PN-AAZ-979

LAN=56430

Drought Tolerance in Winter Cereals

Proceedings of an International Workshop 27–31 October 1985, Capri, Italy

Edited by

Dr J. P. Srivastava
Leader, Cereal Improvement Program, ICARDA, Aleppo, Syria

Dr E. Porceddu
Director, CNR–IPRA, Institute of Agricultural Biology, University of Tuscia, Viterbo, Italy

Dr E. Acevedo
Physiology/Agronomist, Cereal Improvement Program, ICARDA, Aleppo, Syria

Dr S. Varma
Head of Editing and Publications, ICARDA, Aleppo, Syria

A Wiley-Interscience Publication

JOHN WILEY & SONS
Chichester · New York · Brisbane · Toronto · Singapore

Copyright © 1987 ICARDA

All rights reserved

No part of this book may be reproduced by any means, or transmitted, or translated into a machine language without the written permission of the publisher.

Library of Congress Cataloging-in-Publication Data:

Drought tolerance in winter cereals

'A Wiley-Interscience publication.'
1. Winter grain—Breeding—Congresses. 2. Winter grain—Drought resistance—Congresses. 3. Winter grain—Ecology—Congresses. I. Srivastava, J. P., 1940- .
SB189.5.149 1987 633.1'04912 87-16139

ISBN 0 471 91650 1

British Library Cataloguing in Publication Data:

Drought tolerance in winter cereals:
proceedings of an international workshop
27-31 October 1985, Capri, Italy.
1. Grain-Breeding 2. Mediterranean Climate
I. Srivastava, J. P.
633.1'043'0912 SB189.5

ISBN 0 471 91650 1

Typeset by Acorn Bookwork, Salisbury, Wiltshire
Printed and bound in Great Britain.

Contents

List of Contributors ix

Foreword xiii

Preface xv

Section I The Framework for Winter Cereals Research in the Low-rainfall Areas of Southwest Asia and the Mediterranean

1 Agroclimatological classification of the Mediterranean and Southwest Asian areas 3
M. Frere, G. Maracchi, F. Miglietta, and C. Conese

2 Agroecological models and wheat ideotypes for semi-arid lands 15
F. Miglietta, C. Vazzana, and E. Porceddu

3 Crop genotype–environment interaction 37
Hazel C. Harris, W. Goebel, and P. J. M. Cooper

4 Actual and potential yields of cereal crops in moisture-limited environments 55
H. Ketata

Section II Breeding for Winter Cereals in the Low-rainfall Areas

5 Barley and wheat improvement for moisture-limiting areas in West Asia and North Africa 65
J. P. Srivastava

6 A review of plant-breeding strategies for rainfed areas 79
E. L. Smith

7 Australian plant breeding strategies for rainfed areas 89
D. R. Marshall

8 Breeding strategies for improving cereal yield and stability under drought 101
S. Ceccarelli, M. M. Nachit, G. O. Ferrara, M. S. Mekni, M. Tahir, J. van Leur, and J. P. Srivastava

9 Biochemical and physiological response to heat and water stress in barley 115
A. M. Stanca, M. Odoardi, P. Martiniello, L. Cattivelli, C. Lorenzoni, and N. Marmiroli

10 An attempt to define a new plant ideotype of bread wheat for Mediterranean conditions based on physiological studies 123
B. Borghi, M. Cattaneo, M. Corbellini, and M. Perenzin

11 Physiology and the breeding of winter-grown cereals for dry areas 133
R. A. Richards

12 Breeding for moisture-stressed areas 151
M. Osmanzai, S. Rajaram, and E. B. Knapp

13 Breeding for improved yield in moisture-limiting areas: the experience of Jordan 163
Mahmud Duwayri, A. M. Tell, and F. Shqaidef

14 Use of physiological and morphological traits in breeding programmes to improve drought resistance of cereals 171
John M. Clarke

15 Stability of performance of cereals in low-rainfall areas as related to adaptive traits 191
A. Hadjichristodoulou

Section III Physiological Research for Drought Avoidance and Tolerance and its Implication in Breeding Programmes

16 Drought resistance of wheat for light-textured soils in a Mediterranean climate 203
Neil C. Turner and Marc E. Nicolas

17 Relations among physiological characters in durum wheat under drought 217
A. Rascio, B. Baldelli, Z. Flagella, and G. Wittmer

18 Stress metabolism: its implication in breeding programmes 227
David W. Lawlor

19 Nitrogen metabolism in relation to water stress 241
J. Pearson, N. Smirnoff, G. R. Stewart and L. B. Turner

20 Modelling stomatal conductance in the identification of physiological traits for drought resistance 255
A. M. Castrignano, N. Losavio, M. Mastrorilli, and M. E. Venezian

21 Responses to water deficits in relation to breeding for drought resistance 263
E. Fereres

22 Root characteristics and water use in Mediterranean environments 275
S. C. Brown, P. J. Gregory, and A. Wahbi

23 Opportunities for manipulating root systems to reduce drought stress in wheat 285
Howard M. Taylor and Henry T. Nguyen

Section IV Plant Characteristics Required for Improved Performance in Moisture-limiting Environments—an *ad interim* Assessment

24 Assessing crop and plant attributes for cereal improvement in water-limited Mediterranean environments 303
E. Acevedo

25 Some crop characteristics of wheat and their influence on yield and water use 321
R. B. Austin

26 Use of water balance terms in breeding for drought resistance—the upland rice case 337
R. N. Reyniers

27 Maize in the Mediterranean cropping system—modifying its growth to combat drought 339
R. Kent Crookston and Said Ouattar

28 Drought resistance in crop plants: a critical physiological and biochemical assessment 349
S. K. Sinha

29 Synthesis—tackling the problem of low yield and yield instability of winter cereals in the Mediterranean areas of West Asia, North Africa, and Southern Europe 365
M. C. Saxena and S. K. Sinha

Recommendations 373

Index 375

List of Contributors

E. Acevedo *ICARDA, PO Box 5466, Aleppo, Syria*

R. B. Austin *Plant Breeding Institute, Maris Lane, Cambridge CB2 2LQ, UK*

B. Baldelli *Istituto Sperimentale per la Cerealicoltura, S.S. 16 Km. 675 Cas. Postale, 71100 Foggia, Italy*

B. Borghi *Experimental Institute for Cereal Research, 20079 S. Angelo Lodigiano, Milan, Italy*

S. C. Brown *Department of Soil Science, University of Reading, London Road, Reading RG1 5AQ, UK*

A. M. Castrignano *Istituto Sperimentale Agronomico (MAF), Via C. Ulpiani 5, Bari, Italy*

M. Cattaneo *Experimental Institute for Cereal Research, 20079 S. Angelo Lodigiano, Milan, Italy*

L. Cattivelli *Istituto di Botanica e Genetica Vegetale, Universita di Piacenza, Italy*

S. Ceccarelli *ICARDA, PO Box 5466, Aleppo, Syria*

John M. Clarke *Research Station, Research Branch, Agriculture Canada, Swift Current, Saskatchewan S9H 3X2, Canada*

C. Conese *Institute of Environmental Analysis and Remote Sensing for Agriculture, P. le delle Cascine 18, Firenze, Italy*

P. J. M. Cooper *ICARDA, PO Box 5466, Aleppo, Syria*

M. Corbellini *Experimental Institute for Cereal Research, 20079 S. Angelo Lodigiano, Milan, Italy*

R. Kent Crookston *Agronomy Department, University of Minnesota, St Paul, Minnesota 55108, USA*

Mahmud Duwayri *Faculty of Agriculture, University of Jordan, Amman, Jordan*

E. Fereres *SIA and University of Cordoba, Apartado 240, 14071 Cordoba, Spain*

G. O. Ferrara *ICARDA, PO Box 5466, Aleppo, Syria*

Z. Flagella *Istituto Sperimentale per la Cerealicoltura, S.S. 16 Km. 675 Cas. Postale, 71100 Foggia, Italy*

M. Frere *Division of Plant Production and Protection, FAO, Via delle Terme di Caracalla, Rome, Italy*

W. Goebel *ICARDA, PO Box 5466, Aleppo, Syria*

P. J. Gregory *Department of Soil Science, University of Reading, London Road, Reading RG1 5AQ, UK*

A. Hadjichristodoulou *Agricultural Research Institute, Nicosia, Cyprus*

Hazel C. Harris *ICARDA, PO Box 5466, Aleppo, Syria*

H. Ketata *ICARDA, PO Box 5466, Aleppo, Syria*

E. B. Knapp *CIMMYT Wheat Program, Londres 40, Apdo Postal 6-641 06600 Mexico DF, Mexico*

David W. Lawlor *Physiology and Environmental Physics Department, Rothamsted Experimental Station, Harpenden, Herts. AL5 2JQ, UK*

C. Lorenzoni *Istituto di Botanica e Genetica Vegetale, Universita di Piacenza, Italy*

N. Losavio *Istituto Sperimentale Agronomico (MAF), Via C. Ulpiani 5, Bari, Italy*

G. Maracchi *Institute of Environmental Analysis and Remote Sensing for Agriculture, P.le delle Cascine 18, Firenze, Italy*

N. Marmiroli *Istituto di Genetica, Universita di Parma, Italy*

D. R. Marshall *I A. Watson Wheat Research Centre, University of Sydney Plant Breeding Institute, PO Box 219, Narrabri, NSW 2390, Australia*

P. Martiniello *Istituto Sperimentale per la Cerealicoltura, Fiorenzuola d'Arda (PC), Italy*

M. Mastrorilli *Istituto Sperimentale Agronomico (MAF), Via C. Ulpiani 5, Bari, Italy*

M. S. Mekni *ICARDA, PO Box 5466, Aleppo, Syria*

F. Miglietta *Institute of Environmental Analysis and Remote Sensing for Agriculture, P.le delle Cascine 18, Firenze, Italy*

M. M. Nachit *ICARDA, PO Box 5466, Aleppo, Syria*

Henry T. Nguyen *Department of Plant and Soil Science, Texas Tech University, Lubbock, Texas 79409, USA*

Marc E. Nicolas *Dryland Crops and Soils Research Programme, CSIRO Laboratory for Rural Research, Private Bag PO, Wembley WA 6014, Australia*

M. Odoardi *Istituto Sperimentale per la Cerealicoltura, Fiorenzuola d'Arda (PC), Italy*

M. Osmanzai *CIMMYT Wheat Program, Londres 40, Apdo Postal 6-641, 06600 Mexico DF, Mexico*

Said Ouattar *Institut Agronomique et Vétérinaire Hassan II, BP 6202, Rabat, Morocco*

J. Pearson *University College London, Department of Botany and Microbiology, Gower Street, London WC1E 6BT, UK*

M. Perenzin *Experimental Institute for Cereal Research, 20079 S. Angelo Lodigiano, Milan, Italy*

E. Porceddu *CNR–IPRA Institute of Agricultural Biology, University of Tuscia, Viterbo, Italy*

S. Rajaram *CIMMYT Wheat Program, Londres 40, Apdo Postal 6-641, 06600 Mexico DF, Mexico*

A. Rascio *Istituto Sperimentale per la Cerealicoltura, S.S. 16 Km, 675 Cas. Postale, 71100 Foggia, Italy*

R. N. Reyniers *La Zolad, Batiment 7, 34100 Montpellier, France*

R. A. Richards *Division of Plant Industry, CSIRO, PO Box 1600, Canberra City, ACT 2601, Australia*

M. C. Saxena *ICARDA, PO Box 5466, Aleppo, Syria*

F. Shqaidef *Faculty of Agriculture, University of Jordan, Amman, Jordan*

S. K. Sinha *Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012, India*

E. L. Smith *USAID/MIAC, Institut National de la Recherche Agronomique, PO Box 290, Settat, Morocco*

N. Smirnoff *Department of Biological Sciences, University of Exeter, Exeter, UK*

J. P. Srivastava *ICARDA, PO Box 5466, Aleppo, Syria*

A. M. Stanca *Istituto Sperimentale per la Cerealicoltura, Fiorenzuola d'Arda (PC), Italy*

G. R. Stewart *University College London, Department of Botany and Microbiology, Gower Street, London WC1E 6BT, UK*

M. Tahir *ICARDA, PO Box 5466, Aleppo, Syria*

Howard M. Taylor *Department of Plant and Soil Science, Texas Tech University, Lubbock, Texas 79409, USA*

A. M. Tell *Faculty of Agriculture, University of Jordan, Amman, Jordan*

L. B. Turner *Department of Biological Sciences, University of Sussex, Falmer, Brighton, UK*

Neil C. Turner *Dryland Crops and Soils Research Programme, CSIRO Laboratory for Rural Research, Private Bag PO, Wembley WA 6014, Australia*

J. van Leur *ICARDA, PO Box 5466, Aleppo, Syria*

C. Vazzana *Istituto Agronomia Generale, P.le delle Cascine 18, 50144 Firenze, Italy*

M. E. Venezian *Istituto Sperimentale Agronomico (MAF), Via C. Ulpiani 5, Bari, Italy*

A Wahbi *Department of Soil Science, University of Reading, London Road, Reading RG1 5AQ, UK*

G. Wittmer *Istituto Sperimentale per la Cerealicoltura, S.S. 16 Km. 675 Cas. Postale, 71100 Foggia, Italy*

Foreword

One of the major objectives of the International Center for Agricultural Research in the Dry Areas (ICARDA) is to develop improved winter cereals for the dry areas of West Asia and North Africa. In the case of barley, this scope is wider since ICARDA has the world mandate for this crop within the Consultative Group on International Agricultural Research (CGIAR).

Experience over the years has shown that wheat and barley yields in stressed dryland areas have increased only modestly. The simultaneous occurrence of two or more abiotic stresses such as drought, cold and heat coupled with the high seasonal and interannual variability of the environment slows down the improvement process. The physiological basis of the genetic improvement is not fully understood. However, plant physiologists, based on their knowledge of the underlying processes affecting yield under moisture stress, have suggested many traits to be of importance for increasing yield and stability of yield under such conditions. This knowledge has not yet been applied to improve the effectiveness of plant breeding programs.

In recognition of the need to systematically explore the use of a physiological basis in crop improvement programs, the National Research Council of Italy (CNR — Special Project — IPRA) and ICARDA jointly organized an international symposium 'Improving Winter Cereals for Moisture-limiting Areas', in Capri, Italy. Its primary objective was to encourage a dialogue between plant breeders and physiologists with a view to increasing the stability and production of wheat and barley in rainfed areas, particularly those in West Asia and North Africa. Leading scientists participated in the discussions with the objective of sharing experiences and seeking ways of merging their knowledge. The efficiency of current breeding procedures was reviewed and some more effective approaches were suggested. The outcome of this meeting is presented in this book, which I trust will contribute to science, as well as to a better understanding of the

problems of the ICARDA region. I have no doubt that the knowledge generated from this symposium will be useful in improving food production in dry areas.

MOHAMED A. NOUR
Director General, ICARDA

Preface

This volume is based on the presentations made by a multidisciplinary group of scientists at an international symposium on Improving Winter Cereals in Moisture-limiting Areas, held in Capri, Italy. Though belonging to different disciplines, the participating scientists had a common focus: how the disciplines in which they worked could contribute to improving food production in those crop growing environments where availability of water—or rather the shortage of it—is the major constraint.

The text is organized into four sections. Section I, 'The Framework for Winter Cereals Research in the Low-rainfall Areas of Southwest Asia and the Mediterranean', deals with the role of agroclimatology and of agroecological models in developing a meaningful approach for crop improvement. Section II, 'Breeding for Winter Cereals in the Low-rainfall Areas', reviews and compares the efficiency of current breeding methods and presents some new approaches. Section III deals with 'Physiological Research for Drought Avoidance and Tolerance and its Implication in Breeding Programmes', and section IV with 'Plant Characteristics Required for Improved Performance in Moisture-limiting Environments—an *ad interim* Assessment'. A set of recommendations of the symposium is also included.

While most papers were edited only for style, some had to be substantially revised. Each presentation was followed by a series of lively, thought-provoking discussions which highlighted the importance of a multidisciplinary approach, particularly the integration of agroclimatology and crop physiology with breeding, in accelerating the cereal improvement for dry areas. The discussion section for each paper was developed from tapes and the question-and-answer sheets returned to us by the contributors. The limitation of time did not permit us to clear the editorial changes in papers and the drafts of discussion sections with all contributors, but every possible effort was made to ensure that each paper and its accompanying discussion section reflected the contributors' ideas as accurately as possible. However, we solicit contributors' indulgence for the mistakes of commission and omission that remain.

Grateful thanks are due to the National Research Council of Italy (CNR—Special Project—IPRA) and ICARDA for providing the financial support to hold the workshop and to produce this volume. The success of the symposium was primarily due to the personal interest and wholehearted encouragement of Dr G. T. Scarascia-Mugnozza, Rector, University of Tuscia, Viterbo, and Dr Mohamed A. Nour, Director General of ICARDA.

We thank Ms Parvin Damania of IPRA for her help during the symposium; and Ms Joyce Bendki, Ms Margaret Jones, Mr Hassan Khairallah, and Ms Sylva Cholakian of ICARDA for their assistance in preparation of the manuscript.

J. P. SRIVASTAVA
E. PORCEDDU
E. ACEVEDO
S. VARMA

SECTION I

The Framework for Winter Cereals Research in the Low-rainfall Areas of Southwest Asia and the Mediterranean

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

1

Agroclimatological Classification of the Mediterranean and Southwest Asian Areas

M. FRERE,* G. MARACCHI,† F. MIGLIETTA,† and C. CONESE†
**Division of Plant Production and Protection, FAO, Via delle Terme di Caracalla, Rome, Italy; and † Institute of Environmental Analysis and Remote Sensing for Agriculture, P.le delle Cascine 18, Firenze, Italy*

ABSTRACT

Using the monthly data available with the Agrometeorological Bureau of FAO, we report an agroclimatological classification to characterize the climatic patterns in relation to the growth and development of winter cereals in the Mediterranean areas. The classification needs to be improved further to assess the effect of daily and interannual variability.

The main emphasis was on the water balance equation accounting for the water availability in the soil and its distribution during the growth period. The parameters considered were rainfall, evapotranspiration, and temperature. Temperature was considered to limit the development to levels below the threshold.

A classification method of cluster analysis was used to identify the groups with a high degree of similarity and of principal component analysis (PCA) to build up a linear combination of the original variables accounting for as much of the total variation as possible.

The results of the classification revealed nine types of climate according to the water balance and temperature levels. The plotted results for each station made it possible to draw the main climatic patterns in relation to geographical distribution.

Furthermore, the results could be of help in understanding the most convenient ideotypes for each climatic region. At the same time, useful indications could be obtained to further improve the classification using the daily meteorological data instead of monthly average values.

INTRODUCTION

The effect of climatic environment on plant growth can result in a dramatic reduction in crop productivity, particularly in the sub-arid climates of the Mediterranean region. In that environment lack of adequate rainfall is a serious constraint to winter cereal production and rainfall distribution, more than its total seasonal amount, can adversely influence crop productivity.

A satisfactory solution to increase the productivity of winter cereals can, however, be found through breeding drought-resistant varieties. These breeding programmes should first evaluate the characteristics of the environments where new varieties have to be introduced.

A good definition of plant ideotypes, in fact, can only result from a sound knowledge of local climates and of quantitative genetic responses of the existing germplasm. A knowledge of the climate, on the other hand, will help researchers in parameterizing the enviromental variability by some agro-climatic indexes. The climatic environment can be better defined by the ranges of its temporal variability than, for instance, by its polyannual monthly averages.

For low-rainfall areas, the concept of agroclimates has necessarily to be extended to the interaction of atmospheric variability with soil water storage properties. Unfortunately most of that information is still lacking. Nevertheless, in a first approach to agroclimatic classification, more information can be obtained using multivariate classification and ordination methods.

In this paper we discuss methodological problems and propose some examples of classification. We also outline the need for more complex databases and wider information sources as well as for collection and homogeneous management of the agroclimatic data of the area.

DATABASE AND METHODOLOGY

The climatic data used for this study were obtained from the Agrometeorological Bureau of FAO. The data ranged from Morocco to Turkey along the coastline of the Mediterranean Sea for a minimum of 30 years for each station. In all, data for 210 stations were used. From the original dataset only monthly rainfall, monthly average temperature, monthly maximum average temperature, monthly average of minimum temperature, and evapotranspiration computed by the Penman equation were used for classification and ordination.

The methodology used for data processing was to group the stations with a similar pattern in the base dataset for the parameters named above. The cluster analysis classification and principal component ordination method of Morrison (1967) was used.

The cluster analysis is a multivariate classification technique for displaying

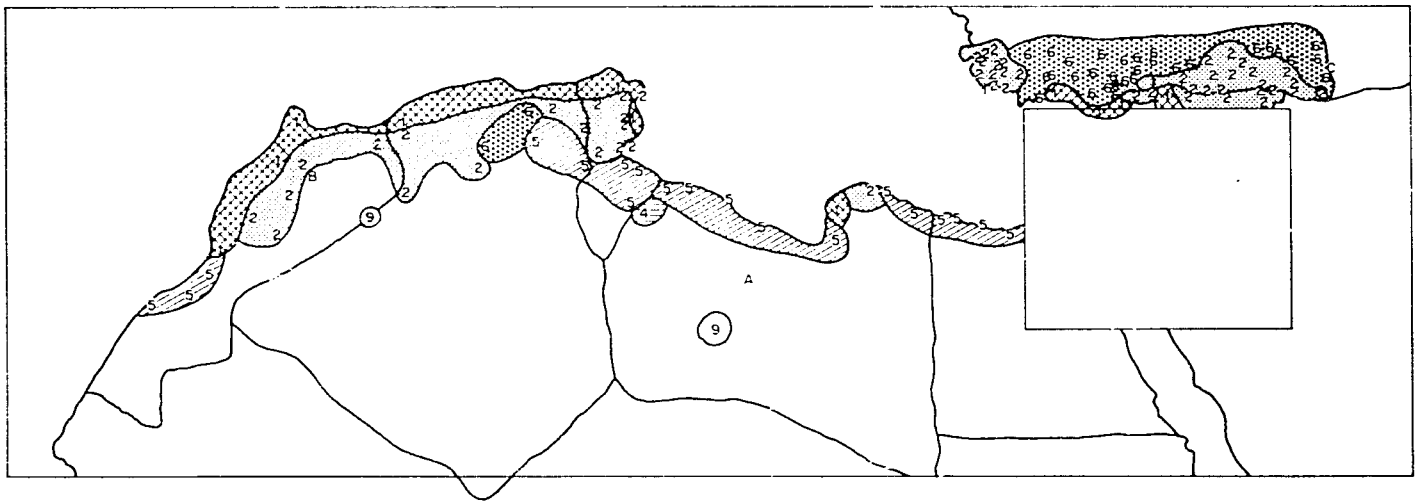


Figure 1. Thematic map of the proposed classification. Classes (climates) are displayed by different grey levels and each number represents the class (see text) and geographical location of the station

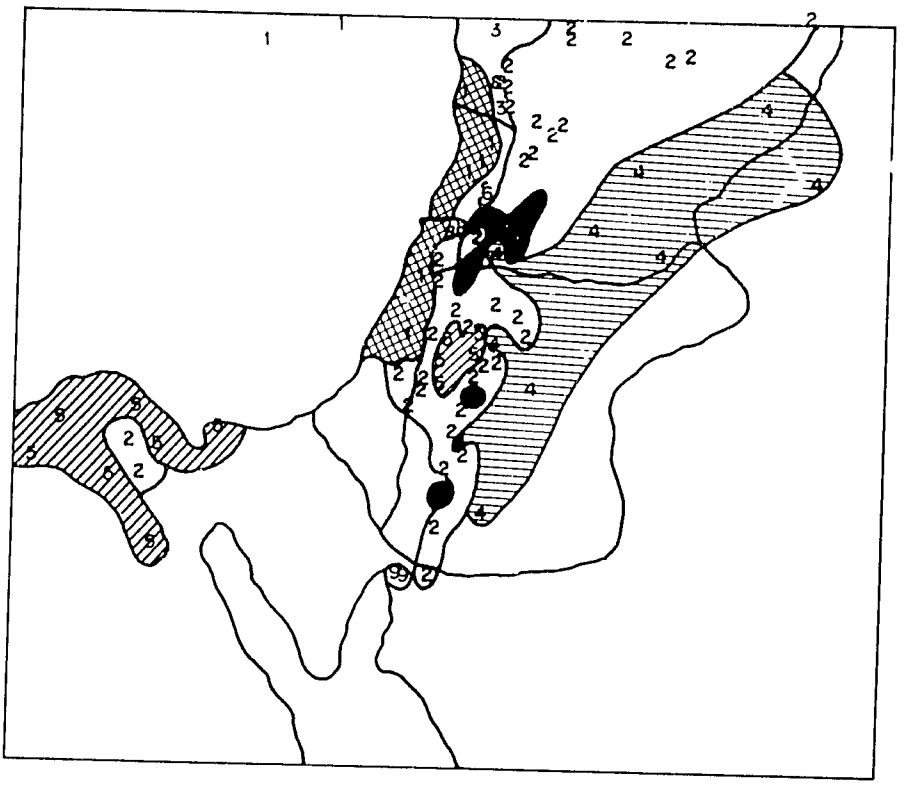


Figure 2. A part of Figure 1 enlarged to show the details

within-cluster variation in relation to between-cluster variation. There are many criteria to assess the similarity leading to the cluster concept, the more common being to judge the between-cluster variation by computation of the distance among cluster centres in comparison with the distance of a cluster member to its cluster centre.

Hierarchical methods allowed the classification of dataset at different levels of similarity (or dissimilarity) among classes. An optimized classification level may be chosen *a posteriori* according to the classification goals.

The principal component analysis (PCA) transforms the original set of variables into a smaller one that accounts for a large part of the variance of the original set. The purpose of the principal component analysis is to determine factors (principal components) in order to explain as much of the total variation in the data as possible with as few of the factors as possible. The principal components are extracted so that the first principal component accounts for the largest amount of the total variation in the data.

The first principal component is a linear combination of the observed

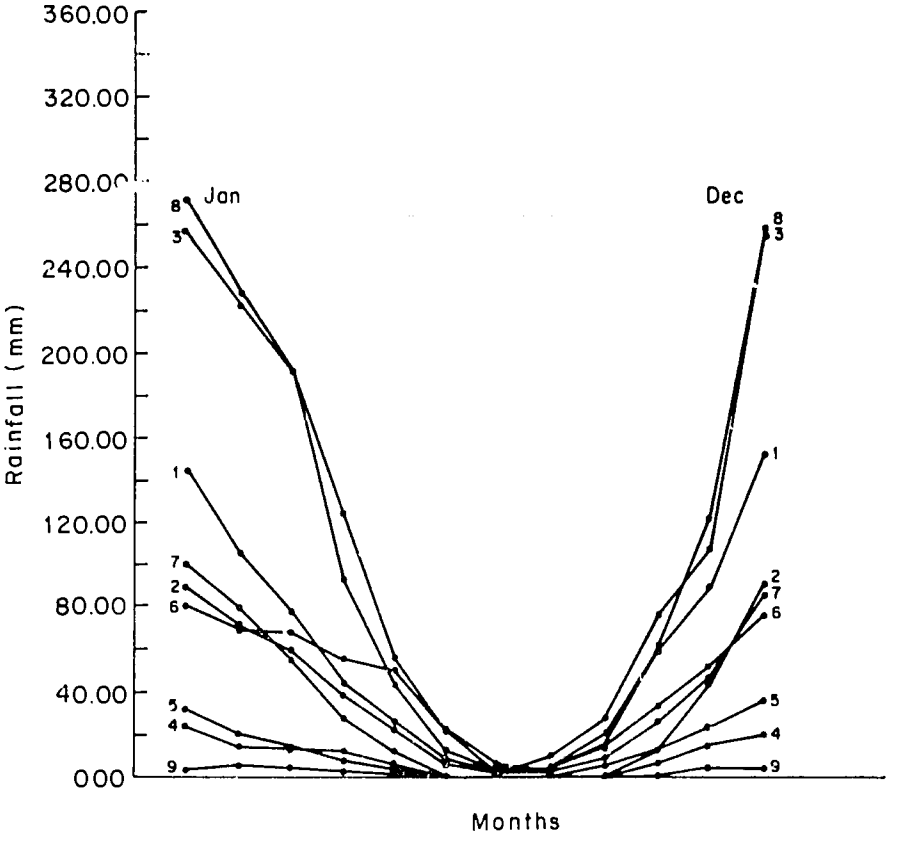


Figure 3. Average rainfall during the year for each class (identified by its ordinal numbers)

variables where the weights have been chosen to maximize the ratio between the variance of principal component and total variation. Thus, a correlation may be found between the principal components and the original variables.

In this sense, the principal component analysis is a useful tool for understanding the relationship between variables and a previously classified dataset, as well as within class unit distribution.

RESULTS

Nine main types of climate, with various numerical consistencies, emerge from this classification.

The location of stations at heights ranging from sea level to mountain levels points to the fact that temperature was not a relevant parameter for grouping.

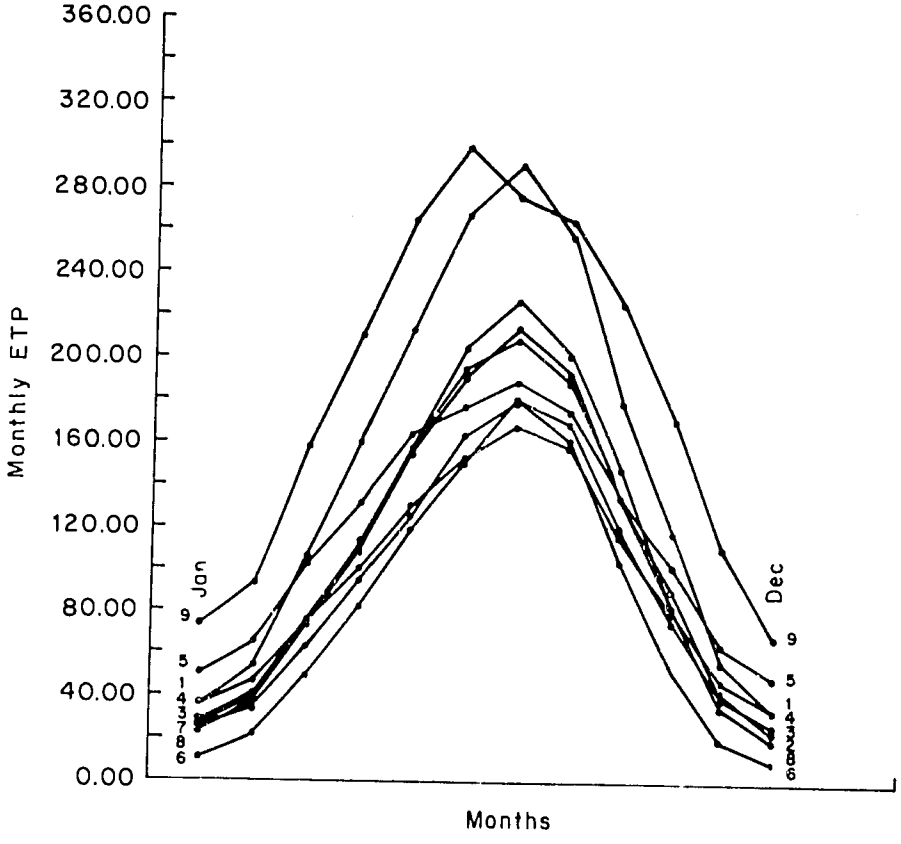


Figure 4. Potential evapotranspiration pattern for each class

That was, however, not the case if we considered the minimum temperature related to the frost events, instead of the average of minimum temperature, but this needs to be further assessed with the daily data.

The most prevailing classes are 1, 2, 5, and 6. From a geographical standpoint (Figures 1 and 2), they are located as follows:

Class 1: along the coastline of the Mediterranean Sea
Class 2: a belt at the interior border of class 1
Class 5: between class 2 and desert areas
Class 6: in the northern area of Turkey

The other classes are related either to mountain or desert areas.

After cluster grouping we computed the balance for the various climatic types according to the ratio between rainfall and evapotranspiration for the winter cereals growing period. Evapotranspiration was computed as 0.75 of potential evapotranspiration (ETP) to account for the water stored in the soil.

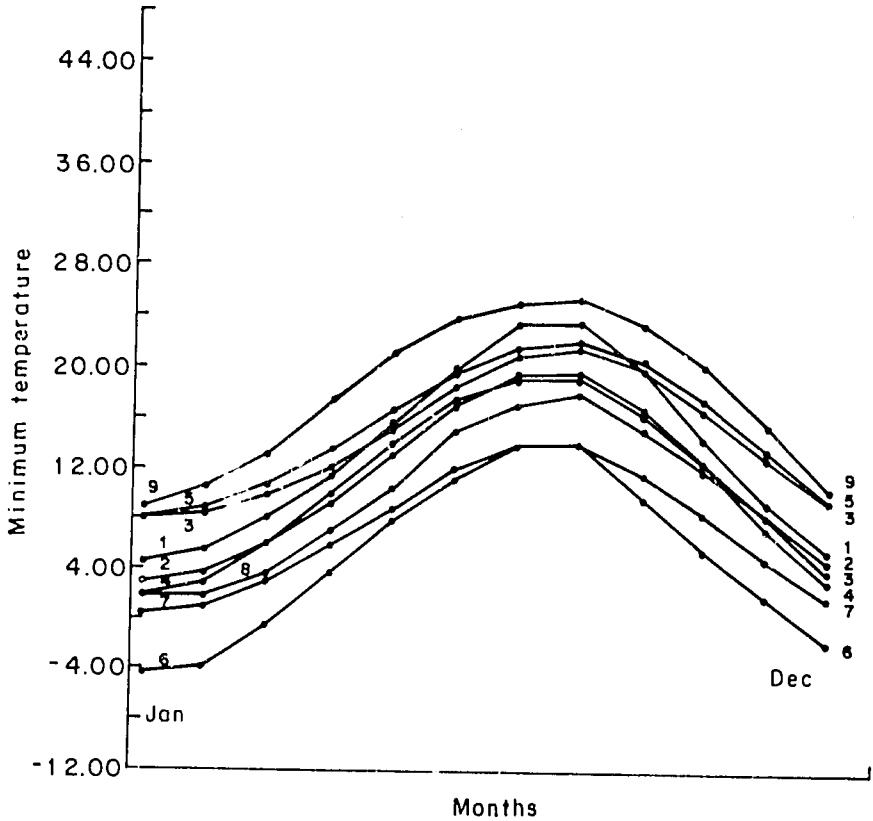


Figure 5. Minimum daily temperature pattern for each class

The crossing point between the rainfall–ETP lines represent the starting point for the growing season.

Figures 3 and 4 show the climatic pattern related to the water balance; the main differences are related to the increasing aridity going from the coastline to the interior. ETP patterns follow the temperature distribution while rainfall patterns differ mainly in the total amount of rainfall with a relatively constant distribution during the autumn–winter–spring period with a maximum in the middle of the growing period. Due to the use of monthly data and interannual average data, the variability is not considered.

The temperature distribution analysis (Figures 5 and 6) puts in evidence the highland areas where some problems may be related to the winter cold.

The PCA ordination is illustrated in Figures 7, 8 and 9. The usefulness of this analysis may be considered, in association with classification, as a tool for displaying the average class association with the main climatic variables. In

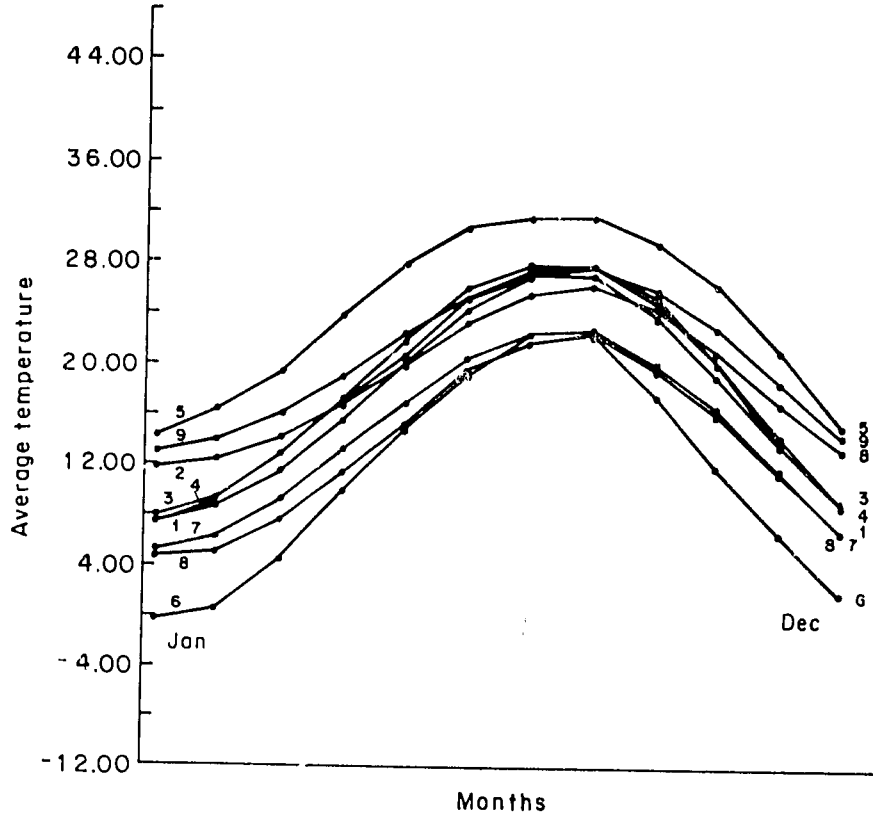


Figure 6. Average daily temperature pattern for each class

Figure 7, the x axis, which is the first extracted component, is highly negatively correlated with the average monthly air temperature during the summer season. The y axis, which is the second extracted component, is negatively correlated with the average monthly rainfall. The graph may, therefore, be split into four regions identifying four extreme climatic patterns of the area studied.

The homogeneity, i.e. the reduced space of the class in the plot, also gives information about the within-class similarity of the stations.

Figure 8 is the plot of the first component (x axis), with the same correlation meaning as above, and the third component. The y axis has correlation both with summer season temperature (positive) and total evapotranspiration (negative). Only the extreme desertic classes 5 and 9, and the class 6 on the other hand, show a non-scattered distribution. The central classes with average thermal levels are overlapped. It is interesting to outline

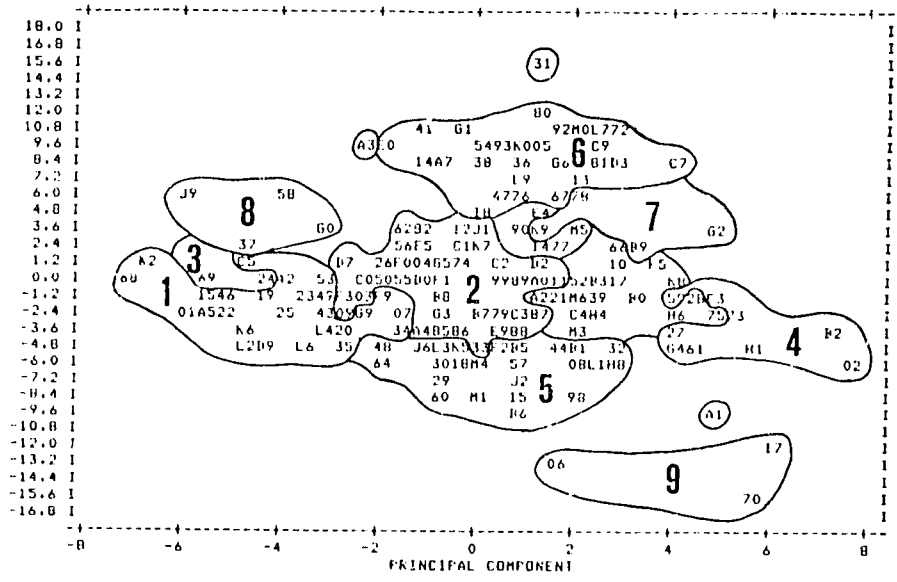


Figure 7. Plot of the first principal component (x axis) against the second one (see text)

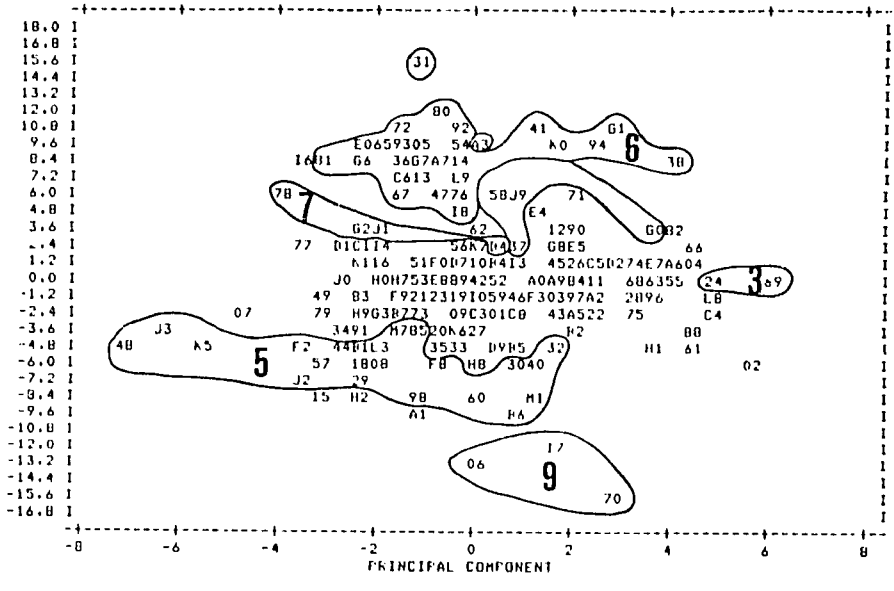


Figure 8. Plot of the first principal component (x axis) against the third one (see text)

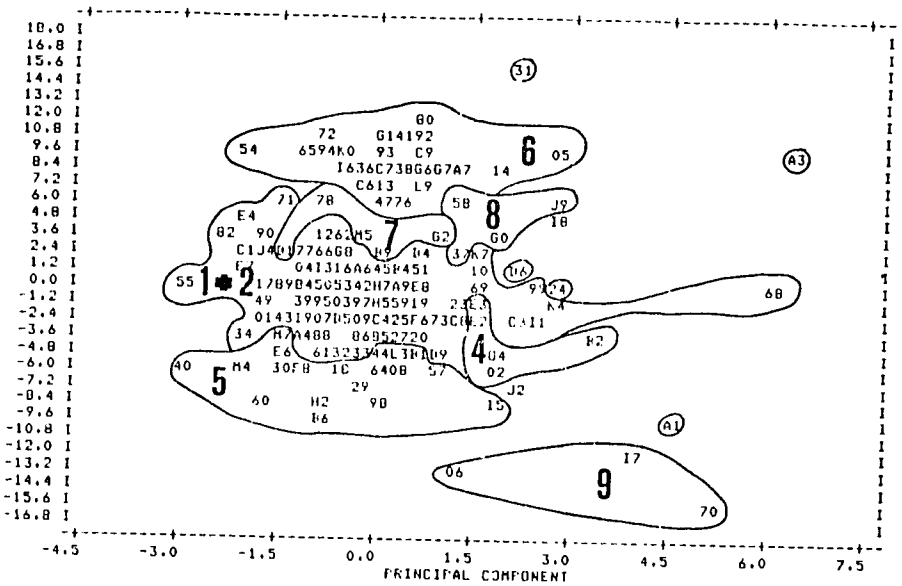


Figure 9. Plot of the first principal component (x axis) against the fourth one (see text)

the stretched shape of class 5 distribution which relates to a high dissimilarity level in ETP values distribution within the class.

In Figure 9 the x axis has the same meaning as above but the fourth component, plotted on the y axis, shows a high correlation with summer season rainfall. This case, which stresses again the differences among extreme classes (5 and 9 on the bottom and 6 and 8 on the top), allows us to interpret how rainfall variability is lower among desertic classes than in more temperate areas.

The PCA analysis, thus, suggests the need for further investigation of the variability within classes from daily meteorological data to derive the agro-climatic classifications as related to interannual variability for the assessment of winter cereal potential productivity.

From the above, some general conclusions can be drawn: the main feature of the climate in an average year is a shortage of water at the beginning and towards the end of growth and development. It means that root growth, foliage cover, vegetative development rate, and grain filling can be modified by this pattern.

The data available on the basis of monthly records and interannual averages are not sufficient to identify accurately the ecological needs of crops. We can conclude from a practical point of view that further data must be added to the database for agro-climatic classification, and also a general description of

soil characteristics is needed to compute the soil water balance more accurately.

REFERENCE

Morrison, D. F. 1967. *Multivariate statistical methods*. McGraw-Hill, New York. 343 pp.

DISCUSSION

S. K. Sinha

How would your classification be affected if you considered the coefficient of variability of rainfall? Could you predict dry-matter production in different zones?

G. Maracchi

We could compute the growing period and the crop necessity in phenological stages. We could predict the dry-matter production on the basis of the climatic model.

H. Ketata

PCA is used when dealing with several correlated characters. You have used rainfall and temperature, each of which you have broken down into 12 levels, making a total of 24 variables. Are you satisfied with the PCA, i.e. how much of the variation is explained by the two first PCs?

G. Maracchi

Yes, we have 24 variables; the two principal components explained 80 per cent of the total variation.

M. Tahir

The information on climatic zoning will stay fragmented and of little practical utility unless a team involving breeders, physiologists, and climatologists works together to work out information on crop modelling and phenology.

G. Maracchi

It is just a starting point. A lot more data is needed even to create climatic zones. However, I agree with you on the need to make a joint effort.

G. T. Scarascia-Mugnozza

We will make a recommendation to create some kind of a team or infrastructure involving climatologists, breeders, and physiologists.

B. Yilmaz

Do you have any plans to work on the relationship between plant type and agroclimatic data for Mediterranean areas?

G. Maracchi

Yes, in the future, after we have built up enough data.

M. S. Mekni

What kind of practical recommendations can we make from the data and type of analysis available? Recommendations are more urgently needed in areas where weather and agroecological data-collection supplies are poor. What can we do about it?

G. Maracchi

We could give some recommendations on the crop calendar and to forecast yield. We can use remote sensing to interpolate the meteorological data.

F. N. Reyniers

(1) Can an NOAA satellite be used to collect daily rainfall data?
(2) What water balance terms should be used to characterize a site with agronomical purposes in mind?

We think Eta is an interesting indicator for tropical agriculture. What about Mediterranean conditions?

G. Maracchi

(1) We can use WOAA for daily temperature.
(2) 0.75 of ET and rainfall.
(3) Yes.

M. Duwayri

You said this information will be of value to farmers in the developing countries. Would you please elaborate how those farmers could use this information?

G. Maracchi

They can use it for crop calendars, choosing the right varieties, and yield forecasting.

J. P. Srivastava

It would be desirable as a first cut to provide an agroclimatological zoning so that breeders can tailor-make genotypes for specific environments. Could you specify what form of cooperation is required from ICARDA and national programmes?

G. Maracchi

The present state-of-the-art allows us to give a first scheme of classification. I recommend the promotion of a joint team to collect data between ICARDA and national institutions.

H. Harris

You have indicated a need to collect large volumes of daily climatic data for more detailed analysis. Have you considered the use of weather generators to simulate stochastic data as an alternative to the logistics of data collection?

G. Maracchi

We think that without any data on interannual variability we cannot use weather stochastic generators.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

2

Agroecological Models and Wheat Ideotypes for Semi-Arid Lands

F. MIGLIETTA*, C. VAZZANA†, and E. PORCEDDU‡
**Institute of Environmental Analysis and Remote Sensing for Agriculture, P.le delle Cascine 18, Firenze, Italy; †Ist Agronomia Generale, P.le delle Cascine 18, 50144 Firenze, Italy; and ‡CNR–IPRA, Institute of Agricultural Biology, University of Tuscia, Viterbo, Italy*

ABSTRACT

A recently developed crop growth model (ACROM) was used to test some hypotheses for the identification of wheat ideotypes in semi-arid lands. First we summarise the model functioning and then test some ideotypes in wheat plant. These are: (1) early vegetative growth, low LAI, (2) root depth, (3) root/shoot ratio, (4) stomatal sensitivity, and (5) hydraulic root resistance.

For each of these studies, we discuss the results of model runs and attempt suggestions for future wheat breeding programmes.

INTRODUCTION

Water limitation is one of the major constraints to crop growth and production in the semi-arid lands of the Mediterranean area. Improvements in crop growth and productivity may be obtained by increasing agronomic production technology and by evaluating and selecting more suitable plant cultivars. This evaluation and selection may be approached exhaustively on the basis of the definition of crop ideotypes.

For semi-arid conditions, we can restrict the concept of ideotype to a crop feature that is a compromise between better adaptation to environmental conditions and productivity.

Generally, partial approaches have been made to describe and define the characteristics of crop ideotypes and the related potential yield of wheat, studying, for example, photosynthetic system performances or root growth

(Greacen *et al.*, 1976; Austin, 1982; Passioura, 1983). On the other hand, much of research has pointed out how only a general analysis and modelling of crop behaviour may be useful in this perspective. For this reason we have tried to verify some hypotheses by using a crop productivity model.

This type of model generally takes into account the interaction of the most important physiological and structural processes in the plant, to describe all total crop behaviour. ACROM (arid crop model), which has been recently developed by the authors, was considered particularly suitable for this purpose, mostly for the root system modelling approach that has been used.

The proposed development must be considered as a methodological way of work. This means that (in any case) further tests and discussion are needed. Model improvement, above all in phenological formalization and grain dry-matter production, and further model validation might produce better results.

Finally, experimental work is still needed to increase knowledge about root systems, general root shape features, and partitioning of root/shoot assimilates as related to the water-use pattern during the life cycle of the crop.

MATERIALS AND METHODS

As described below, a productivity simulation model (ACROM) has been used to test and validate crop ideotypes hypotheses. Due to the lack of meteorological and paedological data on the Mediterranean area, the model's runs have been done using a single meteorological input, an only one soil type has been chosen for tests.

The climatic growing season trend was described by the daily temperature and rainfall records of 1983 of a Sicilian meteorological station (Sciacca) located at 37.05 lat. N (Figure 1).

For paedological variables the model needs a soil tensiometric curve at seven entry points, soil bulk density, saturated conductivity, and an infiltration code ranging from 1 to 10 in relation to soil estimated-rainfall infiltrability. In this case a silty clay–loam soil is used as an example, and its characteristics are shown in Table 1.

THE MODEL

ACROM is a deterministic descriptive model of crop biomass production. A complete description of the model has been developed in Maracchi *et al.* (1985a, 1985b) and recently improved by Miglietta *et al.* (unpublished data).

In this context a brief summary of ACROM's structure and behaviour will be given to better understand the model's adaptability to the arid and semi-arid agricultural environment. In fact, ACROM was conceived to describe crop behaviour mostly as a function of a plant/soil system water

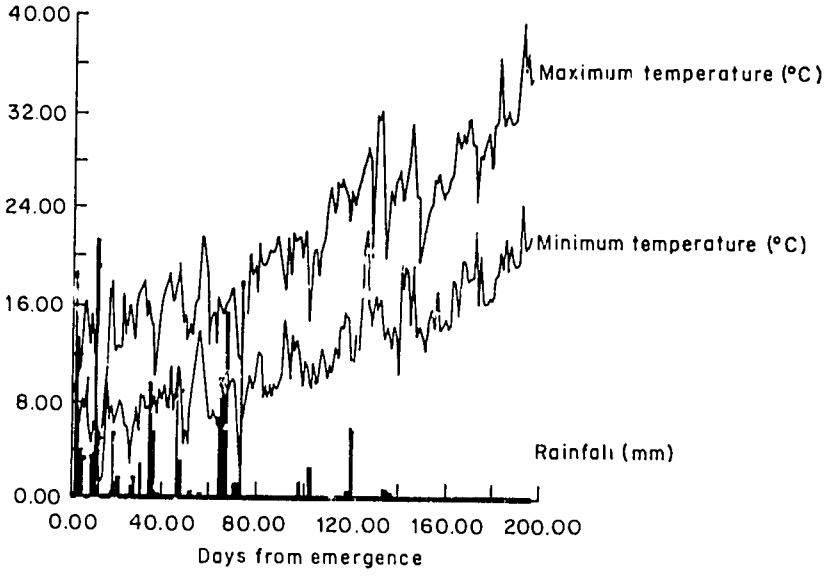


Figure 1. Standard climatic trend of rainfall and temperature for simulated growing season

deficit. Root development and distribution and main ecophysiological aspects of crop growth are outlined and formalized in detail. The general model scheme includes five modules: (1) soil module, (2) root module, (3) plant/water module, (4) photosynthesis module and (5) growth module.

Soil module

The ACROM approach to soil water dynamic modelling follows classical schemes (Hillel and Talpaz, 1976; Feddes *et al.*, 1978) using a multilayered soil approximation, the darcyan flow equation, a linear approximation of tensiometric curve between experimental points (Feddes *et al.*, 1978;

Table 1. Soil characteristics

Soil type	= silty clay-loam
Bulk density	= 1.22
Saturated conductivity	= 50.0 cm/day
Infiltrability code	= 1
Soil depth	= 1.5 m
Soil water % at wilting point (−15 bars)	= 0.0825
Soil water % at field capacity (−0.3 bars)	= 0.225

Rijtema, 1969), and the unsaturated conductivity evaluation on the basis of granulometric patterns of soil. For each simulation these variables are computed and integrated using five main forcing variables: E = soil evaporation, P = rainfall, R = runoff, D = deep drainage, which may be considered as infinite or related to a time constant water table, and S = root water uptake, which is modelled as a function of soil resistance (Feddes *et al.*, 1978) and root shape, root depth, and soil volume explored by roots.

Root module

The module includes both mechanistic and empirical approaches. Empirical aspects of the module relate to allometric constants which may be used in root growth modelling. The assimilation partitioning between root/shoot systems is expressed using two empirical coefficients (Passioura, 1983; Acock, 1984; de Wit *et al.*, 1978) as a function of plant water deficit. The allometric relationship allows us to express root length as a function of root dry matter using an empirical value of root weight per unit length (a = gr/mm) (Passioura, 1983) and another coefficient (L = mm/mm^3) may give the approximate soil volume explored by roots per unit length (Passioura, 1983).

Mechanistic aspects involved in the module refer to root system shape analysis and maximum soil depth of water absorption according to the defined shape. A preliminary definition may be obtained using a general geometric

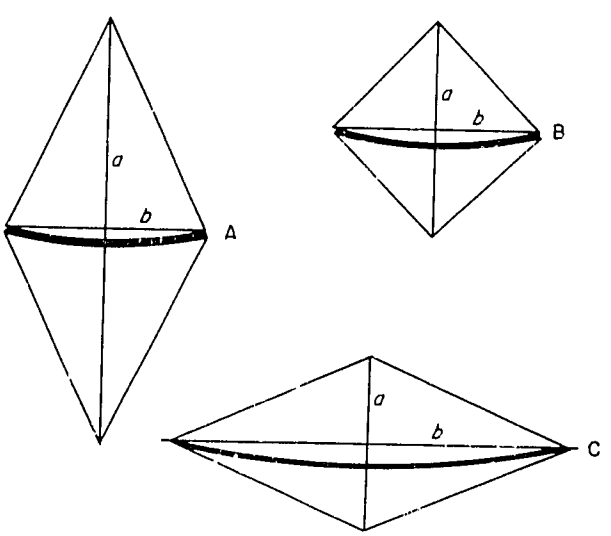


Figure 2. Root shape in the model is defined as in the figure using the a/b ratio as input variable
A—a/b = 0.5
B—a/b = 1.0
C—a/b = 2.0

feature: two basis opposed cones and a ratio B which is given as model input and refers to the dimensional relationship between the double of the cone's height and basis ray, as shown in Figure 2.

Plant/water module

Potential transpiration is used in the model as a forcing variable for plant water balance. Thus actual transpiration T_a is computed in relation to stomatal resistance, and then plant water volume is integrated over time. Leaf water potential (a) can be roughly computed as a linear function of plant water deficit. Finally, computed values of a and radiative levels are used to evaluate stomatal resistance. Figure 3 shows an example of ACROM's approximation as compared with experimental data.

Photosynthesis module

ACROM is a water-limiting crop productivity model. It has thus been designed to use, as input, both daily radiation (PAR) values and monthly

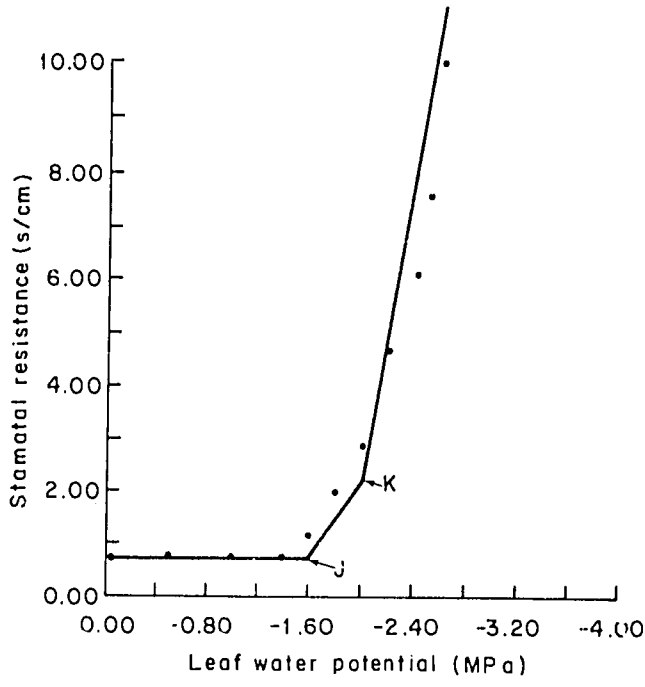


Figure 3. ACROM's approximation for stomatal resistance (solid line) as compared with experimental data (dots) from Turner (1978). Nodal points K, J may be imposed in the model at different leaf water potential levels

average estimates of daily radiation. The rough approximation of the second case is improved in the model by taking into account a coefficient that is applied to estimate radiation values during rainy days, as a reduction factor, and during non-rainy ones, as an increasing factor.

Potential photosynthesis is then computed using radiation and thermal data as meteorological input. Crop canopy structure is modelled on the extinction and transmission coefficients and leaf area index basis, while the actual potential photosynthesis (P_c) at a given radiation level is computed on the basis of the leaf photosynthetic response curve (France and Thornley, 1984):

$$P_c = \frac{I_l P_{max}}{I_l + P_{max}} \tag{1}$$

where

I_l = intercepted PAR

P_{max} = light-saturated value of photosynthetic rate (1.2×10^{-6} kg $CO_2/m^2/s$) (Acock, 1976).

Using the Monsi-Saeki (Saeki, 1960) equation and a combination of it with (1), the final photosynthesis equation may be written as follows:

$$P = \frac{P_{max}}{K}\left\{\ln\left[\frac{\alpha K I_0 + P_{max}(1-m)}{\alpha K I_0 e^{-K\,LAI} + P_{max}(1-m)}\right]\right\} \tag{2}$$

where

α = initial slope of the response curve, i.e. photosynthetic efficiency [13×10^{-9} kg CO_2/J(PAR)]

LAI = leaf area index

K = extinction coefficient

m = transmission coefficient

I_0 = incoming radiation (PAR)(J/m²/s)

Model performance at a given crop leaf area level (LAI = 1.77) is shown in Figure 4.

Growth module

Finally, total shoot dry matter (DM) can be integrated over the time of the simulation as follows:

$$DM = \int_0^n \frac{P_c}{R_s} \times R_{smin} \times (1 - R_p) \times (1 - Dr)\, dt \tag{3}$$

where

Dr = root/shoot dry-matter partitioning ratio, which is expressed as a function of leaf water potential

R_s = actual crop stomatal resistance

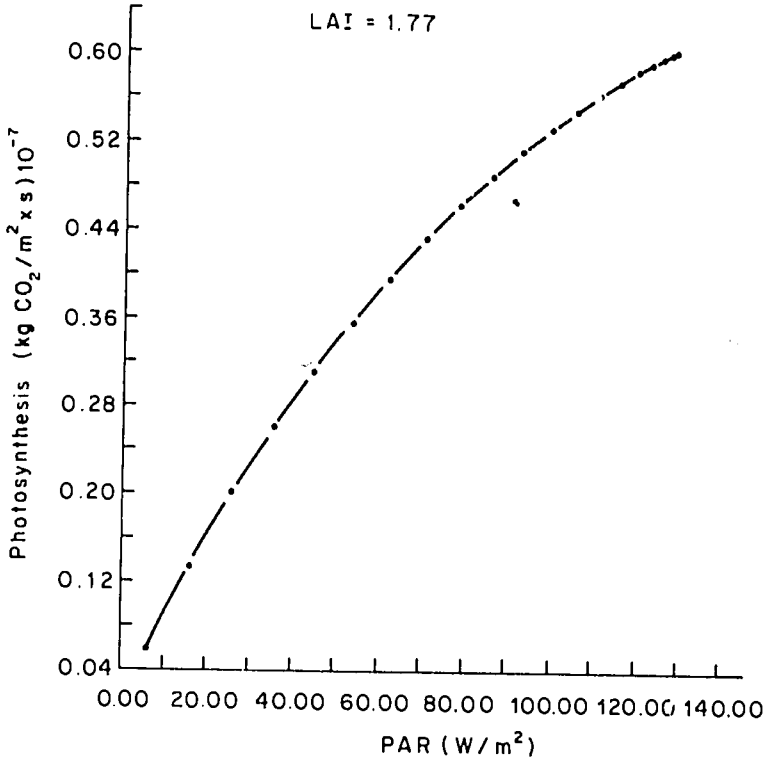


Figure 4. ACROM's potential photosynthesis computation at different incoming radiation (PAR) levels

R_p = crop respiration coefficient
R_{smin} = minimum crop stomatal resistance
n = the total time of the simulation.

Root dry-matter growth is integrated as a difference between total growth value and shoot dry-matter integral. Some of the ACROM's performances for particular days of simulation are given in Figure 5 in order to appreciate general model computation flow over daytime.

EXAMPLES AND DISCUSSION

In this section two different items, classical hypotheses about improvement of cereal adaptation and productivity in semi-arid climates, and simulation responses to these hypotheses will be examined and each theoretical level will correspond to a technical case study of simulation.

According to Passioura's analysis (1983) of the performances of wheat

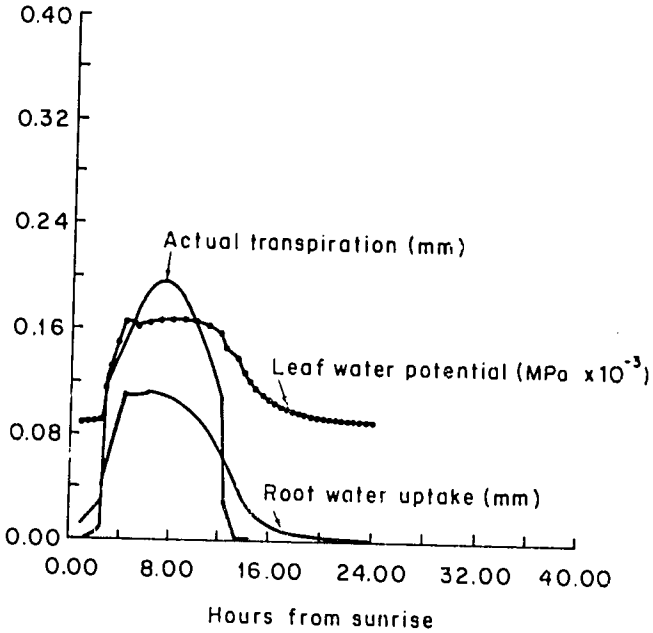


Figure 5. ACROM's performance is shown for a particular day when water stress is evident. The effect of soil water shortage is reflected by limited water uptake, transpiration, and leaf water potential. Simulated stomata closure regulates plant water balance and assimilation

growing with a limiting soil water supply, we can consider that crop yield is a result of an interaction among these factors:

(1) amount of water available to a crop during the growth cycle,

(2) water-use efficiency, i.e. transpired water and accumulated dry-matter ratio per unit time, and

(3) harvest index.

The quantity of water available to a crop depends on the amount of water stored in the soil profile at sowing plus infiltrated rainfall during the crop life. In the semi-arid areas, often the probability of rainfall during the most critical part of the growing season is very low; therefore the soil water storage capacity assumes high relevance for productivity. Water stored in the upper layers may be lost for crop productivity through direct evaporation from the soil surface. Soil evaporation depends largely on the radiative flux reaching the soil in the absence of plant cover or, at low leaf area levels, on exposed areas between plants.

Evaporation from the soil surface can greatly contribute to water-loss mechanisms. It would be useful for such a control to select wheat lines that

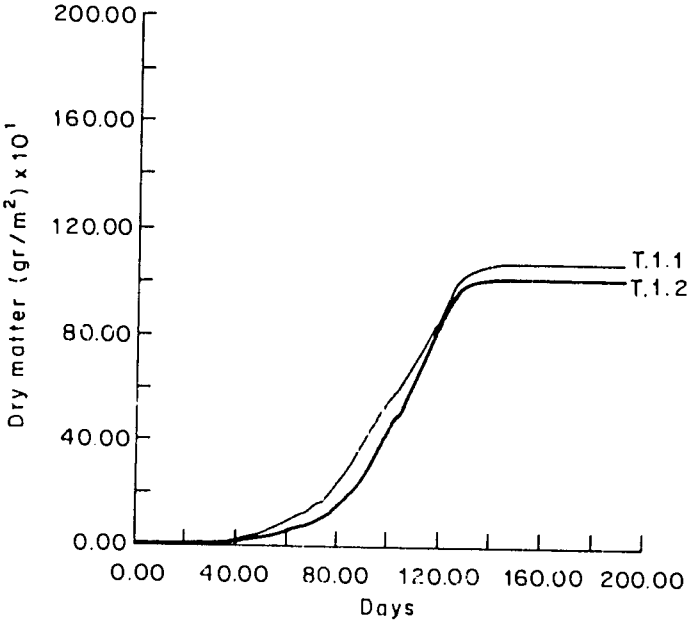


Figure 6. Biomass production over growing season

emerge and establish adequate green stands as fast as possible. Some results can be obtained by increasing wheat density at sowing, but the cost of extra early growth could be strong in terms of water uptake. To avoid any effect on the final harvest index due to reduced available water, we need to have cultivars which are able to make a compromise between early growth and early water use. A low LAI enables the crop to maintain a high water status while using water slowly (Passioura, 1983). In practice, a crop keeping its leaf area index below, for example, 2.5 will suffer only mild drought effects.

Case study 1: early vegetative growth, low LAI

Following these assumptions, input variables of model's runs have been tuned to compare different growth curves and related characteristics of an earlier and later growth ideotype. The first one (T.1.1) is defined as less sensitive to low air temperatures: the lowest growth limit has been chosen at $T = 1°C$ while optimal air temperature values are above $T = 15°C$. For the second one (T.1.2) these values are $T = 5°C$ and $T = 18°C$. Maximum imposed crop LAI was different, ranging from 2 to 3. Figure 6 shows how the model simulation allows the ideotype T.1.1 to have a higher cumulative dry matter than T.1.2. This is in agreement with the hypothesis: a lower leaf area index can maintain leaf water potential at a higher level during the growth of the crop, thus

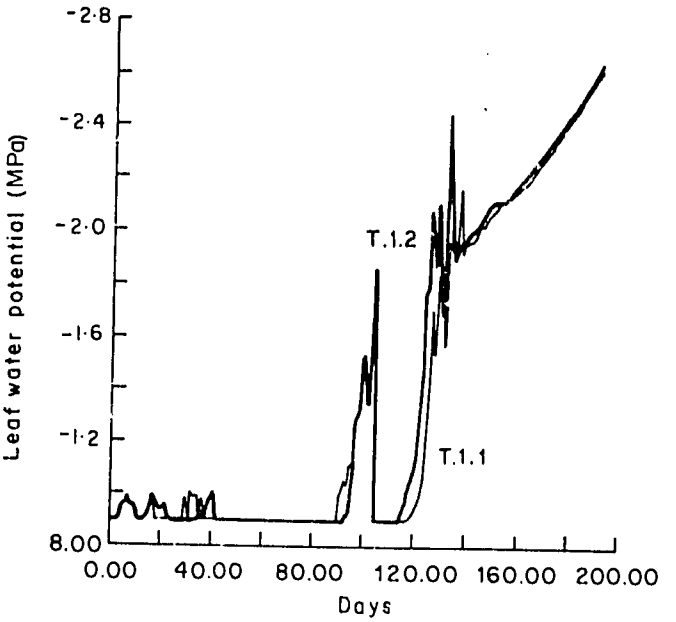


Figure 7. Leaf water potential at midday over growing season

reducing water stress (Figure 7). Earliness allows the crop to avoid drought during the last period (Derera *et al.*, 1969; McKay, 1966, 1970) and contributes in reducing direct evaporation from the soil, promoting a rapid development of leaf area. According to the literature, wheat cultivars with earlier vegetative growth and reduced LAI are more suitable where the amount of available water is the more limiting factor.

McKay (1979) indicates that the type of shoot development is to a large extent related to the root system. A crop can respond to a dry climate by diverting more assimilates to root growth. A more developed root system can allow a better uptake of water from the soil. The development of effective deep root depends on the strong interaction between environmental and genetic factors. A promising way for water-use improvement in wheat could be to breed plants with a vigorous root system at depth.

Hurd (1974) searched for parents having deep roots and included them into a breeding programme. A deeper root system can penetrate as far as the wetting front and uptake the amount of available water. In dry areas, some of the water deeply stored in the soil cannot be used because of the reduced development of roots (Taylor and Gardner, 1960). An additional amount of water extracted by a deeper root system could improve the total biomass production and also increase the harvest index, if water is available towards the stage of grain filling.

Case study 2: root depth

In this example three different root distribution shapes have been compared to evaluate the effect of the depth of the root system on growth and late-season water storage in the soil. Root distribution is defined as having a maximum soil explored depth of 40 cm for T.2.1, 80 cm for T.2.2, and 150 cm, at the soil bottom, for T.2.3. If only the upper layers of soil are explored by roots, when rooting is poor (T.2.1), the crop will suffer water stress in the earlier vegetative phase. The effect on biomass accumulation is very drastic, having at the end 45 per cent of dry matter as compared to ideotype T.2.2 (Figures 8 and 9). The reduced water consumption during early growth may, however, maintain higher water storage in soil after anthesis and during the grain-filling period. Otherwise we must take into account that severe stress during early growth phases may strongly affect crop density.

This first simulation indicated that a deeper root system may give a better use of available soil water. The following strategic step was then to analyse how far this correlation may be stressed. The T.2.3 ideotype was then tuned to have the deepest root system according to the hypothesized soil depth. Results of this simulation are shown in Figures 10 and 11. It is interesting to outline how the increased water consumption with a larger soil water availability may influence water stress, reducing the soil water storage. In fact T.2.3 has a large water consumption during a non-dry season and it has very low leaf water potential during crucial phases.

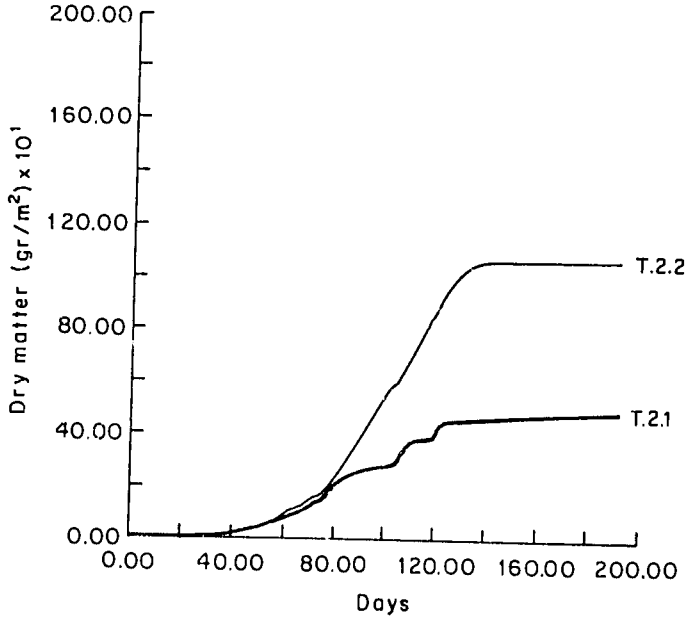


Figure 8. Biomass production over growing season

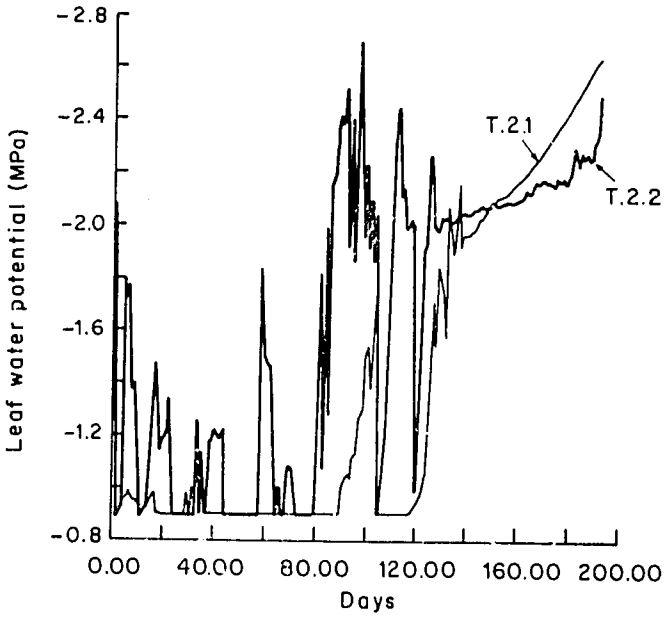


Figure 9. Leaf water potential at midday over growing season

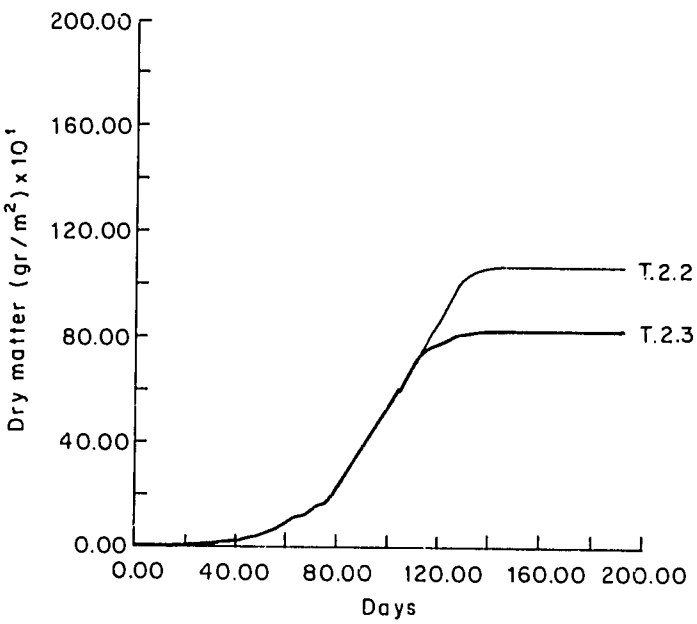


Figure 10. Biomass production over growing season

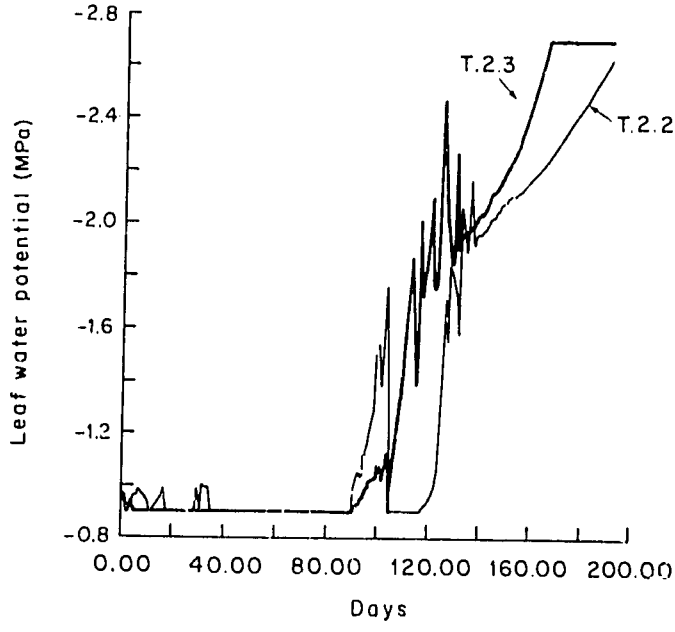


Figure 11. Leaf water potential at midday over growing season

Finally, the hypothesis may be derived that 'root exploring ability' must be in equilibrium between earlier water use and final soil water storage; paradoxically, drought resistance might be improved by decreasing the size of the root system (Porceddu, 1984; Passioura, 1983).

Following previous indications, we must suppose that the ideal wheat crop might have a bigger root system during drought periods and a smaller one when water is not limiting. Ideotype hypothetical strategy to perform such adaptation may be related to plant ability in modifying the partitioning of assimilates between root/shoot systems as a function of water deficiency of tissues. Classical studies (Schultz, 1974) indicate that the root/shoot ratio normally ranges in wheat from 0.1 to 0.3. An adapted cultivar which can modify this behaviour may be hypothesized with a lower root/shoot ratio at high soil moisture levels.

Case study 3: root/shoot ratio

In this simulation test two ideotypes were compared: T.3.1 with a partioning ratio of 0.1–0.3 linearly dependent from leaf water potential, and T.3.2, with a 0.01–0.3 range. Results (Figure 12 and 13) show a more equilibrated water use in T.3.2, allowing the crop to have a higher biomass production. This yield increase is otherwise balanced by a strong decrease in leaf water potential

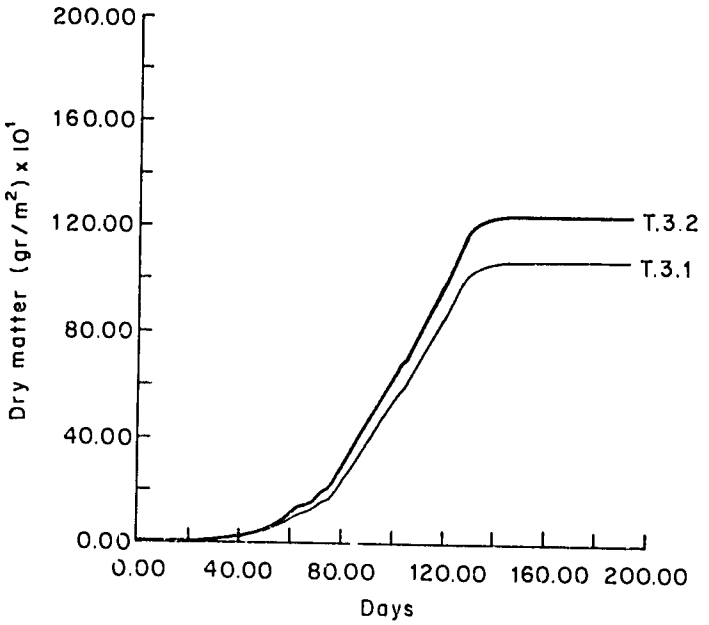


Figure 12. Biomass production over growing season

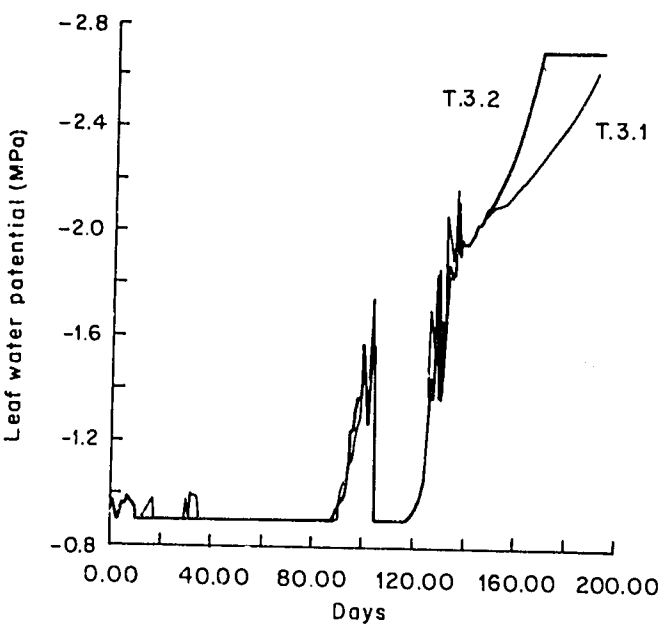


Figure 13. Leaf water potential at midday over growing season

during maturity due to a more relevant transpirative loss. This might reduce the benefit of the lower early water use.

One physiological trait often considered is stomatal resistance. Water-loss regulation in the green part of the plant is performed by stomata and differences in stomatal behaviour appear to explain differences in drought resistance among species (Schmidt, 1983; Kirkham and Kanemasu, 1983). Both stomatal size and sensitivity to leaf water potential changes can influence crop water use. Stomatal resistance was considerably higher in drought-resistant wheat than in susceptible ones. This trait might be of some interest if included in programmes designed to screen wheat cultivars for dry lands.

Case study 4: stomatal sensitivity

Following case study 3, the selected test T.4.1 = T.3.2 may be improved, inducing a more sensitive stomata closure to water stress (T.4.2). Soil water storage might be influenced by changing the water-use pattern. Two ideotypes were characterized in the model with different threshold values for leaf water potential/stomatal resistance relationship. Nodal points (J,K in Figure 3) were:

T.4.1 = -15/-19 MPa
T.4.2 = -12/-15 MPa

Figures 14 and 15 compare the results of simulation for the two ideotypes. A very low final biomass reduction in T.4.2 is related to an important decrease

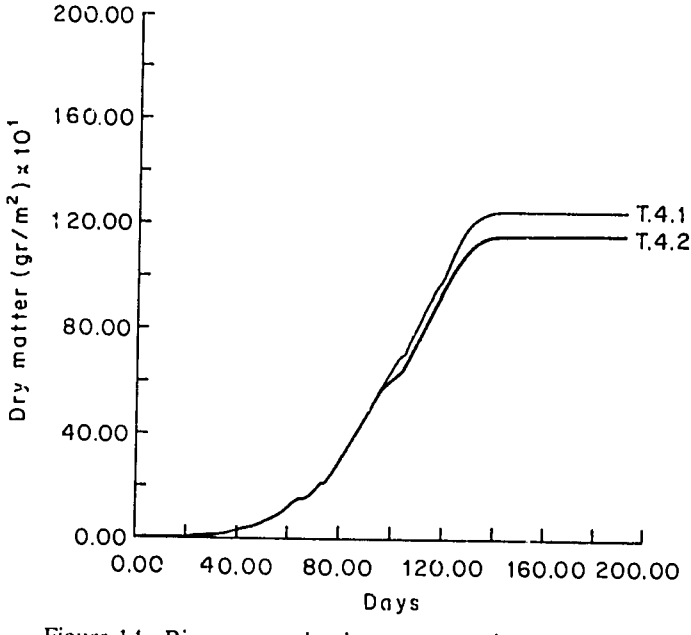


Figure 14. Biomass production over growing season

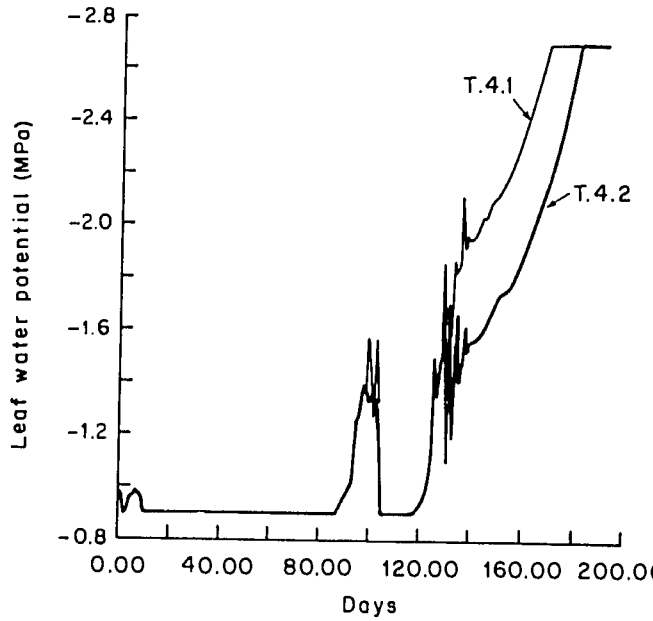


Figure 15. Leaf water potential at midday over growing season

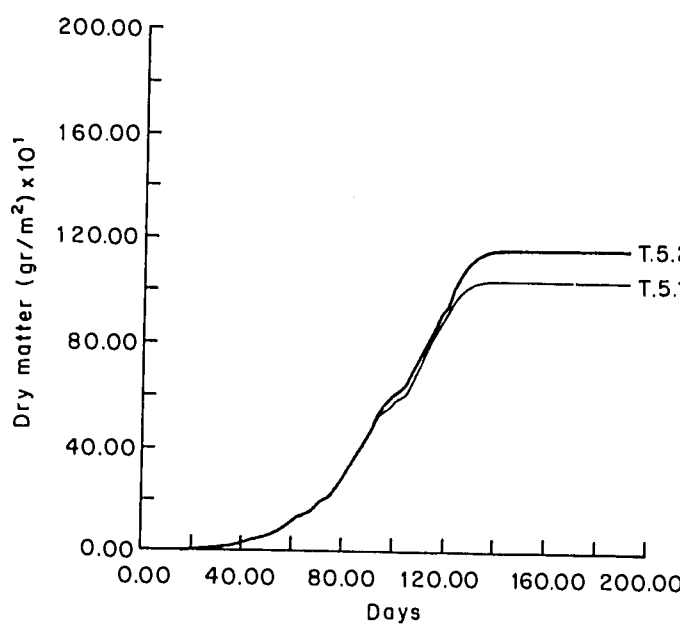


Figure 16. Biomass production over growing season

in water consumption. This seems to be in agreement with ideotype goals for semi-arid lands.

When the wheat crop relies on soil water storage at the time of sowing, the water-use pattern during the life cycle is strongly related to final production; grain yield in this case may depend on the amount of available water at the time of flowering (Nix and Fitzpatrick, 1969). To reduce the amount of water extracted from the soil in order to have a more efficient distribution along phenophases, Passioura (1983) suggests that a good way might be to increase the root hydraulic resistance to water flow, selecting, for example, wheat lines that have small xylem vessels.

Case study 5: hydraulic root resistance to water flow

In this case two new tests, T.5.1 (= T.4.2) and T.5.2 (the last one defined by an increased root hydraulic resistance), were compared. T.5.2 (Figures 16 and 17) shows a higher biomass production and a lower water consumption, confirming that it is relevant to prevent the plant using water too freely during vegetative growth.

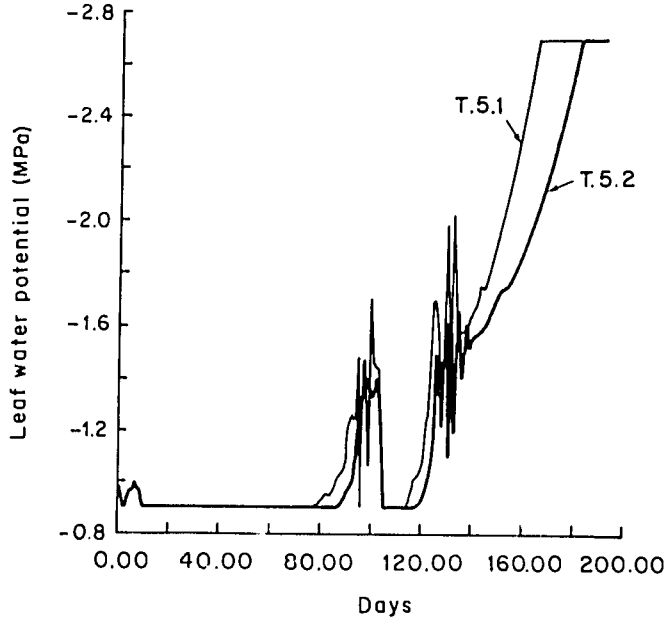


Figure 17. Leaf water potential at midday over growing season

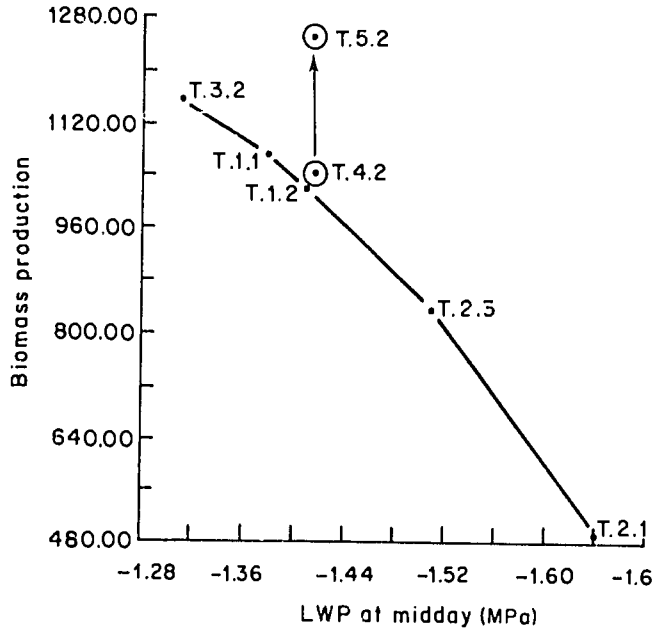


Figure 18. According to case study examples, a quasi-linear relationship can be found among averaged leaf water potentials at midday along the growth cycle and final dry-matter production. Except in cases T.5.1 and T.5.2 a decrease in leaf water potential corresponds to lower production. For the other cases the different functional approach used in the model allows the ideotypes to economize on water during the growth cycle and increase final yield, diverting rapidly from the drawn line

Conclusions

From the above discussed examples of the use of simulation models to test crop ideotypes for semi-arid lands, the first conclusion derived is that this type of approach does not give as misleading results as suggested in the literature. Crop models, when well validated, could be used as controls for ecophysiological traits to be put in breeding programmes.

The final observation relates to the fact that average midday leaf water potential, measured or simulated, is quasi-linearly correlated with crop dry-matter production (Figure 18) (Sojka *et al.*, 1981). All strategies that allow the maintenance of high leaf water potential might be of great interest in breeding programmes for semi-arid regions.

REFERENCES

Acock, B., Thornley, J. H. M. and Warren Wilson, J. 1970. Spatial variation of light in the canopy. Pages 91–102 in *Prediction and Measurements of Photosynthetic Productivity* (Setli, I., ed.). Pudoc, Wageningen, The Netherlands.

Austin, R. B. 1982. Crop characteristics and the potential yield of wheat. *J. Agric. Sci. Camb.* **98**:447–453.

Derera, N. F., Marshall, D. R. and Balaam, L. N. 1969. Genetic variability in root development in relation to drought tolerance in spring wheats. *Exp. Agric.* **5**:327–337.

De Wit, C. T. and others 1978. *Simulation of assimilation, respiration and transpiration*. Pudoc, Wageningen, The Netherlands.

Feddes, R. A., Kowalik, P. J. and Zaradny, H. 1978. *Simulation of field water use and crop yield*. Pudoc, Wageningen, The Netherlands.

France, J. and Thornley, J. H. M. 1984. *Mathematical models in agriculture*. Butterworth.

Greacen, E. L., Ponsana P. and Barley, K. P. 1976. B. Resistance to water flow in the roots of cereals. In *Water and Plant Life. Ecological Studies Analysis and Synthesis*, Vol. 19. Springer, Berlin.

Hillel, D. and Talpaz, H. 1976. Simulation of soil water dynamics in layered soil. *Soil Science*. Vol. ??. ????

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. *Agric. Meteorol.* **14**:39–55.

Kirkham, M. B. and Kanemasu, E. T. 1983. Wheat. In *Crop Water Relation*, Teare, I. D. and Peet, M. M., eds. John Wiley.

McKay, J. 1966. The wheat plant as a model in adaptation to high productivity under different environments. Pages 37–48 in *5th Jugoslav Symposium on Research in Wheat*, Novi Sad.

McKay, J. 1970. An ecological model for yield in small grains. Pages 128–149 in *Seminar series*, Department of Agronomy, Iowa State University, Ames, Iowa, USA.

McKay, J. 1979. Wheat domestication as a shoot/root interrelation process. Pages 875–890 in *Proceedings, 5th International Wheat Genetics Symposium*, New Delhi.

Maracchi, G., Miglietta, F., Raschi, A., Vazzana, C. and Bacci, L. 1985a. A crop model based on simple meteorological inputs for large scale agricultural productivity simulation: *Proceedings of 13th IASTED International Conference on Modelling and Simulation*, Lugano, Italy.

Maracchi, G., Conese, C., Miglietta, F. and Bacci, L. 1985b. An integrated model for agricultural productivity. In press, by FAP-IIASA Laxenburg.

Nix, H. A. and Fitzpatrick, E. A. 1969. An index of crop water stress related to wheat and grain sorghum yields. *Agric. Meteorol.* **6**:321–337.

Passioura, J. B. 1983. Roots and drought resistance. *Agric. Water Manag.* **7**:265–280.

Porceddu, E. 1984. Factors in crop plant adaptation to dry land conditions. Centro Informazione Stampa Universitaria, pp. 5–29.

Rijtema, P. E. 1969. *Soil moisture forecasting*. Institut voor Culturtechniek en Waterhuishouding, Wageningen, The Netherlands.

Schmidt, J. W. 1983. Drought resistance and wheat breeding. *Agric. Water Manag.* **7**:181–194.

Schultz, J. E. 1974. Root development of wheat at the flowering stage under different cultural practices. *Agric. Rec.* **1**:12–17.

Sojka, R. E., Stolzy, L. H. and Fischer, R. A. 1981. Seasonal drought response of selected wheat cultivars. *Agric. J.* **73**:838–844.

Taylor, H. M. and Gardner, J. R. 1960. Relative penetrating ability of different plant roots. *Agron. J.* 52:579–581.

Turner, N. C., Bagg, J. E., Rawson, H. M., English, S. D. and Hearn, A. B. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, CO_2 photosynthesis and adaptation to water deficits. *Aust. J. Plant. Physiol.* 5:179.

DISCUSSION

M. Nachit

(1) What implication does deep rooting have on grain-filling rate?

(2) Could you elaborate on the relationship between stomata closure and leaf temperature increase?

C. Vazzana

(1) The deep rooting genotype is not ideal for dry areas, and this is mainly due to moisture extraction in early developmental stages and not having enough water during the grain-filling stage.

(2) Closed stomata during stress enhance the leaf temperature and this reduces the photosynthetic activity. However, actually in the model, as said in the presentation, no heat exchange is considered.

H. M. Taylor

Your simulation model shows that deeper root systems reduce yield. Experience shows that deeper root systems in fully wetted soil increase yield. Why do your simulations show the opposite effect?

C. Vazzana

There is a large consumption of water in the early stage of the grain-filling period. In the model, changing the hypothesized root geometry allows the plant to have a deeper root system and so water consumption in the early growth phases is changed; the stored water is freely consumed and rapidly exhausted. Soil water storage is freely consumed and rapidly exhausted. We think that this may really happen (Passioura, 1983).

B. Yilmaz

Is there any relation between coleoptile length and/or crown depth on yield?

C. Vazzana

At the present time we don't take into account the relation between coleoptile and yield. We take into account only the LAI.

D. Lawlor

The information given on stomatal resistance against leaf water potential: was it assumed, calculated, or measured? Is the relationship of a general type? Did you simulate the effect of smaller stomatal changes at higher water potential? Increasing resistance increases the vapour pressure gradient around the leaves, but may not produce a proportional decrease in evaporation.

C. Vazzana

We validated the response used in the model for stomatal resistance against leaf water potential with experimental data. The model itself calculates stomatal resistance as a function of leaf water potential previously computed in the plant water module. The relationship seems to be of a general type. We did not simulate the effect of smaller stomatal changes at high leaf water potentials, but we could do it.

R. A. Richards

How was dry-matter production calculated from water use in simulation studies and were any corrections made for changes in stomatal conductance or differences in vapour pressure as time progressed?

C. Vazzana

In the model, the water used by the plant influences the leaf water potential and stomatal resistance. The latter acts on actual photosynthesis and hence on dry-matter production. We do not take into account the effect of senescence on stomatal activity, but we compute the effect of decreasing LAI.

R. B. Austin

How did you simulate the dry-matter distribution among the different organs of the shoot? Was the performance of the model greatly sensitive to variation in the above?

C. Vazzana

Only a relationship between dry matter and leaf area is considered in the model. Other shoot components are actually neglected in the computation. We think that improvement in this relationship may be substantial due to high sensitivity of the model. The easiest way to approach this problem might be to formulate different crop architectures.

S. K. Sinha

(1) You have used water potential changes as the main criterion of water stress. However, water potential changes with the stage of growth even in an irrigated crop. Did you take these changes into consideration?

(2) There is a strong effect of water stress on senescence. Does your model take the rate of senescence into consideration in relation to the sink size? When you validate your models, do you use some existing varieties. If yes, they could be better described as plant types rather than ideotypes.

C. Vazzana

We take into consideration the change in water potential connected with the change in root/shoot water balance. We don't consider senescence at the moment; however, the model computes a decrease in LAI after anthesis. Yes, a durum wheat variety, 'CRESO', is being used for validation. When we talk about ideotypes, we only change crop characteristics as input data in the model.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

3

Crop Genotype–Environment Interaction

HAZEL C. HARRIS, W. GOEBEL, and P. J. M. COOPER
ICARDA, PO Box 5466, Aleppo, Syria

ABSTRACT

In most semi-arid regions where winter cereals are grown under dryland conditions, productivity is limited not only by low and/or uncertain rainfall, but also by both low and high extremes of temperature. The interaction of these stresses is discussed in relation to winter rainfall areas of the Mediterranean region.

Means of reducing the effects of these stresses by either the application of sound agronomic practices or modification of cultivars are considered, and illustrated with data from agronomic trials and computer simulation studies.

INTRODUCTION

The environment of crops is comprised of several elements. In any one season and location, weather conditions, soil factors, and cultural practices interplay to determine to what extent the yield potential of a given genotype will be expressed. When crops are grown for on-farm production, cultural practices are determined to a large degree by the social and economic circumstances of the producer and vary according to his resources and goals, the information available to him, government policies, infrastructure support, and numerous other factors. It is not the purpose of this paper to consider these socioeconomic components of the environment, but they should not be overlooked in consideration of strategies for crop genotype improvement.

This paper examines the influence of interrelationships of weather, soil, and management factors on the productivity of crop genotypes in moisture-limiting environments. Attention has been focused on those regions of the world where spring-type temperate cereals are sown in the autumn (fall) and harvested in late spring or early summer. These regions include predomin-

antly Mediterranean-type and subtropical climates. The interaction of environmental factors is illustrated using data from our programme which we believe to be directly relevant to much of the Mediterranean Basin and to have considerable relevance for other winter-rainfall areas. Reference is made to the implications of this interaction for other areas where appropriate.

CONSTRAINT IDENTIFICATION

Moisture supply

Rainfall patterns in winter cereal growing regions, where moisture supply is limiting, range from the classical Mediterranean-type distribution where rain is received only during the six months of the year spanning the winter, through areas where rainfall is uniformly distributed through the year, to zones where as much as 80 per cent of rain may fall in summer and cereals are grown during the winter using stored soil moisture. It is characteristic of all of these areas that rainfall not only is low, but its distribution is highly variable both between and within seasons.

One of the consequences of this variability for research, and probably particularly for genotype evaluation, is that it becomes extremely difficult to interpret data from field trials. The occurrence of water stress of differing degrees in succeeding seasons, or at different growth stages from season to season, means that genotype evaluation needs to be carried out in several seasons and locations to arrive at conclusions regarding genotype performance. Even then, the range of environments covered may not represent the full range to which a new genotype may be exposed. We believe that the choice of environments for genotype evaluation is extremely important. Testing sites should be carefully chosen to span the environmental range of areas for which material is targetted in order to generate information not only on genotype performance, but also on the environments themselves and on plant–environment interactions.

The question of the length of the period over which genotype testing should be carried out deserves attention. In variable environments how long is long enough to adequately assess genotype performance? We will return to this later.

The numerous methods which have been developed to test relative genotype–environment interactions (e.g. Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Fischer and Maurer, 1978) have provided useful interpretations in some circumstances but in others have been found wanting. Probably, the main reason for the lack of wide applicability of the first two mentioned methods is that only final yield is used as a measure of crop performance and no account is taken of the fact that yield development is itself complex. The final yield (or that part of it, namely, the grain, which is

most commonly measured) represents the summation of the ability of a cultivar to adapt to a series of stresses and their interactions which may be encountered during the life cycle. In other words, grain yield almost always represents the integration of a season's effects rather than a single identifiable occurrence. Grain yield can be achieved by different pathways, depending on the physiological stage at which stress occurs and on the adaptive response of the cultivar. The details of such adaptive responses form the subject matter of other papers in this meeting and will not be pursued here.

Temperature limitations

There is a strong interaction between the temperature and moisture components of the crop growth environment, particularly at both high and low extremes of temperature.

High temperature

The temperature regime of moisture-limiting environments, where winter cereals are grown as defined in the introduction, is virtually always characterized by a rapid rise of temperature in the spring (Figure 1) to a level where temperatures during much of each day are well above the optimum for the growth of temperate grasses. One consequence is that respiration rates are markedly increased, leading to lower net assimilation and dry-matter accumulation rates.

A second consequence of high temperature in spring is that the rate of physiological development is increased and the onset of the process of senescence occurs more quickly. This reduces the time available for crop growth and even under well-watered conditions may cause a marked erosion of the yield potential of a cultivar. Strong temperature–genotype interactions shown by McDonald *et al.* (1983) include both of these effects, but suggest genotype differences do exist.

A third, and most important, consequence of high spring temperatures is the increase in the saturation vapour pressure deficit of the atmosphere which they cause. This increase leads to a reduction in the efficiency of water use due to the inverse relationship between carbon fixation and vapour pressure deficit (Tanner and Sinclair, 1983). In the regions being considered, spring-type cereals planted in autumn develop during winter and early spring and reach maximum canopy development and thus maximum transpiration rates at the time of this increased evaporative demand. The size of the evaporative load frequently exceeds the capacity of the soil–plant continuum to maintain the supply of water to transpiring crop surfaces and, even where soil moisture reserves are high, daytime water deficits occur within the crop canopy. These are exacerbated by the fact that in these environments spring either marks the

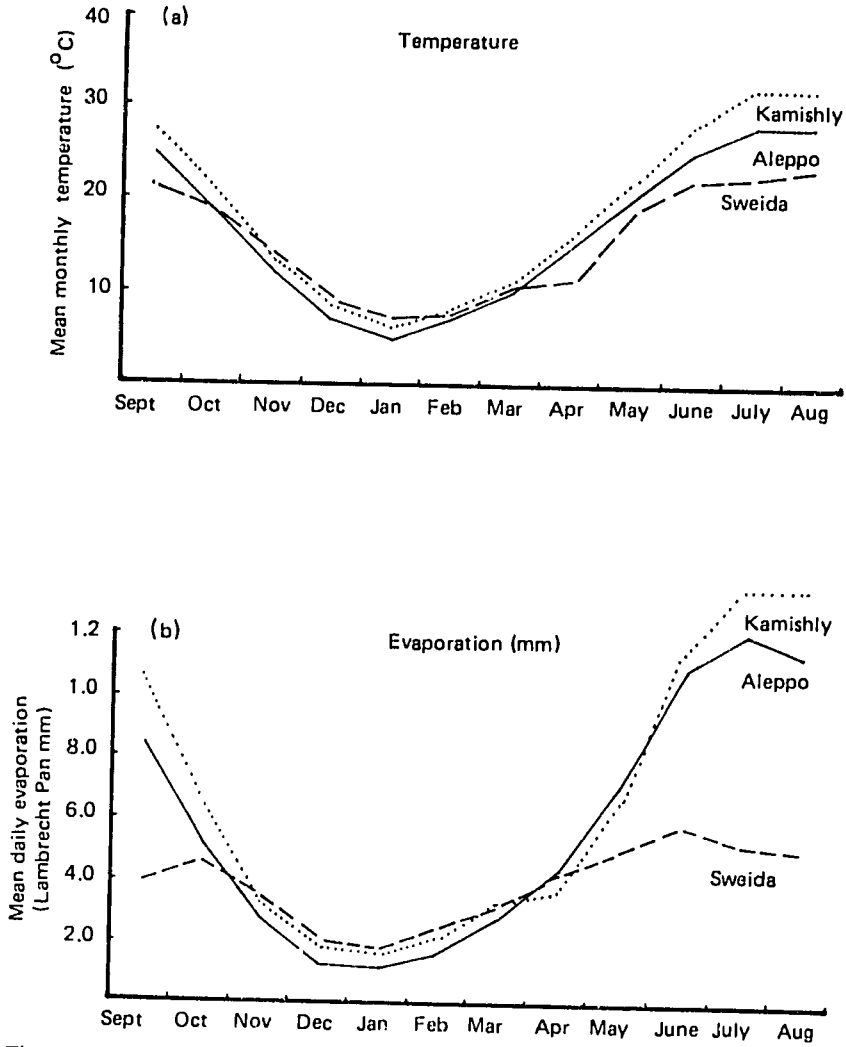


Figure 1. Monthly mean temperature and mean daily evaporation for three locations in Syria. Data supplied by the Meteorological Department, Ministry of Defence, Syrian Arab Republic

end of the rainfall season in winter-rainfall areas or may coincide with a period of low probability of rain in regions where rain is more uniformly distributed throughout the year. Frequently, therefore, the water supply to a crop is inadequate to meet the demand placed upon it. Some, and often severe, water stress in the grain-filling stage of crop growth is virtually inevitable in the environments we are considering. Quantitative effects of these stresses are considered later.

Low temperature

The effects of low temperatures on the productivity of winter-grown cereals clearly vary with geographical area. Attention in the following discussion again is focused on those areas where spring-type cereals are grown during the winter. Interactions with the moisture regime will be considered under two headings: the effect of low temperature on growth and the effect of freezing damage on development and yield.

Low temperatures and growth

In much of the area defined above, and particularly in the Mediterranean region, low winter temperatures restrict crop growth rates. This results in slow development of full ground cover by crops. Poor ground cover allows increased evaporative loss from bare soil surfaces which reduces the water available for crop use (e.g. Slayter, 1967; Jury, 1979; and for the specific environment, Cooper, 1983). It is well documented that dry-matter production is linearly related to the amount of water transpired and that the efficiency with which transpired water is used is greater at lower than at high evaporative demands (e.g. Tanner and Sinclair, 1983). Further, it has been shown that, except in very severe postanthesis drought, grain yield is directly related to biomass in the late vegetative/early reproductive stage of growth (Fischer, 1979). It therefore has been argued that the greater the proportion of crop growth which can take place early in the season, the greater will be the efficiency of water use (Fischer, 1981). Obviously, slow winter growth will reduce the efficiency, whereas any increase in winter growth could markedly increase it. This will be considered quantitatively later.

Freezing damage, crop development, and yield

Freezing damage has been observed in our experimental programme at several stages of growth. In the seedling growth stage, freezing in conjunction with wet (waterlogged) conditions caused quite extensive plant death in the 1984–5 season. This occurrence is possibly rare. Loss of leaf area in the early stages of growth (prestem elongation) of both wheat and barley with screen night temperatures less than about −8°C occurs more frequently, the severity of damage probably being greater when mild temperatures precede the frost event. Reduction in canopy size through this effect can be expected to lead to similar water-use inefficiencies to those noted in the preceding paragraph.

Freezing damage following the commencement of stem elongation also occurs in the environments we are considering, and the effect of this on crop

grain yield is likely to be much more severe. The degree of severity will depend on the stage of development and the form the damage takes. In Syria, temperatures below about −8°C in early stem elongation caused death of the main stem of both wheat and barley, but tillers were unaffected or suffered only leaf burn. The crops recovered to give reasonable yields, but flowering and maturity of damaged crops appeared to be delayed by a few days and some yield reduction undoubtedly occurred, although this cannot be quantified (Stapper, 1984; Shepherd, 1985).

Frost damage at later growth stages is a recognized hazard of semi-arid environments. When quite mild frosts (*ca.* < −3°C) occur in the late elongation, booting, or heading stages, severe yield reduction may result (Single, 1975). At these stages of growth there is little opportunity for recovery as crops enter periods of high temperature and water deficit.

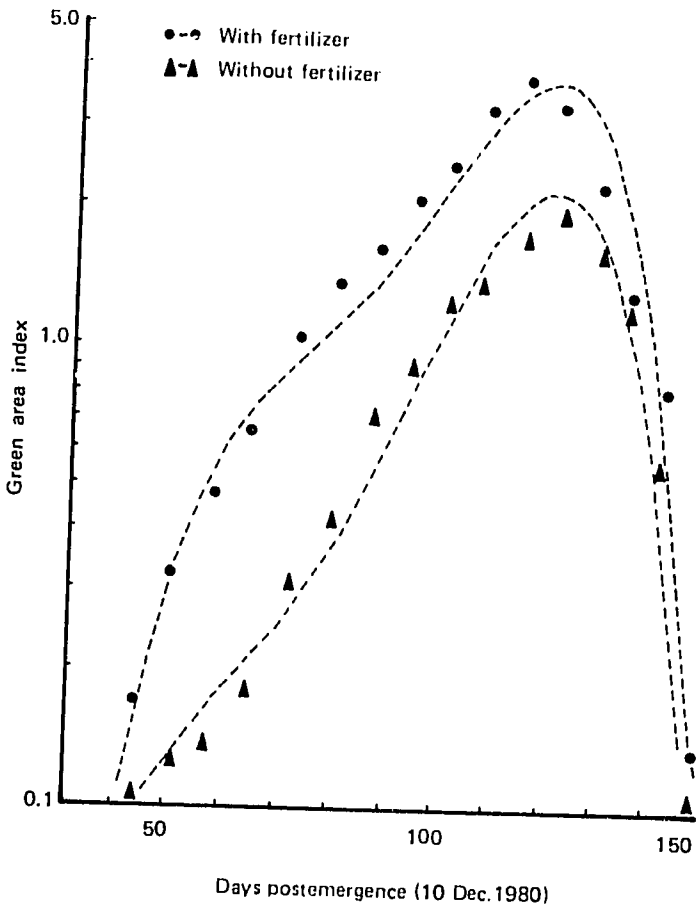


Figure 2. Seasonal change in GAI of Beecher barley with and without added fertilizer, northern Syria (1980–1). (From Cooper, 1983)

The physiology of freezing damage in cereals, especially wheat, is reasonably well known. The severity of damage is related to the growth stage at which it occurs and appears to be increased when relatively high day temperatures immediately precede frost events (Single, 1975).

Given the complexities of the interactions of freezing temperatures with crop growth stage and previous conditions, it is not surprising to find that the effects of the damage on crop yields are poorly quantified. It should be noted in particular that the temperatures cited above are only approximate.

MODIFICATION OF GENOTYPE-ENVIRONMENT INTERACTIONS

Some interactions of crop genotypes with environment may be modified by agronomic practices. One clear example is cited below. Alternatively, longer-term breeding programmes are required. Both processes are costly—the

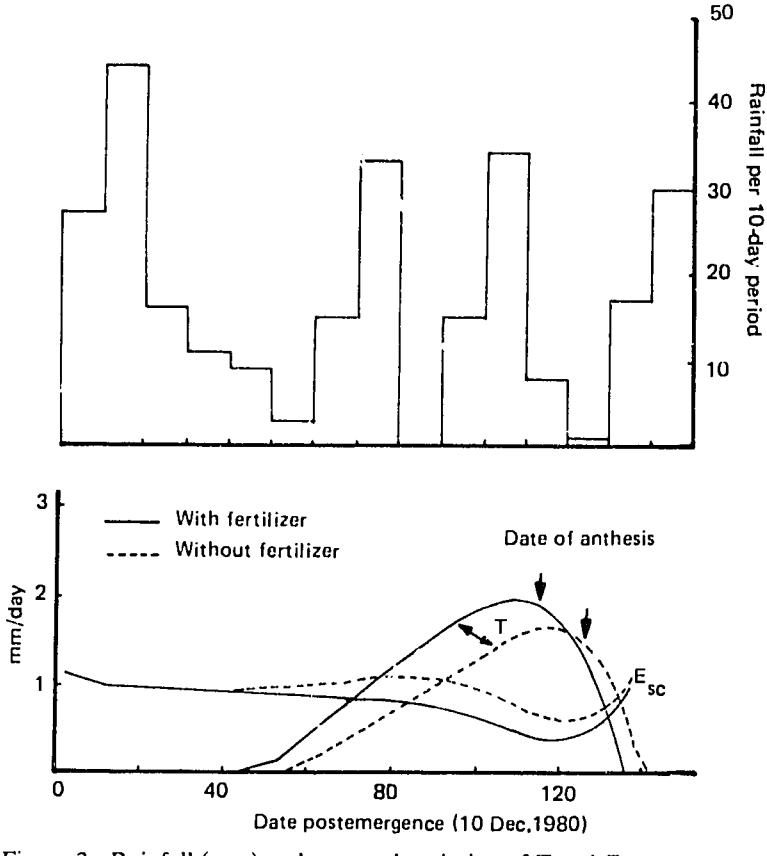


Figure 3. Rainfall (mm) and seasonal variation of T and E_{sc} of Beecher barley with and without added fertilizer, northern Syria (1980–1). (From Cooper, 1983)

former due to the need to test the efficiency of practices in a range of seasonal conditions; the latter, in first producing and then testing new cultivars, is even more time and resource demanding. One means by which it may be possible to make these processes more efficient is through the judicious use of computer simulation models in conjunction with environmental data, to explore alternative strategies. Some examples of the application of such a tool are also given below.

Plant nutrition

The amelioration of phosphorus deficiency has been shown to markedly increase the efficiency of water use by barley crops in northern Syria. Figures 2 and 3 show the seasonal pattern of green area index (GAI) and the effect of differences in GAI on seasonal water use, respectively. Fertilizer clearly increased the rate of early canopy development and crop transpiration (T) but reduced soil evaporation (E_{sc}). Total season water use was virtually the same for unfertilized (220 mm) and fertilized (216 mm) crops but total dry-matter yields were 3.6 and 4.9 t/ha, respectively. The water-use efficiency (WUE) was thus increased by 42 per cent. Fertilizer reduced the total growth period of the crop by 7 days, and the increase in WUE for grain production was 26 per cent (Cooper, 1983).

Time of sowing

Studies on the time of sowing of cereal crops have, in the short term, been less conclusive, with results varying between seasons and between sites within seasons (ICARDA, 1981) depending on the rainfall distribution. However, when the question was addressed in the longer term using a regionally calibrated simulation model for wheat genotypes (Stapper, 1984) and 20 years of daily weather data*, it was shown that small but consistent increases in yield can be expected from earlier sowings (Figure 4).

The ability to sow earlier will depend on the timing of rains at the start of the season. Figure 5 shows model predictions of moisture-dependent germination presented as the cumulative probability (for four sites) of germination having taken place. The wide spread of germination dates (55–65 days) may indicate a need for different genotypes to make the best use of the variable length of the growing season.

Earlier sowing also may entail a risk of early postemergence drought which may cause seedling death. This effect is not included in the model as no data on it are available. Probabilities of the occurrence of short-term droughts at this time have been examined by Keatinge *et al.* (1985).

* Data supplied by the Meteorological Department, Ministry of Defence, Syria.

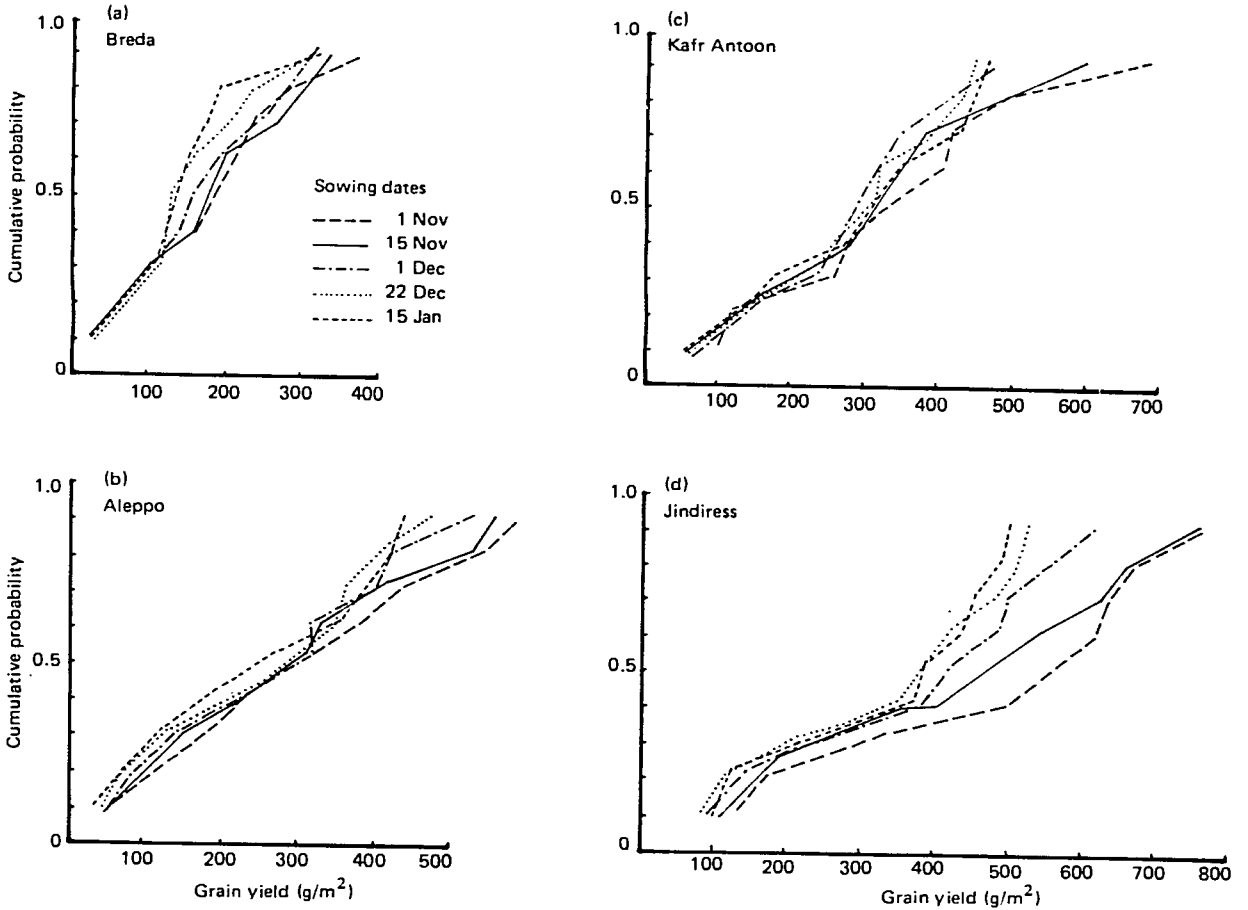


Figure 4. The cumulative probability distribution of simulated yields of a medium season spring wheat cultivar sown on five different dates at (a) Breda, (b) Aleppo, (c) Kafr Antoon, and (d) Jindiress, northern Syria. (From Stapper, 1984)

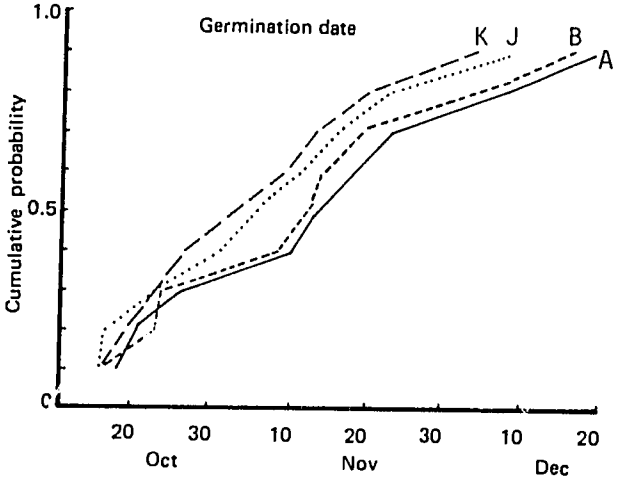


Figure 5. The cumulative probability distribution for simulated time of germination of wheat sown at four locations (K = Kafr Antoon; J = Jindiress; B = Breda; A = Aleppo) in northern Syria. The simulations used 20 years of climatic record for each location. (From Stapper, 1984)

Crop maturity type

Another long-term question which has been addressed using the model is that of the 'best bet' maturity type for wheat in northern Syria. The results (Figure 6) indicate that, as might be expected, early cultivars are best suited to drier sites (*ca.* < 350 mm) where the advantage of yield stability in lower-rainfall years outweighs their inability to fully exploit the best seasons. However, a longer season type is more suited where mean rainfall exceeds 450 mm.

This analysis of crop-type environment interactions is currently being expanded to other areas in Syria, and it is planned that it will be extended to other parts of the Mediterranean region as weather data for other countries become available to us.

We suggest that this form of use of a simulation model can greatly assist in the definition of breeding strategies in variable climates. Similarly, by the quantification of a minimum set of parameters which describe the photothermal responses and important morphological characters of individual genotypes, this model (SIMTAG) should be able to be used to address the question of the length of the testing period raised earlier.

The interaction of soil depth, maturity type, and season

The interaction of soil depth, crop maturity type, and seasonal variability, as predicted by the model, is illustrated in Figure 7. This analysis indicates that

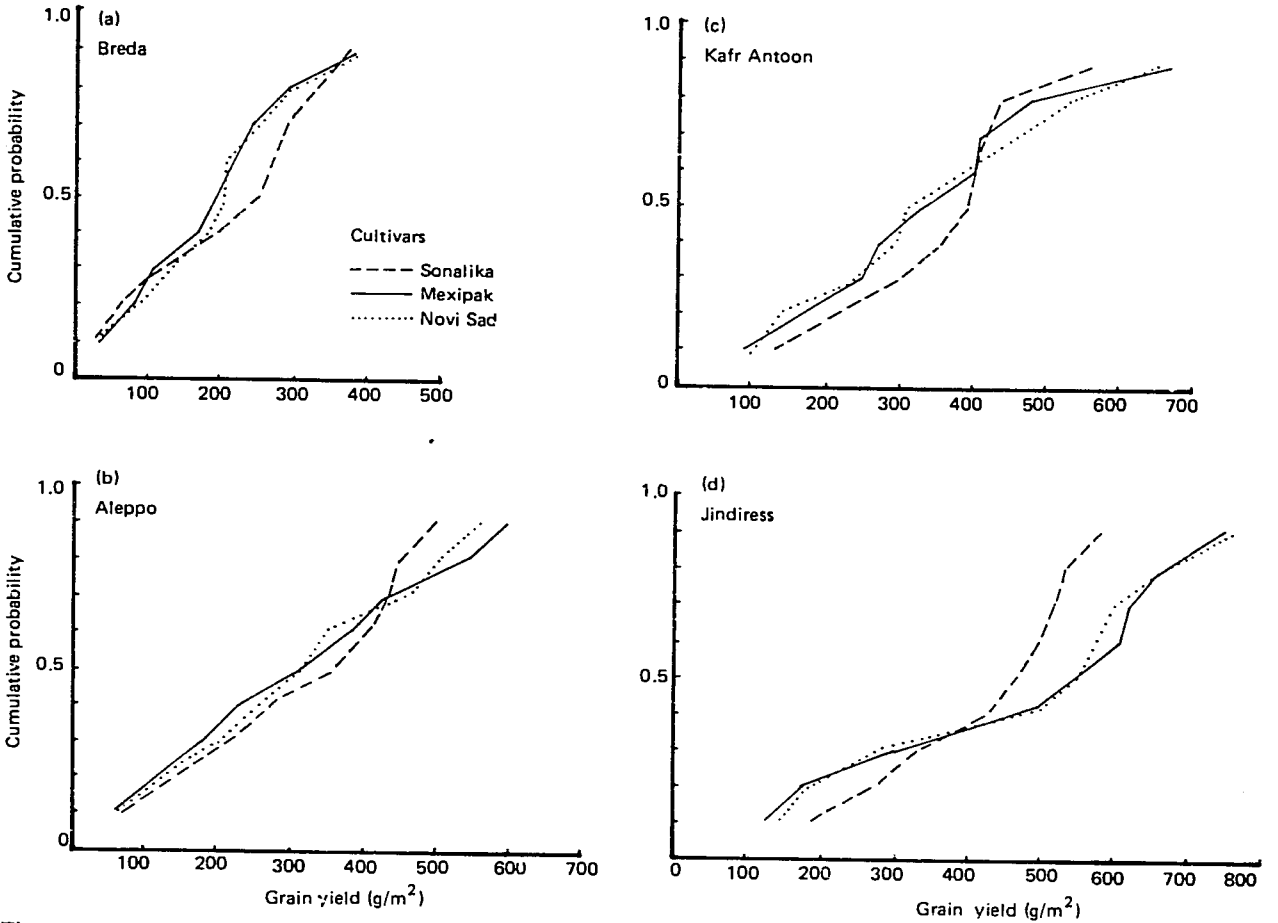


Figure 6. The cumulative probability distribution for simulated grain yields of three spring wheat cultivars of differing maturity sown early November at (a) Breda, (b) Aleppo, (c) Kafr Antoon, and (d) Jindiress. The simulations used 20 years of climatic record for each location. (From Stapper, 1984.)

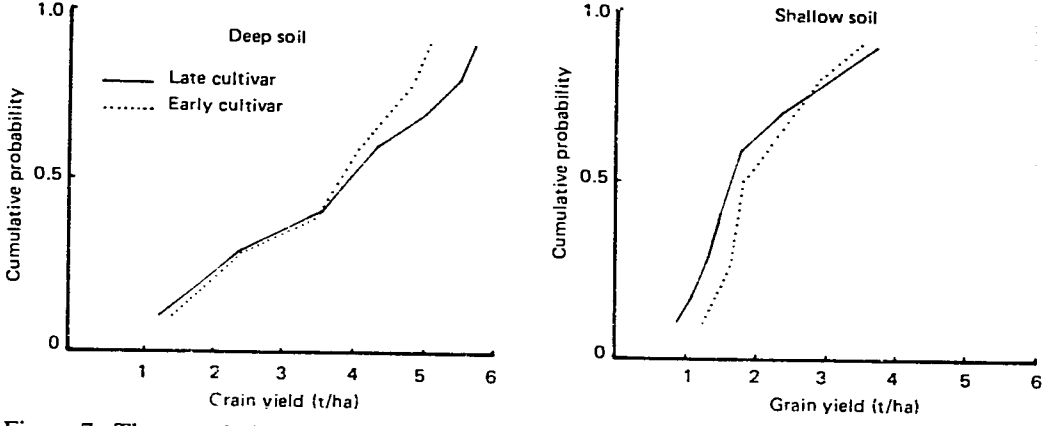


Figure 7. The cumulative probability distribution of simulated grain yields of an early and a late spring wheat cultivar sown on deep and shallow soil. The simulations used 25 years of climatic record from Sweida, southern Syria

for a deep soil with good water-holding capacity in the environment of Sweida in southern Syria, a later cultivar will perform almost as well as an early one in years with some stress, and will outperform the early one in good years. However, on shallow soil an early cultivar will provide a yield advantage over a late one in all but the most favourable years. Such interactions have obvious implications for both breeding strategies and the selection of sites for genotype evaluation.

CONCLUSIONS

A number of points arise from the foregoing discussion which we believe should be addressed by a meeting of this nature.

(1) It is important that the environment for which breeding is undertaken should be clearly defined, particularly with respect to the upper and lower extremes of stress-inducing environmental variables. How well do breeders currently explore this environmental variability for the purpose of defining strategies?

(2) A good deal is known about the effect of stresses at different growth stages on the adaptive strategies existing in plants. How well are these quantified for breeding material?

(3) How are testing sites for new genotypes selected? Is information on environmental variables collected in conjunction with yield evaluation in order to facilitate the interpretation of yield responses?

(4) The occurrence of very extreme stress events is sometimes used in breeding programmes to select heavily for apparent resistance to the stress. What are the limits to which such strategies should be taken? In other words, what should be regarded by breeders as an appropriate event on which to select: a one in five years event, one in ten years, one in twenty years?

(5) Finally, we return to the socioeconomic component of the environment, which is not surprising since our research deals with farming systems. What are the needs of the clients of breeding programmes, governments and farmers, in respect to the environmental variability we are considering? What level of yield variability can be accepted by the social systems with which we deal? How well can we define this and how should such information be incorporated into breeding strategies?

REFERENCES

Cooper, P. J. M., 1983. Crop management in rainfed agriculture with special reference to water use efficiency. Pages 63–79 in *Nutrient Balances and the Need for Fertilizers in Semi-Arid and Arid Regions*. International Potash Institute, Bern.

Cooper, P. J. M., Keatinge, J. D. H. and Hughes, G. 1983. Crop evapotranspiration—a technique for calculation of its components by field measurements. *Field Crops Research* 7:299–312.

Eberhart, S. A. and Russell, W. A. 1966. Stability parameters for comparing varieties. *Crop Science* **6**:36–40.

Finlay, K. W. and Wilkinson, G. N. 1963. The analysis of adaptation in a plant-breeding programme. *Australian Journal of Agricultural Research* **14**:742–754.

Fischer, R. A. 1979. Growth and water limitations to dryland wheat yields in Australia: a physiological framework. *Journal of the Australian Institute for Agricultural Science* **45**:83–94.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through the breeding of crops. *Plant and Soil* **58**:249–278.

Fischer, R. A. and Maurer, R. 1978. Drought resistance in spring wheat cultivars. I. Grain yield response. *Australian Journal of Agricultural Research* **29**:897–912.

ICARDA (International Center for Agricultural Research in the Dry Areas). 1981. Soil, water and nutrient research—1979/80 by the Farming Systems Research Program, Project report 3. ICARDA, Aleppo, Syria.

Jury, W. A. 1979. Water transport through soil, plant and atmosphere. Pages 180–199 in *Agriculture in Semi-Arid Environments* (Hall, A. E., Cannell, G. H. and Lawton, H. W., eds.). Springer-Verlag, Berlin.

Keatinge, J. D. H., Dennett, M. D. and Rodgers, J. 1985. The influence of precipitation regime on the management of three-course crop rotations in northern Syria. *Journal of Agricultural Science, Cambridge* **104**:281–287.

McDonald, G. K., Sutton, B. A. and Ellison, F. W. 1983. The effect of time of sowing on the grain yield of irrigated wheat in the Namoi Valley, New South Wales. *Australian Journal of Agricultural Research* **34**:229–240.

Shepherd, K. D. 1985. Growth and yield of barley in Mediterranean-type environments. Unpublished Ph.D. thesis. University of Reading. Reading, England.

Single, W. V. 1975. Frost injury. Pages 364–383 in *Australian Field Crops*, Vol. 1, *Wheat and Other Temperate Cereals* (Lazenby, Alec and Matheson, E. M., eds.). Augus and Robertson, Sydney.

Slayter, R. O. 1967. *Plant-water relationships*. Academic Press, London. 366 pp.

Stapper, M. 1984. Simulations assessing the productivity of wheat maturity types in a Mediterranean climate. Unpublished Ph.D. thesis. University of New England, Armidale, NSW, Australia.

Tanner, C. B. and Sinclair, T. R. 1983. Efficient water use in crop production: research or re-search? Pages 1–27 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R. and Sinclair, T. R., ed). American Society of Agronomy.

DISCUSSION

N. C. Turner

What were the yield and grain size in the phosphates fertilizer study referred to? Your data suggested that high phosphate fertilizer use brought the date of anthesis forward by a considerable period. Have similar experiments been conducted varying the sowing density or cultivars with similar dates of anthesis but differing in tillering to test the role of early canopy development on water use by the crop versus that lost from the soil and its influence on yield?

H. Harris

Total biomass yields were 5 t/ha with fertilizer, 3–5 t/ha unfertilized. The harvest index of the fertilized crop was lower than the unfertilized one, implying lower 1000-grain weight. These data are available but not to hand here.

No, these experiments have not been carried out.

G. Ortiz Ferrara

Data presented are based on four locations in Syria representing a radius of no more than 100 km. What will be the feasibility to implement the models you are proposing based on data from more distant and/or perhaps more representative locations from North Africa and the Middle East region?

H. Harris

It is planned to do this when weather data become available to us.

S. K. Sinha

In late growing experiments, was there the same seed rate? Because of photoperiod and vernalization sensitivity the early sown crop would produce more tillers, but not the late sown. Did you compensate it? What was the soil moisture profile at the harvest in early and late sown crops?

H. Harris

The same seeding rate (= 250 plants/m^2) was used. At these populations, similar to those used by farmers, very few tillers survive in the environment. Tiller number is adjusted internally by the model depending on water supply and radiative energy load prior to heading.

All crops used all the water available in any season, i.e. total water use is dependent on rainfall. However, the model predicts that there will be substantial shifts in the proportions either transpired or lost through soil evaporation. The latter increases with later sowings due to loss by evaporation prior to sowing and smaller canopy development in late-sown crops, causing more soil evaporation.

M. Duwayri

Does the model take into consideration the monthly temperature during the growing season along with the amount of rainfall?

H. Harris

The model operates on daily values of rainfall, maximum and minimum temperatures and radiation. It thus incorporates the effect of all these variables on crop growth.

R. A. Richards

What is the difference between the plus and minus P treatment in the proportion of seasonal precipitation lost by evaporation from the soil surface. Is it related to P rate and do farmers in the region already use P?

H. Harris

The proportions were of the order of 50 per cent from unfertilized crops and 25 per cent from fertilized ones. P rate has not been evaluated.

No, farmers in dry areas do not have access to P fertilizer. The aerial extent of the applicability of these results is currently being investigated with a view to reassessment of fertilizer supply policy.

A. Hadjichristodoulou

Information obtained by using three or four varieties of different earliness, i.e. to study the effect of earliness, has limited value and cannot be generalized, because the varieties differ also in genes controlling other traits. Do you think that if one uses varieties of the same earliness will get the same results?

H. Harris

The model has been designed to accept descriptors which characterize individual cultivars. It should be able to predict the response of specified cultivars provided this information is used.

A. Hadjichristodoulou

Do you have data from the region on the effect of intraseasonal variation in precipitation on yield? Any difference in response of varieties? Data from Cyprus (Institute of Agricultural Science, 1982) show that fortnightly distribution of precipitation explained 61–98 per cent of yield variation depending on variety while only 5–70 per cent was explained by the amount of annual precipitation. More detailed analysis showed that the precipitation during sowing time and grain filling was the most important, but this effect also varied with variety.

H. Harris

Data of this type are needed to verify model predictions.

Howard Taylor

How did you define soil depth? Depth to those soil characteristics that stop root development?

H. Harris

The two soil depths used were: for deep soil 180 cm, with a potential water storage capacity of 200–250 mm; and for shallow soil 40 cm, with a water storage capacity of 80–90 mm. In the case of the deep soil, free drainage is assumed below the specified depth. In the shallow soil, the subtending material would be either $CaCO_3$ or rock.

M. Tahir

Don't you think that by making a recommendation of early planting and early types the crop will be exposed to higher risks of frost damage as was indicated by you—a damage of 90 per cent in early types?

H. Harris

The recommendations on maturity types shown included the effects of potential frost damage through the use of daily maximum and minimum temperatures in the simulation. One site where frost damage would be a problem was not discussed. At the sites discussed frost damage is not considered to be a problem for early cultivars except in extreme conditions such as 1984–5.

S. C. Brown

You suggested that the breeding of cereals for the arid areas should be done at the extremes of environmental conditions as well as between the extremes. You have also mentioned the importance of phosphate fertilizer for increasing productivity. There is evidence that yields of landrace varieties, presumably developed under low or zero fertilizer application conditions, are at least equal to those of 'improved' varieties bred under high available nutrient conditions. In contrast, under low or zero fertilizer applications, yields of landrace varieties usually exceed by a significant margin the yields of the 'improved' varieties. Since agriculture is at present generally low input and the level of inputs in the future are uncertain, would it not be better insurance to breed under zero or very low rather than medium or high fertilizer input conditions?

H. Harris

I was referring specifically to testing of genotypes when I suggested that locations covering the extremes of conditions should be used. Obviously, there are limits to which breeding in low nutrient conditions can be carried. In the extreme, no yields would be possible. The question of selecting under low productivity environments versus higher yielding ones will be addressed in a later paper (Ceccarelli *et al.*).

T. C. Hsiao

In your model evaluation of fertilizer effect on canopy development and water-use efficiency, soil evaporation was shown to continue at a relatively high level throughout the season. How is soil evaporation estimated? My understanding is that soil evaporation should decrease markedly when the surface dries or when canopy cover is good.

H. Harris

Soil evaporation was estimated by the method of Cooper *et al.*, using measurements of soil water under both crop and fallow and adjusting for radiation interception by the crop. This is a dry site and GAI normally reaches a maximum of only *ca.* 3–4.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

4

Actual and Potential Yields of Cereal Crops in Moisture-limited Environments

H. KETATA
ICARDA, PO Box 5466, Aleppo, Syria

ABSTRACT

The observed yield of a crop is the expression of its genetic yield potential in a given environment. Cereal production data indicate that realized yields on the farm are generally inferior to those obtained under controlled field conditions in rainfed areas.

Seasonal rainfall is the most important factor affecting yields in the rainfed areas of North Africa and the Middle East. Up to 82 per cent of the variation in grain yield was found to be determined by seasonal rainfall in areas receiving 133–454 mm with 11–19 kg/ha being produced for each additional millimetre. Other important factors include rainfall distribution, soil characteristics, temperature, evaporative demand, and biological stress.

Yields in rainfed areas of North Africa and the Middle East can be increased by an appropriate crop rotation, adequate fertilization, and early planting. A 6-week delay in planting time resulted in yield reductions of 42 per cent in barley and 22–32 per cent in wheat.

Breeding cereal cultivars adapted to rainfed areas is a prerequisite to raising yield potential in those areas. At ICARDA, multilocation screening of early generations and yield testing of advanced material in targetted dry environments has provided improved germplasm combining high yield potential and consistent performance both on research sites and on farmers' fields. Examples are the lines Rihane (barley), Korifla (durum wheat), and Flk's'-Hork (bread wheat).

Farmers in the dry areas hesitate to make any substantial investments because of the high risk of total crop failure. Favourable credit, pricing, and insurance policies have to be developed for encouraging the farmers to adopt the improved technology.

INTRODUCTION

Although the genetic yield potential of a crop is determined by its genetic make-up, the measured yield potential, i.e. the maximum observed yield, is a characteristic of both the genotype and the surrounding environment. In fact, the yield potential of a crop or genotype should be defined as the maximum yield attainable under a given environment. Several factors make up the environment of a crop and determine the maximum crop yield. A number of those factors, including rainfall, temperature, light, and carbon dioxide are uncontrollable. Other factors, including crop type, crop management, and socioeconomic systems may be manipulated by man to best meet his needs.

YIELD POTENTIAL AND YIELD GAP

The maximum theoretical grain yield for wheat under optimum growing conditions was estimated to be around 37,500 kg/ha by Mac Key (1981) and 20,000 kg/ha by Hanson *et al.* (1982). However, the actual highest grain yield in the field has not been more than 15,650 kg/ha. While research reports from different parts of the world do often indicate grain yields of over 10,000 kg/ha, yield estimates are usually based on small plots grown under controlled conditions, and actual yields at the farm level are frequently much lower.

The gap between potential and realized yields varies depending on the technology, environment, and socioeconomic factors. It is relatively small in developed countries but alarmingly large in many areas of the developing countries. In Tunisia, for example, the yield gap depends to a large extent on farm management and is somewhat larger in the drier areas of the country (Table 1). In Syria, the yield gap for wheat and barley ranged between 60 and 160 per cent, based on a comparison of on-farm research plots with farmers' fields in 1984–85.

Past cereal research has emphasized crop improvement for high-rainfall, high-input environments, and led to increased yields in those environments.

Table 1. Average cereal grain yields at research station and on farm for different rainfall levels in Tunisia (1983–4 and 1984–5)

	Grain yield (t/ha)		
Rainfall (mm)	Research	Progressive farmer	Average farmer
450–700	5.5	4.5	2.5
350–450	3.5	2.5	1.5
200–350	2.0	—*	0.7

*No progressive cereal farmers for this rainfall level.

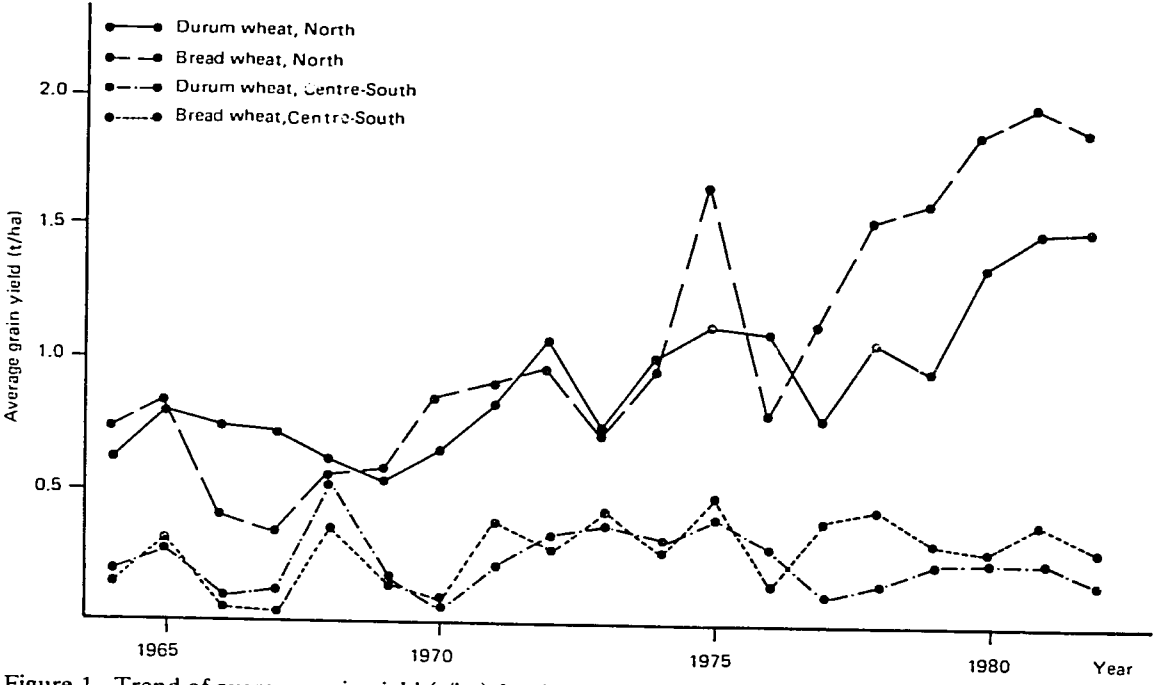


Figure 1. Trend of average grain yield (t/ha) for durum and bread wheat in two contrasting rainfall zones (north and centre-south) of Tunisia

In contrast, yields in less favourable areas have remained low (Anon., 1982; Srivastava and Winslow, 1985). A typical case is depicted in Figure 1 for the yield trend for wheat in Tunisia over a 19-year period in two contrasting environments with subhumid areas in the north (350–700 mm of annual rainfall) and dry areas in the centre-south (200–350 mm). This trend is characteristic of most cereal-growing areas in North Africa and the Middle East. With the increasing population density in the region, increasing food production for cereals has become a major challenge to decision makers and agricultural workers. It is therefore essential to determine the major cereal production constraints and develop ways to alleviate them.

PRODUCTION FACTORS

Moisture stress is the most important constraint to increasing grain yield in rainfed cereal areas. Data in Table 2 demonstrate the positive effect of increased moisture on grain yield of wheat and barley in Syria in 1980 and 1981 when rainfall was favourable. Data from 1983 to 1985 indicate that seasonal rainfall in Syria accounted for up to 82 per cent of cereal grain yield with 11–19 kg/ha being produced for each additional millimetre within the range of 133–454 mm (Table 3). The effect of rainfall, however, becomes confounded when extremes of other environmental factors prevail. For example, in the 1985 season low temperatures during January, February, and March drastically affected yield in Syria. Even in 'normal' years, a sizeable portion (up to 37 per cent) of the variation in grain yield may not be explained by total seasonal rainfall (Table 3). Other environmental factors affecting yield under moisture-limited conditions include rainfall distribution, soil characteristics, temperature, light, evaporative demand, biological stress, and crop management.

Table 2. National average grain yield (t/ha) of rainfed and irrigated wheat and barley for five years in Syria. (The Annual Agricultural Statistical Abstracts, 1983, Syrian Arab Republic, Ministry of Agriculture and Agrarian Reform)

	Wheat		Barley	
Year	Rainfed	Irrigated	Rainfed	Irrigated
1979	0.72	2.39	0.35	1.35
1980	1.38	2.75	1.30	2.43
1981	1.48	2.82	1.03	2.21
1982	1.09	2.52	0.40	1.99
1983	1.07	2.47	0.67	2.02

Table 3. Effect of seasonal rainfall on grain yield of barley and wheat at dry sites in Syria

Year	Rainfall range (mm)	Crop	Regression parameters*		
			n	b (kg/ha/mm)	R^2
1983	186–380	Barley	12	19.2	0.82†
	226–454	Bread wheat	15	12.0	0.70†
	226–454	Durum wheat	15	12.3	0.74†
1984	133–300	Barley	7	11.1	0.43
	166–374	Bread wheat	12	10.8	0.69†
	166–374	Durum wheat	13	12.7	0.63†
1985	171–416	Barley	12	−3.3	0.12
	213–438	Bread wheat	10	6.1	0.23
	213–438	Durum wheat	11	7.5	0.24

*n = number of sites.
b = coefficient of linear regression of grain yield (kg/ha) on rainfall (mm). The value −3.3 for barley in 1985 estimates zero.
R^2 = coefficient of determination for the above regression.
†Significant at $P = 0.01$.

Efficient management of the crop microenvironment has been found to be a key factor to increasing cereal biological yield in moisture-limited areas (Bolton, 1979; ICARDA, 1983, 1984). Early planting, proper fertilization, and appropriate crop rotation were found to increase water-use efficiency (WUE). Results from Syria (Table 4) and Jordan (Anon., 1984) have consistently shown the beneficial effect of early planting on grain yields in dry areas.

Olsen (1980) reported that responses to fertilizers are less pronounced in drier than more humid areas. However, most dry areas have calcareous soils and tend to be low in available P. Results at ICARDA indicate more frequent responses to P than N in drier areas of Syria, where added P was found to increase WUE and hasten barley maturity.

Fallowing is commonly practised in rainfed cereal-growing areas. Results at ICARDA (1984) show that in a fallow/barley rotation, fallowing consistently increased the amount of available N and stored moisture in comparison with a barley/barley rotation. In the Great Plains of the United States (Fenster, 1980), fallowing resulted in a twofold yield increase of winter wheat. However, in rainfed areas with more than 250 mm of annual rainfall, a medic/wheat rotation may be more beneficial (Bakhtri, 1980).

Weed control also affects cereal yields. However, the results in dry environments are not always consistent with regard to the economics of chemical weed control which depends on the degree of infestation, type of weeds, and moisture level (Anon., 1984).

Table 4. Effect of sowing date on grain yield (kg/ha) of barley, durum, and bread wheat at Tel Hadya (230 mm), Syria, 1983–4

Crop	Sowing date		Percent reduction (%)	Rate of yield reduction (kg/ha/day)
	12 Nov. 1983	28 Dec. 1983		
Barley	3105	1805	42	28
Durum wheat	2331	1815	22	11
Bread wheat	2368	1619	32	16

While suitable cultural practices are needed to maximize the expression of genetic potential, breeding cereal cultivars adapted to rainfed areas is a prerequisite to raising the cereal yield potential in those areas. The breeder is here challenged to develop cultivars that are able to withstand drought and yet respond favourably under less stressful conditions. Desirable plant type, variety structure, crop duration, and reaction to diseases (Table 5) are examples of key attributes sought in hybridization and selection programmes. At ICARDA, multilocation screening of early generations and yield testing of advanced material in the target dry environments has provided new lines combining high yield potential and consistent performance both at research sites and on farmers' fields under varying degrees of biophysical and biological stresses. Examples are the barley line Rihane, the durum wheat line Korifla, and the bread wheat line Flk's'-Hork.

TRANSFER OF TECHNOLOGY

Development of improved production technology alone, however, is not sufficient for insuring increased yields at the farm level. The new technology

Table 5. Desirable characteristics of cereal cultivars for dry areas

Characteristic	Desirable feature
Plant type:	
Tillering	High potential, determinate type
Height	Medium tall under normal conditions
Varietal structure	Some degree of genetic heterogeneity or heterozygosity
Maturity	Early (for efficient use of reserve moisture and escape terminal drought)
Reaction to diseases	Resistance to most damaging diseases in dry areas such as common bunt, loose smut, root and foot rot for wheat, and powdery mildew and scald for barley

has to be successfully introduced to the farmer through extension services. Farmers in dry areas usually hesitate to make any substantial investments, even when they are convinced of the usefulness of new technology, simply because the risk of failure is always high in those harsh environments. It is, therefore, for the decision makers to intervene to minimize the risk factor by establishing a favourable policy of credit, price, and insurance. It is only when the risk factor is minimized that the probability of adoption by the farmer will be high.

The task of narrowing the yield gap at the farm level in dry areas is extremely difficult and requires the combined efforts of agronomists, breeders, extension specialists, sociologists, decision makers, and, above all, farmers.

REFERENCES

Anonymous, 1982. Present situation of rainfed agriculture. Pages 3–8 in *Regional Study on Rainfed Agriculture and Agroclimatic Inventory of Eleven Countries in the Near East Region*. FAO, Rome, Italy.

Anonymous, 1984. Cereal improvement in the dry areas: a report on the Jordan Cooperative Cereal Improvement Project, 1978/79 to 1982/83. ICARDA, Aleppo, Syria. 94 pp.

Bakhtri. Naceur. 1980. Introduction of medic/wheat rotation in the North African and Near East countries. Pages 118–125 in *Rainfed Agriculture in the Near East and North Africa: Proceedings of the FAO Regional Seminar on Rainfed Agriculture in the Near East and North Africa*, May 1979, Amman, Jordan. FAO, Rome, Italy.

Bolton, F. E. 1979. Agronomic yield constraints in rainfed cereal production systems. Pages 2–16 in *The Gap between Present Farm Yield and the Potential: Major Constraints and Possible Solutions. Proceedings of the 5th Cereals Workshop*, Vol. II, 5–9 May 1979, Algiers, Algeria.

Fenster, C. R. 1980. Soil management for rainfed wheat production. Pages 306–323 in *Proceedings of the 3rd International Wheat Conference*, 22 May–3 June 1980, Madrid, Spain.

Hanson, H., Borlaug, N. E. and Anderson, R. G. 1982. *Wheat in the Third World*. Westview Press, Boulder, Colorado, USA. 174 pp.

ICARDA (International Center for Agricultural Research in the Dry Areas). Annual report 1983. ICARDA, Aleppo, Syria.

ICARDA (International Center for Agricultural Research in the Dry Areas). Annual report 1984. ICARDA, Aleppo, Syria.

Mac Key, James. 1981. Cereal production. Pages 5–23 in *Cereals: A Renewable Resource, Theory and Practice* (Pomeranz, Y. and Munck, Lars, eds.). American Association of Cereal Chemists, Saint Paul, Minnesota, USA.

Olsen, R. A. 1980. Soil fertility management under rainfed wheat production—opportunities and constraints. Pages 279–305 in *Proceedings of the 3rd International Wheat Conference*, 22 May–3 June 1980, Madrid, Spain.

Srivastava, J. P. and Winslow, M. D. 1985. Improving wheat and barley production in moisture-limiting areas. Rachis 4(1):2–8.

DISCUSSION

B. Yilmaz

Do you recommend high-tillering ability with high seeding rate or low seeding rate?

H. Ketata

Higher-tillering potential combined with good plasticity was found to be associated with higher yields in moisture-limiting environments. Seed rate in these environments should not be too high. Studies have shown no effect on grain yield when seed rates were in the range of 80–160 kg/ha.

F. N. Reyniers

How do you justify the recommendation for high-tillering variety for drought environments? For rice, we recommend medium-tillering variety, for such environments.

H. Ketata

Wheat and barley are usually grown in environments which are very different from those where rice is grown. High-tillering potential with genetic plant plasticity for its expression provides the plant with a mechanism of buffering the environmental variation. For low seed rates, or low germination, or poor stand, the plant can tiller more and take advantage of the available resources (moisture, nutrients, etc.). Genotypes with relatively higher tillering potential were found to be better yielding than other genotypes in moisture-limiting areas.

M. Tahir

Recommendation of high-tillering capacity is based on the agroclimatic pattern as well as our studies on the landrace varieties of barley and wheat from West Asia and North Africa where the rainfall comes during winter months and summers are dry. The plant has to go through a long vegetative phase with no moisture stress followed by a short reproductive phase. This recommendation should also be looked into for other desirable characteristics of a successful variety such as medium to short head size, medium grain size, and short reproductive phase. These characteristics help in avoidance of terminal moisture stress.

SECTION II

Breeding for Winter Cereals in the Low-rainfall Areas

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

5

Barley and Wheat Improvement for Moisture-limiting Areas in West Asia and North Africa

J. P. SRIVASTAVA
ICARDA, PO Box 5466, Aleppo, Syria

ABSTRACT

West Asia and North Africa encompass two major types of environment: a coastal Mediterranean environment with cool, wet winters and hot, dry summers; and a second that includes highlands over 1000 m above sea level, where winters are long and severe and summers short and hot. In these environments bread wheat, durum wheat, and barley are the major crops grown for food and animal feed. During the growing season, usually October/November to May/June, lack of moisture and occurrence of such stresses as cold, heat, or soil salinity damage or kill the crop. Long stretches without rain or short dry or hot spells during critical growing stages reduce grain yields.

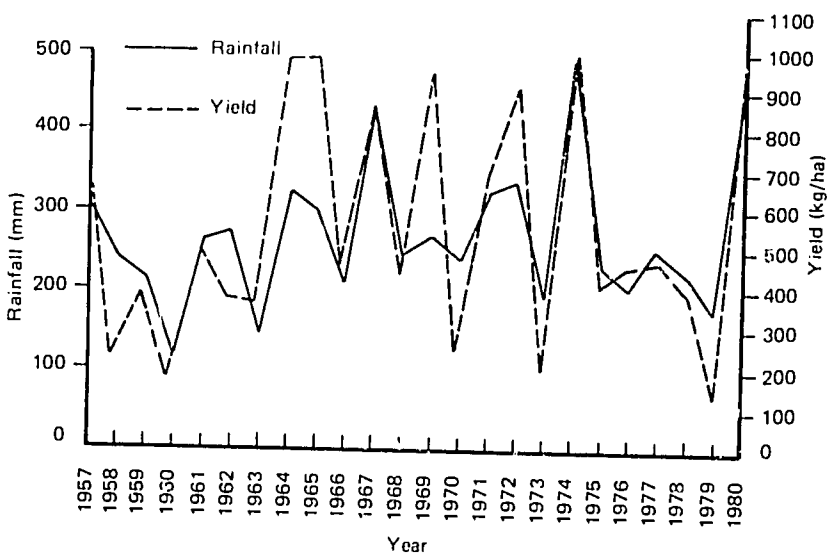
Incorporating genetic resistance into plants can help them tolerate biotic stresses which often limit their productivity. Coupled with better agronomic practices this can improve not just productivity but also yield stability. Characterization of the target environment is important in this process, as is the heritability of plant characteristics beneficial in specific environments. It is important to define the level of moisture stress and production level for applying the appropriate breeding and selection strategy. Breeding and selection methods employed at ICARDA for developing barley and wheat germplasm for dry areas essentially comprise: (1) screening and development of genetic stocks possessing resistance/tolerance to prevailing stresses in the region, (2) incorporation of desired traits in the crosses required in the target environment, (3) exposure of early generation populations to the environments in which they will be grown, (4) use of modified bulk procedures, and (5) multienvironment testing through a network of national programmes. Genetic variability in local landraces, primitive forms, and wild progenitors of barley and wheat have proved to be very useful.

INTRODUCTION

Within the Consultative Group on International Agricultural Research (CGIAR) system, the International Center for Agricultural Research in the Dry Areas (ICARDA) has a global responsibility for barley improvement and a joint mandate with the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) for wheat improvement in West Asia and North Africa. In the ICARDA region about 97 per cent of durum wheat, 65 per cent of bread wheat, and essentially all of barley is grown without irrigation under rainfed conditions. In cooperation with national and international institutions, the Cereal Improvement Program at ICARDA endeavours to increase the productivity as well as stability of production of barley and wheat in rainfed areas.

CHARACTERIZATION OF THE AGROENVIRONMENTAL CONDITIONS

Barley, durum wheat, and bread wheat together cover 70 per cent of the land devoted to food crops. The choice of the cereal grown is mostly determined by moisture. Within the zone of 300–600 mm of annual precipitation, farmers in wetter areas (and farmers having irrigation facilities) favour bread wheat and



Source: Factors Affecting Wheat Production in Jordan. Ministry of Agriculture, Jordan, University of Jordan and ICARDA.

Figure 1. Relationship between rainfall and wheat yields in Jordan, 1957–80

those in moderate rainfall areas favour durum wheat. In more arid zones, with 200–300 mm of rain, farmers usually grow barley. The unpredictable rainfall, and hot dry summers, typical of the region, have important implications for agricultural researchers. One of these, obviously, is the drought tolerance of cereal varieties.

The region has diverse and variable climatic conditions. Rainfall and temperature regimes can differ considerably over short distances, and interannual variation is high. Broadly speaking, there are two major agro-climatic zones in which cereals are grown. One zone has a Mediterranean climate characterized by hot, dry summers and cool, but not frigid winters in which rainfall is concentrated. Crops are grown mostly during the winter. The second zone consists of various highland areas over 1000 m and areas of continental climate where winters are cold and summers are hot and dry. Snowfall during winter is a major source of soil moisture. Crops are usually planted in the autumn, though spring plantings are important in parts of Turkey, Afghanistan, and Pakistan.

In the rainfed areas of West Asia and the Mediterranean basin, drought, heat, and cold predominate. Drought may be present alone or in combination with a thermal stress, or a given thermal stress may prevail at various stages of

Table 1. Barley area and yields in the ICARDA Region (1982–4). (FAO Production Yearbook, 1984)

Country	Area harvested (1000 ha)	Grain yield (kg/ha)
Afghanistan	340	1060
Algeria	811	622
Cyprus	52	1718
Egypt	50	2636
Ethiopia	860	1214
Iraq	942	700
Iran	1883	970
Jordan	37	439
Lebanon	5	1224
Libya	257	325
Morocco	2108	791
Pakistan	250	709
Saudi Arabia	6	2103
Syria	1463	446
Tunisia	505	659
Turkey	3096	1970
Yemen Arab Republic	43	1020
Others	5	—
Total	12,713	

crop development. Furthermore, stress patterns may differ in each of the various climatic zones (ICARDA, 1985). Figure 1 indicates the relationship between rainfall and wheat yields in Jordan which is typical of much of the low to moderate rainfall wheat-production area in West Asia and North Africa, and highlights the dependence of winter cereal production on precipitation. Even when the crop is grown in an 'optimum moisture environment' occasional periods of drought may occur during the growing season and reduce crop production. The use of technologies to alleviate the effects of climatic stresses, such as irrigation, fertilization, and tillage is limited in the region. Therefore, genetic manipulation of plants to minimize the effects of climatic stresses is an important endeavour for rainfed areas.

Many regions of the world have succeeded in improving wheat yields, particularly in favourable crop-growing conditions, through the introduction of semi-dwarf, high-input-responsive varieties. However, such high-yielding varieties have not met with great success in the dry areas of West Asia and North Africa. Traditional methods of cultivation and landraces of improved local cultivars predominate in most of these areas. The barley and wheat

Table 2. Wheat area and yields in the ICARDA Region (1982–4). (FAO Production Yearbook, 1984)

Country	Area harvested (1000 ha)	Grain yield (kg/ha)
Afghanistan	2330	1232
Algeria	1670	590
Cyprus	14	1298
Egypt	566	3433
Ethiopia	656	1261
Iraq	1003	664
Iran	6011	1003
Jordan	77	801
Lebanon	17	1218
Libya	253	576
Morocco	1839	1121
Pakistan	7314	1584
People's Democratic Republic of Yemen	15	1000
Saudi Arabia	308	2725
Sudan	142	1096
Syria	1204	1159
Tunisia	800	963
Turkey	9105	1875
Yemen Arab Republic	50	985
Total	33,375	

Table 3. Approximate percentage distribution of wheat area according to moisture environment in major production regions of the developing world. (Byerlee and Winkelmann, 1980)

Region	Moisture environment		
	Irrigated	Adequate rainfall	Semi-arid rainfed
Middle East/North Africa	14	34	51
South Asia	73	4	23
East Asia	25	39	37
Latin America	9	49	43
All developing countries	34	28	37

yields in the region (Tables 1 and 2) are among the lowest in the world. Small farmers and those in very dry areas (Table 3) are particularly vulnerable to moisture stress that limits crop production. Barley and wheat varieties with tolerance to moisture stress would provide stability and increased yields. Their benefit would be even higher if accompanied by modifications in

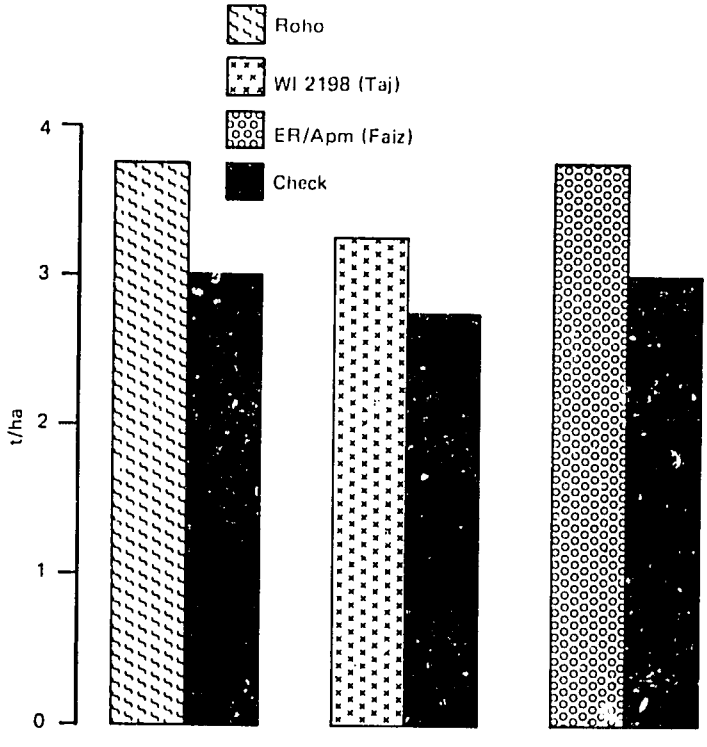


Figure 2. Grain yield of three barley varieties in Tunisia (means of three years, 1982–4)

Table 4. Grain yield (kg/ha) of Tadmor, a pure line selected from a local cultivar of barley, in sites receiving less than 250 mm of annual rainfall

Material	Bouider 1984–5	Mean of five locations 1985–6
Tadmor	2428 a	1785 a
Local cultivar	1633 b	1580 b

Values followed by different letters are significantly different ($P < 0.05$).

cropping systems and cultural practices that would minimize the adverse effects of drought.

Research efforts are under way to combine drought tolerance with increased yield and stability of production as well as other desirable traits such as resistance to important diseases and pests. In the case of barley, through a joint Tunisia-ICARDA barley-improvement project, three varieties have been released in Tunisia which yield significantly higher than the existing commercial varieties (Figure 2). Rihane 'S', another barley line, has performed well in several countries in the moderate rainfall (250–350 mm) areas. In the severe moisture stress areas (less than 300 mm rainfall), selections from the locally adapted landraces seem to be most promising. For example, Tadmor, a line selected from the locally adapted landrace in Northern Syria, has performed best in 200–300 mm rainfall areas of Northern Syria (Table 4).

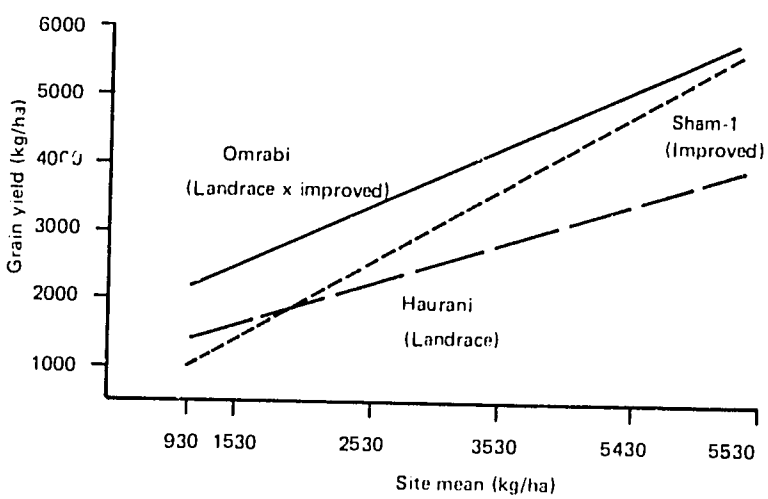


Figure 3. Yield stability of a landrace (Haurani), in comparison to a landrace × improved variety (Omrabi) and improved variety (Sham-1)

Nachit and Ketata (1986) reported superior performance of Omrabi, a durum wheat line derived from a cross involving 'Haurani', a landrace adapted to 250–400 mm rainfall areas in Syria and Jordan, and Jori, C-69, a high-yielding variety in favourable environments (Figure 3). They also noted that a new durum line, 'Sebou', derived from a cross involving 'Crane' (a variety adapted to favourable conditions) and a strain of *T. polinicum*, a primitive wheat adapted to arid conditions, outyielded Haurani in on-farm trials at several locations for 3 years in Syria. Algeria released a durum variety 'Sahl' in 1986, developed from a cross between *T. dicoccum* and 'Crane' 'S' variety. 'Korifla' has outyielded the locally adapted line 'Haurani' for 4 years in on-farm trials throughout Syria in zone B (250–350 mm precipitation) (Figure 4).

Bread wheat varieties Sham 2 and Sham 4 have been released in Syria for

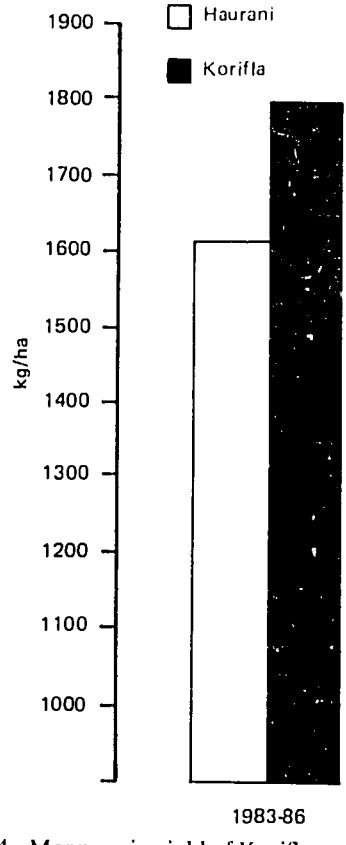


Figure 4. Mean grain yield of Korifla compared to Haurani in on-farm trials in zone B, 250–350 mm rainfall, in Syria

their superior yields in bread-wheat-growing areas. They have also performed well in rainfed conditions in Turkey, Lebanon, Jordan, and North Africa. Improved yield of these and other varieties clearly indicates the possibilities of improving yield and yield stability in the rainfed areas by employing suitable production technologies and varieties developed for moisture-limiting areas.

CHOICE OF CROP SPECIES

A better characterization of the agroclimatic zone in the region may lead to a more rational distribution of the area traditionally cropped with barley, durum wheat, and bread wheat. Data collected by Saari and Srivastava (1977) from the region suggest that barley utilizes water more efficiently than wheat at low to moderate moisture levels (Table 5). Wright (1978) reported that similar calculations from 40 yield trials in Turkey indicated that barley was always more efficient than wheat under less than 450 mm of rainfall. However, the socioeconomic structure, farmers' needs, and pricing policies greatly affect the cropping systems in the region.

Barley and wheat improvement strategy for moisture-limiting areas requires a discussion of basic elements of its production systems, the environment, the genotypes, and their complex interactions.

THE ENVIRONMENT

A better understanding of the target environment with respect to prevailing environmental and biological stresses, their intensities, and frequency of occurrence at a given growth stage of the crop is necessary before choosing appropriate breeding and selection methods. Given the fact that yield is the integrated product of genotypic expression in a given environment, Figure 5 shows how our definition of a stress environment can affect the decisions regarding breeding strategies. If the production potential of the target envi-

Table 5. Kilograms of grain produced by barley and wheat per millimetre of moisture. (Saari and Srivastava, 1977)

Moisture (mm) (rainfall or irrigation)	kg grain/mm moisture	
	barley	wheat
200	7.5	1.1
300	8.0	6.1
400	8.7	5.6
500	3.4	8.7
600	5.6	7.8
700	4.7	11.6

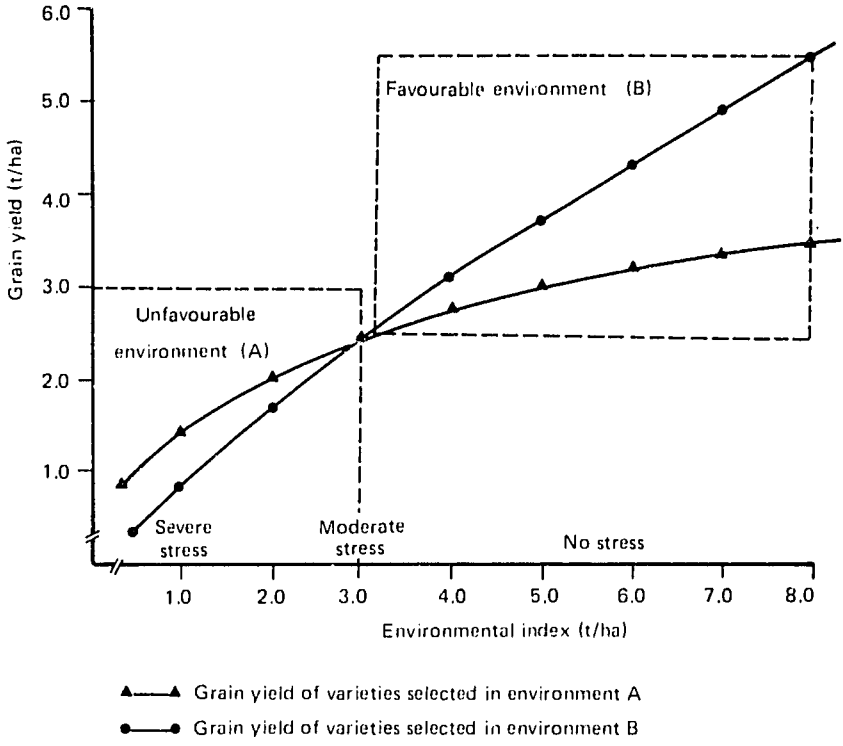


Figure 5. Grain yield of two wheat varieties in unfavourable (A) and favourable (B) crop-growing environments

ronment is 3 t/ha and above, then selection could be effectively practised in favourable crop-growing conditions. However, if the environment stresses limit the yield potential to 3 t/ha and below, then it would be more efficient to select plants directly under these environments. In this environment selection for resistance/tolerance to drought and other prevailing stresses is of much more importance than for maximizing yields in favourable environments.

General adaptation to a wide range of environments representing different stresses may cost the plant some yield sacrifice; therefore, best fitness in one range of environments may be achieved by concentrating on development of germplasm suitable for that environment. Austin (1987) reported the effect on yield of selection for different plant attributes at three levels of water availability and found that an attribute that is beneficial in one environment, with a particular level and pattern of water availability, may be detrimental or of no effect in another one. He indicated that selection in appropriate conditions for the attributes tested would benefit yield in one of two of the environments, but usually not all three. Nachit and Ketata (1986) suggested

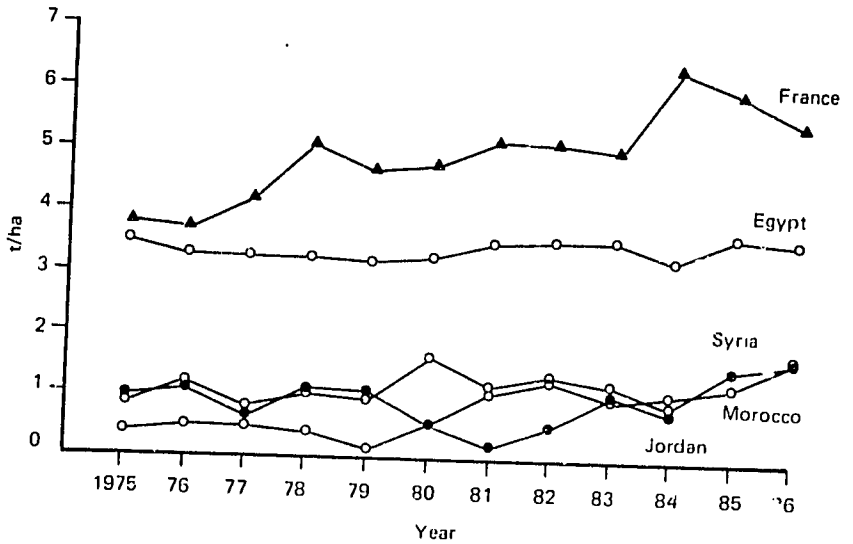


Figure 6. Wheat grain yield in five countries representing a range of agro-climatic conditions

that phenotypic variation over the environments due to differences among the testing sites can be significantly reduced through subzoning, using agro-climatological information and appropriate statistical procedures such as cluster analysis. When they used this analysis on regional durum yield trials, the portion of the total variation due to differences among sites came down from 80 per cent for all the 22 locations to 18 per cent for a cluster of four relatively homogeneous locations.

Wheat grain yield in five countries representing three agroclimatic conditions are presented in Figure 6. France represents an equable climate and high-input environment where yields are high and the interannual coefficient of variation in yield is low. Egypt represents an irrigated and intensive cropping system, good yields, and stability of production. Jordan, Morocco, and Syria represent low-input rainfed agriculture and low yields and a high interannual coefficient of variation in yield. Much of the barley and wheat in West Asia and North Africa is produced in similar areas where yields are not only low but interannual variation in yield causes considerable unpredictability of production.

Therefore, a breeding programme will be more effective if genetic material is developed to meet the specific needs of the target environment. Climate, particularly differences in rainfall and temperature, has been used to classify germplasm into those destined for wet, moderate, or dry environments; those destined for warm or cool environments; those for short or long maturity; and those for low- or high-elevation climates. A number of statistical procedures

has been employed with varying degrees of success to group environments, but much remains to be added to our understanding to better characterize different production environments. Attempts to predict the rainfall and its distribution in a particular area have been unsatisfactory, particularly in the lower rainfall areas where the interannual variability is the greatest. The importance of defining agroclimatological zones, not only in terms of rainfall and evaporation but also in terms of pests and diseases, cannot be overemphasized and should be an important cooperative activity.

GERMPLASM IMPROVEMENT

It is possible to modify crop growth environments through the use of sound agronomic principles, crop rotations, and fertilization. Improvements in water-use efficiency have been achieved by these practices. However, availability of varieties with specific adaptations which better match their phenologies to the favourable crop periods and with genetic resistance/tolerance to yield-limiting stresses would lead to further yield increase and stability of production.

Both barley and wheat are presumed to have originated in West Asia, where their wild progenitors, primitive forms, and landraces grow in varying moisture stress conditions, with a cold and wet vegetative phase and a hot, dry, and short grain-filling period. In their natural environments, these plants are well adapted to prevailing stresses and may possess many desirable traits that could be utilized in the breeding programmes. It is important to collect and make special efforts to evaluate these germplasms for useful and potentially useful traits. Broadening the diversity of germplasm used in national programmes merits special efforts. Development of elite germplasm for rainfed breeding programmes is one of the very important activities in the cereal programme at ICARDA and this would make germplasm improvement for moisture-limiting areas easier and more efficient.

The next step in breeding for resistance to moisture stress is to identify traits that could be beneficial in the target environment and to establish that selection for the trait(s) and recombination with other desirable characters are feasible. Reliable laboratory and field screening techniques should then be available to screen potential germplasm and to develop genetic stocks with known sources of resistance. It is important to determine the heritability of the trait and its relationship to yield performance in the target environment (Clarke, this volume).

For most traits that appear to contribute towards drought tolerance, the genes involved and their heritabilities are not known. Physiologists have proposed several morphological and biochemical traits that may be associated with drought resistance. They argue that progress in breeding would be faster and more certain in outcome if there were a better knowledge of the

significance for yield of particular attributes and how this depends on environmental factors (Cornish, 1950; Austin, 1987). Although most of the achievements in crop improvement have been made by the 'empirical approach', physiological and genetical advance in understanding the complexities of drought resistance in plants will certainly accelerate the rate of progress in improving barley and wheat yields in moisture-limiting areas.

Efficiency of selection

Employment of efficient techniques of selection is the key to success in plant breeding. Any procedure that can discard undesirable germplasm in early generations adds efficiency and cost effectiveness to the variety improvement efforts. No one set of selection procedures is likely to fit all arid and semi-arid production areas. It is desirable to examine and evaluate available techniques for each situation and/or to develop the most appropriate ones. Breeding and selection methods employed at ICARDA for developing barley and wheat germplasm for dry areas have been described by Ceccarelli and Mekni (1985), Nachit (1983), Ceccarelli (1986b), Nachit and Ketata (1986), Ortiz Ferrara and Mulitze (1986), and Srivastava (1987). They essentially comprise: characterization and identification of elite parental lines possessing resistance/tolerance to moisture stress and other stresses prevailing in the region; incorporation of desired traits in the crosses for a target environment; exposure of early generation populations to the environments in which they will be grown; use of modified bulk procedures; and multienvironment testing through a network of national programmes. This requires a great deal of coordination and effort of a multidisciplinary group of scientists from national and international centres as well as specialized institutions.

Several studies have considered the effect of different growing conditions on response to selection for grain yield. Opinions vary on whether favourable or moisture stress environment will maximize the efficiency of selection if the target area is a dry environment. As indicated earlier (Figure 5), a better understanding of the degree of moisture stress in the target environment may assist in determining the type of nursery environment that will allow maximum progress from selection. Allen *et al.* (1978) computed averages of the yield means, the error variance estimates, and genotypic variance estimates for each of the favourable, intermediate, and unfavourable environments. They reported mean yields in the unfavourable environments to be less than one-half those in the favourable environments and concluded that the use of intermediate environment as test sites was preferable over either high or low yield environment. Nachit and Ketata (1986) compared 210 durum wheat lines both in intermediate and unfavourable environments and found that genotypes that performed well in the intermediate conditions did not always give higher yields under unfavourable conditions. Their results indicated that selection from segregating populations in the unfavourable environment

generated lines with higher grain yields in rainfed sites in Syria as compared to lines derived through selection in more favourable environments. Ceccarelli (1986a, 1986b), working with barley at different sites representing a range of moisture stress, reported a superior efficiency of selection under moisture stress conditions when the objective is to identify genotypes for drought environments. Srivastava *et al.* (1983) suggested that it is desirable to determine the range of moisture stress that may occur in the majority of years and to evaluate the germplasm derived from carefully planned crosses, even in early generations, at sites selected to represent those environments. Any functional new technique that could be developed for use on a large scale would greatly simplify selection procedures and therefore requires a great deal of sustained effort by physiologists and plant breeders.

Yield stability

Our knowledge about plant characteristics and mechanisms of response to moisture stress is very little and our understanding of the mechanisms whereby different varieties respond differently to different environments is even less. However, the significant role of genotype–environment interaction is a predominant feature of rainfed experiments. Cornish (1950) reported that 70–80 per cent of the variance of yield from 296 locations in South Australia for the years 1896–1941 was due to interannual variation in rainfall. Multilocation testing is an integral part of variety development procedures used by breeders for determining the performance of a genotype at several carefully selected sites representing a range and type of moisture stress that the plant may encounter over the years at a particular site. The selected genotypes are subjected to intensive 'on-farm' evaluations for 3–4 years in the region of intended use before a variety is released for commercial cultivation.

Nonetheless, the inherently large interseasonal variability, lack of satisfactory breeding procedures, and suitable experimental design make the task to improve yield stability in moisture-limiting areas slow and difficult. It is imperative to develop improved and functional methodologies to define agroenvironmental boundaries for varietal adaptation and to develop germplasm with specific adaptation to the target environment with increased yield and yield stability. For moisture-limiting areas, breeders may consider sacrificing some wide adaptability in favour of specific adaptation to cope with prevailing stresses that limit yield and stability of production.

REFERENCES

Allen, F. L., Comstock, R. E. and Rasmusson, D. C. 1978. Optimal environments for yield testing. *Crop Sci.* 8:747–751.

Austin, R. B. 1987. The climatic vulnerability of wheat. In *International Symposium on Climatic Variability and Food Security*, 6–9 February 1987, New Delhi, India.

Byerlee, D. and Winkelmann, D. F. 1980. Accelerating wheat production in semi-arid developing regions. Economic and policy issues. Pages 328–362 in *Proceedings of the 3rd International Wheat Conference*, Madrid, Spain.

Ceccarelli, S. 1986a. Tolerance to climatic stress. In *Proceedings of the 5th Barley Genetic Symposium*, 6–12 October 1986, Osaka, Japan.

Ceccarelli, S. 1986b. Breeding strategies to improve barley yield and stability in drought-prone environments. Presented at the Meeting on Drought Tolerance in Plants: Genetic and Physiological Aspect, 20–23 October 1986, Amalfi, Italy.

Ceccarelli, S. and Mekni M. S. 1985. Barley breeding for areas receiving less than 250 mm annual rainfall. *Rachis* 4(2):3–9.

Cornish, E. A. 1950. The influence of rainfall on the yield of wheat in South Australia. *Aust. J. Sci. Res.* 3:178–218.

Ferrara, G. O. and Mulitze, D. 1986. Bread wheat breeding for the low-rainfall, non-irrigated areas of West Asia and North Africa. In *Proceedings of the International Wheat Conference*, 2–5 May 1986, Rabat, Morocco.

ICARDA (International Center for Agricultural Research in the Dry Areas), 1985. Annual report 1985. ICARDA, Aleppo, Syria.

Nachit, M. M. 1983. Use of planting dates to select stress tolerant and yield stable triticale genotypes for the rainfed Mediterranean environment. *Rachis* 3(1):37.

Nachit, M. M. and Ketata, H. 1986. Breeding strategy for improving durum wheat in Mediterranean rainfed areas. In *Proceedings of the International Wheat Conference*, 2–5 May 1986, Rabat, Morocco.

Saari, E. E. and Srivastava, J. P. 1977. Improvement and stabilization of production of the winter cereals: potential in a single-crop system. Middle East and Africa Agricultural Seminar, the Ford Foundation, 1–3 February 1977, Tunis, Tunisia.

Srivastava, J. P., Jana, S., Gautam, P. L. and Nicks, R. E. 1983. Parallel selection: an approach to increase grain yield and stability. Pages 725–733 in *Proceedings of the 6th International Wheat Genetics Symposium*, Kyoto, Japan.

Srivastava, J. P. 1987. Development of crop germplasm with improved resistance to environmental and biotic stresses. In *International Symposium on Climatic Variability and Food Security*, 6–9 February 1987, New Delhi, India.

Wright, B. C. 1978. The agronomic uniqueness of barley. In *The 4th Regional Winter Cereal Workshop on Barley*, Vol. 2, 24–28 April 1977, Amman, Jordan.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

6

A Review of Plant-breeding Strategies for Rainfed Areas

E. L. SMITH
USAID/MIAC, Institut National de la Recherche Agronomique, PO Box 290, Settat, Morocco

ABSTRACT

Various plant-breeding strategies are examined and discussed. Emphasis is placed on wheat-improvement strategies for semi-arid conditions. One strategy that has been successful in the Southern Great Plains of the United States is the use of the F_2 progeny method of breeding. In this method, head selections are made in F_2 bulks and subsequent selection is made among (but not within) F_3 head rows. Promising subpopulations as identified in replicated trials are then rogued or reselected for uniformity. Cultivars derived by this method retain some degree of heterogeneity which may add to yield stability. Multilocation testing, including on-farm trials, provides a database for predicting agricultural worth of new varieties. Such a system of trials also serves to examine yield stability parameters of individual genotypes. Multilocation testing strategies can be of special value in water-limited conditions. Successful breeding strategies must include consideration of disease and insect resistance, including gene deployment, germplasm evaluation, and prebreeding programmes. The plant architecture approach to breeding, in which selection is based on yield components, offers some possibility of increasing yield potential, especially when target environments can be defined with precision. However, this breeding strategy has not as yet had much impact on practical breeding programmes. Selection based on physiological traits such as leaf canopy temperature, cell osmotic adjustment, leaf water potential, and stomatal resistance may lead to improved drought resistance. For most physiological traits, however, screening is as yet not feasible on a scale required by plant breeders. Initially, physiologic response could be established for a series of genotypes for use as parents to produce genetically variable populations for selection.

INTRODUCTION

No one set of breeding strategies will likely fit all semi-arid situations or rainfed production areas. Various breeding systems and procedures must be examined and evaluated for each situation. Nevertheless, some generalizations are useful. This report deals with a number of plant-breeding strategies that appear to have merit in rainfed production areas. Emphasis is on wheat-improvement problems in semi-arid regions.

F_2 PROGENY METHOD OF BREEDING

In semi-arid zones, certain types of modified bulk breeding methods may have advantages over the 'classical' pedigree method of selection. One wheat-breeding strategy that has been successful in the Southern Great Plains area of the United States and which is currently employed in the programme at Oklahoma State University is the use of the F_2 progeny method of breeding.

This is a modified bulk breeding method in which head selections are made in genetically variable populations in the F_2 generation. In our programme in Oklahoma we take heads from promising F_2 populations (seeded at normal densities) in multiples of 100 heads (up to 600 per F_2 population). This technique fits with our use of 100-cell planting trays. Selection in the F_2 is based primarily on highly fertile heads from vigorous plants of the proper height and maturity classes. Normally 100 heads are taken from each F_2 population, but occasionally up to 600 heads will be taken from particularly promising crosses. The following year, F_3 head rows are grown (a total of approximately 40,000 per year) with occasional sets of standard cultivars to serve as checks. In the F_3 generation, selection is made among rows. There is no within-row selection. Selection is based on plant height, maturity, disease reaction, and general vigour. After harvest of selected rows, seed samples are examined for desirable grain characteristics. We normally save about 2000 rows.

In the F_4, the F_2 subpopulations are grown in four-row plots 3 m in length with a standard cultivar check planted in every tenth plot. This nursery is seeded at two locations (non-replicated). One planting is made at our main station which is in a reasonably favourable rainfall zone and in which good disease development occurs. The other planting is made at a more droughty location where differences in performance characteristics are recorded. Notes taken at the two locations are used to identify promising subpopulations (500–1000) which are then examined for 1000-kernal weight and bread-making quality. Normally some 200–400 subpopulations are saved in inclusion in preliminary yield trials.

Preliminary yield trials are grown at three locations each year (two replications per location). Two of the locations are the same as mentioned above for

the F_4s. The third location is at a site of rather severe drought stress. Thus, the three locations provide a good range with regard to levels of drought stress. The most promising subpopulations coming from the preliminary yield trials move into advanced levels of testing at seven locations in the state. These sites, again, represent a good range in drought stress conditions.

The objective of this breeding strategy is to identify yield potential and to some extent stability of yield early on in the breeding programme. Obviously, with this method, there will be heterogeneity for a number of traits in those subpopulations reaching the advanced testing stage. At that point, the most promising lines will be rogued or reselected for uniformity. If they are reselected, the basic seed will be reconstituted by compositing a number of reselections of similar agronomic type. A finished cultivar coming from this system of breeding will intentionally be somewhat heterogeneous, although it will have 'acceptable' uniformity in terms of 'field appearance'. We believe that a certain amount of heterogeneity confers yield stability in our target zone. With this breeding strategy, seed-certifying agencies must be flexible enough to accept heterogeneous cultivars. We have had no serious difficulties with our seed inspection authorities since we have formally described the variability within cultivars of this type.

OKLAHOMA WHEAT YIELDS

It is generally held that breeding for drought conditions is more difficult than breeding for more favourable conditions. The greater degree of difficulty is due to increased complexity of genotype–environment interactions associated with yield and yield-related traits in stress situations. The difficulty increases even more in situations characterized by unpredictable rainfall and temperature patterns (the reader is referred to considerations of G × E interactions by Allard and Bradshaw, 1964).

In spite of these difficulties genetic improvement for yield is possible in semi-arid conditions. We have examples from a number of regions. One example is that for winter wheat in Oklahoma (USA). In Oklahoma, average wheat yields have increased from about 1000 kg/ha in the mid-1950s to 2000 kg/ha at the present time. This represents an average increase of more than 2 per cent per year. When we partition this increase into genetic and non-genetic influences we find that half of the increase is due to plant breeding. The other half comes through improved cultural practices, better crop management, and more effective pest control measures.

The plant-breeding progress noted in the above example was made primarily through the use of empirical breeding approaches—by concentrating on yield and kernel weight differences at selected locations providing various levels of drought stress. It should be pointed out that this increase in yield was accompanied by changes in plant type. As new cultivars replaced older ones,

there was a shift towards earlier maturity, shorter plant stature, increased spike fertility, and better disease resistance.

MULTILOCATION TESTING

Multilocation testing is a strategy widely employed in plant breeding; it is routinely used in most national and regional programmes and is utilized on an extensive scale by international plant-improvement centres. Multilocation testing has much merit in variety development programmes and is of special interest to breeders in semi-arid zones for its utilized genotype performance in natural stress environments.

Multilocation testing constitutes a system of trials which are generally replicated over years as well as locations. The object of this system of trials is to predict performance of breeders' lines and new varieties in relation to standard cultivar checks. Systems of trials are satisfactory only if they predict, with an acceptable degree of accuracy, agricultural performance under farmers' conditions. To improve the predictive value of agricultural worth, a system of 'on-farm trials', used as a supplement to on-station trials, offers some advantages. When properly conducted, on-farm trials should predict, with greater accuracy, the performance of new cultivars under the system of management employed by the farmer. They also serve as demonstration plots and can be used to publicize new cultivars.

Multilocation testing also provides information on yield stability over different environments. From the standpoint of variety development, the ideal situation would be to have a highly stable genotype with a high-yield potential (Smith, 1982). However this ideal situation may be difficult to achieve since the high-yield potential tends to be associated with lack of stability. This may be due, at least in part, to the fact that in most breeding programmes yield itself, rather than stability of yield, has been the main criterion for selection. Regression analysis of genotype performance on environmental index provides a description of relative stability of individual genotypes (Eberhart and Russell, 1966). This technique, when used with other performance parameters, should be useful in programmes dealing with yield and yield stability in semi-arid conditions.

As far as the plant breeder is concerned, the major limitation of multilocation testing is that selection pressure is applied at the final stage of breeding, at which point genetic variability is usually limited. Consideration should be given to multilocation selection systems that could be employed earlier in the breeding programme to take advantage of greater genetic variability. Some type of modified bulk breeding system could be utilized in which individual plants are selected from potentially superior bulk populations as identified by performance across several locations.

SITES FOR SELECTION

Now for a comment about sites for selection. In water-limited production zones the choice of site for early generation selection needs some consideration. Within the target zone, the breeders will normally have access to a number of potential selection sites differing in degree of stress, ranging from severe stress to non-stress conditions. The breeder may be tempted to use a site of severe stress for early generation selection, especially if it represents stress conditions to be found in a major part of the target zone.

This, I believe, is a mistaken strategy. A site characterized by severe stress is prone to crop failure which results in a loss of time and effort. In addition, it is difficult to detect intergenotypic differences for production traits when plants are severely stressed. A better strategy would be to use a site of moderate stress for initial selection and then conduct progeny tests under both stress and non-stress conditions. This approach would be consistent with systems developed empirically by a number of successful plant-breeding programmes.

BREEDING FOR DISEASE AND INSECT RESISTANCE

Any breeding strategy for rainfed conditions must include consideration of disease and insect resistance. We must continue to give high priority to 'defensive' breeding to provide adequate protection to the crop. Disease and insect resistance has played an important role in most successful breeding programmes. Genetic resistance, when it can be had, is the most effective and inexpensive means of alleviating production constraints posed by pathogens and insect pests (see the review articles by Parlevliet, 1981; and Jenkins, 1981).

A successful strategy must recognize the problems of physiological specialization of the causal organism and be ready with sources of resistance to combat new physiologic races. In order to locate new sources of resistance, a search may have to be made through much of the germplasm base of the crop species or even through related species and genera. When resistant genes are found in poorly adapted types or related species, a programme of parent building (prebreeding) may be required to put the new gene into an adapted background genotype so that it can be more effectively used by the breeder.

Consideration must be given to strategies of gene deployment (for race-specific genes). Possible strategies include: use of resistant genes one at a time, multiple resistance systems, multiline varieties, and various systems of deploying resistant genes on a regional basis. The most effective gene deployment strategy is one that provides adequate protection to the crop while at the same time prolonging the useful life of the gene in question.

Non-specific genes for resistance, usually of polygenic inheritance patterns, should be considered also. Although non-specific gene systems tend to be more difficult to handle in the breeding programme, they have the advantage of durable resistance, providing protection against a series of physiologic races of the pathogen. Nonspecific genes may confer a lower level of resistance, but even so they can still be useful. In this connection, Simmonds (1979) states: 'high resistance . . . is good to have if it can be got without compromising other characters, but the examples of many successful varieties shows us that . . . middling resistances wisely used can be agriculturally very satisfactory.'

The success of 'defensive' breeding depends to a large extent on the availability of suitable screening techniques. These are systems of environmental control designed to facilitate the identification of resistant plants within genetically variable populations. Satisfactory screening techniques have been developed for a number of pathogens and insect pests. However, for others, more efficient screening techniques are needed. Breeding for disease and insect resistance requires cooperation between the breeder and the pathologist/entomologist. Close cooperation is especially important for the development and efficient use of screening techniques. A team effort is the best approach.

PLANT ARCHITECTURE

Since the advent of Donald's ideotype concept (Donald, 1968), the plant architecture approach to breeding has been rather thoroughly studied. In this approach, selection is based on yield components rather than on yield itself (for wheat the major yield components are: number of tillers per unit areas, average weight per grain, and average number of grains per spike). This, then, is a system of indirect selection which utilizes selection indices either stated or implied. The theory is attractive but the required characterization of 'model' components for the target environment has been difficult to achieve. In all probability, there is no one ideal (model) architecture for any particular environmental situation. Plant-breeding experience tells us that different genotypes can make the same yield through different yield component pathways.

Although the plant architecture approach appears to have some merit in breeding for increased yields (Rasmusson, 1984), it has not as yet had much impact on practical plant-breeding programmes. Major difficulties in using this approach are: (1) yield component compensation and (2) allometric relationships of size of organs of the plant. Neither system is well understood at the present time.

However, as a result of plant architecture studies we have learned something about character interrelationships and the contributions of various

organs to grain yield. These studies have reinforced earlier observations that larger grain size, at least in barley and wheat, may contribute to yield stability in water-limited situations.

MORPHOPHYSIOLOGICAL TRAITS

There has been a substantial increase in the number of physiologically oriented studies on drought tolerance during the past 10 years. We have gained a great deal of new information on the subject but so far we have not been able to translate this information into procedures that can be utilized on a scale of sufficient magnitude to be used efficiently in breeding programmes.

Over the years, a number of drought-related traits have been identified. These include: leaf canopy temperature, cell osmotic adjustment, cell membrane stability, leaf water potential, stomatal resistance, leaf rolling index, and leaf waxiness. For the most part, however, the relationship of these traits to grain yield has not been established with any degree of certainty. The problem lies with complex environmental influences affecting the trait in question and yield itself. The expression of drought-related traits may vary from one set of environmental conditions to another.

In wheat, for example, the total above-ground part of the plant (biological yield) in a water-limited production area is directly related to the water supply (Passioura, 1981). Although biological yield offers little hope of modification through breeding, the harvest index which reflects the ratio of grain to total biological yield appears to be amenable to genetic improvement for enhanced drought tolerance.

In terms of drought tolerance, the root system of the plant merits additional study. We know that wheat genotypes differ in types of root systems and in rooting depths. Seminal roots are important in some situations while coronal roots are important in others. If the crop depends on moisture stored in the soil profile, a deep root system would be beneficial. However, breeding for deeper rooting patterns would be counterproductive in situations of shallow soils with limited water-holding capacity, especially when the crop is produced on seasonal rainfall. The breeder, then, must determine which type or rooting pattern is needed in his particular area of production before launching into a breeding programme aimed at root modification.

Roots are rather difficult to study but initially, in a breeding programme, rooting patterns could be established for a series of genotypes for use as parents to produce genetically variable populations for selection.

Although attempts by breeders and physiologists to collaborate in the development of drought-tolerant cultivars have not been very successful, a note of optimism appears in a recent review article (Blum, 1984). In this article Blum suggests that results of recent studies are of sufficient promise to stimulate better cooperation between breeders and physiologists. The poten-

tial benefits to be gained by such cooperation are enormous, and collaborative efforts between breeders and physiologists should be encouraged.

REFERENCES

Allard, R. W. and Bradshaw, A. D. 1964. Implications of genotype–environment interactions in applied plant breeding. *Crop Sci.* 4:503–507.

Blum, A. 1984. Breeding crop varieties for stress environments. *CRC Critical Reviews in Plant Sciences* 2(3):199–238.

Donald, C. M. 1968. The breeding of crop ideotypes. *Euphytica* 17:385–403.

Eberhart, S. A. and Russell, W. A. 1966. Stability parameters for comparing varieties. *Crop Sci.* 6:36–40.

Jenkins, J. N. 1981. Breeding for insect resistance. Pages 291–308 in *Plant Breeding* (Frey, K. J., ed.), Vol. II. The Iowa State University Press, Ames.

Parlevliet, J. E. 1981. Disease resistance in plants and its consequences for plant breeding. Pages 309–364 in *Plant Breeding* (Frey, K. J., ed.), Vol. II. The Iowa State University Press, Ames.

Passioura, J. B. 1981. The interaction between the physiology and the breeding of wheat. Pages 191–201 in *Wheat Science—Today and Tomorrow* (Evans, L. T. and Peacock, W. J., eds.). Cambridge University Press, Cambridge.

Rasmusson, D. C. 1984. Ideotype research and plant breeding. Pages 95–120 in *Gene Manipulation in Plant Improvement* (Gustafson, J. P., ed.). Plenum Press, New York.

Simmonds, N. W. 1979. Principles of crop improvement. Longman, New York.

Smith, E. L. 1982. Heat and drought tolerant wheats of the future. Pages 141–147 in *Proceedings of the National Wheat Research Conference*, 1982. USA-ARS, Beltsville, Maryland.

DISCUSSION

M. Nachit

Which phenological attributes have changed through the breeding process in your programme during the last hundred years? What implications has dryland root rot resistance for drought resistance?

E. Smith

The attributes that have changed during the breeding process (1890–1980) were the maturity and the height (early + short). We are selecting the lines that survived the dryland root rot and reincorporating these into parents.

R. B. Austin

Yields in Oklahoma have increased from 0.8–0.9 t/ha (1950s) to 2–2.2 t/ha (present). Have they become more variable? Has the climate become more favourable or less variable over the period?

E. Smith

Production (yield) is perhaps more variable now than in the early 1950s. In some years as much as 25 per cent of the acreage is abandoned. In the late 1950s there was a period of favourable weather; since then weather patterns have fluctuated from unfavourable to favourable.

E. Porceddu

You have shown that high-yielding varieties yield less than landraces in poor environments. Would this be the result of early generation selection in a good environment?

E. Smith

Yes, perhaps. Also, selection has been based on average yield over several sites. For increased emphasis on drought stress, we should pay more attention to the yields and stressed environments.

G. Ortiz Ferrara

Considering the F_2 progeny row (or modified pedigree method) you use in your programme, at what stage in the selection phase do you apply selection pressure for quality and which quality characteristics do you consider most important?

E. Smith

Quality evaluation consisting of protein percentage, mixing time, mixing tolerance, specific sedimentation, and flour yield is routinely conducted in the F_4 generation. For specific crosses, some quality evaluation is conducted in F_3 (especially for protein where high-protein parent lines are involved in the cross).

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

7

Australian Plant Breeding Strategies for Rainfed Areas

D. R. MARSHALL
I.A. Watson Wheat Research Centre, University of Sydney Plant Breeding Institute, PO Box 219, Narrabri, NSW 2390, Australia

ABSTRACT

Most Australian winter cereals are grown under dryland conditions in areas of limited and variable rainfall. As a result, increased drought resistance has been a major aim of many Australian breeding programmes since their inception. Yet few breeders have systematically tested or selected for drought resistance *per se*. Rather, the emphasis has been on increasing yield potential and average yields. Progress has been made in increasing average yields but the increases have been modest and progress slow and erratic.

This modest progress has led to considerable criticism of current breeding strategies. It has frequently been suggested that yield *per se* is a poor indicator of drought resistance and that greater progress could be made by selecting for other attributes specifically related to drought resistance. Many such selective criteria have been proposed in the literature. However, except for rare pilot studies, such tests have largely been ignored by plant breeders because it has seldom been demonstrated that indirect selection for increased yield via these criteria is more effective than direct selection for yield. Instead, Australian breeders have concentrated on improving the efficiency of traditional breeding procedures via increased mechanization and computerization and improved analytical procedures. However, there has also been substantial interest in more radical alternative approaches to yield improvement and we will now briefly discuss two of these.

INTRODUCTION

Australia is a dry country—overall the driest continent on earth. As a result, improved drought resitance has been an important objective in breeding

programmes since the initiation in Australia of purposeful plant breeding in wheat by William Farrer in the late 1880s. Further, plant–water relations in arid and semi-arid environments have long been a major focus of research by Australian plant physiologists and agronomists. In the context of the present conference this raises two important questions. First, what lessons, in terms of devising efficient breeding strategies for moisture-limiting environments, have the local breeders learnt from this century of practical experience and research? Second, which of these lessons, if any, are of relevance to breeders in other regions or countries with broadly similar climates?

In attempting to answer these questions I will first consider the breeding procedures used in the past, since some of the earlier Australian wheats have been important as cultivars or parents in many of the drier regions of the world. I will then consider current breeding strategies and briefly describe several future alternatives now under investigation.

THE PAST

For the first hundred years following European settlement in 1788, wheat production was confined to relatively small areas in the cooler, higher rainfall regions of Australia. During the next 50 years production increased dramatically (from ≤1M ha in 1880 to ≥7M ha in 1930) and shifted to the hotter, more arid inland areas (growing season rainfall May to October of 175–375 mm). The first wheats grown in Australia, the red and white Lammas and Tuscans and Purple Straw types of English origin, were recognized as potentially the highest-yielding wheats available at that time (Vavilov, 1951). However, these cultivars were poorly adapted to the expanding Australian wheat belt. The critical deficiencies were their late maturity and associated excessive early vegetative growth and tillering which caused them to be highly susceptible to drought during flowering and grain filling. They were also susceptible to stem rust so that even in wet years they were often low yielding due to rust epidemics.

Not surprisingly the early Australian breeders were concerned with overcoming these deficiencies and their aims reflected this concern. For example, Farrer (1898) stressed the importance of earliness, sparse tillering, narrow leaves, and the ability to fill plump grain under severe drought in adapting wheat to the more arid inland areas. Farrer's contemporaries had similar objectives. Richardson (1914) even included short strong straw and high 'migration ratio', the equivalent of the harvest index, in his aims. These objectives are remarkably similar to those of many modern breeders in areas with similar climates (e.g. Hurd, 1971; Hadjichristodoulou, 1981). Perhaps the first important lesson to learn here, as a reminder of the great difficulty in making major advances in drought resistance research, is that at a practical level breeding aims have advanced little in more than 80 years.

Drought resistance germplasm sources

Early Australian wheat breeders pursued a vigorous programme of germplasm introduction in their search for drought-resistant stocks. Ultimately, three sources of germplasm proved of critical importance. A short list of cultivars which played a significant role in the extension of the Australian wheat belt into drier areas is given in Table 1 to illustrate this point. The first important source of germplasm was southern Africa. Gluyas Early, selected from South African material, and its derivatives, Nabawa and Bencubbin, were among the dominant wheat cultivars in Australia, particularly in the drier states of South Australia and Western Australia, from the 1900s to the 1950s. The second important source of germplasm was India. These introductions were an important source of earliness (Macindoe and Walkden-Brown, 1968) as well as reduced height, high harvest index, and limited tillering (Richardson, 1914). The third important source of germplasm appears to

Table 1. Some important varieties in the extension of wheat production in Australia into lower rainfall areas

Variety	Pedigree‡	Year released
Farmers' selections		
Steinwedel	Selection from Champlains' hybrid (American)	Late 1880s
Early Gluyas	Selection from Wards' Prolific (South African)	1890s
Bred varieties		
Federation	Purple Straw 14A//improved Fife/Etawah	1901
Currawa	Northern Champion/Cretan†//Little Club	1912
Canberra	Federation/Volga*†	1914
Nabawa	Early Gluyas/Bunyip	1915
Ghurka	Gallipoli/3/Currawa//India 4E/Federation	1924
Bencubbin	Nabawa/Early Gluyas	1929
Gabo	Bobin selection/Gaza†//Bobin selection	1945
Spica	Three Seas/Kamburico†//Pusa 4/Flora	1952

*Originally designated as skinless barley.
†Involved hybrid between *T. aestivum* and *T. durum*.
‡Pedigrees from Macindoe and Walkden-Brown (1968).

have been tetraploid wheats, particularly *T. durum*, from arid Mediterranean climates. The pedigrees in Table 1 suggest that cultivars carrying *T. durum* germplasm have made a significant contribution to the extension of the wheat belt into the drier areas of Australia, despite the relatively few interspecific hybrids made and used in breeding programmes (Macindoe and Walkden-Brown, 1968).

This suggests that *T. durum* offered genes for adaptation to dryland conditions not readily available in *T. aestivum*. If this suggestion is valid, it has important implications for breeders in the region serviced by ICARDA. This region is particularly rich in landrace populations of tetraploid wheats which have often evolved in harsh environments, and represent the pinnacle of adaptation to those harsh environments. Crossing these highly drought-resistant tetraploids with the best available, in terms of yield potential, bread and durum cultivars should generate significant scope for dryland yield improvement.

THE PRESENT

The present-day breeders face very different circumstances to their pioneering counterparts. Farrer and his contemporaries could expect to make gains in drier areas simply by breeding for earliness. Obviously, this is no longer possible. Once a suite of cultivars that flower at the optimum time is available, no more progress is possible via this route. Similar arguments can be made about other easily measured or observable traits of moderate to high heritability, such as height and tillering.

In this situation, a breeder can seek to identify other easily observable traits or adaptations that contribute to yield under drought and select for these. Alternatively, he can breed for yield directly. These different approaches have been termed the analytical approach and the empirical approach, respectively (Richards, 1982).

Analytical approach

Under this approach yield potential and drought resistance are presumed to be controlled by separate and distinct genetic systems. Breeding requires the identification of the drought resistance traits and their incorporation into high-yielding and well-adapted genotypes. It is assumed that because yield is the ultimate expression of many individual processes and their interaction with the prevailing climate and crop environment, selection for these drought-conferring traits will be more efficient than for yield itself. It is also assumed that the traits selected do not decrease yields in better environments (Richards, 1982).

Many morphological, physiological, and biochemical traits have been proposed as indirect selection criteria for improved drought resistance. A partial list is given in Table 2. However, in general, such proposals have been ignored by practising winter cereal breeders. The reasons are simple. First, it has often not been adequately demonstrated that the suggested criteria do improve drought resistance or yields in water-limiting environments. Second, even where it has been demonstrated that a particular trait does improve drought resistance, it is usually not clear that its effects are substantial enough to warrant its incorporation into all cultivars released. Third, even where it can be demonstrated that a particular trait measurably increases drought resistance and increases yield in water-limiting environments to a sufficient degree to warrant mandatory incorporation of that trait in all cultivars, it is usually not clear that indirect selection for increased yield using this trait will be more effective than direct selection for yield itself.

There are nevertheless several interesting pilot studies in progress to assess the value of several traits as indirect selection for drought resistance. These

Table 2. Some proposed indirect selection criteria* for improved yield in water-limiting environments

1. *Morphological traits*
   - Awns
   - Leaf waxiness
   - Small and/or narrow leaves
   - Low stomate density
   - Root weight/fineness
   - Root depth
   - Root xylem vessel diameter
2. *Physiological traits*
   - Dehydration avoidance
     - stomatal regulation
     - osmotic adjustment
     - leaf rolling
     - excised leaf water retention ability
   - Dehydration tolerance
     - cell membrane stability
3. *Metabolic traits*
   - Proline accumulation
   - Abscisic acid level
   - Betaine accumulation

*See Hall *et al.* (1979), Turner and Begg (1981), Blum (1982), Richards (1982), and Morgan (1984), and papers reviewed by these authors.

include leaf glaucousness, root xylem vessel diameter and reduced tillering (Richards, 1982), osmoregulation (Morgan, 1984), and carbon isotope discrimination (Richards, 1984).

Empirical approach

In the light of perceived deficiencies in the analytical approach, emphasis in Australian cereal-breeding programmes has been on increasing yield potential and average yields rather than on increasing drought resistance *per se*. While the broad aim of these programmes, i.e. increasing yields in water-limiting environments, can be described as traditional, the philosophies and technologies adopted cannot. Indeed, there have been dramatic changes in the so-called traditional breeding programmes in Australia over the last two decades.

The most significant philosophical change has been the widespread adoption of early-generation multilocation yield testing. This change was motivated by experience which indicated that, while selection for easily observable and simply inherited characters, such as disease resistance and plant height, in spaced F_2 progenies or F_3 progeny rows was effective, visual selection for yield was not. Indeed, plants visually selected for yield in early generations were often no higher yielding on average over sites and years than random selections from the same populations. Such results have led many breeders to the view that selection for improved performance will only be effective if based on yield tests over a range of sites (location/years) representative of the target environment.

This viewpoint has an obvious practical corollary. Breeders must be able to yield-test large numbers of lines at a representative set of locations each year. As a consequence of this corollary, Australian breeders have concentrated on improving the efficiency of yield testing through increased mechanization and computerization and improved analytical procedures. With respect to mechanization, the most significant advances have come with the introduction of magazine seed-loading systems, the cone seeder, and the self-propelled plot harvesters (Portmann, 1983). These machines have greatly increased the potential of breeders to sow and harvest large numbers of yield plots. However, realization of this potential without greatly increased staff has only been possible with the introduction of computers as an everyday adjunct in breeding programmes. Without computers the benefits would have been largely lost because the bookkeeping and data processing would have been prohibitive.

With current machinery and computing systems the number of yield plots which can be routinely handled by breeders is impressive. For example, Portmann (1983) estimated that the number of plots handled per man per year has increased from 700 in 1969 to a massive 10,000 by 1983. As a result

of such increases in plot-handling capabilities the size of many Australian cereal breeding programmes has increased so that the largest now grow 40–80 thousand yield plots per year (Portmann, 1983; Hollamby *et al.*, 1983).

The increase in large-scale yield testing has also spawned increased interest and substantial developments in testing and analytical procedures. One area of major concern has been ways of identifying suitable test sites, particularly early in the programme, when the number of lines to be tested is large and the number of sites small. Several alternative procedures have been proposed and are being further evaluated (e.g. Pederson and Rathjen, 1981; Brennan *et al.*, 1981). Another major area of concern has been optimal experimental designs for large numbers of entries, and how these may be analyzed and interpreted. A significant advance here has been the development of the 'nearest neighbour (NN) analysis' (Wilkinson *et al.*, 1983), which has quickly gained wide currency in Australia but which is still highly controversial.

The rapid adoption over the last decade of new technologies by Australian breeders has important implications for plant physiologists and others developing drought screening tests. Clearly, if breeders have the capacity to grow 10,000 yield plots per man each year and say, 2000 lines grow on five sites in single replicate plots, then any alternative test must be able to handle at least that many lines cheaper or more reliably if it is to be competitive. Many tests have been promoted in the past as being 'simple, cheap, and reliable'. Future tests will indeed have to meet all these criteria to be adopted by breeders.

THE FUTURE

Measurable progress has been made in increasing average yields in Australia in recent decades. However, progress has been modest compared to the absolute gains made over the same period in more favourable conditions such as in the United Kingdom (Turner and Begg, 1981). Further, all indications are that while the rate of progress may increase with improved technologies it is still likely to remain modest. As a consequence, while breeders generally regard the empirical approach as the only dependable route to improved yields in regions with relatively low and uncertain rainfall, they are nevertheless interested in alternative approaches which may result in more rapid or substantial increases in yield or water-use efficiency. Several such alternative approaches have been advocated in the literature in recent years. I consider two which have attracted the interest of cereal breeders.

Development of longer growing season cultivars

The first proposed means of increasing yields is by the development of longer growing season cultivars. Emphasis has traditionally been given in drier

environments to shorter season cultivars which use less water during the preflowering period so more is available during the critical flowering and grain-filling period. Such cultivars are more reliable in drier areas or years. However, they are also less capable of responding to more favourable moisture regimes.

In subsistence agriculture, stable yields, particularly in the poorer years, and a minimum of crop failure are obviously critically important. Similarly, in less-developed countries with small local markets, where prices are high in poor years and excess production virtually worthless in good years, stability is also important. In sharp contrast, in developed countries, with relatively stable or controlled prices, good storage, and access to worldwide markets, high average yields are the critical factor. Proponents of longer-season wheats argue that they will increase average yields, even in low input environments, because the potential yield increases in the good years far outweigh the potential losses in the bad years.

One of the difficulties with this concept in Australia was ensuring that the longer-season cultivar flowered at the optimum time, i.e. as soon as the frost risk is acceptably low—in spring before the onset of drought and heat. In other words, the growing season can only be lengthened by early sowing. This problem was eventually resolved by the development of semi-dwarf daylength-insensitive winter wheats with a relatively low vernalization requirement of 4–5 weeks. Such wheats may be sown over an extended period from mid-April to mid-July in New South Wales and still flower around the optimum time. Unfortunately, the first such wheat developed in Australia, WW33 (Pugsley, 1973), was not approved for cultivation because of deficiencies in its quality, although it has subsequently been released in California as 'Phoenix'. However, in recent years several WW33 derivatives have been released in Australia and appear to be competitive in yield with hard spring wheats (Martin, 1981). If they are quickly and readily accepted by farmers it will indicate that such cultivars may have a place in dryland wheat production in many regions of the world.

Frost resistance

The second proposed means of increasing yield is indirectly via increased frost resistance during stem elongation and heading. In Australia, spring radiation frosts can cause severe damage to wheat during the reproductive stages of development. Such damage can arise at temperatures in a standard meteorological screen of −2°C or less. Frost during stem elongation produces tiller mortality, whereas frost after ear emergence can reduce seed set and may result in complete sterility (Fletcher, 1984; Single, 1985).

The danger of spring frosts during reproductive development precludes early flowering. As a consequence, the crop faces rapidly rising evaporative

demand and mean daily temperatures, often coupled with limited or no rainfall, during the flowering and grain-filling period. It has been argued that by improving frost resistance it would be possible to move flowering and grain filling earlier during the cooler spring months and therefore improve water-use efficiency and grain yield (Fletcher, 1984). Trials in frost-free areas in central Queensland strongly supported this concept and indicated that grain yield of a number of genotypes was highest when anthesis occurred in mid-winter (Woodruff, 1983; Woodruff and Tonks, 1983). Unfortunately, progress in improving frost resistance has been limited (Fletcher, 1984) but further progress appears possible (Single, 1985). Given the potential yield advantage of earlier flowering frost-resistant cultivars, this problem deserves more attention from cereal breeders in water-limiting environments than it has received to date.

REFERENCES

Blum, A. 1982. Evidence for genetic variability in drought resistance and its implications for plant breeding. Pages 53–68 in *Drought Resistance in Crops with Emphasis on Rice*. International Rice Research Institute, Los Banos, Phillipines.

Brennan, P. S., Byth, D. E., Drake, D. W., Densey, I. H. and Butler, D. G. 1981. Determination of the location and number of test environments for a wheat cultivar evaluation program. *Aust. J. Agric. Res.* **32**:189–201.

Farrer, W. J. 1898. The making and improvement of wheat for Australian conditions. *Agric. Gaz. NSW* **9**:131–168, 241–250.

Fletcher, R. J. 1984. Breeding for frost resistance in early flowering wheat. Pages 615–619 in *Proceedings of the 6th International Wheat Genetics Symposium*, 1983, Kyoto, Japan.

Hadjichristodoulou, A. 1981. Aspects of barley breeding for dry Mediterranean regions. *Barley Genet.* **IV**:383–388.

Hall, A. E., Foster, K. W. and Waines, J. G. 1979. Crop adaptation to semi-arid environments. Pages 148–179 in *Agriculture in Semi-Arid Environments* (Hall, A. E., Cannell, G. H. and Lawson, H. W., eds.). Ecological Studies, Vol. 34. Springer-Verlag, Berlin and Heidelberg, Germany.

Hollamby, G. J., Wilson, R. E. and Bayraktar, A. 1983. Extending the wheat breeding philosophy to farmers—the Roseworthy programme. Pages 358–360 in *Proceedings of the Australian Plant Breeding Conference* (Driscoll, C. J., ed.), 14–18 February 1983, Adelaide, South Australia. University of Adelaide, Adelaide, Australia.

Hurd, E. A. 1971. Can we breed for drought resistance? Pages 77–78 in *Drought Injury and Resistance in Crops* (Larson, K. L. and Rachter, J. D., eds.). CSSA special publication 2, Crop Science Society of America.

Macindoe, S. L. and Walkden-Brown, C. 1968. Wheat breeding and varieties in Australia. Scientific bulletin 76, NSW Department of Agriculture. 225 pp.

Martin, R. H. 1981. In Farrer's footsteps. *J. Aust. Inst. Agric. Sci.* **47**:123–131.

Morgan, J. M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* **35**:299–319.

Pederson, D. G. and Rathjen, A. J. 1981. Choosing trial sites to maximise selection response for grain yield in spring wheat. *Aust. J. Agric. Res.* **32**:411–424.

Portmann, P. A. 1983. Machines and computers—then, now and next. Pages 18–23 in *Proceedings of the Australian Plant Breeding Conference* (Driscoll, C. J., ed.). 14–18 February 1983, Adelaide, South Australia. University of Adelaide, Adelaide, Australia.

Pugsley, A. T. 1973. At last—semi-dwarf wheats for Australia. *Bulk Wheat* **8**:34–35.

Richards, R. A. 1982. Breeding and selecting for drought resistance in wheat. Pages 303–316 in *Drought Resistance in Crops with Emphasis on Rice*. International Rice Research Institute, Los Banos, Phillipines.

Richards, R. A. 1984. An analytical approach to breeding for higher wheat yields in droughted environments. Pages 29–30 in *Proceedings of the 4th Assembly of Wheat Breeding Society of Australia*, August 1984, Toowoomba, Queensland. Queensland Wheat Research Institute, Toowoomba, Australia.

Richardson, A. E. V. 1914. Wheat breeding in Australia. *J. Dept. Agric., Vic.* **12**:644–655.

Single, W. V. 1985. Frost injury and the physiology of the wheat plant. *J. Aust. Inst. Agric. Sci.* **51**:128–134.

Turner, N. C. and Begg, J. E. 1981. Plant–water relations and adaptation to stress. *Plant and Soil* **58**:97–131.

Vavilov, N. I. 1951. *The origin, variation, immunity and breeding of cultivated plants*. Ronald Press, New York. 364 pp.

Wilkinson, G. N., Eckert, S. R., Hancock, T. W., Mayo, O., Rathjen, A. J. and Sparrow, D. H. B. 1983. A new statistical methodology for design and analysis of plant breeding and varietal field trials. Pages 59–65 in *Proceedings of the Australian Plant Breeding Conference* (Driscoll, C. J., ed.), 14–18 February 1983, Adelaide, South Australia. University of Adelaide, Adelaide, Australia.

Woodruff, D. R. 1983. The effect of a common date of either anthesis or planting on the rate of development and grain yield of wheat. *Aust. J. Agric. Res.* **34**:13–22.

Woodruff, D. R. and Tonks, J. 1983. Relationship between time of anthesis and grain yield of wheat genotypes with differing developmental patterns. *Aust. J. Agric. Res.* **34**:1–11.

DISCUSSION

M. S. Mekni

Since the most important yield jump in cereal breeding in Australia has been obtained through increases in HI, following the adoption of semi-dwarfs, have Australian breeders sacrificed straw yield? Are you breeding for straw yield?

D. R. Marshall

It is true that, as recent yield increases in Australia have been primarily due to increases in harvest index associated with Rht genes, straw yields have decreased. However, in contrast to many countries in the Mediterranean region, cereal straw is not regarded in Australia as an important annual feed. Australian farmers often do stock stubble after harvest but this is to control weeds and to assist in stubble breakdown.

N. C. Turner

There are some pilot breeding programmes for physiological characters in Australia. In the light of your comments in your paper do these have no validity?

D. R. Marshall

As I noted in my paper, there are a few notable exceptions to the general rule that plant breeders have not adopted the selection criteria proposed by plant physiolo-

gists. One notable exception is the use of leaf emergence by Dr J. Syme in Queensland in breeding successful varieties. Another is the physiologist, J. Morgan, in Tamworth, NSW, using osmoregulation as a selection criterion for drought resistance.

F. N. Reyniers

How do you use the rank of your varieties in multilocation trial?
With my experience it could be used in two ways:
(1) to have specific variety for specific drought stress,
(2) cross varieties which perform well in different types of drought.

D. R. Marshall

The rank of varieties in trials is used primarily to decide which varieties to release to farmers. We are prepared to release varieties for specific areas, if this is necessary. However, we prefer to use multilocation tests to select cultivars which are acceptable.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

8

Breeding Strategies for Improving Cereal Yield and Stability under Drought

S. CECCARELLI, M. M. NACHIT, G. O. FERRARA, M. S. MEKNI, M. TAHIR, J. VAN LEUR, and J. P. SRIVASTAVA
ICARDA, PO Box 5466, Aleppo, Syria

ABSTRACT

The main objective of the cereal-breeding activities of ICARDA (International Center for Agricultural Research in the Dry Areas) is to increase yield and yield stability of barley, durum wheat, and bread wheat under the environmental fluctuations of rainfed agriculture. The key strategy employed involves targetted crosses and multilocation testing and selection of early segregating populations to identify genotypes capable of coping with the erratic and unpredictable climatic conditions of dry areas. A modified bulk method is used for the selection of early segregating populations. Additional strategies are the use of landraces and wild relatives of these crops.

By using the traditional approach (selection for grain yield) it has been found that in barley the F_3 families derived from F_2 selected under unfavourable conditions were more vigorous in the early stages of growth, taller, earlier in heading, and with larger yields than the F_3 derived from F_2 selected under favourable conditions. A high and negative correlation coefficient was found between the drought susceptibility index and grain yield at the driest site, whereas at the wettest site the correlation coefficients were lower and in some cases positive. Similar results have been obtained with durum wheat and bread wheat advanced lines, indicating that, within the rainfall range of the trials (178–380 mm for barley and 277–600 mm for durum wheat and bread wheat), segregating populations and lines with the largest grain yield under favourable conditions are more drought susceptible than those with the largest grain yield under drought. This indicates the existence of certain traits which are desirable under drought but undesirable under favourable conditions, or vice versa.

These results, confirmed by the data from the 1985–6 season, indicate that selection under stress conditions is expected to be more efficient than

selection under favourable conditions when dry areas become the target environment.

INTRODUCTION

The improvement of yield and yield stability of barley, durum wheat, and bread wheat under rainfed conditions is the main objective of the cereal breeding activities of ICARDA (International Center for Agricultural Research in the Dry Areas).

Barley, durum wheat, and bread wheat are grown under varied rainfed conditions in the ICARDA region: barley, mainly under lower rainfall and often harsh environment; bread wheat under higher rainfall or irrigated conditions; and durum wheat in moderate rainfall areas.

Wherever the three crops are grown under rainfed conditions in a Mediterranean type of climate, year-to-year fluctuations in the amount, frequency, and duration of rain are higher, and other factors such as low temperatures in winter and high temperatures during the terminal grain-filling period also influence crop growth and yield. Often, biotic stresses such as low nutrient level, diseases, insect pests, and poor crop management also limit production. Similar factors, although with different intensity and timing, limit grain yield when barley and wheat are grown in areas more than 1000 m above sea level with a continental Mediterranean climate.

Breeding for moisture-limited environments and, in general, for stress environments, raises two main issues. The first is whether breeding for stress environments should rely on selection under favourable conditions and subsequent testing of selected material in stress environments, or on direct selection under stress conditions. The second issue is related to direct selection for yield (also called the traditional or empirical approach) as opposed to selection for morphological and/or physiological attributes, which are assumed to have a cause–effect relationship with yield in a moisture-limited environment (the analytical or reductionist approach).

In this paper we present the current strategies and methodologies of the Cereal Program at ICARDA in relation to those two issues, as well as some experimental data which we have generated to test and monitor our current strategies.

Breeding strategies

The breeding strategies common to all three crops are targetted crosses, multilocation testing and selection of early segregating populations, and the use of modified bulk methods as a means to identify genotypes capable of coping with the erratic and unpredictable climatic conditions typical of dry areas and to reduce the effect of large environmental variability which limits

the efficiency of selection in dry areas. Additional strategies are the use of landraces and wild relatives (Ceccarelli and Mekni, 1985; Srivastava and Winslow, 1981; Tahir *et al.*, 1983).

Multilocation testing is an extension of the 'parallel selection' initiated at ICARDA in 1978 on durum wheat evaluated under rainfed and supplementary irrigation within one location. The results of parallel selection revealed that 'selection under low fertility dry farming conditions is more successful in identifying drought-tolerant genotypes than selection in the fertile high-moisture environment' (Srivastava *et al.*, 1983).

Most of the multilocation testing and selection is now carried out within the Aleppo Province, in northern Syria, which offers the unique opportunity of evaluating breeding materials between 175 and 450 mm of annual rainfall within a distance of 100 km. Additional environments are provided by early, normal, and late planting at ICARDA's main experimental station at Tel Hadya (Syria). The experimental station at Terbol (Lebanon) is used as a high-rainfall environment (Table 1).

This approach is expected to have two major advantages. First, from a practical viewpoint, it allows the evaluation of the genotype–environment interaction in a given year or, stated differently, of the range of phenotypic responses of a given genotype (or family) to a range of climatic events and stresses (amount and distribution of rainfall, temperature, diseases, and pests pressure) which may occur at a given location over a number of years. Second, from a methodological viewpoint, it generates a wealth of information on the issue of whether breeding for stress environments should rely on selection under good conditions and subsequent test in stress environments or on direct selection under stress conditions. Followers of the first strategy assume that varieties that give good yields in favourable conditions will also yield relatively well in unfavourable conditions. Selection is easier because in favourable conditions genetic variability and heritability are higher. This strategy

Table 1. Locations and environments used by the cereal-breeding programmes at ICARDA, with long-term annual rainfall as well as total rainfall in 1984–5

Location or environment	Long-term annual rainfall (mm)	1984–5 rainfall (mm)	Crop*
Bouider	175	178	B
Breda	273	277	B,DW,BW
Tel Hadya (late planting)		300	B,DW,BW
(normal planting)	342	380	B,DW,BW
(early planting)		450	DW,BW
Terbol	600		B,DW,BW

*B = barley, DW = durum wheat, BW = bread wheat.

also assumes that genotypes selected in dry environments will have a low yield potential in good environments. Although the argument for selection in favourable conditions has been supported by some experimental data (Frey, 1964; Roy and Murty, 1970; Mederski and Jeffers, 1973; Richards, 1982), the greater efficiency of the second strategy (direct selection under stress conditions); has been emphasized by many workers (Aufhammer *et al.*, 1959; Burton, 1964; Hageman *et al.*, 1967; Johnson *et al.*, 1968; Hurd, 1968, 1971; Boyer and McPherson, 1975; Johnson, 1980; Bidinger, 1980; Buddenhagen, 1983).

Selection in environment Y when the target environment is X is a special case of correlated responses to selection (Falconer, 1960), which is given by

$$CR_x = \frac{r_A h_y}{h_x} R_y$$

where CR_x is the correlated response in the target environment (X), R_y is the direct response in environment Y, h_y and h_x are the root squares of heritabilities in environments X and Y, and r_A is the genetic correlation between grain yields in the two environments. Figure 1 shows the relationship between r_A and the ratio CR_x/R_y when the ratio between heritabilities in the

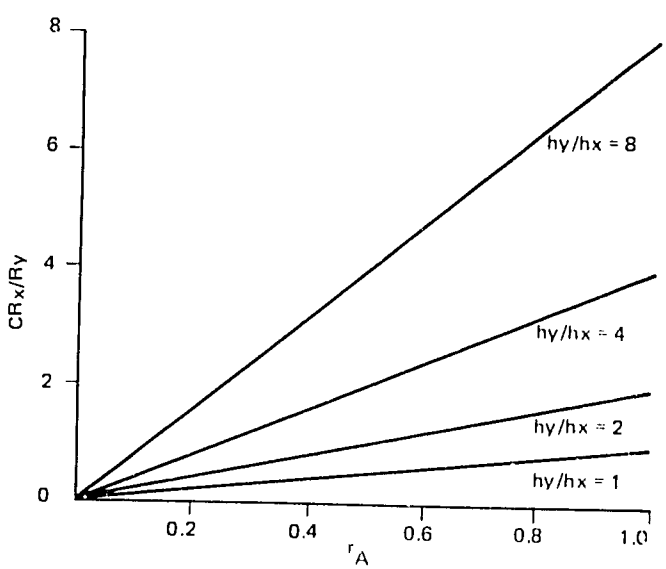


Figure 1. Relationship between genetic correlation coefficients between yields in environments Y and X and the ratio between correlated response in environment X when selection is done in environment Y over direct response at different ratios of heritability in the two environments

two environments is equal to 3, 4, 2, and 1. If the heritability for a given character is similar in the two environments, it will be more efficient to carry out the selection in the environment in which the material is expected to be grown, in spite of the value of the genetic correlation coefficient. On this issue and based on the magnitude of genetic correlations between yields in stress and non-stress environments, and on the ratio of genetic variances in stress and non-stress environments, selection for tolerance to stress is expected to produce a negative correlated response on mean yields in non-stress environments (Rosielle and Hamblin, 1981). This conclusion, which is supported by the data of Langer *et al.* (1979), indicates that direct selection in stress environments will decrease yield in a non-stress environment unless genetic variances in stress environments are considerably greater than those in non-stress environments and genetic correlations are positive and close to 1.

Recent results on F_3 bulk families of barley (Figure 2) indicated no relationship between broad sense heritability and level of stress measured as grain yield per millimetre of rainfall, which suggests that direct selection in dry areas could be more efficient than selection in favourable environments regardless of the magnitude of the genetic correlation.

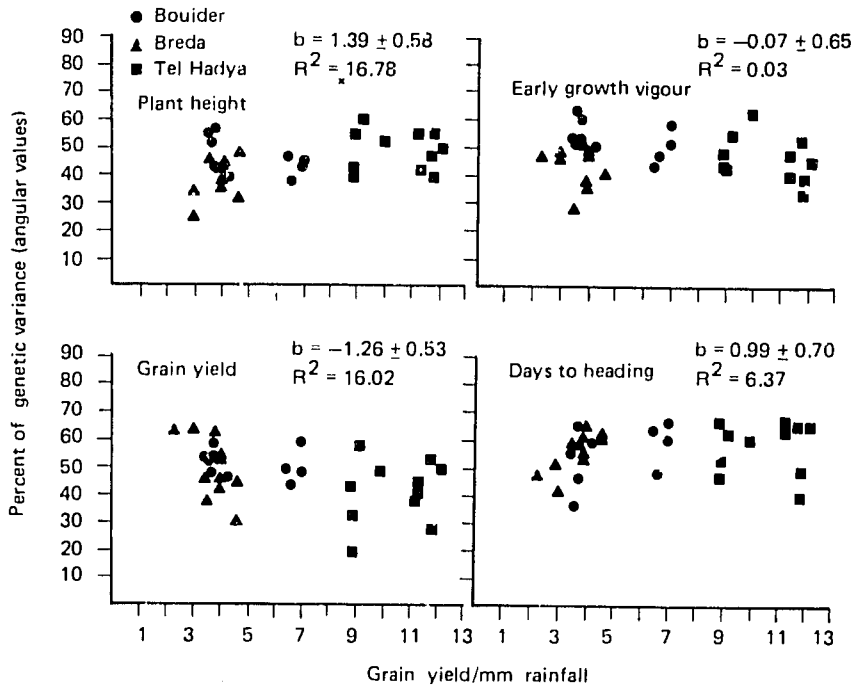


Figure 2. Relationships between broad sense heritability and moisture stress measured as grain yield per millimetre of rainfall

Table 2. Agronomic characters and drought susceptibility index (DSI) in F_3 bulk families derived from F_2s selected in 1983–4 at Breda, Tel Hadya, and both locations

Selected at	Cold tolerance	Early vigour	Plant height	Days to heading	Grain yield (kg/ha)	DSI
Breda	3.06	2.93 a	56 a	152.6 b	1880 a	0.73 a
Tel Hadya	2.97	3.11 b	53 b	153.4 c	1772 b	0.75 b
Both locations	3.04	2.91 a	54 b	150.2 a	1850 a	0.73 a

Each value is the average of 26 families, 3 locations, and 5 trials, with the exception of the drought susceptibility index which is the average of 26 families and 5 trials.

Values followed by the same letter(s) are not significantly ($P < 0.05$) different. For DSI a significant level of 10 per cent was used.

Some additional evidence in favour of a higher efficiency of direct selection under dry conditions was observed in barley by comparing three groups of F_3 families derived from F_2s selected only at Breda, only at Tel Hadya, or at both locations. No significant differences were observed between the three groups of F_3 families for cold tolerance (Table 2). Compared with the group selected at Tel Hadya, the group selected at Breda was more vigorous in the early stages of growth, taller, earlier in heading, and more productive. The group selected at both locations was not significantly different from the group selected at Breda except for shorter plants and earlier heading. The drought susceptibility index (Fischer and Maurer, 1978; Fischer and Wood, 1979) was slightly lower ($P = 0.10$) in the groups selected at Breda and at both locations, indicating that the material in these two groups tended to have a higher drought resistance. Although significant, the differences were not large, probably due to (1) the severe drought at Breda and Tel Hadya in 1983–4 and (2) the inefficiency of the visual selection of F_2. However, these

Table 3. Grain yield (kg/ha) of three groups of F_3 families derived from F_2 selected only at Breda, only at Tel Hadya, and at both locations, and evaluated at Bouider, Breda, and Tel Hadya

Selected at	Grain yield*		
	Bouider	Breda	Tel Hadya
Breda	921 a	1037 a	3675 a
Tel Hadya	827 b	928 b	3577 a
Both locations	891 ab	1033 a	3628 a

*Means followed by the same letter(s) are not significantly ($P < 0.05$) different.

data suggest an advantage of direct selection under dry conditions over selection in more favourable conditions.

The data in Table 2 also indicate that the traditional approach is not necessarily opposed to the analytical approach because, through the study of correlated responses to selection, it may generate information on which characters are more frequently associated with larger yields in a moisture-limited environment. Examples of these characters are early growth vigour, long culm, and earliness (Table 2).

The larger grain yield found in the two groups of families selected only at Breda and those selected both at Breda and Tel Hadya has to be attributed to their better adaptation to drier areas (Table 3). It is interesting to note that neither group lost the ability to respond to the favourable environment at Tel Hadya.

In barley (Table 4) a high negative correlation coefficient was found between the drought susceptibility index (S) and grain yield at the driest site, indicating that larger yields are associated with higher levels of drought resistance, whereas at the wettest site the correlation coefficients were much lower (even if significant) and in two cases positive. Positive and significant correlation coefficients between S and grain yield in wet environments have been reported by Fischer and Maurer (1978) and have been interpreted as an indication of the existence of traits which are desirable under drought and undesirable under favourable conditions, or vice versa. In spite of the low value of the correlation coefficient between the drought susceptibility index and grain yield at Tel Hadya, selection for high and low grain yield at this location is expected to increase drought susceptibility (Table 5), whereas selection for large grain yield at Bouider is expected to increase drought resistance. At both locations the F_3 families with the largest grain yield were significantly more cold tolerant, more vigorous in the early stages of growth, and taller than the F_3 families with the lowest grain yield. Selection for large and small grain yield at Bouider is also expected to determine a correlated

Table 4. Correlation coefficients among drought susceptibility index and grain yield at different levels of moisture stress in barley

Trial	*N*	Bouider (178 mm)	Breda (277 mm)	Tel Hadya (380 mm)
F_3 bulk families	729	−0.769*	0.510*	0.249*
Elite yield trials	42	−0.833†	0.384*	0.298
Advanced yield trials	168	−0.866†	0.086	0.270†
Landraces—1	49	−0.719*	0.630*	0.134
Landraces—2	36	−0.769*	0.784*	0.102

*$P < 0.01$.
†$P < 0.001$.

Table 5. Average grain yield (kg/ha), plant height, cold tolerance, early growth vigour, days to heading, days to maturity, and drought susceptibility index (DSI) in contrasting environments of F_3 families of barley selected for grain yield under favourable (Tel Hadya) and unfavourable (Bouider) conditions

Character	Selection at Bouider			Selection at Tel Hadya		
	Top 5%	Bottom 5%	Difference	Top 5%	Bottom 5%	Difference
Grain yield at Bouider	1686	274	1412‡	929	758	171
Grain yield at Tel Hadya	3935	3565	370*	5367	2508	2859‡
Plant height at Bouider	53.2	38.3	14.9‡	43.8	44.6	−0.8
Plant height at Tel Hadya	72.8	73.8	−1.0	79.5	63.6	15.9†
Cold tolerance	2.7	3.6	−0.9‡‡	3.0	3.3	−0.3‡
Early growth vigour	2.7	3.5	−0.8‡	2.4	3.3	−0.9‡
Days to heading (Bouider)	148.4	158.3	−9.9‡	150.4	156.0	−5.6†
Days to heading (Tel Hadya)	142.2	143.2	−1.1	141.1	142.4	−1.3
Days to maturity (Bouider)	171.9	173.4	−1.5‡	172.0	172.7	−0.7*
Drought susceptibility index	0.83	1.17	−0.34	1.05	0.97	0.08*

*$P < 0.05$.
†$P < 0.01$.
‡$P < 0.001$.

response at Tel Hadya. On the contrary, selection for large and small grain yield at Tel Hadya is expected to produce insignificant effects when the material is grown at Bouider.

These data indicate that direct selection under dry conditions is more efficient than selection under favourable conditions or, stated differently, that high yield potential under favourable conditions is not a useful selection criterion to identify superior genotypes for dry areas. In fact, in the top 5 per cent of the F_3 families for grain yield at Tel Hadya, there are only three families which are also included in the top 5 per cent for grain yield at Bouider.

The implications of these results, obtained with early segregating populations, are obvious. In a breeding programme for dry areas it is essential to screen early segregating populations, possibly as early as the F_2 generation, in the target environment, to avoid the risk of losing highly drought-resistant genotypes by selecting for one or more cycles in a favourable environment.

Similar results have been obtained in durum and bread wheat by evaluating 210 lines in the advanced yield trials grown in five different environments ranging from Breda to Terbol.

With the exception of bread wheat planted late at Tel Hadya (Table 6), where probably heat stress, in addition to moisture stress during the final stages of crop development, affected grain yield, the correlation coefficient between the drought susceptibility index and grain yield was high and negative at the driest location, negative but progressively smaller with normal and late planting at Tel Hadya, and positive in the higher rainfall environment (Terbol). Similar to barley, selection for high grain yield in durum and bread wheat under favourable conditions is expected to cause an increase in drought susceptibility, although the correlated response would probably be small in bread wheat due to the low value of the correlation coefficient (r = 0.413). In less favourable environments, larger grain yields become progressively

Table 6. Correlation coefficients among drought susceptibility index and grain yield at different levels of moisture stress in bread wheat (BW) and durum wheat (DW)

Location or environment	Rainfall (mm)	Correlation coefficient	
		BW	DW
Breda	277	−0.836	−0.71
Tel Hadya (late planting)	300	−0.041	−0.31
(normal planting)	342	−0.484	−0.32
(early planting)	450	−0.154	−0.18
Terbol	600	−0.413	−0.76

Table 7. Average grain yield (kg/ha), plant height, days to heading, early growth, days to maturity, and drought susceptibility index (DSI) in contrasting environments of bread wheat lines selected for grain yield under low- and high-rainfall conditions

Character	Low rainfall (LR)			High rainfall (HR)		
	Top 5%	Bottom 5%	Difference	Top 5%	Bottom 5%	Difference
Grain yield (LR)	3347	1663	1684‡	1991	2623	−632‡
Grain yield (HR)	5235	5438	−203	6032	4163	1869‡
Plant height (LR)	80.0	66.0	14.0‡	68.5	74.0	−5.5
Plant height (HR)	75.5	77.5	−2.0	82.5	76.5	6.0
Days to heading (LR)	140.4	141.8	−1.4	142.2	141.4	0.8
Days to heading (HR)	151.3	149.6	1.7	149.9	151.2	−1.3
Days to maturity (LR)	177.4	178.8	−1.4‡	179.0	177.7	1.3*
Days to maturity (HR)	192.7	193.2	−0.5	194.7	193.1	1.6*
Drought susceptibility index	0.71	1.37	−0.66‡	1.33	0.73	0.60‡

*$P < 0.05$.
†$P < 0.01$.
‡$P < 0.001$.

Table 8. Average grain yield (kg/ha), plant height, cold tolerance, days to heading, and drought susceptibility index in contrasting environments of durum wheat lines selected for grain yield under low- and high-rainfall conditions

Character	Low rainfall (LR)			High rainfall (HR)		
	Top 5%	Bottom 5%	Difference	Top 5%	Bottom 5%	Difference
Grain yield (LR)	1419	699	720‡	986	1205	−219
Grain yield (HR)	4361	4083	278	5125	2836	2289‡
Plant height (LR)	65	59	6*	58	60	−2
Plant height (HR)	70	68	2	76	65	11†
Cold tolerance	5.0	3.8	1.2*	6.3	3.7	2.6‡
Days to heading	170	174	−4*	173	175	−2
Drought susceptibility index	0.91	1.14	0.23‡	1.04	0.92	0.12†

*$P < 0.05$.
†$P < 0.01$.
‡$P < 0.001$.

associated with low values of drought susceptibility index (higher drought resistance).

Therefore, it should be expected that (1) lines selected under favourable conditions will be different from those selected in unfavourable conditions and that (2) selection for large grain yield in favourable conditions does not cause a carry-over effect in moisture-limited environments.

This can be tested by comparing grain yield of the top and bottom 5 per cent of the lines in contrasting environments (Tables 7 and 8). In bread wheat, the lines with the highest and lowest grain yield at Breda (low rainfall) were found to give similar yield when evaluated at Terbol (high rainfall). By contrast, the top and bottom 5 per cent of the lines for grain yield at Terbol were found to differ significantly ($P < 0.05$) at Breda, the bottom 5 per cent producing a larger yield than the top 5 per cent. The lines selected for large grain yield under low rainfall were significantly ($P < 0.001$) taller and earlier in maturity than those selected for low grain yield. By contrast, selection for large grain yield in a high-rainfall environment did not affect plant height and favoured late-maturing genotypes. This is additional evidence for the existence of traits which are of advantage under drought and are a disadvantage or neutral in an optimum environment. Similar to the findings in barley, lines selected for large grain yield under low rainfall are more drought resistant than those selected for low grain yield, whereas lines selected for large grain yield under high rainfall are more drought susceptible than those selected for low grain yield.

In durum wheat the top and bottom 5 per cent of the lines for grain yield under low and high rainfall did not differ significantly in grain yield in the contrasting environments of high and low rainfall, respectively. Similar to what we found in barley, favourable conditions did not allow the identification of the most drought-tolerant durum wheat genotypes. Durum wheat lines with larger grain yield in moisture-limiting conditions were taller, more cold tolerant, and earlier than those with lower grain yield. Plant height and cold tolerance are also conducive to larger yields in a favourable environment, whereas earliness does not appear to be as important as in an unfavourable environment.

In conclusion, it appears that in all three crops a high yield potential under favourable conditions is not an efficient selection criterion to identify the higher yielding material for rainfed and stress conditions. The results also suggest that this is due to a different architecture of plant characteristics associated with yield under stress and non-stress conditions.

REFERENCES

Aufhammer, G., Fischbeck, G. and Grebner, H. 1959. Testing drought resistance in spring cereals. *Z. Acker. Pflanzenbau* **110**:117–134.

Bidinger, F. 1980. Breeding for drought resistance. Pages 452–454 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, N. C. and Kramer, P. J., eds.). John Wiley, New York.

Boyer, J. S. and McPherson, H. G. 1975. Physiology of water deficits in cereal crops. *Adv. Agron.* **27**:1–23.

Buddenhagen, I. W. 1983. Breeding strategies for stress and disease resistance in developing countries. *Ann. Rev. Phytopathol.* **27**:385–409.

Burton, G. W. 1964. The geneticist's role in improving water-use efficiency by crops. 'Research on Water', Special publication 4, American Society of Agronomy, Madison, Wisconsin.

Ceccarelli, S. and Mekni, M. S., 1985. Barley breeding for areas receiving less than 250 mm annual rainfall. *Rachis* **4**(2):3–9.

Falconer, D. A. 1960. *Introduction to quantitative genetics*. The Ronald Press Company, New York.

Fischer, R. A. and Maurer, R. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. *Aust. J. Agric. Res.* **29**:897–912.

Fischer, R. A. and Wood, J. T. 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. *Aust. J. Agric. Res.* **30**:1001–1020.

Frey, K. J. 1964. Adaptation reaction of oat strains selected under stress and non-stress environmental conditions. *Crop Sci.* **4**:55–58.

Hageman, R. H., Leng, E. R. and Dudley, J. W. 1967. A biochemical approach to corn breeding. *Adv. Agron.* **19**:45–86.

Hurd, E. A. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. *Agron. J.* **60**:201–205.

Hurd, E. A. 1971. Can we breed for drought resistance? Pages 77–88 in *Drought Injury and Resistance in Crops* (Larson, K. L. and Eastin, J. D., eds.). Special publication 2, Crop Science Society of America, Madison, Wisconsin.

Johnson, D. A. 1980. Improvement of perennial herbaceous plants for drought-stressed western rangelands. Pages 419–433 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, M. C. and Kramer, P. J., eds.). Wiley Interscience, New York.

Johnson, V. A., Shafer, S. L. and Schmidt, J. W. 1968. Regression analysis of general adaptation in hard red winter wheat (*Triticum aestivum* L.). *Crop Sci.* **8**:187–191.

Langer, I., Frey, K. J. and Bailey, T. 1979. Associations among productivity, production response, and stability indexes in oat varieties. *Euphytica* **28**:17–24.

Mederski, H. J. and Jeffers, D. L. 1973. Yield response of soybean varieties grown at two soil moisture stress levels. *Agron. J.* **65**:410–412.

Richards, R. A. 1982. Breeding and selecting for drought resistance in wheat. Pages 303–316 in *Drought Resistance in Crops with Emphasis on Rice*. The International Rice Research Institute, Manila, Philippines.

Roy, N. N. and Murty, O. R. 1970. A selection procedure in wheat for stress environment. *Euphytica* **19**:509–521.

Rosielle, A. A. and Hamblin, J. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Sci.* **21**:943–946.

Srivastava, J. P., Jana, S., Gautam, P. L. and Niks, R. E. 1983. Parallel selection: an approach to increase yield and stability. Pages 725–733 in *Proceedings of the 6th International Wheat Genetics Symposium*, 1983. Plant Germplasm Institute, Faculty of Agriculture, Kyoto University, Kyoto, Japan.

Srivastava, J. P. and Winslow, M. D. 1981. Improving wheat and barley production in moisture-limiting areas. *Rachis* **4**(1):2–8.

Tahir, M., Muhammad, S. and Nachit, M. M. 1985. Cereal breeding for semiarid high-elevation areas of ICARDA region. Pages 647–656 in *Proceedings of the 6th International Wheat Genetics Symposium*, 1983. Plant Germplasm Institute, Faculty of Agriculture, Kyoto University, Kyoto, Japan.

DISCUSSION

A. Hadjichristodoulou

Did you observe any difference in the range of height of individual varieties in your top 5 per cent and bottom 5 per cent yielding varieties? And is there any association between range (or stability of height) and grain yield?

S. Ceccarelli

No, but this information will be given in the final paper.

S. C. Brown

My question is directed to you although I would really like to address it to all breeders. Nutrient as well as drought stress is very important for breeding for the dry areas, particularly in relation to root characteristics. Do you use fertilizer or nutrient availability levels similar to those farmers use at present, or are likely to use within the next few years?

S. Ceccarelli

We are currently evaluating parents, segregating populations, and advanced lines at fertilizer levels that are likely to be adopted by farmers in the near future.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

9

Biochemical and Physiological Response to Heat and Water Stress in Barley

A. M. STANCA,* M. ODOARDI,* P. MARTINIELLO,*
L. CATTIVELLI,† C. LORENZONI,† and N. MARMIROLI‡
**Istituto Sperimentale per la Cerealicoltura, Fiorenzuola d'Arda (PC), Italy; †Istituto di Botanica e Genetica Vegetale, Universita di Piacenza, Italy; and ‡Istituto di Genetica, Universita di Parma, Italy*

ABSTRACT

Evidence is presented of the production of stress proteins in response to high temperature and water stress in barley seedlings. A brief period at 37°C induced the production of heat shock proteins and increased the capacity of the seedlings to recover from exposure to higher temperatures (42–45°C). In particular, a 70 kD HSP was found. Novel proteins appeared after PEG induced water stress.

Laboratory physiological screening methods were also used for selection among genotypes. A lack of correlation among the response to physiological tests at different stages of growth led to the postulation that the genetic mechanisms of drought tolerance are independent and process-specific for each stage of barley development.

INTRODUCTION

Interest in crop response to environmental stresses has increased greatly in recent years because severe losses may result from heat, cold, drought, and high concentrations of toxic mineral elements (Lewis and Christiansen, 1981; Blum, 1985). Unfavourable temperatures and lack of water limit the expression of full genetic yield potential of the plant (Kramer, 1980).

Any reduction in crop yield depends upon the extent of stress and the stage of development of the crop during the stress. In fact, crop plants differ in their sensitivity to stress factors according to their stage of growth from germina-

tion to maturity. Several modifications in partitioning the dry matter to harvestable yield components have been reported (Hanson and Nelsen, 1980; Martiniello, 1984; Vaadia, 1985; Blum, 1986). An understanding of the mechanisms of stress and their genetic control would help in developing improved crop management and breeding techniques and therefore in increasing crop production in unfavourable environments.

This paper deals with the impact of induction of stress proteins on the acquisition of thermotolerance, and with the development of physiological methodologies for drought resistance screening in barley (*Hordeum vulgare* L.).

BARLEY RESPONSE TO HIGH TEMPERATURE

Heat stress inactivates some basic cellular processes and induces the synthesis of novel proteins (Mascarenhas, 1984). We are studying the regulation

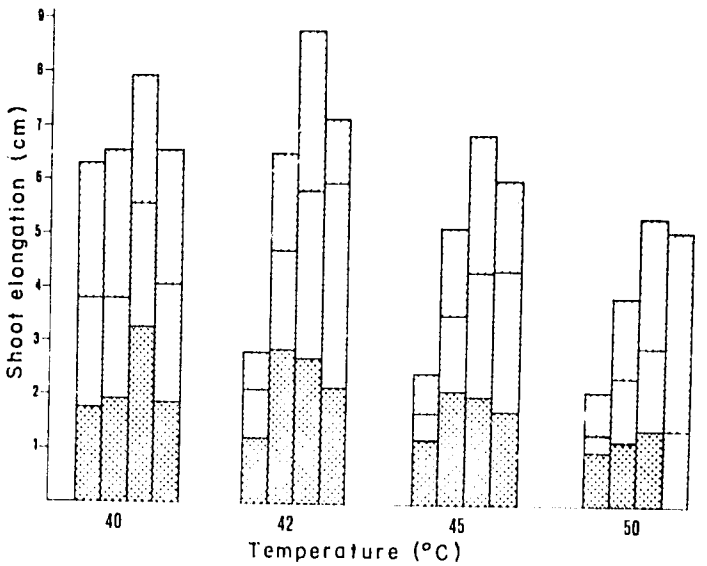


Figure 1. Acquisition of thermotolerance in barley seedlings following exposure to 37°C for various times. Duplicate samples of 50 seedlings, grown at 25°C, with protruding axis 1 cm long, were either directly exposed to 40, 42, 45, and 50°C for 2 h (first bar from the left in each group of four histograms) or preshocked at 37°C for 30 (second bar), 60 (third bar), and 120 min (fourth bar) before the shock at 40, 42, 45, and 50°C for 2 h. Shoot elongation was determined 24 (gridded), 48 (horizontal hatching), and 72 h (diagonal hatching) after the transfer of seedlings from the stress to the normal (25°C) growing temperature

mechanisms that give rise to the production of stress proteins and the role of these proteins in the acclimation of plants to high temperatures.

A brief period at a relatively high temperature (37°C) increases the capacity of barley seedlings (Figure 1) to recover from exposure to temperatures which otherwise inhibit the growth of the plant (42–45°C). This thermoprotection of seedlings is associated with the induction of heat shock proteins (HSPs). The production of HSPs starts at temperatures several degrees below those that completely inactivate general protein synthesis and growth of the plant (34–37°C).

Identification and isolation of specific heat shock genes was attempted through classical molecular genetic approaches. The SDS polyacrylamide electrophoresis demonstrated the appearance of six major HSPs with MW 22, 47, 70, 85, 94, and 100 kD (Marmiroli *et al.*, 1986). In particular, a 70 kD HSP similar to the animal 70 kD HSP was found by molecular hybridization between the mRNA from heat-shocked seedlings and a specific probe for the HSP of *Drosophila* and yeast, as well as immunoprecipitation with an antibody specifically reactive towards animal and plant 70 kD protein. Apparently, the induction of HSPs seems to provide protection for plant cells from heat-induced death or heat-induced inactivation of some basic cellular process.

Synthesis of individual proteins has also been followed in plants subjected to water stress under different experimental protocols: growth in the presence of osmotic solutions or with a limited supply of water. As in maize (Bewley *et al.*, 1983), the synthesis of some proteins increases and of some others decreases in barley seedlings maintained at high concentration of polyethylene glycol (PEG 6000), but a discrete set of novel proteins appears (Figure 2). It is possible that these induced proteins have a role in water stress resistance similar to that of HSPs in heat resistance.

PHYSIOLOGICAL SCREENING METHODOLOGY

Extensive work has been done in recent years on the genetic improvement of drought resistance in cereals using empirical screening techniques for selecting new cultivars for areas with limited soil moisture (Weltzien and Srivastava, 1981).

Our approach is based on the assumption that drought resistance can be enhanced, beyond the empirical approach, by using physiological tests for selection among genotypes. However, the success of this approach will require evidence that the characters tested in the laboratory reflect drought tolerance under field conditions also.

Three laboratory tests have been applied to 50 barley genotypes (cultivars and breeding materials): (1) seed germination in osmotic solution (GOS), (2) dry-matter increase in seedling (DW1–DW0) after a period of thermal stress

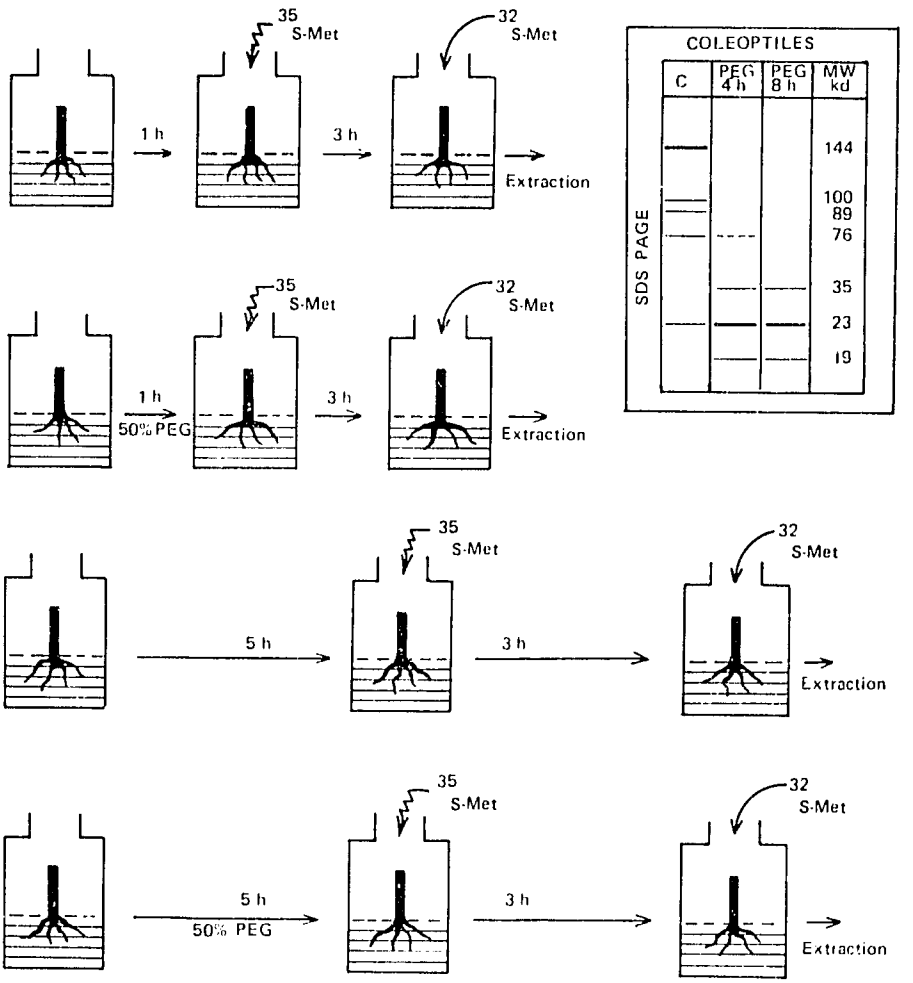


Figure 2. Diagram of the water stress experiment on barley seedlings. Treatments with and without 50% polyethylene glycol (PEG 6000) were applied for 4 and 8 h. Seedlings were labelled at 24°C in the presence of ^{35}S-methionine for 3 h. On the right: protein pattern after SDS-PAG electrophoresis of excised coleoptile extracts following water stress. C = control without stress; 4 h osmotic stress, 8 h osmotic stress. Molecular weight (MW) determined with MW markers run on the same gel

carried out in greenhouse, and (3) evaluation of the stability of the cellular membrane in the presence of osmotic stress applied at flowering time (LEOS).

The physiological tests gave the opportunity to identify variability among genotypes. A group of 16 genotypes (Table 1) was selected and evaluated in the laboratory and in field trials at three locations in southern Italy where

Table 1. Grain yield and physiological test responses (GOS = germination under osmotic solution; $DW_1 - DW_0$ = seedling dry-matter increase after thermal stress; LEOS = loss of electrolytes under osmotic stress) of some barley genotypes (d = two-row; P = six-row)

Genotype	Ear type	Grain yield (kg/ha)	GOS (%)	$DW_1 - DW_0$ ($g \times 10^{-2}$/plant)	LEOS (%)
Georgie	D	5170	30.7	20.7	54.3
Gitane	D	4630	54.7	14.0	69.4
Igri	D	4680	6.4	24.5	63.4
Panda	D	4370	1.8	12.9	67.2
Pepite	D	3430	8.3	15.0	78.8
Arda	D	4580	2.7	18.3	49.0
Alpha	D	4180	29.3	13.2	67.7
Porthos	D	4770	36.1	15.0	55.1
Tipper	D	4460	14.7	18.6	73.0
Arma	P	3740	1.3	9.5	75.6
Fior 26	P	4120	2.1	8.5	69.9
Robur	P	4040	0.7	6.7	75.5
Pirate	P	4330	0.1	25.4	68.5
Vetulio	P	3690	3.0	8.6	69.6
Barberousse	P	4600	2.4	19.9	75.5
Jaidor	P	4050	2.4	17.6	77.8
LSD (0.05)		3.3	6.9	3.1	5.7

conditions of drought are frequent (Cagliari, Catania, and Foggia). The highest value for correlation between grain yield and physiological test response (Table 2) was found with electrolyte leakage (LEOS), suggesting that this test was a good indicator of drought-tolerant lines. The average grain yield of the genotypes with high scores in the physiological tests was 15 per cent higher than the mean yield of the discarded ones (4590 kg/ha versus 3940 kg/ha). Of these genotypes, only Georgie showed good drought tolerance at three stages of development. Other genotypes showed different responses at different stages. Tipper seemed to be highly resistant at the early

Table 2. Correlations among grain yield and physiological tests in barley

Yield	GOS	$DW_1 - DW_0$	LEOS
	0.48*	0.56†	−0.69†

*$P < 0.05$.
†$P < 0.01$.

Table 3. Barley genotypes with high test values

Cultivar	GOS	Cultivar	$DW_1 - DW_0$	Cultivar	LEOS
Gitane*	54.7	Igri†	24.5	Arda†	49.0
Porthos†	36.1	Georgie‡	20.4	Georgie‡	54.3
Georgie‡	30.7	Tipper†	18.6	Porthos†	55.1
Alpha†	29.3	Arda†	18.3	Igri†	63.4
Tipper†	14.7	Barberousse*	19.9	Panda*	67.2

*Genotypes with a positive value in one test.
†Genotypes with a positive value in two tests.
‡Genotypes with a positive value in three tests.

stage of growth, while Arda and Igri were tolerant from tillering to maturity (Table 3). All these materials, except Barberousse, are two-row types and within the two-row cultivars both spring and winter types exhibited tolerance. This means that the two-row materials could be utilized for developing winter or spring cultivars with a good chance of adaptation for extremes of environment.

These results indicate that genetic variability for drought tolerance can be identified by physiological laboratory tests applied at different stages of growth (seed, seedling, and adult plant). These data, however, do not give any information about the physiological mechanisms that underlie the correlations between stress tolerance in field conditions and the performance in the laboratory tests. It appears that the genotypes showing positive reactions to laboratory tests possess some genetic mechanisms for recovering their normal growth rate after the stress.

The lack of correlation (Table 4) among the responses to physiological tests at different stages of growth indicates that the genetic mechanisms of drought tolerance are independent and process-specific for each stage of development (Sullivan and Ross, 1979; Levitt, 1980; Trapani and Motto, 1984; Martiniello and Lorenzoni, 1985).

The genotypes that gave positive response to these tests have been introduced in breeding programmes for drought tolerance based on the development of synthetic populations through the recurrent selection method. The objective is to increase the frequency of favourable genes and to maintain in

Table 4. Correlations among physiological tests in barley

	GOS	$DW_1 - DW_0$
$DW_1 - DW_0$	0.05 ns	—
LEOS	−0.32 ns	−0.38*

*$P < 0.05$.

the population a large amount of genetic variability by cyclic selection. From these improved populations advanced breeding material can be extracted: (1) parents for further cycles of recurrent selection, (2) new varieties, and (3) lines as parents for developing F_1 commercial hybrids.

ACKNOWLEDGEMENT

Research work for this paper was supported in part by the Italian Ministry of Agriculture, Progetto 'Cereali: Subprogetto Orzo', and in part by CNR-Italy, Special Grant IPRA subproject 1, paper 1011.

REFERENCES

Bewley, J. D., Larsen, K. M. and Papp, J. E. T. 1983. Water-stress-induced changes in the pattern of protein synthesis in maize seedling mesocotyls: a comparison with the effects of heat shock. *J. Exp. Bot.* **34**:1126–1133.

Blum, A. 1985. Breeding crop varieties for stress environments. *CRC Review in Plant Science* **2**:199–238.

Blum, A. 1986. The effect of heat stress on wheat leaf and ear photosynthesis. *J. Exp. Bot.* **37**:111–118.

Hanson, A. D. and Nelsen, C. E. 1980. Water: adaptation of brops to drought-prone environments. Pages 77–152 in *The Biology of Crop Productivity* (Carlson, P. S., ed.). Academic Press, New York.

Kramer, P. J. 1980. Drought, stress, and the origin of adaptations. Pages 7–20 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, N. C. and Kramer, P. J., eds.). John Wiley, New York.

Levitt, J. 1980. *Responses of plants to environmental stress*, 2nd edition. Academic Press, New York.

Lewis, C. F. and Christiansen, M. N. 1981. Breeding plants for stress environments. Pages 151–178 in *Plant Breeding* (Frey, K. J., ed.), Vol. II. The Iowa State University Press, Ames.

Marmiroli, N., Restivo, F. M., Odoardi Stanca, M., Terzi, V., Tassi, F. and Lorenzoni, C. 1986. Induction of heat shock proteins and acquisition of thermotolerance in barley seedlings (*Hordeum vulgare* L.). *Genet. Agrar.* **40**:9–25.

Martiniello, P. 1984. Drought resistance in maize: methods of detection and breeding considerations. *Genet. Agrar.* **38**: 267–307.

Martiniello, P. and Lorenzoni, C. 1985. Response of maize genotypes to drought tolerance tests. *Maydica* **30**:353–361.

Mascarenhas, J. P. 1984. Molecular mechanisms of heat stress tolerance. Pages 391–423 in *Application of Genetic Engineering to Crop Improvement* (Collins, G. B. and Petolina, J. G., eds.). Martinus Nijhoff and Dr W. Junk, Dordrecht, The Netherlands.

Sullivan, C. Y. and Ross, W. M. 1979. Selecting grain sorghum for drought and heat resistance. Pages 263–281 in *Stress Physiology in Crop Plants* (Massel, H. and Staples, R. C., eds.). John Wiley, New York.

Trapani, N. and Motto, M. 1984. Combining ability for drought tolerance tests in maize populations. *Maydica* **29**:325–334.

Vaadia, Y. 1985. The impact of plant stress on crop yields. Pages 13–40 in *Cellular and Molecular Biology of Plant Stress* (Key, J. L. and Kosuge, T., eds.). Alan R. Liss, New York.

Weltzien, H. C. and Srivastava, J. P. 1981. Stress factors and barley productivity and their implications in breeding strategies. Pages 351–361 in *Barley Genetics*, Vol. IV. Editorial Subcommittee, 4th International Barley Genetics Symposium, Edinburgh.

DISCUSSION

D. W. Lawlor

(1) Are you selecting plants for drought resistance on the basis of absence of damage to membranes?

(2) Would you select for drought resistance based on higher or lower level of production of heat shock proteins?

(3) Do you also find low molecular weight HSPs as well as 70 kD?

A. M. Stanca

(1) Yes.

(2) We don't know yet.

(3) Yes, 22 and 47 kD HSPs.

M. Nachit

How different is the production of heat shock proteins in the tropical crops (maize and sorghum) in comparison to that in the temperate crops (wheat and barley)?

A. M. Stanca

Synthesis of HSPs has been noted to accompany thermal shock in maize seedings. A 70 kD HSP has been found in maize and barley. The other HSPs found in barley were similar but not totally identical to the HSPs of maize. Another similarity between maize and barley was the continuous synthesis of several normal proteins in addition to the HSPs at temperatures between 34 and 40°C.

R. A. Richards

If the characteristics you discussed are so closely correlated with yield then why is it that they are still maintained in populations grown in dry areas? Why hasn't natural selection reduced their frequency?

A. M. Stanca

Populations selected in dry areas have some mechanism to protect the cellular membranes. We found a negative correlation between grain yield and percentage of damaged membranes in stressed environments.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

10

An Attempt to Define a New Plant Ideotype of Bread Wheat for Mediterranean Conditions Based on Physiological Studies

B. BORGHI, M. CATTANEO, M. CORBELLINI, and M. PERENZIN
Experimental Institute for Cereal Research, 20079 S. Angelo Lodigiano, Milan, Italy

ABSTRACT

We summarize results obtained for five years on the identification of the environmental and genetical factors limiting the productivity of bread wheat in Italy. The cultivated Italian varieties did not seem to fully exploit the favourable growing conditions induced with modern agricultural practices. The new plant ideotype proposed should have a longer grain-filling period associated with higher values of leaf area duration (LAD), and higher rates of carbon and nitrogen remobilization towards the kernel. We illustrate new selection criteria based on physiological traits and the use of recurrent selection.

The history of wheat cultivation in Italy is similar to that of several other countries but the evolution towards a modern agriculture took place at the beginning of this century.

Several factors of both genetic and agronomic origin were responsible for the very low yields of the Italian wheats. The cultivated varieties, very old local populations, appeared too tall, late in ripening, and highly susceptible to lodging and rust attacks. In the 1930s, after the pioneer work of Strampelli, new semi-dwarf varieties which were also early enough to escape the late rust attacks became available.

The present Italian bread wheat varieties originate from breeding activity

carried out during this century, with not less than five generations of varieties characterized by increasing productivity. This justifies the wide use of Italian germplasm in breeding programmes in several East European and South American countries (Vallega, 1974).

The continuous intercrossing among Italian varieties produced in the 1970s a group of genetically related high-yielding varieties. During the last 10 years the Italian breeders have been mainly concerned with the genetical improvement of bread-making quality. The new varieties possess a better bread-making quality but are not superior to the older ones in productivity. In our opinion a further improvement in yield requires new breeding strategies that consider biochemical and morphophysiological traits to assure high yield combined with an acceptable bread-making quality.

Studies based on growth analysis carried out in recent years show that the traditional Italian varieties appear to be 'programmed' for a fast filling of the grain—in less than 4 weeks after flowering they reach the maximum seed weight. This characteristic, in our environmental conditions, is very important because in May–June we can frequently observe a progressive reduction of the water available in the soil together with a rise in temperatures. These conditions accelerate the final process of ripening and such acceleration is better tolerated by the early ripening varieties.

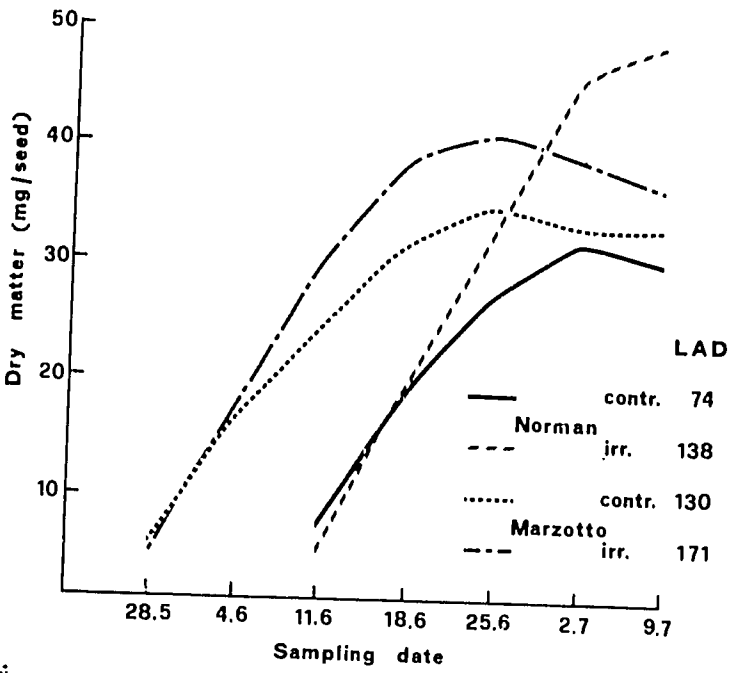


Figure 1. Kinetics of dry-matter accumulation in the grain of the typical Italian variety Marzotto and of the English variety Norman

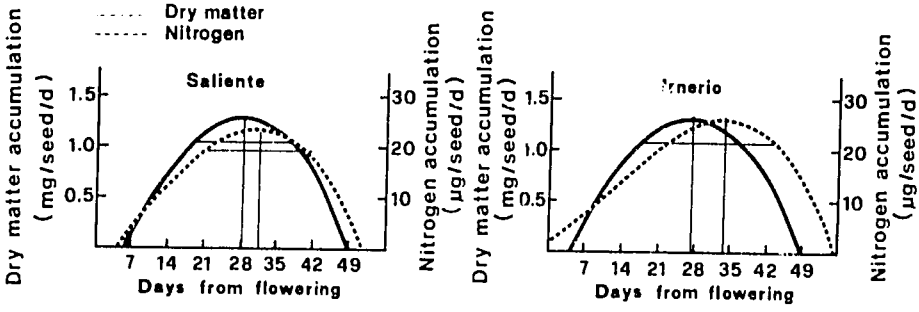


Figure 2. Relative growth rates of dry matter and nitrogen in the kernel. The values represent the mean of three locations. (From Corbellini and Borghi, 1985)

The traditional plant model, essentially based on stress avoidance, however, presents several limitations in a modern agriculture. In fact, the Italian varieties seem unable to exploit fully the favourable environmental conditions introduced with the new agronomical practices such as irrigation, late N application, chemical control of foliar diseases, or conditions occurring naturally (low temperatures, rains) at the end of the life cycle (Borghi *et al.*, 1982, 1983). Figure 1 shows the kinetics of dry-matter (DM) accumulation in the grain of the typical Italian variety Marzotto and of the English variety Norman. Irrigation after flowering remarkably increased the leaf area duration (LAD) in both varieties but kernel size increased steadily only in the English variety.

Remarkable differences in the patterns of dry-matter accumulation into grain are also evident between the Italian varieties Irnerio and Saliente (Corbellini and Borghi, 1985). Irnerio accumulates grain proteins later than Saliente (Figure 2). The green area in Irnerio remains functional for a longer time, as demonstrated by the length of the interval between heading and complete desiccation, which is 2–3 days more than in Saliente. This particular behaviour of Irnerio can explain why, in recent years, this variety has become a leading one in Italy; it also explains, however, why its protein content is generally lower than that of other varieties. It is in fact likely that

Table 1. Biological characteristics of two varieties (mean values of three locations)

Varieties	Plant height (cm)	Biological yield (kg/ha)	HI	NHI	Dry matter in vegetative organs (g/m^2)	
					Maximum	Translocated
Irnerio	74	9320	0.41	0.69	713	210
Saliente	87	10050	0.43	0.72	765	232

Table 2. Effect of plant desiccation at different times from flowering on the varieties Irnerio (I) and Saliente (S)

Treatments	LAD*		Kernel weight*		Compensation†	
	I	S	I	S	I	S
Control	100	100	100	100	9.5	8.4
29 days	98.3	99.9	94.6	91.3	−0.3	7.5
24 days	90.6	92.3	77.4	77.4	3.1	14.1
17 days	84.7	83.9	65.6	63.7	11.9	14.7
$\bar{x}$ treatments	91.2	92.0	79.2	77.5	4.9	11.2
	ns		ns		†	

*In per cent of the control.
†Increase in kernel weight in degrained spikes relative to intact spikes.
‡$P < 0.01$.
ns = not significant.

drought and/or heat stresses, which frequently occur in the final period of grain filling and which do not greatly affect yield, prevent the migration of nitrogen compounds from the green organs towards the kernel.

In contrast to Irnerio, Saliente shows a higher biological yield, associated with high HI and NHI, a better capacity to store dry matter in the vegetative organs after flowering, and to relocate it into grain (Table 1). This can be better seen from the behaviour of these two varieties under stress conditions. Stress was induced with a chemical desiccant applied at different periods after flowering. Using the method suggested by Blum *et al.* (1983), we evaluated the capacity of the plants to sustain kernel growth after the destruction of photosynthetic organs. Saliente showed a greater ability to sustain grain filling under stress conditions (Table 2). On the average of more than a hundred trials, however, Saliente yielded only 0.6 per cent more than Irnerio, but in nearly all locations it showed a higher protein content.

Table 3. Effect of leaf removal on yield components and protein content. (From Borghi *et al.*, 1985)

Treatments	Seeds/ spikelet	Kernel weight (mg)	Grain yield/ spike (g)	Protein content (%)
Control	2.9	41.8	2.44	16.5
Only flag leaf	2.9	39.8	2.35	13.8
Flag leaf removed	3.0	41.8	2.49	12.9
No leaves	2.5	35.3	1.74	11.1
LSD (0.05)	0.36	4.74	0.48	2.0

Table 4. Effect of spike degraining on yield components and protein content. (From Borghi *et al.*, 1985)

Treatments	Seeds/ spikelet	Kernel weight (mg)	Protein content (%)
T1 Control	2.9	41.8	16.48
T3 One spikelet out of two	2.7	41.1	20.07
T4 Two lateral flowers/spikelet	1.9	45.5	16.62
T5 Lateral flowers removed	1.8	30.5	20.80
T6 Top half of the spike removed	3.3	44.2	19.86
T7 T3 + T4	1.9	42.9	21.48
T8 Two spikelets/spike	3.2	38.9	19.00
LSD (0.05)	0.45	3.2	2.17

Other studies on carbon and nitrogen partitioning within the plant using the traditional method of sink and source manipulation (Borghi *et al.*, 1985) have shown that, in Italian conditions, the green surface of the wheat plant is generally sufficient to supply the amount of photosynthates necessary for a complete development of grains (Table 3). On the contrary, in the presence of a sink/source ratio which has been artificially shifted in favour of the source, starch accumulation, considering the number of endosperm cells, cell expansion, number of amyloplasts (Brocklehurst, 1979), is hampered significantly by physical constraints, while the seed apparently did not either oppose any resistance or play any major role in accepting differential levels of all the nitrogen potentially translocatable into grains (Table 4). It must be emphasized that the GPC increase was mostly a consequence of the stimulated synthesis of gliadin and glutelin fractions while NPN and water-soluble proteins increased less (Table 5). The question is how these observations can be exploited in a breeding programme.

A possible answer could be: producing F_1 hybrids. The recent discovery of very effective chemical hybridizing agents (CHA) has opened new pos-

Table 5. Increase (%) of the different nitrogen solubility classes and of total protein in degrained spikes. The values refer to the single kernel and are the average of 2 years. (From Borghi *et al.*, 1985)

Varieties	NPN	Alb + Glob	Gliad	Glut	Res	Tot Prot
Demar 4	47.1	38.4	127.5	80.7	56.2	72.4
Fiorello	33.7	27.0	56.2	62.7	43.7	47.4
Mec	70.1	35.0	82.7	57.5	49.2	56.1
Mean	50.3	33.5	88.8	67.0	49.7	58.6

Table 6. Productivity of the commercial hybrid HO1 (Festin × Frandoc) in comparison with the best variety within each location

Locations	Grain yield (kg/ha)		Variety name
	Hybrid HO1	Best variety	
1	7980	7780	Demar 4
2	9970	8730	Irnerio
3	10610	9070	Tommaso
4	8100	7610	Aurelio
5	6340	6180	Chiarano
6	5440	5340	Loreto
7	5160	4200	Aurelio
8	9940	9320	Chiarano
9	7230	7050	Saliente
10	3250	3760	Orso
11	5530	5450	Pandas
12	5220	5950	Pandas
13	5710	6280	Chiarano
14	5750	4780	Irnerio
15	6940	7670	Salvia
16	9660	9050	Leopardo
Mean	7050	6760	

sibilities for raising yield. At present it is very difficult to foresee the future role of wheat hybrids. However, preliminary trials carried out at several locations show that the first commercial hybrid available on the market can successfully compete, within each location, with the best traditional varieties (Table 6). The pattern of grain filling and the evolution of green area in the first experimental hybrids produced in Italy showed that the hybrids and higher values of LAI and LAD associated with higher HI, a higher rate of dry-matter accumulation, and longer duration of the grain-filling period than in parental lines (Figure 3). In other words, the best hybrids seem to present all the desired physiological traits that one could expect in a wheat plant.

Apart from the new way opened by the possibility of producing hybrids, an important conviction has grown among the wheat breeders: the negative correlation generally found between grain yield and protein content could be overcome by selecting for a higher biomass associated with 'efficiency of remobilization', a trait which positively affects both grain yield and protein content (Corbellini and Borghi, 1985). The first goal in the conditions of Southern Europe, where bread wheat is grown under an intensive crop system, should be achieved, however, without increasing plant height.

It is necessary to determine how to measure these characters through

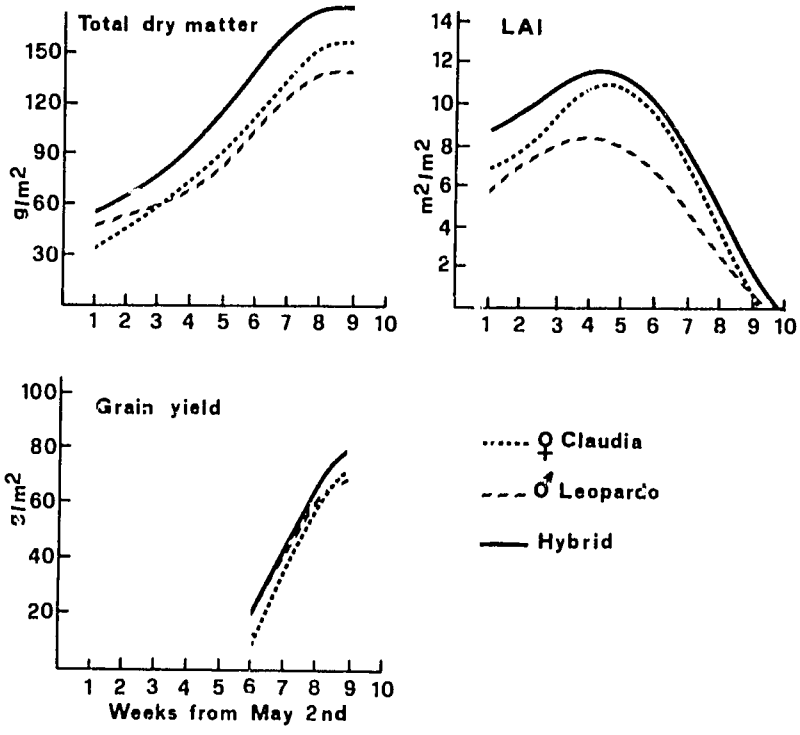


Figure 3. Growth analysis of the varieties Claudia and Leopardo and of their hybrid

simple morphological or physiological traits that can be taken into account during the early stages of selection.

The traditional evaluation of GPC alone does not allow one to distinguish superior lines from those producing a high GPC simply because of their low seed number or their rapid senescence, which generally affects starch storage more adversely than protein accumulation. On the other hand, the early direct evaluation of GY is time consuming and scarcely correlated with the potential yield of most advanced lines. Stem weight loss from flowering to ripening is a relatively easy character to measure; however, according to Hunt (1979) the decrease in stem weight from flowering to harvesting is only weakly related to ear weight.

We suggest selecting for stem and leaf thickness and to increase the storage capacity of the last internode by introducing the character 'solid stem', a typical trait of durum wheat but also found in some old bread wheat varieties. Another important trait to select for is the duration of effective grain filling. Under the environmental conditions of Southern Europe, the duration of grain filling more than the rate of N or dry-matter accumulation is defective in

the presently cultivated genotypes; on the contrary, as previously mentioned, they already have high rates of accumulation because, in order to escape from late rust attacks, they were selected for early maturation (Borghi *et al.*, 1985).

Therefore, we propose to include, along with such traits as plant height, spike size, leaf erectness, and resistance to diseases, the visual selection for thicker and/or solid stem, for a moderate earliness associated with a late desiccation of green parts. After harvesting, the selected plants or lines could be further screened for plump seed, for GPC, and, eventually, for HI and NHI.

To incorporate in one genotype all the positive morphophysiological characteristics by the traditional pedigree method is a very hard task. The time has come for the wheat breeder to pay more attention to the possibility of applying recurrent selection.

The recent availability of effective chemical hybridizing agents and the derived possibility of increasing genetical recombination and selection pressure will greatly enhance the possibility of combining, after one or two cycles of random mating, all the desired characteristics in a single gene pool.

REFERENCES

Blum, A., Poiarkova, H., Golan, G. and Mayer, J. 1983. Chemical desiccation of wheat plants as a simulator of postanthesis stress. I. Effect on translocation and kernel growth. *Field Crops Res.* 6:51–58.

Borghi, B., Monotti, M., Guiducci, M., Pierotti, F., Boggini, G. and Corbellini, M. 1982. Environmental and genetical effects on plant growth, grain filling and productivity in bread wheat. In *Limites de Potentialité de Production du Blé dans Différents Systèmes de Culture et dans Différentes Zones Mediterranéennes*, 30 September and 1–2 October 1981, Bari. pp. 9–26.

Borghi, B., Corbellini, M., Boggini, G. and Pogna, N. E. 1983. Kinetics of dry matter accumulation and composition changes in developing bread wheat kernel. *Z. Acker- und Pflanzenbau* **152**:224–237.

Borghi, B., Corbellini, M., Cattaneo, M., Fornasari, M. E. and Zucchelli, L. 1985. Modification of the sink/source relationships in bread wheat and its influence on grain protein content. In press.

Brocklehurst, P. A. 1979. Control of grain morphogenesis in wheat and its relation to grain yield. Pages 41–44 in *Crop Physiology and Cereal Breeding* (Spiertz and Kramer, eds.). Wageningen.

Corbellini, M. and Borghi, B. 1985. Accumulation and remobilization of dry matter and protein in four bread wheat varieties. *Z. Acker- und Pflanzenbau* **155**:1–11.

Hunt, L. A. 1979. Stem weight changes during grain filling in wheat from diverse sources. Pages 923–929 in *Proceedings of the 5th International Wheat Genetics Symposium*, IARI, New Delhi.

Vallega, J. 1974. Wheat improvement. Historical perspective of wheat breeding in Italy. *Proceedings of the 4th FAO/Rockefeller Foundation Wheat Seminar*, 21 May–2 June 1973, Tehran, Iran.

DISCUSSION

D. R. Marshall

You indicated that spring frost was a major constraint in your attempts to increase the length of the grain-filling period. Have you attempted to breed for frost resistance? If not, why not?

B. Borghi

In spite of the serious efforts by breeders to improve earliness, no successful variety which is 5 days earlier than S. Pastore has been obtained in South European countries in the last 20 years. Probably a reasonable amount of time is required for spike differentiation. I also believe that the period from flowering to harvesting could be extended by selecting genotypes for this character.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

11

Physiology and the Breeding of Winter-grown Cereals for Dry Areas

R. A. RICHARDS
Division of Plant Industry, CSIRO, PO Box 1600, Canberra City, ACT 2601, Australia

ABSTRACT

The breeding of higher-yielding wheats for dry areas has been little influenced by physiology in the past. This paper discusses how physiological processes and traits that affect them may be modified by breeding and hence increase yields in the future. We make reference to different rainfed environments and discuss the following physiological processes and ways to improve them: (1) crop transpiration, by improving water extraction and decreasing surface water evaporation; (2) water-use efficiency, by increasing glaucousness, the amount of discrimination of the stable isotope ^{13}C during the fixation of CO_2, improving cool temperature vigour, and altering root/shoot partitioning; and (3) harvest index, by increasing hydraulic resistance in the seminal roots and by modifying leaf area development using determinate tillering genotypes. Our breeding programme aims to increase yields in dry areas by improving each of the above processes. Results from this programme are discussed, as are ways to validate the worth of specific traits and ways to incorporate traits into existing breeding programmes.

INTRODUCTION

There are abundant suggestions in the literature of physiological and morphological characteristics that, if selected, may improve yields under drought. It is surprising that traits suggested to improve yield under drought are more numerous than those proposed to improve yields in the absence of drought. This apparent imbalance may be for a variety of reasons, the more important being an intrigue with drought and the need to stabilize seasonal yield

variations and reduce the calamity that drought is to individual farmers and nations.

The aim of plant breeders in semi-arid regions is to increase yields under drought and hence reduce the difference in yield achieved in good and bad years. They are impressed by the extent of variation in their populations and are confident they can manipulate that variation if a particular trait is known to be advantageous under drought. Breeders may therefore be tempted to select for traits suggested in the literature, particularly as there is a tendency to believe that certain touchstones may exist that will give rapid yield advances. However, it is very difficult for the breeder to decide which characteristics to select. As the intensity and timing of drought varies with region and season it is not uncommon for disagreement to arise among physiologists as to the value of a particular trait. Also, since drought affects many traits simultaneously, changing one may have an unexpected effect elsewhere on the plant so that again there may not be agreement as to which traits are likely to improve yield. It is not unexpected, therefore, that plant breeders have become a little cynical of how physiology can contribute to crop improvement under drought and they may be reluctant to risk adding another trait to select for in their breeding programme, particularly as empirical breeding methods continue to make advances in yield.

The purpose of this paper is to discuss traits we have chosen in our breeding programme that we think have good prospects of improving the yield of winter-grown cereals. I shall also discuss factors important in the choice of traits and the evaluation of their worth.

A FRAMEWORK IN WHICH TO CONSIDER YIELD WHEN WATER IS LIMITED

To choose traits likely to increase yield under drought, we rely very much on a very simple model first proposed by Passioura (1977) and discussed by Fischer and Turner (1978), Richards (1982), and Passioura (1983). This model is applicable to any water-limited crop. In its simplest form it states that

$$\text{Above-ground dry matter (AGDM)} = T \times \text{WUE}$$

where T is the amount of water transpired by the crop and WUE is the efficiency in which this water is used. If the crop produces grain and this has the same value as straw, as it does in many parts of the West Asia and North Africa region that we are considering at this meeting, then these two components are all we need to consider. However, if grain is the economic product then a partitioning component is introduced into the model. It then becomes

$$\text{Grain yield} = T \times \text{WUE} \times \text{HI}$$

where HI, the harvest index, is the ratio of grain to AGDM. When considering ways to increase yield by breeding this model is useful for two reasons. First, the components are largely independent of each other. Thus, if one component is increased by breeding little change should occur in the other components and grain yield should increase. Examples where this may not be the case will be alluded to later. The second reason this model is useful is because it focuses directly on the processes that affect productivity in dry environments. Indiscriminant recommendation of selection criteria is therefore avoided.

Environmental considerations

Before discussing individual traits, it is stressed that each must be considered in relation to the rainfall pattern in the region, the approximate water balance, the soils, and the optimum crop phenology. To not do so may lead to failure.

Traits will be considered in relation to three typical rainfall patterns. These encompass the possible range in seasonal precipitation (Figure 1). Type A is a Mediterranean pattern typical of the West Asia, North Africa region. Here fallowing is ineffective, most of the rain falls in winter before the crop has reached full ground cover, and drought is common from around the time of anthesis through to maturity. The other rainfall patterns are represented by B, where the crop relies on summer rainfall and hence on water stored in the soil from a previous fallow, and C, where rain may occur at any time of the year. Although there is some unpredictability in all patterns, particularly in the amount of rainfall, type C is the most unpredictable as there is no certainty of rain at any time. Fallowing therefore may or may not be effective in C.

Within these rainfall patterns I will assume that cereals are sown just before the winter depression in temperature and that flowering and grain filling occur

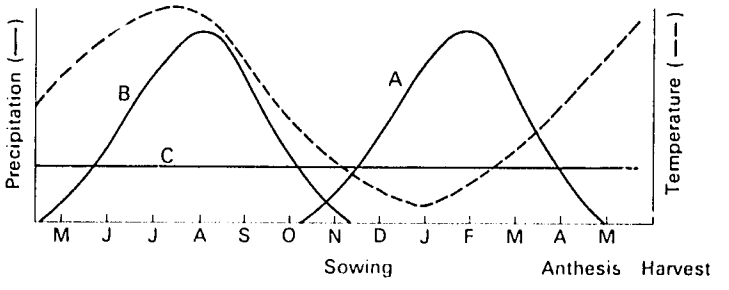


Figure 1. Representation of three rainfall patterns in relation to temperature and crop phenology that encompass the range of environments where wheat is grown in winter

in spring when evaporation is rapidly increasing. In each of these rainfall patterns I consider seedling drought to be unimportant relative to drought later in the season. Terminal drought is almost inevitable as potential evapotranspiration exceeds actual evapotranspiration.

In the absence of nutrient deficiencies, limitations other than drought to crop growth and yield of winter cereals may be waterlogging and cold temperature in winter, frost during reproductive growth, and high temperature during spring. In a particular region, or season, any of these factors may have a greater effect on yield than drought. Thus, if the risk of any of these is reduced by an improvement in crop management or breeding then yields may increase more than if there were an improvement in a genotype's drought resistance.

Breeding considerations

In the traits to be discussed, their choice was guided not only by their likely influence on yield when water is limited but also by the range of genetic variation in the character, whether its measurement is repeatable, and whether it can be selected for easily and quickly. It is assumed that the breeder has the capacity to add another trait to the already extensive range that is required in the selection and release of a new variety. With the above considerations in mind, the use of this model in our wheat-breeding programme will be discussed.

CROP TRANSPIRATION

Ignoring drainage, runon and runoff, the supply of water to the crop depends on the amount of water stored in the soil at sowing plus precipitation during the season. Soil water is depleted by evaporation from the soil surface and extraction by roots for transpiration. There are two ways where breeding may increase the total amount of water used by the crop. One is to increase the depth of rooting to increase the total water extracted from the soil. The other is to increase the relative proportion of water transpired to water evaporated from the soil surface.

Increasing soil water extraction

In many regions, the ICARDA region included, careful studies have shown that cereal crops extract all the available soil water by maturity. An increased rooting depth achieved by breeding is unlikely to be effective in these situations. However, in some areas water remains in the soil at maturity. Usually this water is below the root zone, as in some parts of India where crops grow on water stored deep in the soil following the monsoon season and

as in some areas of Australia (see, for example, Passioura, 1983). Here selection for a greater rooting depth should have a very high priority in a breeding programme as it has a good chance of increasing grain yield. Unfortunately this is very difficult so that indirect techniques are required. Turner and Nicolas (this volume) discuss one such technique that measures differences in canopy temperatures.

Increased osmoregulation may be another way of increasing soil water extraction. Morgan and Condon (1986) found that among wheat lines differing in osmoregulation, lines with high osmoregulation extracted 40 per cent more water than low lines at soil depths between 40 and 140 cm. It has also been found that wheats with high osmoregulation have an increased tiller survival and kernel number per tiller than low lines (Morgan 1983); this was attributed to the maintenance of turgor in the flag leaf at about the time of meiosis. A pilot breeding programme has been initiated at Tamworth, Australia, to screen lines derived from a bread wheat and a durum wheat breeding programme for osmoregulation. Screening is being done in the glasshouse on the flag leaf and lines are being evaluated for yield in field plots. Results show that lines with high osmoregulation yield better than low lines at all yield levels (J. M. Morgan, personal communication).

Decreasing surface water evaporation

Reducing surface water evaporation (E) relative to transpired water (T) by genetic means is a second promising way that may increase the total amount of water transpired and hence grain yield. E is unlikely to be substantial in crops growing on stored soil water (type B in Figure 1); however, when there is rain during the season before canopy closure (as in A and C of Figure 1) it is large. Estimates of E as a proportion of evapotranspiration (ET) in crops in Syria ranged from a minimum of 32 per cent in a fertilized wheat crop where ET was 370 mm to 62 per cent in an unfertilized barley crop where ET was 220 mm (Cooper *et al.*, 1983). These surprisingly high estimates are not uncommon. In South Australia, French and Schultz (1984) found in a study conducted over 12 years with 61 sites that an average of one-third of ET was lost by evaporation from the soil surface. This represents a considerable loss in yield.

Although some water loss from the soil surface is inevitable, a reduction should be possible. There is considerable genetic variation among winter-grown cereals in leaf area display that may increase the rate at which full ground cover is achieved, and this may reduce E. The most notable variation is in early vegetative growth habit. Some genotypes are very prostrate, others have long floppy leaves, yet others are very erect; some genotypes are more vigorous, i.e. have a higher relative leaf expansion rate (RLER) or relative growth rate (RGR), and reach canopy closure earlier. A simple calculation to

determine the effect of a small improvement in RGR, i.e. during the exponential phase of growth, is very instructive. Assume that genotype X has a 5 per cent higher RGR than genotype Y (0.105 g/g/day against 0.100 g/g/day). This would result in X having 50 per cent more dry matter than Y at the end of 100 days of exponential growth.

We have selected lines visually that differ in growth habit and also lines that differ in early vigour by measuring AGDM at about the five-leaf stage. These traits appear to be highly heritable so that it may not be difficult to develop contrasting lines to grow in the field to evaluate their importance.

A different approach to this same problem is to select plants with a greater capacity to intercept water and channel it down the leaves and stem to the ground, hence increasing the store of water immediately below the plant rather than between the rows where it would otherwise be evaporated. This is an interesting idea that may be feasible using genotypes with erect leaves and a rigid midrib.

Ways to reduce E discussed above are based on genetic manipulation. It should not be overlooked that E may also be altered by crop management such as smaller row spacing or nitrogen fertilizer at sowing, and these should also be explored.

WATER-USE EFFICIENCY

Water-use efficiency (WUE), defined as the amount of above-ground dry matter per unit of water transpired, has been considered invariant. Thus, Tanner and Sinclair (1983), in a review of WUE in crop production, considered it unlikely that WUE could be altered genetically. Rather they considered that increasing the efficiency of water use by increasing T relative to E, as discussed above, or improving the ratio of grain to ET by increasing the harvest index may be the only way to achieve increased yields when water is limited. Evidence from field-grown plants supports this notion. I am not aware of any experiments which have shown that increased grain yields in water-limited areas, achieved by breeding, have come from an improved WUE. But then few, if any, experiments have partitioned ET in studies comparing old and recently bred cultivars. However, if increased yields have resulted from an improved WUE, then recently bred genotypes should have been found with a higher AGDM than older genotypes. In the numerous studies where this has been examined it is only wheats selected for high yield under irrigation in Mexico (Waddington *et al.*, 1986) and spring barleys selected specifically for a high biomass in England (Hanson *et al.*, 1985) that an increased AGDM has been found. In our experiments where we have measured above-ground biomass in the field and WUE in large soil containers in the glasshouse, we have not found consistent differences between old and new varieties of cultivated wheats. However, in the glasshouse experiments we did find cultivated wheats had a higher WUE than their diploid and

tetraploid ancestors. This apparent lack of improvement in the WUE among cultivated wheats through breeding is worrying.

Despite the above discussion, sustained attempts to improve WUE are required as any increase may have far-reaching effects in dry environments. There are numerous traits that could conceivably increase WUE, if selected. They can be separated into simple morphological traits that are easily manipulatable, such as awns, pubescence and glaucousness, more complexely inherited traits such as carbon isotope discrimination, specific leaf weight and abscisic acid, and finally traits that on the surface appear unrelated to WUE such as cool temperature, vigour, and dry-matter partitioning to roots. Instead of discussing each of these characters briefly, a few only have been chosen where recent data suggest a significant effect on WUE.

Glaucousness

This refers to the bluish-white bloom of wax on photosynthetic surfaces formed from about the time of flag leaf emergence. Although several major wax inhibitor genes are present in wheat, most breeding materials lack these genes and glaucousness is then controlled by numerous minor genes, each having a small effect. It is with this latter material that we have produced near-isogenic lines. It has been found that the grain yield of the glaucous lines is, on average, 8 per cent more than the non-glaucous lines when grown in water-limited environments (Richards, 1983b). This has been attributed to several factors, all of which affect WUE by changing the evaporative water loss from the leaf. These are that glaucous lines have: (1) a decreased transpiration at night, (2) lower transpiration for a given rate of photosynthesis during the day, (3) cooler photosynthetic surfaces, presumably because of the increased reflectance of light (which may also lead to our observation of less leaf firing on days of extreme evaporative conditions). Further discussion of glaucousness in wheat and its apparent importance in water-limited conditions, particularly as it effects WUE and not the total amount of water transpired or the harvest index, can be found in Johnson *et al.* (1983), Richards (1983b), and Richards *et al.* (1986).

These results give some hint that other traits in cereals could, if selected, also affect evaporation from the leaf surface and hence WUE. These traits and their possible advantage may be: erect leaf posture—effect on radiation shedding, small leaf size—effect on boundary layer, and convective heat transfer.

Carbon isotope discrimination

The naturally occurring stable isotope of carbon, ^{13}C, is discriminated against during the fixation of carbon in C_3 plants. Theory predicts that the amount of discrimination, Δ, is determined by the intercellular partial pressure of CO_2

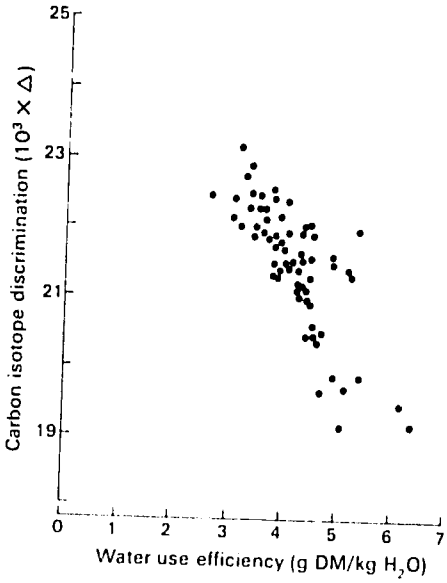


Figure 2. Relationship between carbon isotope discrimination, Δ, and WUE of wheat genotypes in different drought treatments grown in 1 m long pots. Δ was determined on leaves at maturity and WUE calculated between sowing and maturity. (Adapted from Farquhar and Richards, 1984)

(P_i), which in turn is regulated by variation in both stomatal conductance and assimilation capacity (Farquhar *et al.*, 1982). High WUE would be associated with a low Δ and a low P_i. This is achieved when stomatal conductance is small relative to assimilation capacity. Figure 2 shows that this theory was confirmed in droughted wheat in large pot experiments (Farquhar and Richards, 1984). It has subsequently been confirmed in pot experiments on barley and peanuts (Hubick, Farquhar, and Shorter, unpublished results).

Measurement of Δ to estimate total growth relative to water use has many features attractive to breeders. Δ can be determined on fresh or stored, immature or mature plants, leaves, stems, or grain, providing plant material was grown in the same environment. Very small samples only are required. Determination of Δ using a ratio mass spectrometer can be automated and large numbers can be measured over a year as samples are easily stored.

The potential value of Δ as a rapid measure of the WUE of a genotype will depend primarily on three criteria. First, Δ must be correlated with WUE in large field plots. Such data are not yet available. However, in field experiments where we have measurements of Δ but not of water use of a diverse

group of genotypes, variation in Δ was *positively* correlated with AGDM at two sites where there was little water shortage (Condon, Richards, and Farquhar, unpublished data). AGDM averaged 10/t/ha at these two sites. This relationship is opposite to that found under dry conditions. The way we interpret this result is that when there is adequate water there are stomatal limitations to growth so that genotypes with a high Δ and hence a high P_i have higher assimilation rates and relative growth rates. This finding provides evidence of the difficulty in combining high yield in both wet and dry conditions into one cultivar.

It is, nevertheless, worth pointing out that under some water-limited conditions a high Δ and hence a low WUE may not be incompatible with high yield. In environment A in Figure 1, where water is often not limiting until about the time of canopy closure, fast-growing genotypes (i.e. with high Δ) may be favoured for two reasons. First, to reduced E and, second, as more growth in winter is cheaper in terms of water than the equivalent growth when it is warmer later in the season. The second point will be discussed in more detail shortly.

A second criterion that Δ must satisfy for it to be useful in breeding is that there must be variation in Δ, and its measurement should have as little error as possible. Δ has been found to vary widely among genotypes. In a sample of 100 hexaploid wheats grown in the same field environment the range in Δ values was 4×10^{-3}, which is large and corresponds to substantial variation in WUE. Furthermore, measurements of Δ on fifteen advanced breeding lines grown 300 km apart in very different field environments were highly correlated, as were measurements of plants in pots and in field plots in different environments (Figure 3).

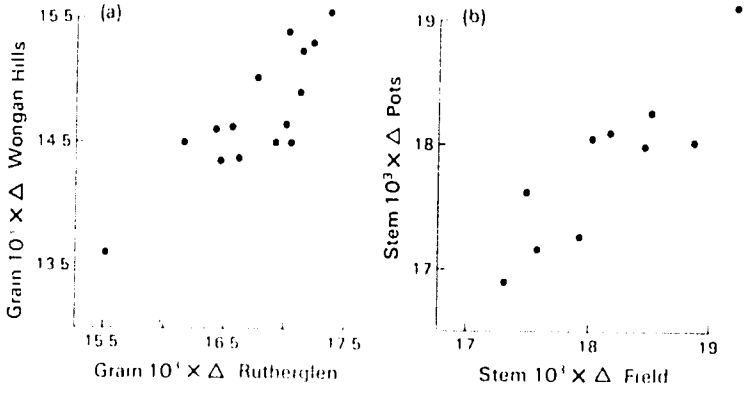


Figure 3. Relationship between carbon isotope discrimination, Δ, determined (a) on grain from two sites 2000 km apart ($r = 0.82$) and (b) stems from plants in pots grown at Canberra and from 8.6/m² experimental plots grown 300 km away ($r = 0.91$). (Condon, Richards, and Farquhar, unpublished data)

The third criterion that Δ must satisfy is that it have insignificant pleiotropic effects. In experiments using 1 m long pots we have not found Δ to adversely influence either water use or HI over a range of different droughted environments (Richards, Townley-Smith, and Farquhar, unpublished work). However, based on our findings at wet field sites, discussed above, it may well be that if genotypes with low Δ are associated with slower growth their increased WUE may be offset by an increased E in environments A and C in Figure 1.

Since we believe the measurement of Δ integrates the diffusion of CO_2 and H_2O into and out of the leaf in relation to assimilation capacity over an entire growing season, we consider it may have considerable potential in breeding. Clearly, we are only beginning to understand its significance.

Root/shoot partitioning and cool-temperature vigour

The third category of characters may appear to bear no relation to WUE. These are cool-temperature vigour, dry-matter partitioning to roots, and phenology. Passioura (1983) has discussed the possible consequences of a high root/shoot ratio in a crop. It is worth highlighting again the calculation made before of the effect of a 5 per cent increase in RGR. The theoretical 50 per cent greater AGDM achieved after 100 days of exponential growth could also arise if one genotype partitioned 5 per cent more of its assimilate to the roots than another. When WUE is expressed as the ratio of AGDM to water used, then the genotype that partitioned less to the roots would not only have a higher WUE but also earlier canopy closure, thereby reducing E. This reduction in root/shoot ratio may be very important in superficially increasing WUE and deserves further exploration.

Improved cool-temperature vigour is proposed as another way of increasing WUE because of the tight relationship between WUE and vapour pressure deficit of the air. Calculations derived from Fischer (1979) show that at Wagga Wagga, Australia, growth during the coldest months, June and July, is 25 per cent more efficient in terms of water than growth in September (WUE = 87 kg/ha^2/mm; cf. 70 kg/ha^2/mm). In December WUE decreases to 28 kg/ha^2/mm so that growth during June and July is three times more efficient than during December. Improved growth during winter will, as Fischer points out, be better from the point of view of WUE as well as decreasing E. Thus the message here is very clear. Growth should be maximized during the coolest period and careful attention should be given to a phenology that most efficiently matches the seasonal change in WUE.

HARVEST INDEX

Maximizing AGDM at maturity under water-limited conditions is first achieved by maximizing its components: (1) water transpired by the crop and

(2) the water-use efficiency. Maximizing grain yield then becomes a function of the harvest index. In considering ways to increase HI of water-limited crops by genetic manipulation three findings are relevant. The first is that increased yields of recently released cereal varieties compared to older ones grown under optimal conditions have generally been achieved by an increased HI rather than an increased AGDM (e.g. Austin *et al.*, 1978). There is little doubt that this increased HI, achieved primarily by selection under optimal conditions, has also contributed to better yields in dry conditions. The second is that although the HI of current cultivars grown in good conditions is about 0.5, when grown as a dryland crop their HI is typically around 0.35 and often less. Thus a considerable amount of the potential yield is not being realized. The third is that in dryland crops it is the balance between dry matter produced (and hence water used) before and after anthesis that is important in determining HI (Passioura, 1977). Thus, if a crop exhausts most of the soil water before anthesis, little will be left for grain filling and this will result in a low HI. It follows that the HI of water-limited cereal crops may first be increased by selecting genotypes with a high HI under optimal conditions. When this is achieved HI may then be further increased by altering the amount of pre- and postanthesis water use.

In dryland crops transpiration is linearly related to leaf area up to an LAI of about 3. It follows that water use is directly related to leaf area throughout much of the crop's life so that a reduced rate of leaf area development should conserve water for grain filling. It may also mean that in the period just before anthesis when kernel number is very sensitive to drought the crop water status will be better and this may reduce any catastrophic effect on kernel number if drought is severe. Conserving water early in the crop's life for later use is particularly relevant to environment B in Figure 1. Whether it is also effective in A and C will depend on whether E is significantly affected by a slower leaf area development. Experiments over two years at Merredin, Western Australia, where the mean average rainfall is 310 mm and is typical of an A-type environment, suggest that more conservative early growth may also increase yield and HI in that environment (Islam and Sedgley, 1981).

We have chosen five plant characteristics as having the potential to improve HI and thereby grain yield from the joint considerations of their effect on leaf area development and the extent of genetic variation. They are seminal root hydraulic resistance, flowering time, determinate tillering, early growth rate, and leaf size. In all of these traits we have attempted to develop contrasting lines or populations to determine their effect on HI. Several experiences in producing these lines are worth relating. In selecting for a reduced leaf size, a correlated response was found in final leaf number with the net effect of no change in leaf area. In developing contrasting lines for flowering time, it was found that the early lines were also shorter so that it was difficult to separate out these two traits for their effect on harvest index and grain yield.

Table 1. Mean grain yield of lines containing small and normal diameter xylem vessels, in three seasons in southern Australia. Lines are backcross-3 derivatives of the commercial variety Kite. April to October rainfall was 228 mm at Condobolin, and 243 and 549 mm at Wagga Wagga in 1982 and 1983, respectively

Xylem vessel diameter	Grain yield (t/ha)		
	Condobolin 1981	Wagga Wagga 1982	Wagga Wagga 1983
Small (50 μm)	0.90	0.96	3.46
Normal (60 μm)	0.81	0.88	3.35
LSD (5%)	0.07	0.08	0.16

Increased hydraulic resistance in the seminal roots

Increased root hydraulic resistance was first proposed by Passioura (1972). Work subsequently has shown this can best be achieved by decreasing the diameter of the main xylem vessel in the seminal roots (Richards and Passioura, 1981a, 1981b). A summary of results obtained in two dry and one wet environment in southern Australia show the potential of this character (Table 1). In all environments lines with small xylem vessels yielded more than lines with larger vessels. The yield advantage was greatest in the driest environments. Thus, there is no yield penalty in having small xylem vessels in good seasons. This yield data corroborates Passioura's original hypothesis, which was that when the top soil is dry, plants rely on the seminal root system to collect water deep in the profile and lines with small vessels will be unable to meet the plant's water requirements on days of high evapotranspiration. Plants will adjust their growth accordingly and conserve some water before flowering for use later and this should result in higher yields. On the other hand, when the top soil is wet, the nodal root system, which seems to be unaffected, will override the effect of the small xylem vessel in the seminal roots and growth will not be affected.

Determinate tillering

The other traits chosen have a more direct effect on the development of leaf area and hence water use. The traits were chosen following a study where leaf area was manipulated in wheat to determine effects on yield in dry environments (Richards, 1983a). Flowering time and determinate tillering are likely to be the most influential. Determinate tillering will be discussed here, and the reader is referred to Fischer (1981) for a full discussion on a change in

flowering date. Determinate tillering wheats (Atsmon and Jacobs, 1977) and barleys (Donald, 1979) are now available. Few, if any, tillers develop so that often there is only a single main shoot per plant. They offer several advantages. First, control over leaf area development and hence the opportunity to modify pre- and postanthesis water use and thereby HI as shown by Islam and Sedgley (1981). This may also lead to the avoidance of severe drought in the period between flag leaf emergence and anthesis. Second, it is a way of eliminating sterile tillers so that there is no water wasted in their production during vegetative growth. Third, flowering is more synchronous, which should increase HI when drought is terminal. The final advantage they offer over conventional wheats is in the control of population density. This may be varied at sowing according to soil type, site, or soil water storage.

Higher yields of the determinate tillering cereals over conventional types in dry environments have been found by Donald (1979), Islam and Sedgley (1981), and Richards (1983a). In the former two studies higher yields were achieved in an A-type environment. It is likely that the effect would be greater in B- and C-type environments where E is less. We have developed near-isogenic wheat lines for this character and they have been tested in several wet environments in both western and eastern Australia. Grain and dry-matter yields of the determinate and conventional tillering lines sown at different densities were indistinguishable (Richards and Delane, unpublished work). We know therefore that there are no yield disadvantages in this material when stand establishment is good. We wait with interest for data from drier environments.

INDEPENDENCE OF FACTORS AFFECTING YIELD

When first discussing each of the three components of the model, I pointed out the apparent independence of each. However, in considering the different traits in the context of the environment where crops will be grown it is clear that this is not completely so and there may be pleiotropic effects that reduce the effectiveness of the trait. In this context it is important to determine whether an increased WUE is generally associated with slower growth during winter and therefore a higher HI or E depending on the environment, and also to determine the relative importance of seasonal WUE with fast- or slow-growing genotypes in relation to variation in E. The interactions among these factors will become clearer with the development and testing of near-isogenic lines for the many different traits.

VALIDATION OF TRAITS

To determine the worth of any trait, genotypes must be developed that have a genetic background as similar as possible, but which contrast in the expression

of the trait. These genotypes, called either isogenic lines or isogenic populations, depending on how they are developed, must then be tested in field plots free of edge effects in environments that are representative of the area where the trait may be successful.

The choice of method to develop contrasting lines depends on the trait. In our work we considered that traits such as narrow xylem vessels in the seminal roots or determinate tillering are unlikely to exist in breeders' populations, but theoretical considerations would suggest they have a very good chance of improving yields in some environments. These two traits, although under the control of several genes, are reasonably heritable, so we chose a backcrossing programme to introduce them into the best available commercial varieties. Then, if they did yield well in field trials, they could be released to farmers very quickly. In the case of the narrow xylem vessel characteristic, two experiences are worth recounting that are relevant to attempts to incorporate a new characteristic into an existing cultivar. The first is the considerable yield penalty associated with using a poorly adapted donor parent. The donor parent in this case was a Turkish landrace wheat. More breeding work than anticipated was required to achieve the yield level of the recurrent parent. The second point refers to the difficulty in keeping ahead of changes in pathogen populations. Lines derived from one of the two recurrent parents became susceptible to a new race of stem rust in the first year of evaluation of backcross-5 F_4 lines. If it is possible to use as a recurrent parent a cultivar with close relatives containing other resistance genes, then much of the breeding work will not be lost if there is a change in the pathogen population.

For traits that already exist in breeders' populations, backcrossing can again be used to produce isogenic lines; however, other methods are also available that may be better or quicker. If the trait is simply inherited and the heterozygote can be identified, then the heterozygote can be selected each generation until at least the F_5 or later generation. Seed is increased to enable the extreme homozygotes to be bulked to give near-isogenic lines. We have used this method to develop lines differing, for example, in glaucousness, awns, and pubescence, among others. For traits in breeders' populations that are controlled by numerous genes and where the heterozygote cannot be identified, the development of isogenic populations is appropriate. We have used this technique to develop lines that differ in early growth, among others. The extreme expressions of the character are selected in F_2 or some other bulk population. Progeny from the selected plants are then tested for the character and extreme lines are bulked to provide the contrasting populations. A useful variation to this method we have used for some traits is to select in backcross-1 F_2 or backcross-2 F_2 populations. This enables more closely related populations to be developed. For example, 87.5 per cent of the genes are derived from one parent if plants are selected from a backcross-2 population.

The above approach will test the worth of a particular trait and is designed to inform. A more empirical approach more suited to breeding programmes is to advance lines containing the trait to the F_4 or F_5 generation when sufficient seed is available to sow plots large enough to be free of edge effects. This may require that lines containing the trait be 'nursed' so that they are well represented. If the trait imparts any yield advantage then lines containing the trait should advance to later generations without any conscious selection. Although this method is very efficient in a breeding programme unfortunately it gives little information to others of the value of a trait.

CONCLUDING REMARKS

Breeding for increased yields in dry regions can take several different forms. Empirical methods have been very successful and they should continue to be so. They will also be an integral part of any attempt to improve yields when physiological processes are selected. If increased yields are to continue it is important that both methods proceed in parallel. In this paper I have discussed our breeding programme as I believe it provides a valuable framework to view the formation of yield when water is limited. It enables traits to be selected that have a good probability of increasing yield when selected alone and perhaps a greater chance when traits are pyramided together.

Although most characteristics that influence yield should fit into one of the three processes that determine yield, there are likely to be some that are more intangible. One such characteristic has been referred to as 'sink strength'. When there is adequate water there is evidence that photosynthesis during grain filling depends in part on the sink size which in turn depends on kernel number (King *et al.* 1967; Rawson *et al.*, 1976; Fischer *et al.*, 1981). Similar evidence has been found when water is limited. For example, some genotypes have an exceptional ability during grain filling to continue accumulating dry matter at a rate which is disproportionate to the water used up to that time (Condon, unpublished results) leading to a high HI and WUE. Several factors may be involved. A decreased respiration may be one. This has not been discussed but it deserves further study as any decrease through breeding, as has been achieved in ryegrass, should result in a higher WUE. Another factor may be the joint contribution of a high dry matter at anthesis and osmoregulation. It is not implausible that a high dry matter sets a high potential kernel number whereas osmoregulation buffers the crop to drought in the preanthesis period, when kernel number is most susceptible, the net result being the establishment of a large sink (high dry matter and kernel number).

Clearly there remains considerable potential to further improve yields of winter-grown cereals in dry regions based on a consideration of the processes

influencing yield and the assiduous choice of traits. When I last reviewed breeding more drought-resistant wheats (Richards, 1982), three characteristics (phenology, tillering, and awns) were identified as being proven to be advantageous in some dry environments. In the intervening years considerable progress has been made and there is no reason why this should not continue.

REFERENCES

Atsmon, D. and Jacobs, E. 1977. A newly bred 'Gigas' form of bread wheat (*Triticum aestivum* L.): morphological features and thermo-periodic responses. *Crop Sci.* **17**:31–35.

Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. M. and Taylor, M. 1978. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci.* **94**:675–689.

Cooper, P. J. M., Keatinge, J. D. H. and Hughes, H. 1983. Crop evapotranspiration—a technique for calculation of its components by field measurements. *Field Crops Res.* **7**:299–312.

Donald, C. M. 1979. A barley breeding program based on an ideotype. *J. Agric. Sci.* **93**:261–269.

Farquhar, G. D. and Richards, R. A. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* **11**:539–552.

Farquhar, G. D., O'Leary, M. H. and Berry, J. A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* **9**:121–137.

Fischer, R. A. 1979. Growth and water limitation to dryland wheat in Australia: a physiological framework. *J. Aust. Inst. Agric. Res.* **45**:83–89.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through breeding of crops. *Plant and Soil* **58**:249–278.

Fischer, R. A. and Turner, N. C. 1978. Plant productivity in the arid and semi-arid zones. *Ann. Rev. Plant Physiol.* **29**:277–231.

Fischer, R. A., Bidinger, F., Syme, J. R. and Wall, P. C. 1981. Leaf photosynthesis, leaf permeability, crop growth, and yield of short spring wheat genotypes under drought. *Crop Sci.* **21**:367–373.

French, R. J. and Schultz, J. E. 1984. Water use efficiency of wheat in a Mediterranean-type environment. I. The relationship between yield, water use and climate. *Aust. J. Agric. Res.* **35**:743–764.

Hanson, P. R., Riggs, T. J., Klose, S. J. and Austin, R. B. 1985. High biomass genotypes in spring barley. *J. Agric. Sci.* **105**:73–78.

Islam, T. M. T. and Sedgley, R. H. 1981. Evidence for a 'uniculm effect' in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. *Euphytica* **30**:277–282.

Johnson, D. A., Richards, R. A. and Turner, N. C. 1983. Yield, water relations and surface reflectances of near-isogenic wheat lines differing in glaucousness. *Crop Sci.* **23**:318–325.

King, R. W., Wardlaw, I. F. and Evans, L. T. 1967. Effect of assimilate utilization on photosynthetic rate in wheat. *Planta* **77**:261–276.

Morgan, J. M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* **34**:607–614.

Morgan, J. M. and Condon, A. G. 1986. Water use, grain yield, and osmoregulation in wheat. *Aust. J. Plant Physiol.* **13**. In press.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. *Aust. J. Agric. Res.* **23**:745–752.

Passioura, J. B. 1977. Grain yield, harvest index and water use of wheat. *J. Aust. Inst. Agric. Sci.* **43**:117–120.

Passioura, J. B. 1983. Roots and drought resistance. *Agric. Water Management* **7**:265–280.

Rawson, H. M., Gifford, R. M. and Bremner, P. M. 1976. Carbon dioxide exchange in relation to sink demand in wheat. *Planta* **132**:19–23.

Richards, R. A 1982. Breeding and selection for drought resistance in wheat. Pages 303–316 in *Drought Resistance in Crops with Emphasis on Rice*. International Rice Research Institute, Manila, Philippines.

Richards, R. A. 1983a. Manipulation of leaf area and its effect on grain yield in droughted wheat. *Aust. J. Agric. Res.* **34**:23–31.

Richards, R. A. 1983b. Glaucousness in wheat, its effect on yield and related characteristics in dryland environments, and its control by minor genes. Pages 447–451 in *Proceedings of the 6th International Wheat Genetics Symposium* (Sakamoto, S., ed.), Kyoto, Japan.

Richards, R. A. and Passioura, J. B. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* **21**:249–252.

Richards, R. A. and Passioura, J. B. 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* **21**:253–255.

Richards, R. A., Rawson, H. M. and Johnson, D. A. 1986. Glaucousness in wheat: its development, and effect on water-use efficiency, gas exchange and photosynthetic tissue temperatures. *Aust. J. Plant Physiol.* **13**. In press.

Tanner, C. B. and Sinclair, T. R. 1983. Efficient water use in crop production: research or re-search? Pages 1–27 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R. and Sinclair, T. R., eds.). American Society of Agronomy.

Waddington, S. R., Yoshida, M. and Ransom, J. K. 1986. The yield potential of durum wheat released in Mexico between 1960 and 1984. *Crop Sci.* In press.

DISCUSSION

B. Borghi

You indicated glaucousness as an important trait to select for. Considering that the differences between glaucous and non-glaucous lines appear mainly related to the chemical composition of the epicuticular wax (presence or absence of B-dicktones) and not to the amount of wax per unit of leaf area, I would like to know your opinion about the possibility of selecting lines with higher amounts of wax in order to reduce water transpiration.

R. Richards

We have no information on whether an increased amount of wax will reduce transpiration. Glaucousness, as we have considered, means that wax must be present so that reflectance is increased, which appears to result in a cooling of the photosynthetic surface. We have observed this in lines near-isogenic for glaucousness but with the same amounts of wax. The glaucous lines yield more grain and dry matter than non-glaucous ones in dry environments. It is for this reason we have concentrated on glaucous wheats rather than the amount of wax.

N. C. Turner

Do you see narrow xylem vessels of the seminal roots being useful in a Mediterranean environment in which the majority of rain comes after sowing?

R. Richards

Although this character has primarily been considered for crops grown predominantly on stored soil water, there is no reason why it should be disadvantageous in a Mediterranean environment. Indeed, if the rainfall during the season is very low, particularly before anthesis, then winter cereals with a narrow xylem vessel diameter may give a yield advantage.

N. C. Turner

The comparisons between the values from Wongan Hills and Rutherglan were correlated, but not on a one-to-one basis. Does this mean that we cannot screen for WUE efficiency by this technique between a range of environments?

R. Richards

Yes, Δ will vary from location to location depending on the vapour pressure difference. Thus, as with almost all characteristics, selection should be done on plants grown in the same environment. However, because values were correlated in very different environments it is possible that by using a series of standard genotypes selections could be made in different sites according to their ranking and the standards.

J. M. Clarke

(1) What is the cost of the equipment to measure carbon isotope discrimination?
(2) What is the possible rate of screening? As I understand, one can easily store samples for later measurement.

R. Richards

(1) A ratio mass spectrometer is approximately US$100,000.
(2) Approximately 40 samples per day can be measured. However, with refinements and less precision this value could be doubled. Δ determinations are done on dried plant material. Hence samples are easily stored and measured at any time.

M. S. Mekni

How much of the initial intensity of the character in the landrace (xylem diameter) have you recuperated? Also, how much of the yield of Kite have you recuperated? The understanding is that the character is valuable only when it leads to yield increases in the recurrent parent.

R. Richards

The diameter of the xylem vessel in the seminal roots of our best selections is little different from the donor landrace wheat. The yields of our best BC3 lines were equal to Kite. We are currently testing BC5 lines. We consider the character valuable as, when conditions are wet, yields are the same as those of comparable lines with a large or standard vessel diameter; however, when conditions are dry, yields of lines with the small xylem vessel are higher.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

12

Breeding for Moisture-stressed Areas

M. OSMANZAI, S. RAJARAM, and E. B. KNAPP
CIMMYT Wheat Program, Londres 40, Apdo Postal 6–641, 06600 Mexico DF, Mexico

ABSTRACT

CIMMYT's approach to breeding for drought resistance is based on wide adaptation, high yield, and stability (i.e. input efficiency and input responsiveness) for semi-arid regions. This approach involves testing of F_2, F_5, and F_6 in optimal conditions, and of F_3 and F_4 in water stress. The assumption is that high-yield potential at the optimum and stress levels can be combined. This is confirmed by analysis of the input-efficient and input-responsive cultivar Veery 'S', which has a high genetic yield potential and exhibits superior yield performance across the entire range of environments.

Methods used at CIMMYT for identifying drought resistance are yield-performance evaluation under reduced irrigation, low-rainfall conditions, gradient irrigation, and multilocational international testing. Wide adaptation, high yield and yield stability—the most important characteristics of CIMMYT germplasm—are derived through the application of the shuttle breeding system in Mexico, using alternate sites of a contrasting nature. High fertility and optimum moisture are applied in the F_2, F_5, and F_6 generations at Ciudad Obregon The F_3 and F_4 generations are grown under low fertility and reduced moisture conditions at Huamantla and Ciudad Obregon. Advanced lines produced through this system undergo reduced irrigation, rainfed, and optimum moisture conditions. The lines performing well under all three conditions are internationally tested in various drought environments.

INTRODUCTION

Wheat is one of man's principal foods. It is grown everywhere except in the tropics and is the world's major source of protein and calories. Breeding, physiology, and production research for wheat have traditionally focused on

increasing yield potential. While the average yield per unit area has risen manyfold in high-moisture environments, increases in production under dry conditions have been less impressive.

The genetics of drought-related characters is complex and not adequately understood. Crop plants occupy diverse environments. These factors make it difficult for breeders to develop genotypes adapted to arid conditions. Understanding drought resistance mechanisms, along with quantifying and clearly explaining the relationship between plant characters and drought resistance, would reduce the dependence on empirical methods and help in the development of cultivars with a high and stable yield under moisture-limiting conditions.

The major climatic factors affecting crop production in dry areas are yearly precipitation and its distribution pattern, relative humidity, average temperature, and soil type and depth (Quizenberry, 1981).

WHEAT DISTRIBUTION ACCORDING TO MOISTURE ENVIRONMENTS IN DEVELOPING COUNTRIES

Of about 241 million hectares of wheat planted worldwide, 105 million are grown in the developing world and 136 million in developed countries (CIMMYT, 1981). According to Byerlee and Winkelmann (1980), the developing world's wheat areas can be divided into irrigated regions, rainfed environments with generally adequate moisture, and semi-arid environments where moisture is often a limiting factor (Table 1). The total area is more or less equally distributed among the three categories of environments.

Thirty-seven per cent of the Third World wheat area is semi-arid, where moisture is the most serious production constraint. The Middle East/North Africa region represents 59 per cent of this area, with the largest area being in

Table 1. Approximate percent distribution of wheat area according to moisture environment in major production regions of the developing world. (Byerlee and Winkelmann, 1980)

	Moisture environment		
Region	Irrigated	Adequate rainfed moisture	Semi-arid rainfed
Middle East/North Africa	14	34	51
South Asia	73	4	23
East Asia	25	39	37
Latin America	9	49	43
All developing countries	34	28	37

Turkey. In South and East Asia, the countries with the largest semi-arid area are India and China. Argentina ranks first in semi-arid area among Latin American countries.

DROUGHT CLASSIFICATION

The term 'drought' describes a condition in which available soil moisture is reduced to the point where the plant cannot absorb it rapidly enough to compensate for transpiration. Drought occurs as a result of low precipitation, high temperature, or wind. It is not a uniform phenomenon, and a plant's reaction depends on the stage of development at which drought occurs. Some plant processes are relatively insensitive to water stress, while others are distinctly affected.

Drought resistance is the plant's ability to obtain and retain water, as well as continue its metabolic functions during a period of low water potential in its tissue. It is the result of many, often independent, morphological and physiological characters whose interaction has not yet been clearly explained. Arnon (1972) defined drought resistance as the ability to survive drought conditions without injury. Levitt (1972) divided drought resistance into drought avoidance and drought tolerance. He stated that drought-avoiding plants maintain a high internal water potential, in spite of low environmental water availability. Kozlowski (1968) classified dry region plants into four groups: drought escaping, drought evading, drought enduring, and those that resist by storing up a water supply to be used when soil moisture is scarce. To plant breeders, drought resistance is the ability of one genotype to be more productive with a given amount of soil water than another (Quizenberry, 1981).

The drought resistance mechanisms of interest to agronomists concern productivity. Yield is the integrated result of a number of interrelated physiological processes. Moisture stress can affect photosynthetic processes, growth (which provides photosynthetic tissue), and seed formation (which provides a reservoir for photosynthates). Many morphological changes in leaves and other green organs appear to improve resistance through higher water-use efficiency (WUE) and photosynthate accumulation. Metabolic changes could be involved in the drought resistance of the plants exposed to severe stress. Nitrate reductase activity and the accumulation of proline and abscisic acid (ABA) are reported to be associated with drought resistance.

There are three stages of physiological research concerning drought. The first relates plant characteristics to stress survival. The second is the investigation of drought-resistance-related differences within a species. The third is the development of simple, rapid methods for measuring the characteristics identified in the previous stages.

BREEDING FOR DROUGHT RESISTANCE

Increased productivity of crops grown under less-than-optimum conditions can be achieved either by developing improved cultural practices or by breeding varieties that are more productive under stress. The latter strategy is dealt with here.

Although the need for crop varieties better adapted to semi-arid conditions is widely recognized, plant breeders disagree on how to meet this need. Some believe that drought resistance can be obtained simply by selecting for high yield. This commonly used approach assumes that some superior yielding varieties at the optimum level will also yield relatively well at suboptimum levels (Arnon, 1972; Rajaram and Nelson, 1982). In such varieties drought resistance may be present as an unidentified component of performance stability. During the breeding process, yield and performance stability are handled together.

The second major breeding approach maintains that the maximum yield potential is irrelevant and that a superior variety for semi-arid growing conditions must be developed and tested in a semi-arid environment. Varieties developed in such a programme often show a narrow adaptation to the relevant environment and are said to have high genotype–environment interaction (Blum, 1979).

Smith (1982) suggested that the ideal variety would have a highly stable yield combined with a high-yield potential. However, in his correlation studies, the higher-yield potential of short-statured genotypes was achieved at the expense of yield stability. Thus, he proposed a 'middle of the road' genotype that could give a high-yield potential in all environments except those of either extremely high or extremely low production conditions.

CIMMYT's concept of breeding for semi-arid environments

Here we elaborate on and propose modifications to the CIMMYT's drought-breeding concept presented by Rajaram and Nelson (1982). The long-term objective of CIMMYT is to develop germplasm with a high-yield stability, disease resistance, and a high-yield potential under all conditions.

The result of this approach has been the development of high-yielding, input-efficient, and input-responsive varieties which have rapidly gained worldwide acceptance. Worrall *et al.* (1980) analysed the data from 14 years of the International Spring Wheat Yield Nursery (ISWYN) distributed by CIMMYT. Their analyses show that CIMMYT wheats and their derivatives perform well and fit into nearly every wheat-growing environment, including semi-arid zones. Based on ISWYN data they concluded that CIMMYT's breeding programme has been effective in developing high-yielding spring

wheat germplasm and that significant progress is being made in breeding for stability over a wide range of environments.

Pfeiffer (1984) analysed the data from the ISWYNs distributed by CIMMYT from 1964–5 to 1978–9. He concluded that:

(1) High-yielding varieties (HYVs) are at least as stable as locally developed varieties (LDVs) under all environmental conditions (but on a higher yield plateau).

(2) HYVs are at least as input efficient as LDVs (and generally more so) under all environmental conditions.

(3) HYVs are significantly more responsive than LDVs to improved production conditions.

(4) 'True' HYVs combine all three of the above characteristics. In other words, CIMMYT germplasm displays a combination of input efficiency and input responsiveness. traits needed for better adaptation to highly variable growing conditions.

Figure 1 illustrates the analysis of the input-efficient, input-responsive variety Veery 'S', which has a high genetic yield potential and exhibits superior yield performance across the entire range of environments, including moisture stress. Its coefficient of regression is not much higher than that of the mean of all entries, but its yield is consistently above the mean yield of all other entries. According to the CIMMYT breeding philosophy, a variety must

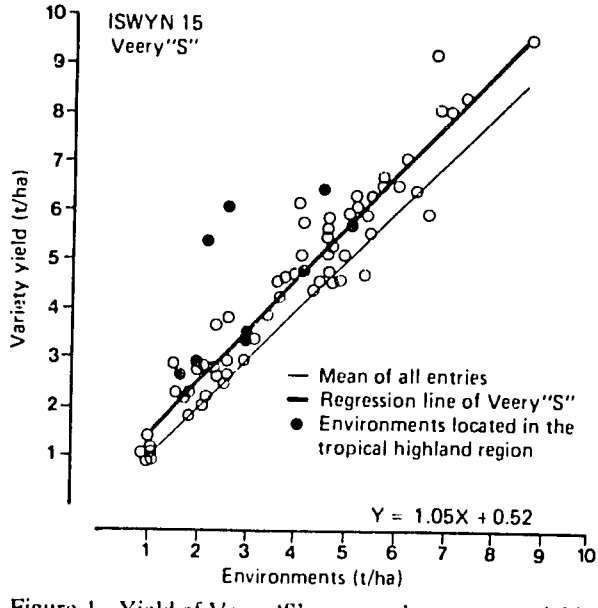


Figure 1. Yield of Veery 'S' regressed over mean yields of 73 locations in the fifteenth ISWYN

be relatively efficient in low-input situations, but must also respond to better moisture and fertilizer availability.

Identification of drought resistance at CIMMYT

Key points in a drought resistance breeding programme are resistance mechanisms, the stages at which a crop faces water stress, and the severity of the stress. Lewis and Christiansen (1981) suggest that stress environments be selected at a level that differentiates between stress-susceptible and stress-resistant genotypes. The following methods are used to identify germplasm for drought resistance at CIMMYT:

1. *Evaluation of performance under reduced irrigation and limited rainfed conditions to identify advanced lines or varieties with increased WUE*

Many advanced lines have been tested at Ciudad Obregon, Sonora, under both well-watered (five irrigations) and stress (two irrigations) conditions and the results are very encouraging. Lines such as Genaro 81 and Lira 'S' were suitable for both regimes (Table 2). The Huamantla location is used to screen varieties and advanced lines under natural rainfed conditions. The soil is sandy and the long-term average annual rainfall is less than 500 mm.

2. *Gradient irrigation (line source) to identify cultivars with WUE*

Hanks *et al.* (1976) described line sprinkler systems that can be used to create a continuous water gradient for studying the drought response of genotypes.

Table 2. Yield performance of six wheat varieties and advanced lines under two irrigation regimes in Ciudad Obregon, Sonora, 1982

	Yield under five irrigations		Yield under two irrigations	
Variety	kg/ha	Rank	kg/ha	Rank
Genaro 81	7461	1	4745	2
Lira 'S'	6920	2	4747	1
Veery 'S'	6819	3	4378	5
Neelkant 'S'	6758	4	4585	4
Junco 'S'	6346	5	4681	3
Tanager 'S'	5202	6	3637	6
LSD (5%)	639		711	

At Ciudad Obregon, a sprinkler system was installed to apply water in a linear fashion with the amount decreasing as the distance from the irrigation line increased. To evaluate the system's usefulness in screening for moisture stress performance, 25 genotypes were sown perpendicular to the irrigation line. Five plots were harvested at 3-metre intervals to obtain information on the relative performance of each genotype at differing levels of applied water. Average yield was positively correlated with the amount of water applied. The genotype response was evaluated using regression analysis. The lines found to be the best adapted for water stress situations were Junco (bread wheat), Yavaros (durum), and Civet 71 and Pika'S' (triticale).

3. *Multisite international trials for identifying drought resistance*

Multilocation testing has been of great value to CIMMYT wheat-breeding programmes in identifying cultivars that perform well over a range of environments including moisture stress situations. The ISWYN was the first systematically organized international yield trial. Begun in 1964 by CIMMYT, it was designed to disseminate the new spring wheat varieties throughout the world and to obtain information on yield, disease resistance, stability and wide adaptation, particularly from national wheat-breeding programmes. CIMMYT also distributes the Drought Screening Nursery (DSN) to provide genetic material to national programmes in semi-arid areas around the world.

Through these programmes, input-efficient, input-responsive, and stable varieties, such as Anza 7C, Pavon 76, Nacozari 76, Glennson 81, Seri 82, Ures 81, and Genaro 81 have been identified and used as parents for building future varieties. The programmes have produced promising results not only in irrigated areas of the world, but also in semi-arid regions (Rajaram *et al.*, 1984).

CIMMYT drought resistance breeding techniques.

The CIMMYT approach is to breed varieties at a high-yield potential level, alternated with moisture stress conditions, on the assumption that input efficiency and input responsiveness can be combined. The analyses of Worrall *et al.* (1980) and Pfeiffer (1984) support this assumption.

The most important traits of CIMMYT germplasm—wide adaptation and yield stability across varied environments—have been derived through application of the 'shuttle breeding' principle, using alternate sites of contrasting conditions. The CIMMYT programme involves two crop cycles per year:

(1) A summer cycle in Huamantla, Tlaxcala, at an elevation of 2500 m and 19°N, where genotypes are screened for resistance to drought under rainfed and sandy soil environments. Planting is done in May, when daylength is increasing.

Table 3. A generalized breeding scheme employed at CIMMYT for moisture stress conditions

Generation	Location	Environmental condition	Selection method
P (parents)			
F_1		Well-watered	
F_2	Ciudad Obregon	Well-watered	Individual plant selection
F_3	Huamantla	Stress	Modified Bulk
F_4	Ciudad Obregon	Stress	Modified Bulk
F_5	Toluca	Well-watered	Individual plant selection
F_6	Yaqui	Well-watered	Bulking of lines
Yield trial*	Ciudad Obregon	Well-watered and stress	
Yield trial*	Huamantla	Stress	

*The outstanding yielding lines in both environmental situations are internationally distributed in the DSN to obtain more information on drought resistance and yield performance.

(2) A winter nursery in Ciudad Obregon at 28°N, with an elevation of 40 m, where materials are screened for high-yield potential under optimum conditions. Planting is done in November, when daylength is decreasing. Testing here can be done under conditions of optimum moisture and reduced irrigation simultaneously.

Ciudad Obregon has dry weather from October to May and a long-term seasonal average rainfall of 48.2 mm. This is considered a suitable environment for drought trials by regulating the number of irrigation applications. In a breeding programme for optimal conditions, five to six irrigations are applied to produce a good crop of wheat. In our drought experiments, plants receive only one or two irrigations to facilitate the selection of lines. The lines selected are further tested in Huamantla under rainfed conditions. A schematic representation of germplasm flow and the handling of the segregating generation are shown in Table 3. High fertility and optimum moisture are applied in the F_2, F_5, and F_6 generations. The F_3 and F_4 generations are grown under low fertility and reduced moisture or rainfed conditions. Selection during the irrigated and well-fertilized generations of F_2, F_5, and F_6 are conducted normally. Rust epidemics are created and susceptible plants are discarded. Good tillering capacity, head development, leaf retention capability, and grain plumpness are the characters evaluated in the individual plant and line selections.

The following characters are important for drought stress situations and are considered in selecting materials grown under limited moisture and low fertility in the F_3 and F_4 generations:

Delayed leaf senescence (longer leaf retention)
Tiller viability
Reduced spike sterility
Grain plumpness
Relatively higher test weight
Relatively higher yield

Advanced lines produced are simultaneously subjected to optimum and stress conditions yield trials. The lines showing high performance in both conditions are included in the Drought Screening Nursery (DSN) and distributed to CIMMYT's cooperators in moisture stress regions.

REFERENCES

Arnon, I. 1972. Crop production in dry regions. Pages 1–72 in *Systematic Treatment of the Principal Crops*, Vol. II. Barnes & Nobb, New York.

Blum, A. 1979. Genetic improvement of drought resistance in crop plants: a case for sorghum. Pages 429–445 in *Stress Physiology in Crop Plants* (Mussel, H. and Staples, R. C., eds.). Wiley Interscience, New York.

Byerlee, D. and Winkelmann, D. F. 1980. Accelerating wheat production in semi-arid developing regions. Economic and policy issues. Pages 328–362 in *Proceedings of the 3rd International Wheat Conference*, Madrid, Spain.

CIMMYT, 1981. World wheat facts and trends. Report One: an analysis of changes in production, consumption, trade, and prices over the last two decades. CIMMYT, Mexico. 19 pp.

Hanks, R. J. Keller, J., Rasmussen, V. P. and Wilson, G. D. 1976. Line source sprinkler for continuous irrigation crop production studies. *Soil Sci. Am. J.* **40**:426–429.

Kozlowski, T. T. 1968. Introduction. Pages 1–21 in *Water Deficit and Plant Growth* (Kozlowski, T. T., ed.), Vol. I. Academic Press, New York.

Lewis, C. F. and Christiansen, M. N. 1981. Breeding plants for stress environments. Pages 151–177 in *Plant Breeding II. Proceedings of Plant Breeding Symposium 112* (Frey, K. J., ed.), 16 March 1979, Ames, Iowa. Iowa State University Press. Ames, Iowa.

Levitt, J. 1972. *Response of plant to environmental stress*. pp. 322–445. Academic Press, New York.

Pfeiffer, W. H. 1984, Ertragsleistung, Ertragsstabilitaet und Adaptation von Sommerweizen auf regionaler und globaler Ebene-Analyse einer serie von internationales sortenversuchen ueber 15 Jahre und 973 Umwelten. Dissetation Universitaet Hohenheim, Federal Republic of Germany.

Quizenberry, J. E. 1981. Breeding for drought resistance and plant water use efficiency. Pages 193–212 in *Breeding Plants for Less Favorable Environments* (Christiansen, M. N. and Lewis, C. F., eds.). Wiley Interscience, New York.

Rajaram, S. and Nelson W. L. 1982. Wheat production system in arid and semi-arid regions. Presented to International Summer School on Agriculture, Royal Society of Dublin, pp. 305–324.

Rajaram, S., Skovmand, B. and Curtis, B. C. 1984. Philosophy and methodology of an international wheat breeding program. Pages 33–60 in *Gene Manipulation in Plant Improvement* (Gustafson, J. P., ed.). Plenum Press, New York.

Smith, E. L. 1982. Heat and drought tolerant wheats of the future. Pages 141–147 in *Proceedings of the National Wheat Research Conference*, Beltsville, Maryland.

Worrall, W. D., Scott, N. H., Klatt, A. R. and Rajaram, S. 1980. Performance of CIMMYT wheat germplasm in optimum and suboptimum production environments. Pages 30–37 in *Proceedings of the 3rd International Wheat Conference*, Madrid, Spain.

DISCUSSION

A. Hadjichristodoulou

In your presentation you mentioned that longer leaf area duration and moderate tillering are among your objectives in breeding for low-rainfall areas. Do you have any data to prove that the chosen levels for the two traits are better than other levels?

Mahmoud Osmanzai

I presented CIMMYT's long-term objective to develop germplasm that possesses (1) high-yield potential under favourable and stress conditions, (2) stable and wide adaptation, and (3) disease resistance. I did not intend to prove or disprove selection criteria, but I presented the criteria in selecting materials grown under limited moisture and low fertility in F_3 and F_4 generations. They are:

Longer leaf area duration or delayed leaf senescence
Moderate tillering ability
Grain plumpness
High test weight and
Yield *per se*.

E. Acevedo

Could you expand on the soil moisture conditions under which reduced irrigation trials are performed? In my experience plant responses to stress vary according to previous growth and stress history.

Mahmoud Osmanzai

I presented the performance of six cultivar/genotypes under five and two irrigation regimes. The water infiltration at the site of the experiment was low. I agree that response of plants (crops) to water stress varies according to the growth stage of the crop, degree of stress, and previous history of stress.

M. Tahir

The yields of 3.8 and 3.3 tons/ha under grain-filling stress and severe stress, respectively, seem to be still very high. Could you please explain the type of stress you were referring to? What was the total moisture (mm) during the crop season for the crop under severe stress?

Mahmoud Osmanzai

In Obregon where the experiments were conducted, the seasonal average rainfall is 48.2 mm only. The moisture stress depended on the amount of water applied. Normally, when only about 300 mm of water was applied, the grain yield reduction was approximately 40–50 per cent as compared to non-stressed plots.

S. K. Sinha

What was the initial soil moisture when you applied two or five irrigations? How much total water was used by different contrasting treatments?

Mahmoud Osmanzai

The initial soil moisture varies, but we gave irrigation to allow seedling emergence. The amount of water used by different contrasting types was not measured.

S. Ceccarelli

(1) Can an environment which gives over 4 t/ha be defined as a stress environment?
(2) Please clarify the breeding strategies for rainfed areas with regard to the selection environment.

E. B. Knapp

Unfortunately there don't yet seem to be any generally accepted criteria for quantifying stresses, and particulary 'drought stress', across different soil and atmospheric environments. Our programme goal is to apply selection pressure (to a degree generally encountered by the wheat plant) on the early generation material in order to elicit an adaptive response. In later generations (F_5 and beyond) the material is evaluated for yield. The particular case you point out represents yield trials at the same location with and without selection pressure for reduced moisture. The best six lines averaged 6785 kg/ha without moisture stress and 4464 kg/ha under limited moisture—a reduction of 32 per cent. Until we have evidence to the contrary, we consider this to represent an expression of the adaptive response to limited moisture. However, I agree that it might help to clarify the question of 'degree' of stress if we also looked at the six worst performing lines for comparison.

With regard to your second question; our general strategy for all wheat-growing environments is basically the same. We try to supply the national programmes with a pool of germplasm that is better than they already have. Of course, we are delighted if they identify something so well adapted to their conditions that it can be released as it is. Normally, however, we would expect the national programmes to refine the material for even better adaptation.

Mahmoud Osmanzai

CIMMYT's philosophical approach to breeding for drought resistance is based on wide adaptation. High yield and stability are necessary in any variety to be recommended for semi-arid regions. The variety must be able to give a relatively high yield under low-input conditions, but must possess the genetic potential for higher yields under optimum environmental conditions such as moisture and fertilizer availability. A schematic representation of germplasm flow and the handling of segregating generations was presented. The F_3 and F_4 generations are grown under low fertility and reduced moisture conditions. High fertility and optimum moisture are applied in the F_2, F_5, and F_6 generations. Advanced lines produced through this system are subjected to selection of desirable types simultaneously under reduced irrigation, rainfed situation, and optimum conditions.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

13

Breeding for Improved Yield in Moisture-limiting Areas: The Experience of Jordan

MAHMUD DUWAYRI, A. M. TELL, and F. SHQAIDEF
Faculty of Agriculture, University of Jordan, Amman, Jordan

ABSTRACT

Selection in a favourable environment did not result in superior lines for stress environments. However, selection in a stress environment resulted in some superior lines that were promising also for a favourable environment. Furthermore, selection of the seed weight ratio in the two contrasting environments appeared to be more promising than selection on the basis of the dry-matter or grain yield ratio.

INTRODUCTION

Frequent occurrence of drought is considered to be the main reason for low wheat yields in semi-arid areas in general and in Jordan in particular. Attempts to introduce high-yielding semi-dwarf varieties in Jordan have not been successful because the grains shrivel under rainfed conditions. Keim and Kronstad (1979) stated that under severely stressed conditions, performance of high-yielding cultivars was the same or even poorer than the previously developed cultivars, indicating the need for adaptation of improved cultivars to a wide range of moisture conditions. Therefore, a poor yield of wheat under stress was related to its inability to avoid stress, resulting in a severe reduction in tiller number and grain-bearing spikes (Keim and Kronstad, 1981). Yield improvement in wheat may be accomplished by manipulating the components of yield such as spikes per unit area, kernel number per spike, and kernel weight (Knott and Talukdar, 1971; Sidwell *et al.*, 1976).

Stork, a semi-dwarf wheat cultivar, produces high grain yields under optimum conditions, while Hourani, a semi-tall wheat, produces a reasonable yield, but the grain is not as satisfactory as that of Stork, under optimum conditions (M. Duwayri, unpublished data). Duwayri (1984) reported that the stress-simulated treatments produced the poorest yields and that Stork was inferior to Hourani in grain yield in those treatments.

McNeal *et al.* (1978) stated that both kernel weight and kernel number per spike were useful for selection for yield, but spike number per plant was not. Knott and Talukdar (1971) suggested that yield could be increased by selecting for an increased kernel weight. Our breeding strategy is to select high-yielding varieties with desirable grain weight.

MATERIALS AND METHODS

An experiment was conducted at Jubeiha and Ramtha stations. The annual variability in rainfall at these stations is shown in Table 1.

A total of 122 durum wheat lines in the F_7 generation, resulting from the cross Hourani X Stork, and the parental lines were planted in a randomized complete block design with two replications. Hourani is a locally adapted cultivar in moderate rainfall areas of Jordan and Syria, while Stork is a high-yielding, early maturing durum wheat variety. Each plot consisted of six rows, 5 m long and 25 cm apart. The seeding rate was 80 kg/ha for both locations. Dates for seeding were 29 and 27 October 1984 and dates of harvesting were 6 June and 29 May 1985 at Jubeiha and Ramtha, respectively.

Data were recorded for plant height, dry matter, grain yield, harvest index,

Table 1. Annual rainfall (mm) in the past 10 years for Jubeiha and Ramtha

Year	Jubeiha	Ramtha
1975–6	346	241
1976–7	441	216
1977–8	656	221
1978–9	359	120
1979–80	563	343
1980–1	491	181
1981–2	549	173
1982–3	664	274
1983–4	483	191
1984–5	448	243
Average	500	220

Table 2. Agronomic characteristics of the parents and the F_7 population grown at Jubeiha and Ramtha, 1984–5

	Dry matter yield (kg/ha)		Grain yield (kg/ha)		Harvest index		1000-seed weight (g)	
	Jubeiha	Ramtha	Jubeiha	Ramtha	Jubeiha	Ramtha	Jubeiha	Ramtha
Stork	5466	3240	2158	946	0.39	0.29	47.2	30.9
Hourani	6600	3216	2096	890	0.32	0.28	42.9	34.6
Population $n = 122$	6829	2783	2289	768	0.33	0.28	43.0	32.5

and thousand-seed weight. The top ten lines based on their performance for the above traits at Jubeiha and Ramtha were selected.

RESULTS AND DISCUSSION

The agronomic characteristics for parents and the F_7 population are presented in Table 2.

Stork produced less dry matter than Hourani at Jubeiha but was slightly better in grain yield at both locations. The harvest index was higher for Stork than Hourani at Jubeiha, while at Ramtha, the drier site, the difference was reduced. This was expected due to the high rainfall at Jubeiha. Though the thousand-seed weight of Stork was higher by 10 per cent than Hourani at Jubeiha, it dropped to 90 per cent of that of Hourani at Ramtha. The overall means of dry-matter and grain yields of the population were higher than the

Table 3. Dry-matter yield (kg/ha) of the top ten lines grown at Jubeiha and Ramtha, 1984–5

Line number	Top yielder at Jubeiha	Yield at Ramtha	Line number	Top yielder at Ramtha	Yield at Jubeiha
130	10650	3126	83	3976	5570
128	9480	2910	3	3820	3200
127	9350	2646	125	3700	8200
92	9200	2306	120	3696	8510
65	9160	2710	105	3690	7610
43	9090	2800	1	3680	4770
47	9076	2166	108	3626	5690
68	9020	2950	93	3450	8400
67	9000	2786	73	3360	6770
99	8800	2750	84	3310	5950
Average	9282	2715		3631	6467

Table 4. Grain yield (kg/ha) of the top ten lines grown at Jubeiha and Ramtha, 1984–5

Line number	Top yielder at Jubeiha	Yield at Ramtha	Line number	Top yielder at Ramtha	Yield at Jubeiha
97	3480	660	105	1200	2556
130	3410	906	83	1110	1916
129	3330	670	116	1106	2440
127	3330	756	100	1020	3000
67	3230	660	71	1016	2950
120	3220	1010	28	1010	1740
92	3200	496	120	1010	3220
124	3186	576	93	996	2966
68	3160	696	60	990	2096
36	3136	640	122	970	2430
Average	3268	707		1043	2531

highest parent at Jubeiha and were intermediate for harvest index and thousand-seed weight at both locations.

The top ten lines for dry-matter production at Jubeiha and Ramtha are listed in Table 3. It was interesting to note that the lines selected at Jubeiha were not in the rank of the top ten at Ramtha, and vice versa. This indicates the necessity to practise selection in the target environment. Seventy lines produced higher dry-matter yield than the superior parent at Jubeiha. However, none of the lines selected at Jubeiha were superior to any parent in dry-matter production at Ramtha. Furthermore, selection of the top ten lines for dry-matter yield at Ramtha gave four lines that were superior to parents or the population average at Jubeiha.

The average grain yield of the top ten lines at Jubeiha was 3268 kg/ha (Table 4). However, only two of these lines produced higher yields than the population average when grown at Ramtha. All top ten lines selected, based on their grain yield performance at Ramtha, were better than the parents or the population average. Six of those selected from Ramtha produced higher grain yields than the population average at Jubeiha (Table 4).

Many lines at both locations were superior to their parents in kernel weight. Furthermore, the selected ten lines for this trait at one location produced lines that gave a mean kernel weight equal to that of the best parent at the other location (Table 5).

The top ten lines for harvest index at Jubeiha were better than the superior parent. The average value for harvest index (0.31) of these lines at Ramtha was better than that for Stork (0.24) at that location. Harvest index values of the top ten lines at Ramtha ranged from 0.32 to 0.36 (mean 0.34) and at Jubeiha from 0.34 to 0.41 (mean 0.38).

Table 5. Thousand-seed weight (g) of the top ten lines grown at Jubeiha and Ramtha, 1984–5

Line number	Top yielder at Jubeiha	Yield at Ramtha	Line number	Top yielder at Ramtha	Yield at Jubeiha
26	49.8	39.5	66	40.5	46.8
71	49.8	32.8	126	40.0	46.5
8	49.0	37.3	26	39.5	49.8
60	49.0	32.0	78	39.5	47.3
68	49.0	34.3	118	39.5	47.5
117	49.0	30.8	39	38.8	47.8
24	48.5	36.8	22	38.5	44.0
49	48.5	34.0	44	38.5	46.8
29	48.0	37.3	134	38.5	45.6
73	48.0	37.8	73	37.8	48.0
Average	48.9	35.3		39.1	47.0

Other traits that are thought to be useful in breeding for stress are the ratios of the values of dry-matter and grain yields and the single-seed weight in a favourable environment to the values of the corresponding lines in a stress environment (Jubeiha/Ramtha in this case). Data on the lowest ratio concerning dry-matter yield are presented in Table 6. None of the lines selected on this bases was superior to either the population average or the better parent at Jubeiha, whereas eight of these lines were superior to the population mean at Ramtha. Furthermore, those lines were not superior in grain yield at Jubeiha

Table 6. Agronomic characteristics of the lowest ten lines in the Jubeiha/Ramtha ratio of dry-matter yield grown in Jubeiha and Ramtha, 1984–5

Line number	Dry-matter yield (kg/ha)			Grain yield (kg/ha)			1000-seed weight (g)		
	Jubeiha	Ramtha	Ratio	Jubeiha	Ramtha	Ratio	Jubeiha	Ramtha	Ratio
1	4670	3680	1.30	736	620	1.19	39.0	30.5	1.28
30	4000	2875	1.39	1456	740	1.97	43.8	29.8	1.47
83	5570	3976	1.40	1916	1110	1.73	41.3	33.3	1.24
28	4570	3230	1.42	1740	1010	1.72	46.3	30.0	1.54
31	2320	1640	1.42	746	430	1.73	38.3	30.3	1.27
111	4470	3150	1.42	1346	800	1.68	41.6	33.3	1.25
108	5690	3626	1.57	2086	926	2.25	40.6	32.0	1.27
23	4690	2940	1.60	1516	700	2.16	44.3	29.5	1.50
86	3940	2386	1.61	1410	640	2.20	44.8	33.3	1.34
60	5400	3120	1.73	2096	990	2.12	49.0	32.0	1.53
Average	4532	3062	1.49	1505	797	1.88	42.9	31.4	1.37

and five lines produced grain yields higher than the population mean at Ramtha. Similar results were obtained for the thousand-seed weight.

The use of the grain yield ratio as a selection criterion resulted in poor yielding lines at Jubeiha, and just five lines were higher than the population mean at Ramtha. The selected lines were poor in dry-matter yield at Jubeiha but five of them produced a reasonable yield at Ramtha. Single-seed weight of these selected lines was superior to the mean of the population at both locations.

The use of the seed weight ratio as a character for selection resulted in a lower mean of the ten selected lines at Jubeiha than the population mean or any of the parents, with two lines approaching the values of the superior parent (Stork). However, the mean of those lines at Ramtha was above the mean of the superior parent and the population, and two lines had a seed weight of 40 mg. Six of these lines produced a higher dry-matter yield than the population mean at Jubeiha. The mean dry-matter yield of these lines at Ramtha was equal to the population mean. Two lines seemed to possess stable dry-matter and grain yields.

REFERENCES

Duwayri, M. 1984. Comparison of wheat cultivars grown in the field under different levels of moisture. *Cereal Res. Commun.* **12**:27–34.

Keim, D. L. and Kronstad, W. E. 1979. Drought resistance and dryland adaptation in winter wheat. *Crop Sci.* **19**:574–576.

Keim, D. L. and Kronstad, W. E. 1981. Drought response of winter wheat cultivars grown under field stress conditions. *Crop Sci.* **21**:11–14.

Knott, D. R. and Talukdar, D. 1971. Increasing seed weight in wheat and its effect on yield components and quality. *Crop Sci.* **11**:280–283.

McNeal, E. H., Qualset, C. O., Baldridge, D. E. and Stewart, V. R. 1978. Selection for yield and yield components in wheat. *Crop Sci.* **18**:795–799.

Sidwell, R. J., Smith, E. L. and McNew, R. W. 1976. Inheritance and interrelationships of grain yield and selected yield related traits in a hard red winter wheat cross. *Crop Sci.* **16**:650–654.

DISCUSSION

E. Acevedo

Is there any evidence that germination at a low water potential is an indicator of plant resistance to water stress? If not, wouldn't this character have a counter-productive effect in shallow sowing, increasing a false start in low-rainfall Jordanian environment?

M. Duwayri

Germination ability at a low water potential when coupled with long coleoptile is very important for stand establishment in the semi-arid regions. To overcome the possibility of germination when there is a shortage of moisture afterwards, seeds should be planted deep enough in the soil so there is residual moisture in the soil

from the previous fallow or in such a way that the moisture reaching the seeds from the early rain will be enough for the growth of the seedlings till the next rains.

S. K. Sinha

In response to the question by Acevedo. Germination at a low water potential is important for areas when the crop is planted on receding soil moisture, as in central India. Farmers prefer a local variety, Pissi Local, because it ensures a good crop stand. However, germination at the low water potential phase does not mean drought resistance.

G. Ortiz-Ferrara

Have you studied any morphological or metabolic characteristics present in Hourani that give the wide adaptation under the low-rainfall conditions of Jordan?

M. Duwayri

Our studies showed that Hourani possessed long and heavy awns; it also has a large flag leaf area. These are important traits for production under dryland conditions. However, limited studies done on the relative water content at various stages did not show differences from other cultivars which are thought to be drought susceptible.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

14

Use of Physiological and Morphological Traits in Breeding Programmes to Improve Drought Resistance of Cereals

JOHN M. CLARKE
Research Station, Research Branch, Agriculture Canada, Swift Current, Saskatchewan S9H 3X2, Canada

ABSTRACT

Improvement of drought resistance of cereals through the use of physiological and morphological traits is a complex, time-consuming process. Traits must be fully evaluated in terms of heritability and relationship to yield under various environmental conditions before breeding strategies can be developed and put into use. Since there are so many factors, both within the plant and in its environment, involved in the response to drought, progress towards improving drought resistance will be much more difficult than the gains that have been made in areas such as rust resistance of wheat. Progress is likely to be greatest where there is a research team of sufficient size and which receives adequate long-term funding.

Germplasm screening, preservation, and exchange plays an important role, and will continue to be of great importance in the future, in efforts to improve drought resistance of cereals. There is inadequate variability for many potentially useful drought resistance traits in the germplasm pools used by cereal breeders in many countries. We should all, therefore, be encouraged to collect, screen, preserve, and exchange germplasm, as well as to share information and ideas, to broaden the genetic bases of our major crops, and to foster progress in drought resistance improvement.

We have sufficient knowledge, in general terms, of how to go about using physiological techniques in breeding for drought resistance. Our challenge is to fully evaluate and start using physiological and morphological traits in practical breeding programmes.

INTRODUCTION

Drought resistance improvement through plant breeding is an extremely complex problem. This complexity arises because of the number of physiological, morphological, and biochemical systems within the plant which are related to drought resistance. Compensation of one system for another and interactions with the environment make it even more difficult to correlate physiological or morphological traits with yield under drought conditions (Jordan *et al.*, 1983; Clarke *et al.*, 1984). Therefore, an integrated approach to the problem is required, as suggested in the literature (Townley-Smith and Hurd, 1979). Unfortunately, however, very few good integrated investigations have been made. Many isolated studies of drought resistance mechanisms have been conducted and published, but little attempt has been made to relate this knowledge to the crop system as a whole.

Yield has, and always will be, an important selection criterion in breeding for drought resistance, since performance at the whole-plant level integrates genotypic and environmental factors. In environments with considerable year-to-year variation in precipitation, highly drought-resistant genotypes may not be desirable, given that such genotypes are often unresponsive to favourable moisture conditions. Genotypes with a high-yield potential buffered by a few drought resistance traits will yield well under favourable conditions and not substantially less than highly drought-resistant genotypes under drought conditions. The challenge to plant and environment scientists, with of course the cooperation of breeders, is to improve the success of selecting genotypes with high and stable yields under drought stress.

USE OF PHYSIOLOGICAL TECHNIQUES IN BREEDING

An integrated approach to drought resistance in a breeding programme should consist of several major steps (Table 1). First, the drought problem in the target environment must be defined, including the consistency of the incidence of drought and its timing in relation to crop development. From this information a partial crop ideotype can be developed, with particular emphasis on matching crop phenology to the target environment. In some environments, for example, it may be possible to choose either winter or spring growth habits, or to select the most appropriate planting date. The

Table 1. Approaches to improvement of drought resistance in cereals

1. Define the drought problem and propose ideotypes.
2. Identify drought resistance traits and develop screening techniques.
3. Evaluate trait heritability and relationship to yield.
4. Screen germplasm for suitable sources of the trait.
5. Utilize appropriate sources in breeding programmes.

Table 2. Useful traits for cereal ideotypes for various drought stress environments

Environment	Resistance mechanism	Useful traits
1. Continuously increasing stress	Stress avoidance (conserve water for grain-fill)	Reduced tillering Excised-leaf water retention Reduced seminal root xylem vessel diameter Glaucousness Early maturity
	Stress tolerance	Photosynthesis at low water potential Osmoregulation
2. Early-season stress	Stress tolerance	Germination at low soil moisture levels Osmoregulation Photosynthesis at low water potential
3. Stress during grain-fill	Stress avoidance	Glaucousness, leaf rolling Extensive root system Remobilization of pre anthesis carbohydrates
	Stress tolerance	Heat tolerance Osmoregulation Photosynthesis at low water potential

desirability of various drought resistance traits will vary somewhat with the stage of crop development at which stress occurs (Table 2). Water conservation mechanisms (drought avoidance) tend to be more important when the crop is grown under conditions of limited water supply and continually increasing stress than when stress occurs during grain-filling only. Drought tolerance mechanisms are desirable in the latter situation to maximize photosynthetic productivity.

The second major step is the identification of morphological, physiological, or biochemical traits related to drought resistance. Before this can be done, the physiologist must have a range of apparently drought-resistant and sensitive genotypes to study. Finding such genotypes is not always easy. For example, does one study high and low yielding lines with the assumption that the yield difference is due to drought resistance differences? This approach will possibly miss important traits which often are found in low-yielding or otherwise agronomically unsuitable genotypes. It may be preferable to rate

drought resistance by comparing relative yield depression by drought, such as by a drought susceptibility index (Fischer and Maurer, 1978), when choosing genotypes for use in physiological studies. This approach too, in my experience, may be unsatisfactory where there is year-to-year variation in timing and intensity of drought stress.

During the search for traits, it is important to study as many genotypes as possible. I suggest using at least twelve genotypes, or more if possible, to address the expected genetic variation for a trait, since empirical studies with two or three genotypes quite often lead to erroneous conclusions. This is not to say that basic drought physiology studies of a few genotypes are of no use—indeed, such studies frequently provide the information and stimulus to plan applied studies. The use of near-isogenic pairs can be a valuable tool for evaluating drought resistance traits (Johnson *et al.*, 1983). Even here, however, one should probably look at several pairs derived from diverse sources of the trait being evaluated to get some idea of the effect of 'genetic environment' on the trait.

When an interesting trait is identified and suitable screening techniques for identifying it have been developed, the third major phase of the study is to evaluate the heritability of the trait and its relationship to yield under drought conditions. Unfortunately, this important step has been taken with very few proposed drought resistance traits, resulting in many potential screening techniques being passed over by breeders unwilling to commit scarce resources to screening for unproven traits. To fully evaluate the heritability and utility of the trait, it is probably best to use diverse sources of the trait, screened from germplasm collections, in crosses with adapted genotypes. If the drought resistance trait proves to be heritable and related to yield under water stress conditions, breeding strategies can be developed and further germplasm screening can be undertaken.

There are many reports in the literature of potential drought resistance traits in cereal crops (Table 3), and since many of these have been reviewed elsewhere (Clarke, 1981; Simpson, 1981; Townley-Smith and Hurd, 1979), it is unnecessary to do so here. The utility of particular characteristics as selection criteria in a breeding programme will depend upon the ease and cost of screening as well as upon the heritability. Traits that are highly heritable and related to an easily measured agronomic trait such as yield may require little or no screening other than to select suitable parents. Ease of screening will also determine the stage of the breeding process at which the procedure can be applied.

Screening for root system size, for example, is labour intensive and only relatively low numbers of genotypes can be screened. This technique, therefore, is more likely to be applied to a search for potential parental genotypes than to screening of hybrid lines. Townley-Smith and Hurd (1979) noted that selection of potential parents with drought resistance traits, no matter how

Table 3. Examples of proposed wheat drought resistance traits

Mechanism	Trait	Screening capability*	Reference
1. Drought avoidance			
(a) Water uptake			
	Extensive root system	L	Hurd (1968)
	Reduced xylem vessel size in seminal root	L–M	Passioura (1972) Richards and Passioura (1981b)
(b) Reduction of water loss			
	Stomate number	L	Kazemi *et al.* (1978)
	Stomatal conductance	L–M	Jones (1977)
	Abscisic acid	L	Wright (1977)
	Leaf temperature	H	Blum *et al.* (1982)
	Excised-leaf water loss	H	Clarke and McCaig (1982b)
	Epicuticular waxes	M	Johnson *et al.* (1983)
2. Drought tolerance			
	Germination in osmoticums	M–H	Gul and Allen (1976)
	Seedling growth in osmoticums	M	Blum *et al.* (1980)
	Photosynthetic rate	L	Kaul and Crowle (1974)
	Osmoregulation	L	Morgan (1983)
	Heat tolerance	M	Smika and Shawcroft (1980)

*L = low numbers of genotypes; M = moderate; H = high.

cumbersome, is useful because it reduces the number of crosses that the breeder has to make and evaluate. Conversely, a rapid screening technique such as leaf temperature measurement with an infrared thermometer can be used to process thousands of lines, and can be applied at any stage of cultivar development.

Although we have at our disposal many sophisticated and expensive instruments for use in physiological studies, we should not overlook simpler technologies which may in fact be faster and more easily used in breeding programmes. As I have already mentioned, rapid screening techniques can be more readily used at any stage of cultivar development than can slower techniques. Visual screening techniques are particularly versatile and can be of considerable practical value. O'Toole *et al.* (1984), for example, found that a visual leaf-rolling score was a good indicator of water stress in rice. Gravimetric techniques, such as the one I will discuss below, also show promise and do not require sophisticated or expensive technology.

We have, I believe, sufficient knowledge of how to go about using physiological techniques in breeding for drought resistance. Our major thrust

should now be to put together research teams to identify new or confirm previously suggested drought resistance traits, and then to take the necessary further steps to evaluate the traits for use in practical breeding programmes. It has to be recognized by research administrators and funding agencies, however, that such research teams require long-term financial support in order to make significant gains. Those unfamiliar with plant breeding are always taken aback when informed that crosses made now may, if all goes well, produce new cultivars in 12–16 years. It is clear, then, that research teams established now will take a number of years to begin producing drought-resistant cultivars.

With this brief general discussion of techniques, I would now like to discuss several traits which have been studied in sufficient detail to at least obtain a preliminary assessment of their utility in practical wheat-breeding programmes. My emphasis on excised-leaf water retention capability at the expense of other traits is not entirely because of my personal bias, but reflects an attempt to avoid topics that are likely to be covered in more detail by other participants in this seminar.

PROMISING SELECTION TRAITS FOR WHEAT

Excised-leaf water retention

The history of this trait goes back almost 50 years. Bayles *et al.* (1937) observed differences among spring wheat (*Triticum aestivum* L.) cultivars in the rate at which excised plants lost water. Twenty years later, Sandhu and Laude (1958) observed that excised plants of drought-resistant winter wheat cultivars lost water more slowly than less resistant cultivars. More recently, Dedio (1975) found differences in excised-leaf water loss rate among wheat genotypes (*T. aestivum* L. and *T. turgidum* L. var. durum). These reports suggested that excised-leaf water loss rate was perhaps a drought resistance screening trait worthy of further investigation. As a result, the wheat physiology/breeding team at Swift Current began detailed investigations of the trait in 1980.

The first studies looked at environmental and phenological influences on the trait. Differences in water loss rate were observed among genotypes grown under rainfed and irrigated conditions in the field (Clarke and McCaig, 1982a). Leaves sampled from irrigated plots lost water more quickly than those from rainfed plots (Table 4), which indicated that drought hardening influenced water loss rate. This was later confirmed by Jaradat and Konzak (1983). There tend to be some genotype–environment interactions for expression of the retention trait, but these usually consist more of changes of ranking than of changes in significant differences among genotypes. Consequently, it should be possible to screen for the trait under a variety of

Table 4. Excised-leaf water loss by durum wheat leaves sampled from rainfed and irrigated environments (6-h wilting period)

Cultivar	Water loss (g/g) Rainfed	Irrigated
Cando	1.22	1.62
Coulter	1.26	1.72
Hercules	1.09	1.46
Lakota	1.18	1.70
Macoun	1.19	1.80
Pelissier	0.77	1.31
Wascana	1.15	1.69
Wakooma	1.00	1.58
AS5	1.12	1.61
CC2B	1.01	1.67
DT363	1.03	1.48
DT367	1.04	1.75
EZ2E	1.00	1.60
HB5C	1.09	1.57
KA3	1.10	1.34
S3	1.01	1.63
Mean	1.08	1.60

Source of variation	DF	Mean square
Environment	1	12.921*
Error A	10	0.283
Cultivar	15	0.155*
C × E	15	0.041
Error B	150	0.051

*Significant $P < 0.01$.

environmental conditions. However, preliminary studies indicated that relative water loss rate of some cultivars differs in field- compared to greenhouse-grown plants (Clarke, 1983), so it may not be possible to screen genotypes in controlled environments.

Differences among cultivars tend to disappear after anthesis, so the retention trait is operative only during the vegetative growth stage. It is not clear whether the change after anthesis is due to physiological changes or to physical factors such as leaf 'firing'. In any event, it is preferable to screen material prior to anthesis.

The simplicity of measuring excised-leaf water retention gravimetrically

makes it very attractive, both from the standpoint of speed and cost. It may be possible to rate excised-leaf water retention visually as well (Clarke and McCaig, 1982a). Visual rankings could separate high and low retention types and it may be possible to select the top lines from a segregating population in this manner.

There is a potential interaction between rolling of excised leaves and retention capability. We have observed differences among and within genotypes in degree and rate of rolling. Rolling reduces the rate of water loss by excised leaves, but it is clearly not the only factor causing the genotypic differences in water loss rate (Figure 1). So far, we have been unable to relate ratings of leaf rolling, using a scale similar to that of O'Toole and Moya (1978), in excised leaves with that of intact leaves on field-grown plants. We have had great difficulty in scoring leaf rolling in field material and question its importance as a drought avoidance trait in our environment. Jones (1979)

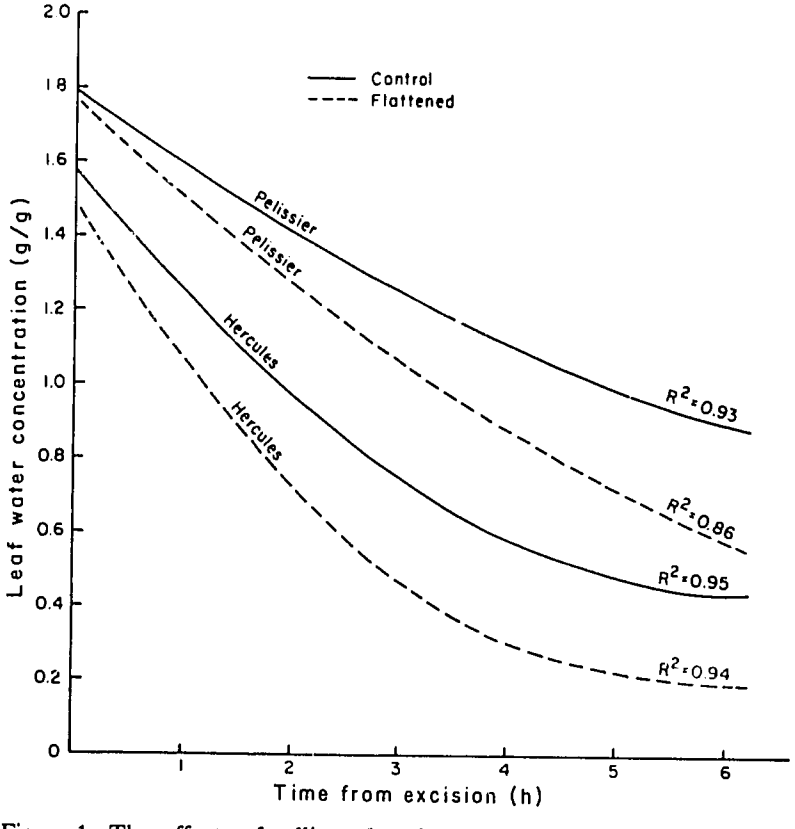


Figure 1. The effects of rolling of excised Pelissier and Hercules durum wheat leaves on rate of water loss (control leaves allowed to roll normally, flattened leaves held flat during the wilting period)

reported that leaf rolling of wheat was poorly correlated with leaf water potential.

After it was confirmed that the excised-leaf technique showed some promise we refined our sampling procedures to allow handling of substantial numbers of genotypes. A set of sampling dishes was constructed, which allowed convenient processing of 200 plots at a time. Three people can take

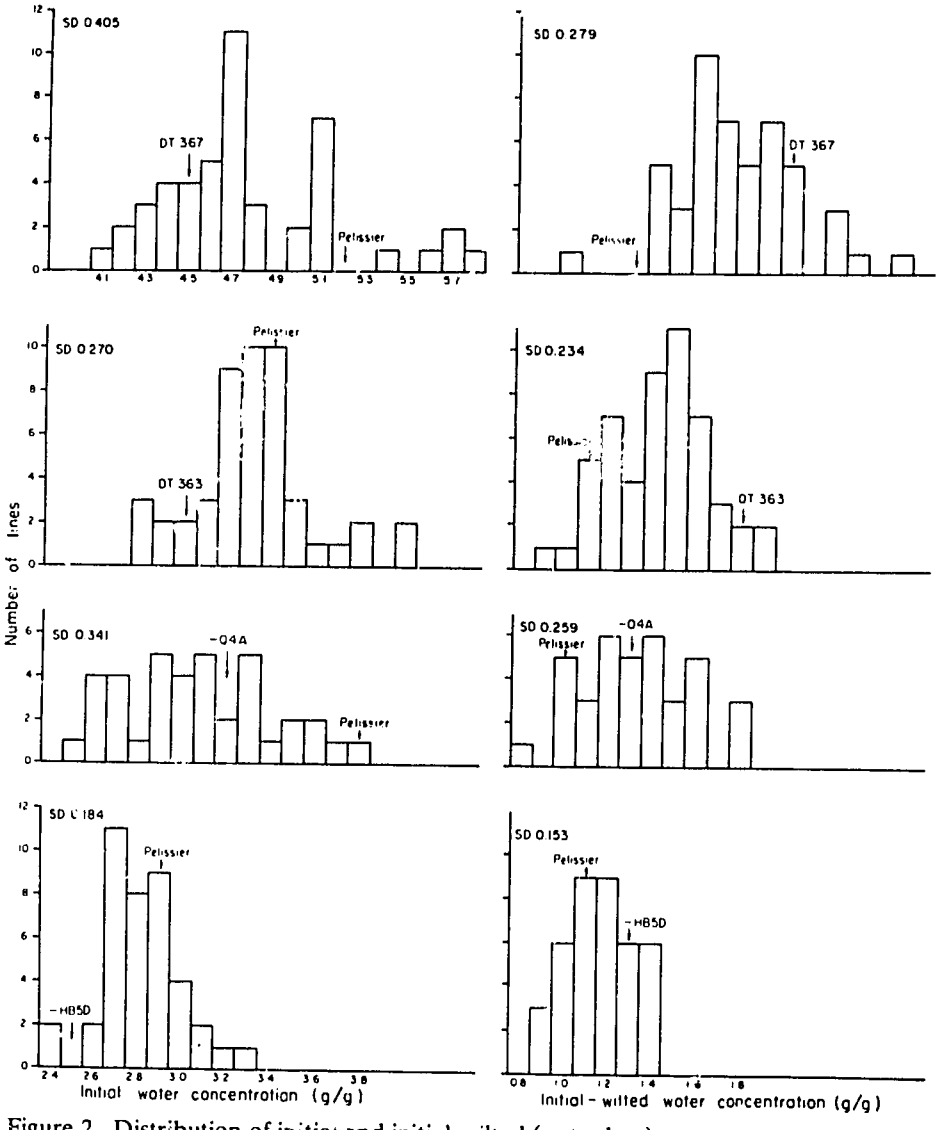


Figure 2. Distribution of initial and initial-wilted (water loss) water concentrations of excised leaves of the F_8 lines and parents of four durum wheat crosses

the samples, which consist of four to six of the newest, fully expanded leaves per plot, in about 30 minutes. Weighing on an electronic balance interfaced with a portable data entry terminal (PDET) or microcomputer takes one person a further 20 minutes per weighing. The samples are weighed three times during routine screening: immediately after sampling, after a period of wilting, and after oven drying. Previously we used a wilting period of 6 h in a controlled temperature room (20°C, 50% RH), followed by oven drying overnight. This allowed us to sample 200 plots per day. More recently we have switched to wilting the leaves for 2 h at 28-30°C, followed by high-temperature drying in an oven for about 1 h. This has enabled us to sample 400 plots per day—200 in the morning and 200 in the afternoon.

The next step in the evaluation of the excised-leaf water-retention trait was to determine its heritability and relationship to yield. Preliminary studies of durum wheat lines from a high-retention (Pelissier) by low-retention (Hercules) cross indicated a positive relationship between water retention and yield (Clarke and McCaig, 1982b). Eight crosses were made to further evaluate this relationship, all involving the high-retention parent Pelissier. Lines were field tested in the F_4, F_6, and F_8 generations (Clarke and Townley-Smith, 1986). Forty to 50 random lines from each cross were grown in the F_4 and F_6 generations; only the four crosses exhibiting the greatest differences were grown in the F_8.

The distribution of initial water concentration and leaf water loss of the lines varied among crosses (Figure 2). In all crosses and years, initial water concentration of Pelissier tended to be near the high end of the distribution, and leaf water loss tended to be near the low end of the range. The distributions of leaf water loss do not support Dedio's (1975) hypothesis that the high-retention parent contributes one or a few dominant genes governing retention.

Table 5. Standard unit heritabilities for initial leaf water concentration and excised-leaf water loss determined by regressing F_4 on F_6 and F_6 on F_8, for durum wheat crosses

	F_4/F_6		F_6/F_8	
Cross	Initial water concentration	Loss	Initial water concentration	Loss
DT363/Pelissier	0.61†	0.49†	0.34*	0.36†
DT367/Pelissier	0.08	0.30*	0.41†	0.10
7461-Q4A/Pelissier	0.10	0.39*	0.38*	0.38*
7562-HB5D/Pelissier	0.34*	0.14	0.15	0.31

*Correlation coefficient significant at $P < 0.05$ (n = 39–50).
†Correlation coefficient significant at $P < 0.01$ (n = 39–50).

Both initial water concentration and leaf water loss were heritable in some crosses and years (Table 5). The two characters showed consistent heritability in DT363/Pelissier and 7461-Q4A/Pelissier, while in 7562-HB5D/Pelissier there was low heritability for the characters. The apparent lack of heritability in the latter cross is not surprising because of the narrow difference in water concentration between the parents. Similarly, intrageneration heritability estimates were greater than 0.30 for over 70 per cent of the cross-years. That some of the heritabilities were high is encouraging in light of the number of environmental and physiological factors interacting with the water loss rates of excised leaves.

Correlations between yield and leaf water loss were generally low and non-significant. Comparisons of the yields of the ten fastest and ten slowest water losers within crosses and years, however, showed significant differences in most crosses (Table 6). Where yields were different, fast water losers outyielded slow water losers in some cross-years, while slow water losers outyielded fast water losers in other cross-years.

This differing pattern was probably due to both genetic and environmental factors. In the case of DT367/Pelissier and DT363/Pelissier, for example, excised-leaf water retention capability was yield-negative in the high-yield environments of 1982 and 1983, but yield-positive under severe drought conditions in 1984, suggesting that the water-retention trait is only beneficial under drought conditions. Similarly, leaf diffusive resistance of wheat was negatively correlated with yield in a well-watered environment (Shimshi and Ephrat, 1975), but positively correlated under water stress (Jones, 1977). The crosses 7461-Q4A/Pelissier and 7562-HB5D/Pelissier, however, showed the water-retention trait to be yield-positive or yield-neutral regardless of environment. We are growing some of the lines under rainfed and irrigated conditions to further study the yield relationship.

An area of the excised-leaf water-retention trait that we have ignored is the underlying physiological or morphological reasons for the differences which

Table 6. Grain yields of fast and slow excised-leaf water-losing durum wheat lines

Cross	F_4 yield* (1982) (g/m²)		F_6 yield (1983) (g/m²)		F_8 yield (1984) (g/m²)	
	Fastest	Slowest	Fastest	Slowest	Fastest	Slowest
DT363/Pelissier	453†	440	334‡	320	149	155‡
DT367/Pelissier	406†	395	334‡	318	4.8	6.2†
7461-Q4A/Pelissier	422	444‡	289	301†	151	150
7562-HB5D/Pelissier	303	367‡	280	286	141	151†

*Yields of ten lines with fastest and ten lines with slowest excised-leaf water loss rate.
†Marked means significantly greater at $P < 0.05$ according to t-test.
‡Marked means significantly greater at $P < 0.01$ according to t-test.

we and others have observed. Presumably, one is largely measuring cuticular transpiration (Jordan *et al.*, 1984), since our measurements of excised leaves with a porometer indicate very rapid and complete closure of stomata following leaf excision. Membrane permeability to water and concentrations of osmotically active compounds may be involved as well. Recently we acquired instruments which will allow us to investigate the relationship between leaf water-retention capability and factors such as photosynthetic rate, water potential, and stomatal diffusive resistance.

Preliminary field studies of the relationship between excised-leaf water-retention capability and stomatal diffusive resistance show either no relationship or a low-order negative correlation (Table 7). In theory, if the excised-leaf technique is measuring cuticular transpiration, there is not necessarily a relationship between stomatal diffusive resistance and water-retention capability. However, a correlation could arise through mutual association of the two factors with a third factor such as membrane permeability to water or accumulation of osmotically active compounds.

We have screened numerous genotypes for the leaf water-retention trait. In 1984 we screened over 4000 durum lines obtained from ICARDA (International Center for Agricultural Research in the Dry Areas) via the University of Saskatchewan. All of these lines are contained in the USDA Small Grains Collection. A broad range of excised-leaf water-retention capabilities was observed in this material, ranging from better than our best local check, Pelissier (which, incidentally, was introduced into North America from Algeria in 1905), to worse than our worst local check (Table 8). The lines were also rated for other agronomic traits such as height and maturity, and for morphological traits such as leaf size and attitude, tillering, glaucousness, and leaf rolling.

Table 7. Correlations between excised-leaf water loss and stomatal diffusive resistance of field-grown durum wheats in 1985

Trial	Environment	Date	Correlation coefficient r	Number of observations n
Cultivar screening	Rainfed	14 June	0.10	150
Cultivar screening	Irrigated	14 June	0.03	150
Cultivar screening	Rainfed	27 June	−0.21*	150
Cultivar screening	Rainfed	11 July	−0.26*	150
Cultivar screening	Irrigated	11 July	−0.31*	150
Durum crosses	Irrigated	26 June	−0.08	196
Durum crosses	Rainfed	10 July	−0.11	196
Durum crosses	Irrigated	10 July	−0.13	196
Germplasm screening	Rainfed	28 June	−0.34*	192

*Significant $P < 0.01$.

Table 8. Excised-leaf water loss ratings of 3560 durum genotypes of diverse origin grown at Swift Current, Canada, in 1984

Water loss	Class‡	Number of lines
Very low	< 0.53	116
Low*	0.53–0.84	815
Moderate	0.85–1.13	1217
High†	1.14–1.61	1045
Very high	> 1.61	367

*Range of best local check (Pelissier).
†Range of poorest local check (Hercules).
‡Relative to mean of four check cultivars (Pelissier, Hercules, Kyle, Wakooma).

In 1985, 640 of the lines, representing high- and low-retention types, were selected within several of the agronomic and morphological classes for further field studies in replicated tests. We hope to identify high-retention parents to utilize in crosses to further evaluate the retention trait as well as to assess the relationship between retention capability and agronomic/morphological traits.

The excised-leaf water-retention capability may be of interest in other cereals as well. We screened triticale (*X-Triticosecale* Wittmack) lines from the 1981–2 CIMMYT International Triticale Screening Nursery and found genotypic differences of similar magnitude to those observed in wheat. Jordan *et al.* (1984) concluded that measurement of water loss from excised leaves of sorghum (*Sorghum bicolor* L. Moench) was a fast, simple way to measure a cuticular transpiration rate.

In summary, the excised-leaf water-retention trait seems to be somewhat heritable, and is positively related to yield under drought stress. Sophisticated technology is not required to screen for the trait, and large numbers of samples can be processed with small labour input. Further research is required to develop practical selection strategies for the trait and to confirm its desirability in particular environments.

Root characteristics

Root systems have been of interest in drought resistance studies. Wheat genotypes with extensive root systems have been suggested for environments with moisture available deep in the soil profile (Hurd, 1974). For wheat crops grown essentially on stored soil moisture alone, however, Passioura (1972) suggested a reduction in root system size to conserve water for the grain-

filling growth period. A reduction in effective root system size can be made by reducing xylem vessel size in seminal root axes or by reducing the numbers of seminal root axes (Richards and Passioura, 1981a). Through screening of wheat germplasm, Richards and Passioura (1981b) concluded that reduction of xylem vessel size was the most effective means of reducing effective root system size because of more genetic diversity and higher heritabilities than for a number of seminal axes. The heritability estimates obtained by Richards and Passioura (1981b) for reduced xylem vessel size (narrow-sense 52 per cent, broad-sense 71 per cent) suggest that the trait could be very useful in breeding programmes. Variation in xylem vessel size has been reported in barley (*Hordeum vulgare* L.) as well (Irvine and Therrien, 1985).

Epicuticular waxes

Epicuticular wax depositions produce glaucousness or 'bloom' on plant surfaces, and appear to be a drought resistance characteristic in many species, including wheat (Fischer and Wood, 1979). Total wax deposition in sorghum tends to increase under hot, dry conditions (Jordan *et al.*, 1983), but there is no consistent relationship between wax amounts and glaucousness. Rather, glaucousness seems to be related to the composition and pattern of deposition of wax (Troughton and Hall, 1967). In a study of near-isogenic wheat lines, Johnson *et al.* (1983) reported that glaucous lines outyielded non-glaucous lines in irrigated and rainfed situations but not in extremely dry environments. These authors concluded that glaucousness did not appear likely to limit yields in non-drought environments. Glaucousness reduced photosynthetic rate in sorghum (Chatterton *et al.*, 1975). Selection for glaucousness in a breeding programme should be quite easy and rapid, either by visual means or by measurement of reflectivity.

Osmoregulation

Osmoregulation, the adjustment of osmotic potential through accumulation of solutes, contributes to the ability of plants to tolerate water deficits. It has been demonstrated in sorghum and sunflower that the water potential at which stomata closed decreased as osmotic potential decreased, thereby ensuring maintenance of gas exchange and photosynthesis under water stress (Turner *et al.*, 1978).

Morgan (1983) has proposed, and currently uses, screening of wheat genotypes for osmoregulation in a breeding programme. He screens lines by applying artificial stress in the greenhouse. Under field drought conditions, lines selected for high osmoregulation yielded 1.6 and 1.5 times greater than low osmoregulation lines in the F_4 and F_6 generations, respectively. Moderate

numbers of advanced breeding lines or potential parents can be screened using this technique.

Leaf temperature

Measurement of leaf or canopy temperature has received some interest as a drought resistance screening technique, particularly with the advent of portable infrared thermometers. Ehrler *et al.* (1978) reported that wheat canopy temperature provided a good indication of plant water potential when comparing environments with varying degrees of water stress. Clarke and McCaig (1982a) found, however, that a hand-held infrared thermometer detected no consistent differences among wheat cultivars within environments. Significant correlations between leaf temperature and leaf water potential of wheat genotypes were reported by Blum *et al.* (1982). Genotypic variation in leaf temperature has also been observed in soybean (*Glycine max* L. Merr.) grown in stressed environments (Harris *et al.*, 1984).

Although remote measurement of leaf temperature can be extremely fast and simple, the technique has several limitations. Some degree of drought stress is required to obtain an expression of genotypic differences (Blum *et al.*, 1982; Harris *et al.*, 1984), which would limit the consistency with which a breeder could use the technique. A second major limitation is that remote leaf temperature measurement requires a dense canopy which covers the soil surface (Clarke and McCaig, 1982a; Blum *et al.*, 1982), since high soil surface temperatures would bias the leaf temperature measurements. This limitation makes it impossible to use infrared leaf temperature measurement on early-generation lines where seed availability limits plot size, and also limits the time available to make measurements on larger plots. In our environment, for example, we have a very limited 'window of opportunity' for measuring leaf temperature between canopy closure and leaf necrosis. Indeed, under extreme drought stress, complete canopy closure may never be achieved.

Remobilization of stored carbohydrates

There is evidence to suggest that remobilization of non-structural carbohydrates accumulated during the vegetative growth phase contributes to grain filling in cereal crops subjected to postanthesis stress (Bidinger *et al.*, 1977). As well, there are genotypic differences in the amount of non-structural carbohydrates (McCaig and Clarke, 1982) and in the remobilization of carbohydrate as suggested by stem weight loss after anthesis (Rawson *et al.*, 1977).

Screening for either non-structural carbohydrates or postanthesis stem weight loss would be rather tedious in a breeding programme. Blum *et al.*

(1983) have proposed a technique to measure remobilization indirectly. The technique consists of simulating postanthesis stress by application of desiccants to kill photosynthetic tissue. Grain size is subsequently evaluated to determine ability to maintain grain growth through remobilization. Such a screening procedure would be quite rapid, but variations in the date of anthesis among genotypes would have to be accounted for.

REFERENCES

Bayles, B. B., Taylor, J. W. and Bartel, A. T. 1937. Rate of water loss in wheat varieties and resistance to artificial drought. *J. Am. Soc. Agron.* **29**:40–52.

Bidinger, F. R., Musgrave, R. B. and Fischer, R. A. 1977. Contribution of stored preanthesis assimilate to grain yield in wheat and barley. *Nature* **270**:431–433.

Blum, A., Sinmena, B. and Ziv, O. 1980. An evaluation of seed and seedling drought tolerance screening tests in wheat. *Euphytica* **29**:727–736.

Blum, A., Mayer, J. and Gozland, G. 1982. Infrared thermal sensing of plant canopies as a screening technique for dehydration avoidance in wheat. *Field Crops Res.* **5**:137–146.

Blum, A., Boiarkova, H., Golan, G. and Mayer, J. 1983. Chemical desiccation of wheat plants as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. *Field Crops Res.* **6**:51–58.

Chatterton, N. J., Hanna, W. W., Powell, J. B. and Lee, D. R. 1975. Photosynthesis and transpiration of bloom and bloomless sorghum. *Can. J. Plant Sci.* **55**:641–643.

Clarke, J. M. 1981. Case examples of research progress in drought-stress physiology: wheat. In *Water Stress on Plants* (Simpson, G. M., ed.). Prager Scientific, New York.

Clarke, J. M. 1983. Differential excised-leaf water retention capabilities of *Triticum* cultivars grown in field and controlled environments. *Can. J. Plant Sci.* **63**:539–541.

Clarke, J. M. and McCaig, T. N. 1982a. Evaluation of techniques for screening for drought resistance in wheat. *Crop Sci.* **22**:503–506.

Clarke, J. M. and McCaig, T. N. 1982b. Excised-leaf water retention capability as an indicator of drought resistance of *Triticum* genotypes. *Can. J. Plant Sci.* **62**:571–578.

Clarke, J. M. and Townley-Smith, T. F. 1986. Heritability and relationship to yield of excised-leaf water retention in durum wheat. *Crop Sci.* **26**. In press.

Clarke, J. M., Townley-Smith, T. F., McCaig, T. N. and Green, D. G. 1984. Growth analysis of spring wheat cultivars of varying drought resistance. *Crop Sci.* **24**:537–541.

Dedio, W. 1975. Water relations of wheat leaves as screening tests for drought resistance. *Can. J. Plant Sci.* **55**:369–378.

Ehrler, W. L., Idso, S. B., Jackson, R. D. and Reginato, R. J. 1978. Wheat canopy temperature: relation to plant water potential. *Agron. J.* **70**:251–256.

Fischer, R. A. and Maurer, R. 1978. Drought resistance in spring wheat cultivars. I. Grain yield response. *Aust. J. Agric. Res.* **29**:897–912.

Fischer, R. A. and Wood, J. T. 1979. Drought resistance in spring wheat cultivars. III. Yield association with morpho-physiological traits. *Aust. J. Agric. Res.* **30**:1001–1020.

Gul, A. and Allen, R. E. 1976. Stand establishment of wheat lines under different levels of water potential. *Crop Sci.* **16**:611–615.

Harris, D. S., Schapaugh, Jr, W. T. and Kanemasu, E. T. 1984. Genetic diversity in

soybeans for leaf canopy temperature and the association of leaf canopy temperature and yield. *Crop Sci.* **24**:839–842.

Hurd, E. A. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. *Agron. J.* **60**:201–205.

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. *Agric. Meteorol.* **14**:39–55.

Irvine, R. B. and Therrien, M. C. 1985. Effective xylem radius of the subcrown internode of barley (*Hordeum vulgare* L.). *Can. J. Plant Sci.* **65**:211–214.

Jaradat, A. and Konzak, C. F. 1983. Screening of wheat genotypes for drought tolerance: 1. Excised-leaf water retention. *Cereal Res. Comm.* **11**:179–186.

Johnson, D. A., Richards, R. A. and Turner, N. C. 1983. Yield, water relations, gas exchange, and surface reflectance of near-isogenic wheat lines differing in glaucousness. *Crop Sci.* **23**:318–325.

Jones, H. G. 1977. Aspects of water relations of spring wheat (*Triticum aestivum* L.) in response to induced drought. *J. Agric. Sci.* **88**:267–282.

Jones, H. G. 1979. Visual estimation of plant water status in cereals. *J. Agric. Sci.* **92**:83–89.

Jordan, W. R., Monk, R. L., Miller, F. R., Rosenow, D. T., Clark, L. E. and Shouse, P. J. 1983. Environmental physiology of sorghum. I. Environmental and genetic control of epicuticular wax load. *Crop Sci.* **23**:552–558.

Jordan, W. R., Shouse, P. J., Blum, A., Miller, F. R. and Monk, R. L. 1984. Environmental physiology of sorghum. II. Epicuticular wax load and cuticular transpiration. *Crop Sci.* **24**:1168–1173.

Kaul, R. and Crowle, W. L. 1974. An index derived from photosynthetic parameters for predicting grain yields of drought-stressed wheat cultivars. *Z. Pflanzenzuecht* **71**:42–51.

Kazemi, H., Chapman, S. R. and McNeal, F. H. 1978. Variation in stomatal number in spring wheat cultivars. *Cereal Res. Comm.* **6**:359–365.

McCaig, T. N. and Clarke, J. M. 1982. Seasonal changes in nonstructural carbohydrate levels of wheat and oats grown in a semiarid environment. *Crop Sci.* **22**:963–970.

Morgan, J. M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* **34**:607–614.

O'Toole, J. C. and Moya, T. B. 1978. Genotypic variation in maintenance of leaf water potential in rice. *Crop Sci.* **18**:873–876.

O'Toole, J. C., Turner, N. C., Namuco, O. P., Dingkuhn, M. and Gomez, K. A. 1984. Comparison of some crop water stress measurement methods. *Crop Sci.* **24**:1121–1128.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. *Aust. J. Agric. Res.* **23**:745–752.

Rawson, H. M., Bagga, A. K. and Bremner, P. M. 1977. Aspects of adaptation by wheat and barley to soil moisture deficits. *Aust. J. Plant Physiol.* **4**:389–401.

Richards, R. A. and Passioura, J. B. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* **21**:249–252.

Richards, R. A. and Passioura, J. B. 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* **21**:253–255.

Sandhu, A. S. and Laude, H. H. 1958. Tests of drought and heat hardiness of winter wheat. *Agron. J.* **50**:78–81.

Shimshi, D. and Ephrat, J. 1975. Stomatal behavior of wheat cultivars in relation to their transpiration, photosynthesis and yield. *Agron. J.* **67**:326–331.

Simpson, G. M. 1981. Case examples of research progress in drought-stress physiology: sorghum. In *Water Stress on Plants* (Simpson. G. M., ed.). Prager Scientific, New York.

Smika, D. E. and Shawcroft, R. W. 1980. Preliminary study using a wind tunnel to determine the effect of hot wind on a wheat crop. *Field Crops Res.* **3**:129–135.
Townley-Smith, T. F. and Hurd, E. A. 1979. Testing and selecting for drought resistance in wheat. In *Stress Physiology in Crop Plants* (Mussell, H. and Staples, R., eds.). John Wiley, New York.
Troughton, J. H. and Hall, D. M. 1967. Extracuticular wax and contact angle measurements on wheat (*Triticum vulgare* L.). *Aust. J. Biol. Sci.* **20**:509–525.
Turner, N. C., Begg, J. E. and Tonnet, M. L. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. *Aust. J. Plant Physiol.* **5**:597–608.
Wright, S. T. C. 1977. The relationship between leaf water potential and the levels of abscisic acid and ethylene in excised wheat leaves. *Planta* **134**:183–189.

DISCUSSION

H. Ketata

Are you satisfied with the criterion of water loss from excised leaves? I have noticed low heritability values, which varied with crosses and had an inconsistent correlation with yield.

J. M. Clarke

There is a requirement to further evaluate the relationship between water loss and yield, which we are doing. The heritabilities were variable, and should be looked at in other genetic backgrounds. I think this study illustrates the point I made earlier that it is very difficult to get a consistent relationship between potential drought resistance traits and yield. I think the trait looks promising, but a little more research will be required to develop appropriate breeding strategies.

S. K. Sinha

(1) What is the relationship between leaf water loss and the rate of transpiration?
(2) Are the leaves of low leaf water loss types small and thick?

J. M. Clarke

(1) I mentioned that we are just now beginning to evaluate such a relationship, and I cannot give a good indication of any relationship at this stage.
(2) At this point we have no indication of a strong relationship between loss and leaf morphology, but are investigating several morphological factors in relation to loss rates.

M. C. Saxena

(1) Regarding the technique, please could you indicate why you have decided upon a 2-h wilting period?
(2) What is the environmental condition (temperature, RH, etc.) in which the leaves are allowed to lose water?
(3) Could you quantify the classes (very low, low, moderate, high, very high water losses) for actual loss of water?

J. M. Clarke

(1) The wilting time is chosen to show good separation of genotypes and will vary with the temperature and humidity conditions under which wilting occurs.
(2) Presently we use 28–30°C at 25–36% RH, our ambient laboratory conditions.
(3) The classes were based upon the mean values of four check cultivars sampled at the same time. The classes were set so that the low-loss class corresponded to

the range for Pelissier (our low-loss rate check) and the high-loss category corresponded to the range for Hercules (high-loss rate check).

M. Tahir

(1) On the basis of your studies on water loss rate can you generalize whether tetraploid or hexaploid species have a lower water loss rate?

(2) What is the heritability of this trait?

J. M. Clarke

(1) I have observed a similar range of genetic variability for excised leaf water loss in *Triticum aestivum*, *T. durum*, and triticale.

(2) We have observed standard unit heritabilities of 30–45 per cent in about half of the cross/generation in the comparisons that we have studied.

D. Lawlor

Have you looked at the relationship of weight to leaf area, as leaf area determines the water loss in the field, and whether the leaf area/weight value in various types could be a source of error and confusion?

J. M. Clarke

I feel that in the absence of any large differences in leaf area/weight ratio, expression of water loss on the basis of leaf dry weight avoids this problem. So far we have not observed a great variation in leaf area/weight ratios.

M. Nachit

(1) Could you please elaborate on the use of leaf rolling techniques in the segregating populations and (2) its relationship with the leaf water retention, and (3) on the scores used for leaf water retention and which scores must have drought-resistant lines?

J. M. Clarke

(1) We looked at leaf rolling in both excised leaves and in the field, but could demonstrate no consistent relationship, partly because of extreme variability among plants within genotypes in the field.

(2) Rolling of leaves reduces water loss, both in the intact plant and in excised leaves. Differences among genotypes in the degree of rolling by excised leaves does not account for the major genotypic differences in water loss by excised leaves.

(3) The scores used for water loss in our germplasm screening were based on means of four repeated checks. I would say that low to very low loss rates could be useful in environments where conservation of water for use during grain filling is important.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

15

Stability of Performance of Cereals in Low-rainfall Areas as Related to Adaptive Traits

A. HADJICHRISTODOULOU
Agricultural Research Institute, Nicosia, Cyprus

ABSTRACT

Under low-rainfall conditions barley has been shown to be more stable than wheat. Yields of even the same variety, sown under uniform agronomic practices at several locations and years, vary significantly because of fluctuations in the environmental conditions, especially the amount and distribution of precipitation. Breeding for stability of performance under variable conditions is a complex and difficult task because selection pressure is variable and unpredictable. This affects the efficiency of traditional breeding programmes, as some useful genotypes may be discarded and those with only specific adaptation may be promoted. One of the approaches to improve stability is the identification of adaptive traits that affect yield response to environments, and formulation of a breeding programme to alleviate their adverse effects. This is achieved by studying the stability or plasticity of adaptive traits and their effects on consistency of performance. Screening techniques applicable to F_2 to F_5 generations or to yield trials are described for some adaptive traits.

The studies revealed that the optimum range for earliness should be determined for each region after a long-term testing, and this information can then be used to select plants within that range. The varieties tested differed in the stability of their heading date. The traits of high-tillering capacity per plant and high plasticity of tiller number per plant (low variance of tiller number per unit area) can be used for selecting consistently high-yielding lines. In segregating populations, plants with high and uniform tillering should be selected. A screening method for stability of number of tillers per unit area is described.

Varieties with stable height, high and stable thousand-grain weight, disease resistance, and awned spikes are expected to give high and stable performance.

INTRODUCTION

In moisture-limited areas, yields of cereals are low and variable. Breeding improved varieties appears the most efficient way to achieve high and stable yields in all environments in dry areas, in combination with suitable agronomic practices. Stability refers to consistency of high and above-average performance over a wide range of conditions and implies the genetic potential of varieties to exploit fully the available environmental resources. In the regression analysis models (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) these varieties will have the average regression coefficient $b = 1$, and as small a deviation from the regression as possible. Stable varieties will have $b = 0$ or close to zero. Hadjichristodoulou (1985) found that in most cases the highest-yielding varieties had $b = 1.0$.

Consistency in performance of new varieties plays a decisive role in their adoption by farmers. In this paper a review of the available experimental evidence on breeding for stability is presented, and the use of morphological and physiological traits as selection criteria for the development of cereal varieties with stable performance under unpredictable conditions of environment is discussed.

RESULTS AND DISCUSSION

Yield variation and its causes

Yields of cereals are known to vary widely with environmental conditions. To quantify this variation, cereal varieties selected in Cyprus were tested in eight different trials in 13–47 environments with more or less uniform management practices. The term environment here refers to different combinations of locations and years. The variation was very high, and barley yields ranged from 732 to 6142 kg/ha, durum wheat from 355 to 8636 kg/ha, bread wheat from 799 to 8636 kg/ha, and triticale from 2413 to 8523 kg/ha. Valid comparisons of these ranges among species could not be made because they were not necessarily grown in the same trials.

These significant variations in yield of the same varieties were caused by variations in environmental factors such as precipitation and its distribution, soil type and fertility, seed-bed preparation, temperature, weed control, and diseases and pests. In low-rainfall areas the annual amount and seasonal distribution of precipitation varies widely with year and location (Hadjichristodoulou, 1982). The relative contribution of precipitation to variation in yield in the Mediterranean region has been studied by Lomas and Shashoua (1973), Hadjichristodoulou (1982), and other workers. These studies revealed that the amount of precipitation explained 5–79 per cent and its distribution 61–93 per cent of the variation in yield, depending on the variety and country.

Breeding for stability

Variation in yield may be partitioned into the variation caused by genotype–location or genotype–year interactions. In the first case, varieties or populations with specific adaptation can be selected for each region, thus eliminating this source of variation. The year-to-year variations in the climatic conditions at a given location can be minimized by developing stable varieties (Allard and Bradshaw, 1964).

The available methods (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Lewontin, 1966) can be used to evaluate the fixed lines for stability of their performance, but not to develop such lines. Thus, there is a need to develop new procedures for breeding varieties with consistently high yield under diverse environmental conditions. To achieve this, it is necessary to develop suitable selection criteria for important adaptive traits, which can be used in segregating populations (F_2 to F_5) or in nurseries grown in one environment with increased probability that the selections will perform well in different environments as well.

An attempt was made to identify the morphological and physiological traits or yield components that are important contributors to yield under low-rainfall conditions and to study their influence on stability of performance. The traits studied are described below.

Tillering capacity

The number of productive tillers per unit area is one of the main yield components. Variations in tiller number usually cause variation in grain yield. Factors that affect tiller number per unit area are: (1) seed rate, seed-bed preparation, sowing depth, soil-moisture conditions at sowing and soon after, seed germinability, bird or insect damage, etc., and (2) tillering capacity of varieties.

In low-rainfall areas, even if all agronomic practices affecting stand are used correctly, drought conditions during the sowing period may affect the stand significantly (Hadjichristodoulou *et al.*, 1977; Photiades and Hadjichristodoulou, 1984). Thus, selection of varieties with a high plasticity for number of tillers per plant should alleviate the adverse effects of variations in stand establishment and result in a more stable number of tillers per unit area. To accomplish this, it is necessary to establish that plasticity of tiller number is genetically controlled. Several trials were conducted during 1981–5, which showed significant differences in the variance $s^2 \log x$ of tiller number per square metre among barley and wheat genotypes (Hadjichristodoulou, 1983, 1985).

Furthermore, studies on the relation between yield, tiller number per unit area, and variance of tiller number for six-row and two-row barley genotypes revealed that those with a low variance and a high mean tiller number per

square metre gave high and stable yields (Hadjichristodoulou, 1985). The implications of this finding in a breeding programme are:

(1) In spaced-sown segregating populations single plants with a high and uniform tillering only should be selected.

(2) In F_4 to F_6 generation, genetically fixed families are harvested in bulk and are normally tested in nurseries. These should be sown at low, medium, and high seed rates. Selected lines, expected to perform well under a wide range of conditions, should have a relatively high number of tillers at the lowest seed rate, a high mean, and a narrow range for number of tillers (Hadjichristodoulou, 1985).

Kirby and Faris (1972) discussed the effects of tillering on barley and suggested that under favourable conditions the low tillering types should produce the maximum yield but, in dry areas, high tillering might be necessary to exploit the environment fully.

Contrary to the finding of this study that high plasticity for number of tillers is required, Donald (1968) suggested breeding wheat ideotypes capable of producing only single culms. However, he acknowledged that, with single-culm ideotypes, partial failure of stand establishment or any winter killing will not be compensated by an increased rate of tillering by surviving plants. He stressed that a uniculm wheat seems to have prospective limitations in an environment of erratic seasonal rainfall, and concluded that one to three tillers per plant, according to environmental conditions, would suffice for dry areas.

Earliness

The time of maturity or heading affects yields. Studies on the effect of distribution of precipitation on grain yield showed that increased precipitation during heading to the maturity period of barley had positive effects on yield (Hadjichristodoulou, 1982). When a large number of unselected lines were screened in a given environment, the relation between heading date and yield was more or less curvilinear (Figure 1). The performance of lines varied with year, depending on the distribution of precipitation; relatively early lines produced high yields if drought occurred late in the growing season and relatively late-maturing lines if precipitation was adequate during the late stages of maturity.

In Cyprus, where about 50–100 lines each of barley, durum wheat, and bread wheat are tested each year at one to four locations, a study was conducted on the relation of heading date with yield. It was found that the heading date of the successful barley varieties fell within the range of 4 days earlier and 4 days later than that of Anthenais, a variety that has been a top yielder for 25 years (Hadjichristodoulou, 1981a). In durum wheat, the successful new varieties have a heading date 5–10 days earlier than the

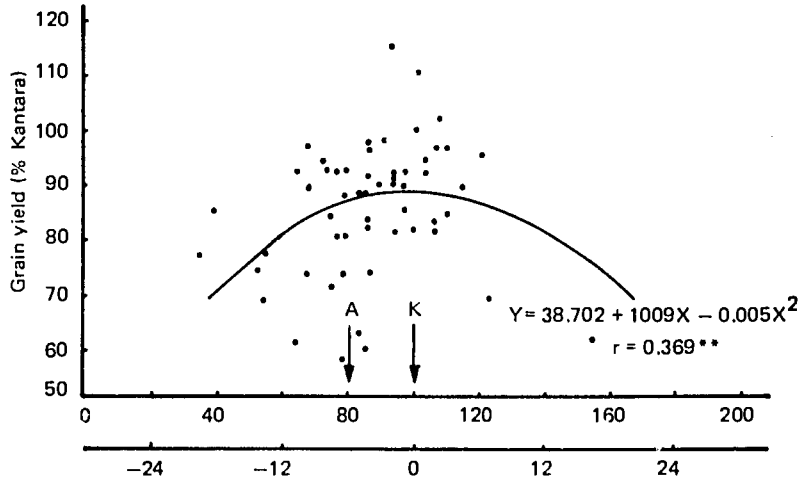


Figure 1. Heading date: above as percentage of Kantara, below as differences in actual number of days

heading date of the local variety, Kyperounda (Hadjichristodoulou and Kari, 1984). It can be concluded that:

(1) The unpredictable complex interactions between earliness and distribution of precipitation in dry areas complicate breeding for stability.

(2) For each region an optimum earliness range can be determined after long-term studies with a large number of genotypes. In breeding for stability of performance, single plants or genetically fixed lines expected to perform well must have a crop duration within that optimum range. Once this optimum is established, plants can be selected from segregating populations for that range.

Plant height

Under conditions of uncertain amounts of precipitation and its distribution, a line may grow too tall and lodge under good moisture conditions or be too short in dry seasons. The variations in plant height may become one of the causes of variation in grain yield. In Cyprus, lines grown at a dry location resulted in 2 per cent lodging (short plants), while at a wetter location lodging was 35 per cent (tall plants). Tall varieties tended to give higher yield than short varieties at the location where plants were short (Hadjichristodoulou, 1981a). By contrast, at the location where plants were tall and lodged, short varieties gave higher yields. In Cyprus, the mean height under dryland conditions of the highest-yielding wheat varieties is 75–85 cm and of barley 80–95 cm.

The variation in yield caused by instability of height can be eliminated by breeding varieties for less-variable height. Evidence for significant differences among varieties for the variance of plant height in barley was presented by Hadjichristodoulou (1981a) and in durum wheat by Hadjichristodoulou and Kari (1984).

Significant differences in stability ($s^2 \log x$) of plant height were found in Cyprus in the 1981–2 season for some of the 42 wheat genotypes tested in eighteen environments (range for $s^2 \log x$ of 0.004–0.0018). The tall varieties were more variable in height when non-transformed data were used ($r = 0.64$, $P < 0.05$), but when transformed data were used there was no significant correlation between plant height and variance ($r = 0.08$ NS).

In barley, significant differences were obtained in $s^2 \log x$ for height, range 0.004–0.017 for 45 six-row types and 0.004–0.013 for 15 two-row types. For six-row types there was a positive correlation ($r = 0.55$; $P < 0.05$) between plant height and variance of non-transformed data.

Screening for stability of height can be made by comparing the range of height of lines grown in two environments, one with optimum growing conditions and the other with moisture and soil fertility stress.

Thousand-grain weight

Under low-rainfall conditions in Cyprus, thousand-grain weight of barley genotypes was positively correlated with grain yield (Hadjichristodoulou, 1981a), but at Cambridge, UK, Pushman and Bingham (1975) working with winter wheat found non-significant correlations. In three trials grown at three locations in 1983–84, a significant correlation between grain weight and yield was found only in two trials at one location (Dromolaxia). At this location,

Table 1. Correlation coefficient between grain yield and thousand-grain weight of barley varieties (36 observations, 1983–4)

	Location					
	Laxia		Dromolaxia		Akhera	
Trial	r	Mean 1000-grain weight (g)	r	Mean 1000-grain weight (g)	r	Mean 1000-grain weight (g)
35/1/E	0.034 NS	36.6	−0.013 NS	32.8	0.271 NS	34.1
35/1/D			0.333*	35.5	0.157 NS	34.0
35/1/C			0.588*	31.4	0.141 NS	37.6

*$P < 0.05$.
NS = not significant.

the mean thousand-grain weight was lower than that at other locations and genotypes with a high thousand-grain weight tended to produce a high yield (Table 1).

If environmental conditions become favourable during the grain-filling period, the crop can compensate for a reduced number of tillers and/or lower number of flowers fertilized due to unfavourable conditions earlier in the season, by producing heavy grains. The thousand-grain weight will be lower if the crop suffers from stress during the grain-filling period. The observation made in this study and those reported by other workers suggest that under moisture stress certain genotypes can remain greener and produce better-filled grains than others. Assuming other effects to be equal, it is reasonable to believe that the adverse effect of moisture stress during the grain-filling period on the yield of such genotypes will be less than on fast senescing ones under moisture stress conditions. In such a case, the yield of genotypes with a high mean and low variance in thousand-grain weight will be affected less than the yield of those with a high variance, even if the mean is high. Variance for thousand-grain weight is a genetically controlled trait. All five barley varieties tested gave significantly different variances for thousand-grain weight (Hadjichristodoulou, 1981a). Kantara, a recently released variety in Cyprus after many years of testing, has a high mean thousand-grain weight and low variance.

Disease resistance

In general, diseases affect cereal crops more in high-rainfall areas than in dry areas. However, under certain conditions diseases may cause yield reductions even in low-rainfall areas (Hadjichristodoulou and Kari, 1985). Strategies to limit the effects of diseases have been discussed earlier (Hadjichristodoulou, 1981b). Breeding for disease resistance appears to be one of the most effective long-term strategies. Under varying rainfall conditions, performance of high-yielding lines resistant to diseases will be more stable than that of susceptible ones.

Awn length

Awns of cereals are generally believed to increase yields under low-rainfall conditions. Grundbacher (1963) reviewed the experimental evidence on this and concluded that in hot dry regions awns increased yields while in humid areas the effect of awns was variable. Similar conclusions were reached by Bingham (1974). The physiological mechanism of the awn function is not clear, but it is known that awn photosynthetic ability is affected by drought less than that of leaves (Grundbacher, 1963; Evans *et al.*, 1972, cited by Bingham 1974). Indeed, all barley and wheat varieties grown in low-rainfall

areas are awned. It can be concluded that in these areas awns contribute to high and stable performance. This trait is highly heritable and can be selected easily in segregating populations and in nurseries.

ACKNOWLEDGEMENTS

This work was supported by the Cereal Improvement Program of the International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, as part of the Collaborative Program between ICARDA and the Agricultural Research Institute, Nicosia. The author is thankful to the technical staff of the Institute for their assistance in field work and in recording and analysing the data.

REFERENCES

Allard, R. W. and Bradshaw, A. D. 1964. Implications of genotype–environment interactions in applied plant breeding. *Crop Sci.* **4**:503–508.

Bingham, J. 1974. Physiological objectives in breeding for high grain yield under irrigated and rainfed conditions. Pages 127–139 in *Proceedings of the 4th FAO/Rockefeller Foundation Wheat Seminar*, 21 May–2 June 1973, Tehran. FAO, Rome, Italy.

Donald, C. M. 1968. The breeding of crop ideotypes. *Euphytica* **17**:385–403.

Eberhart, S. A. and Russell, W. A. 1966. Stability parameters for comparing varieties. *Crop Sci.* **6**:36–40.

Finlay, K. W. and Wilkinson, G. N. 1963. The analysis of adaptation in a plant breeding programme. *Aust. J. of Agric. Res.* **14**:742–754.

Grundbacher, F. J. 1963. The physiological function of the cereal awn. *Bot. Rev.* **29**:366–381.

Hadjichristodoulou, A. 1981a. Aspects of barley breeding for dry Mediterranean regions. Barley genetics IV. Pages 383–388 in *Proceedings of the IV International Barley Genetics Symposium*, 22–29 July 1981, Edinburgh, UK.

Hadjichristodoulou, A. 1981b. Cereal diseases in Cyprus—control strategies. Technical Bulletin 38, Agricultural Research Institute, Nicosia. 12 pp.

Hadjichristodoulou, A. 1982. The effects of annual precipitation and its distribution on grain yield of dryland cereals. *J. Agric. Sci., Cambridge* **99**:261–270.

Hadjichristodoulou, A. 1983. Breeding wheat for semi-arid conditions through stability or plasticity of adaptive traits. Pages 657–661 in *Proceedings of the 6th International Wheat Genetics Symposium*, 28 November–3 December, Kyoto, Japan.

Hadjichristodoulou, A. 1985. The stability of number of tillers of barley varieties and its relation with consistency of performance under semi-arid conditions. *Euphytica* **34**. In press.

Hadjichristodoulou, A. and Kari, A. 1984. Karpasia, a high-yielding new durum wheat variety with improved grain quality characteristics. Technical Bulletin 57, Agricultural Research Institute, Nicosia, 7 pp.

Hadjichristodoulou, A. and Kari, A. 1985. On the feasibility of chemical control of diseases of barley and wheat varieties grown at several environments. Technical Bulletin 70, Agricultural Research Institute, Nicosia.

Hadjichristodoulou, A., Della, A. and Photiades, J. 1977. Effect of sowing depth on

stand establishment, tillering capacity and other agronomic characters of cereals. *J. Agric. Sci., Cambridge* **89**:161–167.

Kirby, E. J. M. and Faris, D. G. 1972. The effect of plant density on tiller growth and morphology in barley. *J. Agric. Sci., Cambridge* **78**:281–288.

Lewontin, R. C. 1966. On the measurement of relative variability. *Syst. Zool.* **15**(2):141–142.

Lomas, J. and Shashoua, Y. 1973. The effect of rainfall on wheat yield in an arid region. Pages 531–578 in *Plant Response to Climatic Factors, Proceedings of Uppsala Symposium*, 1970, UNESCO.

Photiades, I. and Hadjichristodouloua, A. 1984. Sowing date, sowing depth, seed rate and row spacing of wheat and barley under dryland conditions. *Field Crops Res.* 9:151–162.

Pushman, M. Fiona and Bingham, J. 1975. Components of test weight of ten varieties of winter wheat grown with two rates of nitrogen fertilizer application. *J. Agric. Sci., Cambridge* **85**:559–563.

DISCUSSION

D. Marshall

You have shown that barley tillers better than wheat so that it has a higher and more stable number of tillers per square metre. Have you looked at increasing the seeding rate of wheat to compensate for its lower tillering ability and, if so, what did you find?

A. Hadjichristodoulou

The optimum seed rate of wheat is about 50 per cent higher than that of barley under our conditions, because of the lower tillering capacity. However, under unpredictable conditions causing poor stand establishment, wheat plants do not have the plasticity that barley plants have to fill the empty gaps with tillers.

B. Yilmaz

Is barley earlier than durum and bread wheat after anthesis?

A. Hadjichristodoulou

This varies with variety and season. For the highest yielding lines the difference in anthesis is about 10–15 days.

H. Harris

Given that main stems survive the stress better than tillers, and given that you report differences in plant establishment, are you confident that the differences in fertile tiller numbers you report are genetic and that they do not reflect differences in establishment?

A. Hadjichristodoulou

The number of tillers reported refers only to productive tillers counted at the dough stage. There were no or few non-productive tillers at that stage. All the varieties were treated uniformly, i.e. three seed rates (10, 70, 130 kg/ha) and six sites. Thus, for all varieties there were low, medium, and high numbers of plants. Those differences in variance that were statistically significant were genetic.

M. Nachit

Could you elaborate on the importance of early plant establishment for barley, durum wheat, and bread wheat and their importance for rainfed conditions?

A. Hadjichristodoulou

We studied the differences among the species (barley, durum wheat, and bread wheat) in stability of tiller number per square metre and their mean tiller number in eighteen environments. Barley is known to have better stand establishment than wheat, but we have not measured this character.

M. S. Mekni

Variance for tiller number per unit area, as well as variance for height, both fairly simply inherited, can be affected by several factors, such as plant density, depth of seeding, etc. How reliable are the variances for those two characters between species and within a given species?

A. Hadjichristodoulou

The inheritance of tiller number and plant height is known but we do not know the genetic control of the variance (or stability) of tiller number per unit area or of plant height. The differences in stability for the two traits were statistically significant only between certain varieties, not among all of them. A test on stability, repeated in the second year for some varieties, gave similar results. There was no difference between barley and wheat in stability of height ($s^2 \log x = 0.008$) but tiller number was more stable in barley than wheat.

P. Martiniello

At this stage you are considering each trait separately. Would it not be more desirable to apply a multiplicative index which considers more than one trait simultaneously to cope with the complex environmental stresses?

A. Hadjichristodoulou

At this stage we are studying individual traits. It is necessary to establish the effects of modifying each trait on grain yield and stability. It is also necessary to collect information on the genetic control of stability and plasticity of the traits. Then one can proceed with the application of multiplicative indices for high yield and stability of performance.

SECTION III

Physiological Research for Drought Avoidance and Tolerance and its Implication in Breeding Programmes

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

16

Drought Resistance of Wheat for Light-textured Soils in a Mediterranean Climate

NEIL C. TURNER and MARC E. NICOLAS
Dryland Crops and Soils Research Programme, CSIRO Laboratory for Rural Research, Private Bag PO, Wembley, WA 6014, Australia

ABSTRACT

Three characteristics are considered desirable in order to maximize grain yield per unit of rainfall for wheat growing on deep freely draining, light-textured soils in a Mediterranean climatic zone. These are early vigour, deep roots, and a high degree of assimilate transfer from the stem and leaves to the grain. This paper describes an experiment designed to measure these characters in 90 lines and cultivars of bread wheat. We present first results for 22 of the 90 lines. Early vigour, scored visually, was shown to be closely correlated with the dry matter accumulated per unit area by the five-leaf stage, and with the dry weight per plant when final plant populations were between 50 and 150 plants per square metre. Early vigour, as measured by dry matter per plant at the five-leaf stage, was positively correlated with final yield in unirrigated wheat. Root depth was to be indirectly assessed by infrared thermometry as water deficits developed in the spring, but gusty winds, poor canopy development, and differences in stomatal conductance at similar water contents suggested that it has limited usefulness in dryland cropping programmes. We assessed assimilate transfer by desiccation of irrigated plants 10–15 days after anthesis. Preliminary results showed that potassium iodide was the chemical desiccant that most closely resembled drought effects.

INTRODUCTION

Agriculture in Australia's Mediterranean climatic zones is based on a low-input, extensive wheat/sheep farming system in which various lengths of

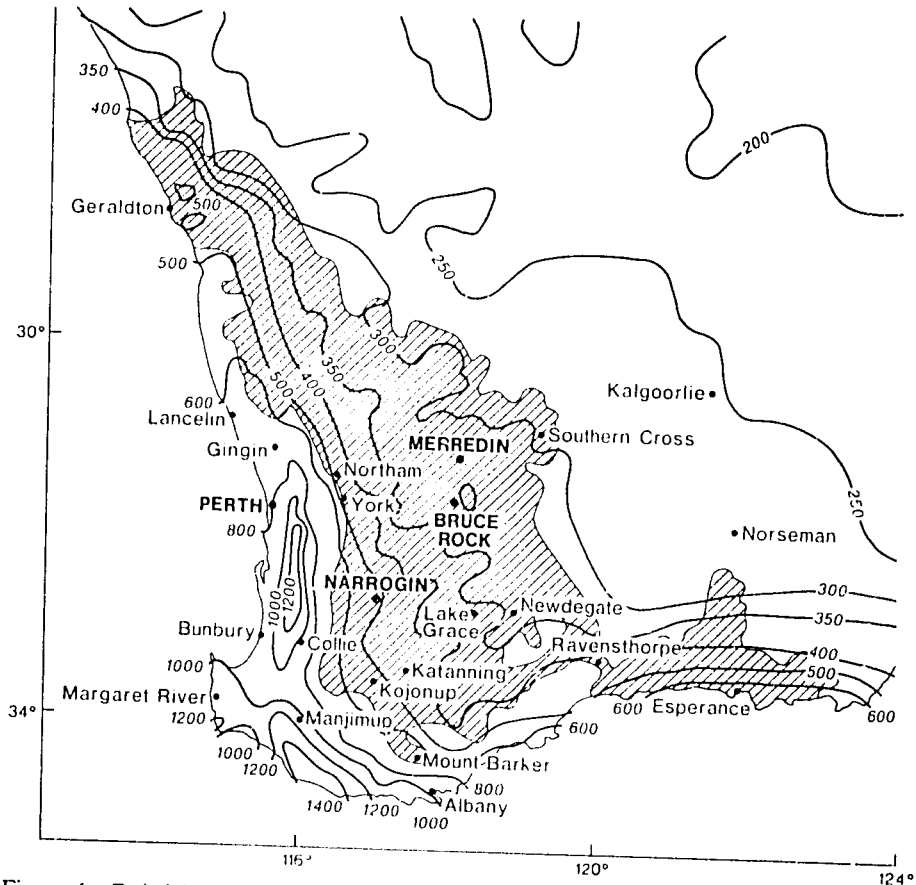


Figure 1. Rainfall isohyets and cropping region for Australia's south-western Mediterranean climatic zone

self-sown annual legume pastures are interspersed with one or more years of cereal crops, principally bread wheat. In the past decade there has been an increase in the proportion of cropping and a partial replacement of pasture legumes by grain legumes, notably lupins, for a break in the cereal cycle. Wheat production in south-western Australia occurs principally in the zone receiving 300–500 mm annual rainfall (Figure 1). Climatically this zone is similar to that of the ICARDA region except that the seasons are offset by 6 months. Figure 2 compares the rainfall and temperatures for Aleppo, Syria, with those for Merredin in the drier eastern portion of the West Australian wheatbelt (annual rainfall 327 mm) and Narrogin in the wetter western portion of the West Australian wheatbelt (annual rainfall 505 mm). Aleppo is intermediate in precipitation between Narrogin and Merredin and has a stronger continental influence, with higher summer temperatures and lower

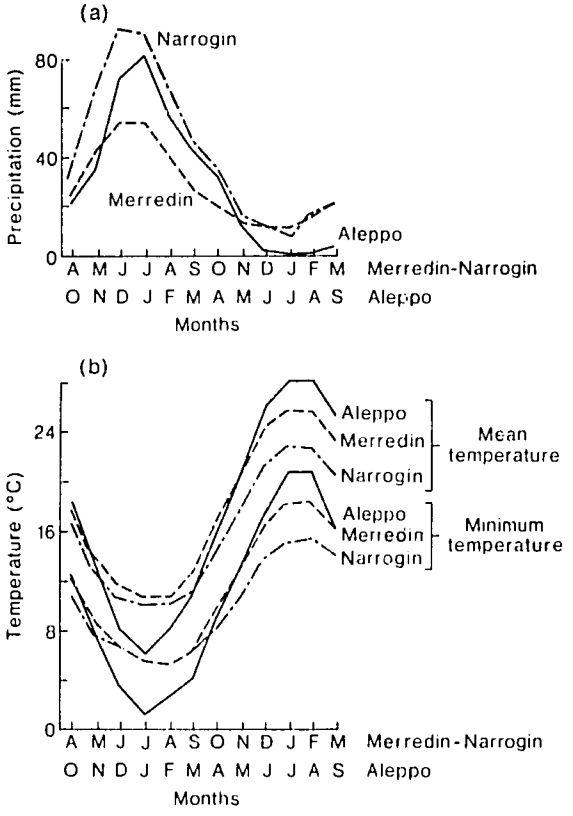


Figure 2. Mean monthly precipitation, mean monthly temperature, and mean monthly minimum temperature for Aleppo, Syria, and Narrogin and Merredin, Australia

winter temperatures than both Merredin and Narrogin. Both Australian centres have higher summer rainfall than Aleppo, reflecting the occurrence of cyclonic rain of tropical origin in some years. The cropping cycle, like the climatic cycle, is offset 6 months from that in northern Mediterranean regions with sowing occurring in mid to late May and the crop being harvested in November.

A marked feature of much of the cropping zone of south-western Australia is the predominance of light-textured surface soils. While some of these sandy soils are underlain by heavy clay subsoils at 0.2–1.5 m, wheat is often grown on deep sandy soils which contain no clay subsoil layers within the root zone. The soils are free draining and have an average water-holding capacity of about 50 mm/m. These characteristics lead to losses of rainfall by deep drainage below the root zone during the wet winter months when the crop is

still small and vegetative, and to water deficits in the spring as rainfall decreases, evaporation increases, and the water in the soil is rapidly depleted.

Fischer (1981), Turner and Begg (1981), and Turner (1982) suggested characters that, from analysis, should benefit yields under Mediterranean climatic conditions. The three characters that we consider of principal importance for wheat production on light-textured soils in a Mediterranean climatic zone are: (1) early vigour, (2) deep rooting habit, and (3) high assimilate transfer to the grain during grain filling.

A project has been initiated to test the importance of these characters for yield under water-limited conditions and the genetic diversity available for the improvement of these characters in wheat. This paper reports on the rationale behind the choice of characters, the methodologies employed, and the early results; final results will only be available after the completion of this paper.

MAXIMIZING GRAIN YIELD PER UNIT OF RAINFALL

The objective of all dryland farming in water-limited environments is to maximize economic yields per unit of growing-season rainfall. Grain yields in water-limited environments are a function of three largely independent factors (Passioura, 1977):

$$\text{Grain yield} = \text{water use} \times \text{water-use efficiency} \times \text{harvest index}$$

Current evidence suggests that wheat grown on light textured soils in a Mediterranean-type climate has restricted production per unit of rainfall because of high water loss through deep drainage early in growth and a low harvest index from water deficits at the end of the season (Turner, 1986a).

We postulate that a wheat plant with early vigour will maximize water use and minimize water loss during the winter months when rainfall is plentiful and that deep roots will maximize the use of the water available throughout the profile, particularly as the soil dries in the spring. A high transfer of assimilates to the grain will maximize the harvest index under conditions of terminal drought and reduce the proportion of dry matter produced early in growth that is left as straw. While it is recognized that vigorous early shoot growth may restrict root growth and may deplete water in the profile before anthesis, thereby restricting the water available for grain filling (Fischer, 1979), evidence from studies in wheat on deep sandy soils suggests that such feedback mechanisms do not necessarily occur. Vigorous early growth resulting in high dry-matter yields by anthesis resulted in improved grain yields and no decrease in the harvest index (Figure 3). We conclude from the results in Figure 3 that on the deep sandy soils early growth enables greater root development so that yields are not restricted by water limitations at the end of the season.

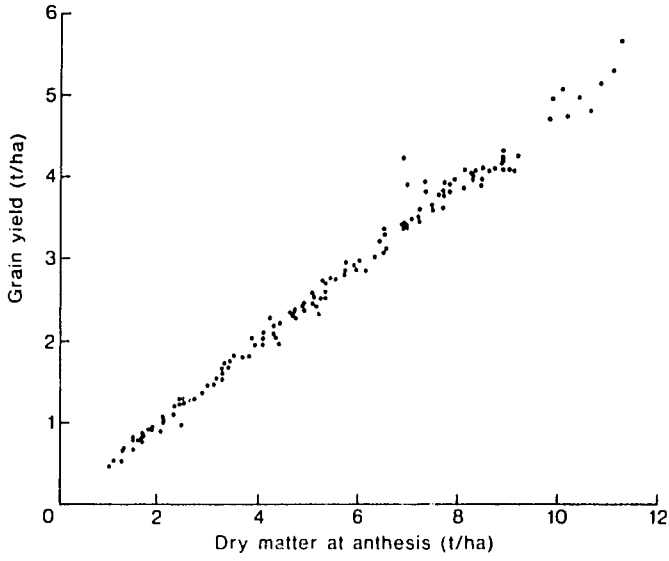


Figure 3. Relationship between grain yield and dry-matter yield at anthesis for wheat, given a wide range of tillage and fertilizer treatments. (From J. Wilson, J. Hamblin, A. Brown, and R. Delane, unpublished work)

EXPERIMENTAL LAYOUT

In order to test whether our suggested characters are beneficial to yield under water-limited conditions, an experiment was conducted in 1985 at Bruce Rock, Western Australia, where the annual average rainfall is 334 mm. The soil was a deep, yellow, slightly acid (pH = 5.4 in calcium chloride) sand containing less than 7 per cent clay. Ninety lines of wheat representing current recommended varieties, older varieties that are no longer grown, and a selection of advanced lines and cultivars from Australia and overseas were sown on 24 June 1985. In this paper data for only 22 of the lines are presented. These 22 lines are representative of the range of material studied (Table 1). The wheat was sown in rows 19 cm apart in 5 m × 2.5 m plots in six replicate blocks. Sowing rate was adjusted to give an expected plant density of 100–150 plants/m^2. The plots were fertilized with 35 kg N/ha and 18 kg P/ha. Half of the blocks were irrigated from early September onwards to reduce water deficits. Flowering occurred between 24 September and 12 October and the plots were harvested from 12–26 November.

The season was exceptionally dry. Growing-season (April–October) rainfall at the site was 137 mm compared with the long-term district average of 260 mm (Table 2). In particular, rainfall in April, May, and June was well

Table 1. Cultivars and lines of wheat grown in the field study at Bruce Rock, Western Australia, in 1985 and reported in this study

Recommended cultivars in South-western Australia:
Bodallin
Egret
Gutha
Kite
Kulin
Tincurrin
Warigal
Wailki
Grown in South-western Australia, but no longer recommended:
Gamenya
Halberd
Millewa
Old variety:
Darkan
Grown elsewhere in Australia:
Condor
Phoenix
Overseas cultivars:
Barkaee
Mongolia
Pembina
Experimental lines:
Somaclonal line 5
Somaclonal line 6
Somaclonal line 8
Cook isoline 49C
Cook isoline 58C

Table 2. Rainfall at the experimental site (mm) in 1985 compared with the long-term average monthly rainfall (mm) for the district

	April	May	June	July	August	September	October
Experimental site	5	6	15	53	28	23	7
District average	22	42	57	52	41	26	20

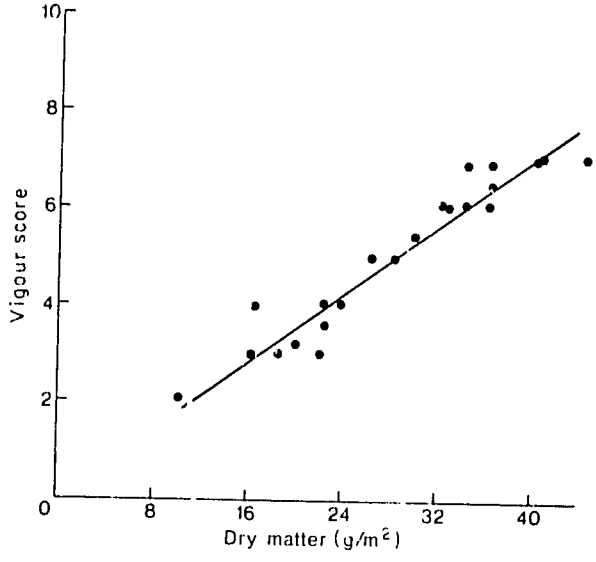


Figure 4. Relationship between visual score for early vigour and dry matter per unit area at the five-leaf stage in 22 wheat cultivars

below average, leading to a date of sowing about one month later than normal. Since rainfall on any one date never exceeded 19 mm, the soil was never wet below 0.6 m, leading to restricted rooting.

Early vigour

On 27 August when the plants were at the five-leaf stage, early vigour was assessed visually using a score of 1 to 10 where 1 was low vigour and 10 was high vigour, and by dry-matter sampling. The oven-dry weight of all plants in 0.5 m^2 together with the number of plants was measured. On a selection of 22 of the lines the vigour scores varied from 2 to 7 and the dry matter per unit area varied from 9 to 44 g/m^2. The vigour score was closely correlated with the dry matter per unit area (Figure 4). Due to the poor soil moisture conditions at sowing, the range of final plant densities varied from 40 to 200 plants/m^2 among the 22 lines. The vigour score was poorly correlated with dry matter per plant due to the fact that high vigour scores were attributed to plots with high plant emergence and low vigour scores to sparse plots. However, the correlation was quite acceptable for the medium density (50–150 plants/m^2) plots (Figure 5). Clearly, for visual scoring of early vigour reasonably uniform seeding and emergence is required, but the good correlation between vigour score and dry matter per plant for plant populations

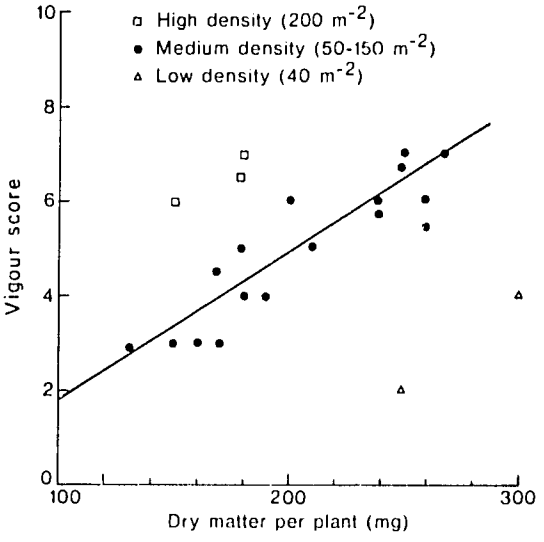


Figure 5. Relationship between visual score for early vigour and dry matter per pla t at the five-leaf stage in 22 wheat cultivars that had final plant populations of 40, 50–150, and 200 plants/m^2

varying threefold suggests that plant densities do not need to be too uniform for acceptable results.

Early vigour, as measured by dry matter per plant at the five-leaf stage, was positively correlated with final grain yield per plant in the unirrigated plots (Figure 6). However, one of the high vigour lines had a low grain yield and three of the low vigour lines had high grain yields. The poor-yielding high vigour line is a very late-maturing line poorly suited to growth under the conditions of this study. The three high-yielding, low early vigour lines clearly have other attributes that enable them to yield under water-limited conditions. Nevertheless, the data strongly suggest that early vigour is a major determinant of yield under moisture-limiting conditions.

Deep roots

While techniques exist for the measurement of rooting depth in seedlings (Rumbaugh and Johnson, 1983), the necessity to sample 540 plots at or near flowering precluded the direct measurement of rooting depth by sampling or by methods such as water extraction. We therefore planned to measure rooting depth indirectly by measuring the development of stress in the postanthesis period by infrared thermometry. The technique is based on the principle that the leaf temperature increases relative to air temperature as the

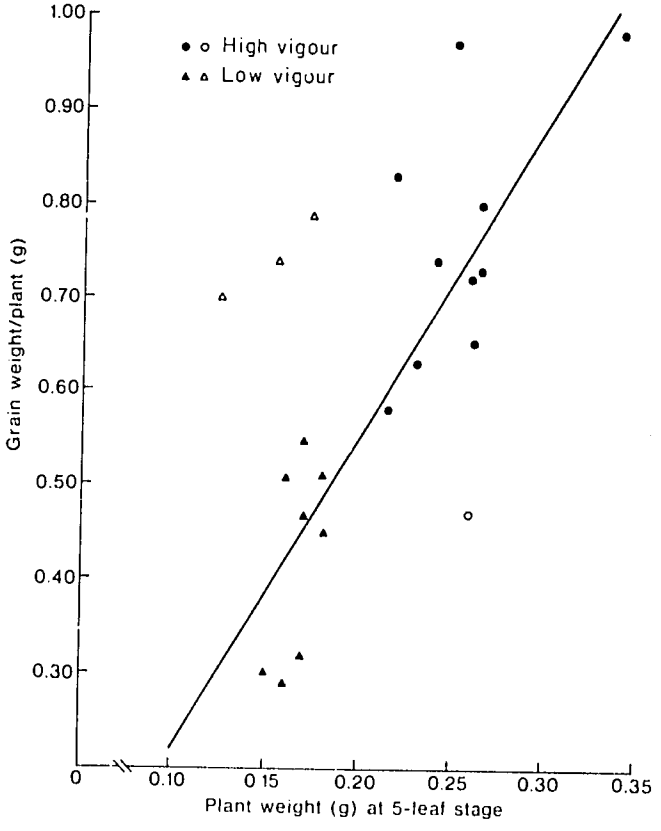


Figure 6. Relationship between grain weight per plant at maturity and dry matter per plant at the five-leaf stage in 22 wheat cultivars that had high or low early vigour. Open symbols identify lines not considered when fitting the linear regression

crop becomes stressed and transpiration decreases (Jackson, 1982). Blum *et al.* (1982) developed the technique as a screening tool for dehydration avoidance or postponement. While several factors are involved in dehydration postponement (Turner, 1986b), maintenance of water uptake by deep and prolific roots is a major component. Thus, provided other factors such as stomatal conductance or leaf rolling do not vary across genotypes, infrared thermometry can be used as an initial screen for lines likely to have deep roots. In practice the technique requires a rapid measurement of leaf-to-air temperature differences across the lines once water deficits begin to develop (Blum *et al.*, 1982). Blum (1983) worked with crops that were irrigated prior to the development of a postanthesis stress cycle. Since irrigation is less likely to lead to the expression of differences in root depth and more likely to show differences in stomatal or leaf rolling responses to water deficits, we preferred

to use the technique on the unirrigated plants as water deficits developed naturally after anthesis.

For reliable results the technique depends on uniform wind speeds (O'Toole and Hatfield, 1983) and complete canopy cover. Since dry soil has a temperature several degrees or tens of degrees above the temperature of the canopy, soil must not enter the field of view of the thermometer or must be uniformly present in each cultivar. We found that neither condition prevailed in the present study. Gusty winds at the experimental site made comparisons among cultivars difficult. Moreover, the late establishment of the crop meant that full ground cover did not occur in any plot. While a low angle across the plots was used to minimize the presence of soil in the field of view, a photographic record showed that some soil was always in the field of view and the amount varied with the cultivar. The amount of soil present in the field of view varied from 5 to 12.5 per cent in three cultivars selected at random. Moreover, measured leaf conductances on five of the cultivars as water deficits developed showed that the conductances varied more than twofold at similar relative water contents (Table 3). As differences among lines in stomatal conductance will influence the leaf temperature, we therefore conclude that infrared thermometry is unlikely to be useful as a screening tool for root depth in wheat lines. Furthermore, it may prove difficult to use as a tool for assessing dehydration postponement in dryland crop-breeding programmes.

Assimilate transfer

Blum *et al.* (1983a, 1983b) have shown that assimilate transfer to the grain under drought can be simulated by spraying well-watered plants with a

Table 3. Leaf conductances, both absolute values and relative to the irrigated controls, and relative water contents of five wheat cultivars measured in the unirrigated plots between 1200 and 1430 h on 26 September 1985. Conductances were measured with the Delta-T porometer

Cultivar	Stomatal conductance		Relative water content (%)
	Absolute ($mmol/m^2/s$)	Relative (%)	
Gamenya	152	36	93.1
Gutha	215	51	96.9
Bass	269	52	79.6
Halberd	353	94	93.7
Wailki	214	70	93.1

Table 4. Effect of desiccants, drought, and defoliation applied 10 days after anthesis on grain weight of Gutha wheat. Values are expressed as percentages of the untreated controls (weight = 47.7 mg/gr). The desiccants were sprayed on the whole plant or only the leaves. The mean coefficient of variation for the various treatments was 12.6 per cent

Treatment	Desiccant sprayed on	
	Whole plant	Leaves only
Desiccant spray:*		
(a) Magnesium chlorate	20.1	22.5
(b) Sodium chlorate	23.4	29.8
(c) Potassium iodide	29.4	49.6
Drought	26.7	
Defoliation		71.2

*Magnesium and sodium chlorate were used as 4% solutions and potassium iodide as a 0.3% solution.

desiccant 14 days after anthesis. The desiccant used was magnesium chlorate (4% solution). A high relative grain weight after desiccation normalized for grain weight in the untreated plants is taken as an indication of a high transfer of assimilates from the leaves and stems to the grain. A. Blum (personal communication) has reported lines with an ability to transfer 45 per cent more of their assimilates to the grain than normal.

Prior to using the technique in the field, we assessed the effect of a range of desiccants on the grain weight of Gutha wheat. The plants, grown in pots in a glasshouse at 22/15°C day/night temperatures, were sprayed with the desiccants 10 days after anthesis. Either the whole plant or leaves only were sprayed. At the same time, some plants were defoliated and others were left unwatered to provide a drought treatment. Table 4 shows the results for three of the desiccants. While the drought treatment reduced the grain weight by almost 75 per cent, defoliation of the leaves reduced the grain size by 30 per cent. With the exception of the potassium iodide, the other treatments reduced grain weight to a greater extent than the drought treatment. The treatment of only the leaves indicated the reason for this. When applied to the leaves magnesium chlorate reduced the grain weight by 77.5 per cent and sodium chlorate reduced the grain weight by 70 per cent, suggesting that the chemicals were transported to the grain and affected grain growth. The potassium iodide treatment was the chemical that best simulated the effect of drought and had least effect when applied to the leaves only; the chemical also desiccated the lower leaves first and then the upper leaves, giving the appearance of accelerated senescence rather than desiccation.

We utilized both sodium chlorate (1% solution), which is more readily available than magnesium chlorate, and potassium iodide (0.2% solution) in the field study. The study was conducted on the irrigated plants which were sprayed 15 days after anthesis. The results will be compared with the effects of the drought that occurred at the site on grain weight.

CONCLUSIONS

Our first results suggest that there is considerable variation among wheat lines in early vigour and that high early vigour results in high yields under water-limited conditions. The study has also highlighted that infrared thermometry may prove difficult in screening for dehydration postponement and root depth in dryland wheat lines. Finally, our preliminary results indicate that magnesium chlorate is too severe a desiccant to simulate drought effects and propose the use of potassium iodide as a preferable chemical.

The study will continue in 1986. In addition to more studies on the role of early vigour, root depth, and assimilate transfer in a selection of the lines from the 1985 study, we propose to look in further depth at the variation in early vigour to see whether it is genetic or environmental. Additionally, we plan to study the mechanisms of assimilate transfer, particularly the role of osmotic adjustment and membrane stability under stress, on the quality and quantity of assimilated transferred.

ACKNOWLEDGEMENTS

The study was supported by the Wheat Industry Research Council of Australia and the Wheat Research Committee of Western Australia. The Wheat Research Committee of Western Australia also provided, in part, travel funds for N. C. Turner to attend the conference. We thank Michael Rayner for technical assistance.

REFERENCES

Blum, A. 1983. Genetic and physiological relationships in plant breeding for drought resistance. *Agri. Water Mang.* **7**:195–205

Blum, A., Mayer, J. and Gozlan, G. 1982. Infrared thermal sensing of plant canopies as a screening technique for dehydration avoidance in wheat. *Field Crops Res.* **5**:137–146.

Blum, A., Poiarkova, H., Golan, G. and Mayer, J. 1983a. Chemical desiccation of wheat plants as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. *Field Crops Res.* **6**:51–58.

Blum, A., Mayer, J. and Golan, G. 1983b. Chemical desiccation of wheat plants as a simulator of post-anthesis stress. II. Relations to drought stress. *Field Crops Res.* **6**:149–155.

Fischer, R. A. 1979. Growth and water limitation to dryland wheat yield in Australia: a physiological framework. *J. Aust. Inst. of Agri. Sci.* **45**:83–94.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through breeding of crops. *Plant and Soil* **58**:249–278.
Jackson, R. D. 1982. Canopy temperature and crop water stress. *Adv. Irrig.* **1**:43–85.
O'Toole, J. C. and Hatfield, J. L. 1983. Effect of wind on the crop water stress index derived by infrared thermometry. *Agron. J.* **75**:811–817.
Passioura, J. B. 1977. Grain yield, harvest index, and water use of wheat. *J. Aust. Inst. Agric. Sci.* **43**:117–120.
Rumbaugh, M. D. and Johnson, D. A. 1983. Changes in alfalfa cultivars grown in a semiarid environment. *Crop Sci.* **23**:477–480.
Turner, N. C. 1982. The role of shoot characteristics in drought resistance of crop plants. Pages 115–134 in *Drought Resistance in Crops with Emphasis on Rice*. International Rice Research Institute, Los Banos, The Philippines.
Turner, N. C. 1986a. Improving crop water use—what are the options? In *Putting W.A. Scientists on Notice. Proceedings of the 1986 Wheat/Sheep Review*. Farm Management Foundation of Australia, Mosman Park, Australia. In pres.
Turner, N. C. 1986b. Crop water deficits: a decade of progress. *Adv. Agron.* **39**. In press.
Turner, N. C. and Begg, J. E. 1981. Plant-water relations and adaptation to stress. *Plant and Soil* **58**:97–131.

DISCUSSION

M. Nachit

Commenting on early vigour, your results are in accordance with our data. However, our experience with infrared has been exciting. Would you please elaborate on the stress level when you recorded the data of the experimental plots?

N. C. Turner

Our measurements were made with moderate stress around anthesis. The preferred time would be under more severe stress during grain filling. Nevertheless, the stage is immature if the early crop development is poor because of poor seasonal conditions and one is measuring soil temperatures.

T. C. Hsiao

You are attempting to select for early vigour as well as deeper rooting. It seems to me this is self-contradicting since more carbon allocation to the shoot, associated with early vigour, would mean less carbon allocation to roots.

N. C. Turner

Although this may be theoretically true, our evidence suggests that this is not practically true. The reason for this is that deep roots and early vigour may allow better utilization of the soil and atmospheric resources.

Howard Taylor

Your programme is using infrared thermometry to monitor root water supplying power. You gave no indication whether you are monitoring nutrient uptake. Are you working on soils where the nutrient uptake rate is non-limiting to wheat growth and yield?

N. C. Turner

Nutrient levels were aimed to be non-limiting in relation to phosphorus and micronutrients. Nitrogen was applied at levels moderately above the current farmer practice. Part of the possible advantage from early vigour and deep roots may arise from better utilization of fertilizer nitrogen.

S. K. Sinha

Do you think that higher dry-matter production before anthesis would be the same both in 300 and 500 mm zones? Could you give any figures (percentage before anthesis) for both zones?

N. C. Turner

In general there is little difference in water availability before anthesis in the environments we are studying. With temperatures similar during the winter at the two sites, there is unlikely to be any differences in dry-matter production at anthesis. However, where temperatures and rainfall between sowing and anthesis do differ we would expect differences in dry-matter production.

J. M. Clarke

Do you envision problems in the Blum desiccation technique due to variation in anthesis date among genotypes? If so, how could such difficulties be overcome?

N. C. Turner

We are applying the desiccants at 15 days after anthesis so that all lines will be desiccated at the same physiological stage. I see no problems with this approach.

A. Hadjichristodoulou

When selecting for early vigour one may end up selecting too-early types which have a short growing period, do not utilize all moisture because they mature early, and, finally, give low yields. Early vigour may be of use when it deals with genotypes of the same maturity.

N. C. Turner

Certainly early vigour may be linked with earliness in some lines, but we are noting anthesis date and will be comparing early vigour in lines with similar maturities.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

17

Relations among Physiological Characters in Durum Wheat under Drought

A. RASCIO, B. BALDELLI, Z. FLAGELLA, and G. WITTMER
Istituto Sperimentale per la Cerealicoltura, S.S. 16 Km. 675 Cas. Postale, 71100 Foggia, Italy

ABSTRACT

We evaluated the tolerance of 25 cultivars to drought and heat stress by two tests of membrane stability—an osmotic and a heat test.

We estimated the injury to cell membranes by measuring the electroconductivity of an aqueous medium containing leaf discs previously stressed *in vitro* either by a solution 40% w/v PEG 6000 or by a temperature of 50°C. We studied the tolerance of the cultivars to the two types of stress at five different stages of development, but did not correlate the two tests. We found a significant interaction between 'stage of development' and 'variety' for the osmotic but not for the heat test.

We also calculated the trends of percent injury over time for the mean varietal response, but correlations were not significant.

The second experiment concerned leaf-water relations. Under limited water conditions the osmotic potential showed a tendency to decrease in the non-irrigated treatment; however, at initial stages we observed significant differences between the varieties, with Appulo having more negative values than Valforte.

Water stress did not modify the relationship, which was a varietal characteristic, between RWC and water potential.

The turgor pressure decrease, when RWC decreased, was greater in Valforte than Appulo, which suggests that the latter has a greater cell wall elasticity.

Stomatal conductance declined when the RWC decreased in a similar way in the two treatments and varieties.

In Italy almost 65 per cent of the durum wheat area is located in semi-arid areas, where the rainfall usually ranges from 420 to 490 mm per year and

seasons with less than 300 mm are frequent. The problem of increasing the yield in these areas, traditionally devoted to this crop, is a serious one.

Until 15 years ago, the main objective of the Italian breeders was to impose earliness, the only way considered practicable for avoiding the water deficit which usually occurs from April. Two important examples of such genotypes are Capeiti 8 and Appulo, still widely cultivated in southern Italy in spite of their height and their susceptibility to lodging and to rusts and mildew attacks. A second breeding approach, started in the 1960s, and including the use of interspecific crosses with bread wheats carrying genes for dwarfism and sources of resistance to diseases, produced in the 1970s a great number of very interesting semi-dwarf varieties, resistant to lodging and tolerant to the more dangerous foliar diseases.

In spite of several positive characteristics, including the ability to make use of higher quantities of nitrogen and therefore produce very high yield, this new generation of durum cultivars (Valgroup, Creso, etc.) has not been widely grown in southern Italy, probably because of their lateness. They were judged in the first instance to be insufficiently tolerant to drought and very demanding as to soil conditions.

In order to define a better strategy for the future, at the end of the 1970s the Foggia Section of the Cereal Experimental Institute decided to start a research programme on applied physiology for determining a new plant ideotype of durum wheat better adapted to conditions in southern Italy and based on morphophysiological traits.

The research carried out in this context dealt with the growth analysis, the nitrogen accumulation pattern, and the relations between morphological and physiological yield components (Wittmer, 1979; Wittmer *et al.*, 1982; Iannucci *et al.*, 1983; Rascio *et al.*, 1984; Baldelli *et al.*, 1986).

The second part of our programme, already in progress, concerns:

(1) the evaluation of several *in vitro* tests for screening for drought resistance or tolerance;

(2) a basic study on water relations in the leaves.

Drought tolerance may be measured by analysing the different metabolic or physiological functions. Some authors reported that cell membrane stability plays a critical role under conditions of moisture stress. Recently considerable importance has been attributed to cell membrane thermostability as a measure of plant tolerance to high temperatures.

The tests for drought and heat tolerance developed by Sullivan and Ross (1979) for sorghum were applied by us on durum wheat. Both tests are based on the leakage of electrolytes from cell membranes after imposing *in vitro* stress.

Twenty-five cultivars of durum wheat were tested for drought and heat tolerance at five different stages of development. The percent of injury was calculated as follows:

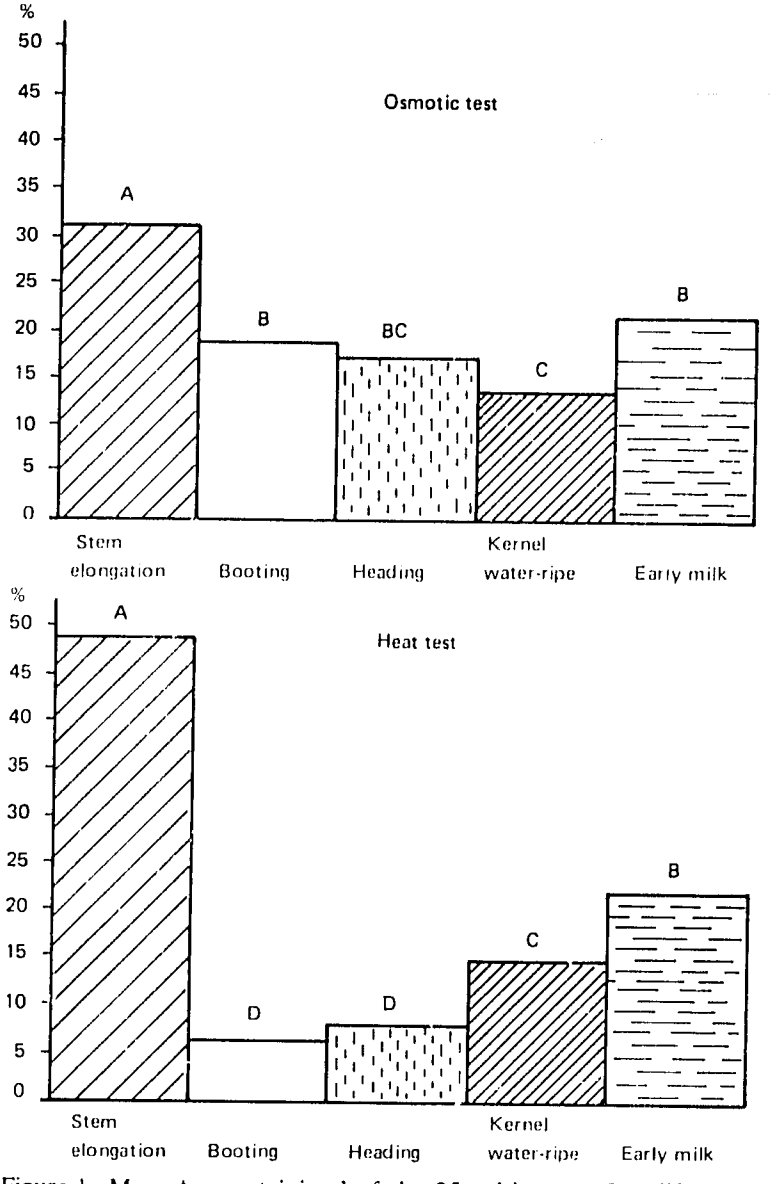


Figure 1. Mean 'percent injury' of the 25 cultivars at five different stages of development

$$\text{Percent injury} = 1 - \frac{1 - T1/T2}{1 - C1/C2} \times 100$$

where T is treatment, C control, 1 before autoclaving, and 2 after autoclaving.

The maximum differences among varieties were found during stem elongation. At this stage, all the cultivars showed the highest values of injury for both tests. In Figure 1 the mean response to the osmotic and heat stress at the different stages is shown. In the drought tolerance test a decrease of percent injury was found from stem elongation to caryopsis water ripe, but there was an increase of the membrane damage at the early milk stage. In the heat tolerance test, the increase of percent injury was observed at the booting stage. The combined analysis of variance showed a phenological stage–variety interaction for drought tolerance.

A regression was calculated to analyse the behaviour of percent injury during plant development for both drought and heat tolerance. The two different regressions showed a similar trend but were not correlated (Figure 2). In none of the growth stages were the varietal responses to these tests correlated. It probably meant that each test measured a different kind of

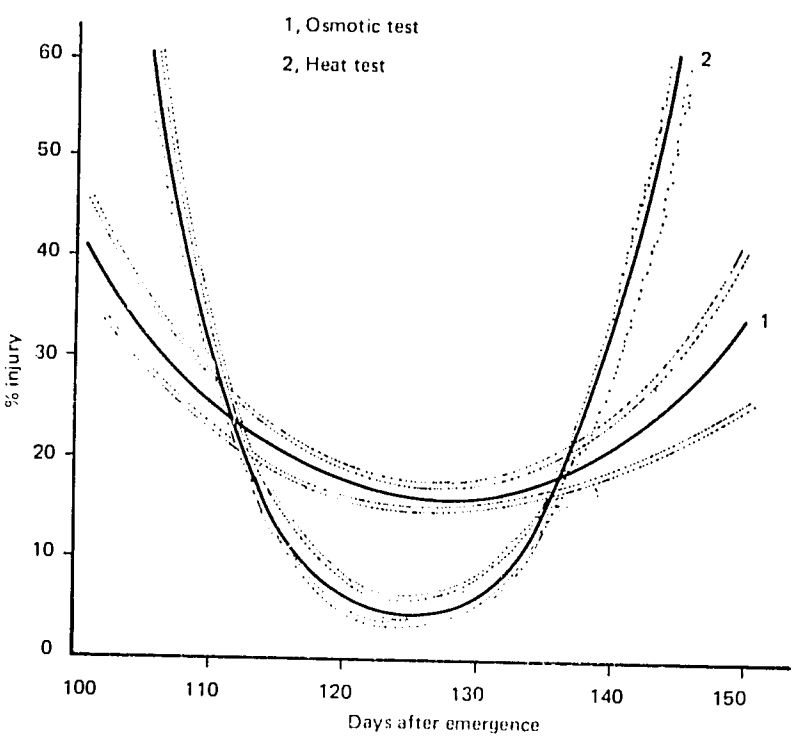


Figure 2. Trend of 'percent injury' over time

damage to the cell membrane. Moreover cell membrane resistance is only one of the several physiological factors determining drought and heat rolerance.

In our opinion, the consequences of these results for plant breeding are as follows:

(1) It is desirable to screen genotypes when moisture stress in the field is more frequent due to interaction between phenological stage and variety for the osmotic test.

(2) With each test we selected only one physiological character related to drought tolerance. It may be better to utilize several tests which evaluate different physiological or metabolic factors in order to have an integrated genotypic response to drought.

The second aspect studied was the characterization of the internal water status in two durum wheat varieties that represent two phases of breeding for the last 20 years: Appulo, a traditional variety that is considered adequately tolerant to drought, depending on agronomic practices, and Valforte, a recently released variety.

To test these varieties, two treatments were imposed: 'irrigated' and 'non-irrigated'. During the booting-milk stage at 08.00 h and 12.00 h, on cloudless and windless days, the following parameters on the youngest fully expanded leaves were measured:

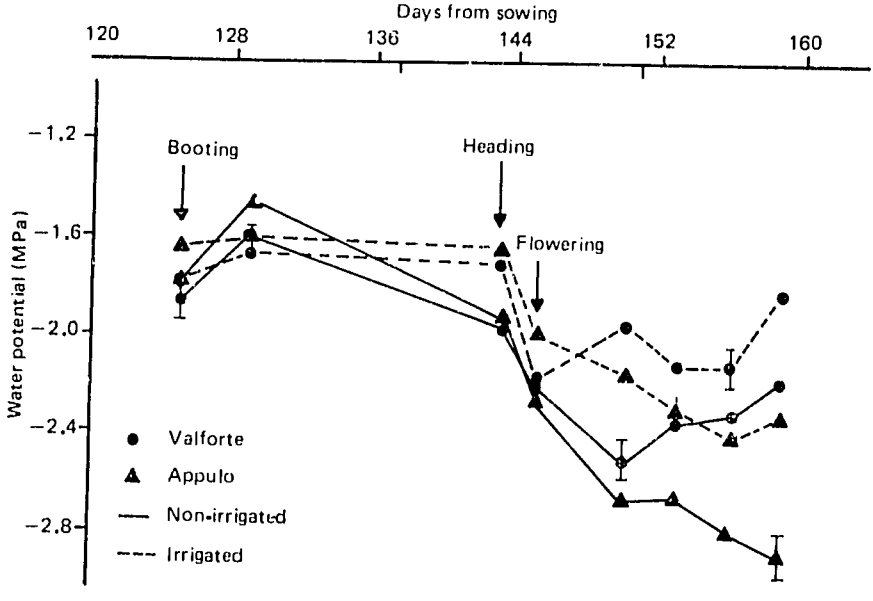


Figure 3. Midday leaf water potential of upper expanded leaves. The arrows show the dates of irrigation. Vertical bars denote standard error (only when it was greater than or equal to 0.15 MPa) of four replications

Relative water content (method of Barrs and Weatherley)
Water potential (pressure chamber)
Osmotic potential (cryoscopic method)

The osmotic potential at full turgor was determined, collecting the samples at 08.00 h and keeping them in distilled water for 3 hours (Hsiao *et al.*, 1984).

Figure 3 shows midday leaf water potential from 22 April to 24 May. There were significant differences between treatments starting from the heading stage, while the differences between varieties appeared later: Appulo showed higher water potential than Valforte during the milk stage.

The relationships between relative water content and water potential (Figure 4) showed a great relative water content in Valforte than in Appulo, when leaf water potential decreased, while the stress history of the plant did not affect this relationship.

The ability to retain a larger amount of water, at any given leaf water potential, may be due to a greater rigidity of the cell wall, but may also result from accumulation of osmotically active solutes in cells. For this reason, the seasonal trends of midday leaf water potential and osmotic potential at full turgor in the non-irrigated treatment were compared. The latter determination was preferred to the midday one because to study the active osmotic adjustment it is necessary to eliminate changes due to dehydration.

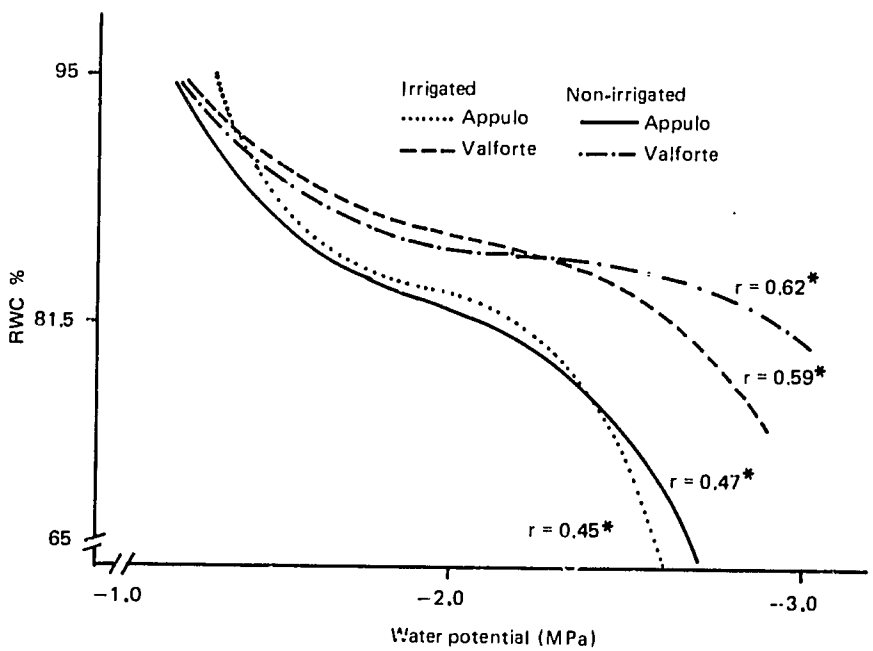


Figure 4. Relationships between relative water content (RWC) and water potential. Lines are fitted according to the curvilinear regression

Table 1. Values of solute potential at full turgor, modulus of elasticity, and RWC at zero turgor for unstressed winter wheat cultivars

Varieties	Solute potential at full turgor (MPa)	Modulus of elasticity ϵ	Relative water content at zero turgor (%)
Appulo	−1.33	2.6	66
Valforte	−1.50	5.0	77

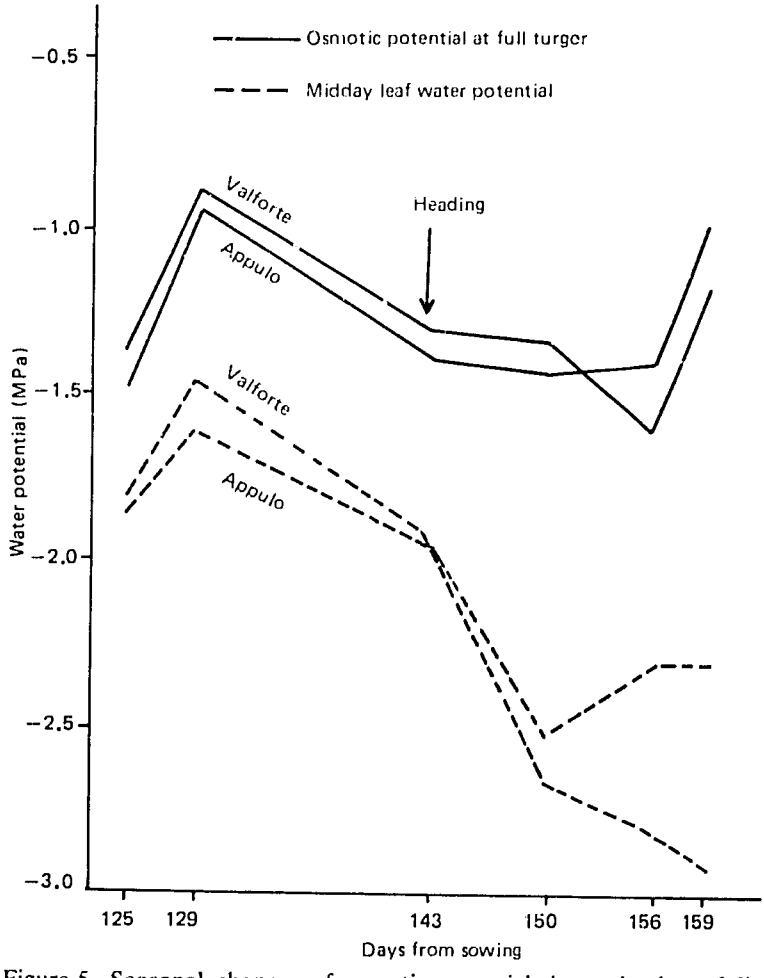


Figure 5. Seasonal changes of osmotic potential determined on fully rehydrated leaves and midday water potential. Each point represents the average of four measurements

As water potential fell, the osmotic potential decreased at a slower rate, so that there was a decrease in the turgor potential. It was lower in Valforte than Appulo because the osmotic potential did not differ between varieties, while the water potential was lower in Valforte during the milk-development stage.

Valforte, which shows lower turgor potential (P) but greater RWC values, probably has more rigid cell walls than Appulo. The bulk volumetric elastic modulus ϵ (which is inversely related to the cell wall elasticity) may be given by (Hellkvist *et al.*, 1974)

$$\epsilon = \frac{\Delta P}{\mathrm{RWC}} \times 100$$

assuming that the bound water in the leaf is negligible at RWC values reached in this study.

The pressure–volume curves (Wilson *et al.*, 1979) seemed to confirm what has been observed in the field. Table 1 shows the osmotic potential at full pressure potential, relative water content at plasmolysis (or zero turgor potential point), and bulk modulus of elasticity (ϵ) obtained by the above technique, applied to plants grown unstressed for 30 days in the field.

Some authors (Coyne *et al.*, 1982) thought that varieties with highly elastic cell walls have to lose more water to develop a sufficient water potential gradient to extract water from a drying soil. In the Mediterranean environment, however, whose particular attribute is climatic variability, the high cell wall elasticity may be an important adaptive feature against the early loss of turgor.

REFERENCES

Baldelli, G., Wittmer, G., Platani, C., Rascio, A. and Flagella, Z. 1986. Correlazioni tra i componenti della produzione nel frumento duro a diverse densita di semina. *Rivista di Agronomia*. In press.

Coyne, P. I., Bradford, J. A. and Deweld, G. L. 1982. Leaf water relations and gas exchange in relation to forage production in four asiatic bluestems. *Crop Sci.* **22**:1036–1040.

Hellkvist, J., Richards, G. P. and Jarvis, P. G. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. *J. Appl. Ecol.* **11**:637–667.

Hsiao, T. C., O'Toole, J. C., Yambao, E. B. and Turner, N. C. 1984. Influence of osmotic adjustment on leaf rolling and tissue death in rice (*Oryza sativa* L.). *Plant Physiol.* **75**:338–341.

Iannucci, A., De Santis, G., Baldelli, G., Rascio, A. and Wittmer, G. 1983. Modello di accumulo della sostanza proteica nel grano duro: analisi di varieta tradizionali e recenti. *Monografie di Genetica Agraria* **5**:253–271.

Rascio, A., Baldelli, G. and Wittmer, G. 1984. Analisi di alcuni componenti fisiologici e morfologici della produzione del frumento (*Triticum durum* Desf.). *Rivista di Agronomia* **1**:35–41.

Sullivan, C. Y. and Ross, M. 1979. Selecting for drought and heat resistance in grain

sorghum. Pages 263–281 in *Stress Physiology in Crop Plants* (Mussel, H. and Staples, R. C., eds.). John Wiley, New York.

Wilson, J. R., Fischer, M. J., Schulze, E. D., Dolby, G. R. and Ludkow, M. M. 1979. Comparison between pressure–volume and dewpoint–hygrometry techniques for determining the water-relations characteristics of grass and legumes' leaves. *Oecologia (Berl.)* **41**:77–88

Wittmer, G. 1979. Fisiologia della pianta di frumento. *Agricoltura Ricerca, anno II.* **8**:40–48.

Wittmer, G., Iannucci, A., De Santis, G., Baldelli, G., De Stefanis, E., Brando, A., Ciocca, L. and Rascio, A. 1982. Adattamento e fattori fisiologici limitanti la produttivita del frumento duro. *Rivista di Agronomia* **2**:61–70.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

18

Stress Metabolism: Its Implication in Breeding Programmes

DAVID W. LAWLOR
Physiology and Environmental Physics Department, Rothamsted Experimental Station, Harpenden, Herts. AL5 2JQ, UK

ABSTRACT

Attainment of large rates of plant dry-matter production under water stress depends on the maintenance of metabolism, principally carbon dioxide and nitrate assimilation. Translocation of assimilates and synthesis of proteins and other cellular constituents are essential for the growth of the photosynthetic surface (and reproductive and storage organs) and for efficient photosynthesis per unit area of leaf. Interactions between metabolic processes in assimilation and growth are not quantitatively understood; nor is regulation of metabolism by environmental factors, including water stress. Water stress operates at the physiological and whole-organ level, e.g. via stomatal closure which decreases CO_2 supply and thereby photosynthesis and increases the ratio of photorespiration to photosynthesis. Water stress inhibits the photosynthetic mechanism, probably ATP synthesis, and changes the amounts and type of carbon and nitrogen compounds formed. A decrease in ATP synthesis but maintenance of reductant synthesis may lead to accumulation of secondary metabolites, e.g. amino acids (particularly proline), glycine betaine, and hormones. Changes in assimilation of carbon and in accumulation of metabolites may be used to identify and select plants differing in response to stress. Accumulation of particular metabolites may not confer resistance to, or increase productivity under, stress. We discuss the value of altering metabolism and the possibilities of improving conventional screening methods and of applying genetic engineering techniques. By combining measurements of photosynthesis as a function of CO_2, light, etc., and of selected metabolites under defined water stress we might be able to assess the value of particular metabolic features for increasing production in drought-prone environments and their potential in conventional breeding and in genetic modification.

INTRODUCTION

Yield of crops is determined by many processes (Figure 1) originating in the genetic information of the nucleus, chloroplast, and other organelles of the higher plant cell (Weeks, 1981; Le Rudulier and Valentine, 1982). The information controls the synthesis of structural proteins and enzymes which synthesize other cell components (e.g lipids and proteins of membranes, cell walls, etc.). Cells grow and multiply, forming leaves and vegetative and reproductive structures, often with storage function. Photosynthesis provides directly, or via storage, the energy and materials required for metabolism.

Plants are adapted to a range of complex environments (Vaadia, 1985), varying in temperature, light, and (the topic of this paper) water stress. Inadequate and often very erratic rainfall is, in many parts of the world, the limiting factor in crop production, decreasing growth (Hsiao, 1973) because transpiration exceeds water supply from the soil. Consequently plants lose water and cell water, osmotic, and turgor potentials decrease. Metabolism is sensitive to changes in ionic strength and composition (Wyn Jones and Gorham, 1983) and to the concentration of metabolic control molecules. The supply of substrates (e.g. CO_2, NO_3^-) from the environment or from other metabolic processes in the cell or from other organs also affects metabolism. Mild waterstress decreases cell expansion and thereby growth of leaves (Hsiao, 1973) and may slow photosynthesis through accumulation of assimilates. Photosynthesis of leaves under greater water stress is slowed by stomatal closure and the ratio of photorespiration (P_r) to net photosynthesis (P_n) may increase due to the decrease in the CO_2/O_2 ratio within the leaf (Lawlor and Fock, 1975; Lawlor, 1979). Also with an inadequate CO_2 supply photosynthetic cells may become photoinhibited under large solar energy

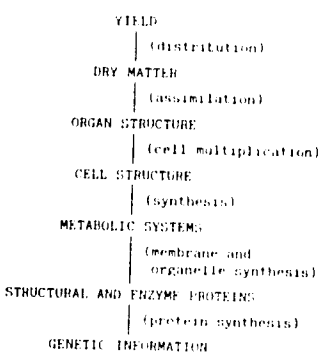


Figure 1. Organizational levels in crop production; water stress affects processes at all stages

loads (Sharp and Bower, 1985). Severe water stress inhibits photosynthesis and causes imbalance between metabolic processes which greatly alters the content of metabolites, etc., and disrupts cellular function (Lawlor, 1983).

Evolution (and recently selection and breeding for man's requirements) had adapted plants to particular environments in which they are most productive and efficient in their use of light energy, CO_2, etc. When environmental factors are outside the 'norm' to which the plant's metabolic systems are adapted (its 'design limits' in engineering terms), then the efficiency of metabolism decreases, growth becomes erratic, and yield falls. Metabolism of droughted plants is altered in many ways, as the vast literature testifies (e.g. Hsiao, 1973; Hanson and Hitz, 1982). Recently, analysis of drought effects has concentrated on (1) stomatal control of water loss and CO_2 exchange in relation to plant and cell water content, and water, osmotic, and turgor potentials (Fischer and Turner, 1978), (2) cell and organ expansion in relation to water balance (Hsiao, 1973), (3) the role of osmotic potential in the regulation of cell water balance and for the protection of metabolism against desiccation (Wyn Jones and Gorham, 1983), (4) regulation of photosynthesis and respiration, including the associated carbon and nitrogen metabolism (Lawlor, 1979, 1983), and (5) accumulation of metabolites which alter osmotic potential and may protect metabolism from damage, allowing plants to survive drought and/or increase production of assimilates (Hanson and Hitz, 1982).

Understanding of events caused by water stress at the level of gene expression, in basic metabolism and in accumulation of metabolites, is incomplete and poorly related to agronomic production under stress. Current effort is directed towards protection from severe drought (Hanson and Hitz, 1982) and less to increasing production under more mild stress, and also concentrates on secondary metabolite rather than primary photosynthate production.

At present, analysis of the ability of plants to be productive under stress is best performed at the whole crop and organ levels of organization, rather than by studying individual metabolic processes (Zelitch, 1980). Measurements are generally made on the complete production system, in the normal environment, and integrate the processes at lower levels of organization. Such studies lack the information to describe the system in mechanistic terms and to show how it is controlled by the environment, so cannot lead directly to modifications. These must be made at the molecular level, even if the changes are to be expressed in the whole organ.

Stress metabolism has been studied on many plant species, using different methods of applying stress, and the rate of stress development and its severity have varied widely. Recently selection for 'drought resistance' has been based on accumulation of nitrogenous compounds, such as amino acids (Hanson and Hitz, 1982) (particularly proline) and glycine betaine (Hanson and Grumet,

1985), or hormones (e.g. abscisic acid). However, there is only indirect evidence of the value of metabolite accumulation in maintaining plant production (Blum and Ebercon, 1976). The effects of proline or glycine betaine on stabilizing isolated enzymes, in decreasing osmotic potential, and in promoting the growth of bacteria under osmotic stress (Le Rudulier and Valentine, 1982) show that they increase metabolic stability. Accumulation of such metabolites in higher plant cells may reflect the operation of similar, beneficial mechanisms. However, the control of photosynthesis in relation to secondary metabolism has not been adequately investigated (Lawlor, 1983) and it is not clear if photosynthesis will benefit from changes in, say, proline content. Uncertainty about which metabolic processes should be modified or of the value of metabolite accumulation stems from the lack of understanding of metabolism under water stress (Hsiao, 1973; Lawlor, 1983).

Conventional plant breeding allows metabolic characters to be combined and increased in the genome; also isogenic lines enable the effects of a single gene change in a uniform genetic background to be tested, and the metabolic consequences analysed. Similarly genetic material may be incorporated by genetic manipulation techniques (Le Rudulier and Valentine, 1982), giving specific genetic and metabolic modifications. Although both breeding and genetic engineering are technically feasible, uncertainty about the key metabolic processes may limit their efficient application to improving yield under drought. To quote Hanson and Grumet (1985), 'genetic engineering of stress-resistance will necessarily be a series of shots in the dark' and this is also applicable to conventional breeding. Despite this, the role of glycine betaine in osmotic adjustment and increasing production of barley under stress is being studied (Hitz *et al.*, 1982), and attempts are being made to introduce 'resistance genes' for water and related stresses into plants (Le Rudulier and Valentine, 1982). The value of genetic manipulation and isogenic lines may lie in the increased understanding of the interactions between metabolism and production gained from analysis of the system modified by introduction of single gene changes.

PHOTOSYNTHESIS UNDER DROUGHT

Total photosynthesis largely determines dry-matter production of crops: put at its simplest, the rate of assimilation per unit ground area is a function of crop leaf area LA, the rate of net photosynthesis per unit leaf area P_n, and the rate of crop respiration R:

$$\text{Net dry-matter production} = \text{LA} * P_n - R$$

Total crop water loss depends on LA and the rate of evaporation per unit leaf area E:

$$\text{Water loss} = \text{LA} * E$$

In moisture-limiting environments, increasing crop production by increasing LA (either by breeding or abundant fertilization) is not a simple option, for greater LA increases water loss which may cause greater water stress, and increase yield variability and loss of production (Vaadia, 1985). Also E and P_n are dependent upon stomatal conductance g, as E is related to the difference in water vapour pressure between the intercellular spaces (v_i) and air (v_a) and g_w, the conductance to water vapour, by

$$E = g_w (v_i - v_a)$$

and P_n is determined by the partial pressure of CO_2 in the intercellular spaces (c_i) and atmosphere (c_a) by

$$P_n = g_c (c_a - c_i)$$

where the conductance for CO_2, $g_c = g_w/1.6$, to correct for the diffusion coefficients of water vapour and CO_2 in air (Farquhar and Sharkey, 1982). Clearly, water loss and photosynthesis are related by g and LA and thus crop dry-matter production and water loss are closely coupled; although separation of the two would be advantageous, it is not possible (Vaadia, 1985). Water-use efficiency (WUE = dry-matter production/water used) depends on the net dry matter produced over the season and the accumulated water loss.

An option for increased production and WUE, and decreased water loss would be to select plants for greater P_n and smaller E. The principles (Farquhar and Sharkey, 1982) involved in selection for optimum photosynthesis are illustrated in Figure 2, which shows theoretical relationships between P_n and c_i for a leaf in light which saturates photosynthesis. The slope of the curves indicates the efficiency of the complete chain of processes leading to carboxylation. The maximum rate of photosynthesis, P_{max}, gives the capacity of the system independent of stomatal conductance, and with saturating CO_2 and light. By comparing the relationships for different genotypes under different conditions, e.g. of water stress or temperature, selection may be made for photosynthetic efficiency and high rate in relation to environment. Also, measurement of g shows how it regulates assimilation.

A number of strategies for optimizing P_n and E may be envisaged. Leaves with small maximum rates of P_n (Figure 2, line A) may decrease E by decreasing g, without a large fall in c_i. This would slow water loss and minimize water stress but at the expense of crop production. Plants with large potential rates of P_n and small g_w (Figure 2, line B) would, in theory, decrease water loss and maintain assimilation, but would suffer a large reduction in c_i. As a low ratio of CO_2/O_2 adversely affects photosynthesis of C_3 plants, because it increases the proportion of assimilate lost by photorespiration (see next section), permanently small g and large potential P_n are incompatible; even short-term stomatal closure may damage leaf functions. If the carboxylation efficiency were much larger (Figure 2, idealized response) then g and c_i

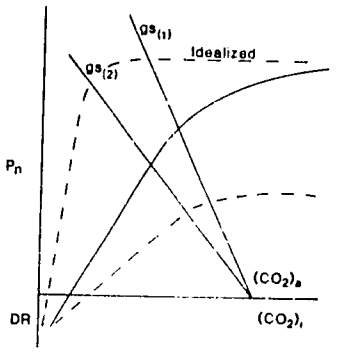


Figure 2. Photosynthetic response to intercellular carbon dioxide $[CO_2]_i$ at a given ambient $[CO_2]_a$ and two stomatal conductances, g_1 greater than g_2, for different photosynthetic capacity

could fall greatly without affecting P_n. The resemblance of this curve to that of C_4 leaves is marked and illustrates the need for increased photosynthetic efficiency if large rates of dry-matter production are to be achieved with minimum water loss. An alternative strategy of large P_n and g would only be effective if the crop grew so fast that water stress did not develop; this approach is only found in plants growing in very wet habitats. Decreasing g has a larger effect on water loss than on assimilation when CO_2 and g maintain c_i so that P_n is on the plateau of the response curve, but generally P_n is maintained below P_{max}; P_n, g and c_i appear to be optimized below maximum capacity for photosynthesis (Farquhar and Sharkey, 1982).

In breeding programmes it would be essential to select for high P_{max} and efficiency, particularly under stress, and for small total water use and large WUE. However, plants with efficient water use are not necessarily more resistant to water stress (Lawlor, 1979); that depends largely on the degree of change in water content and turgor potential and the effects on metabolism. Water use and dry-matter production must be optimized for long-term stability rather than maximum yield under good conditions. The differences in the photosynthetic characteristics of plants are sufficient to justify exploitation in breeding programmes. In wheats, modern higher ploidy varieties have small P_n (at given c_i, light, etc.) compared to primitive wheats, although they have a larger area per leaf (Zelitch, 1980). Dry-matter production and WUE of wheats might be improved under stress by increasing P_n and efficiency of modern varieties, decreasing their LA and g, but retaining greater assimilate storage capacity.

Both photosynthetic rate and efficiency are decreased by water stress and poor nutrition; the responses of P_n to c_i and light for winter wheat crops grown

in the field at Rothamsted with different nitrate supplies and with or without irrigation (rain excluded by automatic rain shelters) are shown in Figure 3. Drought or lack of nitrogen decreased both carboxylation efficiency and P_{max}. The initial slope of the light response curves (Figure 3b) shows that P_{max} and light harvesting efficiency also decreased with water and nitrogen stress during growth. These effects of slowly developing stress are similar to those observed with rapid water stress which decreased both carboxylation efficiency and P_{max} in proportion to leaf water potential (Lawlor and Khanna-Chopra, 1983), although in other studies (Sharkey and Badger, 1982) P_{max} decreased but not efficiency and in others stress had little effect on assimilation. For P_n response curves to be useful indicators of resistance to stress, conditions under which they should be measured need to be established.

Measurement of photosynthetic response curves allows the effect of defined treatments on the metabolic processes to be analysed. By stressing plants of different genotypes over periods of days and correlating the changes in assimilation with water balance, a preliminary screen would be possible. Subsequent comparisons would be made in the field and followed through the breeding programme, to confirm the responses or to evaluate the effects of other tissue characteristics, e.g. osmotic adjustment, on photosynthesis. Measurements may be made with existing gas exchange techniques (Farquhar and Sharkey, 1982) both in the laboratory and field (light and CO_2 may now be controlled with relative ease although temperature is more difficult), and microprocessor-based data acquisition and calculation greatly reduce the labour. Although it would not be possible to screen large numbers of crosses in a breeding programme, the technique is applicable to selection of parental lines and evaluation of potentially useful material.

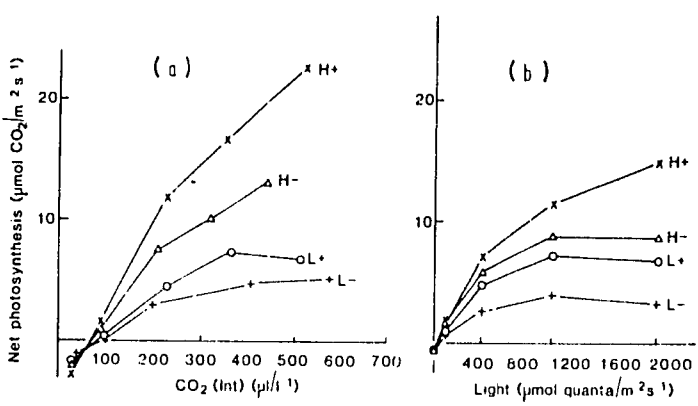


Figure 3. Response of net photosynthesis to (a) intercellular CO_2 and (b) light (measured in the laboratory) for the flag leaf of winter wheat (cv. Avalon) grown in the field with high (H) or low (L) nitrate supply with (+) or without (--) nitrate irrigation

METABOLISM AND CARBON DIOXIDE ASSIMILATION

Photosynthesis of C_3 plants, such as wheat, depends (Figure 4) on the capture of light energy by the chloroplast pigments and the efficiency with which the energy is used to synthesize reducing power (reduced ferredoxin and NADPH) and the phosphorylated metabolic 'energy currency' ATP. NADPH and ATP are used in the regeneration of ribulose bisphosphate (RuBP), the acceptor of CO_2. RuBP carboxylase-oxygenase (RuBPc-o) is the enzyme which catalyses the reaction of CO_2 with RuBP, producing 3-phosphoglyceric acid; it also catalyses the oxygenation of RuBP with O_2, producing phosphoglycolate. 3-Phosphoglyceric acid is converted, via many metabolic steps, to carbohydrates and (to a smaller extent) to amino acids, in reactions that depend on the nitrogen supply. Phosphoglycolate is ultimately metabolized in leaf cells to carbohydrates but with loss of CO_2 in the process of photorespiration. The ratio of P_r to P_n depends on the RuBPc-o characteristics and on the CO_2 and O_2 partial pressures in the tissue: P_r/P_n increases with a large O_2/CO_2 ratio and also with increasing temperature, particularly above 30°C. Water stress decreases g and thereby c_i, leading to an increase in the P_r/P_n ratio (Lawlor, 1979; Lawlor and Fock, 1975). The affinity of RuBPc-o for O_2 and CO_2 is very similar in all crop plants, and has not been changed by selection or breeding methods, possibly because several changes to the amino acid sequences at the enzyme active site are required. Genetic engineering techniques may enable an enzyme to be constructed with low oxygenase activity. This would be a considerable benefit to photosynthesis under drought conditions.

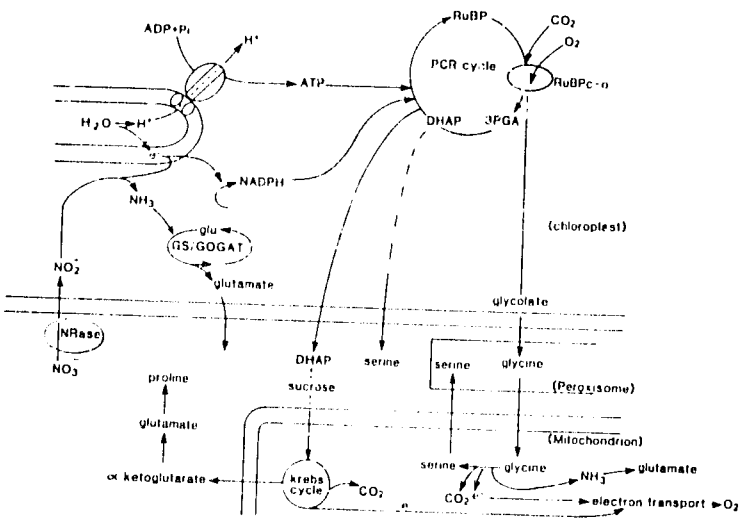


Figure 4. Simplified scheme of carbon and related nitrogen metabolism in the C_3 leaf

The decrease in P_n that occurs in stressed leaves has been ascribed to several changes in metabolism. In the longer term, loss of RuBPc-o activity, partly due to loss of protein, is probably important. There is progressive and roughly proportional decrease in most components of the photosynthetic apparatus under stress, linked to senescence. In more rapidly and severely stressed leaves, there is evidence (Boyer and Younis, 1983) that ATP synthesis (photophosphorylation) is a very sensitive metabolic process. Photophosporylation depends on the transport of electrons and protons in the chloroplast and the activity of the enzyme, coupling factor (CF_0 to CF_1). Amounts of ATP in stressed tissues decrease (Figure 5) with loss of turgor and changes in the ionic composition of cells, which alters the conformation of coupling factor and inhibits activity (Younis *et al.*, 1979).

ATP synthesis appears to be more sensitive to water stress than is reduction of NADP as the reductant status of stressed leaves is very large (Lawlor and Khanna-Chopra, 1983) when ATP is much decreased (Figure 5). Inhibition of ATP production and an imbalance with reductant will have serious consequences for all cellular processes (Lawlor, 1983; Pradet and Raymond, 1983). If energy absorbed by the light-harvesting pigments is not dissipated by photosynthesis, photoinhibition may occur, unless other processes can dissipate the energy. There is a clear indication from chlorophyll fluorescence that energy accumulates in the light-harvesting apparatus. However, there is controversy about photoinhibition as a cause of decreased P_n (Sharp and Boyer, 1985).

SECONDARY CARBON AND NITROGEN METABOLISM

One aspect of stress metabolism which continues to attract much interest is the changes in metabolite pools, particularly of nitrogen-containing compounds (Hanson and Hitz, 1982) formed in secondary reactions removed from photosynthesis (Figure 4). However, the complexity of metabolism makes it difficult to analyse the changes, particularly as the severity and rate of stress development impose different conditions on the leaves. In general, mild stress decreases growth but not assimilation, and carbohydrates may accumulate. Stress, which decreases P_n but not demand for assimilates by secondary metabolism, results in smaller pools of RuBP, 3-phosphoglyceric acid, and carbohydrates. However, with more severe and rapid stress, amino acids accumulate in leaves, and there is marked depletion of carbohydrates. Very severe stress, which almost stops P_n, greatly increases the amounts of amino acids, particularly proline (Lawlor and Fock, 1977), of the nitrogen-containing glycine betaine, and of hormones (Hsiao, 1973; Hanson and Hitz, 1982). Probably under these conditions ATP synthesis is inhibited and its content decreases, yet NADPH (and NADH) accumulate (Figure 5) (Lawlor and Khanna-Chopra, 1983). These conditions may favour production of

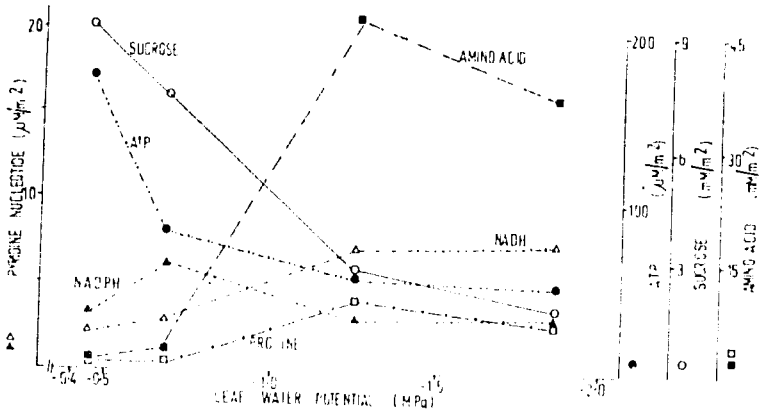


Figure 5. Changes in the amount of ATP, NADPH, NADH, sucrose, and total amino acid and proline in rapidly stressed leaves of wheat

ammonia by nitrate and nitrite reductases; ammonia is converted to glutamate and subsequently other amino acids are synthesized as the reduced cellular state favours their synthesis and yet demand from growth is stopped. Proline, for example, is produced from glutamate in a reaction which is probably mitochondrial and consumes reductant, not ATP. It is significant that proline accumulates when P_n is inhibited (and dark respiration occurs), and light energy is still captured so that electron transport continues to make reductant. Proline accumulation in higher plants is probably the end product of disrupted metabolism (Lawlor, 1983). Similarly, accumulation of glycine betaine, derived from the phosphatydyl choline of membranes (Hanson and Hitz, 1982), the appearance of myoinositol (Lawlor and Fock, 1977), and accumulation of polyamines (Flores *et al.*, 1985) with severe stress, suggest strongly that metabolite accumulation is a damage response in many species. Glycine betaine, however, occurs in halophytes under non-stress conditions; it has beneficial effects on enzyme stability *in vitro*, suggesting that it may have a particular role in resistance to salinity and water stress (Hanson and Hitz, 1982; Le Rudulier and Valentine, 1982). The accumulation of relatively small amounts of proline in crop plants has, as yet, not been shown to confer an advantage to cellular stability or for increased assimilation and yield (Blum and Ebercon, 1976), although, by analogy with bacteria, a protective role in metabolism is expected (Le Rudulier and Valentine, 1982). Evidence for the ability of accumulated metabolites to maintain productivity in crop plants is circumstantial.

PROTEIN SYNTHESIS AND STRESS

Under mild to severe stress, protein synthesis slows (Hsiao, 1973) due to loss of polyribosomes, possibly caused by ATP shortage. Impaired protein syn-

thesis may change cell function and increase senescence of stressed leaves. Perhaps damage to the protein synthesizing mechanism, or associated metabolic processes, is responsible for the synthesis of 'shock proteins' similar to those caused by heat shock in many organisms (Key *et al.*, 1985). Such proteins may be the product of metabolic disturbance without advantage. However, they may protect the protein-synthesizing system or other metabolic processes or have regulatory functions which enable the plant to adjust to stress. As with accumulation of other metabolites, the function of 'shock proteins' is equivocal. They may be useful in stress studies and breeding to indicate the susceptibility of the tissue to damage or its capacity to adjust to stress. Examination of the relation of protein synthesis to carbon metabolism and the ability of the tissue to survive drought might resolve these questions and show if shock proteins are of direct use as a screen for drought resistance. There is much interest in protein synthesis under stress because of the potential for genetic engineering (Key *et al.*, 1985).

METABOLIC INDICATORS OF USE IN BREEDING AND SELECTION

To be useful as indicators of plant adaptation to drought, metabolites should (1) be produced in well-characterized reactions, (2) accumulate in reproducible fashion in response to quantified stress, both degree and duration, (3) have clear functions in metabolism, e.g. as substrate or control molecules, and (4) have a well-understood mode of action in stressed tissue. Metabolites currently employed as selection criteria do not meet these theoretical requirements on present experimental evidence. Proline, for example, does not meet criteria 1, 3, or 4. Accumulation of substances or changes in the rates of complete processes, e.g. carbon fluxes in metabolic pathways such as sucrose synthesis, may be used to indicate severity of stress as well as the resistance of different genotypes to it. However, it is unlikely that any one metabolite or process will provide an unequivocal measure of 'drought resistance'. Comparison of photosynthesis and amounts of selected metabolites under defined stress may be a way of evaluating genotypes. Selection or production of genetic material with contrasted characteristics would enable their resistance to be tested and related to yield, etc.

The following aspects of metabolism and physiology could be of potential value in breeding programmes:

(1) Amounts of plant structure (e.g. light-harvesting membranes) or of soluble proteins or activities of enzymes (e.g. RuBPc-o). They relate only rather approximately to the potential capacity for photosynthesis. etc. Their relationship to drought resistance is unclear and it is difficult and time-consuming to measure them.

(2) Amounts of metabolites from photosynthesis or secondary reactions often correlate with particular stress thresholds (Hsiao, 1973; Hanson and

Hitz, 1982; Lawlor, 1983). They indicate metabolic functions and can be correlated with growth and production. The most useful of these are amino acids and indicators of membrane damage, e.g. myoinositol. They link to other physiological changes, e.g. osmotic adjustment (Wyn Jones and Gorham, 1983), and may be analysed by routine automated chemistry, and can therefore be used widely in selection.

(3) Measurement of carbon fluxes, e.g. by radiotracer techniques (Lawlor and Fock, 1975, 1977), provides information about short-term metabolic changes with stress. Methods are demanding, time-consuming, and difficult to interpret, particularly if conditions are changing rapidly.

(4) Photosynthesis, measured by gas exchange with light and CO_2 responses, integrates all associated metabolic processes, indicates efficiency, and can be related both to the stomatal and metabolic activity (Farquhar and Sharkey, 1982). Techniques are advanced, and relatively rapid, and they can be used in the field on droughted crops. Measurements can be combined with tracer studies and metabolite sampling for detailed analysis of the drought responses.

CONCLUSIONS

Measurements of metabolic change provide an insight into the mechanisms of plant production under drought, although no one process unequivocally meets the criterion of predicting improved productivity and yield stability. Gas exchange measurements integrate all metabolic processes associated with photosynthesis and may be used to select genotypes for 'drought resistance'. Methods are established and equipment is available; P_n should be correlated with soluble metabolites (amino acids and sugars) and with crop dry-matter production and yield. This approach will show the effects and value of particular metabolic changes and provide material for breeding programmes and for genetic manipulation. Such detailed analysis is impractical for evaluation of large numbers of genotypes. Progress is most likely where a combination of characters is selected in parental material, incorporated into the required genetic background, and the results evaluated on selected genotypes in the environment for which they are intended. Thus a combination of physiological and metabolic studies will provide information for selection and assessment of plants to increase yield under stress.

REFERENCES

Blum, A. and Ebercon, A. 1976. Genotypic responses in sorghum to drought stress. III. Free proline and drought resistance. *Crop Sci.* **16**:428–431.

Boyer, J. S. and Younis, H. M. 1983. Molecular aspects of photosynthesis at low leaf water potentials. Pages 29–33 in *Effects of Stress on Photosynthesis* (Marcelle, R., Clysters, H. and von Pouche, M., eds.). Martinus Nijhoff/Dr W. Junk, Publishers, The Hague.

Farquhar, G. D. and Sharkey, T. D. 1982. Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* **33**:317–345.

Fischer, R. A. and Turner, N. D. 1978. Plant productivity in the arid and semi-arid zones. *Ann. Rev. Plant Physiol.* **29**:277–317.

Flores, H. E., Young, N. D. and Galston, A. W. 1985. Polyamine metabolism and plant stress. Pages 93–114 in *Cellular and Molecular Biology of Plant Stress*. Alan R. Liss, New York.

Hanson, A. D. and Grumet, R. 1985. Betaine accumulation: metabolic pathways and genetics. Pages 71–92 in *Cellular and Molecular Biology of Plant Stress*. Alan R. Liss, New York.

Hanson, A. D. and Hitz, W. D. 1982. Metabolic responses of mesophytes to plant water deficits. *Ann. Rev. Plant Physiol.* **33**:163–203.

Hitz, W. D., Ladyman, J. A. R. and Hanson, A. D. 1982. Betaine synthesis and accumulation in barley during field water-stress. *Crop Sci.* **22**:47–54.

Hsiao, T. C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* **24**:519–570.

Key, J. L., Kimpel, J. A., Lin, C. Y., Nagao, R. T., Vierling, E., Czarnecka, E., Gurley, W. B., Roberts, J. K., Mansfield, M. A. and Edelman, L. 1985. The heat shock response in soybean. Pages 161–179 in *Cellular and Molecular Biology of Plant Stress*. Alan R. Liss, New York.

Lawlor, D. W. 1979. Effects of water and heat stress on carbon metabolism of plants with C_3 and C_4 photosynthesis. Pages 304–326 in *Stress Physiology in Crop Plants* (Mussell, H. and Staples, R. C., eds.). John Wiley, New York.

Lawlor, D. W. 1983. Integration of biochemical processes in the physiology of water-stressed plants. Pages 35-44 in *Effects of Stress on Photosynthesis* (Marcelle, R., Clijsters, H. and van Pousse, M., eds.). Martinus Nijhoff, The Hague.

Lawlor, D. W. and Fock, H. 1975. Photosynthesis and photorespiratory CO_2 evolution of water-stressed sunflower leaves. *Planta* **126**:247–258.

Lawlor, D. W. and Fock, H. 1977. Water stress induced changes in the amounts of some photosynthetic assimilation products and respiratory metabolites of sunflower leaves. *J. Exp. Bot.* **28**:329–337.

Lawlor, D. W. and Khanna-Chopra, R. 1983. Regulation of photosynthesis during water stress. Pages 379–382 in *Advances in Photosynthesis Research* (Sybesma, C., ed.). Martinus Nijhoff/Dr W. Junk, Publishers, The Hague.

Le Rudulier, D. and Valentine, R. C. 1982. Genetic engineering in agriculture: osmoregulation. *Trends Biochem. Sci.* **5**:431–433.

Pradet, A. and Raymond, P. 1983. Adenine nucleotide ratios and adenylate energy charge in energy metabolism. *Ann. Rev. Plant Physiol.* **34**:199–224.

Sharkey, T. D. and Badger, M. R. 1982. Effect of water stress on photosynthetic electron transport, photophosphorylation, and metabolite levels of *Xanthium strumarium* mesophyll cells. *Planta* **156**:199–206.

Sharp, R. E. and Boyer, J. S. 1985. Loss in chloroplast activity at low leaf water potentials in sunflower: the significance of photoinhibition. Pages 41–49 in *Cellular and Molecular Biology of Plant Stress*. Alan R. Liss, New York.

Vaadia, Y. 1985. The impact of plant stresses on crop yields. Pages 13–40 in *Cellular and Molecular Biology of Plant Stress*. Alan R. Liss, New York.

Weeks, D. P. 1981. Protein biosynthesis: mechanisms and regulation. Pages 491–529 in *The Biochemistry of Plants* (Stumpf, P. K. and Conn, E. F., eds.). Vol. 6, *Proteins and Nucleic Acids* (Markus, A., ed.). Academic Press, New York.

Wyn Jones, R. G. and Gorham, J. 1983. Osmoregulation. Pages 35–58 in *Encyclopedia of Plant Phsiology N.S.* Vol. 12, *Physiological Plant Ecology III* (Lange, O. L., Nobel, P. S., Osmond, C. B. and Ziegler, H., eds.). Springer-Verlag, Berlin.

Younis, H. M., Boyer, J. S. and Govindjee 1979. Conformation and activity of chloroplast coupling factor exposed to low chemical potential of water in cells. *Biochim. Biophys. Acta* **548**:328–340.

Zelitch, I. 1980. The close relationship between net photosynthesis and crop yield. *Bioscience* **32**:796–802.

DISCUSSION

N. C. Turner

Where you compared the net photosynthesis at different CO_2 levels and light levels in high and low nitrogen regimes and with and without stress, were the leaf water potentials and stress history of the leaves similar?

D. Lawlor

Leaf water potentials of the irrigated treatments were similar but the droughted were not. Large nitrogen rate increased water loss from the soil and leaf water potential in that treatment was smaller than in low nitrogen.

S. K. Sinha

You have shown the effects of drought on various metabolic processes. Do you think that leaf and dry matter integrate these effects, and hence serve as good selection criteria?

D. Lawlor

Yes, metabolic changes are many and complex. Dry-matter production, yield, leaf area, etc., integrate the effects of environment on metabolic steps in their production, so they are the best single indicator of response.

E. Porceddu

There is evidence of great variation among and within species of wheat in SOD activity when under stress. Have you found any similar evidence?

D. Lawlor

No, I have no evidence but there may be differences, perhaps as there are in relation to light.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

19

Nitrogen Metabolism in Relation to Water Stress

J. PEARSON,* N. SMIRNOFF,† G. R. STEWART,* and L. B. TURNER‡
**University College London, Department of Botany and Microbiology, Gower Street, London WC1E 6BT, UK; †Department of Biological Sciences, University of Exeter, Exeter, UK; ‡Department of Biological Sciences, University of Sussex, Falmer, Brighton, UK.*

ABSTRACT

We consider the role of nitrate and organic nitrogen compounds in relation to water stress and also aspects of nitrogen acquisition, biosynthesis, and cycling. We analysed both laboratory- and field-grown plants (on a line-source sprinkler) for metabolites, such as nitrate, proline, and other amino acids. In the barley varieties tested these all increase in concentration with increased water deficit. Such compounds are thought to act as osmoticants. Total reduced nitrogen also increases in drought-stressed plants, and we questioned the so-called drought susceptibility of nitrate reductase. The quantitative changes of amino acids in stressed barley have been used to construct a metabolic index of stress which correlates very well with rates of water loss from leaves. This may be useful in characterizing the susceptibility of plants to drought stress.

INTRODUCTION

The essence of crop improvement, be it through breeding or management practices, is perhaps best expressed by Jonathan Swift in *Gulliver's Travels*:

> . . . He gave it for his opinion that whoever could make two ears of corn, or two blades of grass to grow upon a spot of ground where only one grew before; would deserve better of mankind, and do more essential service to his country, than the whole race of politicians put together.

In arid and saline areas the problem is that we have hardly managed to get one blade of grass to grow.

In this contribution we want to consider some of the ways in which plant nitrogen metabolism is affected by osmotic stress: drought and salinity. The reason for doing so is that not only is nitrogen an important nutritional component for plants but it is also found in solutes that often comprise an important part of a plant's total osmotica. In this latter respect it may play an important role in controlling the water relations of plants in drought-stressed environments. The amino acid proline, for example, can comprise 1–2 per cent of the total dry weight in water-stressed barley (Aspinall and Paleg, 1981), or in salt-stressed *Triglochin maritima* it may be as much as 10 per cent (Stewart and Lee, 1974). Therefore, a knowledge of the processes involved in nitrogen transformations, within plants under drought stress, may point to desirable metabolic traits needed to improve crop varieties for growth in arid environments.

Under stress a plant may compensate at genotypic and phenotypic levels by using existing structures or pathways, or it may modify its status by forming new structures or switching on new pathways. Either way the end result is represented by the two extremes of adaptation or death. In studying metabolic changes it is vital that we know where on this continuum the stressed plant lies. Conclusions about processes and the role of metabolites, such as proline, are difficult if the plant is dead or dying. One such method of overcoming this problem that is particularly applicable to the study of crop plants in dry areas is that of the line-source sprinkler (LSS). Water is supplied to plants at times of stress such that those nearest the sprinkler receive an adequate supply, while those furthest away receive hardly any. Plants can then be sampled along the irrigation gradient. In this way changes along the continuum unstressed—(adapted)—stressed can be more easily studied.

It is convenient to regard plant nitrogen metabolism as three areas which overlap and interact with each other. This emphasizes that an alteration in one of these areas can have repercussions in either or both of the other areas. Under stress it is generally possible to observe changes in almost every facet of nitrogen metabolism.

NITROGEN METABOLISM

Acquisition

In arid soils the predominant form of available nitrogen to non-leguminous crops is in the form of nitrate. Soil availability apart, two components of the acquisition of nitrate are involved: uptake and transformation or assimilation. It is likely that in the absence of transformation there will be a limit to the rate of uptake.

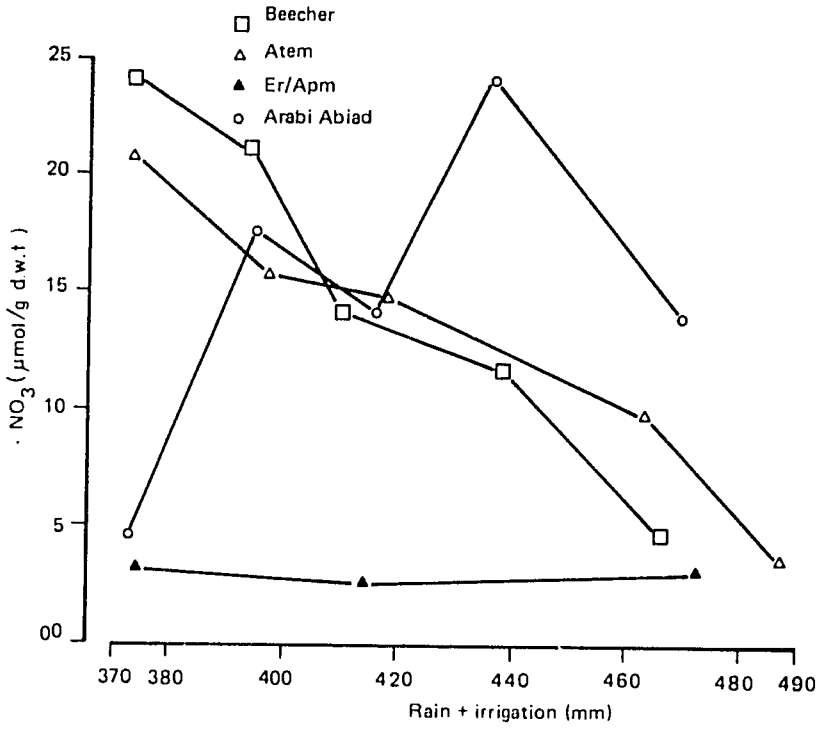


Figure 1. Nitrate accumulation in the shoot of four barley varieties grown on the LSS at ICARDA, Tel Hadya, Syria, 1985

Experiments on mostly laboratory-grown plants suggest that nitrate will accumulate under drought stress, while at the same time the activity of nitrate reductase, the first enzyme of nitrate assimilation, will decline (Hanson and Hitz, 1983). Four LSS-grown barley varieties (Beecher and Er/Apm, improved varieties for drylands; Atem, a north European improved variety; and Arabi Abiad, a Syrian landrace) showed differing responses of nitrate accumulation under drought stress (Figure 1). Beecher and Atem showed a six- to sevenfold increase in shoot nitrate accumulation down the irrigation gradient. Arabi Abiad gave no consistent response, while the nitrate content of Er/Apm remained relatively low and constant. Increasing irrigation can mean increased nitrate leaching from the soil; thus availability rather than uptake may be primarily affected. However, plants grown in nutrient solution with 6 mM nitrate and then given incremental doses of PEG 6000 every 3 days were still able to increase their shoot and root nitrate concentrations more than threefold (Figure 2).

This increase in nitrate concentration under water stress could be due to the

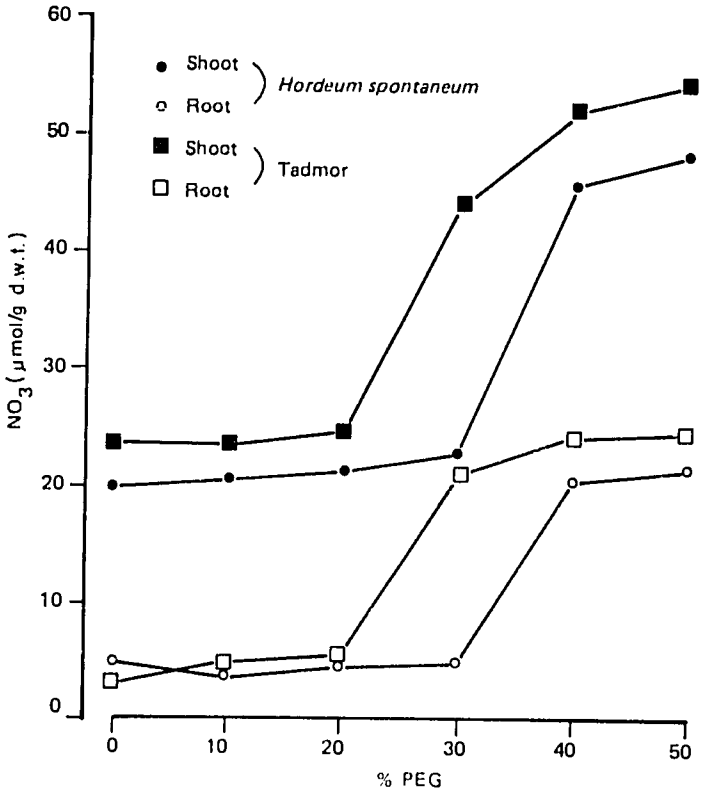


Figure 2. Nitrate accumulation in the shoot and root of *Hordeum spontaneum* and a landrace barley, Tadmor, grown on successive incremental PEG 6000 concentrations

inhibition of nitrate reductase activity due to its drought sensitivity (Sinha and Nicholas, 1981). However, Smirnoff *et al.* (1985) showed that nitrate reductase activity in Er/Apm and Arabi Abiad, when grown on an LSS, did not decline, even when leaf water potentials were as low as −2.5 to −3.5 MPa. These plants when given rapidly applied water stress in the laboratory showed decreases in nitrate reductase activity of 40–85 per cent of the control. Further tentative evidence that its activity may not be so readily inhibited by drought stress in plants under field conditions is given in Figure 3, where we give a comparison of tissue nitrate against tissue total nitrogen (not including nitrate). Apart from Er/Apm, where no significant changes occurred, there is a reasonable positive correlation between tissue nitrate and total nitrogen.

Can we, therefore, regard nitrate accumulation under increased water deficit as an adaptive response: If *Suaeda maritima* is drought stressed on PEG 6000 without NaCl, then it can accumulate nitrate to levels as high as

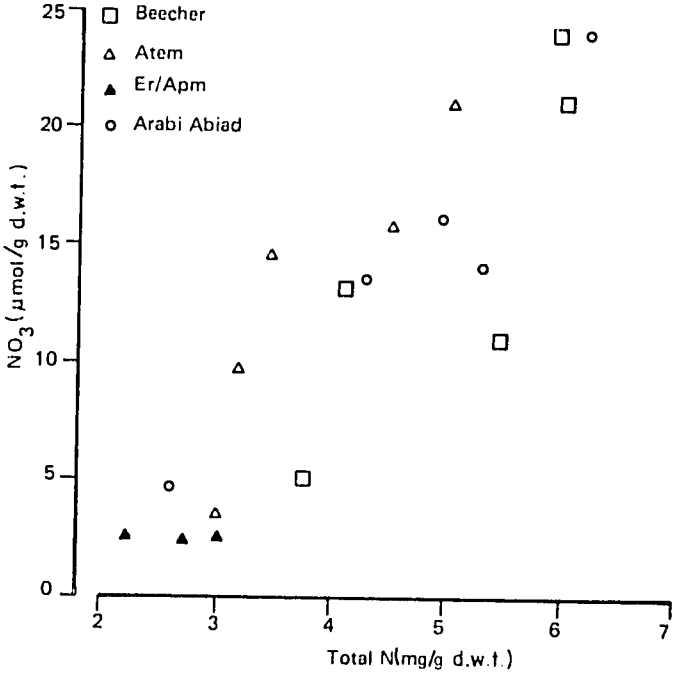


Figure 3. The correlation of shoot tissue nitrate with total nitrogen in four barley varieties

300 mM. There is also quite a good correlation between nitrate concentration and leaf water potential (unpublished). The implications are that nitrate can act as an osmoticant. In lettuce it has been shown that nitrate may act as an alternative osmoticant when organic acid and sugar concentrations are reduced under low light intensities (Blom-Zandstra and Lampe, 1985).

Total plant nitrogen content can be said to reflect the rates of acquisition, although for individual tissues (roots, leaves, seeds, etc.) the other two processes of assimilation and cycling will be directly involved. Figure 3 has already intimated that total tissue nitrogen in barley may increase with increasing drought stress. The same seems to be true of other non-nodulated crops, provided soil nitrate is not limiting (Hanson and Hitz, 1983). The total nitrogen content of two barley varieties grown on well-fertilized soil on an LSS at two locations in Syria verifies these findings (Figure 4). Again the notion of nitrate reductase activity being drought susceptible can be questioned, as clearly nitrogen acquisition and assimilation is seemingly increased under water stress.

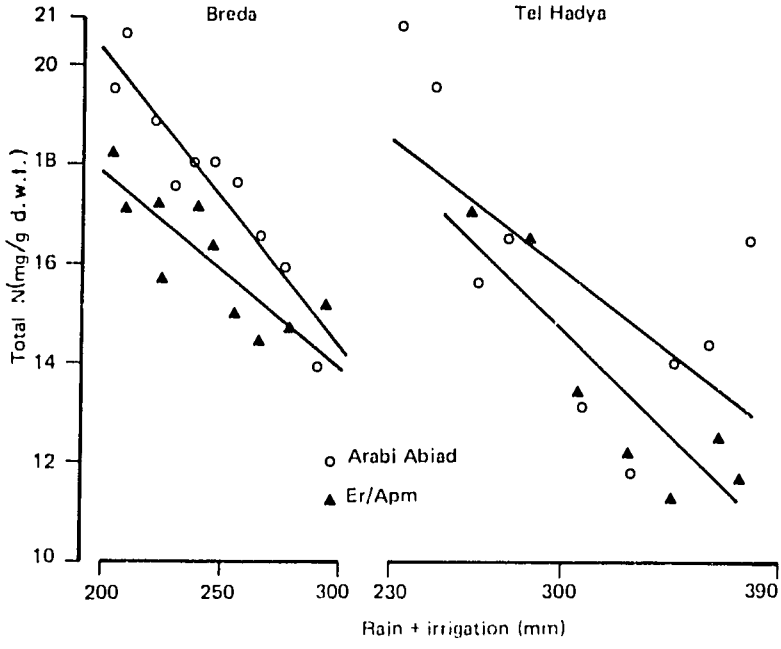


Figure 4. Total nitrogen content of straw plus grain for two barley varieties: Arabi Abiad and Er/Apm. Plants were grown on fertilized plots on an LSS at two locations in Syria in 1984. The regression factors are Breda: Arabi Abiad $r = -0.95$ and Er/Apm $r = -0.85$; Tel Hadya: Arabi Abiad $r = -0.66$ and Er/Apm $r = -0.67$

Biosynthesis

While the role of nitrate reductase in tissues experiencing water deficit can be questioned, it is generally agreed that nitrite reductase and the GS/GOGAT mechanisms are not so readily affected (Sinha and Nicholas, 1981; Taylor *et al.*, 1982).

With respect of intermediary nitrogen metabolism, much attention has been focused on proline and the betaines in relation to drought and salinity exposure. However, it must be pointed out that proline is by no means the only amino acid that alters in plants under stressed conditions. Several others accumulate: asparagine, phenylalanine, isoleucine, valine, and leucine. Others that generally decrease are aspartate and glutamate (Stewart and Lahrer, 1980). Asparagine, for example, though usually present in relatively large amounts in unstressed tissue shows a small increase with increasing water deficit (Figure 5). Figure 5 also makes the point that total amino acids increase in concentration with drought stress. This increase is over and above the levels accounted for by both proline and asparagine. During water stress

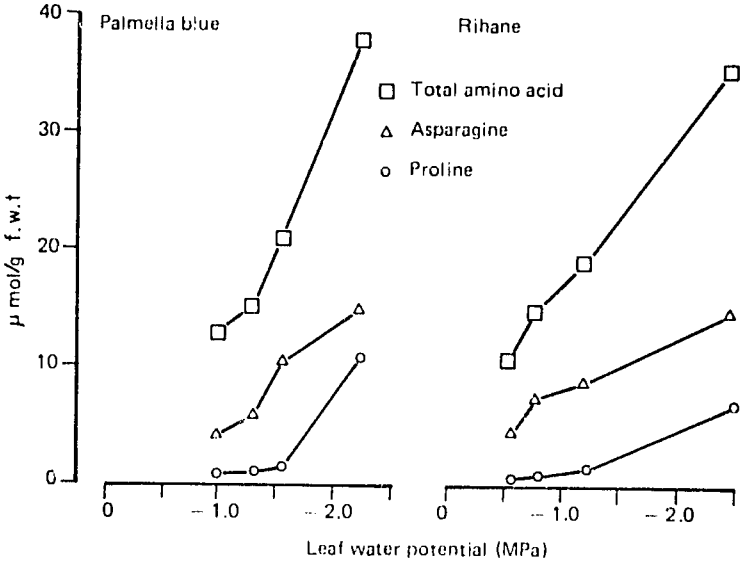


Figure 5. Metabolites in the leaves of two barley varieties grown in pots from which water has been withheld

polyribosomes disaggregate and it is known that protein synthesis is inhibited (Bewley *et al.*, 1983; Hsiao, 1970); paradoxically some protein hydrolysis may also occur. More interesting are the possible implications of altered pathways of protein synthesis. This has been pursued with respect to heat-shock proteins (mentioned earlier at this meeting). Is it possible that drought-shock proteins may also be discovered (Bewley *et al.*, 1983)?

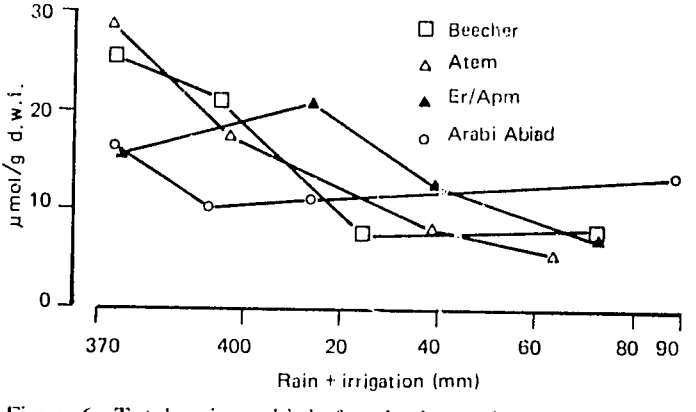


Figure 6. Total amino acids in four barley varieties grown on an LSS at Tel Hadya, 1985

The data showing total amino acid concentration in the LSS-grown varieties (Figure 6) are less clear, mainly because there was too much rainfall during the course of the field experiment. Yet with Beecher and Atem the trend towards amino acid accumulation at the drier end of the LSS is evident.

Other nitrogen-containing secondary metabolites have also been implicated in drought-stress tolerance (Turner and Stewart, 1986). Figure 7 shows the rates of increase, or decrease, of putrescine in four barley varieties against the change in leaf water potential. Plants were grown in pots from which water was withheld and then compared to well-watered controls. The two most drought-tolerant varieties, Rihane and Alger ceres, have a greater capacity to accumulate putrescine, whereas in the least tolerant, Roho, putrescine levels decline.

Cycling

In briefly considering the cycling of metabolites it must be emphasized that the timing and duration of water stress will have different repercussions on photosynthesis and photorespiration (C_3 plants). This will greatly affect both the history of the buildup of metabolites and their subsequent mobilization. Barley is predominantly a shoot assimilator of nitrate and so translocation of nitrate to the shoot is important. This movement may be inhibited if the

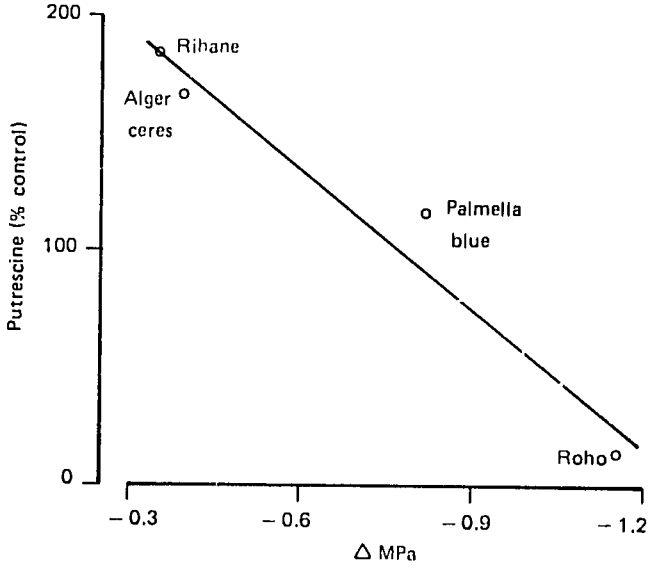


Figure 7. Leaf putrescine concentrations in four barley varieties compared to rates of leaf water loss. Plants were grown in pots from which the water had been withheld for 7 days

transpiration rate declines due to water deficit. Further, export of reduced nitrogen, or other metabolites, from leaf to root, other leaves, and grain, has several stages that must be sensitive to changes in plant water status. Enzymes involved in either *de novo* synthesis or protein hydrolysis and amino acid catabolism could be affected. Movement to and through the phloem to the target site, as well as subsequent transformations and synthesis, may also be altered under stress (Hanson and Hitz, 1983).

BIOCHEMICAL ASPECTS IN RELATION TO CROP BREEDING FOR ARID ENVIRONMENTS

From the data presented in the previous sections it is clear that in barley, although the overall changes in nitrogen metabolism are similar, the extent of these changes show marked intervarietal differences. There is also a degree of intravarietal variation that is more evident in the landrace Arabi Abiad. Selection for some of this genotypic variation with regard to the crop physiology may be useful, provided desirable traits can be characterized. For instance, the evidence for barley suggests that the more drought-tolerant varieties have a lower water potential threshold before nitrate, proline, and amino acids in general begin to accumulate. In this respect a useful metabolic or physiological trait must: (1) have diagnostic value, (2) be readily measured or quantified, (3) preferably show a wide heritable variation, and (4) be easy to select for.

In order to comply with the above criteria we have worked on constructing a metabolic index of stress. This is based on changes in the amino acid content. The idea of an index of stress is not a new one; indeed indices have been constructed purely from visual assessment of damage to plants during stress. This index could revolve around those amino acids that increase (numerator) and those that decrease (denominator):

$$\frac{\text{Pro} \times \text{Phe} \times \text{Isol} \times \text{Val} \times \text{Leu}}{\text{Asp} \times \text{Glu}}$$

Figure 8 shows the close correlation of the index with rates of leaf water loss from five barley varieties (cf. Figure 7). However, the techniques for individual amino acid quantification are time consuming and at best might only be useful for looking for favourable parents for crosses. As proline has by far the highest concentration than any other amino acid formed in barley under stress, then an index of proline/total amino acids might be more useful. This has the advantage that simple colorimetric techniques can be used, and it could be possible to screen modest numbers of offspring from crosses. The index for the four LSS barley varieties has been calculated against grain yield (Table 1). The higher values for the gas chromatograph are probably due to

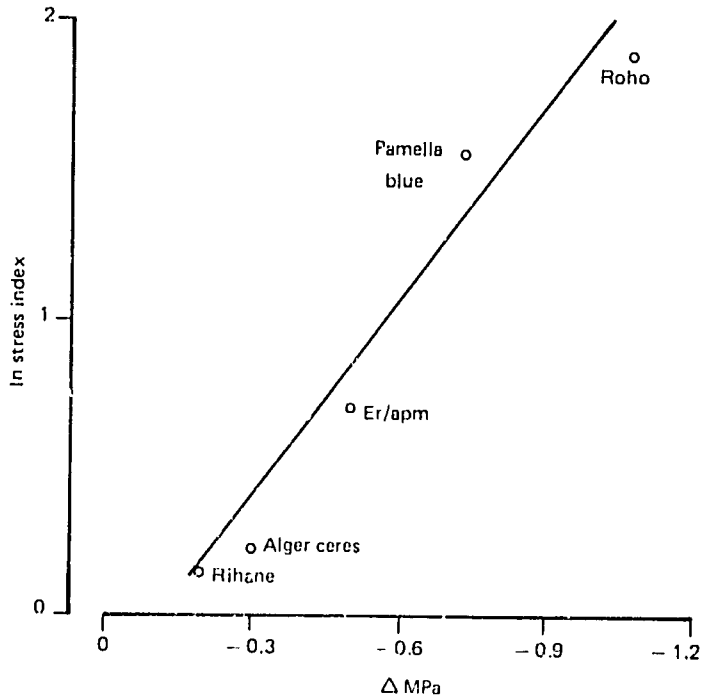


Figure 8. Plot of the natural log of the stress index against rate of leaf water loss for five barley varieties

the greater sensitivity of this technique. There is a strong negative correlation of grain yield with both indices (both $r = -0.99$).

We have already heard from Dr Marshall that any screening technique must be rapid and simple, and capable of characterizing offspring numbering tens of thousands. One such technique which we are currently analysing is the effect of stress on grain fill. Proline cycling from leaves, or possibly the awns,

Table 1. Index of proline/total amino acids for four varieties of barley receiving only 373 mm rainfall. Plants were grown at Tel Hadya, Syria, 1985

Variety	Index		Grain yield (kg/ha)
	Colorimetric	Gas chromatography	
Arabi Abiad	0.122	0.334	3976
Beecher	0.216	0.461	3489
Er/Apm	0.356	—	3016
Atem	0.522	0.675	2035

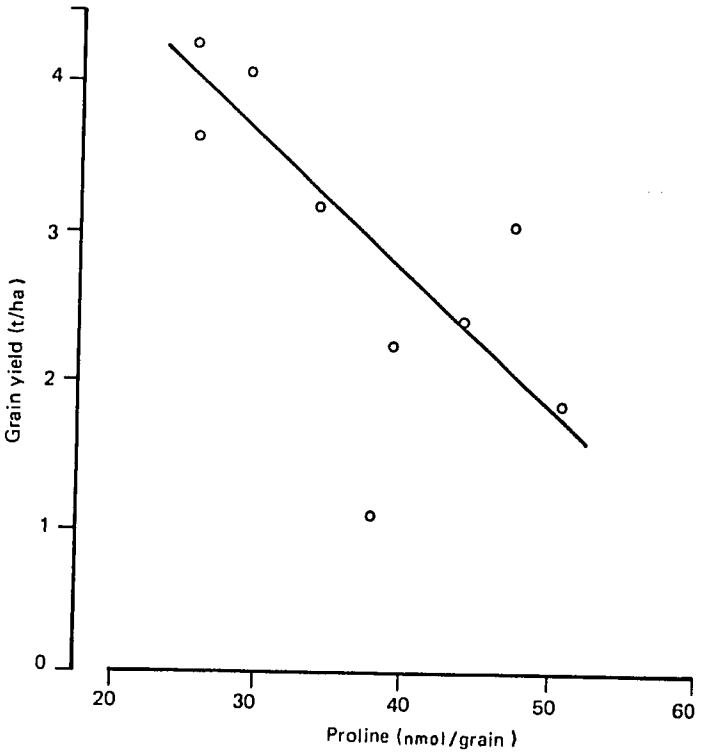


Figure 9. Correlation of grain yield with grain proline content in Arabi Abiad, a landrace barley

to the grain may reflect the history of the drought stress during grain maturation, and therefore it could be a useful aid to metabolic profiling. In this way there is no need to spend time growing progeny before sampling, and results can be compared readily with grain yield. Preliminary results (Figure 9) do indicate that there is a marked correlation between grain proline and final yield in Arabi Abiad.

CONCLUSIONS

Even if physiological and metabolic profiling is not a realistic means of screening large numbers of offspring from crosses, it may still help the plant breeder in several ways. As far as we know within the entire barley genome there is a limit to the degree of drought tolerance that can be achieved. Physiological characterization of ancient relatives, landraces, and improved varieties can assess these likely limits. It is impossible to conceive of barley

being dessication tolerant as with the mosses and resurrection plants, or that it can be made truly drought tolerant like the desert succulents. In the end there has to be a price paid for drought tolerance. If it is attainable it may only come as a result of drastic yield reductions. Even the accumulation of osmoticants such as proline or nitrate come at a price—the use of energy for uptake and production and the waste of potential resources they represent (Oertli and Jenka, 1985). In studying barley in terms of water use the physiologist might just as easily ask how flood tolerant is it? In this way barley's potential genotypic position on the full spectrum of flood tolerance to true drought tolerance could be assessed.

ACKNOWLEDGEMENTS

J. Pearson and N. Smirnoff gratefully acknowledge the financial support of the Overseas Development Administration and the help of the International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. Thanks also to Philip Ladley for his technical assistance and to David Rhodes (Purdue University, USA) for useful discussions on the metabolic stress index.

REFERENCES

Aspinall, D. and Paleg, L. G 1981. Proline accumulation: physiological aspects. Pages 205–241 in *The Physiology and Biochemistry of Drought Resistance in Plants* (Paleg, L. G. and Aspinall, D., eds.). Academic Press, Sydney, Australia.

Bewley, J. D., Larsen, K. M., and Papp, J. E. 1983. Water-stress-induced changes in the pattern of protein synthesis in maize seedling mesocotyls: a comparison with the effects of heat shock. *J. Exp. Bot.* **34**:1126–1133.

Blom-Zandstra, M. and Lampe, J. E. M. 1985. The role of nitrate in the osmoregulation of lettuce (*Lactuca sativa* L.) grown at different light intensities. *J. Exp. Bot.* **36**: 1043–1052.

Hanson, A. D. and Hitz, W. D. 1983. Whole-plant response to water deficits: water deficits and the nitrogen economy. Pages 331–343 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R. and Sinclair, T. R., eds.). American Society of Agronomy, New York.

Hsiao, T. C. 1970. Rapid changes in levels of polyribosomes in *Zea mays* in response to water stress. *Plant Physiol.* **46**:281–285.

Oertli, J. J. and Jenka, B. 1985. The theoretical basis for determining osmotic adjustment. *J. Plant Physiol.* **121**:391–395.

Sinha, S. K. and Nicholas, D. J. D. 1981. Nitrate reductase. Pages 145–169 in *The Physiology and Biochemistry of Drought Resistance in Plants* (Paleg, L. G. and Aspinall, D., eds.). Academic Press, Sydney, Australia.

Smirnoff, N., Winslow, M. D., and Stewart, G. R. 1985. Nitrate reductase activity in leaves of barley (*Hordeum vulgare*) and durum wheat (*Triticum durum*) during field and rapidly applied water deficits. *J. Exp. Bot.* **36**:1200–1208.

Stewart, G. R. and Lahrer, F. 1980. Accumulation of amino acids and related compounds in relation to environmental stress. Pages 609–635 in *The Biochemistry of Plants*, Vol. 5. Academic Press, London.

Stewart, G. R. and Lee, J. A. 1974. The role of proline accumulation in halophytes. *Planta* **120**:279–289.

Taylor, A. A., De Felice, J. and Havill, D. C. 1982. Nitrogen metabolism in *Poterium sanguisorba* during water stress. *New Phytologist* **90**:19–25.

Turner, L. B. and Stewart, G. R. 1986. The effect of water stress upon polyamine levels in barley (*Hordeum vulgare* L.) leaves. *J. Exp. Bot.* **37**:175–182.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

20

Modelling Stomatal Conductance in the Identification of Physiological Traits for Drought Resistance

A. M. CASTRIGNANO, N. LOSAVIO, M. MASTRORILLI, and M. E. VENEZIAN
Istituto Sperimentale Agronomico (MAF), Via C. Ulpiani 5, Bari, Italy

ABSTRACT

We propose a model that utilizes the response of stomatal conductance (K_s) to net radiation (R_n), vapour pressure deficit of the atmosphere (VPD), and leaf water potential (ψ_l).

We carried out the model calibration on the basis of the data from both stressed and irrigated durum wheat. The calculated parameter values appeared to be higher in well-watered plants for: (1) the maximum of K_s under non-limiting light conditions and the rate of reaching this maximum and (2) the minimum threshold of ψ_l for the beginning of stomatal opening. We observed lower values in stressed plants for these parameters: (1) rate of stomata closing at the increasing VPD and (2) rate of stomatal response to increasing ψ_l.

We then discuss some speculations on the possibility of utilizing the values of the considered physiological traits in breeding for drought resistance.

INTRODUCTION

Screening of genotypes for high yield under arid conditions should be based on simple and rapid analytical procedures. The measurement of plant water status and stomatal conductance K_s can be used as a tool to evaluate the genotype response to water deficit; the leaf water potential ψ_l is a good overall indicator of the plant water status and the stomata opening, which is related to the water status of the leaf, and can be used for the estimation of the rate of water vapour flow (O'Toole *et al.*, 1984).

The crops respond differently to moisture deficit: some genotypes can tolerate the water stress, reducing the sensitivity of stomata to lower values of leaf water potential; on the other hand, the genotypes capable of maintaining a relatively high water potential, when exposed to drought stress, could be selected as drought avoiders.

The cultivation of durum wheat is of great importance in the Mediterranean area but its yield fluctuates from year to year primarily due to the climatic conditions, and drought is considered the main cause of yield reduction.

A mathematical model that can predict the stomata conductance behaviour on the basis of some ecophysiological variables has been calibrated on durum wheat in southern Italy under rainfed as well as supplementary irrigation conditions, as a means to screen wheat lines most suitable for dry regions.

MATERIAL AND METHODS

We grew durum wheat under two different water supply conditions: rainfed and irrigated (88 mm water applied at two different times) and measured stomatal conductance and leaf water potential (Scholander *et al.*, 1965) during the flowering and seed-setting stages for two growing seasons.

Stomatal conductance was measured at different levels of radiation and air humidity by a steady-state diffusion porometer equipped with a thermocouple sensor to measure leaf temperature. The K_s of the wheat flag leaf was estimated by $K_s = K_{sab} + K_{sad}$, where K_{sab} and K_{sad} are abaxial and adaxial conductance, respectively (Brun *et al.*, 1973).

During the period of measurements, net radiation, air temperature, and relative humidity were determined and the actual vapour pressure deficit (VPD) was estimated and expressed in megapascals.

Because many factors affect K_s, we propose a phenomenological model for the stomata response to the main ecophysiological variables, on the basis of the functions between K_s and R_n, VPD and ψ_l; these functions representing the K_s response to each variable—the others being constant—were obtained by Jarvis (1976) from the data from crops grown under controlled conditions and checked later experimentally.

Assuming the effects of the variables R_n, VPD, ψ_l, acting at the same time in the field, to be multiplicative and neglecting synergic effects, the resulting global function for the stomatal conductance is:

$$K_s(R_n, \text{VPD}, \psi_l) = f(R_n) f(\text{VPD}) f(\psi_l)$$

The first term on the right-hand side of the equation:

$$f(R_n) = \frac{P_1 P_2 R_n}{P_1 + P_2 R_n}$$

relating K_s to R_n is a rectangular hyperbola and its parameters are

P_1 = asymptotic value of K_s under non-limiting light and optimal conditions for the other variables

P_2 = slope of the function K_s versus R_n for $R_n \rightarrow 0$

The second term:

$$f(\text{VPD}) = 1 - P_3 \times \text{VPD}$$

relating K_s to VPD is linear and its parameter P_3 is the rate of stomata closing at the increase of VPD. Finally, the third term:

$$f(\psi_l) = 1 - e^{-P_4(\psi_l - P_5)}$$

relating K_s to ψ_l is an exponential function with two parameters:

P_4 = rate of stomata response to increasing ψ_l

P_5 = lower threshold value of ψ_l for the beginning of stomatal opening

We used an iterative process, implemented on a minicomputer using the Marquardt method, to estimate the parameters (Marquardt, 1963; Draper and Smith, 1966). The standardized residual, i.e. the ratio of the residual (measured K_s − predicted K_s) to the standard error of the residual, was estimated for each observation. The objective criterion used to test the model depended on the value of standardized residual: observations with standardized residual greater than two were neglected.

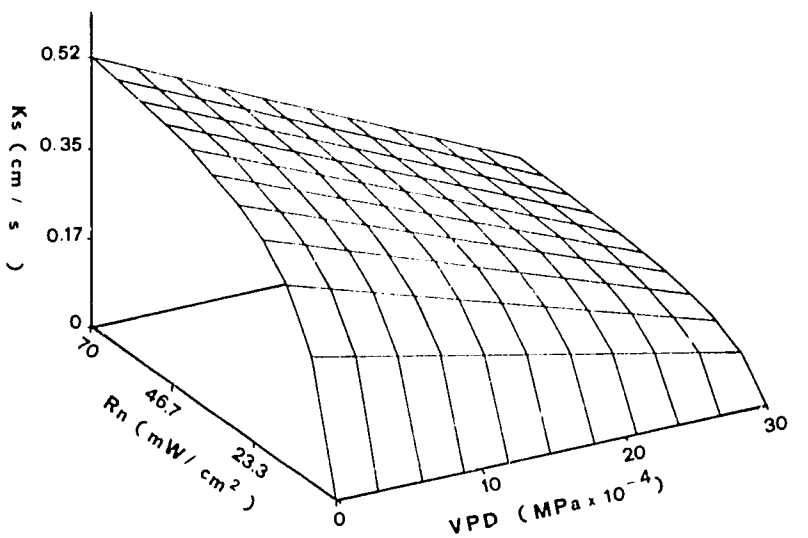


Figure 1. Surface response of K_s to R_n and VPD on rainfed plants (ψ_l = −3 MPa)

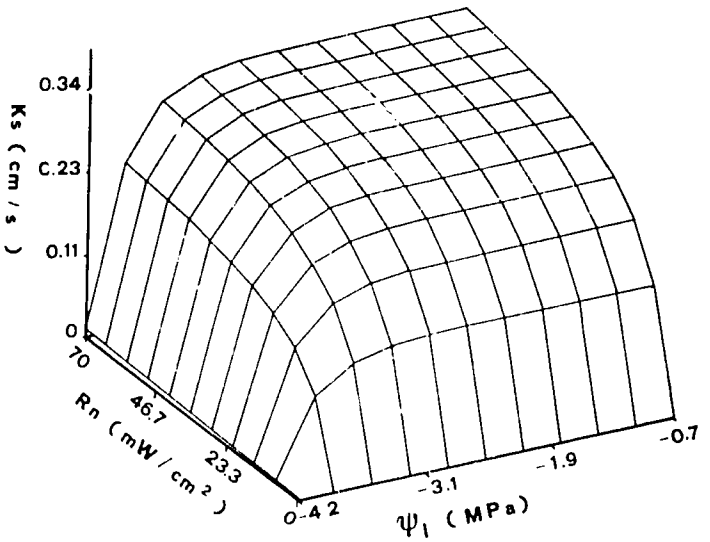


Figure 2. Surface response of K_s to R_n and ψ_l on rainfed plants (VPD = 15 MPa × 10^{-4})

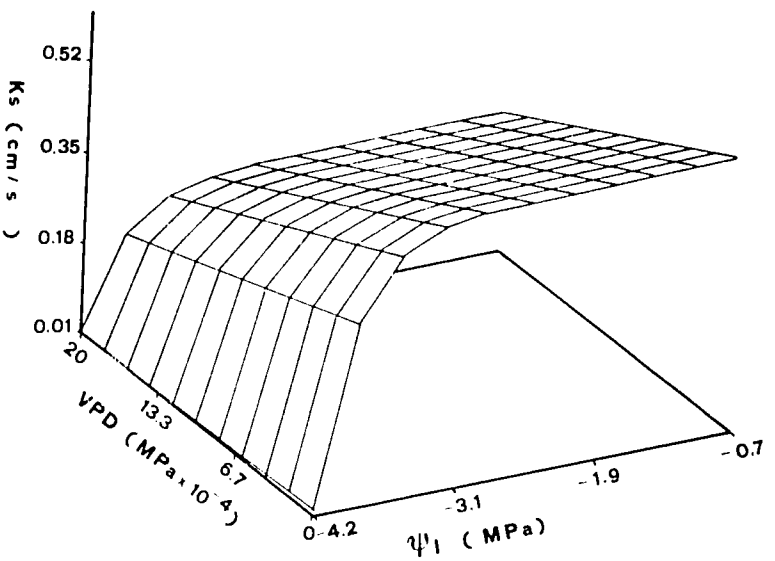


Figure 3. Surface response of K_s to VPD and ψ_l on rainfed plants (R_n = 56 mW/cm^{-2})

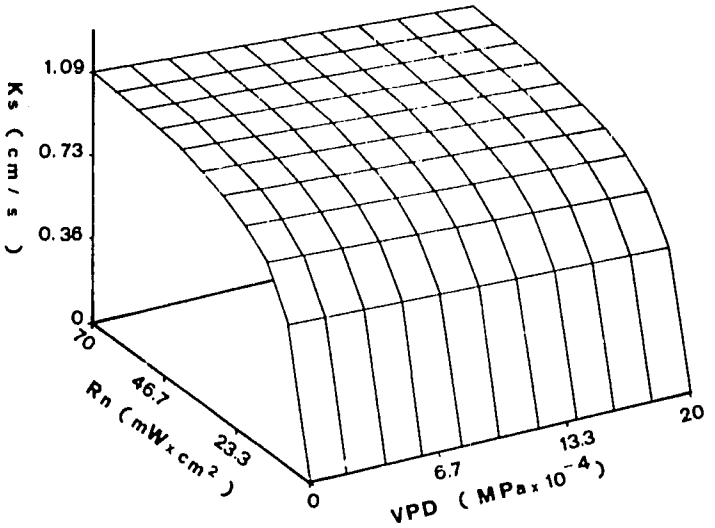


Figure 4. Surface response of K_s to R_n and VPD on irrigated plants ($\psi_l = -3$ MPa)

RESULTS AND DISCUSSION

We carried out the model calibration by utilizing two sets of data on durum wheat grown under two different water supply conditions.

The surface responses of K_s to two changing ecophysiological variables and the third one unchanged are shown in Figures 1, 2, and 3 for the rainfed treatment and Figures 4, 5, and 6 for the irrigated one. The main factors controlling stomatal conductance appear to be R_n and ψ_l; the VPD appears to affect this behaviour only in rainfed plants. Moreover, rainfed plants are characterized by generally less conducting and more sensitive stomata to changes of VPD and ψ_l if compared to irrigated plants.

Table 1 shows the estimated parameter values and their standard errors ($P = 0.05$).

Corresponding parameter values between rainfed and irrigated plants differed significantly. In particular, it seemed that the peak values of stomatal conductance (P_1)—obtained at the same light saturation levels—were higher in irrigated plants due to a higher soil water supply; the stomata of irrigated plants were found to be more sensitive, i.e. they responded with a higher opening rate (P_2) to the increase of the net radiation and, at the same time, were less sensitive to the increase of vapour pressure deficit (P_3) and to the leaf water potential variations (P_4). Moreover, rainfed plants showed a lower threshold value for the beginning of stomatal opening (P_5).

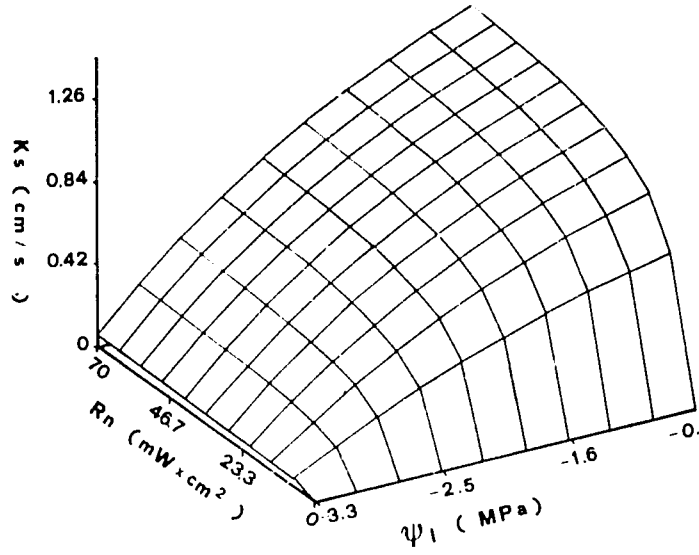


Figure 5. Surface response of K_s to R_n and ψ_l on irrigated plants (VPD = 15 MPa × 10^{-4})

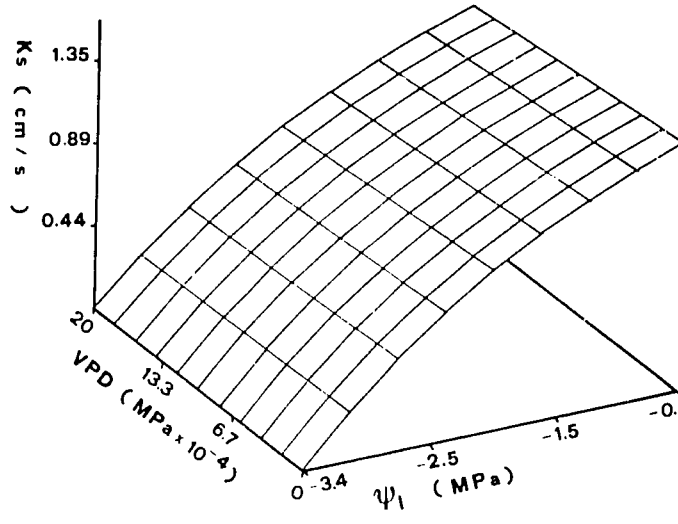


Figure 6. Surface response of K_s to VPD and ψ_a on irrigated plants (R_2 = 56 mW/cm^2)

Table 1. Estimated parameter values and their standard errors ($P = 0.05$)

	Rainfed plants		Irrigated plants	
Parameter	Values	SE	Values	SE
P_1	0.484	0.022	2.020	0.057
P_2	0.084	0.012	0.404	0.051
P_3	210.672	19.081	64.735	18.224
P_4	3.434	0.824	0.406	0.017
P_5	−4.289	0.098	−3.758	0.081

The parameter values obtained by the model calibration could be utilized as a guideline to choose those attributes that may allow identification of wheat genotypes most suitable for arid conditions.

Indeed, as reported by many workers, the differences in stomatal opening and closing rate may supply useful information about the total capacity of a plant to withstand water shortage (Shackel *et al.*, 1982). In plants of *Elaeis guineensis* (Jacq.) grown under dry conditions a higher yield was found to be associated with a more rapid stomata closing as the water stress was starting (Adjahoussou and Louguet, 1984). The other important factor that can change the crop response to drought is the ability for poststress recovery (Blum, 1984; Williams, 1984). Finally, the ability to keep stomata open at lower leaf water status has been considered a drought resistance character by many workers (Blum, 1984; Louguet, 1984; Adjahoussou and Louguet, 1984), and many genetic studies have reported that the leaf conductance and water potential have a fairly good inheritability.

Based on the above information and our own experimental results, we made attempts to identify the most suitable drought resistance traits for a genotype: a lower peak value of K_s, stomata less sensitive to increasing solar radiation and more sensitive to increasing VPD to limit water loss; more sensitive stomata to leaf water potential variations, i.e. stomata quickly closing at decreasing ψ_l and rapidly opening at rising ψ_l after a rain or an irrigation in order to facilitate the poststress recovery; a lower threshold value of ψ_l for the beginning of stomata opening to enable plants to photosynthesize even under low water supply conditions.

Plant breeders can select lines for K_s optimal values, assuming it to be a dynamic function affected by many environmental factors on the grounds of the parameter values obtained through the model proposed here.

ACKNOWLEDGEMENT

Research work for this paper was supported by CNR, Italy: Special grant IPRA-Subproject 1, paper 776. All four authors contributed equally to this paper.

REFERENCES

Adjahoussou, D. F. and Louguet, Ph. 1984. Correlations entre les résistances stomatiques de divers croisements de palmier à huile (*Elaeis guineensis* Jacq.) et al tolérance à la sécheresse. Actes coll. *Résistance à la Sécheresse en Milieu Intertropical*, Dakar, 1984. pp. 213–221.

Blum, A. 1984. Selection criteria for improving drought resistance in sorghum: a review. Actes coll. *Résistance à la Sécheresse en Milieu Intertropical*, Dakar, 1984. pp. 273–283.

Brun, L. J., Kanemasu, E. T. and Powers, W. L. 1973. Estimating transpiration resistance. *Agron. J.* **65**:326–328.

Draper, N. R. and Smith, H. 1966. *Applied regression analysis*. Wiley, New York.

Jarvis, P. G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. Lond. B.* **273**: 593–610.

Louguet, P. 1984. Interrelations entre les mouvements des stomates et la resistance à la sécheresse chez les vegetaux cultives: cas du mil. Actes coll. *Résistance à la Sécheresse en Milieu Intertropical*, Dakar, 1984. pp. 185–197.

Marquardt, D. 1963. An algorithm for least squares estimation of nonlinear parameters. *J. Soc. Indust. Appl. Math.* **11**:2.

O'Toole, J. C., Turner, N. C., Namuco, O. P., Dingkuhn, M. and Gomez, K. A. 1984. Comparison of some crop water stress measurement methods. *Crop Sci.* **24**:1121–1128.

Scholander, P. F., Hammel, H. T., Bradstreet, E. D. and Hemmingsen, E. A. 1965. Sap pressure in vascular plants. *Science, New York* **148**:339–346.

Shackel, K. A., Foster, K. W. and Hall, A. E. 1982. Genotypic differences in leaf osmotic potential among grain sorghum cultivars grown under irrigation and drought. *Crop Sci.* **22**:1121–1125.

Williams, J. H. 1984. Some physiological reasons for genotype × drought interactions in groundnuts. Actes coll. *Résistance à la Sécheresse en Milieu Intertropical*, Dakar, 1984. pp. 237–244.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

21

Responses to Water Deficits in Relation to Breeding for Drought Resistance

E. FERERES
SIA and University of Cordoba, Apartado 240, 14071 Cordoba, Spain

ABSTRACT

In recent years, substantial knowledge has been accumulating on crop responses to water deficits under relevant environmental conditions. Osmotic adjustment, root growth under water stress, and maintenance of green area and of gas exchange are among the responses postulated to benefit crop performance under limited water supply.

In breeding for drought resistance, use of current knowledge on crop responses to water deficits is limited by at least two problems. First, drought resistance is a complex attribute of a crop community and it is not clear how specific adaptive mechanisms are integrated in determining yield under water stress. Therefore, selecting for any single adaptive mechanism may not result in any yield improvement under drought. There is also a lack of available techniques for rapid screening of large numbers of genotypes. Notwithstanding these limitations, an understanding of crop responses to water deficits is essential to define breeding strategies. We present a case study on sunflower to demonstrate how physiological and agronomic knowledge can be used in assisting breeding efforts for drought resistance.

INTRODUCTION

The study of plant responses to water deficits has been one of the major research topics in plant physiology for decades. An important justification for such efforts is that, on a global scale, drought is the main environmental factor limiting plant productivity (Boyer, 1982). Improvements in productivity have depended heavily on plant breeding to increase the genetic yield potential of crops. It is therefore critical to apply the knowledge on plant responses to

water deficits to the breeding efforts designed to overcome the limitations that drought imposes on crop productivity.

There has been little use of water stress studies in breeding programmes, however. One reason is that most breeding programmes are designed to increase the genetic yield potential of crops in the absence of drought or any other environmental limitation. This is because both empirical evidence and theoretical considerations (Rosielle and Hamblin, 1981) suggest that the greatest progress in improving mean productivity would be achieved by selecting under optimal conditions. On the other hand, many water stress studies have been conducted under controlled conditions and the observed responses are of questionable relevance to processes influencing crop yield under field conditions. Until recently, the major form of interaction between stress physiologists and plant breeders started with the physiologists' suggestions of an apparently important trait to select for (usually at the lower levels of biological organization), and ended among the difficulties in devising rapid screening tests for the trait and the general skepticism of the plant breeder.

While the above-mentioned approach has not been productive, recent advances in the understanding of crop responses to water deficits in the field (e.g. Turner and Kramer, 1980; IRRI, 1982) as well as multidisciplinary studies on the role of water in crop production (e.g. Taylor *et al.*, 1983; Stone and Willis, 1983) will certainly assist current and future efforts in breeding for drought resistance. There is little doubt now that such efforts are warranted in many arid areas of the world where varieties bred under optimal conditions never approach their yield potential.

Progress in breeding for drought resistance will require a number of concerted efforts. First, the drought patterns must be characterized and quantified in terms of probability levels. Then a number of potentially useful agronomical and physiological traits must be identified and genetic variation within the germplasm pool must be found. Also, the adaptive value of the selected traits must be demonstrated, preferably through the development of isogenic lines differing in the degree of expression of the particular traits. Furthermore, efficient breeding methods must be designed, incorporating rapid screening procedures for the traits involved. Evaluation of promising lines in several environments representing a range of relevant drought situations is imperative. Also, as simulation models become more realistic they could aid in designing specific breeding strategies (Jordan *et al.*, 1983).

It is evident that breeding for specific, suboptimal environments will require a deeper understanding of yield-determining processes (Blum, 1983), and this is where knowledge on crop responses to water deficits may be best put to use. We review here some responses to water deficits that may be relevant in breeding for drought resistance. Emphasis is given to our efforts directed at evaluating the potential for increasing sunflower yields under the dryland conditions of southern Spain.

YIELD RESPONSES TO WATER DEFICITS

In several crop species there is evidence of genetic variability in their yield responses to water deficit (Fischer and Maurer, 1978; IRRI, 1982). An assessment of such variability may be obtained by conducting yield trials in several drought-prone environments (Blum, 1983) by simulating a range of water deficits using a line-source sprinkler system (Garrity *et al.*, 1982) or simply by comparing genotype performance under drought and under optimal water supply through irrigation (Fischer and Maurer, 1978). Using the last scheme, rainfed and irrigated yields may be combined to evaluate the drought susceptibility of various genotypes and its relation to yield potential (Fischer and Maurer, 1978).

Over the last five years we have evaluated the genetic variability of sunflower cultivars at Cordoba, Spain, under rainfed and irrigated conditions (Fereres *et al.*, 1986). In all experiments we found a substantial variation in both dryland and potential yield. Variation in yield potential among commercial hybrids was mainly related to the length of the growing season, while dryland yields varied even within the same maturity range. The variability in dryland yield among genotypes of similar length of season was explained by variation in the harvest index (HI) (Figure 1), indicating that drought-resistant cultivars are capable of maintaining high HI values when subjected to water deficits. Adjustments in seed number were of primary importance in the maintenance of the HI under drought, while there was less variation in individual seed weight among the genotypes studied (Fereres *et al.*, 1986).

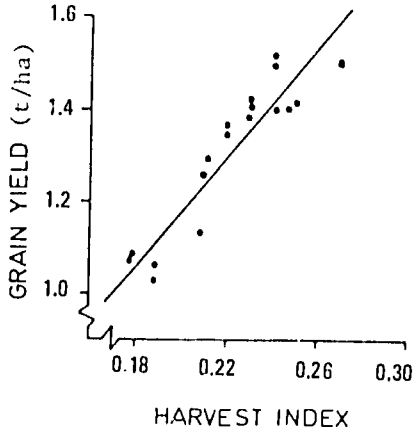


Figure 1. Relationship between harvest index and rainfed grain yield for sunflower genotypes of similar length of season. (Adapted from Fereres *et al.*, 1986)

One important limitation of evaluating genotype performance on the basis of the rainfed and irrigated yield in a single experiment is the year-to-year variation in drought patterns, which can be significant even under predictable Mediterranean conditions. Such climatic variability can change the relative ranking from year to year (Fischer and Maurer, 1978; Fereres *et al.*, 1986). If yield response is the major criterion in a breeding programme, more extensive genotype evaluation may be performed by (1) varying planting dates which normally result in different water stress levels, (2) using soils that differ in their water-holding capacity (within those representative of the typical soils in the target area), and (3) conducting experiments at several locations known to differ in rainfall or drought patterns. The above considerations also emphasize the limitations of the empirical yield trials when they are used as the only tool in drought resistance breeding programmes. It is therefore desirable to include in such programmes aspects of physiological responses to water deficits as well as studies of soil and climatic variability within the target areas.

PHYSIOLOGICAL RESPONSES TO WATER DEFICITS

Too often, genotypic differences in physiological responses to water deficits have been pursued with the expectation that they would correlate with presumed differences in yield under drought. A more fruitful approach may be to study the variation in physiological responses only after consistent differences in yield have been found among the genotypes considered. As stated above, selection based on physiological responses should not start unless the benefits of such responses in terms of yield advantage have been demonstrated using isogenic lines differing in response levels. Progress using this approach has been shown for ABA accumulation in wheat (Quarrie, 1981), accumulation of proline and glycine betaine in barley (Hanson and Hitz, 1982), and for other metabolic responses (see this volume). An interesting example is that of proline accumulation. For more than a decade, accumulation of proline, described as a response to water stress (Hsiao, 1973), was proposed as a mechanism conferring adaptive value to plants under water deficits (e.g. Singh *et al.*, 1972). Only until a critical study on the role of proline in the adaptation of barley to water deficits was conducted by Hanson and others (summarized by Hanson and Hitz, 1982) was it possible to demonstrate that accumulation of proline does not confer a yield advantage to barley in drought situations.

Associations between specific metabolic responses and yield under drought must be weak at best. Alternative studies which evaluate several physiologial and agronomic responses of genotypes differing in drought resistance (Blum *et al.*, 1983; Aggarwall and Sinha, 1984; Nicolas *et al.*, 1985) offer more promise in the development of physiologically based breeding programmes.

GROWTH, WATER RELATIONS, AND CROP PRODUCTIVITY

To explain the yield differences among sunflower genotypes we studied a number of morphological and physiological responses of cultivars which had contrasting behaviour under water deficits (Gimenez and Fereres, 1986). As reported earlier by Takami *et al.* (1982), we also found no evidence of genetic variability in short-term leaf-growth responses to water deficits. However, there were drastic differences among genotypes in long-term leaf area development and dry-matter accumulation (Gimenez and Fereres, 1986). Twofold differences in LAI and leaf area duration among cultivars were observed, and some of the late genotypes produced 50–60 per cent more dry matter than early cultivars.

Genotypic differences in leaf water relations have often been described in the literature, although rarely have they constituted a basis for breeding programmes. An exception is that reported by Morgan (1983) who successfully used osmoregulation as a selection criterion for breeding drought-resistant wheat. Osmotic adjustment has been associated with higher yields in a comparative study of two sorghum hybrids (Wright *et al.*, 1983). Its adaptive advantage was attributed to the maintenance of high leaf conductance under low water potential. In contrast, in another comparative study with two cotton genotypes (Quisenberry *et al.*, 1985), higher yields were recorded in the genotype which exhibited earlier stomatal closure. Thus, maintenance of stomatal opening under a limited water supply may or may not benefit yields, depending on whether there is sufficient water to complete the crop life cycle.

Our studies with sunflower on water relations (Gimenez and Fereres, 1986) have not shown large differences in osmotic adjustment among genotypes. However, the small differences observed were enough to induce nearly a twofold difference in leaf conductance for a given low water potential value (around −2.5 MPa). In some years, we detected genotypic differences of about 0.5 MPa in predawn leaf water potential near the end of the season (Gimenez and Fereres, 1986).

Few studies have shown how genotypic differences in growth and water relations in the field may affect the seasonal patterns of assimilate utilization and distribution. Gimenez and Fereres (1986) computed for several sunflower genotypes an approximate balance sheet of the glucose equivalents produced and utilized during the reproductive period (Table 1). The use of glucose equivalents is justified by the high oil (around 50 per cent) and protein content of the sunflower seed. The estimates presented in Table 1 indicate the quantitative differences between the two genotypes in canopy photosynthetic efficiency during the reproductive period. The late genotype (Sungro) apparently assimilated more per unit leaf area duration, indicating

Table 1. Computation of glucose equivalents (GE) required for the rainfed production of an early and a late sunflower genotype during the reproductive period. (Adapted from Gimenez and Fereres, 1986)

Genotype	Y (GE/m^2)	R (GE/m^2)	T (GE/m^2)	LAD_F (days)	E (GE/m^2/day)
$A_1 \times R_7$	384	562	227	57.4	9.0
Sungro	446	554	419	37.1	15.7

Y, grain yield; R, respiration; T, translocation from vegetative parts to the grain; LAD_F, leaf area duration after flowering; and E, canopy photosynthetic efficiency after flowering $(Y + R - T) \div LAD_F)$.

greater rates of photosynthesis when subjected to water deficits late in the season. This idea is supported by the higher leaf conductances under water stress observed in Sungro after flowering (Gimenez and Fereres, 1986).

EFFICIENCY OF WATER USE

The analysis of Tanner and Sinclair (1983) suggests that it would be unlikely to find genotypic differences in water-use efficiency (WUE) for biomass. Loomis (1983) also emphasized that evaporative demand is a major factor influencing WUE. Our data in Figure 2a show differences among sunflower genotypes in WUE for biomass. Sunflower in southern Spain is planted at the end of winter and develops into the hot summer. The late genotypes thus require an additional 30–75 mm of water to produce the same amount of biomass as that produced by the early genotypes which develop faster during the period of low evaporative demand.

Similar differences in WUE for grain yield are shown in Figure 2b, since the harvest index of the late cultivars tends to be lower due to the more severe water deficits (Fereres *et al.*, 1986). Differences in WUE for oil yield are less pronounced (Figure 2c) because of the typically higher seed oil content of the late genotypes. From the standpoint of WUE it can be concluded that early sunflower genotypes may be more appropriate in situations of limited water supply.

Genotypic variation in seasonal evapotranspiration (ET) must be due to differences in soil water extraction. Figure 3 shows the soil water extraction for two contrasting sunflower genotypes. The late genotype explored substantially greater soil depth, transpiring water that was not available to the early genotype. That additional subsoil water extraction was mostly due to a longer root growth period rather than to differences in apparent root-growth rates (Figure 3). Obviously, water must be available to those genotypes capable of exploring the deep subsoil.

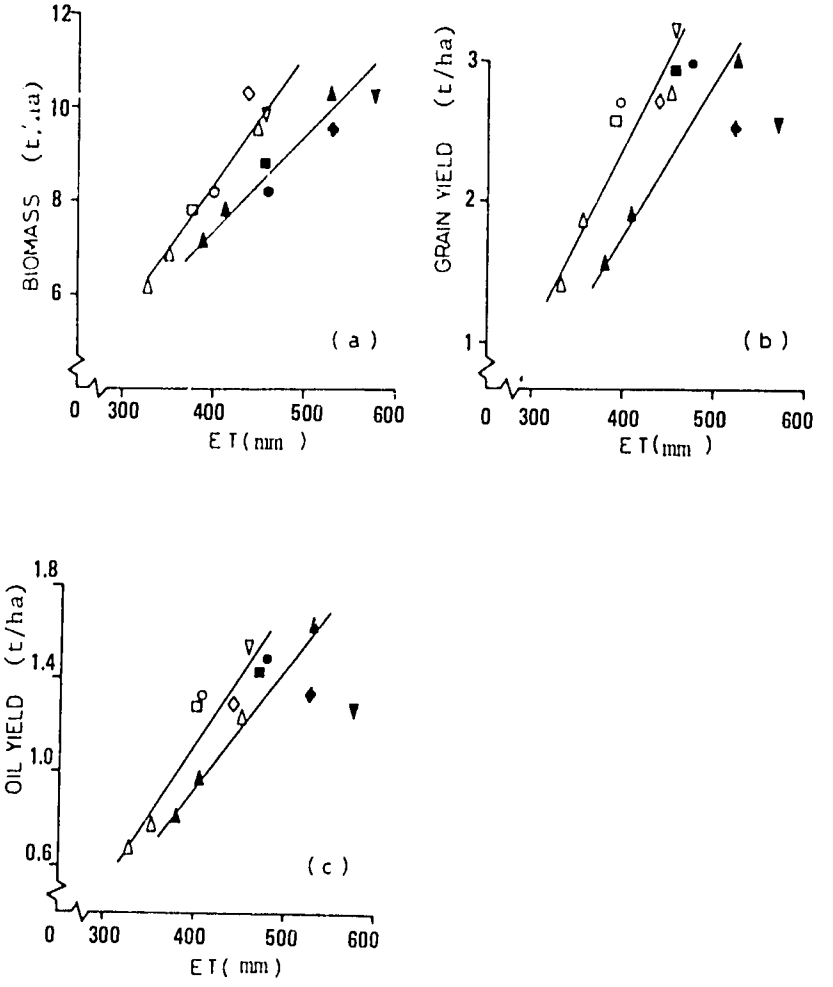


Figure 2. Relationships between evapotranspiration and (a) biomass, (b) grain, and (c) oil yield for five early (open symbols) and five late (closed symbols) sunflower cultivars. Data obtained at Cordoba, Spain, between 1981 and 1985

CONCLUSION

Drought escape has been a successful tactic in increasing the yields of many crop species grown under limited water supply. Early genotypes of sunflower have higher WUE (Figure 2) and may complete their life cycle in southern Spain before the hot summer arrives. It would seem to be desirable to select for short-season genotypes in that situation. However, experimental data over

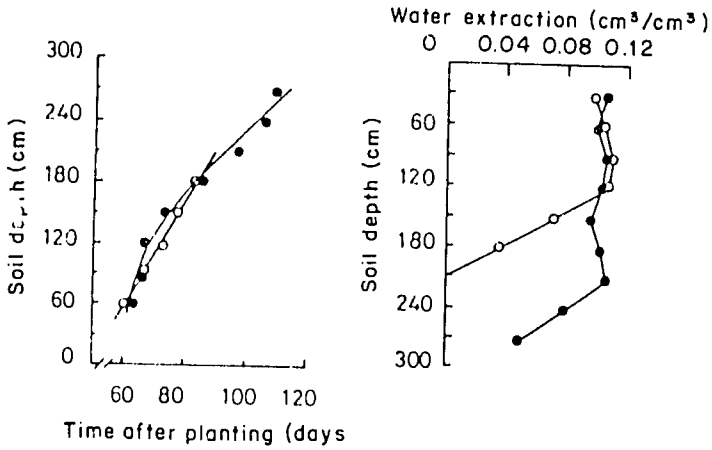


Figure 3. Soil water extraction and evolution of the time of initiation of root water extraction for an early $A_4 \times R_7$ (open circles) and a late sunflower cultivar (Contiflor, closed circles). (Adapted from Gimenez and Fereres, 1986)

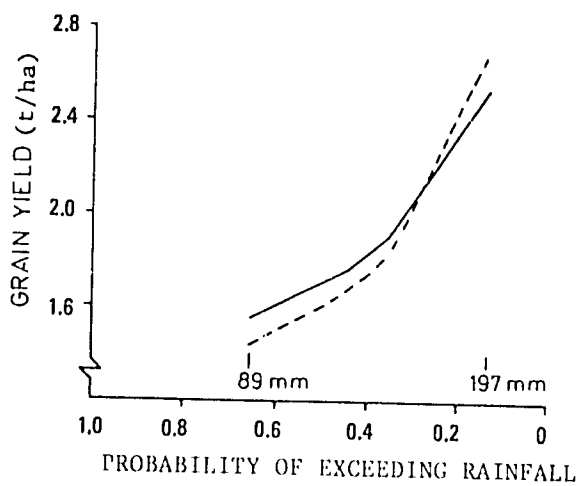


Figure 4. Dryland sunflower grain yield as a function of the probability of exceeding april through June rainfall at Cordoba for an early (dashed line) and a late (solid line) cultivar. Lines have been drawn using five years of data. The two numbers in the graph indicate the extreme amounts of rainfall measured during those years (1981–5)

the last five years suggest that late genotypes yield as much or more than the early ones when sufficient water is available in the subsoil. This apparent paradox may be clarified by plotting the experimental data in terms of probabilities (Figure 4). When rainfall from April to June is substantial, it enables the early genotype to complete its life cycle with less yield loss than the later cultivar. Such a situation occurs at Cordoba, however, only once every three to four years (Figure 4). In all other cases, yield of the late genotype is higher if the subsoil has been replenished by winter rainfall (annual rainfall at Cordoba is 650 mm, mostly between October and March). From consideration of Figure 4, it may be concluded that sunflower breeding for the dryland conditions of south-western Spain should be based on long-season germplasm.

Finally, it took five years of field experimentation to collect the data presented in Figure 4. Similar information could be obtained in a much shorter time period if realistic simulation models were available for hypothesis testing. Such models will therefore become invaluable tools to breed plants for specific environments in the future.

ACKNOWLEDGEMENTS

I thank Dr C. Gimenez for cooperation in the experiments and Dr H. F. Rapoport for editorial comments.

REFERENCES

Aggarwal, P. K. and Sinha, S. K. 1984. Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought-environment. *Ann. Bot.* **53**:329–340.

Blum, A. 1983. Breeding programs for improving crop resistance to water stress. Pages 263–275 in *Crop Reactions to Water and Temperature Stresses in Humid, Temperate Climates* (Raper, Jr, C. D. and Kramer, P. J., eds.). Westview Press, Boulder, Colorado, USA.

Blum, A., Mayer, J. and Gozland, G. 1983. Associations between plant production and some physiological components of drought resistance in wheat. *Plant, Cell and Envir.* **6**:219–225.

Boyer, J. S. 1982. Plant productivity and environment. *Science* **218**:443–448.

Fereres, E., Gimenez, C. and Fernandez, J. M. 1986. Genetic variability in sunflower cultivars under drought. I. Yield relationships. *Aust. J. Agric. Res.* In press.

Fischer, R. A. and Maurer, R. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. *Aust. J. Agric. Res.* **29**:897–912.

Garrity, D. P., Sullivan, C. Y. and Ross, W. M. 1982. Alternative approaches to improving grain sorghum productivity under drought stress. Pages 339–356 in *Drought Resistance in Crops with Emphasis on Rice* (IRRI, 1982). IRRI, Los Baños, Laguna, Philippines.

Gimenez, C. and Fereres, E. 1986. Genetic variability in sunflower cultivars under drought. II. Growth and water relations. *Aust. J. Agric. Res.* In Press.

Hanson, A. D. and Hitz, W. D. 1982. Metabolic responses of mesophytes to plant water deficits. *Ann. Rev. Plant Physiol.* **33**:163–203.

Hsiao, T. C. 1973. Plant responses to water stress. *Ann. Rev. Plant Physiol.* **24**:519–570.

IRRI. 1982. *Drought resistance in crops with emphasis on rice*. IRRI, Los Baños, Laguna, Philippines.

Jordan, W. R., Dugas, Jr. W. A. and Shouse, P. J. 1981. Strategies for crop improvement for drought-prone regions. Pages 281–299 in *Plant Production and Management under Drought Conditions* (Stone, J. F. and Willis, W. O., eds.). Elsevier Science Publisher, Amsterdam, The Netherlands.

Loomis, R. S. 1983. Crop manipulations for efficient use of water: an overview. Pages 345–371 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R. and Sinclair, T. R., eds.). ASA, Madison, Wisconsin, USA.

Morgan, J. M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* **34**:607–614.

Nicolas, M. E., Lambers, H., Simpson, R. J. and Dalling, M. J. 1985. Effect of drought on metabolism and partitioning of carbon in two wheat varieties differing in drought-tolerance. *Ann. Bot* **55**:727–742.

Quarrie, S. A. 1981., Genetic variability and heritability of drought-induced abscisic acid accumulation in spring wheat. *Plant, Cell and Envir.* **4**:147–151.

Quisenberry, J. E., Wendt, C. W., Berlin, J. D. and McMichael, B. L. 1985. Potential for using leaf turgidity to select drought tolerance in cotton. *Crop Sci.* **25**:294–299.

Rosielle, A. A. and Hamblin, J. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. *Crop Sci.* **21**:943–946.

Singh, T. N., Aspinall, D. and Paleg, L. G. 1972. Proline accumulation and varietal adaptability to drought in barley: a potential metabolic measure of drought resistance. *Nature New Biol.* **236**:188–190.

Stone, J. F. and Willis, W. O. (eds.). 1982. *Plant production and management under drought conditions*. Elsevier Science Publishers, Amsterdam, The Netherlands.

Takami, S., Rawson, H. M. and Turner, N. C. 1982. Leaf expansion of four sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. II. Diurnal patterns during stress and recovery. *Plant, Cell and Envir.* **5**: 279–286.

Tanner, C. B. and Sinclair, T. R. 1983. Efficient water use in crop production: research or re-search? Pages 1–25 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R. and Sinclair, T. R., eds.). ASA, Madison, Wisconsin, USA.

Taylor, H. M., Jordan, W. R. and Sinclair, T. R. 1983. *Limitations to efficient water use in crop production*. ASA, Madison, Wisconsin, USA.

Turner, N. C. and Kramer, P. J. (eds.). 1980. *Adaptation of plants to water and high temperature stress*. John Wiley. New York.

Wright, G. C., Smith, R. C. G. and Morgan, J. M. 1983. Differences between two grain sorghum genotypes in adaptation to drought stress. III. Physiological responses. *Aust. J. Agric. Res.* **34**:637–651.

DISCUSSION

H. Harris

You have not commented on the characteristic of sunflower to shed its radiation load at relatively high plant water potentials. Could you comment on this characteristic and speculate on its possible usefulness in cereals for the areas we are considering?

E. Fereres

Such response is very significant and decreases radiation interception at midday by 50–70 per cent at a time when the evaporative demand is highest. A similar response has been observed in grain sorghum where leaf angle changes substantially, leaves becoming more erect under moderate water stress. I suppose that the same mechanism could be useful to winter cereals which have an architecture similar to that of sorghum.

R. B. Austin

The annual rain in your area is about 650 mm. Sunflower roots extract water to a depth greater than 2.5 m. Is their actual evapotranspiration greater than the annual rainfall and, if so, what are the consequences?

E. Fereres

The evapotranspiration of dryland sunflower crops varies between 330–450 mm depending on year and genotype. In our typical wheat–sunflower rotation, there is a high probability (> 40 per cent) that the soil profile will be refilled to the depth that sunflower roots extract water before this crop is planted every other year.

D. Lawlor

You showed that there is substantial contribution of stored material to late grain filling. Do the early sowings and greater biomass provide a larger storage capacity for remobilization under drought?

E. Fereres

The suggestion is correct. Long-season genotypes planted in winter produce large amounts of biomass, which is apparently remobilized during grain filling.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

22

Root Characteristics and Water Use in Mediterranean Environments

S. C. BROWN, P. J. GREGORY, and A. WAHBI
Department of Soil Science, University of Reading, London Road, Reading RG1 5AQ, UK

ABSTRACT

Experiments in controlled as well as field conditions showed the existence of differences between barley varieties in both spatial patterns and rates of root growth. Barley plants grown in controlled conditions for 8 weeks showed a fourfold range of root length and a twofold range in leaf area, although the two measures were not correlated. In field-grown crops, fertilizer application increased the total root length and there were small, but significant, differences between varieties. From stem elongation until maturity, the local landrace, Arabi Abiad, had a longer root system below 15 cm than the variety Beecher. The rate of water uptake from each soil layer increased as root length increased to 1 cm root/cm^3 soil.

In Mediterranean environments, the depth of rooting is generally limited to the depth of profile wetting, and about 50 per cent of the rainfall is lost by evaporation from the soil surface. The timing of root growth, the root length in a soil layer, and the rapid growth of leaves to cover the soil are therefore important for maximizing water use and the production of dry matter. These may be affected by the application of fertilizer and by the choice of variety.

INTRODUCTION

Differences between plant species in the size and shape of root systems are well established. Differences within species have also been found (O'Brien, 1979; Richards and Passioura, 1981), although the magnitude and consequences of the differences are only now being assessed. Taylor (1980) reviewed the assumption that plants need deep, vigorous root systems in drought-prone

environments and concluded that rooting depth, root length in specific soil layers, and the resistance to water flow within the root were all relevant attributes of such a root system.

The characteristics of a desirable root system will vary with edaphic and climatic conditions. First, where water is stored deep in the soil profile, a deep root system will be necessary (Hurd, 1974). Second, where the amount of rainfall is uncertain and the crop must survive on stored water in the soil, a sparse root system extracting water at a slow rate but for a prolonged period may be advantageous (Passioura, 1972). Finally, where evaporation from the soil surface is a major component of the total water use, a dense root system may ensure that a greater proportion of the water is transpired.

The purpose of this paper is to show the extent of varietal variation in some root characteristics of barley grown in glasshouse and field conditions and to indicate the characteristics that may be important for water use in Mediterranean environments.

THE MEDITERRANEAN ENVIRONMENT

The Mediterranean climate is characterized by winter rainfall that peaks at the time when temperature and radiation are at their minimum (Harris *et al.*, this volume). In northern Syria, rainfall decreases after March and temperature increases rapidly, so the autumn-sown crops frequently experience drought during the grain-filling stage. The field work referred to in this paper was done at sites in northern Syria in collaboration with the International Center for Agricultural Research in the Dry Areas (ICARDA). Jindiress has a mean annual rainfall of 472 mm and Breda 283 mm. The soils at both sites contain appreciable quantities of smectite and are classified as a Palexerollic Chromoxerert (Jindiress) and a Typic Calciorthid (Breda).

METHODS FOR ASSESSING ROOT GROWTH

Glasshouse experiments at the Department of Soil Science, University of Reading, and field experiments at ICARDA sites in Syria were carried out to compare the growth and development of roots and shoots of a range of barley varieties.

In the glasshouse, a range of varieties was grown in three rooting media: nutrient solution, sand with perlite watered with nutrient solution, and sandy loam soil from the University of Reading Farm at Sonning. The mean temperatures were 19°C for roots and 24°C for shoots.

In field experiments, up to six barley varieties were used to examine relations between water use and root and shoot growth. Roots were sampled using a 10 cm diameter Jarratt auger in 15 cm increments down the soil profile. Roots were separated from the soil by washing with water and dead

roots and debris were removed by hand. In both glasshouse and field studies, root length was measured by counting intersections with a 1 cm grid (Tennant, 1975). Root and shoot weights were measured after drying at 80°C and the green area of shoots was measured with a planimeter. Selected results from these experiments are presented here; full descriptions appear elsewhere (Brown *et al.*, 1987; Cooper *et al.*, 1987; Wahbi, 1986).

VARIATION IN ROOT AND SHOOT GROWTH OF BARLEY VARIETIES

Barley varieties show significant variation in both rates of root and shoot growth and the ratio of root length to leaf area during early growth (Figure 1). While it is easy to demonstrate such differences in controlled conditions, it is rare for substantial differences to be demonstrated in the field. However, Brown *et al.* (1987) compared Arabi Abiad (a local landrace) with Beecher (an improved, widely adapted variety) and showed that although the total

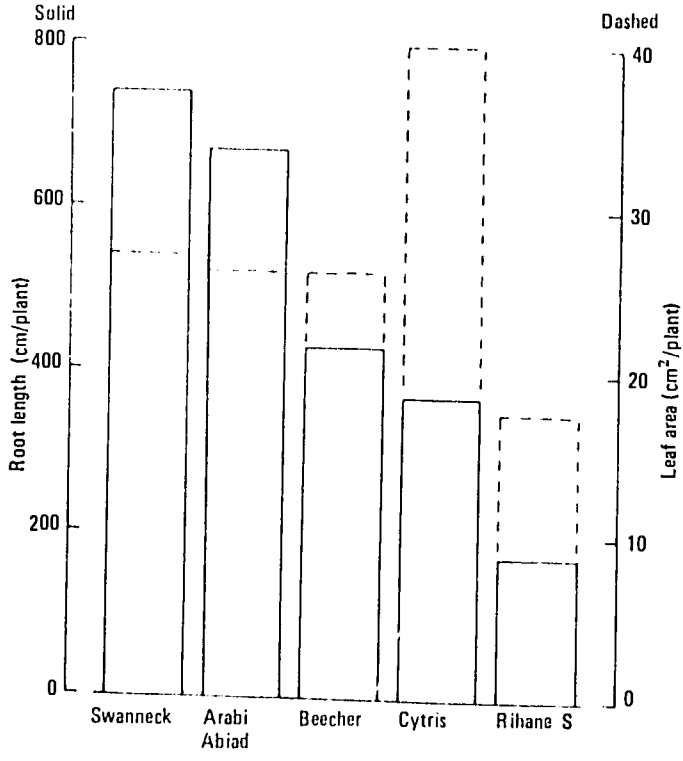


Figure 1. Root length and leaf area of five barley varieties at the six-leaf stage. The plants were grown in nutrient solution in a glasshouse

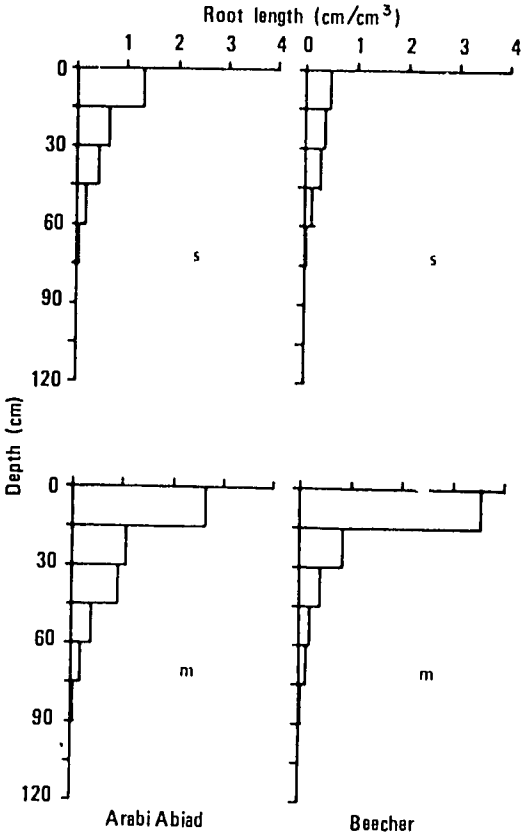


Figure 2. Root length of Arabi Abiad and Beecher at the beginning of stem extension (s) and maturity (m). Both crops were grown at Breda in 1982–3 and given fertilizer

length of both root systems was similar, Arabi Abiad had a significantly greater root length below 15 cm at the beginning of stem extension and at maturity (Figure 2).

Similarly, differences exist in the shoot growth. Table 1 shows the ranking of varieties according to shoot weight. In the glasshouse experiment there was some interaction between the rooting medium and variety; nevertheless, there were consistent differences between varieties. The ranking order of the varieties in the field was similar to that in the glasshouse at an equivalent stage of growth.

Rihane was generally worse than other varieties during early growth and Arabi Abiad, Beecher, and Cytris were generally better than average. How-

Table 1. Ranking of shoot weights of barley varieties at the four- to six-leaf stage, beginning of stem extension (s) and maturity (m). Plants were grown in the glasshouse in nutrient solution (n.s.), sand with perlite (s.p.), and soil, and in the field at Breda.

	Arabi Abiad	Beecher	Cytris	Matnan	Rihane	Swanneck
Glasshouse (5 leaves)						
n.s.	2=	2=		1	5	4
s.p.	1	3=		3=	5	2
soil	2=	1		2=	5	2=
Breda 1982–3						
s	1	2				
m	1=	1=				
1983–4						
6 leaves	2=	2=	1	4	6	5
s	1=	1=	1=	4	6	5
m	1=	1=	1=	6	4=	4=
1984–5						
4 leaves	2	4=	1		3	4=
s	1	4=	2=		2=	4=
m	1=	1=	4=		3	4=

ever, Swanneck grew well in the glasshouse but was worse than average in the field. Differences between glasshouse and field results may be due to differences between varieties in response to temperature (mean air temperatures of 24 and 9°C, respectively) and to frost, which occurred only in the field experiments. Further work is necessary to explain the variation in results between media and to design simple techniques that might allow screening of larger numbers of varieties.

Table 1 also shows that, in most cases, the ranking of varieties grown in the field changed little between stem extension and maturity. In all years, Arabi Abiad had the highest shoot weight at both stem extension and maturity, and weights of Rihane and Swanneck were generally among the lowest throughout the growth period. Cytris was unusual in its fast rates of growth initially but during 1984–5 its ranking fell in later growth. Generally, the potential for high productivity is determined by high growth rates during early growth but this potential may not be achieved if frost or severe drought curtail later growth.

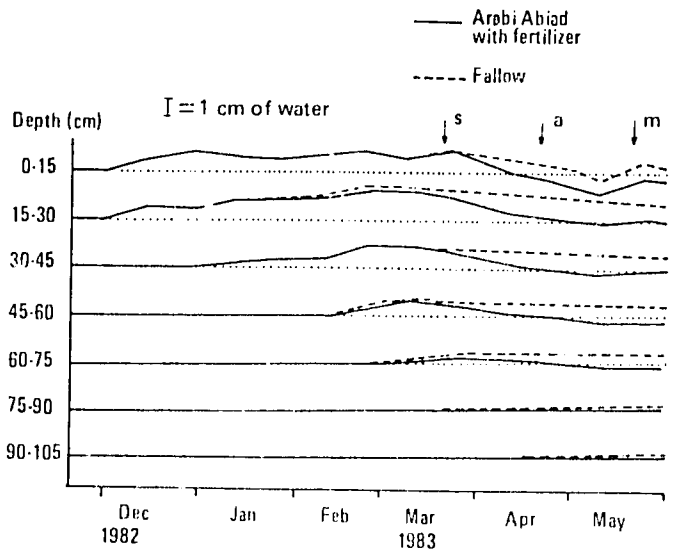


Figure 3. Cumulative change in soil water content of 15 cm depth increments at Breda under Arabi Abiad with fertilizer and fallow during the 1982–3 growing season. Times of the beginning of stem extension (s), anthesis (a), and maturity (m) are indicated for the barley crop

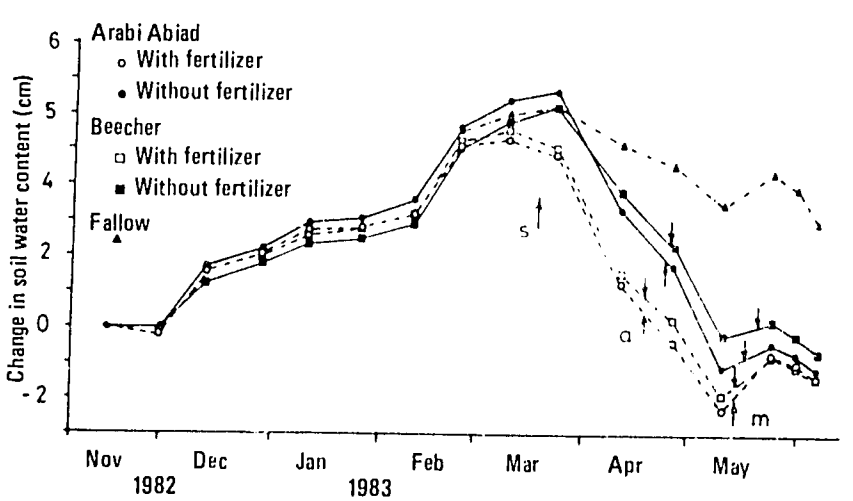


Figure 4. Change in soil water content at Breda under Arabi Abiad, Beecher, and fallow, both with and without fertilizer. Times of the beginning of stem extension (s), anthesis (a), and maturity (m) are indicated

WATER USE BY BARLEY

Water use by a crop of barley grown at Breda during the 1982–3 season will be used to illustrate the features of the Mediterranean environment. Figure 3 shows that water penetrated slowly down the profile during the winter to reach its maximum depth in March (90 cm in the fallow and 75 cm under barley). The total water content of the soil profile also increased during the winter period, reaching a maximum in about mid-March (Figure 4); thereafter evaporative demand exceeded rainfall and the profile dried again either by crop extraction of water or evaporation directly from the soil surface or both (Cooper, 1983; Gregory *et al.*, 1984). The depth of wetting varies from season to season and site to site, depending upon the total rainfall and its distribution within the growth season.

Effects of fertilizer applications and of variety on water use are shown in Figure 4. Total water use for the whole season was similar for all treatments (see Cooper *et al.*, 1987, for details) and approximately equal to the seasonal rainfall, as was found in other studies (Cooper, 1983; Gregory *et al.*, 1984). However, application of fertilizer increased the soil water extraction rate during March and also the total water use by about 10–20 mm. The differences between varieties were smaller than the effects of fertilizer and Arabi Abiad used more water than Beecher. Earlier use of water by Arabi Abiad and by crops given fertilizer was associated with longer root systems, particularly below the surface 15 cm (see Figure 2 for effects of variety and Brown *et al.*, 1987, for effects of fertilizer). Figure 5 shows that at both Jindiress and Breda, the mean rate of water extraction for individual soil layers during the period of drying was related to the root length present in that layer. Water was extracted at a maximum rate by about 1 cm root/cm^3 soil. Measurements for the 0–15 cm layer have not been included in this figure because of the substantial evaporation from the soil surface that occurs from this layer; in deeper soil layers almost all of the change in soil water content is due to uptake by roots.

CONCLUSIONS

This paper shows that there are differences between varieties in the growth of roots. In the glasshouse, differences in root length, shoot weight, and leaf area occurred; in the field, varieties of barley differed in both total root length and in the distribution of root length within the soil profile. How might such differences be exploited to use water most effectively in the production of dry matter in Mediterranean environments?

Varieties with deeper rooting systems are unlikely to result in increased production because rooting depth is largely restricted by the depth of wetting and because water stored below the mean depth of wetting can only be

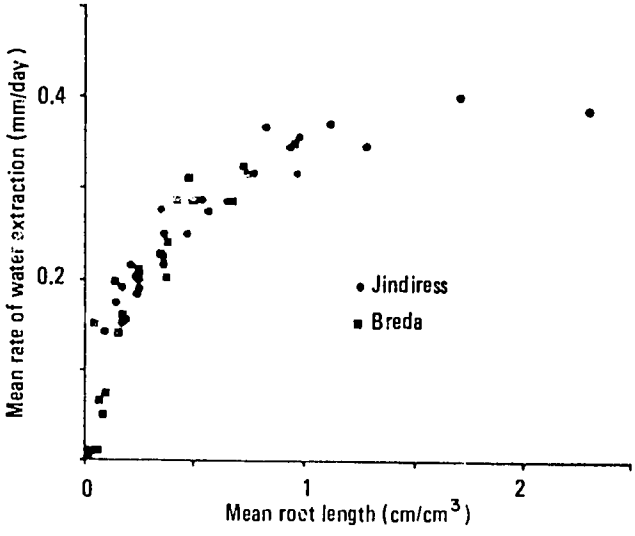


Figure 5. Relation between the mean rate of water extraction calculated from the beginning of stem extension to maturity, and mean root length for 15 cm depth increments between 15 and 120 cm. Results from Arabi Abiad and Beecher varieties both with and without fertilizer at Jindiress and Breda, during 1982–3

exploited once. There is therefore little to be gained from increasing the potential for deep rooting (cf. Hurd, 1974).

In the Mediterranean climate, the soil surface remains damp for most of the winter period and up to 50 per cent of the seasonal rainfall is lost during this period by evaporation directly from the soil. This large loss of water means that little is gained by having a sparse root system and attempting to save water for grain filling (Passioura, 1972). Indeed, growth during the winter period is highly desirable because water is transpired that would otherwise be lost from the soil surface and the ability to grow rapidly in early spring (late February and March), when saturation deficits are lower than during grain filling, also leads to greater transpiration efficiency (Richards, this volume). In varieties currently available, anthesis occurs early enough in most years to allow sufficient water for adequate grain filling.

Figure 5 shows that there is a definite relationship between the rate of water extraction from a soil layer and the root length in that layer. The distribution of root length is therefore important for optimizing water use and varieties having more roots deeper in the profile from early in the spring may be able to use water more efficiently to produce dry matter than those with sparse roots at depth. However, there is also a need for roots to take up nutrients and the

length per unit volume required for adequate rates of uptake may differ from that for water (van Noordwijk, 1983). This may be particularly important during early growth when shortage of nutrients (especially phosphate), rather than of water, frequently limits growth.

ACKNOWLEDGEMENTS

We are most grateful to Drs P. J. M. Cooper and J. D. H. Keatinge for their collaboration in work at ICARDA. We also thank the Overseas Development Administration (UK) for financial support.

REFERENCES

Brown, S. C., Keatinge, J. D. H., Gregory, P. J. and Cooper, P. J. M. 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 1. Root and shoot growth. *Field Crops Res.* **16**:53–56.

Cooper, P. J. M. 1983. Crop management in rainfed agriculture with special reference to water use efficiency. Pages 63–79 in *Proceedings of the 17th Colloquium*. The International Potash Institute, Bern, Switzerland.

Cooper, P. J. M., Gregory, P. J., Keatinge, J. D. H. and Brown, S. C. 1987. Effects of fertilizer, variety and location on barley production under rainfed conditions in northern Syria. 2. Soil water dynamics and crop water use. *Field Crops Res.* **16**:67–84.

Gregory, P. J., Shepherd, K. D. and Cooper, P. J. M. 1984. Effects of fertilizer on root growth and water use of barley in northern Syria. *J. Agric. Sci. Cambridge* **103**:429–438.

Hurd, E. A. 1974. Phenotype and drought tolerance in wheat. *Agric. Met.* **14**:39–55.

O'Brien, L. 1979. Genetic variability of root growth in wheat (*Triticum aestivum* L.). *Aust. J. Agric. Res.* **30**:587–595.

Passioura, J. B. 1972. The effect of root geometry on the yield of wheat growing on stored water. *Aust. J. Agric. Res.* **23**:745–752.

Richards, R. A. and Passioura, J. B. 1981. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* **21**:253–255.

Taylor, H. M. 1980. Modifying root systems of cotton and soybean to increase water absorption. Pages 75–84 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, N. C. and Kramer, P. J., eds.). John Wiley, New York.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. *J. Ecol.* **63**:995–1001.

van Noordwijk, M. 1983. Functional interpretation of root densities in the field for nutrient and water uptake. Pages 207–226 in *Root Ecology and its Practical Application*. International Symposium, Gumpenstein, 1982. Bundesanstalt, Gumpenstein, A-8952, Irdning, Austria.

Wahbi, A. 1986. Varietal variation in root growth of barley and its influence on water use. Ph.D. thesis. Reading University, UK.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo, and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

23

Opportunities for Manipulating Root Systems to Reduce Drought Stress in Wheat

HOWARD M. TAYLOR and HENRY T. NGUYEN
Department of Plant and Soil Science, Texas Tech University, Lubbock, Texas 79409, USA

ABSTRACT

This paper first describes the general characteristics of wheat root systems and then some opportunities for modifying axial resistance in the seminal roots and the subcrown internode. We also discuss opportunities for and consequences of modifying root length densities with depth. Finally, we discuss opportunities for modifying aluminum tolerance, penetration into compact soil layers, and cereal cyst nematode resistance.

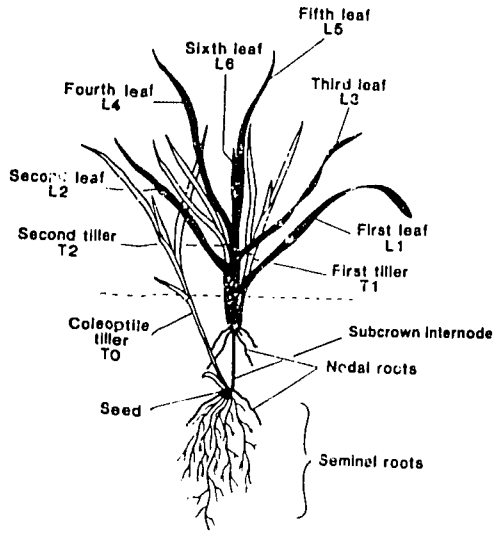
INTRODUCTION

There are four general approaches that we can use to manipulate root systems for more efficient or more complete extraction of water from a soil profile. We can: (1) modify the soil environment to reduce some soil constraint to rooting or to water flow, (2) change from a species susceptible to a specific soil constraint to one more tolerant, (3) alter crop management, such as changing row spacing, plant population, or planting date, and (4) breed and select strains within species.

This article concentrates on breeding and selecting wheat root systems to improve drought resistance. A general discussion of the other three approaches is presented elsewhere (Taylor, 1983).

THE WHEAT ROOT SYSTEM

The wheat root system usually consists of seminal and adventitious (nodal) roots and a subcrown internode (Figure 1). The seminal roots occur at the



WHEAT PLANT

Figure 1. Sketch of a wheat seedling as modified from Klepper *et al.* (1983)

depth of planting and arise from root primordia found in the seed. The seminal root system consists of a radicle and up to five roots associated with the scutellar and epiblast nodes. The xylem of a seminal root is dominated by a single large metaxylem vessel in the center of the stele. This metaxylem vessel is usually larger in the radicle than in the other seminal roots. Wheat plants can grow to maturity using only their seminal roots (Locke and Clark, 1924).

Adventitious roots arise mainly at crown depth, but can arise at seed depth when a coleoptilar tiller develops (Klepper *et al.*, 1983). The number of adventitious roots depends on the extent of tillering (Klepper, 1986) but adventitious roots do not develop into continuously dry soil (Passioura, 1974). There are several metaxylem vessels about equal in diameter and some smaller vessels in the xylem of adventitious roots.

The crown usually develops 20–40 mm below the soil surface (Chambers, 1963), but crown depth is somewhat affected by cultivar and temperature (Hunt *et al.*, 1983).

The main axis between the seminal root attachments and the crown is the subcrown internode. Xylem in the subcrown internode consists of seven to ten groups of vessels, each usually containing two large (12–25 μm) and several smaller vessels (Cornish, 1981). Because seminal root location is fixed by seeding depth, and crown depth usually occurs 20–40 mm below the soil surface, length of the subcrown internode increases with seeding depth.

OPPORTUNITIES FOR MODIFYING THE SEMINAL ROOT SYSTEM

The water-uptake rate from a soil volume depends on evaporative demand, on rooting density, on water potential difference between soil and xylem, and on radial resistance to flow of water from bulk soil to the root xylem (Taylor and Klepper, 1978). It is usually considered that radial resistance from soil to root xylem is a major impediment to water flow; however, magnitudes and locations of this resistance are the subject of very active investigations and methods of evaluating this resistance are time consuming and often not very accurate. For these reasons, it seems inappropriate at this time to suggest that plant-breeding opportunities exist there.

There is opportunity, however, to select plants for more appropriate resistances axially in the xylem of seminal roots. Axial resistance there is often considered to obey the Poiseuille equation; thus

$$\Delta P = \frac{8ql\eta}{\pi r^4} \tag{1}$$

where

ΔP = pressure drop (pascals) along a tube of length l (m)
q = rate of flow (m^3/s)
η = viscosity of water (1.1×10^{-3} P/sec at 16°C)
r = radius of the tube (m).

It will be noted that a unit decrease in radius of the tube will increase by 16 times the pressure drop required to maintain flow at a specified rate. The resistance to flow of water through the xylem is considered to be insignificant in most plants (Cowan and Milthorpe, 1968; Kramer, 1969); however, Passioura (1974) calculated that a pressure drop as great as 4 MPa/m of xylem might be required to maintain an average flow rate when only seminal roots are supplying water to the plant tops.

Both Passioura (1974) and Greacen *et al.* (1976) considered that the upper part of the seminal root system could be a bottleneck to the rapid and efficient utilization of subsoil water if adventitious roots had not yet developed sufficiently. Passioura (1974) discussed two situations: (1) when water was restricted to the top meter of soil and periods of severe drought were likely and (2) when much water was contained below one meter and periods of mild drought were likely. Passioura (1974) concluded that substantial axial resistance would be an advantage to the wheat plants in the first case and a substantial disadvantage in the second case.

Substantial axial resistance can develop if only a few roots are delivering water to the subcrown internode or if their metaxylem vessels have sufficiently small radii. Richards and Passioura (1981b) investigated over a thousand wheat accessions for the nature and extent of genetic variation in

the number of xylem vessels. They concluded that xylem vessel diameter was more tractable in selection programmes than number of axes because no entry had substantially fewer axes than average, but some landrace wheats had acceptably narrow vessels. Estimates of narrow-sense heritability using regression of F_3 progeny means on F_2 parental values were high (71 per cent) for xylem vessel diameter. A significant response to selection was achieved for this trait in each of the six segregating populations (Richards and Passioura, 1981b).

Richards and Passioura (1981a) examined environmental effects on the number of seminal axes and xylem vessel diameters for six hexaploid wheat cultivars. They concluded that environmental influences are unlikely to be significant unless hydraulic resistances already are large because of genetic influences on vessel diameter. They estimated that vessel diameter should be less than 60 μm or that seminal axes should average less than two per plant for this resistance to be significant in subsoil water conservation.

Passioura (1983) stated that breeding for decreased xylem vessel diameter in seminal roots is preferable to breeding for decreased leaf area in regions that rely predominantly on stored soil water. His reasoning was that, during good rainfall years, an adventitious root system will develop and take over the water supply function from the high resistance seminal root system. If low leaf areas were achieved for benefits in drought years, however, the low leaf area genotype probably will not yield adequately in good rainfall years. Richards (1982) has suggested that it may still be worth while modifying leaf area development in wheat genetically to improve yields under some dryland conditions.

In addition to high axial resistances, other attributes of seminal roots are important in drought resistance. These attributes are root elongation rate, rooting depth, and rooting density. Rapid root elongation rates are very important in seedling establishment and persistence, especially when prolonged surface soil dryness occurs soon after seeding. Under these conditions, adventitious roots do not develop from the crown and a drying front becomes progressively deeper with time. Elongation rate of the seminal roots must be rapid enough for a substantial portion of the root length to stay in moist soil ahead of the drying front or the wheat plants will suffer drought stress. This dry surface soil condition often occurs after wheat seeding time on the Southern Great Plains where the authors are located.

There are significant differences among cultivars of wheat in rooting depth, density, and elongation rates. Campbell and Lefever (1977) examined the length of seminal roots for 43 cultivars and experimental lines of wheat after they were grown in a nutrient solution. There were major differences among the various entries. Hurd (1968) used glass-fronted boxes to examine the growth of seminal roots of seven cultivars of spring wheat. He found that the Thatcher cultivar had a greater length of roots below 0.3 m depth and

suggested that this greater root length was the reason that Thatcher yielded so well under the semi-arid conditions of Saskatchewan. Derera *et al.* (1969), also using glass-fronted boxes, found significant differences among 15 wheat lines in their rates of root penetration and in rooting depth. Köpke *et al.* (1982) found a close correlation between differences among cultivars in root growth within soil-filled containers and those tnat occurred at trench profile walls.

The field and the glass-fronted box methods require so much time to finish an evaluation that the most we should expect from them is to identify some genetic materials that can be incorporated into breeding programmes without further evaluation of progeny root systems. Glass or plastic tubes slanted 15–20° from the vertical can be used to characterize cultivar rooting traits (Nilsson, 1973a, 1973b) and for limited progeny testing (Kaspar *et al.*, 1984). The nutrient solution technique (Reid, 1977), when applicable, can be used to screen thousands of seedling root systems.

OPPORTUNITIES FOR MANIPULATING ROOTING DENSITY

McGowan and Tzimas (1985) have suggested that water uptake by wheat root systems can be described by the equation

$$U = L_v \frac{\psi_s = \psi_{x(min)}}{R} \qquad (2)$$

where

U = rate of change of soil water storage (m^3 H_2O/m^3 soil/day)
L_v = root length density (m roots/m^3 soil)
ψ_s = soil water potential (m)
$\psi_{x(min)}$ = time-averaged xylem potential at which water inflow into the root is zero (m)
R = effective resistance (day/m)

They found that the wheat plants in their study produced more roots than were necessary for efficient water uptake. In their study, actual/potential evapotranspiration was about 1.0–1.2 at anthesis when their plants had 2.4×10^4 m roots/m^2 land area (Gregory *et al.*, 1978). In contrast, Proffitt *et al.* (1985) found that actual/potential evporation was maintained at 1.0 with 3.5×10^3 m roots/m^2 soil, or 15 per cent of the rooting intensity found by McGowan and Tzimas (1985). Pavlychenko (1937), Pavlychenko and Harrington (1935), and Walter and Barley (1974) support the values of Gregory *et al.* (1978) while those of Hamblin and Hamblin (1985) and Köpke *et al.* (1982) support the values of Proffitt *et al.* (1985). These differences in rooting are large enough to be real and are significant to the carbon economy of the

plants. Clarkson (1985) estimates that up to 20 per cent of the total photosynthate is exuded from the roots. Rovira (1969) has shown that exudation from wheat is greater from root tips than from other root parts. One can assume that plants with greater root length per land area will have more root tips and greater exudation rates. For these and many other reasons, it seems imperative that we define, with much greater precision than has been done to date, the minimum rooting densities that are necessary to dry various soil layers in reasonable time periods.

Rooting depth of wheat decreases with frequency of watering and rooting density usually decreases with depth (Figure 2). This increased depth of rooting, either seminal or adventitious, and increased density of roots deep within the profile are important if the wheat plants suffer drought but leave substantial quantities of water in the soil profile at harvest. There are substantial differences among cultivars of wheat in rooting density at depths below 0.50 m (MacKey, 1973). A hydroponic system using polystyrene foam and transparent tubes has proven to be an excellent and standard system for evaluating rooting density at depth. One should be extremely careful in pursuing a breeding programme to increase rooting depth and density,

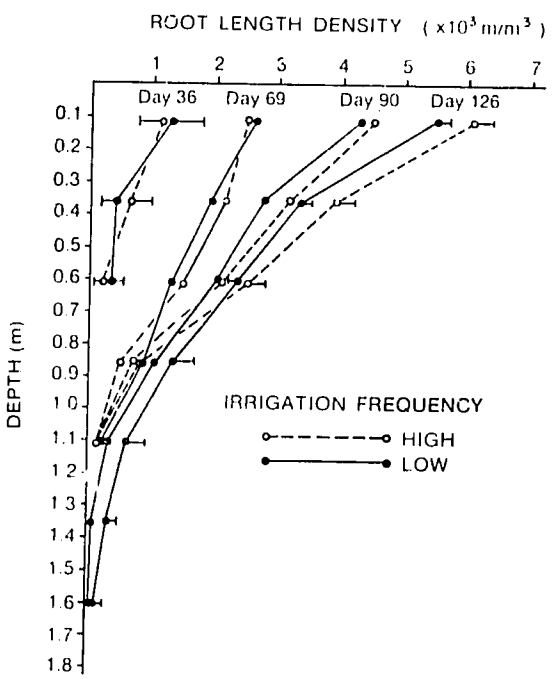


Figure 2. Root length density of wheat as a function of soil depth and irrigation frequency. (*Redrawn from Proffitt* et al., *1985. Reproduced by permission of Agronomy Journal and the authors*)

however, unless the altered rooting results in an increased water supply to plants during grain fill.

OPPORTUNITIES FOR MODIFYING THE SUBCROWN INTERNODE HYDRAULIC RESISTANCE

Wheat is often planted into soil when the surface 0.05–0.15 m is below the permanent wilting percentage, but moist soil exists below those depths. This situation often occurs at wheat seeding time on the Southern Great Plains. Farmers respond to this condition either by planting the seed in dry soil or by planting deep enough to place the seed in moist soil. Some wheat geneticists have selected plants for their long coleoptiles, which allow these plants to emerge even though planted several centimeters deep (Chambers, 1963; Sunderman, 1964). These deep plantings cause long subcrown internodes and possibly cause high resistances along the xylem in the internode.

Under the USA Pacific Northwest conditions, Gul and Allan (1978) found significant genetic variation and high parent–progeny regression heritability estimates (74 per cent) for subcrown internode length. They concluded that selection for this trait should give rapid genetic advance.

Cornish (1981) used a modified Poiseuille equation to study the conducting capacity in subcrown internodes of five lines of wheat. Cornish (1981) used equation (1) after calculating an effective radius r_e, after Wind (1955), using the equation

$$r_e = \left(\sum_i^m r_i^4\right)^{1/4} \tag{3}$$

There were sufficient variations in subcrown internode lengths and effective radii (Table 1) for Cornish (1981) to suggest that water-use rates could be altered substantially by selection of genetic lines and planting depths.

In the situation where the plants are easily established, but have a limited water supply in the soil profile and a terminal drought at maturity, one should select for high subcrown internode resistances (i.e. small vessels). Where seedling establishment is a severe problem, however, one should select plants that have low resistance, even when the subcrown internode is 0.07–0.08 m long.

OPPORTUNITIES FOR MODIFYING ROOT GROWTH IN PROBLEM SOILS

There are many millions of hectares of land that are climatically, physiographically, and hydrologically suited for cultivation, but are idle because of some type of soil-related problems.

One soil-related problem that affects both seminal and adventitious roots of wheat is that of aluminium toxicity. According to recent concepts of soil

Table 1. Subcrown internode length and mean vessel effective radii of the largest seminal root, the three main roots combined, and the subcrown internode of five wheat lines at two planting depths. (After Cornish, 1981)

Depth (mm)	Genotype	Effective xylem radius: Largest root (μm)	Combined root (μm)	Subcrown internode (μm)	Subcrown internode length (mm)
45	AVS16871	32 bc	39 bc	31 bc	39 c
	Cook	29 c	36 cd	30 bc	19 d
	16871/Cook	28 c	34 c	20 bc	20 d
	Kite	36 ab	42 ab	29 cd	24 d
	Kalyansona	37 a	45 a	39 a	19 d
90	AVS16871	32 bc	38 bc	26 d	79 a
	Cook	29 c	35 cd	30 bc	54 b
	16871/Cook	30 c	34 c	28 cd	59 b
	Kite	35 ab	44 a	31 bc	50 b
	Kalyansona	37 a	45 a	33 b	41 c

Means within columns sharing a common superscript do not differ according to Duncan's Range Test ($P \leq 0.05$).

acidity, the potential acidity of a soil is held as Al^{3+}, hydroxy-aluminium ions such as $Al(OH)^{2+}$ or $Al(OH)_2^+$, or as charged hydroxy-aluminium complexes (Coleman and Thomas, 1967). One hydrolysis reaction in soil is

$$Al^{3+} + 2\ H_2O \rightleftarrows Al(OH)^{2+} + 2\ H^+ \qquad (4)$$

When the soil system becomes more acid, the H^+ concentration increases and the reaction moves toward the left, or Al^{3+} increases. Any increase in Al^{3+} concentration reduces root growth of wheat (Campbell and Lefever, 1977).

One of the outstanding successes of screening plants for root systems that tolerate a soil problem has been with the aluminium ion. There are significant differences among wheat cultivars in their tolerance to aluminium ions (Campbell and Lefever, 1977). Cultivars developed in regions with strongly acid soils often possess high levels of aluminium tolerance, while those developed in other regions seldom possess this trait. Selection for aluminium-tolerant cultivars began in Brazil in 1919, although the specific cause of the toxicity was not identified until later (Silva, 1977). In the case of aluminium toxicity of wheat grown in Brazil, planting aluminium-tolerant cultivars is clearly more logical than the use of lime to precipitate the aluminium because the large amounts of limestone seem to encourage the incidence of take-all disease [*Ophiobolus graminis* (Sacc.) Sacc.] (Silva, 1977). In addition, it is very difficult to change the subsoil aluminium activity with additions of lime. The direct toxicity of Al^{3+} ions in solution generally is

the major factor reducing yield on acid soils; however, low pH also tends to increase concentrations of Mn^{2+} and Fe^{2+}. Tolerance to Al^{3+} does not necessarily infer tolerance to other toxic ions. For example, 'Atlas 66' cultivar of wheat is more tolerant to excess Al^{3+} than 'Monon,' but 'Monon' tolerates excess Mn^{2+} better than 'Atlas 66' (Foy *et al.*, 1973). The genetic variation in responses to Al, Mn, and Fe hold exciting promise for improved wheat yields, on soils with low pH. In addition, new plant genetic engineering techniques, including *in vitro* tissue culture selection, are potentially useful and efficient in selection for improving tolerance to all kinds of chemical toxicities (Hanson, 1984).

Since 1974, when cooperative agreements were formalized between CIMMYT and Brazilian research institutions, shuttle breeding for tolerance to aluminium toxicity has shown remarkable progress. With adequate disease resistance, new wheat cultivars will yield up to twice as much as the currently available commercial cultivars grown in Brazil's wheat production areas with acid soils high in soluble aluminium (CIMMYT, 1985).

While one can find soils with significant concentrations of aluminium in drought-prone areas such as parts of West Africa, Brazil, and Australia, a more common problem in dry areas is that of excess salinity. A group of scientists at Davis, California (Epstein *et al.*, 1980), has shown that genetic variability for salt tolerance exists in wheat. They screened over 5000 accessions from the USDA collections and found 34 lines of spring wheat that were capable of producing grain at a salinity 50 per cent that of sea water. Figure 3 shows the percentage survival of 34 salt-tolerant and 30 salt-sensitive selections of wheat (Epstein *et al.*, 1980). Plants of the sensitive populations died within 7 weeks of germination, but those of the tolerant lines survived much longer and 17 per cent of the plants produced viable seeds. In one selection cycle using Kharchia, a salt-tolerant wheat cultivar from India, Epstein *et al.* (1980) found strains that outperformed Kharchia. They concluded that further selection cycles should yield substantial improvement in salinity tolerance. In addition, Srivastava and Jana (1984) have identified 64 promising lines for salinity tolerance (out of 948 accessions tested) of durum wheat and 7 lines of bread wheat (out of 506 accessions). The salinity-tolerant lines exclude salts from uptake by the roots (Greenway and Munns, 1980). Progress in breeding for salinity tolerance has been reviewed recently by Shannon (1984).

The nutrient solution technique is particularly appropriate to use in screening cultivars for tolerance to toxic quantities of chemicals in the soil solution. In fact, Foy (1977) concluded that nutrient solutions were preferable to using soil with the same level of chemical in the soil solution. One can change ion concentration readily in a nutrient solution, but it is almost impossible to change the concentration of a specific chemical in the soil without simultaneously changing concentrations of other chemicals that may affect root growth (Meredith, 1984; Hanson, 1984).

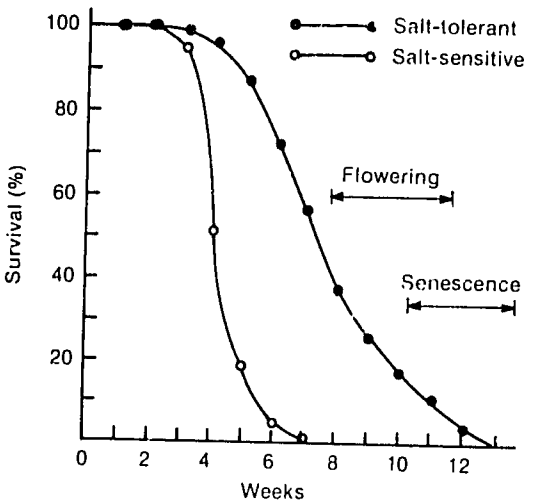


Figure 3. Survival of 34 salt-tolerant and 30 salt-sensitive selections of wheat grown in media salinized to 50 per cent of the salinity of sea water. (*Redrawn from Epstein* et al., *1980. Reproduced by permission of AAAS. Copyright © 1980.*)

In many wheat-growing areas, high-strength layers form readily, especially immediately below the depth of ploughing in sandy soils. Because roots must either grow through existing voids or must push aside the soil particles (Taylor and Klepper, 1978), some researchers have suggested that one should select plants with small-diameter root tips so the roots could more readily grow through soil voids. Williams *et al.* (1982, 1983) compared the ability of large versus small roots of tall fescue (*Festuca arundinacea* Schreb.) to penetrate compact soil. Although subject to more lance nematode (*Hopoloaimus galeatus* [Cobb] Sher.) damage, the large-diameter roots penetrated the soil better than small-diameter ones (Elkins *et al.*, 1977). A. T. P. Bennie (personal communication, 1985) suggests that one should screen plants for high root length density rather than for small root tips. Dr Bennie's logic is that many roots have a greater chance than few roots of finding voids to grow through the compact layers. Plants can be screened for high root length density by the acrylic slant-tube technique (MacKey, 1973; Nilsson, 1973a, 1973b).

Rovira (1979) has suggested that cultivar differences exist for resistance to cereal cyst nematode in both oats (*Avena sativa* L.) and wheat. The opportunity undoubtedly exists for selecting nematode-resistant cultivars of wheat, but any progress to date seems to have been made as a result of observations on top growth and yield.

Vesicular—arbuscular (VA) mycorrhizae increase the absorption, per unit of root length, of phosphorus (Khan, 1975), zinc (Swaminathan and Verma, 1979), bromine and chlorine (Buwalda *et al.*, 1983), and copper (Gildon and Tinker, 1983). Not enough is known about wheat cultivar differences in VA infection, in VA persistence in soil or root, or in VA effectiveness in increasing ion uptake to allow us to recommend or reject a research programme based on selecting cultivars for enhanced uptake of ions under field situations. It seems to us that phosphorus fertilisation of soil is the preferred treatment for the present time if uptake of phosphorus is limiting cereal growth and yield.

CONCLUSION

Wheat root systems vary from one cultivar to another due to genetic potential, but environment interacts strongly with genetic potential to control root growth and effectiveness. There is opportunity to select cultivars that reduce the effect of each adverse soil condition, at least within certain ranges. Selection of resistant cultivars is only one approach and it may be economically preferable to overcome the adverse soil condition through modifying the soil itself, through changing from wheat to another, more tolerant species, or through modifying soil management.

Finally, one should not assume that more root growth, a deeper root system, or one with less resistance to water or ion movement will necessarily yield more grain. Yield is controlled by many factors, only partly due to the rooting parameters.

REFERENCES

Buwalda, J., Stribley, D. P. and Tinker, P. B. 1983. Increased uptake of bromide and chloride by plants infected with vesicular-arbuscular mycorrhizae. *New Phytol.* **93**:217–225.

Campbell, L. G. and Lefever, H. N. 1977. Correlation of field and nutrient culture techniques of screening wheat for aluminum tolerance. Pages 277–286 in *Plant Adaptation to Mineral Stress in Problem Soils* (Wright, M. J., ed.). Proceedings of Workshop, NAL, Beltsville, Maryland, 22–23 November 1976. AID, Washington, DC.

Chambers, S. C. 1963. Deep sowing of wheat—the effect on root systems. *W. Aust. J. Agric.* **4**(4th series):287–289.

CIMMYT. 1985. CIMMYT annual report 1984. CIMMYT, Mexico.

Clarkson, D. T. 1985. Factors affecting mineral nutrient acquisition by plants. *Ann. Rev. Plant Physiol.* **36**:77–115.

Coleman, N. T. and Thomas, G. W. 1967. The basic chemistry of soil acidity. In *Soil Acidity and Liming* (Pearson, R. W. and Adams, F., eds.), Vol. 12. Agronomy. pp. 1–42.

Cornish, P. S. 1981. Resistance to water flow in the intracoleoptile internode of wheat. *Plant and Soil* **59**:119–125.

Cowan, I. R. and Milthorpe, F. L. 1968. Plant factors influencing the water status of plant tissues. Pages 137–193 in *Water Deficits and Plant Growth*. I. *Development, control and measurement* (Kozlouski, T. T., ed.). Academic Press, New York.

Derera, N. F., Marshall, D. R. and Balaam, L. N. 1969. Genetic variability in root development in relation to drought tolerance in spring wheats. *Exp. Agric.* **5**:327–338.

Elkins, C. B. Haaland, R. L. and Hoveland, C. S. 1977. Grass roots as a tool for penetrating soil hardpans and increasing crop yields. Pages 21–25 in *Proceedings of the 34th South. Past. Forage Crop Improvement Conference*.

Epstein, E., Norlyn, J. D., Rush, D. W., Kingsbury, R. W., Kelly, D. B., Cunningham, G. A. and Wrona, Anne F. 1980. Saline culture of crops: a genetic approach. *Science* **210**:399–404.

Foy, C. D. 1977. General principles involved in screening plants for aluminum and manganese tolerance. Pages 255–267 in *Plant Adaptation to Mineral Stress in Problem Soils* (Wright, M. J., ed.). Proceedings of Workshop, NAL, Beltsville, Maryland. 22–23 November 1976. AID, Washington, DC.

Foy, C. D., Fleming, A. L., and Schwartz, J. W. 1973. Opposite aluminum and manganese tolerances of two wheat varieties. *Agron. J.* **66**:751–758.

Gildon, A. and Tinker, P. B. 1983. Interactions of vesicular–arbuscular mycorrhizal infections and heavy metals in plants. II. The effects of infection on copper uptake. *New Phytol.* **85**:263–268.

Greacen, E. L., Porsana, P. and Barley, K. P. 1976. Resistance to water flow in the roots of cereals. Pages 80–100 in *Water and Plant Life* (Lange, O. L., *et al.*, eds.). Springer-Verlag, Berlin.

Greenway, H. and Munns, R. 1980. Mechanisms of salt tolerance in nonhalophytes. *Ann. Rev. Plant Physiol.* **31**:149–190.

Gregory, P. J., McGowan, M., Biscoe, P. V. and Hunter, B. 1978. Water relations of winter wheat. I. Growth of the root system. *J. Agric. Sci., Camb.* **91**:91–102.

Gul, A. and Allan, R. E. 1978. Inheritance of subcrown internode length, crown depth, and crown-tissue regrowth in winter wheat cross. *Crop Sci.* **18**:438–440.

Hamblin, A. P. and Hamblin, J. 1985. Root characteristics of some temperate legume species and varieties on deep, free-draining entisols. *Aust. J. Agric. Res.* **36**:63–72.

Hanson, M. R. 1984. Cell culture and recombinant DNA methods for understanding and improving salt tolerance of plants. Pages 335–359 in *Salinity Tolerance in Plants: Strategies for Crop Improvement* (Staples, R. C. and Toenniessen, G. H., eds.), John Wiley, New York.

Hunt, L. A., McKersie, B. D. and Tanner, D. G. 1983. Crown depth in eastern soft white winter wheats. *Crop Sci.* **23**:613–614.

Hurd, E. A. 1968. Growth of roots of seven varieties of spring wheat at high and low moisture levels. *Agron. J.* **60**:201–205.

Kaspar, T. C., Taylor, H. M. and Shibles, R. M. 1984. Taproot-elongation rates of soybean cultivars in the glasshouse and their relation to field rooting depth. *Crop Sci.* **24**:916–920.

Khan, A. G. 1975. The effect of vesicular–arbuscular mycorrhizal associations on the growth of cereals. II. Effect on wheat growth. *Ann. Appl. Biol.* **80**:27–36.

Klepper, Betty. 1986. Origin, branching and distribution of root systems. In *Root Development and Function—Effects of the Physical Environment* (Lake, J. V., Rose, D. A. and Gregory, P. J., eds.). Cambridge University Press. In press.

Klepper, B., Rickman, R. W. and Belford, R. K. 1983. Leaf and tiller development on wheat plants. *Crop Sci.* **23**:1002–1004.

Köpke, U., Bohm, W. and Jachmann, H. 1982. Rooting patterns of three winter wheat

cultivars in a field and greenhouse experiment. *Z. Acker- und Pflanzenbau* **151**:42–48.

Kramer, P. J. 1969. *Plant and soil water relationships: a modern synthesis*. McGraw-Hill, New York. 482 pp.

Locke, L. F. and Clark, J. A. 1924. Development of wheat plants from seminal roots. *J. Am. Soc. Agron.* **16**:261–268.

MacKey, J. 1973. The wheat root. Pages 827–842 in *Proceedings of the 4th International Wheat Genetics Symposium*. MO Agricultural Experimental Station, Columbia.

McGowan, M. and Tzimas, E. 1985. Water relations of winter wheat: the root system, petiolar resistance and development of a root abstraction equation. *Expl. Agric.* **21**. In press.

Meredith, C. P. 1984. Selecting better crops from cultured cells. Pages 503–528 in *Gene Manipulation in Plant Improvement* (Gustafson, J. P., ed.). Plenum Press, New York.

Nilsson, H. E. 1973a. Varietal differences in resistance to take-all disease of winter wheat. *Swedish J. Agric. Res.* **3**:89–93.

Nilsson, H. E. 1973b. Method for the study of roots and root diseases under controlled culture conditions. *Swedish J. Agric. Res.* **3**:79–88.

Passioura, J. B. 1974. The effect of root geometry on the water relations of temperate cereals (wheat, barley, oats). Pages 357–363 in *Structure and Function of Primary Root Tissue* (Kolek, J., ed.). Veda, Bratislava.

Passioura, J. B. 1983. Roots and drought resistance. *Agricultural Water Management* **7**:265–280.

Pavlychenko, T. K. 1937. Quantitative study of the entire root system of weed and crop plants under field conditions. *Ecology* **18**:62–79.

Pavlychenko, T. K. and Harrington, J. B. 1935. Root development of weeds and crops in competition under dry farming. *Scient. Agric.* **16**:151–160.

Proffitt, A. P. B., Berliner, P. R. and Oosterhuis, D. M. 1985. A comparative study of root distribution and water extraction efficiency by wheat under high- and low-frequency irrigation. *Agron. J.* **77**:655–662.

Reid, D. A. 1977. Screening barley for aluminum tolerance. In *Plant Adaptation to Mineral Stress in Problem Soils* (Wright. M. J., ed.). Proceedings of Workshop, NAL, Beltsville, Maryland, 22–23 November 1976. AID, Washington, DC.

Richards, R. A. 1982. Breeding and selecting for drought resistance in wheat. Pages 303–316 in *Drought Resistance in Crops with Special Emphasis on Rice*. IRRI, Manila, Philippines.

Richards, R. A. and Passioura, J. B. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* **21**:249–252.

Richards, R. A. and Passioura, J. B. 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* **21**:253–255.

Rovira, A. D. 1969. Diffusion of carbon compounds away from wheat root. *Aust. J. Biol. Sci.* **22**:1287–1290.

Rovira, A. D. 1979. Direct drilling—friend or foe to soil-borne root diseases of cereals. Pages 79–93 in *Proceedings of National Direct Drilling Conference*, Gateway Inn, Adelaide, 1979. Imperial Chemicals Incorporated, Australia.

Shannon, M. C. 1984. Breeding, selection and the genetics of salt tolerance. Pages 231–254 in *Salinity Tolerance in Plants: Strategies for Crop Improvement* (Staples, R. C. and Toenniessin, G. H., eds.). John Wiley. New York.

Silva, A. R. da 1977. Application of the genetic approach to wheat culture in Brazil. Pages 223–236 in *Plant Adaptation to Mineral Stress in Problem Soils* (Wright,

M. J., ed.). Proceedings of Workshop, NAL, Beltsville, Maryland, 22–23 November 1976. AID, Wasington, DC.

Srivastava, J. P. and Jana, S. 1984. Screening wheat and barley germplasm for salt tolerance. Pages 273–283 in *Salinity Tolerance in Plants: Strategies for Crop Improvement* (Staples, R. C. and Toenniessin, G. H., eds.). John Wiley, New York.

Sunderman, D. W. 1964. Seedling emergence of winter wheats and its association with depth of sowing, coleoptile length under various conditions and plant height. *Agron. J.* **56**:23–25.

Swaminathan, K. and Verma, B. C. 1979. Responses of three crop species to vesicular–arbuscular mycorrhizal infection on zinc-deficient Indian soils. *New Phytol.* **82**:481–487.

Taylor, H. M. 1983. Managing root systems for efficient water use: an overview. Pages 87–111 in *Limitations to Efficient Water Use in Crop Production* (Taylor, H. M., Jordan, W. R., and Sinclair, T. R., eds.). American Society of Agronomy, Madison, Wisconsin.

Taylor, H. M. and Klepper. Betty. 1978. The role of rooting characteristics in the supply of water to plants. *Adv. Agron.* **30**:99–128.

Walter, C. J. and Barley, K. P. 1974. The depletion of soil water by wheat at low, intermediate and high rates of seeding. *Trans. 10th Int. Cong. Soil Sci. Proc. Moscow* **I**:18–44.

Williams, C. B., Elkins, C. B. and Rodriguez-Kabana, R. 1982. Root size of tall fescue affects yield, stand persistence. Page 3 in *Highlights of Agricultural Research*, Vol. 29. Auburn University Agricultural Experimental Station.

Williams, C. B., Elkins, C. B., Haaland, R. L., Hoveland, C. S. and Rodriguez-Kabana, R. 1983. Effects of root diameter, nematodes, and soil compaction on forage yield of two tall fescue genotypes. *Proceedings of XIV International Grassland Congress*, Lexington, Kentucky, 15–24 June 1981. Westview Press, Boulder, Colorado.

Wind, G. P. 1955. Flow of water through plant roots. *Neth. J. Agric. Sci.* **3**:259–264.

DISCUSSION

N. C. Turner

(1) Is there any evidence that mycorrhiza affect water uptake and whether this accounts for differences in estimates of water uptake efficiency?

(2) Do nodal roots grow as deep as to be effective in extracting water from deep layers as seminal roots?

H. M. Taylor

(1) The evidence is contradictory. Some experiments in the literature have been interpreted as showing that VA mycorrhiza affect water uptake, especially for survival, while other experiments do not show any water uptake benefits from mycorrhiza. In view of my belief that root length densities and root uptake efficiencies are inversely related in many instances, I will not spend my time on experiments to show that VA mycorrhiza are important to field-grown annual plants in waters uptake. Of course, VA mycorrhiza are important in P uptake, even in annuals.

(2) Yes, some wheat genotypes have nodal (crown) roots that go as deep and are as effective as seminal roots in water uptake from deep layers.

S. K. Sinha

A point has been made that wheat plants revive if rains come after a period of severe stress. This could be dependent on the stage of plant development. Prior to grain fill, the assimilates or reserves might be transported to roots, which can revive depending on the damage done to them. However, once the plant has started grain development, the revival may not be possible unless seed development has been impaired.

H. M. Taylor

Your comment is accurate if the revival occurs as a result of new root growth. However, the revival of root uptake of water or nutrients may occur through the remaining functional roots merely because water becomes available to be taken up by the roots or to transport nutrients to the existing roots.

D. R. Marshall

Experience in the northern NSW wheat belt shows that tillers which do not develop crown roots have poor seminal prospects. One suggestion is that deep crowns may allow tillers greater opportunities to develop crown roots. Is there any evidence to support this suggestion?

H. M. Taylor

Yes, the deep crowns are more likely to be located in somewhat wetter soil. The crown roots will not develop to any significant extent in dry soil but can develop into the somewhat moderately dry soil usually found deeper in the plow layer.

R. A. Richards

The reactivation of nodal roots in a dry soil after a rain event may be a very important characteristic for cereals in the ICARDA region. Is there any evidence that cereals have this capacity?

H. M. Taylor

Yes, root system reactivation occurs after a rain, sometimes as a result of new root growth and sometimes because roots that remain, but were not able to function because of lack of water, take up water and start transporting ions.

SECTION IV

Plant Characteristics Required for Improved Performance in Moisture-limiting Environments—an *ad interim* Assessment

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

24

Assessing Crop and Plant Attributes for Cereal Improvement in Water-limited Mediterranean Environments

E. ACEVEDO
ICARDA, PO Box 5466, Aleppo, Syria

ABSTRACT

We discuss a conceptual model to identify traits affecting stress resistance and avoidance for a given environment and assess the importance of some traits in cereal production in stressed Mediterranean environments. We then compare the morphological and physiological attributes between and within cereal species.

INTRODUCTION

Physical or abiotic stresses greatly influence the growth of cereal crops in the rainfed areas of North Africa and Southwest Asia. In these areas, which constitute ICARDA's geographic regional mandate, drought, heat, and cold predominate. Drought may occur alone or in combination with one or more of the thermal stresses, or a given thermal stress may prevail at various stages of crop development. Furthermore, the stress pattern may differ in each of the various climatic zones (ICARDA, 1985; Frere *et al.*, this volume).

Breeding for cereal improvement under such conditions is therefore difficult. When the plant responses to environmental (physical) stresses are included in the improvement process, additional factors must be considered. These are:

(1) There seems to be no single plant trait conferring stress resistance in the form of avoidance or tolerance but there are responses to a combination of traits.

(2) Some traits which help improve the performance of a plant under stress conditions are constitutive (always present) while others are adaptive, i.e. they will express only under a given set of environmental stimuli.

(3) Plant performance is the result of a combination of constitutive and adaptive traits

(4) The response depends on the stress history of the plant since acclimation (short-term responses) may also be present.

(5) If adaptive traits are important to plant response under stress, a target environment for the breeder's selection is needed.

(6) There seems to be a tradeoff between yield and stress resistance.

Two main approaches have been proposed for varietal improvement under stressful environments. The first and most widely used approach relies on grain yield as the main selection criterion, since this parameter integrates all the components in a stressful environment. The second, and most recently introduced for areas where stresses are of high intensity, is the 'analytical' approach. The latter relies on the adaptation mechanisms of a plant in a stressful environment, with the possibility that breeding and selection for these adaptations will contribute to growth and yield under stress. The analytical approach links plant and crop physiology with breeding efforts so as to hasten the otherwise usually slow pace of plant improvement in highly stressed environments (Richards 1982, and this volume; Marshall, this volume). In fact both approaches are complementary.

The key component of the analytical approach is to identify the individual traits conferring stress resistance, which could be separated for further recombination to produce plants with resistance at various stages of growth. To do this an environment (or a set of similar environments) must be first defined in view of the complexity of the stress syndrome. Assuming that the physiological response within the plant to a specific stress is known, a simple plant parameter that correlates with the plant response to the stress must also be found. It should then be proved that genetic variability within a population exists to warrant plant selection. Finally, selection for the trait(s) and their recombination with other characters must be feasible, without any negative effects on such characters as yield, disease resistance, or quality of the final product (Simpson, 1981).

For this study, two Mediterranean environments differing in their long-term rainfall (about 300 and 200 mm) were selected in northern Syria. A wide range of genotypes were fully characterised, to identify specific parameters or attributes representing significant traits conferring survival and productivity at each stage of the life cycle. Since water stress is of major concern in the region, a set of plant attributes was derived based on the conceptual model of Passioura (1977) and Fischer and Turner (1978). The model suggests that yield under water stress may be viewed as the product of transpiration (T), transpiration efficiency (TE), and a partitioning term (F) which, in the case of

grain yield, is the harvest index of the crop. Based on this model, a hypothetical crop ideotype was designed for the Mediterranean environments.

The main features of the environments under consideration may be summarised as follows: (1) low and variable winter rainfall and low temperatures, (2) high probability of early and terminal drought stress, (3) low temperatures during canopy development with the possibility of frost, (4) high temperatures during grain filling, and (5) water availability essentially determined by current rainfall, particularly in low-rainfall areas.

HYPOTHESIS

The proposed model suggests that maximizing the three components, T, TE, and F would maximize yield at a plant or crop level. The following attributes may be derived to maximize T as a fraction of evapotranspiration (ET): (1) early crop establishment with profuse root growth in the top of the soil and sparse root growth at depth, as deep as allowed by the wetting front, (2) fast leaf area development, (3) initial prostrate growth habit, (4) ability to grow under suboptimal temperatures, and (5) resistance to low temperatures and occasional drought.

The plant attributes postulated to maximize TE are as follows:

I. Morphological
   1. Short and narrow leaves, with high specific weight (Nobel, 1980, 1983) to maximize the mesophyll area over the leaf area (A^{mes}/A); erect leaves after stem extension (Evans and Wardlaw, 1976). These attributes would tend to increase photosynthesis.
   2. Relatively high plant resistance to liquid water flow, specially under very dry (approximately 200 mm) conditions such that osmotic and stomatal adjustment is induced.
   3. Properties of the photosynthetic organs that would minimize the energy load during terminal drought and heat stress (Johnson *et al.*, 1983).

II. Physiological
   1. Ability to photosynthesize under stress (drought, cold, heat), coupled with relatively low transpiration rates in the very dry areas.
   2. High sink capacity in the above-ground parts of the plant.
   3. Stomatal adjustment to drought.

The plant attributes postulated to maximize grain yield (F) are:

1. An amount of dry matter at anthesis that would maximize yield (i.e. high sink capacity) (Fischer, 1981).
2. Early flowering as allowed by spring frosts.
3. Relatively fast grain filling as allowed by drought and heat stress.
4. A high proportion of preanthesis assimilates reallocated to the grain and/or a slow leaf senescence (Boyer, 1983).

5. Presence of awns (Turner and Kramer, 1980).
6. High net photosynthesis under drought (heat).

These attributes must be evaluated for their contribution to stress resistance and yield under stress.

The objective of this work is to evaluate a wide range of barley, durum wheat, and bread wheat genotypes for some of the attributes stated in the working hypothesis. Comparisons between as well as within species are being made.

Materials and methods

Seventy-two barley, 20 durum wheat, and 20 bread wheat genotypes were grown at Tel Hadya and Bouider in northern Syria. The genotypes chosen represented contrasting characters of early vigour, growth at low temperature, height under stress, flowering date, and grain-filling period. Genotypes with a high-yield potential and/or good yield stability, pure lines isolated from landraces (in the case of barley), and lines thought to be stress tolerant were also included.

Two experiments were performed at each site with barley and wheat genotypes. In both cases a completely randomized block design with three replicates was used. Plots were 2.4 m wide (12 rows, 20 cm apart) and 5 m long. The sowing rate was adjusted to 250 plants/m^2 for each genotype by correcting for percent germination and kernel weight of the seed.

At Tel Hadya, the wetter site, the soil was fertilized with a preplanting dose of 40 kg of nitrogen/ha in the form of ammonium sulphate and 60 kg of P_2O_5/ha in the form of triple superphosphate. An additional 40 kg of nitrogen/ha was broadcast at mid-tillering. At Bouider, the drier site, the split application of nitrogen was reduced to 20 kg/ha at each time while the preplanting phosphorus was kept at 60 kg P_2O_5/ha. All preplanting fertilizations were incorporated into the soil with the last harrowing. Perforan was used as a preemergence herbicide at a rate of 2.5 l/ha at all sites. Weed control was complemented with Brominal plus applied at a rate of 1.5 l/ha in 400 litres of water at the five-leaf stage.

Table 1. Cereal physiology nurseries, field score

	Minimum	Maximum
Ground cover	1	10
Plant vigour	1	5
Plant wilting	1	5
Leaf rolling	1	5
Plant senescence	1	5

Growth habit: 1, erect; 2, intermediate; 3, prostrate.

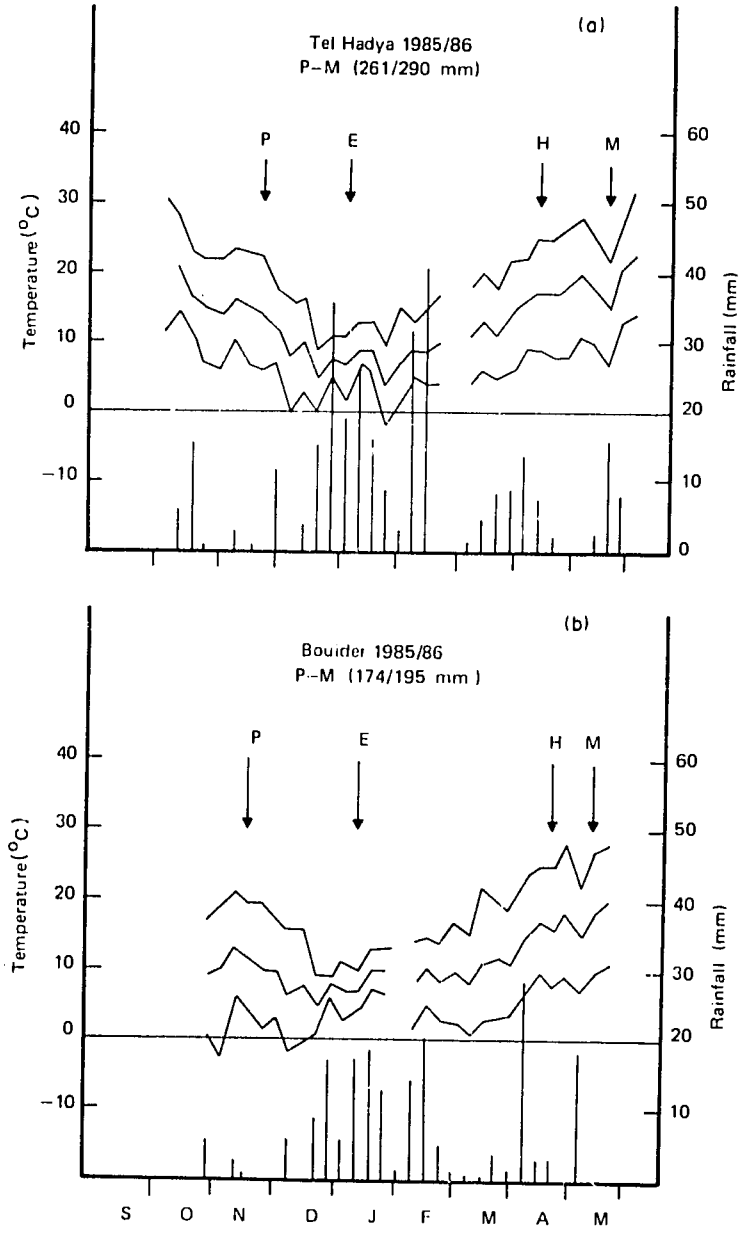


Figure 1. Climodiagrams for Tel Hadya and Bouider. A range of rainfall from planting to maturity is given at each site covering the range in maturity type of the genotypes tested. Arrows indicate times of planting (P), emergence (E), heading (H), and maturity (M)

Observations were periodically taken on development using Zadoks stages. Peduncle length and plant height were measured to determine growth. Water relations measured included water potential using a pressure chamber, leaf moisture release curves around anthesis (the relation between relative water content, RWC, and water potential Ψ), and stomatal conductance. Net photosynthesis was measured with a portable IRGA and related parameters included substomatal CO_2 concentration (calculated) and stomatal conductance. Biological yield (roots excluded), grain yield, and number of spikes per unit surface were determined at harvest. Other crop and plant observations were scored in the field (Table 1) five times during the growing season.

Climatic conditions

Climodiagrams including rainfall and screen temperature for the sites are presented in Figure 1. They are typical for the Mediterranean climate. They show how the opportunity for grain filling decreases, as rainfall decreases, due to terminal drought and heat stresses. Concurrently the risk of a false start or seedling water stress increases.

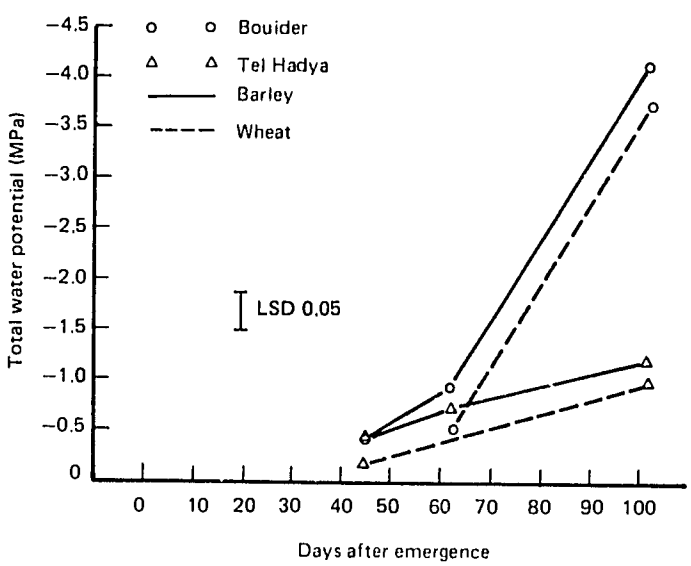


Figure 2. Predawn water potential during the growing season for barley and wheat. Measurements were taken on the last fully expanded leaf at Tel Hadya and Bouider. The LSD is for site comparisons of the pooled populations

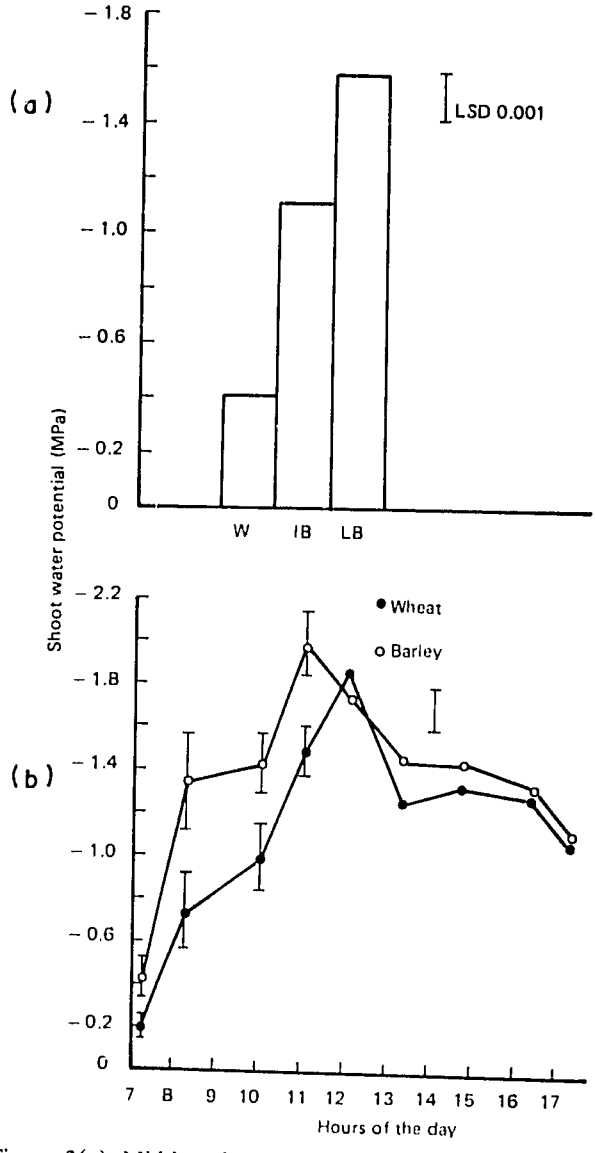


Figure 3(a) Midday shoot water potential in wheat (W), four genotypes; improved barleys (IB), eight genotypes; and barley landraces (LB), four genotypes. Tel Hadya, 38 days after emergence. Zadoks stages 12–13. (b) Daily course of shoot water potential. Wheat, four genotypes; and barley, eight genotypes. Tel Hadya, 55 days after emergence. Zadoks stages 22–24. The bars indicate twice the standard error of the means

Water relations

Figure 2 shows generalized curves of predawn leaf water potential through the growing season at Tel Hadya and Bouider. These curves indicate the contrasting severity of water stress experienced by the genotypes at the two sites.

The working hypothesis postulated that a relatively high resistance to liquid water flow would be desirable for plants growing under drought. Passioura (1977) has long advocated this trait and it is being tested as a breeding objective (Richards and Passioura 1981a, 1981b; Richards, this volume) for cereals experiencing terminal drought stress. The cereal physiology nurseries assembled provided an opportunity to test this trait under natural conditions. Figure 3a shows the shoot water potential of wheat, improved barley genotypes and barley landraces measured at midday at the Tel Hadya site, 38 days after emergence. The day was overcast following rain, the photosynthetically active radiation (PAR) being around 400 μmol/m^2/s during the measurements. The plants were at the two- to three-leaf stage (Zadoks stages 12–13). Nodal root growth had not yet started, nor was it incipient. The plants therefore grew on their seminal root systems. Wheat had a significantly higher Ψ than the improved barleys, which in turn had a significantly higher value than the barley landraces. Figure 3b shows that the shoot water potential of the barley genotypes during the morning was significantly lower than that of the wheat genotypes at the same site even after nodal root development had been initiated (55 days after emergence).

Shoot water potential alone, even when measured with the soil at field capacity, does not prove that there are differences in resistance to liquid water flow between or within species as the water status of a plant results from water uptake and transpiration. Measurements were therefore taken of leaf conductance. Figure 4 shows that the stomatal conductance of barley was significantly lower both at Tel Hadya and Bouider at the tillering stage (Zadoks stages 22–25). These results indicate that barley has a conservative strategy in terms of water use as compared to wheat and the increased resistance to liquid water flow in the plants was in the order wheat < improved barleys < landrace barleys. In terms of rainfall this trend is consistent with the areas where these crops are grown in northern Syria. In fact, landrace barleys are grown in the very low rainfall areas (approximately 200 mm), while wheat and improved barleys are grown in areas receiving 300 mm and above.

There was great variability between genotypes in predawn water potential and stomatal conductance as demonstrated by the physiology nurseries.

It has been suggested during the last decade that the ability of tissues to retain water is an important attribute of plants grown under stress (Acevedo, 1975; Acevedo *et al.*, 1979; Pearson *et al.*, this volume; Morgan, 1983;

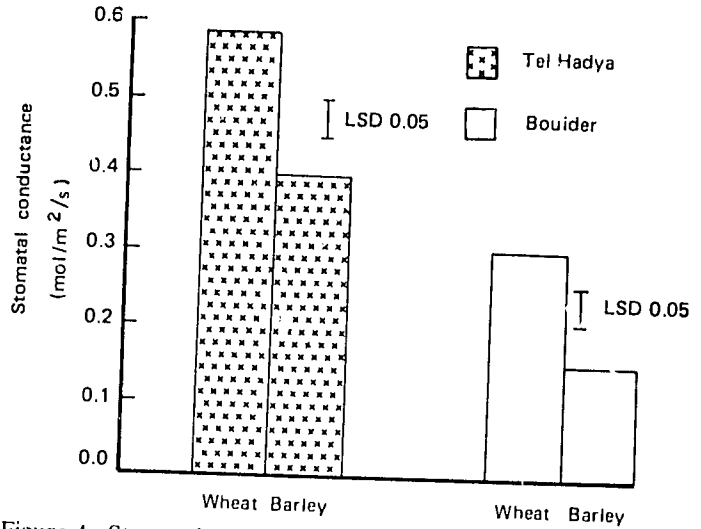


Figure 4. Stomatal conductance in wheat and barley of the last fully expanded leaf. Measurements taken at Tel Hadya and Bouider, 62–63 days after emergence. The accumulated rainfall from planting was 212 mm at Tel Hadya and 141 mm at Bouider

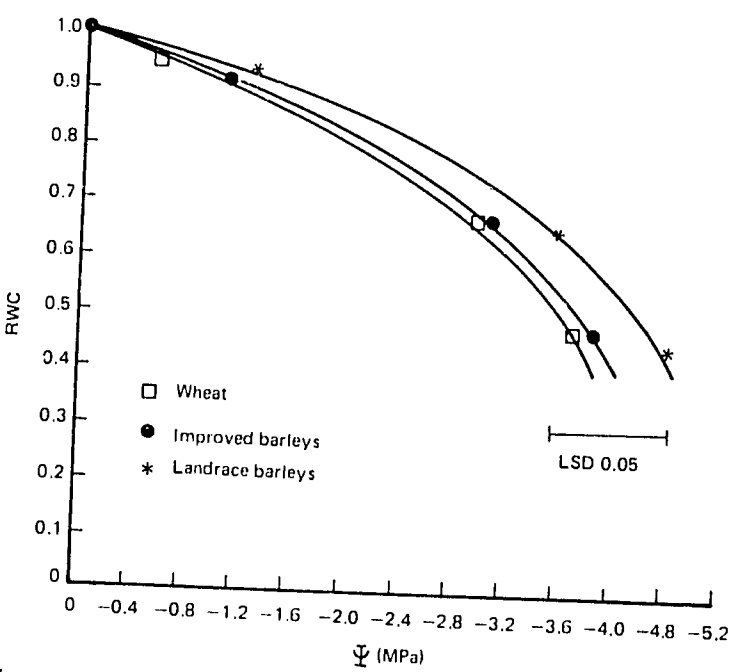


Figure 5. Average moisture release curves for wheat, improved barleys, and barley landraces. Bouider, 72 days after planting, Zadoks stage 51. Samples taken on the flat leaf-2

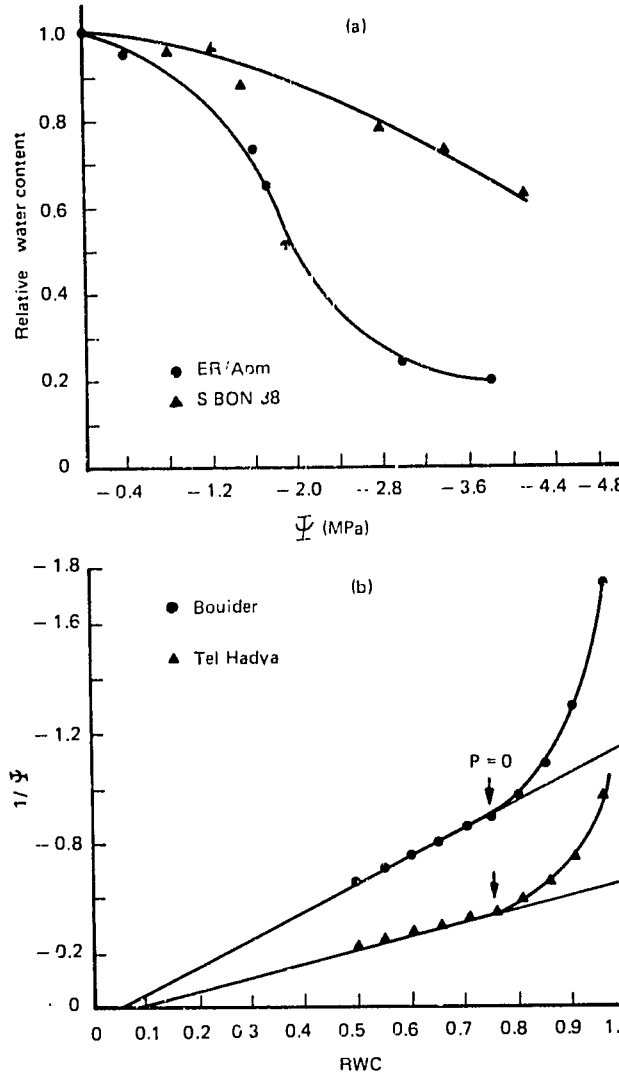


Figure 6. (a) Leaf moisture release curves of contrasting barley genotypes. Measurements taken on predawn samples of the flag leaf-2. Each curve has data points from Tel Hadya and Bouider. The curves were drawn by hand. (b) Moisture release curves as in (a) for a barley landrace showing osmotic adjustment from −1.04 MPa of solute potential at Tel Hadya to −2.17 MPa at Bouider for an RWC of 1.0

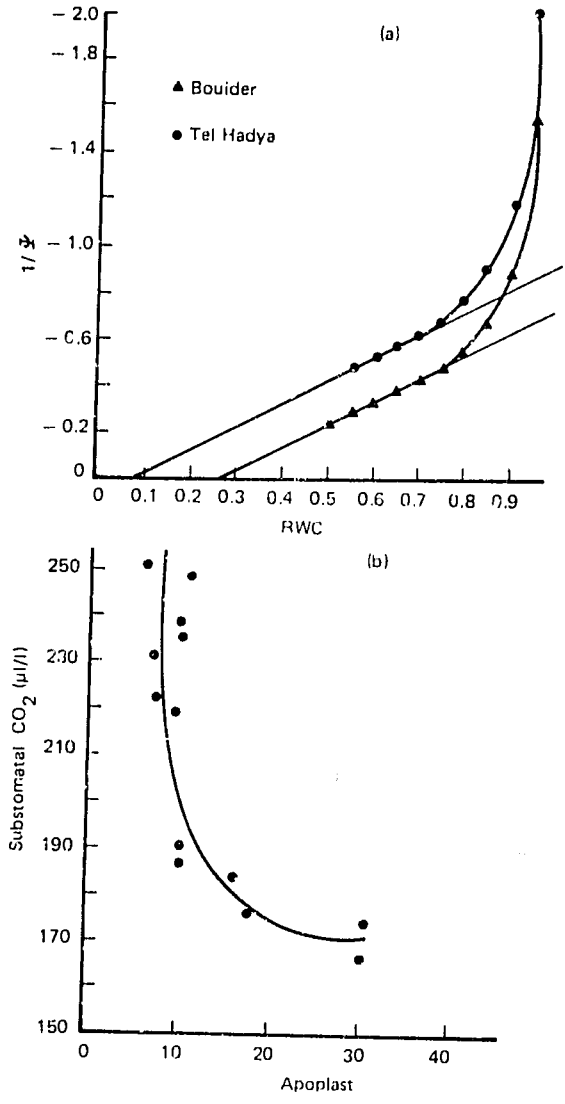


Figure 7. (a) Moisture release curves as in Figure 6a for a barley landrace. Osmotic adjustment and an increase in apoplastic tissue are evidenced at the dry site, Bouider, as compared to the wet site, Tel Hadya. (b) Trend in decreased substomatal CO_2 concentration with increased apoplastic tissue in a range of barley genotypes

Sinclair and Ludlow, 1985). This is usually achieved by osmoregulation. Morgan (1983) advocated osmoregulation as a selection criterion for drought tolerance in wheat. In the working hypothesis, osmoregulation and stomatal adjustment, which are usually associated with each other (Turner and Jones, 1980; Acevedo and Massardo, 1984), was postulated. Leaf moisture release curves in predawn samples taken around anthesis were determined for selected wheat and all the barley genotypes.

Figure 5 shows that there was a tendency for barley landraces to retain more water in the leaf tissue at a given water potential as compared to improved barleys and wheat. Release curves in the barley nursery were more intensively studied. Large differences were found between genotypes. In some, this character was constitutive (the same curve observed at Tel Hadya and Bouider, Figure 6a) with no osmotic adjustment under drought. Others at the dry site, Bouider (Figure 6b), presented an adaptive trait and adjusted osmotically up to about 1 MPa at full turgor (RWC = 1.0). Still other genotypes increased their apoplastic tissue under drought (Figure 7a). This increase may be due to a decreased mesophyll cell size and increased A^{mes}/A, which may be associated with an increased photosynthetic rate under stress. The trend in substomatal CO_2 concentration (Figure 7b) seems to indicate this. The substomatal CO_2 concentration was strongly and negatively correlated with net photosynthesis ($r = -0.83$, $P < 0.001$). Other variables that affect photosynthesis also play a role (Farquhar and Sharkey, 1982).

The shift within a given barley genotype of the leaf moisture release curve (Figure 6a) to the right under stress conditions had a significantly ($P < 0.05$) negative correlation with grain ($r = 0.26$) and biological yield ($r = 0.30$) at the dry site (Bouider). The change in position of the curve was quantified as the value (negative) at which the RWC dropped to 75 per cent, which is roughly the value of zero turgor pressure (Figures 6b and 7a) for barley. The implications of the type of leaf moisture release curve in terms of stability of performance of a variety under drought are yet to be assessed.

Net photosynthesis

Leaf conductance and photosynthesis in wheat dropped drastically under drought at heading as compared to barley (Table 2). On the contrary the barley genotypes seemed to adjust their stomata and kept a higher photosynthesis rate. The mean substomatal CO_2 concentration was lower in barley as compared to wheat at the wet site and increased by 15 per cent in barley but only 8 per cent in wheat under drought. Within barley and wheat genotypes net photosynthesis per unit leaf conductance as well as per unit substomatal CO_2 varied significantly ($P < 0.001$) for similar leaf conductances at the dry site. This finding may have relevance in terms of transpiration efficiency differences between genotypes. The ranges in Table 2 also indicate that there

Table 2. Net photosynthesis (NP), stomatal conductance (CWV) and calculated substomatal CO_2 concentration (Int CO_2) in barley (72 genotypes) and wheat (40 genotypes). Measurements taken at the flag leaf-1 at Zadoks stage 50–59 (ear emergence)

Variable		Barley		Wheat	
		Tel Hadya	Bouider	Tel Hadya	Bouider
NP (μmol CO_2 m^2/s)	$\bar{X}$	14.4	5.4	17.7	2.8
	range	(19.6–8.4)	(15.6–0.8)	(21.4–11.6)	(7.7–0.2)
CWV (mol/m^2/s)	$\bar{X}$	0.39	0.17	0.60	0.07
	range	(0.75–0.21)	(0.47–0.03)	(0.79–0.48)	(0.12–0.03)
Int CO_2 (μl/l)	$\bar{X}$	199	227	212	229
	range	(241–153)	(300–154)	(232–195)	(305–153)

Table 3. Barley physiology nursery at Bouider (174–195 mm). Correlation between plant and crop attributes and yield (72 genotypes)

Crop attribute	Score	Mean (range)	Standard error	Correlation coefficient	
				BioY	GY
Ground cover (10–40 days)	(0–10)	1.9 (0.2–5.5)	0.04	0.38†	−0.21†
Ground cover anthesis	(0–10)	7.7 (4.0–10)	0.09	0.34†	−0.16†
Wilting anthesis	(1R–5S)	2.5 (1–5)	0.07	−0.33†	−0.32†
Leaf rolling (20 days)	(1L–5H)	1.1 (0–2.0)	0.02	0.31†	0.20†
Leaf rolling anthesis	(1L–5H	2.1 (1.5–3)	0.03	−0.11	−0.03
Senescence (grain filling)	(1L–5H)	2.6 (1–5)	0.07	−0.32†	−0.29†
Peduncle length	(Measured)	7.2 (2.7–15.9)	0.16	0.28†	0.40†
Plant height	(Measured)	40.7 (24.0–73.0)	0.60	0.43†	0.29†
Days to heading	(50%)	88 (80–115)	0.29	−0.26†	−0.23†
Days to maturity	(50%)	115 (106–126)	0.32	−0.20†	−0.23†

*$P < 0.05$.
†$P < 0.01$.
$N = 211$.
R = resistance; S = susceptible; L = low; H = high.

is scope for selection for these traits. Osmotic and stomatal adjustment would probably be most important in wheat (Morgan, 1983), while finding lines with higher carboxylation rates would be a goal in both species, particularly in barley. The variability in net photosynthesis within these species is wide (Table 2).

Plant (crop) attributes and yield

Tables 3 and 4 show some crop and plant attributes including their mean and range as well as simple correlations with yield at Tel Hadya and Bouider. A highly significant correlation was found at both sites between ground cover and biological yield (BioY) as well as between ground cover and grain yield (GY). However, the correlation of ground cover at anthesis with GY was weak at Bouider. This might indicate that there may be an optimum ground

Table 4. Barley physiology nursery at Tel Hadya (261–290 mm). Correlation between crop attributes and yield (72 genotypes)

Crop Attribute	Score	Mean (range)	Standard error	Correlation coefficient BioY	Correlation coefficient GY
Ground cover (30 days)	(0–10)	1.6 (0.3–5.5)	0.07	0.39†	0.31†
Ground cover anthesis	(0–10)	7.0 (1.5–9.5)	0.10	0.41†	0.31†
Wilting anthesis	(1R–5S)	1.0 (1.0–1.0)	0.00	—	—
Leaf rolling (30 days)	(1L–5H)	1.6 (0.5–5.0)	0.03	0.04	0.11
Leaf rolling anthesis	(1L–5H)	2.4 (1.5–3.6)	0.03	0.08	0.05
Senescence (grain filling)	(1L–5H)	1.1 (1.0–2.5)	0.02	−0.24†	−0.15*
Peduncle length	(Measured)	16.4 (5.3–28.9)	0.28	0.24†	0.34†
Plant height	(Measured)	78.7 (57.0–110.0)	0.62	0.27†	0.20†
Days to heading	(50%)	92 (85–105)	0.25	−0.20†	−0.35†
Days to maturity	(50%)	120 (114–133)	0.25	0.03	−0.14*

*$P < 0.05$.
†$P < 0.01$.
$N = 211$.
R = resistance; S = susceptible; L = low; H = high.

cover at the dry site for maximum grain yield as postulated by Fischer (1981). Wilting symptoms were highly negatively correlated with yield at the dry site (no wilting was observed at Tel Hadya). Leaf rolling, assessed as the number of turns of the leaves, early in the season was positively correlated with yield at the dry site only. The genotypes showing this trait at this time were not experiencing drought stress and hence it may be a constitutive trait. The same trait at anthesis, however, was negatively correlated with yield at the dry site and had a higher mean for the population. At this stage water stress was probably inducing rolling.

In the working hypothesis it was also postulated that slow leaf senescence would be a desirable trait. This was found to be the case both at Tel Hadya and Bouider (Tables 3 and 4). Peduncle length and plant height had a highly significant correlation with yield at both sites. Days to heading was negatively correlated at both sites but days to maturity was strongly negatively correlated with yield only at the dry site.

If, as shown, early ground cover is a desirable crop attribute, then the growth habit of the plant may play an important role. Table 5 shows that ground cover between 30 and 50 days (tillering stage) is highly and positively associated to a prostrate habit. Plants become erect after shoot extension (70 days), and this is associated with ground cover (score: 1 erect, 3 prostrate) and is highly correlated ($r = 0.38$, $P < 0.01$) with grain yield.

Stepwise multiple-regression analysis of grain yield and crop attributes at the dry site indicated the relative importance of the following variables in the indicated order: head number per square metre > peduncle length > growth habit at anthesis > senescence during grain filling > predawn Ψ at anthesis (flag leaf − 1). At Tel Hadya, the most important variables were ground

Table 5. Barley physiology nursery at Tel Hadya, 1985–6. Simple correlations between ground cover (GC) and growth habit (GH)

	GC1	GC2	GC3
GH1	−0.002	−0.012	0.049
GH2	0.165	0.244†	0.178*
GH3	0.079	0.232†	0.216†
GH4	−0.258	−0.340†	−0.492†

*$P < 0.05$.
†$P < 0.01$.
$N = 216$.
GH score: 1, erect; 2, medium; 3, prostrate.

1, 10 days after emergence
2, 30 days after emergence
3, 50 days after emergence
4, 70 days after emergence

cover > grain-filling period (positively correlated with grain yield) > plant height.

CONCLUSIONS

(1) Barley as compared to wheat seems to have a conservative strategy in terms of water use. This strategy was shown by an increased resistance to water flow within the plant and a decreased leaf conductance to water vapour under well-watered conditions.

(2) Within barley genotypes there were variations in resistance to water flow, the implications of which must be studied in terms of their contribution to 'responsiveness' and 'stability' in production.

(3) Stomata closure at heading was clear in the wheat population at the dry site. The barley genotypes showed a higher stomata conductance. Net photosynthesis was also more depressed in wheat than in barley at this time.

(4) The relative importance of osmotic adjustment to genotype 'responsiveness' and 'stability' needs to be assessed. Both adaptive and constitutive barley genotypes regarding this trait were observed.

(5) An early ground cover was strongly and positively associated with biological yield both at the dry and wet sites. Grain yield was clearly associated with ground cover only at the wet site, indicating that probably an optimum ground cover and/or a more conservative water-use strategy may be needed for the dry site.

(6) Early leaf senescence during grain filling was particularly detrimental at the dry site, both in total biological yield and grain yield.

(7) At both dry and wet sites the number of spikes per square metre seemed to predict the biological as well as grain yield. The same was true for peduncle length.

(8) Leaf rolling during early growth (10–30 D) was significantly correlated with biological and grain yield, being probably a constitutive character at this stage.

(9) In barley, a prostrate habit through stem elongation is highly desirable for increased ground cover. Thereafter, an erect habit with relatively vertical leaves is highly correlated with biological and grain yield.

(10) Sufficient variability within barley genotypes exists in the abovementioned attributes to explore them as selection tools.

ACKNOWLEDGEMENTS

I thank Dr J. P. Srivastava for his support as Leader of the Cereal Improvement Program of ICARDA. The assistance of Messrs. Issam Naji, Moffid Ajami, and Riad Saccal in data collection is deeply appreciated.

REFERENCES

Acevedo, E. 1975. The growth of maize (*Zea mays* L.) under field conditions as affected by its water relations. Ph.D. dissertation. University of California, Davis. 253 pp.

Acevedo, E. and Massardo, C. 1984. Efecto del dificit hidrico en dos etapas del desarrollo en el cultivo del tomate (*Lycopersicon esculentum* Mill.). *Pyton* **44** (2):151–166.

Acevedo, E., Fereres, E., Hsiao, T. C. and Henderson, D. W. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. *Plant Physiol.* **64**: 476–480.

Boyer, J. S. 1983. Subcellular mechanisms of plant response to low water potential. *Agric. Water Manage.* **7**:239–248.

Evans, L. T. and Wardlaw, I. F. 1976. Aspects of the comparative physiology of grain yield in cereals. *Adv. Agron.* **28**:301–359.

Farquhar, G. D. and Sharkey, T. D. 1982. Stomatal conductance and photosynthesis. *Ann. Rev. Plant Physiol.* **33**:317–345.

Fischer, R. A. 1981. Optimizing the use of water and nitrogen through breeding of crops. Page 249–278 in *Soil Water and Nitrogen in Mediterranean-type Environments* (Monteith, J. and Webb, C., eds.). Martinus Nijhoff/Dr W. Junk Publishers, The Hague, the Netherlands.

Fischer, R. A. and Turner, N. C. 1978. Plant productivity in the arid and semiarid zones. *Ann. Rev. Plant Physiol.* **29**:277–317.

ICARDA (International Center for Agricultural Research in the Dry Areas). 1985. Annual report 1984. Aleppo, Syria.

Johnson, D. A., Richards, R. A. and Turner, N. C. 1983. Yield, water relations, gas exchange and surface reflectance of near-isogenic wheat lines differing in glaucousness. *Crop Sci.* **23**:318–325.

Morgan, J. M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* **34**:607–614.

Nobel, P. S. 1980. Leaf anatomy and water use efficiency. Pages 43–55 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, N. C. and Kramer, P. J., eds.). John Wiley, New York.

Nobel, P. S. 1983. *Biophysical plant physiology and ecology*. W. H. Freeman, San Francisco. 608 pp.

Passioura, J. B. 1977. Grain yield, harvest index and water use of wheat. *J. Aust. Inst. Agric. Sci.* **43**:117–120.

Richards, R. A. 1982. Breeding and selecting for drought resistance in wheat. Pages 303–316 in *Drought Resistance in Crops with Emphasis on Rice*. International Rice Research Institute, Manila, Philippines.

Richards, R. A. and Passioura, J. B. 1981a. Seminal root morphology and water use of wheat. I. Environmental effects. *Crop Sci.* **21**:249–252.

Richards, R. A. and Passioura, J. B. 1981b. Seminal root morphology and water use of wheat. II. Genetic variation. *Crop Sci.* **21**:253–255.

Simpson, G. M. 1981. The value of physiological knowledge of water stress in plants. Pages 235–265 in *Water on Plants* (Simpson, G. M., ed.). Praeger Publishers, New York.

Sinclair, T. R. and Ludlow, M. M. 1985. Who taught plants thermodynamics? The unfulfilled potential of plant water potential. *Aust. J. Plant Physiol.* **12**:213–217.

Turner, N. C. and Jones, M. M. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. Pages 87–103 in *Adaptation of Plants to Water and High Temperature Stress* (Turner, N. C. and Kramer, P. J., eds). John Wiley, New York.

Turner, N. C. and Kramer, P. J. 1980. *Adaptation of plants to water and high temperature stress*. John Wiley, New York. 482 pp.

DISCUSSION

M. S. Mekni

Early ground cover might lead to faster depletion of soil moisture if evaporation was small. If that is so, during the winter months, what would be the value of fast initial ground cover in a dry environment? Would you try to verify current belief at ICARDA on usefulness of rapid ground cover?

E. Acevedo

The value of fast initial ground cover is to favour the transpiration component of evapotranspiration, i.e. decrease direct soil evaporation. The crop is also intercepting more solar radiation per unit area in a period during which it is decreasing. At ICARDA we are testing this hypothesis and the results obtained so far seem to support it.

N. C. Turner

You said that planting early gave best yields in the ICARDA region. If water stress occurs after anthesis, does this occur? Observations in Western Australia suggest that water stress after emergence may so hasten anthesis that dry-matter accumulation at anthesis may be low and a later planting may give higher dry matter at anthesis and grain yield.

E. Acevedo

Yes, it does. The experimental evidence for barley grown in sites of 200–300 mm rainfall supports this view. Early planting is usually done in the second half of October. Many of the landraces grown in the very dry area have some vernalization requirement.

M. S. Mekni

Would you care to comment on how important you consider the kernel number in a selection index you would devise for dry areas?

E. Acevedo

In dry areas with terminal drought, kernel number and kernel weight are negatively related. On the other hand, spike number per unit area seems to be highly correlated with yield.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

25

Some Crop Characteristics of Wheat and Their Influence on Yield and Water Use

R. B. AUSTIN
Plant Breeding Institute, Maris Lane, Cambridge CB2 2LQ, UK

ABSTRACT

In favourable environments, cereal yields have at least doubled during the past 30–40 years. These increases in yield have depended jointly on the increased use of fertilizers and other agrochemicals and on the breeding of varieties with greater yield potential. By contrast, in regions of the world where water is a dominant limiting factor, little increase in yield has been achieved. In this paper, we argue that there is scope for increasing yields in such areas, but that improvements in cultural conditions and a much greater effort in breeding are required to achieve this.

To improve the efficiency of cereal-breeding programmes in dry areas, we suggest that research be undertaken to establish the importance for yield and water use of component characteristics for which selection could easily be practised. This approach has been followed at the Plant Breeding Institute, Cambridge, where experiments have been carried out on winter wheat to study the consequences for yield and water use of various plant characteristics. The results showed that high tillering capacity benefited yield except when there was a preanthesis drought, that semi-dwarf (Rht1 or Rht2) lines were slightly more adversely affected by drought than tall ones, that early flowering lines yielded more grain than later flowering ones, and that a high capacity of the leaves to accumulate abscisic acid was associated with increased water-use efficiency.

INTRODUCTION

Genetic limitations to cereal improvement in dry areas

By definition, the major limitation to cereal yields in dry areas is the amount of water available to the crop. At least in the short and medium term, it can be

taken that there is no prospect of irrigating cereal crops on any scale. Therefore, the question arises, given the necessary fertilizer that would be required to support increased grain and/or total dry-matter yield, would the water available to the crop permit such increased yield, i.e. could water-use efficiency be increased? Simple theory, based on the resistance analogue for cabon dioxide and water vapour fluxes into and out of individual leaves exposed to saturating light intensity (e.g. Gaastra, 1959; Jones, 1976), suggests that water-use efficiency is at a maximum when the rate of photosynthesis of a leaf is less than half its rate when not stressed (Figure 1). For crop canopies the rate of photosynthesis at which water-use efficiency is maximum is influenced by additional factors which may be susceptible to genetic modification. The resistance of the crop boundary layer to CO_2 and water vapour transport affects transpiration more than assimilation, and may vary with leaf size, leaf disposition, and canopy structure. This resistance will tend to increase water-use efficiency. Over the period of the growth of a crop, the pattern of water availability and transpirational demand will vary with the weather and with genetically determined characteristics, so affecting phenology and canopy structure, and have a 'feedback' effect on water-use efficiency.

It should be noted that the resistance analogue model is an oversimplification because it takes no account of the fact that the 'carboxylation' or 'mesophyll' resistance is influenced by water stress and that a mechanism operates to maintain C_i, the CO_2 concentration in the air spaces within the leaf, relatively invariant. This mechanism involves direct regulation of stomatal behaviour by C_i. Also, in crop canopies, and over a diurnal cycle, not all the leaves are light saturated, so photochemical steps will be limiting at times. The resistance model requires additional terms to take this into account.

The crop characteristics, as distinct from individual leaf properties which affect water-use efficiency, are individually of second-order importance in comparison to the main effect illustrated in Figure 1, and this is why for a given site and over a limited range of crop yield there is a strong correlation between the dry-matter production of a crop and water use (de Wit, 1958; Day *et al.*, 1978). To increase water-use efficiency and crop yields in drought-prone areas breeders can expect to manipulate the crop characteristics, which individually are of 'second-order' importance, more easily than stomatal and photosynthetic properties. Taking the second-order factors collectively, the scope for yield improvement may be considerable, but it will probably be location specific and may depend on achieving genetic increases in total dry-matter yield. Thus progress in breeding for higher yield in moisture-limited environments will be much more difficult than in those where moisture is not limiting.

As shown later in this paper, there may be scope for increasing water-use

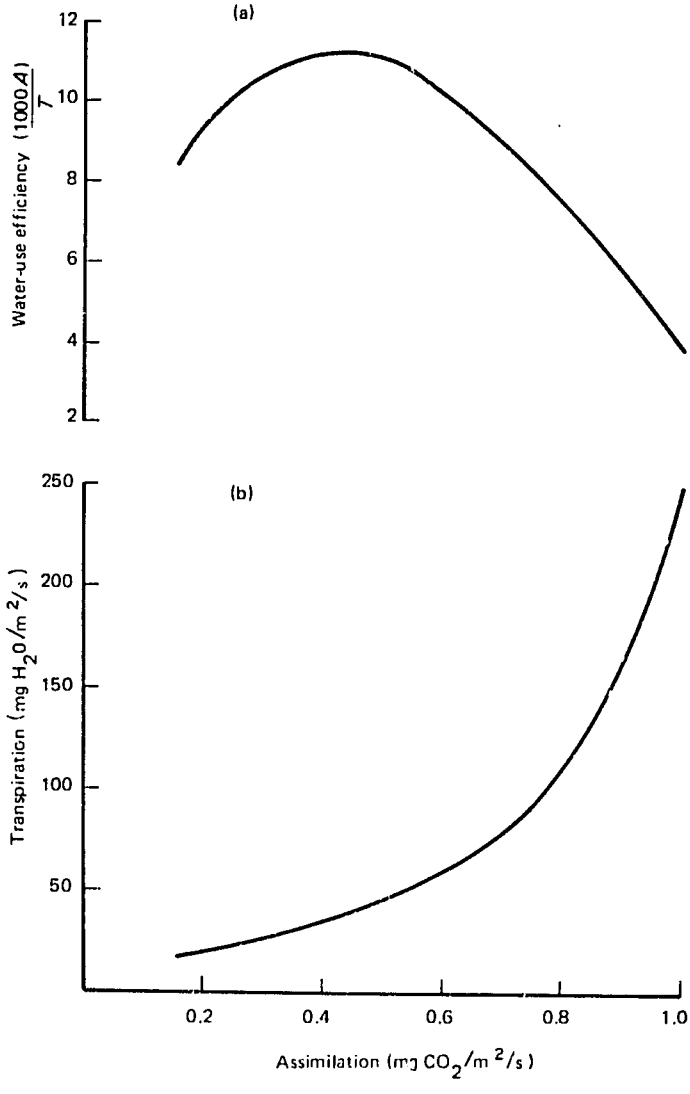


Figure 1. (a) Water-use efficiency as a function of assimilation rate. (b) Rate of transpiration (T) as a function of rate of assimilation (A). Assumptions: stomatal resistance, r_s, equal to 1.0 s/cm. where A = 1.0 mg/m^2/s and T = 250 mg/m^2/s. Cuticular resistance to water vapour transport equal to 20 s/cm. Mesophyll resistance, r_m, equal to 5 s/cm. A is proportional to $1/(r_s + r_m)$ T is proportional to the reciprocal of $1/r_s + 1/r_c$

efficiency by genetically modifying the regulation of stomatal aperture. Genetic increases in the photosynthetic capacity of individual leaves (equivalent to decreasing the r_m in Figure 1) would also increase water-use efficiency provided that there were no compensating pleiotropic effects. So far there is little evidence that this has been achieved by breeders.

As with crop production in more humid regions, increases in dry-matter production should be possible by improving cultural practices, especially by using more fertilizer. During the time that the crop is intercepting most of the incoming radiation, there should not be an increase in the water use of the crop, which is commensurate with the increased dry-matter yield which, of course, will generally be associated with increased grain yield, as agronomic practices are unlikely to reduce substantially the grain/straw ratio.

Cereal improvement in areas not subject to severe drought

In the United Kingdom, as in other countries of western Europe that do not normally experience serious drought, wheat yields have doubled since 1950 and are at present 6–7 t/ha. About half of the increase in yield has been attributed to improved varieties and half to improved cultural conditions (Silvey, 1979). Cultural factors, preeminently the increased use of fertilizer nitrogen, have increased the total amount of dry matter produced per unit area. As there has not been a systematic increase in annual rainfall over the period, nor, as far as is known, an increase in evapotranspiration commensurate with the increase in grain or total dry-matter yield, it follows that the water-use efficiency of the crop, either expressed as grain or as total dry-matter yield per unit of evapotranspiration, has increased.

Where old and new varieties of wheat and of barley have been compared in the same experiment and the complications of differential lodging and disease incidence avoided, it has been found for both crops that genetic gain in grain yield is attributable mainly to the increased grain/straw ratio of the modern varieties. Total dry-matter yields of modern English varieties are only slightly, if at all, greater than those of their predecessors (Austin *et al.*, 1980; Riggs *et al.*, 1981). Of course, past experience is not an infallible guide as to what may happen in the future, but at least it can be concluded that genetic improvements in total dry-matter yield are likely to be much more difficult to achieve than improvements in grain/straw ratios.

A logical approach to breeding cereals for dry areas

Crop simulation models are not yet sufficiently refined to be able to predict with any confidence the effects of crop characteristics on water-use efficiency. Thus, although a number of features can be identified which are likely to be of significance (Table 1), only experiments can measure the actual effect of any

given feature. Direct comparisons of a few cultivars contrasting in the expression of a given feature do not give an adequate assessment of the effects of that feature because the cultivars will vary in numerous other characteristics. If the feature of interest is governed by a major gene, it is a straightforward if tedious task to produce isogenic lines which can then be compared. When the inheritance of the feature is not known, is complex, or has low heritability, the appropriate procedure is to make crosses between contrasting cultivars and select in the F_2 and subsequent generations for the feature under investigation. This procedure gives sets of lines with low or high expression of the feature under investigation, and these *sets* (as distinct from the individual lines) will differ only in respect of the genes that control the feature and any pleiotropic effects on yield, water-use efficiency, etc. If there are any closely linked genes with effects on yield, the lines may also differ in respect of these genes.

With wheat, the plant characteristics studied at Cambridge using this approach have included tillering capacity, mature plant height, flowering date, and the capacity of droughted leaves to accumulate abscisic acid. The results of the experiments are reviewed below briefly but have been published in more detail elsewhere. It is emphasized that the work was undertaken to provide information for wheat breeders in the United Kingdom, where drought is estimated to cause an average loss in yield of 10–20 per cent. The results cannot be regarded as directly applicable to the ICARDA region, but are described to illustrate the approach being advocated.

EXPERIMENTS AND RESULTS

Tillering capacity

The number of ears produced by a crop is a yield component and, if it could be increased genetically without compensating decreases in the other components, there would be a benefit to yield. To investigate this, crosses were made between three pairs of winter wheat varieties. One member of each pair had a low (L) and the other a higher (H) number of ears at maturity. Selection for number of ears was carried out in the F_2, F_3, and F_4 generations and by the F_5 there were consistent, heritable differences between H and L lines in each cross. Four H and four L lines from each cross (24 lines in all) were grown in field experiments in 1978–9 and 1979–80. Also in 1979–80, the eight lines of the cross contrasting the most in ear number were compared in a trial which was sheltered from rain and was irrigated to produce three regimes: fully irrigated (FI); early drought (ED), in which irrigatin was withheld for the 35 days between 1 May and anthesis; and late drought (LD), in which irrigation was withheld for the 61 days from anthesis to harvest.

Table 1. Attributes which may be associated with drought tolerance in barley, correlated attributes, and their probable consequential effects. (Adapted from Austin, 1977)

Attribute	Beneficial effects in Mediterranean environment	Correlated attributes and/or consequential effect	Effect of correlated attribute/ consequential effect
Pattern of response to photoperiod and temperature which reduces duration of life cycle	Early maturity, reduced water use. Improved yield	Reduced plant size, ear size, and number	Reduced potential yield (i.e. yield when water is non-limiting)
Reduced leaf and tiller development	Reduced plant size and water use. Wasteful use of water in growth of tillers destined to die is avoided. Improved yield	Reduced ear size	Reduced potential size
Low stomatal frequency	Increased stomatal diffusion resistance and decreased transpiration	Increased stomatal pore length and maximum width. Larger leaves	Decreased stomatal diffusion resistance and increased transpiration. Increased transpiration and photosynthesis per leaf
Rapid closure of stomatal in response to stress	Reduced transpiration when plants stressed. Yield may be increased, due to increased water-use efficiency	Reduced photosynthesis when plants stressed. Need to dissipate more energy as sensible heat or by re-radiation	Reduced growth and potential yield
Low ABA concentration* throughout growth	Indicates that plant is not stressed	May indicate small plant size and so conservation of available soil water resources	May indicate low-yield potential
High ABA concentration* when water stressed	Stomatal closure, reduced transpiration. Water-use efficiency and yield may be increased	Reduced photosynthesis, leaf expansion, and ear size	May reduce yield potential where stress occurs early
High cuticular resistance to water loss	Reduced transpiration and resistance to desiccation	None known	None known

High rate of light-saturated photosynthesis	Increased water-use efficiency and grain yield	Small, narrow leaves; increased stomatal frequency and possibly decreased stomatal diffusion resistance	Reduced photosynthesis per leaf, reduced leaf boundary-layer resistance, increased transpiration per unit leaf area
Narrower leaves	Heat dissipation from crops may be increased. Reduced respiratory loss and possibly increased yields	High rate of light-saturated photosynthesis. Because boundary-layer resistances reduced, transpiration and photosynthesis may be increased	Water-use efficiency decreased because effect on transpiration is greater than effect on photosynthesis
Dwarf habit and stiff straw	Uncertain, but direct effects on heat loss, transpiration, and photosynthesis likely to be small (effects depend on wind speed)	Major height-reducing genes may have pleiotropic effects on ear size	
Absence of leaf rolling	Indicates plants not stressed, i.e. water uptake satisfies transpirational demand	Rolling reduces transpiration and photosynthesis	Uncertain
Large awns	Increased contribution by awns to grain filling; greater proportion of intercepted radiation dissipated as sensible heat. Water-use efficiency of crop after ear emergence is increased	Unkown	
High concentration of soluble carbohydrates early in grain-filling period	Increased availability of assimilate late in the grain-filling phase	Unknown but may indicate reduced ear growth rates and low-yield potential	
Large, deep root system	Increased ability to extract water from lower parts of soil profile	Decreased availabilty of assimilate for growth of shoots, including ears	
High hydraulic resistance to water transport in roots	Decreased water use during early growth, more available during later stages of growth	Unknown, but water stress in leaves may increase during periods of high irradiance	Decreased assimilation during periods of high irradiance

*The consequences of variations in ABA (abscisic acid) concentration depend on the sensitivity to ABA of the various processes it affects. These sensitivities may or may not vary independently of one another and of the tendency of leaves to accumulate ABA.

Table 2. Grain yield and related characters for high and low ear number selections, 1978–9

	High	Low	SE	H/L
Grain yield (t/ha)	8.33	7.68	0.20	1.13
Number of ears per m^2	556	445	13	1.25
Tiller survival (%)	45.3	45.0	1.1	1.01
Harvest index (%)	47.4	46.1	0.3	1.03

The results (Tables 2 and 3) show that when fully irrigated the H lines had 20 per cent more ears than the L lines and yielded 11 per cent more grain. When they experienced an early drought, more tillers died in the H than in the L lines, and the surviving ears of the H selections had less grain per ear, so the H lines gave an 8 per cent lower yield.

The late drought had, as expected, no effect on the number of ears per square metre, and so there remained a yield advantage of the H over the L lines (6 per cent, as compared to 11 per cent in the fully irrigated treatment of the same experiment). Of particular relevance to the Mediterranean areas was that the H lines had a greater biomass and water use (evapotranspiration) than the L ones, although the H lines were able to extract more water from the soil below a depth of 0.9 m than the L lines during the early drought.

The results from these experiments have been described more fully by Innes *et al.* (1981).

Table 3. Grain yield and related characters for high (H) and low (L) ear number selections, 1979–80

		Grain yield (t/ha)	Ears per m^2	Water use‡ (mm)
(a) Sheltered trial*				
Fully irrigated	H	7.41	448	372
	L	6.68	396	353
Early drought	H	5.96	365	325
	L	6.45	373	317
Late drought	H	7.24	455	280
	L	6.84	370	265
SE		0.23	23	7
(b) Irrigated trial†				
	H	6.21	—	—
	L	5.66	—	—
SE		0.19		

*Selections from one cross.
†Selections from three crosses.
‡May–July inclusive.

Mature plant height

The dwarfing genes of wheat which are insensitive to gibberellic acid, Rht1 and Rht2, are now present in many wheat varieties throughout the world. These varieties are generally called 'semi-dwarf'. Although the original motivation for using the genes was to achieve resistance to lodging in high-yielding environments, it is now established, at least for conditions prevailing in western Europe, that even in the absence of lodging the genes confer a yield advantage. While conclusive evidence from experiments is still lacking, it appears that these two genes are not advantageous in wheat grown in dry areas, or may even be detrimental. Rht3, which is allelic with Rht1 but reduces height much more, confers reduced biomass when compared with Rht1 or Rht2, and has not yet been exploited commercially. Isogenic lines of these genes and the tall control (rht) in each of three different genetic background provided ideal material for studying the effects of the genes on response to drought. As described in the previous section, the lines were compared in drilled trials and in plots sheltered from rain giving F1, ED, and LD treatments.

The results (Tables 4 and 5) show that when fully irrigated the semi-dwarf lines gave 13–15 per cent greater yields than the tall controls. They still gave greater yields than the tall controls when subject either to an early or a late drought, but their yield advantage was less (11 per cent). Looked at in

Table 4. Grain yield, harvest index and water use for semi-dwarf (Rht1 and Rht2), dwarf (Rht3), and tall (rht) isogenic lines in an experiment in 1984 which was sheltered from rain

	Semi-dwarf isolines	Dwarf isolines	Tall isolines
(a) Grain yield (t/ha)			
FI	9.20	8.43	8.00
ED	6.57	—	5.94
LD	8.27	7.18	7.48
	SE 0.24		
(b) Harvest index (%)			
FI	43	47	38
ED	39	—	33
LD	41	43	37
(c) Cumulative water use (mm)			
FI	272	272	284
ED	225	—	225
LD	190	183	202
	SE 5.4		

Table 5. Grain yield of semi-dwarf (Rht1 and Rht2), dwarf (Rht3), and tall (rht) isogenic lines in fully irrigated drilled trials

	Grain yield (t/ha)
Rht1	10.28
Rht2	10.44
Rht3	8.72
rht	9.19
SE	0.18

another way, early drought reduced the yield of the semi-dwarf lines by 29 per cent and the talls by 26 per cent; and late drought reduced the yields by 10 and 7 per cent, respectively. Whichever way these figures are considered, the semi-dwarf lines always yielded more grain than the talls in a given environment, though their yield advantage was somewhat reduced by drought. Therefore, these results do not support the view that the Rht1 or Rht2 genes are disadvantageous, at least in the kinds of drought experienced in this experiment. For any given treatment the total dry-matter yield of the semi-dwarf lines was similar to that of the tall ones. Their water use was also less, though not significantly so. This may have been an artefact of the experiment, caused by advective effects, as the tall lines would have been more exposed to the wind than the dwarf ones. As expected, the Rht3 lines yielded less than the Rht1 and Rht2 lines.

These results were obtained by my colleagues Dr P. Innes and R. D. Blackwell and the isolines were made available by Dr M. D. Gale of the Plant Breeding Institute.

Flowering date

Modern English varieties of winter wheat reach the stage of ear emergence more than two weeks sooner than the very old varieties which were grown in the nineteenth century. There has been a consistent trend to earlier flowering in wheat varieties since the last century. Early flowering is strongly correlated with reduced height but it is not known whether reduced height, in any measure, causes earlier flowering. Experiments have not yet been done to measure how much of the yield advantage of modern varieties can be attributed solely to their earlier flowering.

My colleague, Dr J. Hoogendoorn, undertook to investigate whether earlier flowering would benefit yield among modern wheat varieties. She selected for early and late flowering from the progeny of a cross between

Table 6. Mean grain yields and other characters of early and late flowering lines in irrigated, drilled trials in 1982–3

	Early	Late	SE
Grain yield (t/ha)	8.62	8.15	0.06
Day to ear emergence (Julian days)	152	159	0.2
Number of ears per m^2	516	517	11
Mean grain weight (kg)	50.0	47.2	0.6
No. of grains per ear	34.7	35.3	0.6
Harvest index (%)	48.4	46.4	0.5

Norman and an early flowering French wheat variety, Talent. The F_5 lines fell into four phenotypic classes since Norman has the Rht2 gene and Talent lacks it but has another non-allelic dwarfing gene of smaller effect. For the purpose of this account the results presented are averages over the tall and dwarf groups (there being no interaction between the effects of height and flowering date for yield). The results are given for three drilled experiments carried out during 1982–3 which were irrigated to avoid severe water stress (one on light soil at Trumpington, one on heavy soil on the same farm but with two sowing dates, and one carried out near Edinburgh), and one experiment under the plot shelters.

The results (Tables 6 and 7) showed that in the drilled trials, which experienced some stress, the early selections yielded more grain than the late ones and had heavier grains. Presumably this difference in grain weight

Table 7. Grain yield, harvest index, and water use of early and late flowering lines in sheltered experiment, 1982–3

Treatment and genotype	Grain yield (t/ha)	Harvest index (%)	Water use* (mm)
Fully irrigated			
Early	9.48	39.8	285
Late	9.29	38.4	296
Early drought			
Early	8.06	39.3	237
Late	7.80	38.9	242
Late drought			
Early	8.06	37.5	216
Late	7.07	33.6	221
SE	0.17	0.5	2.8

*May–June inclusive.

occurred because early selections partially escaped the effects of drought. This conclusion is borne out by the results of the sheltered experiment where, in the late drought treatment, early selections yielded almost 1 t/ha more grain than the late ones. When not droughted, or droughted prior to anthesis, yields of early selections were only slightly more than those of the late ones. In all cases, early selections used less water than the late ones. Although they reached ear emergence 7 days sooner than the late selections, early selections matured only 2–3 days in advance of the late ones, as indicated by the date when grain moisture had decreased by 25 per cent.

These results suggest that even in the relatively mild droughts experienced in England, earlier flowering, which does not reduce yield potential, would benefit yield when there was a terminal drought. These results have been described in detail by Innes *et al.* (1985).

Drought-induced abscisic acid accumulation

Abscisic acid (ABA) plays a central role in causing the adaptive responses of plants to drought stress. Within a few minutes of a reduction in turgor in leaf tissue, the concentration of the hormone increases, often 40 or more times the levels present in non-stressed tissue. The hormone causes stomatal closure and appears to stimulate the production of proline. It is rapidly translocated to growing parts of the plant where it reduces cell expansion, and during prolonged episodes of stress (or continued applications to non-stressed plants) causes a reduction in the final size of organs in which cell division and expansion are taking place.

To find out whether there was genetic variation in the capacity of wheat to accumulate ABA, my colleague, Dr S. A. Quarrie, developed an assay system in which leaves, grown in standardized conditions and of a fixed age and position on the plant, were rapidly desiccated and then incubated under controlled conditions which prevented further loss of water. He found that there was substantial variation in drought-induced ABA accumulation (DIAA) among spring wheat varieties (Quarrie, 1981). Subsequently this has also been found for rice, pearl millet, maize, and barley (Henson, 1983; Henson *et al.*, 1981; Pekic and Quarrie, personal communication, 1986; Arachchi, 1985). Two spring wheat genotypes adapted to UK conditions but contrasting in DIAA were crossed and the progeny selected in the F_2 and later generations for high and low DIAA. F_6 lines (20 low and 20 high) were compared in a sheltered experiment and in drilled trials.

The results from the sheltered experiment (Table 8) show that in the fully irrigated and late drought treatments the high ABA lines yielded slightly more grain than the low ABA lines. In all treatments, however, and in irrigated and unirrigated drilled trials, the water-use efficiency for grain yield was greater for H than for L lines by 0.11 t/ha/100 mm. Although not a large

Table 8. Yield, biomass, and water-use efficiency for grain yield for high and low ABA accumulating lines of spring wheat. Sheltered experiment, 1982

Treatment	Grain yield (t/ha)	Biomass (t/ha)	WUE* for grain yields (t/ha/100 mm)
Fully irrigated			
H	7.25	15.10	2.27
L	6.90	14.71	2.16
Early drought			
H	4.92	9.98	2.28
L	5.03	10.44	2.25
Late drought			
H	6.39	13.99	2.96
L	6.02	13.62	2.74
SE	0.10	0.13	0.07

*Water use from May to July inclusive.

difference, this result suggests that selection for high DIAA may be a means of increasing grain yield and water-use efficiency in Mediterranean environments. High lines accumulated 1.8 times more ABA than the low ones, and it is now known that some wheat varieties have a higher DIAA than the high lines studied here, so it may be expected that, by crossing and selecting for higher DIAA, further improvements in water-use efficiency could be achieved.

Further information on these experiments is given by Innes *et al.* (1984).

CONCLUSIONS

High-yielding varieties of wheat and barley remove more nitrogen from the soil than low-yielding ones (Austin *et al.*, 1980) and so it is unlikely that there will be a sustainable yield improvement from breeding programmes alone. There need to be matching improvements at least in fertilizer use, but probably also in other inputs. This is true for crops grown in dry areas, as well as for those in wetter ones.

Grain/straw ratios of barley varieties grown in the dry areas of the Mediterranean region (Gregory *et al.*, 1984) appear to be lower than those achieved with modern varieties of these crops grown in western Europe. In Europe, modern varieties are 70–80 cm tall and have a harvest index of 45–50 per cent. Attempts to breed shorter varieties have not so far met with success for they produce less total dry matter and do not have a greater harvest index. In dry areas, drought often restricts plant height to 70–80 cm or less so it is

questionable whether breeding for reduced height would give an increased harvest index or yield. Furthermore, with terminal droughts which vary in their time of onset, severity, and duration, varieties with high grain/straw ratios may be less stable in yield than traditional types.

If this is so, improvements in grain yield through breeding will depend on increased total dry-matter production. Experience in western Europe suggests that this will be difficult to achieve. It may be especially difficult at low yield levels, where full canopy closure, if it occurs, lasts only for a short period, because under these conditions biomass is likely to be proportional to water use. Some crop characteristics which may confer the capacity to produce increased dry-matter yields are listed in Table 1.

There may be scope for modifying the timing of the life cycle to achieve greater grain yields. Earlier flowering would permit grain filling to occur in cooler conditions when the crop is likely to be less water stressed. The reduced potential yield which may be associated with earlier flowering might be avoided if co-selection for early vigour was practised.

It may be possible to increase water-use efficiency by selecting for high capacity to accumulate the hormone abscisic acid. In addition, more efficient photosynthesis, i.e. greater quantum yield and increased light saturated rate of photosynthesis per unit leaf area, would confer increased water-use efficiency. Variation in these measures of photosynthesis is known among wheat species (Evans and Dunstone, 1970) and among wild diploid forms of *H. spontaneum* (unpublished data), and it may be possible to transfer the features to cultivated barley and hexaploid wheat, so achieving increases in water-use efficiency and yield.

Evidence from studies in other environments and predictions from crop models are not a substitute for the systematic evaluation of the significance of individual plant characteristics for water use and yield. Four examples of the process of 'character evaluation' are described in this paper. These examples show there is scope for improving water-use efficiency by breeding. It is suggested that character evaluation is the only satisfactory way to provide breeders with definitive crop ideotypes.

Finally, perhaps because planners and scientists perceive that most progress can be made in improving yield in favourable environments, relatively little effort has been devoted to crop improvement for dry areas. Yet, because of the greater variability of the environment in dry areas, the heritability of yield is certain to be lower than in more favourable environments. As a consequence, for a given percentage improvement of yield to be achieved by empirical selection, more effort is needed in dry than in wetter areas. If this were recognized and more resources committed to breeding and the relevant science, I would be optimistic about the progress that could be achieved.

REFERENCES

Arachchi, D. M. 1985. Abscisic acid and drought resistance in barley. M. Phil. thesis. University of Cambridge, England.

Austin, R. B. 1977. Improvement of barley for dryland farming. Pages 12–27 in *Proceedings of a Symposium on Plant Improvement for Arid Zones*, Ahwaz, Iran.

Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. L. and Taylor, M. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci., Camb.* **94**:675–689.

Day, W., Legg, B. J., French, B. K., Johnston, A. E., Lawlor, D. W. and Jeffers, W. de C. 1978. A drought experiment using mobile plot shelters: the effect of drought on barley yield, water use and nutrient uptake. *J. Agric. Sci., Camb.* **91**:599–623.

de Wit, C. T. 1958. Transpiration and crop yields. *Versl. Landbouwk. Onderz.* **64**:6.

Evans, L. T. and Dunstone, R. L. 1970. Some physiological aspects of evolution in wheat. *Aust. J. Biol. Sci.* **23**:725–741.

Gaastra, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. *Meded. Landbouwhogeschool, Wageningen* **59**(13):1–68.

Gregory, P. J., Shepherd, K. D. and Cooper, P. J. 1984. Effects of fertilizer on root growth and water use of barley in northern Syria. *J. Agric. Sci., Camb.* **103**:429–438.

Henson, I. E. 1983. Abscisic acid accumulation in detached leaves of rice (*Oryza sativa* L.) in response to water stress: a correlation with leaf size. *Ann. Bot.* **52**:385–398.

Henson, I. E., Mahalakshmi, V., Bidinger, F. R. and Algarswamy, G. 1981. Genotypic variation in pearl millet (*Pennisetum americanum* [L.] Leeke) in the ability to accumulate abscisic acid in response to water stress. *J. Exp. Bot.* **32**:899–910.

Innes, P., Blackwell, R. D., Austin, R. B. and Ford, M. A. 1981. The effects of selection for number of ears on the yields and water economy of winter wheat. *J. Agric. Sci., Camb.* **97**:523–532.

Innes, P., Blackwell, R. D. and Quarrie, S. A. 1984. Some effects of genetic variation in drought induced abscisic acid accumulation on the yield and water use of spring wheat. *J. Agric. Sci., Camb.* **102**:341–351.

Innes, P., Hoogendoorn, J. and Blackwell, R. D. 1985. Effects of differences in date of ear emergence and height on yield of winter wheat. *J. Agric. Sci., Camb.* **105**:543–549.

Jones, H. G. 1976. Crop characteristics and the ratio between assimilation and transpiration. *J. Appl. Ecol.* **13**:605–622.

Quarrie, S. A. 1981. Genetic variability and heritability of drought-induced abscisic acid accumulation in spring wheat. *Plant, Cell and Environ.* **4**:147–152.

Riggs, T. J., Hanson, P. R., Start, N. D., Miles, D. M., Morgan, C. L. and Ford, M. A. 1981. Comparison of spring barley varieties grown in England and Wales between 1880 and 1980. *J. Agric. Sci., Camb.* **97**:599–610.

Silvey, V. 1979. The contribution of new varieties to increasing cereal yields in England and Wales. *J. Nat. Inst. Agric. Bot.* **14**:367–384.

DISCUSSION

E. Smith

With modern wheats in England yielding 11.3 t/ha, has there been any change in number of spikes per square metre and in leaf carriage and patterns as compared to old ones?

R. B. Austin

There are more grains (more ears) per square metre; the duration of the grain-filling period is about the same; no consistent patterns in leaf size, shape, or arrangement are evident.

S. K. Sinha

The present increase in yield has occurred because of an improvement in harvest index, as you rightly say. If an increase in the rate of photosynthesis is achieved, how would the additional dry matter, in terms of yield component, be effective in increasing yield? Where do you think it would be best to put it, considering the aspects of competition?

R. B. Austin

Increased 'photosynthetic efficiency' of individual leaves, if expressed at the crop level in terms of more rapid growth, would benefit yield only if there were suitable adjustments in crop morphology and phenology. Exploited in this way, it should increase yield and water-use efficiency.

N. C. Turner

Have your high and low abscisic lines been tested in low-input Mediterranean environments?

R. B. Austin

No, we have recently sent grain samples to Canberra for testing. However, they are English spring wheats and may not be well adapted to Australian conditions.

A. Hadjichristodoulou

Your finding that late drought affects the yield of late varieties more than that of early varieties is common experience in our dry regions. In these areas the timing of late drought is not predictable and not controlled as in your trials. Do you wish to comment on the next steps to be taken in order to increase yields and improve stability of performance?

R. B. Austin

I agree that our finding is consistent with common experience. I gave my example to illustrate the approach which needs to be followed to determine the optimum flowering date for a given locality (zone). Of course, the optimum will vary with year, so trials over several years will be needed to determine the best compromise.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

26

*Use of Water Balance Terms in Breeding for Drought Resistance—The Upland Rice Case**

R. N. REYNIERS
La Zolad, Batiment 7, 34100 Montpellier, France

SUMMARY

Rice, which is a staple diet in the tropics, is grown mainly in upland conditions in Brazil, with 5.5m ha, and in West Africa, with 1.4m ha. For about 12 years, the improvement in drought tolerance of upland rice varieties has been the subject of research in several institutions: IRAT, EMBRAPA, IDESSA, IRRI, etc. It is important to examine the results and the problems encountered and to propose 'research for the medium term'.

For varietal improvement, selection is made either directly, in functions of drought tolerance, defined by production capacity in drought conditions, or indirectly, according to tolerance factors grouped in functions of their mode of action, e.g. maintaining a favourable water state and control of the elaboration processes of yield adapted to periods of drought.

Direct selection compares varieties at several similar phenological stages during drought. This has enabled IRAT to select and create varieties adapted to drought conditions in West Africa. The results of multilocation trials organized in networks make it possible to select tolerant varieties. At present, direct selection is still the most efficient method.

Indirect selection involves the identification of tolerance factors, screening for the variability for the traits, and incorporation of those traits in a single genotype.

*Full text not received.

Root characteristics, particularly the root depth, stomatic regulation, cuticular resistance, leaf rolling, and osmotic adjustment, are the principal known factors in the water control of upland rice. The leaf area, stomatic regulation, tillering dynamics, distribution of photosynthates, and growth cycle length are the characteristics determining yield and the effect of droughts. Some factors linked to the developmental processes of the reproductive organs and to mineral nutrition in poor soils are not yet well known but could be important.

The tolerance factors, such as root depth, growth cycle length, and stomatic resistance, have been screened for a sufficient number of varieties to make a rough estimation for genetic variability. However, little information is available on screening of segregating generations. These factors are difficult to screen for large populations.

The final stage of accumulation of factors has not really been carried out. It poses practical and theoretical problems. In fact these factors have a cost in productivity, as emphasized by some authors, and the more traits we add the more the productivity will fall. Moreover, their effects are sometimes contradictory, depending on the modalities of the drought.

In view of these difficulties, another avenue is now being explored at the CNPAF.

The first stage consisted of evaluating for each region whether the drought risk could be reduced by the combined choice of sowing date, growth cycle length, and rooting, which are basic agronomic factors. The methodology consists of calculating the satisfaction rate of water requirements (ET_r/ET_m) for the different phases of development by varying the factors indicated. This calculation is carried out by a microcomputer file simulating the water balance, which has been perfected by IRAT. The first results show that for realistic values of these factors, in very vast regions, there may be up to 80 per cent satisfaction of water requirements for the whole cycle, making possible a production expectation of 3 t/ha on fertile soils.

The second stage aims at helping producers attain these optimum values. In the third stage, areas are selected where, even with an optimum combination of these factors, the satisfaction rates of water requirements remain inadequate and where the main drought problem occurs at the productive stage. Here, direct selection is used.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

27

Maize in the Mediterranean Cropping System—Modifying Its Growth to Combat Drought

R. KENT CROOKSTON* and SAID OUATTAR†
**Agronomy Department, University of Minnesota, St Paul, Minnesota 55108, USA; †Institut Agronomique et Veterinaire Hassan II, BP 6202, Rabat, Morocco*

ABSTRACT

Rainfed maize grown in Mediterranean climates suffers from water stress as rainfall ceases and soil moisture reserves are drawn down during grain filling. Researchers have hypothesized that a reduction of early vegetative growth might save soil moisture for maize that would alleviate the effects of the late-season drought. We conducted two studies to test this hypothesis. In both studies, maize was completely defoliated at an early growth stage to reduce its vegetative growth and final production of leaf area. In one study (conducted in the United States), the amount of water provided to the plants was controlled. In the other (conducted in Morocco), the crop relied on the natural rainfall pattern characteristic of the Mediterranean area. Early defoliation helped in soil moisture conservation which benefited grain yield in severe moisture-stress conditions. We do not recommend defoliation as a production practice, but suggest that restricted early vegetative growth be investigated further as a means of improving grain yields of maize in Mediterranean environments.

INTRODUCTION

Maize is becoming an increasingly important component of the rainfed Mediterranean cropping system. The grain is prized as human food, the stover serves as premium cattle feed, and the crop is valuable for rotating with small grain crops, especially when a 'clean-up' crop is needed because of weeds.

Unlike small grain crops, maize is sown at the end rather than at the beginning of the rainy Mediterranean winter season. This leads to frequent water stress problems for at least two reasons. First, the overall crop cycle is shifted towards summer, or into a period of greater heat and water stress. Second, growth conditions during the warm early season favour vigorous vegetative growth. This leads to a rapid depletion of soil moisture, with a resulting shortage of water during grain filling.

Results from studies in the U.S. corn belt suggested that a deliberate reduction of the early vegetative growth of maize might help to conserve soil moisture early in the Mediterranean season, so that more moisture would be available to the crop during grain filling. Crookston and Hicks (1978) reported that early defoliation of maize led to grain yield increases in low-yielding situations. They also observed, as did others, that under high-yielding conditions early defoliation reduced grain yields (Crockett and Crookston, 1980; Crookston and Hicks, 1978; Ferris, 1979; Jeppson and Crookston, 1986; Johnson, 1978). Crookston and Hicks (1981, 1986) reasoned that early defoliation and the resulting reduction of upper plant mass led to an early saving of soil moisture that proved to be advantageous when water stress occurred during grain filling. The same reduction of early plant mass appeared to be a disadvantage in years when plenty of moisture was available during grain filling. They hypothesized that early defoliation of maize might be a profitable production practice in areas where soil moisture is adequate for the crop early in the season, but becomes limiting during grain filling.

We conducted two studies to test this hypothesis. In the first (bucket study) we grew maize in plastic buckets and defoliated half of them at an early growth stage. The objective was to see if defoliation actually resulted in soil moisture savings, and if these savings could be translated into improved grain yields. In the second (field study) we grew and defoliated maize in Morocco in a Mediterranean climate. The two studies are presented and discussed separately.

MATERIALS AND METHODS (BUCKET STUDY)

The maize hybrid 'Trojan TXS 85' was grown in plastic buckets (Volume of 19 liters) which were placed in the field at St Paul, Minnesota, in 1980. Soil water status was monitored daily by tensiometers positioned in the buckets prior to planting, one each at a depth of 30 and 60 cm. The soil in the containers tested at an equivalent of 200:222:670 kg/ha of N:P:K.

Plants were defoliated when they had grown to the five-leaf stage, by cutting the pseudo-stalk (whorl of leaves) with a razor blade at the collar of the second leaf. Treatments were imposed in pairs. A set of defoliated and a matching set of non-defoliated plants were maintained on each of two

identical watering regimes. The first set was placed on its regime immediately after defoliation. The defoliated plants were provided enough water to maintain the soil in their buckets at or above −0.3 bars. The matching set of non-defoliated plants was given the same amount of water as the defoliated plants. All plants in the second set were provided with sufficient water to maintain the soil in their buckets at or above −0.3 bars up until just after pollination. They were then placed on their regime. The non-defoliated plants were again given the same amount of water as the defoliated plants. There were four replications of each treatment set. The experimental design was a randomized complete block.

Results (bucket study)

As expected, defoliated plants withdrew less water from the soil than their non-defoliated counterparts. When the regime was initiated at the five-leaf stage, soil moisture began to decline under the non-defoliated plants within five days (Figure 1) and within 20 days it was 0.4 bars lower than that of the soil under defoliated plants. The accompanying stress was apparently of such a magnitude that growth was reduced or arrested. The defoliated plants thus 'caught up' with the non-defoliated plants, in terms of growth and water

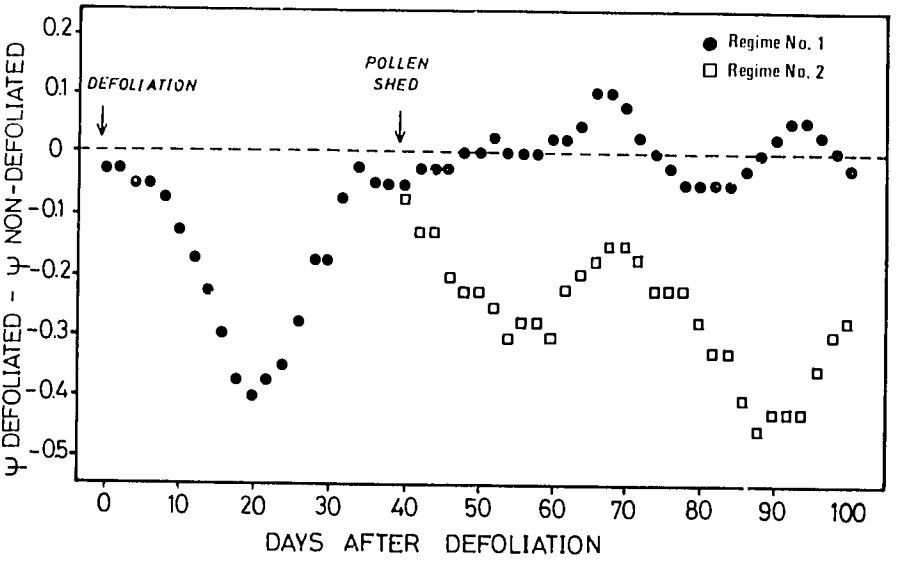


Figure 1. Difference in water potential (ψ = bars) of soil in which defoliated and non-defoliated maize plants were growing. Both plants were provided with the same soil volume and the same amount of water. The water was limited to the 'needs' (see text) of the defoliated plant starting the day after defoliation (regime 1) or the day after pollen shed (regime 2)

Table 1. Yield and yield components of defoliated and non-defoliated maize plants grown in plastic buckets on limited amounts of water. The water was limited to the 'needs' (see text) of the defoliated plants, commencing immediately after defoliation at the five-leaf stage (5LS) or after pollination (P) (compare to Figure 1)

Treatment	Water regime started	Yield of Grain (g/plant)	Yield of Stover (g/plant)	Harvest index	Kernel number	Kernel weight (mg/kernel)
Defoliation	5LS	83 bc	170 b	0.49 ab	381 a	218 ns
Non-defoliation	5LS	72 c	154 b	0.47 b	356 b	274 ns
Defoliation	P	109 a	199 a	0.55 a	343 a	306 ns
Non-defoliation	P	97 ab	198 a	0.49 ab	362 a	258 ns

Values not followed by the same letter in a column are significantly different at the 5 per cent level of probability according to Duncan's multiple range test.

consumption, and 35 days after commencement of the regime both defoliated and non-defoliated plants were using equal amounts of water. The brief period of stress experienced by the non-defoliated plants results in a significant reduction of kernel number per plant (Table 1). Defoliated plants tended to have higher grain yields (14 per cent) and a higher biomass (10 per cent), but these differences were not significant.

When the regime was postponed until after pollination, soil moisture under the non-defoliated plants began to decline immediately (Figure 1), and within 15 days it was approximately 0.3 bars lower than that under the non-defoliated plants. There was apparently no water-use adjustment as occurred with the earlier regime. The defoliated plants again tended to yield more (12 per cent) but the difference was not significant. Stover weight was unaffected (Table 1).

Thus, we were able to confirm that defoliation did result in less water consumption, but did not demonstrate that this had any significant effect on yield. We were not able to draw conclusions regarding a true field situation, however. The limited soil volume within the buckets led to rapid growth compensations unlikely in the field, and we knew that field water supplies would not always match the 'needs' of defoliated plants. We therefore conducted field trials in Morocco where we expected seasonal climate and soil moisture patterns to allow a better evaluation of early defoliation.

MATERIALS AND METHODS (FIELD STUDY)

The field study was conducted during 1982 and 1983 on a clay-loam soil in the Settat area of Morocco. The previous year's crop was wheat. Prior to planting, plots received 90:100:100 kg/ha of N:P:K. Weeds were controlled

by hand. Two local cultivars 'Dra 400' and 'Berrechid' were grown. Plots were overp'anted, during February, and later thinned to a uniform stand density of 53,000 plants per hectare. A randomized complete block design was used in both years. Cultivars served as main plots and treatments as subplots. The first treatment was a check and the second consisted of complete defoliation at the five-leaf stage (as in the bucket study).

In 1982 the soil moisture at defoliation time was adequate for good growth. In 1983 the soil was rather dry at defoliation time. We therefore duplicated the entire experiment in 1983. For one duplicate, the plot area was flood irrigated after defoliation to assure good recovery. The other duplicate received only natural rainfall, which was minimal. In other words, there were three environments in our two-year study (Figure 2).

Plots consisted of 14 rows, each 7 m long, spaced 75 cm apart. The four centre rows were saved for yield (grain and stover) determinations. In 1982, soil moisture was determined gravimetrically at 20 cm intervals to a depth of 1 m until silking. The measurement of soil moisture at harvest was impossible

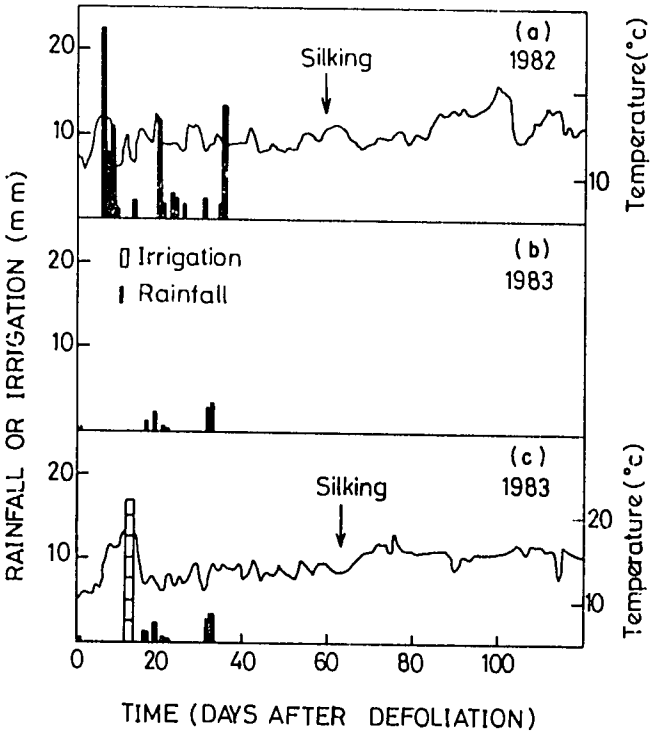


Figure 2. Rainfall and/or irrigation received, and average daily temperature during the field experiments

and we gave up trying to take soil cores after two sample probes were broken. In 1983, a neutron probe was used to monitor soil moisture. Evapotranspiration was calculated from soil water measurements and rainfall data using the classical water balance over each considered period. Water drainage and runoff were assumed to be negligible. Soil moisture values at −15 bars were determined with a pressure plate.

Results (field study)

Defoliation caused about a 10-day delay in leaf area expansion and reduced the final leaf area index by an average of 30 per cent (Figure 3). This is in agreement with the results of others (Crockett and Crookston, 1980; Hsu and Yeh, 1978; Johnson, 1978), who found that early defoliation of maize reduced the final leaf area by 21 to 42 per cent.

There was a close association ($r^2 = 0.67$, $P < 0.01$) between the leaf area index and evapotranspiration. As leaves grew and evapotranspiration increased, soil water reserves beneath control plants were drawn down at a

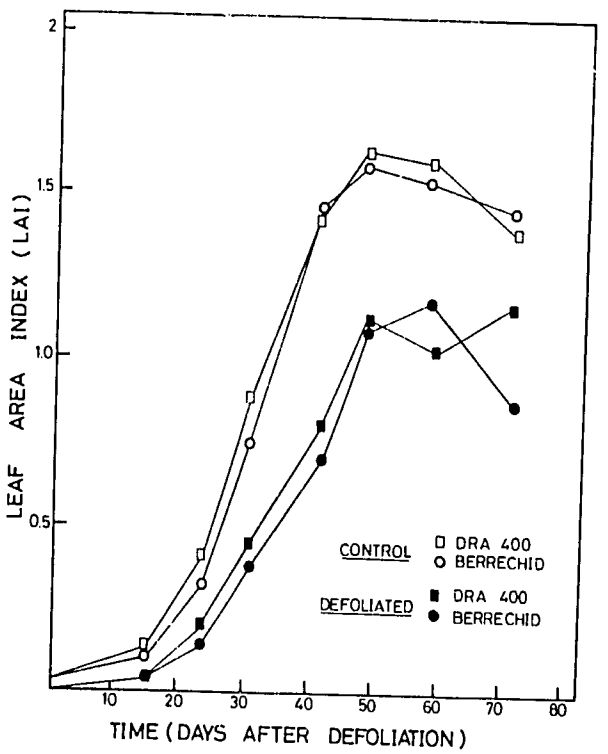


Figure 3. The effect of early defoliation on the leaf area development of the two maize cultivars in 1982

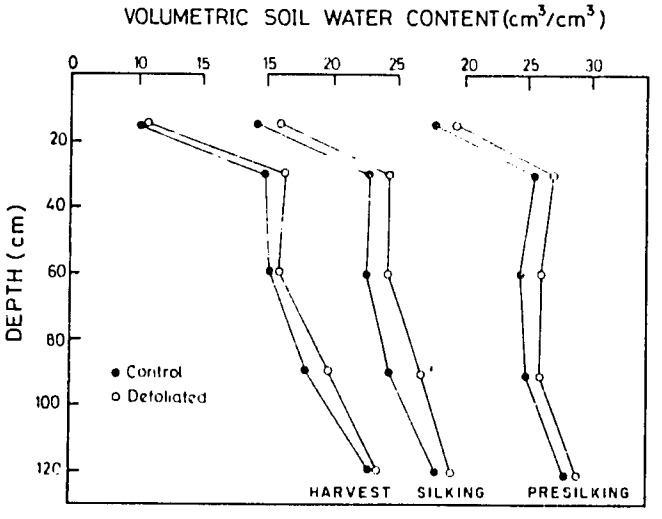


Figure 4. Soil-moisture profiles under control and defoliated maize sampled three times during the 1982 season (environment B)

Table 2. Effect of early defoliation on grain yield, biomass, and harvest index of maize grown under rainfed conditions at Settat, Morocco, in 1982 and 1983. See text and Figure 2 for explanation of environments

Environment	Cultivar	Treatment	Yield of Grain (kg/ha)	Yield of Biomass (kg/ha)	Harvest index
A	Berrechid	Control	91	590	0.17
		Defoliation	121	470	0.25
	DRA 400	Control	210	610	0.29
		Defoliation	183	480	0.36
B	Berrechid	Control	33	340	0.10
		Defoliation	63*	400	0.16
	DRA 400	Control	57	380	0.15
		Defoliation	114*	410	0.28*
C	Berrechid	Control	47	560	0.09
		Defoliation	94*	530	0.18
	DRA 400	Control	141	640	0.22
		Defoliation	153	540	0.28

*Indicates significant difference between control and defoliation (0.05 level of probability).

faster rate than beneath defoliated plants. By silking in 1983, defoliated plots contained an average of 18 mm more soil water than the control plots (Figure 4). This represents substantial water savings, considering the amount of rainfall received during the 1983 season (Figure 2).

The grain yields obtained in this study were very low (mean of 109 kg/ha for control plots). That any grain yield was obtained at all might be regarded as remarkable considering the low amount of rainfall received at the research site during these two years. In 1982, the total rainfall was 161 mm (84 mm after defoliation). In 1983, the total rainfall was 145 mm (12 mm after defoliation).

The effect of defoliation on grain yield was highly dependent on the circumstances. When control yields were below the study mean of 109 kg/ha, defoliation increased yields by an average of 70 per cent (changes usually significant, Table 2). When control yields were above the study mean of 109 kg/ha, defoliation decreased yields by an average of 4 per cent (changes non-significant, Table 2). Thus, there was a strong negative correlation between the control yield level and yield increase following defoliation (Figure 5). A similar trend was observed by Crookston and Hicks (1986), even though the average control yield of their study was 770 kg/ha. Defoliation reduced biomass yield by an average of 9 per cent, but in no case was the effect of defoliation on biomass yield significant (Table 2).

With grain yields increased or unchanged and with biomass yields slightly reduced, there was a consistent upwards shift in the harvest index following

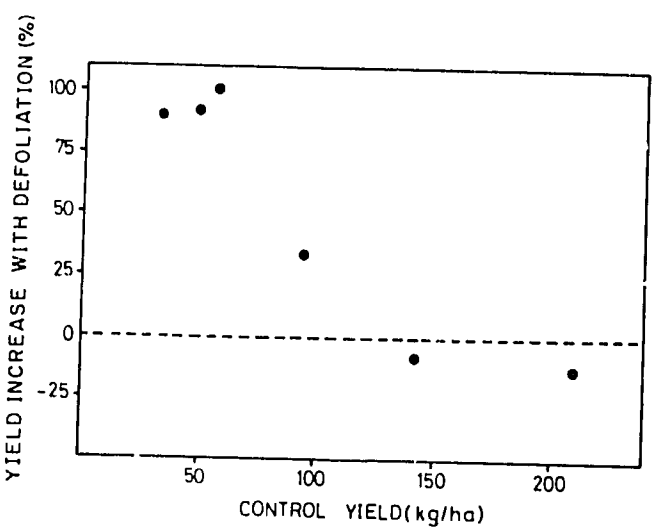


Figure 5. Relationship between level of control yield and relative change in yield following defoliation

defoliation. The average increase in the harvest index was approximately 47 per cent, but individual increases were significant only once. The tendency for the harvest index to be increased following defoliation confirms other reports (Crockett and Crookston, 1980; Ferris, 1979; Jeppson and Crookston, 1986) that early defoliation of maize alters the lifelong pattern of dry-matter partitioning in favour of grain development.

The results of our Moroccan studies with maize are not unlike studies conducted with wheat in the Mediterranean climate areas of Australia. Passioura (1976), Islam and Sedgley (1981), and Richards (1983) demonstrated that wheat made more efficient use of water and yielded better when vegetative growth and/or early water use were reduced.

CONCLUSIONS

We conclude, from our two studies, that early defoliation of maize can result in soil water conservation, and that such conservation can be beneficial to grain yield under moisture-stressed conditions. The increase in the harvest index following defoliation is a growth response which definitely warrants further investigation.

We recommend that restricted early vegetative growth be investigated further as a means of improving grain yields of corn grown in Mediterranean environments. Mechanical defoliation provides a simple experimental technique for evaluating the influence of plant design on water use and yields. We would not recommend defoliation as necessarily the best experimental technique to evaluate growth modification in drought-stressed areas, however. Defoliation is likely to alter root growth which could restrict extraction of available soil water. In a few cases, Crookston and Hicks (1981) found that defoliation resulted in plant death. The development of genetically modified plants or the use of chemical growth suppressants would be likely to offer more opportunities to search for optimum growth modification and improved yields in semi-arid zones where maize will continue to be an important component of the cropping system.

REFERENCES

Crockett, R. P. and Crookston, R. K. 1980. Accounting for increases in the harvest index of sweet corn following early leaf clipping. *J. Am. Soc. Hort. Sci.* **106**:117–120.

Crookston, R. K. and Hicks, D. R. 1978. Early defoliation affects corn grain yields. *Crop Sci.* **18**:485–489.

Crookston, R. K. and Hicks, D. R. 1981. Don't cut corn early. *Crops and Soils* **33**(6):11–14.

Crookston, R. K. and Hicks, D. R. 1986. A second look at the effect of early defoliation on maize yields—an eleven year perspective. *Crop Sci.* In press.

Ferris, R. S. 1979. Influence of genotype and environment on response to early growth-stage defoliation in maize. Ph.D. thesis. University of Minnesota, St Paul.

Hsu, F. H. and Yeh, M. T. 1978. Effects of early defoliation on the agronomic characters and the grain yield of corn. (*Zea Mays* L.). *J. Agric. Ass. China (Taiwan)* **102**:48–58.

Islam, T. M. T. and Sedgley, R. N. 1981. Evidence for a 'uniculm effect' in spring wheat (*Triticum aestivum* L.) in a Mediterranean environment. *Euphytica* **30**:277–282.

Jeppson, R. J. and Crookston, R. K. 1986. Effect of elevated growing-point temperature on maize growth and yield. *Crop Sci.* In press.

Johnson, R. R. 1978. Growth and yield of maize as affected by early-season defoliation. *Agron. J.* **70**:995–998.

Passioura, J. B. 1976. Physiology of grain yield in wheat growing on stored water. *Aust. J. Plant Physiol.* **3**:559–565.

Richards, R. A. 1983. Manipulation of leaf area and its effect on grain yield in droughted wheat. *Aust. J. Agric. Res.* **34**:23–31.

DISCUSSION

A. Hadjichristodoulou

You showed that under stress conditions defoliation at early growth stages increases grain yield of corn. In the Mediterranean countries barley and wheat are grazed at the tillering stage and then harvested for grain. Our studies and those of others show a reduction in grain yield of winter cereals after grazing. I have a feeling that this effect will be more drastic in winter cereals under moisture stress than under more favourable conditions. The experience, thus, with winter cereals is in disagreement with your findings in corn. Do you have any comment on this?

R. K. Crookston

I agree with your 'guess' that small yields would be hurt by early defoliation followed by stress during grain filling. Perhaps the most relevant difference between corn and small grain is that corn cannot compensate by producing more or fewer tillers. The within-the-main-stem compensation of corn apparently provides for a rather unique response.

D. Lawlor

There is evidence in barley and wheat that stresses, such as low nitrogen or water deficits during vegetative growth, decrease the production of tillers, stem, and leaf material but do not affect the growth of reproductive organs, so that the harvest index and often yields are increased.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

28

Drought Resistance in Crop Plants: A Critical Physiological and Biochemical Assessment

S. K. SINHA
Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012, India

ABSTRACT

This review attempts to define drought and drought resistance, analysis of yield of crops, and the effects of water deficit on growth and yield. Several plant processes which occur in time scales ranging from seconds to minutes, hours, days, and months culminate in crop yield under field conditions in a competitive environment. While the importance of short-term responses cannot be denied, their correlation with yield is difficult to expect. It is for this reason that many individual tests have not been found of wider application in selection for drought resistance. A wholistic view of plant growth development and yield components in relation to environment, particularly water availability, is discussed.

The following criteria are suggested for selecting physiologically superior genotypes to conform to the wholistic approach: (1) seedling vigour in *kharif* (rainy season) and slow aerial seedling growth in *rabi* (winter season); (2) canopy temperature lower than the ambient temperature when crop canopy is formed is desirable; (3) assessment of total dry-matter production in relation to soil moisture depletion; and (4) medium capacity of yield components.

INTRODUCTION

Drought is the most common adverse environmental factor limiting crop production in different parts of the world. Drought is often accompanied by relatively high temperatures, which promote evapotranspiration and hence

accentuate its effects, leading to reduced crop yields. Consequently, breeding for drought resistance is a major objective of many research programmes in international and national institutions. This has been so for the past several decades. However, to our disappointment, there has not been any identifiable and measurable success in these programmes, when we compare them with such objectives as 'breeding for yield', 'breeding for disease resistance', and 'breeding for quality'. In fact, this disappointment was sadly expressed by Arnon (1980) when he stated, 'Breeding for drought resistance has been a consistent theme for as long as I remember and probably the greatest source of wasted breeding effort in the whole field of plant breeding.' However, the fact remains that we do hear of drought-resistant varieties in many crops. For example, C306 in wheat, Lalnakanda in rice, and M35-1 in sorghum are some of the better-known examples in India. It is also claimed that a large number of cultures among the Assam Rice Collection exhibit a considerable degree of drought tolerance. Many landraces and wild relatives of several crop species are said to carry drought-resistant genes or traits, which could be utilized profitably in breeding programmes.

Before developing a new strategy it is always good to assess the state-of-the-art in the concerned area. The following questionnaire was prepared and distributed to 75 distinguished plant breeders and plant physiologists in India and abroad to assess the present situation of drought-resistant varieties:

Questionnaire

Name of crop; variety or varieties identified/recognized as drought resistant; duration of these varieties (seedling to maturity) in comparison with other popular high-yielding varieties; yield in a good rainfall and in a drought year; any special morphological or physiological characteristics of the resistant variety; water use in comparison with susceptible varieties; was the variety specifically bred for drought resistance or was it a selection from the existing types?; is there any variety that has been produced specifically fo drought resistance through hybridization?

Many scientists from India and abroad responded to the questionnaire. The following is a summary of their responses:

(1) Some varieties of wheat, barley, sorghum, oats, and rice are recognized as dr. ught resistant.

(2) Most varieties are of medium or long duration. In sorghum, the hybrid CSH-6 is of short duration, but it escapes the drought period. It is not successful in *rabi* (winter season, see below), when the crop actually experiences drought. Under such conditions an average yielding variety M35-1 is most stable, and hence is considered drought resistant.

(3) In good rainfall years, the varieties recognized as drought resistant do not take sufficient advantage of the available water. The average yield is between 2.5 and 3.0 t/ha and is reduced to 1.0 t/ha or less in drought years.

(4) Some wheat varieties, such as Olympia in Australia, have early vigour, whereas others, such as C306 in India, have slow vegetative growth in the initial stages, and they also have a good tillering habit.

(5) The drought-resistant varieties use as much as or more water than susceptible types, such as Olympia and C306 in wheat and Lalnakanda in rice.

(6) Most of these varieties are local selections, or selections from other breeding programmes, which were not meant for 'drought resistance'.

(7) No one claimed to know any variety produced through a hybridization programme on breeding for drought resistance. It was stated that such varieties are in the process of development. For such varieties, the upper limit of yield in rice would be 4 t/ha in good years and 1.5–2.0 t/ha in bad years.

The above information raises the question of why success in breeding for drought resistance has not been comparable to breeding for disease resistance and other characteristics. Have we failed in defining our objectives? Aristotle said, 'This is the alpha and omega of logic, the heart and soul of it, that every important term in serious discourse shall be subjected to the strictest scrutiny and definition. It is difficult, and ruthless, but tests the mind, but once done it is half of any task' (Durant, 1953). The same point was emphasized by Voltaire, an eighteenth century French philosopher, when he said, 'If you wish to converse with me, define your terms.'

DEFINING DROUGHT AND DROUGHT RESISTANCE

There are a large number of definitions of drought resistance, depending upon who defines it: a molecular biologist, a biochemist, a plant physiologist, an agronomist, or a plant breeder. However, the assessment of a farmer for drought resistance is on the basis of economic returns or on his own survival when crops fail to grow to maturity.

Gotoh *et al.* (1979) stated, 'Breeding crop plants for drought-prone conditions requires an appreciation and knowledge of the environmental factors which interact with rainfall deficits to create the array of complexes collectively referred to as "drought". The variability (across and within seasons) and range of these salient environmental factors are extremely location-specific.' Thus it is being increasingly realized that 'drought' from the point of view of a crop is the state when an adequate amount of water, in quantity and distribution, is not available to allow the crop to express its full genetic yield potential. Since the availability of water during the whole plant life is not determined by rainfall alone, but is also dependent on soil characteristics and evaporative demand, the intensity and duration of drought become highly location specific. The pattern of rainfall distribution adds to the uncertainty of stage specificity for experiencing drought. Therefore, in India, where most of the rainfall is received between late June and early September, the concept of

drought is different for *kharif* (monsoon season) and *rabi* (winter season) crops. Accordingly, the concept and magnitude of drought in Europe or the Mediterranean region will be different from the Indian subcontinent. The experience of the past, particularly of precipitation, temperature, and evapotranspiration, could serve as a guide, but cannot be entirely dependable because on the basis of the past 30–50 years of meteorological data no individual year could be classed as a 'normal' year. These records, however, may help in defining the nature of drought at different locations. Thus, a working definition of drought would be water availability, including precipitation and soil moisture capacity, in quantity and distribution during the life cycle of the crop, inadequate for realization of its full yield potential.

An important approach to assessing the drought resistance of a variety is by determining the stability index following the methods of Finlay and Wilkinson (1963) and Eberhart and Russell (1966). In these methods a large number of varieties are grown in a range of environments differing in water availability. The variety that shows maximum stability is considered drought resistant, the criterion of stability being the grain yield. Sinha *et al* (1986) estimated the stability index of seventeen cultures, which included some well-known varieties, belonging to *Triticum aestivum*, *T. durum*, and triticale. Among *T. aestivum*, C306 exhibited better stability and was followed by HD2009 as against Moti, which had the poorest stability (Figures 1 and 2). Thus, at the

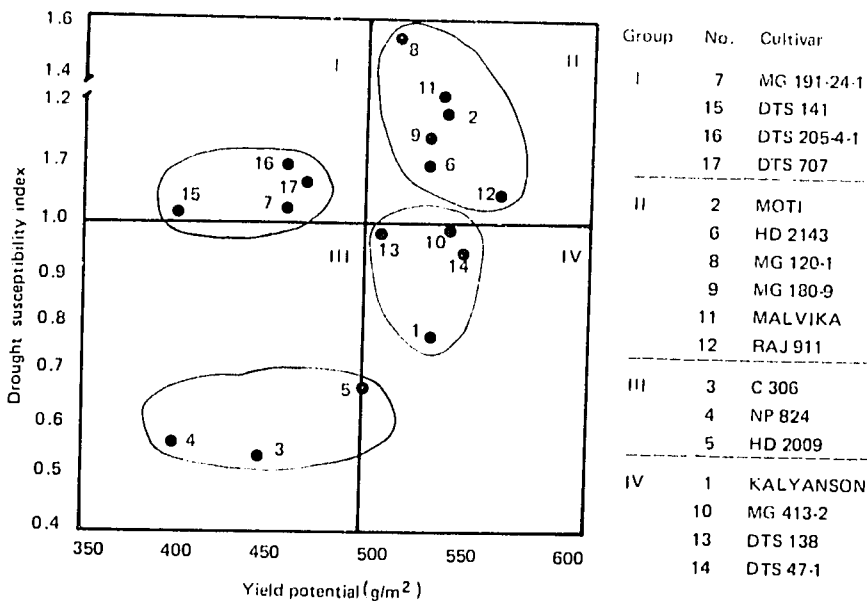


Figure 1. Relationship of yield potential with drought susceptibility index. Genotypes: *Triticum aestivum*, 1, 2, 3, 4, 5, 6; *T. durum*, 7, 8, 9, 10, 11, 12; *T. triticale*, 13, 14, 15, 16, 17.

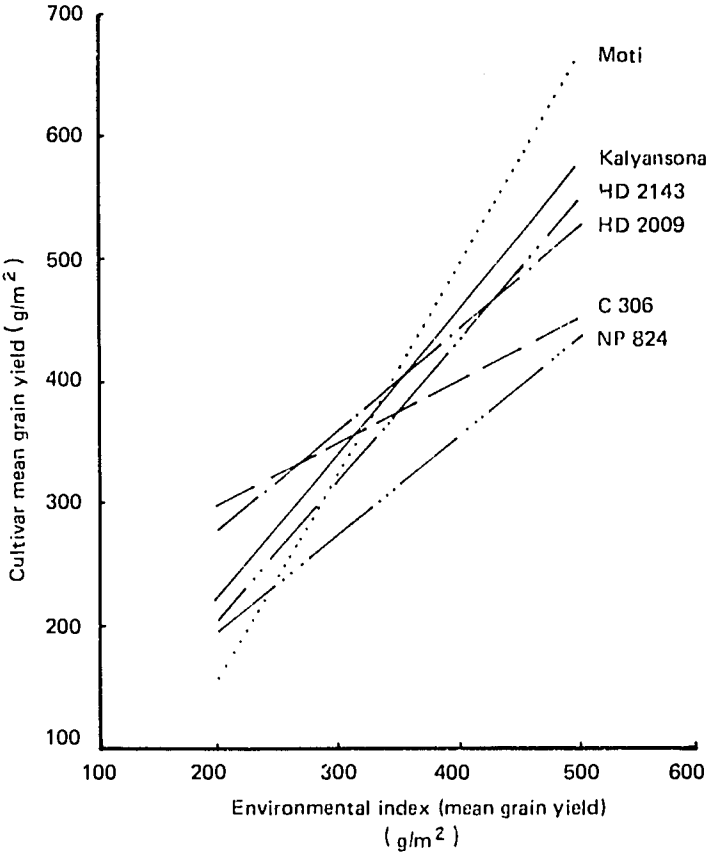


Figure 2. Relationship of cultivar mean grain yield with the environmental index in wheat cultivars

field level, the stability index could be equated with drought resistance. However, it must be recognized that such genotypes are not able to take advantage of a good environment from the point of view of water availability.

Efforts have also been made by biochemists and molecular biologists to define drought resistance. Bewley (1981) reviewed literature on protein synthesis in two mosses (*Tortula ruralis* and *Tortula filicinum*) which were categorized as drought resistant and susceptible. Quick recovery in protein synthesis because of conservation of messenger-RNA was possibly associated with drought resistance. Bewley (1981) very candidly stated that this criterion could not be extended to crop plants.

More recently the interest in molecular aspects of drought resistance has been generated by Le Rudulier *et al.* (1984), by the discovery of osmoregulation genes (osm) in *Escherichia coli*. Osmoregulation was considered the cardinal point in drought resistance of crop plants, though the survival of *E.*

coli mutants was tested in a medium containing sodium chloride. Therefore, for a molecular biologist, the drought resistance is osmoregulation, irrespective of the source of stress, such as the lack of water, salinity, alkalinity, or temperature.

Scientists belonging to different disciplines, therefore, have different perceptions of drought resistance and hence might define it accordingly, as stated below:

Molecular biologist:	Drought resistance as survival of individual cells or unicellular organisms such as *E. coli*, through osmoregulation in saline or PEG-induced water stress
Biochemist:	The tolerance of important biochemical reactions such as protein synthesis, conservation of messenger-RNA, etc., to water deficit in an organism
Physiologist:	Maintenance of growth during water stress and its accelerated resumption on termination of water stress
Agronomist:	Stability in yield performance of a crop or a variety in a water-deficient environment

It is this perception of an individual that becomes the basis of the search for a criterion of drought resistance. However, these perceptions refer to different time scales in the life of a plant which culminate in producing an economic yield. Thus, an integration of events in different time scales is essential for assessing drought resistance in an agronomic sense, which is the ultimate objective of agricultural programmes. It might be useful to define drought resistance as the mechanism/s causing the minimum loss of yield in a water-deficient environment relative to the maximum yield in a water-constraint-free management of the crop. This definition of drought resistance includes the concepts of the relative amounts of water and the relative yield. Therefore, an understanding of the basis of yield is essential to describe the performance of a genotype in a water-limiting and a water-sufficient environment.

Basis of yield in wheat

Although each crop has its own characteristics, every crop passes through different growth phases, starting from sowing to maturity, to culminate in economic yield. It is the differentiation along with growth, which results in the development of economically important structures, such as spikes, inflorescence, tubers, etc., in different crops. Growth basically results in accumulation of dry matter while differentiation and subsequent development leads to

economic yield. It is obvious that any amount of growth or dry-matter production would not help in producing grain yield unless the yield components differentiate and develop appropriately. In a sense we are talking of a dynamic relationship between 'source' and 'sink'. It is their complementation during the differentiation of 'sink', such as panicle, spike, tubers, etc., and subsequently their development that determines yield (Sinha and Khanna. 1975).

It would be appropriate to discuss the specific example of wheat which has been extensively studied in many parts of the world (Asana, 1968; Evans *et al.*, 1975; Fischer, 1983, 1984).

The following phases of growth can be clearly distinguished (Sinha *et al.*, 1982):

(1) Germination to spike initiation
(2) Spike initiation to terminal spikelet formation
(3) Terminal spikelet formation to spike emergence
(4) Spike emergence to grain development and maturity

The above four phases at Delhi take about 26, 25, 40, and 45 days, respectively, if a crop is sown in mid-November and receives adequate irrigation. The duration of these phases changes at different latitudes, leading to changes in crop duration and yield (Sinha *et al.*, 1986). The process of yield realization actually starts after ear or spike initiation. How does the growth achieved earlier or leaf area at this stage determine the yield? From past studies the following main conclusions can be drawn:

(1) Approximately 60–70 per cent of the total dry matter is produced before anthesis.

(2) After anthesis, mainly the flag leaf, peduncle, and ear photosynthesis contribute to assimilation.

(3) Only 15–25 per cent of preanthesis assimilates are mobilized for grain development.

(4) Preanthesis assimilates could be mostly amino acids to mobilize nitrogen from different plant parts.

(5) Eighty to 85 per cent of the total nitrogen is assimilated before anthesis, and is present in leaves and stem.

Thus, current assimilation or photosynthesis and mobilization of the previously accumulated nitrogen are important for grain development. There is now additional evidence to show the following:

(1) When grains develop they trigger senescence of the flag leaf, presumably by enhancing the level of ABA, or ABA-like substances (Morgan, 1980). The main feature of this is the mobilization of protein nitrogen from the flag leaf.

(2) Protein, which is mostly present as RuBP carboxylase in leaves, is mobilized (Sinha and Rajagopal, 1980; Peoples *et al.*, 1980).

(3) There is disruption of chloroplast membranes.

The above processes lead to impairment of photosynthesis and hence carbon assimilation. However, these processes are delayed, if the number of developing grains is low. Thus, the present evidence suggests that eventually the 'sink' disrupts the 'source' or rather shortens the leaf area duration. It is likely that normally some balance is maintained between the 'sink' demand and the 'source'. A disturbance in this balance leads to the disruption of the 'source'.

Effects of drought

Inadequate availability of water in quantity and distribution leads to water deficit and has profound effects on various plant processes. These processes have different time scales in their responses to water deficit or drought (Table 1). Changes in leaf water potential, turgor pressure, and stomatal resistance occur within seconds and minutes while the cell growth, accumulation of proline and betaine, degradation of proteins and polysaccharides are effected in hours.

Observable effects on leaf expansion, shoot and root growth might take days, but the influence on reproductive biology and grain yield is seen in days and months. Thus, plant physiologists and biochemists who seek a criterion of drought resistance which often responds in minutes or hours have an unenviable task of relating it with the final grain yield which is a cumulative effect of various processes over a period of days and months.

An important feature of plant response to drought is that it varies at different stages of plant growth. Often the plant is most sensitive just before panicle emergence or during the period of grain/seed development (Matsushima, 1962). There is now evidence that the genotypes which are identified as drought resistant at the seedling stage do not necessarily exhibit resistance during later stages of growth, particularly the reproductive phase.

Table 1. Plant water status (low) influencing plant characteristics and processes in time scale

Yield	days–months
Flower and fruit development	days–months
Leaf senescence and shedding	days
Root growth	days
Leaf growth	hours–days
Leaf movement	hours–minutes
Cellular metabolism (proline, betaine, abscisic acid accumulation)	hours–minutes
Changes in hydraulic resistance	hours–minutes
Stomatal movement	hours–minutes
Turgor pressure	minutes–seconds

Major changes occur during plant growth. Initially the roots are a major 'sink'. When a plant experiences water stress, it shows senescence of the leaves, but the metabolites are mobilized to the roots (Reddy, Khanna-Chopra, and Sinha, unpublished work). The roots are thus able to grow more and collect more water, or become a source of metabolites if water is again available after a period of stress. As against this, once a plant enters the reproductive phase it mobilizes metabolites from the leaves to the developing grains/seeds. This process is hastened if the plant experiences water stress. Thus, depending upon the size of the 'sink', the senescence of leaves and plant could be influenced; the larger the sink the faster the senescence, and hence greater susceptibility to drought. These effects are possibly caused by synthesis of ABA or ABA-like substances by the grains (Morgan, 1980) and also because ABA is produced in response to water stress. Thus, the combined effect of reproductive sink and stress will have a more detrimental effect on the plant. Experiments using normal and male-sterile lines of sorghum and wheat were performed to test the above hypothesis. In addition, the technique of defruiting was also employed in mung bean (*Vigna radiata*) and cowpea (*Vigna unguiculata*). The seedlings of normal and sterile male plants of sorghum and wheat had a similar response, but during the reproductive phase the normal plants appeared more susceptible to drought (Khanna-Chopra and Sinha, unpublished work). The defruited plants of mung bean and cowpea also exhibited greater tolerance to water stress as compared with the control plants with fruits (Paharia and Sinha, unpublished work; Reddy and Sinha, unpublished work).

These results suggest that the genotypes with a higher 'sink' capacity or those with a higher harvest index would show a greater susceptibility to drought than those with poor 'sink' or poor harvest index. This would also explain why the response of seedlings and the plants at grain development could be different. In fact, the varieties which are identified as drought resistant do have a poor 'sink' or a poor harvest index.

WATER AVAILABILITY AND CROP RESPONSE

Since water is usually a limiting factor in dryland agriculture, it must determine growth and yield. It can be seen from Figure 3 that dry-matter production is a function of water availability in all genotypes of wheat. They all had a linear relationship but there was a difference in slope. For grain yield, this difference in slope suggests that it is a function of dry-matter production and harvest index which could be influenced by the pattern of water availability. However, the total water availability could be used for suggesting suitable plant characteristics at a given location as stated below.

In north India, it is estimated that water availability in a fully charged soil profile after monsoon rains is about 20 cm. On the basis of our present studies

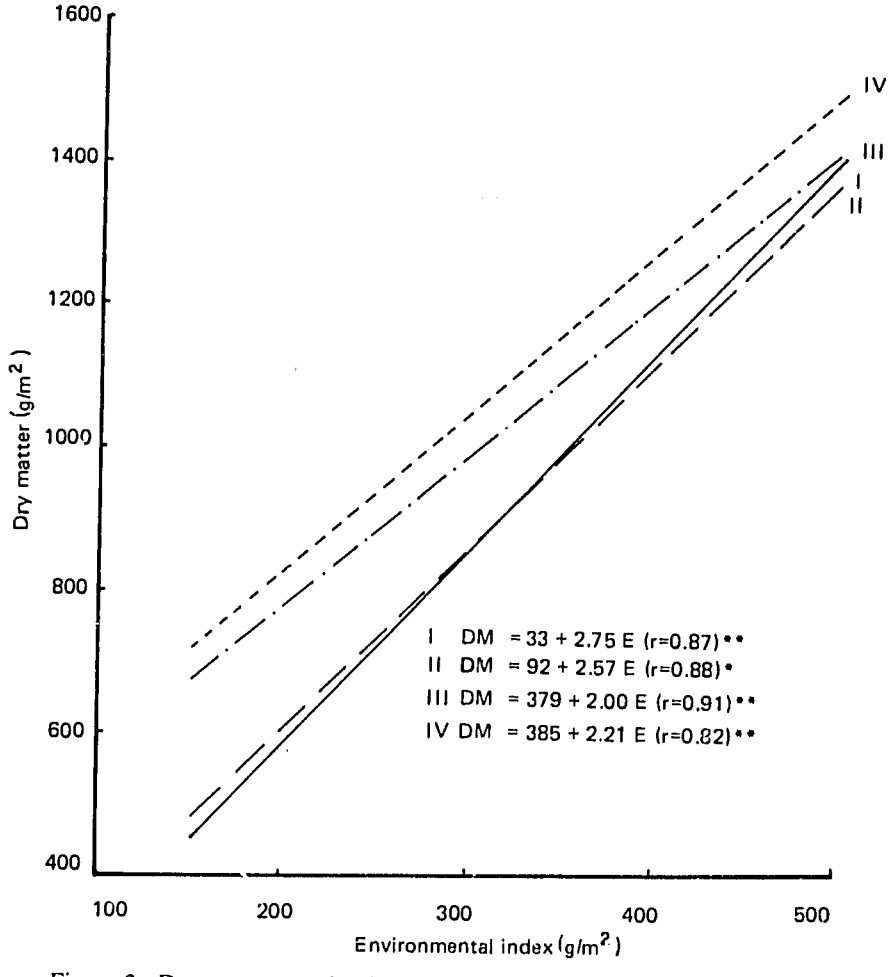


Figure 3. Dry-matter production in relation to water availability in wheat

on water-use efficiency under field conditions, this amount of water is enough to produce 800 g/m^2 of dry matter (Aggarwal and Sinha, 1983). The winter rains would add further to this dry matter. For a 5-cm rain, another 200 g/m^2 could be produced. Therefore, the yield components and phenology of the plant should conform to these requirements. The crop should be able to produce 800 g/m^2 of dry matter if there is no rain but should have the ability to respond to additional water. This would not be possible by a uniculm plant, but a tillering variety would respond to this situation. Of this dry matter, at least 40 per cent should be produced after anthesis. Therefore, about 40 per cent of the total available water should be available at anthesis. In other words, at least 8 cm of water should be present in the soil profile to ensure

postanthesis photoassimilation. This means that early growth of the plant should be slow but, by anthesis, should reach approximately 500 g/m^2 of dry matter. Having reached anthesis, it would be desirable if the spike had a potential of 35 to 40 grains, combined with 250–300 spike-bearing shoots per square metre. Such an ideotype would have to be provided with adequate nutrient supply. For example, a crop producing 1000 g/m^2 of dry matter and 400 g/m^2 of grain would need approximately 110 kg N/ha. If such an amount was not provided, the tillering and spike characters would not reach their potential, despite water availability. Thus, our proposed ideotype of wheat in the stated environment would have the following traits:

(1) Tillering type

(2) Slow early growth, reaching approximately 500 g/m^2 by anthesis

(3) Adequate leaf area at anthesis to produce 300 g/m^2 more after anthesis

(4) 250–300 shoots/m^2

(5) Potential of 35–40 grains of 40 mg each per spike

(6) Medium duration and semi-tall, to ensure adequate preanthesis conservation of assimilates

Indeed, some of these characteristics do exist in some genotypes such as C306, HD2009, etc.

Thus, depending upon the estimated water availability and a particular crop, a suitable location-specific ideotype could be proposed. In many instances it might be necessary to estimate the final yields based on water availability, to assess whether the upper limit was achieved.

SINGLE TRAIT AND DROUGHT RESISTANCE

Several efforts have been made to identify a single character which could serve as the basis of selection for drought resistance. Among these, chlorophyll stability, proline accumulation, betaine accumulation, occurrence of specific fatty acids, and now osmoregulation are noteworthy. Positive correlation of these individual characters to drought resistance (possibly in the agronomic sense) were shown by some workers but negated by others. In recent years, proline accumulation as an index of drought resistance has been extensively debated (Singh *et al.*, 1972; Sinha and Rajagopal, 1975a; Hanson, 1980). That proline could provide protection to enzymes against desiccation or high temperature now seems to be beyond doubt (Sinha and Rajagopal, 1975b; Paleg *et al.*, 1981; Nash *et al.*, 1982). However, a correlation between proline accumulation and drought resistance, estimated on the basis of yield, is difficult to establish because of a number of intervening biochemical, physiological, and differentiation steps. Thus, proline accumulation might have a short-term advantage at the cellular level but it may not be a practically usable selection criterion. The influence of environmental factors,

growth stages, and a relatively low heritability further support this contention (Lewin and Sparrow, 1975; Aspinall and Paleg, 1981). The evidence in support of using betaine accumulation as a criterion for drought resistance is very limited, and may again have importance in cellular functions rather than the whole plant system. Accumulation of ABA as a criterion of drought resistance has not been established either (Quarrie, 1981).

Recently, osmoregulation both in microbes and higher plants has been advocated as a mechanism causing drought tolerance (Le Rudulier *et al.*, 1984; Morgan, 1984). In *E. coli* this evaluation was based in response to salinity stress, and osmoregulation was mostly due to proline accumulation. Salinity stress cannot be equated with water stress for a variety of reasons. Furthermore, in higher plants, such as wheat and barley, the osmoregulation is achieved by accumulation of sugars and inorganic ions (Munns *et al.*, 1979). Proline contributes very little to this phenomenon. If osmoregulation is achieved by accumulation of organic molecules, then partition of assimilates between growth and osmoregulation would become an important factor in determining yield. This could assume even greater significance if water stress developed at the time of grain development. Therefore, it should not be surprising that osmoregulating cultures of wheat had a maximum yield of 1–1.5 t/ha (Morgan, 1984). This, once again, shows that the combination of high yield and drought resistance is an incompatible objective.

The above discussion leads us to the conclusion that it may not be realistic to look for a single trait as a selection criterion for drought resistance.

INTEGRATION

In this review an effort has been made to define drought and drought resistance, analysis of yield of crops, and the effects of water deficit on growth and yield. It should be appreciated that several plant processes which occur in time scales ranging from seconds to minutes, hours, days, and months culminate in crop yield under field conditions in a competitive environment. This relationship is diagrammatically shown in Figure 4. It should be clear from this that while the importance of short-term responses cannot be denied, their correlation with yield is difficult to expect. It is for this reason that many individual tests have not been found of wider application in selection for drought resistance. Therefore, a wholistic view of plant growth development and yield components in relation to water availability would have to be taken for a particular crop. This could be summarized as follows:

(1) Reduced water availability reduces growth and dry-matter production.

(2) Stress at flowering/anthesis has a severe influence, particularly on senescence.

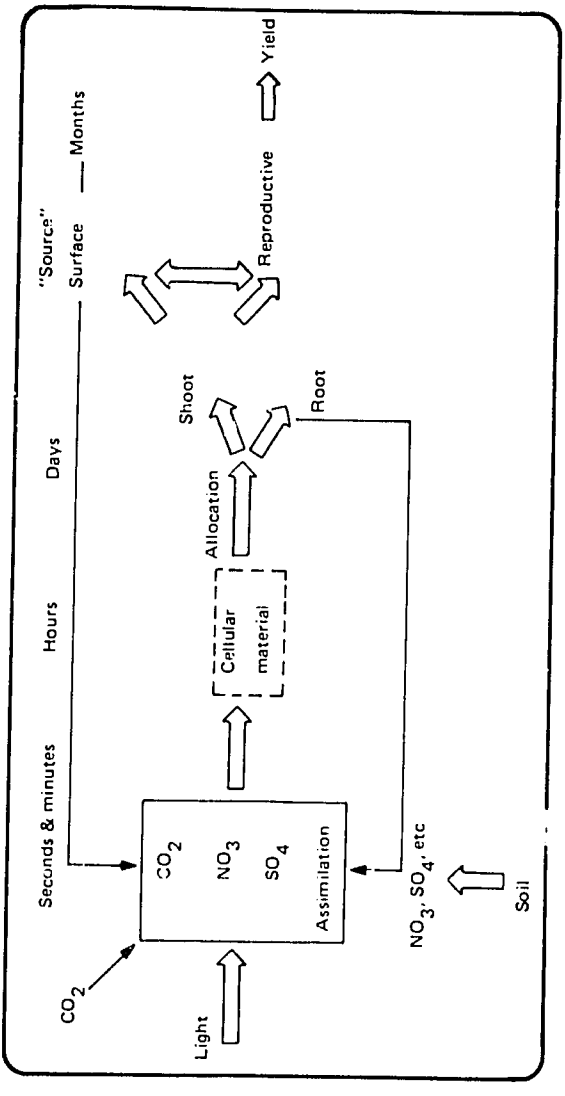


Figure 4. Diagrammatic representation of the relationship between several plant processes that occur in time scales

(3) The larger the sink size, the faster is the leaf senescence. Therefore, the sink potential is not realized.

(4) These effects are possibly accentuated because of increasing canopy temperature.

(5) Intraplant competition for assimilates, particularly between the roots and grains 'sink', impair the former. This in turn further reduces the water-collection ability of roots.

In view of the above, the following attributes are suggested:

(1) In a situation of intermittent rainfall, the genotypes with shorter growing period are selected. However, they should have faster initial growth rates. Such genotypes should have the ability to utilize nitrogen, enabling a high percentage of it to be in leaf tissues. If these genotypes experienced water deficit they would have the capacity to recover and complete their life cycle soon after the cessation of rains. The hybrid CSH-6 of sorghum is such an example.

(2) When the crop is grown with declining soil moisture as in *rabi*, the genotype should have a slower aerial growth combined with delayed differentiation. This plant behaviour ensures better root development and a reasonable number of tillers. By anthesis the crop should attain 500–600 g/m^2 of dry matter, and leave 8–10 cm of water in the soil profile for maintaining adequate photoassimilation in the postanthesis phase. Each spike in wheat should have a potential of 1.0–1.2 g of grain weight. This means that the genotypes should have a tillering capacity along with approximately 40 grains in each spike.

The above attributes could be adopted under limited water availability instead of irrigated or completely rainfed conditions. By providing a uniform population in early stages of growth, the performance of genotypes can be appropriately judged. In *kharif* this is possible because the crop is usually sown after an adequate rainfall. However, in *rabi* it would be advisable to grow the crop after a presowing irrigation to ensure germination and appropriate competition.

Having emphasized the wholistic approach in relation to environment, particularly the water availability, it may be mentioned that the following criteria might prove useful in selecting physiologically superior genotypes to conform to the above-mentioned wholistic approach:

(1) Seedling vigour in *kharif* and slow aerial seedling growth in *rabi*.

(2) A canopy temperature lower than the ambient temperature, when crop canopy is formed is desirable.

(3) Assessment of total dry-matter production in relation to soil moisture depletion.

(4) Medium capacity of yield components.

REFERENCES

Aggarwal, P. K. and Sinha, S. K. 1983. Water stress and water use efficiency in field grown wheat: a comparison of its efficiency with that of C4 plants. *Agricultural Meteorology* **29**:159–167.

Arnon, I. 1980. Breeding for higher yields. Pages 77–81 in *Physiological Aspects of Crop Productivity, Proceedings of 15th Colloquium*. International Potash Institute, Wageningen.

Asana, R. D. 1968. Growth habits of crops of non-irrigated areas. Important characteristics of plant types. *Indian Fmg* **18**:25–27.

Aspinall, D. and Paleg, L. G. 1981. Proline accumulation: physiological aspects. Pages 206–239 in *Physiology and Biochemistry of Drought Resistance in Plants* (Paleg, L. G. and Aspinall, D., eds.). Academic Press, Sydney.

Bewley, J. D. 1981. Protein synthesis. Pages 261–282 in *Physiology and Biochemistry of Drought Resistance in Plants* (Paleg, L. G. and Aspinall, D., eds.). Academic Press, Sydney.

Durrant, W. 1953. *The story of philosophy*. Simon and Schuster, New York.

Eberhart, S. A. and Russell, W. A. 1966. Stability parameters for comparing varieties. *Crop Sci.* **6**:36–40.

Evans, L. T., Wardlaw, I. F. and Fischer, R. A. 1975. Wheat. In *Crop Physiology* (Evans, L. T., ed.). Cambridge University Press.

Finlay, K. W. and Wilkinson, G. N. 1963. The analysis of adaptation in plant breeding programme. *Aust. J. Agri. Res.* **14**:742–754.

Fischer, R. A. 1983. Wheat. In *Potential Productivity of Field Crops under Different Environments*. IRRI, Los Banos, Laguna, Philippines.

Fischer, R. A. 1984. Physiological limitations to producing wheat in semi-tropical and tropical environments and possible selection criteria. Paper presented at Wheat Workshop. CIMMYT. September 1984.

Gotoh, K., Chang, T. T., O'Toole, J. C., Riley, R. and Murty, B. R. 1979. Crop adaptation. Pages 234–261 in *Plant Breeding Perspectives* (Sneep J. and Hendriksen A. J. T., eds). Centre for Agricultural Publications and Documentation, Wageningen.

Hanson, A. D. 1980. Interpreting the metabolic responses of plants to water stress. *Hort. Sci.* **15**:623–629.

Le Rudulier, D., Strom, A. R., Dandekar, A. M., Smith, L. T. and Valentive, R. C. 1984. Molecular biology of osmoregulation. *Science* **224**:1064–1068.

Lewin, L. G. and Sparrow, D. H. 1975. The genetics and physiology of resistance to stress. Barley genetics III. Pages 486–501 in *Proceedings of 3rd International Barley Genetics Symposium*. Garching, 1975.

Matsushima, S. 1962. Some experiments in soil–water–plant relationships in rice. Ministry of Agriculture and Cooperative Federation of Malaya. Div. Agric. Bull. 112. 35 pp.

Morgan, J. M. 1980. Possible role of abscisic acid in reducing seed set in water stressed wheat plants. *Nature* **285**:655–657.

Morgan, J. M. 1984. Osmoregulation and water stress in higher plants. *Ann. Rev. Plant Physiol.* **35**:299–319.

Munns, R., Brady, C. J. and Barlow, E. W. R. 1979. Solute accumulation in the apex and leaves of wheat during water stress. *Aust. J. Plant Physiol.* **6**:379–389.

Nash, D., Paleg, L. G. and Wiskich, J. T. 1982. Effect of proline, betaine and some other solutes on the heat stability of mitochondrial enzymes. *Aust. J. Plant Physiol.* **2**:47–57.

Paleg, L. G., Douglas, T. J., Van Daal, A. and Kaech, D. B. 1981. Proline, betaine and other organic solutes protect enzymes from heat inactivation. *Aust. J. Plant Physiol.* **8**:107–114.

Peoples, M. B., Beilharz, V. C., Waters, S. P., Simpson, R. J. and Dalling, M. J. 1980. Nitrogen redistribution during grain growth in wheat. (*Triticum aestivum*). *Planta* **149**:241–251.

Quarrie, S. A. 1981. Genetic variability and heritability of drought induced abscisic acid accumulation in spring wheat. *Plant Cell and Environ.* **4**:147–151.

Singh, T. N., Aspinall, D. and Paleg, L. G. 1972. Proline accumulation and varietal adaptability to drought in barley: a potential metabolic measure of drought resistance. *Nat. New Biol.* **236**:188–190.

Sinha, S. K. and Khanna, R. 1975. Physiological, biochemical and genetic basis of heterosis. *Adv. Agron.* **27**:123–174.

Sinha, S. K. and Rajagopal, V. 1975a. Proline slows down the loss of nitrate reductase in moisture-stressed plants. *Plant Physiol.* (Suppl.) **56**:225.

Sinha, S. K. and Rajagopal, V. 1975b. Effect of moisture stress on nitrate reductase activity and accumulation of proline in sorghum. Pages 1–9 in *Proceedings of Symposium on Crop Plant Responses to Environmental Stress.* Vivekananda Laboratory for Hill Agriculture, India.

Sinha, S. K. and Rajagopal, V. 1980. Photosynthetic characteristics and nitrate reductase activity during development of flag leaf of wheat. *Photosynthetica* **14**:189–192.

Sinha, S. K., Khanna-Chopra, R., Aggarwal, P. K., Chaturvedi, G. S. and Koundal, K. R. 1982. Effect of drought on shoot growth: significance of metabolism to growth and yield. Pages 153–170 in *Drought Resistance in Crops with Emphasis on Rice.* IRRI, Manila.

Sinha, S. K., Aggarwal, P. K., Chaturvedi, G. S., Singh, A. K. and Kailasnathan, K. 1986. Performance of wheat varieties in a variable water environment. I. Grain yield stability. *Field Crops Res.* In press.

Drought Tolerance in Winter Cereals
Edited by J. P. Srivastava, E. Porceddu, E. Acevedo and S. Varma
© 1987 ICARDA
Published by John Wiley & Sons Ltd

29

Synthesis—Tackling the Problem of Low Yield and Yield Instability of Winter Cereals in the Mediterranean Areas of West Asia, North Africa, and Southern Europe

M. C. SAXENA* and S. K. SINHA†
*ICARDA, PO Box 5466, Aleppo, Syria; †Water Technology Centre, Indian Agricultural Research Institute, New Delhi 110012, India

INTRODUCTION

Special features of the region

The Mediterranean area of West Asia, North Africa, and South Europe is characterized by a highly variable environment, both spatially and temporally. Most of the presentations in this conference stressed this feature of the region. Whereas the moisture stress due to insufficient and/or inappropriate distribution of rainfall was said to be the major factor constraining production, other associated yield retardants identified by the speakers for winter areas were: (1) low-temperature stress, early in the season; (2) high-temperature stress, late in the season; (3) poor soil fertility; and (4) presence of soil salinity and alkalinity in some areas. These factors interact and accentuate the moisture stress and, therefore, make the productivity highly unstable and low.

Agronomic management versus genetic improvement

Due to the vagaries of the environment, the yield gains over the last several years have been very little, as pointed out by J. P. Srivastava, Habib Ketata, and D. R. Marshall. According to D. R. Marshall, for a comparable environment in Australia—when contrasted with the relatively milder environment of North Europe—the yield increases accruing from the genetic improvement

have been rather insignificant. Yield increases over the last decades in North Europe were attributed to both genetic improvement and improved crop management. Several speakers emphasized that both these aspects are almost equally important in effecting significant improvements in productivity and yield stability in the dry rainfed areas of the region. The need for exploiting the interaction between genetic improvement and agronomic management was particularly stressed, which highlights the importance of a close collaboration between agronomists, soil scientists, crop physiologists, and breeders.

Concern was raised that the present conference did not give adequate attention to the agronomic aspects. However, G. T. Scarascia-Mugnozza, chairing the first technical session, emphasized the urgency for a comprehensive review of the work carried out in the past on various aspects of crop management in dry areas of the Mediterranean region. Much of this work has been published in regional languages and thus has not been accessible to all. Future research strategy on crop management will have to be based on the directions provided by this review. Having agreed on this, the conference focused on genetic improvement in its deliberations.

RESEARCH STRATEGY FOR IMPROVED PRODUCTIVITY AND YIELD STABILITY OF CEREALS IN DRY AREAS

Characterization of environments

In view of the enormous variability in the region, a clear characterization of the environment and a definition of the nature of drought stress encountered in different parts of this region was considered a high priority by most of the speakers. G. P. Maracchi presented an interesting account of the efforts to characterize the agroecological zones in West Asia and the Mediterranean region using 30-year average monthly data for rainfall, air temperature, and potential evapotranspiration. However, because the interannual and intra-annual variations were not adequately considered in this analysis, these efforts were of limited value so the speaker recommended that emphasis should be on developing a network for collection of the needed data and that satellite data should also be used. Hazel Harris drew attention to the current efforts in the CGIAR system on agroecological zoning, including the forthcoming Inter-Centre Conference on the subject. The discussion led to the consensus that it offered an expanded opportunity for an interinstitutional collaboration within the region and for establishing a strong linkage between IPRA and ICARDA agroecological zoning.

A clear characterization of 'drought stress' in different parts of the region is needed for designing crop improvement strategies that would suit the target area. Breeders look to agroclimatologists for this information and to crop physiologists and agroecologists to define the probabilities of the occurrence

of environmental extremes. Crop physiologists have to generate information for developing crop models that would provide good indicators to breeders. The progress that could be made by this approach was illustrated by the current modelling efforts presented by Hazel Harris and A. M. Castrignano *et al.* For crop modelling, however, information will be needed on the crop performance in different environments and Hazel Harris requested breeders to collect the relevant information to characterize the environment where the breeding material is evaluated. This information would be greatly useful in validation and fine-tuning of models. Realistic simulation models could go a long way in helping all those involved in improving crop productivity in the dry areas.

Once the agroecological zones are clearly defined and the moisture sufficiency indices developed using the necessary water-balance terms, as described by F. N. Reyniers, the crop physiologists could attempt to suggest the potential crop productivity for each of the subregions so that breeders have a clear crop productivity target in their crop improvement efforts.

Plant ideotype consideration: trait identification and screening

To do away with the hitherto used empirical approach in varietal improvement, there is a need to define suitable plant ideotypes for different agroecological conditions. Attempts to define characters for an ideotype for some specific situations were presented by several speakers from Italy (A. M. Castrignano *et al.*, A. M. Stanca *et al.*, and B. Borghi *et al.*). A. Hadjichristodoulou and M. Duwayri also described the types suitable for the environments encountered in the cereal production areas in Cyprus and Jordan, respectively. Presentations by E. L. Smith, D. R. Marshall, N. C. Turner, S. Ceccarelli *et al.*, and J. M. Clarke also had suggestions for developing ideotypes that would be most suitable for different dry areas. S. Brown, H. M. Taylor, and R. A. Richards discussed the root characteristics desired for different environments. Information on specific phenology and shoot morphological features was presented by E. Acevedo and R. B. Austin.

As expected, there were different opinions on the desirability of a given character for the dry areas, because the nature of moisture stress and other interacting environmental factors vary greatly. Whereas useful information on many major traits was presented, it was obvious that there is a need for additional work on this aspect to establish clear principles with respect to crop phenology, root and shoot morphology, and physiological traits for different environmental conditions to arrive at precise definitions of plant ideotypes for different agroecological situations. This clearly is in the domain of crop physiologists who have to devise appropriate experimental protocols to generate information for defining the right plant ideotypes.

R. B. Austin suggested that for certain characters the system of rain-out shelter could permit identification of genotypic differences, and help in the determination of significance of several physiological and biochemical traits. Such an optimization research is a prerequisite for developing suitable plant ideotypes. J. M. Clarke proposed a simple and pragmatic approach for evaluation of the leaf-water loss characteristics. Use of a line-source sprinkler system was referred to by several speakers as a good tool for creating the needed soil moisture gradients for evaluating genotypes for desirable traits for soil moisture stress tolerance. Crop physiologists and biochemists will, however, need assistance from breeders in identifying a small number of genotypes with extreme values, and some intermediate ones, of the test characters so that these could be used for identifying the relative significance of different characters. Consideration of wild progenitors and landraces will be necessary in these evaluations.

Once the characters are identified by crop physiologists, their heritability will have to be determined. This will require collaborative efforts from both physiologists and breeders.

Since the desirability of a trait might be environment specific, we cannot suggest a common ideotype for all environments. The traits that were most frequently suggested for adapting a cereal genotype to droughty environments included the following:

(1) *Morphological traits*. Emergence and establishment of seedlings in low soil moisture content; tillering; rate of dry-matter accumulation up to anthesis; presence of awns; leaf waxiness; leaf shape and size; stomatal frequency; flag-leaf area and green area duration; root fineness; root depth; diameter of metaxylem vessels in seminal roots; rooting density at depth; subcrown internodal hydraulic resistance; root response to adverse soil conditions; kernel number; kernel plumpness.

(2) *Physiological traits*. Stomatal resistance to water vapour diffusion; osmotic regulation and adjustment; leaf-rolling; excised leaf water retention ability; cell membrane stability; rate of kernel filling; duration of kernel filling; translocation of metabolites from stem to kernel; partitioning of photosynthate between root and shoot at various stages of crop growth.

(3) *Metabolic traits*. Net photosynthetic rate; photorespiration; respiration; abscisic acid (ABA) level; proline accumulation; betaine accumulation; production of heat shock proteins.

Many of the above characters have been a subject of study since 1898 in developing drought-tolerant material, as D. R. Marshall pointed out. However, the way that they are currently being considered is different from the past in that there is a greater interdisciplinary interaction including physiology, biochemistry, agroecology, and genetics and breeding. Barley and wheat as two species differ in their adaptation to drought, barley being more drought tolerant. Therefore, there is a need to exploit those traits for wheat that make barley better adapted to drought. Characters in durum wheat may provide an

'intermediate link' in understanding nature's strategy for adaptation of a crop species to drought.

Whereas there are some good indications for several morphological and physiological traits for their usefulness in adaptation to drought, little is known about the potential biochemical traits. R. B. Austin and D. Lawlor considered the ABA content, which could be potentially exploited. The strong positive relationship between the transpiration and carbon gain through photosynthesis, as illustrated by T. C. Hsiao, would lead one to conclude that there is little possibility of increasing photosynthesis in the winter cereals in a moisture stress environment, unless the biotechnological approaches are used to make substantial modifications in their genetic make-up to incorporate characteristics of C4 plants. Pending that, however, there should be a possibility of identifying genetic differences, in the existing germplasm and related gene pools, for variations in the temperature optima for photosynthesis and respiration so that net photosynthesis could be increased without concomitant increase in the water use to permit improved photosynthetic water-use efficiency. Besides grain, straw is also economically important in the region; hence there is a need for increased total biomass production for the unit amount of water transpired, which at present seems to be possibl only by the above approach. An input from physiologists and biochemists is necessary in this regard.

Breeders need simple morphological and phenological traits which can be used in screening a large number of genotypes quickly. Hence physiologists will have to identify those morphological and phenological traits that are intimately associated with the physiological and biochemical parameters considered important for resistance/tolerance to stresses. Breeders are also interested in knowing the association between resistance characteristics for different abiotic stresses with the aim of incorporating resistance to more than one stress in their genotypes. They are also interested in making assessment of the 'yield cost' that one may have to pay to achieve a certain measure of yield stability. Physiologists have a role to play in providing answers to these questions. They also need to develop quick and reliable screening methods for key physiological and biochemical traits that breeders can use in screening large segregating populations for reducing the numbers of eventual field testing. Such methods as canopy temperature measurement through infrared thermometry, membrane permeability measurements through electrolite leakage following partial desiccation or heat, and assessment of postanthesis translocation of carbohydrates to kernels following chemical desiccation of shoot deserve consideration.

CONSIDERATION IN BREEDING

The principal considerations in breeding for increased yield and stability to drought-prone environments were brought out in the presentations by J. P.

Srivastava, A. Hadjichristodoulou, M. Duwayri, E. L. Smith, D. R. Marshall, S. Ceccarelli *et al.*, M. Osmanzai, A. M. Stanca, and B. Borghi, and the subject evoked a very fruitful discussion. Examples were cited of the progress made for yield improvement in severe or partial stress and non-stress environments by the current breeding methods. Whereas there was an indication of growing realization among breeders of the need to consider specific environmental conditions and crop season available in different target areas for which they breed the genotypes, this can be further refined as more precise information on agroecological zonation becomes available.

It was amply clear that the choice of right parents was crucial in any breeding effort to improve yield and yield stability in stressful environments in the region. Consideration of the following criteria was suggested:

(1) Phenology to match, as best as currently possible, the target environment such that the chances of the crucial phenological stages coinciding with optimum environments are maximized.

(2) Any morphological, physiological, and/or biochemical traits that have so far been identified as important and are, therefore, components of the ideotype for the target area.

(3) Use of landraces and progenitors from the target areas to incorporate adaptation to the environment and to provide the desired buffering for stresses. While laying out the objectives of a breeding programme, it would be necessary not to become overambitious to consider very wide adaptability. Adaptability to specific ecological regions/subregions should be the priority.

Handling of the F_2s derived from the crosses made for adaptation to stressful environments would need special care to ensure that the desirable recombinants are not lost. They will, therefore, have to be grown in the 'medium' stress rather than in the 'extreme' stress environments. The possibility of using specific physiological or biochemical traits to assist in selection should be given the highest consideration by breeders with the necessary input from physiologists and/or biochemists, to reduce the numbers of lines to be evaluated more vigorously subsequently. The subsequent early-generation material has to be so handled as to be most cost effective. Use of the 'modified pedigree' method or 'modified bulk' or other methods was suggested as the alternatives. There appeared a general agreement that the early generation materials should be evaluated in as many environments in the target zone as possible so that the genotypes capable of producing high and stable yields in stress conditions and yet possessing the ability to fully exploit the conditions of favourable environments are identified. While evaluating these breeding materials, efforts should be made to characterize each site as precisely as possible so that the nature of drought to which the material is likely to be exposed could be fully defined. The selected material could eventually be subjected to multilocational testing at regional or international nurseries.

Based on yield performance and stability, the national programmes could then release varieties for their farming conditions.

In conclusion, the meeting provided an excellent opportunity for a multidisciplinary group of scientists from different parts of the world to come together and discuss the problems of improving productivity and yield stability of cereals in stress-prone environments in West Asia and the Mediterranean region. The dialogue started should hasten the pace of research in improving the cereal production in the region.

Recommendations

The workshop considered the research and development needed to accelerate the production of improved varieties of cereals for countries with Mediterranean climates.

It was recognized that the scope for realizing the benefits from improved varieties will be considerably increased when accompanied by improved management practices.

Further work was recommended on the following topics:

1. Assembly, review and evaluation of the results from relevant prior research and experimentation

   It was considered that many of the results from past work are not known by or available to scientists working in the area served by ICARDA. A synthesis of past results would avoid wasteful repetition and provide a sound basis for new work.

2. More precise definition of agroclimatic zones, taking account of socioeconomic factors

   The aim is to define realistic target zones for individual breeding programmes and to provide the information needed to devise appropriate strategies for breeding and selection, and the evaluation of candidate varieties.

3. Research to develop breeding strategies appropriate for defined agroclimatic zones

   (a) The use of simulation models

   An important part of this research will be the use and improvement of simulation models of crop growth which take into account plant characteristics, weather, and soil conditions. These models will enable ideotypes for particular zones to be defined more precisely, taking into account the climate and its variability. They can also be of help in each zone for carrying out selection and trialling, and in identifying parents for crossing.

(b) Evaluation of the consequences for yield and its stability of changing particular plant traits

There is continued discussion on the significance of individual traits for yield. Because of the complexity of plant function and interactions with environments, the unequivocal assessment of traits can be made by incorporating them into isogenic lines with an appropriate genetic background and evaluating the lines in a range of sites and environment in the target agroclimatic zones. It was noted that this approach was being followed in Australia and Britain and that the scientists involved could provide guidance on the methods they use. It was deemed to be especially important to study early growth, root system structure and function, phenology, water-use efficiency, and dry-matter partitioning using this approach. Alternative and simpler methods should be developed.

(c) Efficiency of selection for moisture-limiting areas

More research is needed to develop efficient and cost-effective methods of selection to identify germplasm for moisture-limiting areas. The general consensus was that selection in conditions in which the crop is ultimately to be grown is desirable.

4. Research to exploit useful traits in landraces of wheat and barley and in the wild progenitors of these crops

It was noted that the countries served by ICARDA include the centres of diversity of wheat and barley and their wild progenitors. Although mostly collected and preserved, little work has been done to characterize this germplasm or exploit traits which might be useful in the genetic backgrounds of modern varieties of wheat and barley.

The workshop did not consider what organizational changes, if any, would be needed to ICARDA's programmes to implement effectively these proposals. However, it was recognized that the success of the new work would depend on close collaboration between breeders, physiologists, and climatologists.

Index

Illustrations are indicated by *italic page numbers*, tables by **bold numbers**.

ABA (abscisic acid) accumulation, **326**, 332–3, **333**, 360
ACROM (arid crop) productivity model
  case study applications
    early-growth effects, 23–4, *24*
    hydraulic root resistance effects, 31–2
    root depth effects, 25–7
    root/shoot ratio effects, 27–9
    stomatal sensitivity effects, 29–31
  climatic data used, 16, *17*
  described, 16–17
  growth simulation, 20–1, *22*
  photosynthesis relationships, 19–20, *21*
  root growth models used, 18–19, *19*
  soil characteristics used, 17–18
  water transpiration model used, 19, *19*
Afghanistan
  barley grown in, **67**
  wheat grown in, **68**
Africa, *see* North Africa; West Africa
AGDM (above-ground dry matter)
  relationship to water-use efficiency, 134
Agroclimatological classification, 3–13, 37–43, 66–75, 366–7
  effect on yields of, 74
  ICARDA region, 66–72
  Mediterranean region/Southwest Asia, 3–14
  need to define realistic zones, 373
Agronomic management
  effects on yields, 324, 366
  necessity for review of, 366
Algeria
  agroclimatological classification of, *5*
  barley grown in, **67**
  wheat grown in, **68**
Aluminium toxicity, 291–2
  wheat cultivars tolerant of, 292–3
America, *see* South America; USA
Amino acids, effect of water stress on, 246–8, *247*, *248*
Analytical approach (to breeding), 85–6, 92–4, 102, 304
Asia
  wheat grown in
    area harvested, **68**
    moisture environmental data, **69**, 152–3, **152**
    yield data, **68**
  see also Southwest Asia
Asparagine, effect of water stress on, 246, *247*
Assimilate transfer
  drought-desiccant effect on, 212–14
  see also Remobilization of carbohydrate
ATP
  effect of stress on, 235, *236*
  synthesis of, 234, *234*
Attributes, 362
  effect on barley, **315**, 316–18, **316**
Attributes model, 305–6
  climatic conditions used, *307*, 308
  experimental methods of testing, 306, 308
  photosynthesis affected by, 314, **315**, 316

Attributes model (*contd*)
water relations, effect of, *308*, *309*, 310, *311–13*, 314
yield affected by, 305–6, **315**, 316–18
Australia
Mediterranean climatic zones, 203–4, *204*
rainfall data for, 204, *205*, **208**
soil types in, 205, 207
temperatures in, **205**
Australian breeding strategies, 89–97
analytical approach, 92–4
drought-resistant germplasm sources used, 91–2, **91**
empirical approach, 94–5
frost-resistance development, 96–7
long-season cultivar development, 95–6
original cultivars used, 90, 91, **91**
Australian studies
cultivars studied, **208**
wheat in light-textured soils, 206–14
Awn length, yield affected by, 197–8, **327**

Barley
area harvested in Mediterranean region and West Asia, **67**
cultivars
Alger ceres, 248, *248*, *250*
Alpha, **119**, **120**
Anthenais, 194
Arabi Abiad, 243, *243*, 244, *245*, *246*, *247*, 249, **250**, *250*, *251*, *277*, 278, *278*, 279, **279**, *280*, 281, *282*
Arda, **119**, 120, **121**
Arma, **119**
Atem, *243*, 243, *245*, *247*, 248, **250**
Barberousse, **119**, 120, **120**
Beecher, *42*, *43*, *243*, *245*, *247*, 248, **250**, *277*, 278, *278*, **279**, *280*, 281, *282*
Cytris, *277*, 278, 279, **279**
ER/Apm, *69*, 243, *243*, 244, *245*, *246*, *247*, **250**, *250*, *312*
Fior, 26, **119**
Georgie, 119, **119**, **120**
Gitane, **119**, **120**
Igri, **119**, 120, **120**
Jaidor, **119**
Kantara, *195*, 197
Matnan, **279**
Palmella blue, *247*, *248*, *250*
Panda, **119**, **120**
Pepite, **119**
Pirate, **119**
Porthos, **119**, **120**
Rihane, 60, 70, *247*, 248, *248*, *250*, *277*, 278, 279, **279**
Robur, **119**
Roho, *69*, 248, *248*, *250*
S BON 38, *312*
Swanneck, *277*, 279, **279**
Tadmor, 70, **70**, *244*
Tipper, 119, **119**, **120**
Vetulio, **119**
WI 2198, *69*
drought resistant varieties, 70
drought tolerance attributes for, **326–7**
fallowing effects on, 59, *280*, 281
fertilizer effect on, *42*, *43*, 44, 59
grain size–yield correlation, 196–7
heat shock effects on, 116–17, 122
high-temperature tolerance of, 116–17, *116*
ICARDA studies, 105–9
moisture effects on, 58, **59**, **72**, 105–9
physiological screening methodology for, 117–21
physiological traits of, 117–20
preferred growing zones, 67, 72
rainfall effects on, **58**, 58, **59**, *66*, **72**
root characteristics of, 184, 276–83
sowing time, effects of, **60**
stability of performance compared with wheat, 193, 194, 199
tillering capacity of, 62
water relations for, *308*, *309*, 310, *311–13*, 314
yield
crop/plant attributes, effect on, **315**, 316–18, **316**
in Cyprus, 192
in Mediterranean region and West Asia, **67**
moisture availability effects, 58, **58**, **59**
Betaine, accumulation of, 236, 360
Biochemical traits, breeding for, 93
Brazil
aluminium-tolerant wheat grown, 292, 293

rice acreage grown, 337
Bread wheat
cultivars, *see* Wheat, cultivars
desiccation effects on, **126**
dry-matter accumulation in, *124*, 125
hybrids developed for, 127–8
ICARDA studies, 109, **109**, **110**, 112
ideotype for, 124–30
Italian varieties, 123–4
leaf removal effects on, **126**
moisture availability effects on, *57*, **59**
new varieties, *70*, 71–2
preferred growing zones for, 66
protein content of, **127**
sowing time, effects of, 59, **60**
spike degraining effects on, **127**
yield data in Cyprus, 192
see also Wheat
Breeding strategies
analytical approach, 85–6, 92–4, 95, 102, 304
Australian strategies, 89–97
CIMMYT, 154–9
computerization of data analysis, 94
disease resistance breeding, 83–4
efficiency of selection, 374
empirical approach, 76, 81, 94–5, 102
environmental effects on, 73, 74
F2 progeny method, 80–1
frost-resistance development, 96–7
future objectives for, 369–71, 373–4
insect resistance breeding, 83–4
long-season cultivar development, 95–6
mechanization of testing procedures, 94
moisture-limited areas, 77
morphophysiological traits approach, 85–6, 93–4
multilocation testing, 82, 94, 103
plant architecture approach, 84–5
rainfed areas, 79–87
selection site choice, 83
shuttle breeding, 157–8

Cambridge, Plant Breeding Institute, droughted wheat trials, 325–34
Carbon dioxide assimilation, 234–5
Carbon isotope discrimination
cost of equipment, 150
rate of screening for, 150
water-use efficiency affected by, 139–42
Cereal Improvement Program, 66
CGIAR (Consultative Group on International Agricultural Research) agreement, 66
Chemical hybridizing agents, 127–8
CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo)
breeding philosophy of, 154–6, 161
breeding techniques used, 157–9
identification of drought resistance at, 156–7
long-term breeding objective of, 154–6
research responsibilities, 66
test stations used, 156, 157, 158, **158**
Classification methods, agroclimatological classification, 3–14
Cluster analysis, 4, 6
agroclimatological data, *7*, 8, *8–10*
Computers used, 94–5, 180, 233
Corn, *see also* Maize
Crop productivity simulation models, *see* ACROM productivity model; Simulation models
Cyprus
barley grown in, **67**
wheat grown in, **68**
yield stability trials in, 192–8

Defoliation studies
maize plants, 340–7
wheat plants, *126*
Desiccants, carbohydrate transfer trials, 186, 213, 214
Determinate tillering, **60**
yield affected by, 144–5
Developing countries, moisture environment data for wheat area, **69**, 152–3, **152**
Direct-selection strategy, 102
advantage over favourable-environment selection, 104–9, 166
Jordanian results, **165**, 166
rice breeding, 337
see also Favourable-environment selection strategy; Shuttle breeding technique

Disease resistance
  breeding for, 83–4, 197
  desired characteristic for, **60**
Drought, definitions of, 153, 351–2
Drought resistance
  agronomist's definition of, 352, 354
  approaches to improvement of, **172**
  biochemical traits for, 359–60
  biochemist's definition of, 353, 354
  breeding for, 157–9, 350
  characteristics required, 158–9
  CIMMYT breeding programme for, 154–9
  definitions of, 153, 351, 352–4
  identification of, 156–7
  mechanisms listed, 153, **173**
  metabolic indicators for, 237–8
  molecular biologist's definition of, 353, 354
  morphophysiological traits for, **173**, 174, **175**
  physiological research into, 153
  physiologist's definition of, 351, 354
  questionnaire on, 350–1
Drought shock proteins, 117, *118*, 137, 247
Drought tolerance
  attributes in barley, **326–7**
  measurement of, 218
  yield price paid for, 252, 369
Dry-matter yield
  grain yield affected by in deep sandy soils, 206, *207*
  water availability effect in wheat genotypes, 357, *358*
DSI (drought susceptibility index), 106, **106**
  correlation with grain yield, 107, **107**, *352*
DSN (Drought Screening Nursery), 157, 159
Durum wheat
  cultivars, *see* Wheat, cultivars
  excised-leaf water-retention measurements, 176–83
  ICARDA studies, **109**, **111**, 112
  moisture availability effects on, *57*, **59**
  new varieties, 71, *71*
  physiological characteristics of, 217–24
  physiological traits of, 256–61
  preferred growing zones for, 67
  as source of drought-resistant stock, 92
  sowing time, effects of, 59, **60**
  yield data in Cyprus, 192
  see also Wheat

Earliness
  drought resistance affected by, 24
  stability of, 194–5
  sunflower oil yield affected by, 268–9, *269*, *270*, 271
  wheat yields affected by, 46, *47*, 51, 59, **60**
  yield affected by, 194–5
Early-growth vigour
  Australian light soils, 209–10
  correlation with dry-matter yield, *209*, *210*
  moisture stress effects on, **105**
  visual scoring of, 209
East Asia, moisture environment data for wheat areas, **69**, **152**, 153
Egypt
  agroclimatological classification of, *5*, *6*
  barley grown in, **67**
  wheat grown in
    area harvested, **68**
    yield data, **68**, *74*
Elastic modulus, 224
  turgor adaptability related to, 224
  value quoted for durum wheat, **223**
Empirical approach (to breeding), 76, 81, 94–5, 102
  disadvantages of, 103–4
Environmental factors
  characterization of, 3–13, 37–43, 66–75, 366–7
  genetic correlation between yields affected by, 104–5
  yields affected for specific varieties, 72–5
Ethiopia
  barley grown in, **67**
  wheat grown in, **68**
Evapotranspiration
  soil-water extraction increased, 136–
  surface water evaporation decreased, 137–8
  sunflower plants, *269*
Evapotranspiration potential
  ACROM model use of, 19, *19*
  Mediterranean region, *8*

relationship with rainfall, 8–9
Excised-leaf water retention, 176–83
correlation with stomatal diffusive resistance, **182**
effects of rolling on, 178, *178*, 189
experimental technique described, 179–80
stomatal diffusive resistance correlated with, 182, **182**
values quoted, **177**
yield related to, 180, 181

F2 progeny method of breeding, 80–1
objective of, 81
practical details, 80
Fallowing, 59, *280*, 281
FAO, Agrometeorological Bureau data used, 4
Favourable-environment selection strategy
advantages of, 103
direct-selection strategy preferred to, 104–9
see also Direct-selection strategy; Shuttle breeding technique
Fertilizer
genotype–environment interactions affected by, *42*, *43*, 44, 50, 59
water extraction rate affected by, *280*, 281
yields affected by, *42*, *43*, 44, 59
Flowering date, effect on wheat yields, 330–2, 334
France, wheat yields in, *74*
Freezing damage, 41–3
Frost damage, 42
breeding for resistance to, 96–7
effects on yield, 96–7
genotype–environment interactions affected by, 41–3
Frost-resistant cultivars, 97

GAI (green area index)
fertilizer effect on, *42*, 44
see also LAI (leaf area index)
Genetic correlation, stress-environment selection effect on, 105
Genetic improvement, achievements in, 324, 365–6
Genetic limitations, 321–4
Genotype, *see also* Ideotype concept
Genotype–environment interaction
modification of, 43–53
by maturity type, 46, *47*
by maturity/season/soil, 46, *48*, 49
by nutrition, 44
by time of sowing, 44, *45*
moisture constraints on, 38–9
root characteristics of wheat, 288
temperature limitations on, 39–43
high-temperature limitations, 39–40
low-temperature limitations, 41–3
yield affected by, 192
see also Environmental factors
Germination ability, 168–9
Germplasm improvement, 75–7
efficiency of selection techniques used, 76–7
sources for drought-resistant Australian cultivars, 91–2
yield-stability considerations, 77
Glaucousness, 149, 184
definition of, 139
water-use efficiency affected by, 139, 149
Glucose equivalents, sunflower trials, 267–8, **268**
Glycine betaine, accumulation of, 236
see also Betaine, accumulation of
Growth habit, surface water evaporation affected by, 137, 138

Heat shock proteins, 117, 122
Heat tolerance tests
barley, 116–17
durum wheat, 218–21
Height (of plants)
barley, **327**
desired characteristic for, **60**
moisture stress effects on, **105**
stability of, 195–6
wheat, 329–30
Heterogeneity (in cultivars), 81
HI (harvest index)
definition of, 135
factors affecting, 142–5
sunflower seed yield related to, 265, *265*
High-temperature effects
barley, 116–17, *116*
durum wheat, 218, *219*, 220–2, *220*

High-temperature effects (*contd*)
genotype–environment interactions, 39–40
Hydraulic resistance
barley, **327**
as desirable trait, 310
root system, 144
wheat, 31, 291
yield affected by, 31, 144

ICARDA (International Center for Agricultural Research in the Dry Areas)
barley breeding by, 105–9
bread wheat breeding by, 109, **109**, **110**, 112
breeding strategies used, 102–12
cereal-breeding activities of, 66, 102
durum wheat breeding by, **109**, **111**, 112
experimental stations listed, **103**
research responsibilities, 66
Ideotypes
ACROM model applications, 23–32
bread wheat, 124–30
concept first used, 15
development of, 367–8
plant architecture approach developed from, 84
wheat, 124–30, 359
India
concept of drought in, 351–2
water availability in, 357–8
wheat cultivars grown, 350, 351, 352, *352*, *353*, 359
Infrared thermometry, 185, 210–11, 214
factors affecting, 185, 212
Insect resistance breeding, 83–4
Iran
barley grown in, **67**
wheat grown in, **68**
Iraq
barley grown in, **67**
wheat grown in, **68**
IRAT, rice breeding programme, 337, 338
Irrigated crops
barley, Syrian yield data, **58**
drought resistance identified using, 156–7
in Egypt, 74
physiological characteristics of, *221*, *222*
stomatal resistance modelling for, *259–60*
in Syria, **58**
wheat
percentage in developing countries, **72**
Syrian yield data, **58**
Isogenic lines, 145–6, 374
Israel, agroclimatological classification of, *6*
ISWYN (International Spring Wheat Yield Nursery), 154
data analysed, 155
Italy
barley trials in, 118–21
bread wheat grown in, 123–4
durum wheat grown in, 217–18

Jordan
agroclimatological classification of, *6*
barley grown in, **67**
breeding techniques used, 164–5
rainfall data quoted, **164**
semi-dwarf varieties used, 163, 164
trials results, 165–8
wheat grown
area harvested, **68**
rainfall effect on, *66*
yield data, **68**, *74*

LAI (leaf area index)
ACROM model use of, 20, 34
drought resistance affected by, 23
maize defoliation studies, 344, *344*, 346
see also GAI (green area index)
Landraces, research to exploit, 374
Latin America, moisture environment data for wheat areas, **69**, **152**, 153
Leaf rolling, barley, **327**
Leaf rolling techniques, 178, **178**, 189
Leaf temperature, measurement of, 185, 210–11
limitations of technique, 185, 212
Lebanon
agroclimatological classification of, *6*
barley grown in, **67**
ICARDA test station in, 103, **103**
wheat grown in, **68**

Libya
agroclimatological classification of, *5*
barley grown in, **67**
wheat grown in, **68**
Light-textured soils, Australian studies, 206–14
Limestone, effect on disease susceptibility of wheat, 292
Long-season cultivars, development of, 95–6
Long-term nature of research, 176
Low-temperatures
data for Mediterranean region, *9*
genotype–environment interactions affected by, 41–2
water-use efficiency affected by, 142
LSS (line-source sprinkler) technique
barley studies, 243, *243*, 244
drought resistance identified using, 156–7, 368
sunflower studies, 265

Maize
cultivars
Berrechid, 343, *344*, **345**
DRA 400, 343, *344*, **345**
Trojan TXS 85, 340
defoliation studies
bucket study, 340–2
field study, 342–7
heat shock proteins in, 122
uses as crop, 339
water stress problems in, 340
Marquardt iterative method, 257
Maturity type
desired characteristic for, **60**
wheat yields affected by, 46, *47*, *48*
Mechanization, effect on breeding programmes, 94–5
Mediterranean region
agroclimatological classification of, 5–12
climate characterized, 276
Metabolic stress index
definition of, 249
leaf water loss rate effects on, 249, *250*
measurement of, 249–50
values quoted for barley, **250**
Metabolic traits, 368
breeding for, 93
Metabolism
carbon metabolism, 234–5
indicators for use in breeding, 237–8, 249–52
nitrogen metabolism, *234*, 235–6, 242–9
Mexico, test stations in, 156, 157, 158, **158**
Microprocessor-based data acquisition, 180, 233
Middle East
agroclimatological classification of, *6*
barley grown in, **67**
wheat grown in
area harvested, **68**
moisture environment data, **69**, 152–3, **152**
yield data, *66*, **68**
see also Southwest Asia
Modified bulk breeding methods, 80, 370
Moisture constraints
barley yield affected by, **105**
genotype–environment interactions, 38–9
yields affected by, 58, **58**, **59**, **72**
Monsi–Saeki equation, 20
Morocco
agroclimatological classification of, *5*
barley grown in, **67**
maize defoliation studies, 342–7
rainfall data, *343*
temperature data, *343*
wheat grown in
area harvested, **68**
yield data, **68**, *74*
Morphological traits, 368
bread wheat, 130
breeding for, 85–6, 93–4
transpiration efficiency maximized by, 305
Multidisciplinary teams, coordination of, 76
Multilocation testing, 60, 77, 82–3, 94
advantages of, 103
Australian breeding programme, 94
CIMMYT wheat program, 157
ICARDA programme, 103

NADH, effect of stress on, 235, *236*
NADPH
effect of stress on, 235, *236*

NADPH (*contd*)
synthesis of, 234, *234*
Nitrate accumulation, effect of water stress on, 244–5, *244*
Nitrogen metabolism, *234*, 235–6, 242–9
acquisition processes, 242–5
biochemical indicators for use in breeding, 249–51
biosynthesis processes, 246–8
cycling of metabolites in, 248–9
Nitrogenous compounds
formation of, *234*, 235–6
selection of accumulation ability of, 229–30
NN (nearest neighbour) analysis, 95
North Africa
agroclimatological classification of, *5*
barley grown in, **67**
wheat grown in
area harvested, **68**
yield data, **68**
Nutrient solution technique, 289, 293

Oklahoma (USA), wheat yields quoted, 81, 86
Organizational levels, crop production, *228*
Osmoregulation, 137, 184–5, 314, 353–4, 360

Pakistan
barley grown in, **67**
wheat grown in, **68**
Parallel-selection technique, 103
Passioura model, 134–5, 206, 304
breeding considerations, 136
environmental considerations, 135–6
independence of factors affecting yield, 135, 145
Past research/results, need to review, 373
Phosphorus fertilizer
genotype–environment interactions affected by, *42*, *43*, 44, 50, 59
yields affected by, *42*, *43*, 44, 59
Photosynthesis
barley, **327**
carbon dioxide effects on, 231–2, *232*
drought effects on, 230–3, 314, **315**
simulated in ACROM model, 19–20, *21*
stomatal conductance effects on, 231, **232**

Physiological traits
breeding for, 85–6, 93–4
barley, 117–21
durum wheat, 219–24
examples listed, **175**, 368
harvest index considerations, 142–5
independence of, 145
model used, 134–6
screening for barley, 117–20
screening techniques used, 174, 175, 176–86
sunflowers, 266
transpiration efficiency maximized by, 305
transpiration processes, 136–8
validation of, 145–7
water-use efficiency considerations, 138–42
Poiseuille equation, 287
Polyethylene glycol, water stress induced by, 117, *118*, 243, *244*
Principal component analysis (PCA), 6–7
agroclimatological data, 9–12, *11*, *12*
Proline, accumulation of, 236, 246, *247*, 266, 359
Protein content
bread wheat, **127**
yield and, 128
Protein synthesis
drought resistance affected by, 353
under heat-stress conditions, 117, 122
under water-stress conditions, 117, *118*, 236–7, 247
Putrescine, leaf water loss rate effect on, 248, *248*

Radiation, stomatal resistance affected by, 256, *257–60*
Rain-out shelters, drought-resistance characteristics studied using, 325, 368
Rainfall
data
Australia, 204, *205*, **208**
ICARDA test stations, **103**
Jordan, **164**
Mediterranean region, *7*, *17*
Morocco, *343*
Sicily, *17*
Syria, *43*, *205*, 276, *307*
typical data quoted, *135*
yield variation affected by, 77

yields affected by, 58, **59**, *66*
Recommendations (of the workshop), 373–4
Regression analysis, genotype–environment interactions, **59**, 82
Remobilization of carbohydrate, 185–6, 212–14
see also Assimilate transfer
Resistance analogue model, 322
Rice
acreage in Brazil, 337
acreage in West Africa, 337
breeding of, 337–8
cultivars, Lalnakanda, 350, 351
tillering capacity of, 62
yield limit for, 351
yield potential of, 338
Risk minimization strategies, 61
Root characteristics, 23–7, 85, 183–4
barley, **327**
deep light soils, 210–12
defoliation effects on, maize plants, 347
drought resistance affected by, 183–4
measurement of, 210–11, 212, 282, *282*, 288, 289, 290, 294
screening for, 174
variation for barley varieties, 277–9, *277*, *278*, **279**
water extraction rate affected by, 282, *282*
wheat plants, 285–6
density modified, 289–91
hydraulic resistance modified, 291
problem soils, 291–5
seminal roots modified, 287–9
water uptake equation, 289
Root shape analysis
ACROM model use of, 18–19, 34
case study examples of, 24, 25–7
root distribution defined for, 25
Root/shoot ratio, water-use efficiency affected by, 142
RWC (relative water content), relationship to water potential
barleys, *311*
durum wheat, 222, *222*
wheats, *311*

Salt-tolerant wheat varieties, 293, *294*
Saudi Arabia
barley grown in, **67**
wheat grown in, **68**
Screening techniques
metabolic profiling, 250–1
physiological traits, 174–5, 176–86
root characteristics, 289, 293
Selection techniques, 76–7
Semi-dwarf wheat varieties, 123, 163, 164, 329, **329**, 330, **330**
Shock proteins, 117, *118*, 237
Shuttle breeding technique, 157–8
SIMTAG model, 46
Simulation models
improvement required, 373
inadequacy of, 324–5
need for, 271
see also ACROM model
Sink capacity, drought resistance affected by, 357
Sites (for selection), choice of, 83
Slanted-tube (root measurement) technique, 289, 294
Socioeconomic considerations, 49, 61, 72
Soil characteristics
in ACROM model, 17–18
in Australia, 205, 207
in Syria, 276
Soil depth
definition of, 52
sunflower seed yields affected by, 268, *270*
wheat yields affected by, *48*, 49
Soil water extraction, increase in, 136–7
Soils
toxicity testing in, 293
Sorghum
cultivars
CSH-6, 350, 362
M35-1, 350
excised-leaf water-retention measurements, 183
glaucousness in, 184
heat tolerance tests for, 218
root characteristics of, 184
South America
moisture environment data for wheat areas, **69**, **152**, 153
see also Brazil
South Asia, moisture environment data for wheat areas, **69**, **152**, 153

Southwest Asia
agroclimatological classification of, *6*
see also Middle East
Sowing times, yields affected by, 44, *45*, *46*, 59, **60**
Spain, sunflower trials in, 265–71
Species, factors affecting choice of, 72
Spring plantings, 67
Spring temperatures, genotype–environment interactions affected by, 39–40
Sprinkler systems, drought resistance identified using, 156–7, 243, 244, 265, 368
Stability (of yield), *70*, 77
barley vs. wheat, 193, 194, 199
breeding for, 193–8
effect of single traits on, 359–60, 374
wheat cultivars, 352, *352*, *353*
yield cost for stability, 252, 369
Stomatal closure
ACROM model simulation of, *22*, 29, 34
barley, 314, **327**
photosynthesis affected by, 228
Stomatal conductance
barley, 310, *311*
drought effects on, 314, **315**
global function for, 156–7
measurement of, 256
modelling of, 256–61
photosynthesis affected by, 231, **232**
radiation effects on, 256, *257–60*
vapour pressure deficit effects on, 256, *257–60*
wheat, 310, *311*
Stress metabolism, 228–38, 241–52
Stress-environment selection
physiological traits required for, 264
see also Direct-selection strategy
Sudan, wheat grown in, **68**
Sunflowers
genotype–environment interactions, 267–8
physiological responses to water deficits, 266
water-use efficiency data, 268, *269*
yield responses to water deficits, 265–6
Surface water evaporation
reduction of, 137–8
values quoted, 137

Sweet corn, *see* Maize
Syria
agroclimatological classification of, *6*
barley grown, **67**
factors affecting, *42*, *43*
evaporation data for, *40*, *43*
ICARDA test stations in, 103, **103**
rainfall in, *43*, *205*, 276, *307*
soil types in, 276
temperature data for, *40*, *205*, *307*
wheat grown
area harvested, **68**
new varieties grown, 71–2, *71*
yield data, **68**, *71*, *74*
wheat trials, *45–8*

Take-all disease, 292
Technology transfer, 60–1
Temperature data
Australia, *205*
Mediterranean region, *9*, *10*, *17*
Morocco, *343*
Sicily, *17*
Syria, *40*, *205*, *307*
Temperature limitations
genotype–environment interactions, 39–43
see also High-temperature interactions; Low-temperature effects
Thousand-grain weight
correlation with yield, 196–7
stress environment effects on, 167, **157**
Tillering behaviour, 144–5, 325, 328
desired characteristic for, **60**, 62
factors affecting, 193
stability of, 193–4, 199, 200
yield affected by, 145
Timescales, plant processes, **356**, *361*
Transpiration
as function of assimilation rate, *323*
maximized as fraction of evapotranspiration, 305
Triticale
cultivars
Civet 71, 157
Pika 'S', 157
excised-leaf water-retention measurements, 183
yield data in Cyprus, 192

Tunisia
agroclimatological classification of, *5*
barley grown
area harvested, **67**
cultivars, *69*
new varieties, 70
yield data, **67**
wheat grown
area harvested, **68**
yield data, 55, **56**, *57*, 58, **68**
yield gap in, **56**
Turkey
agroclimatological classification of, *5*, 8
barley grown in, **67**
wheat grown in, **68**

UK, wheat yields in, 324
USA
fallowing practice in, 59
Great Plains, 59, 80, 288, 291
wheat-breeding strategies used, 80, 81

VA (vesicular–arbuscular) infection, wheat affected by, 295
VPD (vapour pressure deficit), stomatal resistance affected by. 256, *257–60*

Water potential
barley crops, *308*, *309*, 310
durum wheat, *221*, *223*
maize defoliation studies, *341*
relative water content related to, durum wheat, *222*
wheat crops, *308*, *309*, 310
wheat ideotypes, *24*, *26*, *27–28*, *30–2*
Water stress resistance experiments, barley seedlings, 117, *118*
Waxiness, 149, 184
see also Glaucousness
Weed control, yields affected by, 59
West Africa
drought-resistant rice varieties grown, 337
rice acreage grown in, 337
Western Australia, deep light soil trials, 207–14
Western Europe, wheat yields in, 324
Wheat
area harvested in Mediterranean region and West Asia, **68**
Australian studies, 207–14
crop characteristics of, 321–34
cultivars
Appulo, 218, 221–4, *221*, *222*, **223**, *223*
AS5, **177**
Atlas 66, 293
Aurelio, **128**
Avalon, *233*
AVS16871, **292**
AZ2E, **177**
Barkaee, **208**
Bass, **212**
Bencubbin, 91, **91**
Bodallin, **208**
C306, 350, 351, 352, *352*, *353*, 359
Canberra, **91**
Cando, **177**
CC2B, **177**
Chiarano, **128**
Claudia, *129*
Condor, **208**
Cook, **292**
Coulter, **177**
Crane, 71
Currawa, **91**
Darkan, **208**
Demar 4, **127**, **128**
DT363, **177**, *179*
DT367, **177**, *179*
DTS47-1, *352*
DTS138, *352*
DTS141, *352*
DTS205-4-1, *352*
DTS707, *352*
Egret, **208**
Federation, **91**
Fiorello, **127**
Flk's'-Hork, 60
Gabo, **91**
Gamenya, **208**, **212**
Genaro 81, 156, **156**
Ghurka, **91**
Gluyas Early, 91, **91**
Gutha, **208**, **212**, 213, **213**
Halberd, **208**, **212**
Haurani, *70*, 71, *71*
HB5C/HB5D, **177**, *179*
HD2009, 352, *352*, *353*, 359
HD2143, *352*, *353*
Hercules, **177**, *178*
HO1 hybrid, **128**

Wheat (*contd*)
cultivars (*contd*)
Hourani, 164, **165**, 169
Imerio, 125–6, *125*, **125**, **126**, **128**
Jori C-69, 71
Junco 'S', **156**, 157
KA3, *177*
Kalyansona, **292**, *352*, *353*
Kharchia, 293
Kite, **144**, **208**, **292**
Korifla, 60, 71, *71*
Kulin, **208**
Kyperounda, 195
Lakota, **177**
Leopardo, **128**, *129*
Lira 'S', 156, **156**
Loreto, **128**
Macoun, **177**
Malvika, *352*
Marzotto, 124, *125*
Mec, **127**
MG120-1, *352*
MG180-9, *352*
MG191-24-1, *352*
MG413-2, *352*
Millewa, **208**
Mongolia, **208**
Monon, 293
Moti, 352, *352*, *353*
Nabawa, 91, **91**
Neelkant 'S', **156**
Norman, *124*, 125, 331
NP824, *352*, *353*
Olympia, 351
Omrabi, *70*, 71
Orso, **128**
Pandas, **128**
Pelissier, **177**, *178*, *179*
Pembina, **208**
Phoenix, 96, **208**
Pissi Local, 169
Q4A, *179*
RAJ911, *352*
S3, *177*
Sahl, 71
Saliente, 125–6, *125*, **125**, **126**, **128**
Salvia, **128**
Sebou, 71
Sham varieties, *70*, 71–2
Spica, **91**
Steinwedel, **91**
Stork, 164, **165**
Talent, 331
Tanager 'S', **156**
Thatcher, 288–9
Tincurrin, **208**
Tommaso, **128**
Valforte, 218, 221–4, *221*, *222*, **223**, *223*
Veery 'S', 155, *155*, **156**
Wailki, **208**, **212**
Wakooma, **177**
Warigal, **208**
Wascana, **177**
WW33 and derivatives, 96
Yavaros, 157
drought-resistant varieties, *70*, 71–2, *71*
factors affecting yield in UK, 324
fallowing effect on, 59
growth phases of, 355
Indian drought-resistant cultivars, 350, 351, 352, *352*, *353*, 359
Italian studies, 123–30
Jordanian trials, 164–9
light-soil drought resistance of, 207–14
maturity type effects on, 46, *47*, *48*, 49
maximum theoretical yield for, 56
physiology of, *286*
rainfall effects on, **58**, **59**, *66*, **72**
root system of, 183–4, 285–6
density modified, 289–91
hydraulic resistance modified, 291
in problem soils, 291–5
seminal-root system modified, 287–9
water uptake equation, 289
salt-tolerant varieties, 293, *294*
soil-depth effects on, *48*, 49
tillering capacity of, 62
time of sowing, effect of, 44, *45*, **60**
water relations for, *308*, *309*, 310, *311–13*, 314
yield
drought effects on, 356–7
factors affecting, 355–6
in Cyprus, 192
in Mediterranean region, **68**
in Syria, **58**, **59**
in Tunisia, *57*
in West Asia, **68**
in Western Europe, 324

WUE (water-use efficiency)
carbon isotope discrimination effect on, 139–42
cool-temperature vigour effects on, 142
definition of, 138
effect of fertilizer on, *43*, **44**
factors affecting, 59
function of assimilation rate, *323*
glaucousness effect on, 139
relationship to above-ground dry matter, 134
root/shoot partitioning effect on, 142
sunflower plants, 268, *269*

Yemen (Arab Republic)
barley grown in, **67**
wheat grown in, **68**
Yemen (People's Democratic Republic), wheat grown in, **68**
Yield gap, **56**
factors affecting, 56–60
risk-minimization in reduction of, 61
Yield stability, *see* Stability (of yield)
Yield variation, causes of, 192