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THE DEVELOPMENT OF A DROUGHT RESISTANT WHEAT GERMPLASM

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CONTENTS

Subject	Page
Summary	2-I
Physiological Attributes Associated With Drought Resistance of Wheat Cultivars in a Mediterranean Environment	3
Variation among wheat cultivars in the response of leaf gas exchange to light	23
Mass selection for grain filling under chemical desiccation stress	38
The evaluation of heat tolerance for yield under field growing conditions	50

SUMMARY

The physiological responses to drought stress of diverse spring wheat materials were studied for three years in the laboratory, growth chambers, greenhouse, rainout-shelter and the field. Heat tolerance of wheat materials were studied in growth chamber experiments and in the field. The response of leaf gas exchange to light in different wheat cultivars was studied as means for understanding variations in potential plant production and the effect of plant selection on potential productivity and stress adaptation. Mass selection for improved grain filling under post-anthesis stress was performed.

The adaptation of wheat to Mediterranean-type drought stress, common to Israel and Portugal, was found to be conditioned primarily by plant phenology. Wheat genotypes of short growth duration have an advantage where total seasonal precipitations are below about 300-400mm. Longer growth duration is advantageous at 600mm or more. Early-maturing genetic materials were developed and are available. Beyond phenology, the most important physiological component in plant adaptation to drought stress was found to be osmotic adjustment. Genetic variation for osmotic adjustment is readily available in the wheat materials studied.

Leaf gas exchange and photosynthetic capacity at light saturation was found to be improved in modern high-yielding cultivars which were selected for high yield under the high radiation environment of Israel. Experimental data as combined with theoretical considerations developed by others allowed to suggest that the improvement of plant production by way of improved photosynthetic capacity is not possible in all environments and the most likely environment for achieving progress in this respect is a high radiation environment, such as Israel or perhaps Southern Portugal.

The most prevalent drought stress in wheat in the Mediterranean climate occurs during grain filling. The chemical desiccation of wheat plants after anthesis, as means for revealing genotypic capacity for grain-filling from stem reserves, was used in mass selection to evaluate effectiveness and progress in selection. The method was efficient in increasing grain filling and improving yield of wheat which was practically devoid of any photosynthetic source after anthesis, as the case is for sever drought stress. The method is considered to be a very simple means for achieving drought tolerance during grain filling without resolving to complex environmental control and laborious procedures of selection.

Physiological Attributes Associated With Drought Resistance of Wheat Cultivars in a Mediterranean Environment

ABSTRACT

In order to evaluate the physiological attributes associated with stable yield production under the semi-arid Mediterranean conditions of Israel, twelve spring wheat (*Triticum aestivum* L.) cultivars were planted in 16 trials (8 trials each in 1985/86 and 1986/87) which received seasonal rainfall (including irrigation) ranging from 230 to 755mm year^{-1}. Under low rainfall conditions, drought stress occurred during the period of stem elongation when the ears grew. Grain filling was largely free of stress. Phenology, yield, yield components and midday canopy temperatures under drought stress were recorded. In additional experiments, data were collected for all cultivars on osmotic adjustment under controlled drought stress, heat tolerance in terms of thermostability of cellular membranes, and the capacity for grain filling from mobilized stem reserves as assessed by the chemical desiccation of plants after anthesis.

The variation in precipitation explained 75% of the variation in mean yield among trials, and the main yield component responsible for yield reduction at low precipitation was ear number, as affected by tiller survival rate. The larger yielding cultivars sustained a higher kernel number per ear in compensation for the reduced number of ears under stress. The yield stability of cultivars under low precipitation was defined by both the joint linear regression method and by the linear regression of yield on precipitation, both of which gave very similar predictions. The magnitude of the intercept of the latter regression was taken as indicator of drought resistance in terms of yield. The variations among cultivars in this intercept was well explained (general linear model R^2=0.78) by corresponding variations in osmotic adjustment, heat tolerance and canopy temperature (75%, 13% and 12% of the total sum of squares, respectively). Grain filling from stem reserve mobilization was not important in this respect, evidently because grain filling was not subjected to drought stress in these trials. Early heading cultivars had a relative yield advantage only when precipitation were less than about 300mm and grain yield was less than about 350 g m^{-2}. Both early heading and heat tolerance were positively correlated with osmotic adjustment across cultivars (r=0.72 and r=0.90, respectively). It was therefore concluded that the main physiological attribute associated with yield stability under conditions of drought stress during the period of ear growth was the capacity for osmotic adjustment, which apparently allowed sustained ear growth under drought stress.

INTRODUCTION

A central issue of the problem of breeding crop cultivars for improved drought resistance is the role of defined physiological attributes in supporting plant production under stress. A clear proof of the importance of given physiological traits for yield production under drought stress is difficult to achieve, for various reasons. Often, attempts were made at obtaining such evidence by comparing the yield of different cultivars, isogenic lines or iso-populations with their physiological responses to drought stress in a field trial. A main problem in such experiments is not necessarily the physiological measurements but rather the estimation of yield. Genetically, yield is characterized by low heritability such that non-genetic variations in yield within and between environments are quite large, especially in drought affected (low yielding) environments (Blum, 1988). Secondly, yield under drought stress is not affected only by the specific physiological responses to stress but also by the yield potential of the genotype (*e.g.* Fischer and Maurer, 1978), which can not be accounted for by physiological measurements of drought response.

In order to allow a proper estimate of genotypic yield response to the environment, plant breeders developed the multi-location testing system from which the stability of any given genotype may be derived, such as the joint linear regression of Finlay and Wilkinson (1963). By this analysis, genotype yield is tested across different environments, where the mean yield (over genotypes) of each of the environments represents an 'environmental index'. In discussing the various forms of stability analysis used in plant breeding programs, Lin *et al.* (1986) pointed out that the analysis by Finlay and Wilkinson (1963) is valuable if some biological meaning can be ascribed to the 'environmental index'. If drought stress is the main environmental factor affecting variation in the environmental index, genotypic yield responses to this variation may be taken to represent their drought resistance in terms of yield production.

There is a very limited insight into the physiological basis of yield stability under semi-arid conditions, even where reliable yield response estimates were obtained. Wheat yield stability across variable moisture regimes was associated with osmotic adjustment, a greater root mass production under drought stress (Blum *et al.*, 1983b), a high capacity for plant reserve mobilization into the growing kernel under stress (Aggarwal and Sinha, 1984), but not with plant height (Laing and Fischer, 1977).

This study was performed in order to evaluate drought resistance in terms of yield stability of wheat cultivars grown under variable moisture regimes in a Mediterranean climate and to associate yield stability with some known physiological attributes of drought resistance.

MATERIALS AND METHODS

Yield trials

Twelve Israeli commercial and experimental spring wheat (*Triticum aestivum* L.) cultivars (Table 1) were tested in 16 trials (8 locations each in 1985/86 and 1986/87 (referred to as 1986 and 1987) in Israel. Trials were grown under rainfed conditions or were given supplemental irrigation in order to

create large variation in the moisture regime between trials. At least 90% of the total annual rainfall was received between wheat planting and harvest. Total annual rainfall (and irrigation) in the different trials ranged from 230 to 755mm (Table 1).

Basal fertilizer, weeds and diseases were managed to ensure that crop growth was not limited. Each trial was sown in a randomized block design with 6 replications. Plot size varied but was always greater than $40m^2$ for mechanical harvesting. All trials were sown with a drill at 15cm row spacing on the optimal date which was between late November and mid-December. Seeding rate was adjusted for each cultivar to result in 280 seeds m^{-2}. Data for heading date, plot yield and kernel weight were collected from all trials and plots. Additional data were collected from 14 trials only. In each of these trials two row sections 2m in length were marked in each plot. For each section data were recorded on seedling number, maximum tiller number (by periodic counts), ear number and mean kernel weight. 'Tiller survival rate' was calculated as the the ratio of ear number to maximum number of stems (including main stems) per unit area. Each row section was threshed and grain yield weighed. Mean kernel number per ear was calculated from row section yield. All data were then averaged per plot.

Physiological tests

In the three driest sites in 1986 (Nir-Oz, Bet Kama and Bet Govrin), canopy temperatures as a relative estimate of cultivar plant water stress (Blum et al., 1982) were measured in all plots when drought stress developed at about Feekes stage 6 to 9, depending on the site. Measurements were performed at midday with an 'Everest' infrared thermometer. It was aimed from the eye level at the centre of the plot at an angle of 45^0 to the direction of the rows. The thermometer never viewed the ground. Target area diameter was approximately 40cm. Two to four measurements were performed in each trial at weekly intervals as long as drought stress progressed. The mean temperature was calculated for each experimental block and plot temperature was then expressed as a percentage of the block mean temperature. Data were then averaged for each plot over dates.

For the measurement of heat tolerance in terms of cell-membrane thermostability, all cultivars were planted in 10L pots in the greenhouse at Bet Dagan on December 3, 1986. Pots contained a fertilized local Vertisol mixed with peat moss. Two plants were established in each pot and were irrigated frequently until Feekes stage 9 (pre-boot), when irrigation was terminated. Plants were water-stressed (for about 10 days, depending on genotype) until symptoms of stress (leaf rolling) developed. Each pot was then irrigated individually, two days after the onset of flag leaf rolling. Two days after irrigation flag leaves were sampled for the measurement of heat tolerance by the electrolite leakage method (Blum and Ebercon, 1981). The drought stress cycle served as a hardening treatment which is required for a reliable separation of genotypes by this measurement. Briefly, 10 pieces (measuring about $1cm^2$) of flag leaves of five plants were sampled into a stoppered vial. Five vials (replications) per cultivar were subjected to heat treatment in a water bath for 1h at 54^0 (treatment). The additional five vials were kept at 10^0 as controls. All vials were then

incubated in 20ml of deionized water for 24h at 10^0, after which the electrolite leakage from the tissues was measured by the electrical conductivity of the medium. Total background conductivity was measured after autoclaving all vials. Percent injury caused by heat stress was then calculated.

In order to measure juvenile plant growth and osmotic adjustment under drought stress, all cultivars were grown in hydroponics in the growth chamber at 12h day, photosynthetically active radiation of 488 μmol m^{-2} sec^{-1} and $10^0/25^0$ night/day temperatures. The hydroponics system was described elsewhere (Blum, 1989) and consisted of aerated full nutrient solution maintained at pH 6.4. Seedlings of all cultivars were established in the pure nutrient culture (control) and grown for two weeks when polyethylene glycol 6000 (PEG) was added to half of the plants at a concentration giving -0.91MPa of solution water potential (stress treatment). PEG was added in two daily increments of half strength each. Three days after adding PEG, eight plants per cultivar were sampled from each treatment for shoot dry matter weight. A second similar sample was taken after 7d. Growth rate was then calculated as Δdry matter $plant^{-1}$ day^{-1}. Injury to growth by PEG was calculated from stress and control growth rates. After the second sample was taken all plants were returned to tap water overnight in order to regain full turgor. Osmotic adjustment was measured next morning as the difference in osmotic potential at full turgor between stress and control treatments. For each treatment/cultivar combination five leaf sections were frozen at -18^0, after which they were thawed and their osmotic potential was measured psychrometrically (Decagon Devices, Pullman, Washington USA).

For the chemical desiccation test, all cultivars were planted at Bet Dagan on November 27, 1987 in a randomized block design with four replications. Each plot consisted of four rows 8m in length with 30cm spacings between rows. Plants were grown under well-watered conditions and were kept free of diseases. With this test (Blum *et al.*,1983a) plants are desiccated after anthesis with magnesium chlorate in order to reveal the capacity to support kernel growth from mobilized stem reserves in the absence of transient photosynthesis, as is the case for late season drought stress. In this trial the date of anthesis was recorded for each plot. Half of each of plot was sprayed to full wetting with 4% solution of magnesium chlorate at 15 days after anthesis in that plot. Each half was then harvested and threshed separately. Percent injury by chemical desiccation was calculated from kernel weights under desiccation and controls.

RESULTS

Yield and its components

The total amount of water received by the trials through rainfall and irrigation combined (this total is termed here as 'precipitation') ranged from 230 to 755 mm. Based on long-term irrigation trials in different regions of Israel it has been established that the potential evapotranspiration of wheat is between 400 and 550 mm, depending on year and location (Shalhevet *et al.*, 1976). Consequently, in this study at least four trials (marked by asterisks in Table 1) that received a total of only 230 to 325 mm of rainfall were evidently under moisture deficit. In these trials water deficit occurred during

February-March, when stems elongated, ears grew and the canopy was becoming quite large, but rainfall received was only between 27 to 47 mm. Some rainfall (51 to 65 mm) was received in these trials during April-May, which allowed grain filling to proceed. These conclusions are corroborated by visual assessments of plant water stress, whereby a degree of leaf rolling was observed in all cultivars in each of these four trials during the second half March and the relief of these symptoms was noted after rainfall during April. In the other twelve trials (Table 1) the amount of rainfall and/or irrigation provided for a reasonable quantity and distribution of moisture supply throughout the season. In all trials, no water stress occurred during the tillering stage of development which took place during December-January (Table 1).

Mean grain yields of the trials ranged from 225 to 657 gr m^{-2} (Fig.1). A strong positive correlation was revealed between the mean yields of the trials and total precipitation (R^2= 75.7). Thus, variations in wheat yield across trials could be ascribed primarily to the effect of the water regime.

A significant cultivar by trial interaction for yield was found through the analysis of variance (not shown) and a stability analysis of yield by the joint linear regression method (Finlay and Wilkinson, 1963) was performed (Table 2). Fits of all regressions were good, as shown by the R^2 values. Regression slopes ranged from 0.73 (SE=0.03) in 'Miriam' to to 1.11 (SE=0.03) in 'Dariel'. Regression intercepts ranged from -60 (SE=15) in 'Bareket' to 98 (SE=14) in 'Miriam'. Similar regressions were performed also between cultivar yields and total precipitation across trials as an environmental index that is independent of cultivar yields (Table 2). These two stability analyses resulted in quite similar predictions for cultivar responses. The intercept of the joint linear regression ($intercept_y$) was well correlated with the intercept of the regression of yield on precipitation ($intercept_p$) across cultivars (r=0.89). The two respective slopes were also highly correlated (r=0.97).

A graphical representation of the yield response to precipitations of several distinct cultivars is presented in Fig.2. These are linear regressions as presented in Table 2, plotted on a log scale of precipitation in order to clarify differences at low precipitation. The mean yields of 'Shafir' and 'Bethlehem' were quite similar (Table 2). However, 'Bethlehem' had a larger yield at precipitation lower than 300mm than 'Shafir' (Fig.2). This difference was independent of phenology, as both had the same mean heading date (Table 2). The relative difference between these two cultivars was well represented by their respective regression intercepts (y and p, Table 2). By definition of Finlay and Wilkinson (1963), 'V652' was a high yielding and stable cultivar, having a $slope_y$ approximating unity, a high mean yield and an $intercept_y$ greater than zero. However, the stability of this cultivar was not good enough for achieving high yield also under low precipitation (Fig.2), as compared with cultivars such as 'Miriam' and 'Bethlehem'. There was a range of rainfall where cultivar yield responses with respect to precipitation crossed-over. This "crossover" occurred within a range of 250 to 350 mm of precipitation (shaded area in Fig.2). For the joint linear regression, this range corresponded with a trial mean yield of about 250 to 350 g m^{-2}. The apparent water-use efficiency

of precipitation was therefore approximately 1g m^{-2} mm^{-1}, in this part of the relationship. In terms of this analysis, the relative drought resistance of cultivars can be defined by their relative yields below the the "crossover", which is reflected in the intercept of the regression of cultivar yield on the environmental index. For example, 'Miriam' and 'Bethlehem' were more drought resistant than "Shafir".

Of the three yield components measured, only the mean number of ears per m^2 was significantly associated with precipitation across trials (Fig.3), indicating that the mean reduction in yield with the reduction in rainfall was largely associated with the suppression of ear number. Mean maximum tiller number was not associated with precipitation across trials. The reduction in ear number with lower precipitation was parallel to the reduction in tiller survival rate (Fig.3), indicating that water stress effect on ear number took place by way of increased tiller abortion rather then by decreased tillering. This was a reasonable outcome of the fact that where drought stress developed it occurred after the tillering stage of development (Table 1, as discussed above).

A general linear model analysis of mean yield and its components across cultivars (Table 3) revealed that kernel number per ear was the most important yield component affecting yield variations among cultivars. Ear number per m^2 was secondary in importance while kernel weight had the least significant effect in this respect.

Components of drought resistance

No simple associations were found between mean yield (or $intercept_y$ or $intercept_p$, as per Table 2) and mean days to heading across cultivars. This was peculiar, as earliness has always been considered to be an important trait under the dryland conditions of this region and early cultivars are indeed planted where rainfall is low. Simple correlations were calculated within each trial between cultivar yield and days to heading. These correlation coefficients were then evaluated against trial mean yields as the 'environmental index' (Fig.4). It was seen that as trial mean yield was reduced the correlation between cultivar yield and days to heading became negative. Conversely, as trial mean yields increased, the respective correlation became positive. Thus, under low yielding and dry conditions (corresponding to a range of about 230 to 350 mm of precipitation; Fig.4), early cultivars had a relative yield advantage. As conditions improved to a mean yield level of 650 gr m^2 (corresponding to a range of about 600 to 755 mm of precipitation; Fig.4), later heading cultivars had a relative advantage in yield. At the medium yield and precipitation levels, days to heading was not associated with cultivar yield.

For all five physiological parameters involved with plant response to drought and heat stress (Table 4), the variations among cultivars were large and significant at $p \leq 0.01$. Nearly a twofold difference between extreme cultivars was seen for injury by chemical desiccation and by heat. Even greater differences were seen for injury to growth by PEG and for osmotic adjustment.

In order to evaluate the associations between the various physiological attributes and drought resistance, the regression $intercept_y$ and $intercept_p$ (Table 2) were each taken to represent the relative

drought resistance of a cultivar in terms of yield. A stepwise regression and a multiple linear regression were performed for each of the two intercepts on the four physiological attributes (as per Table 4). Injury to growth by PEG was not included in the analysis since it could not be considered as independent of osmotic adjustment (Blum, 1989). The results of the two types of regression were similar, so only results for the multiple linear regression are discussed here. The results of this regression as obtained for $intercept_y$ and $intercept_p$ were very similar, only that the model fit was better for $intercept_p$ (R^2=0.78) than for $intercept_y$ (R^2=0.58). Therefore, the analysis is presented only for $intercept_p$ (Table 5).

The relative drought resistance of the cultivar, as expressed by $intercept_p$, increased with osmotic adjustment, and decreased with heat injury and mean canopy temperature under drought stress. The largest relative effect in the model (74.6% of the total sum of squares) was found for osmotic adjustment. The other two parameters had relatively smaller (though very significant) effects (12 to 13 %, respectively). The ability to support kernel growth from mobilized stem reserves, as represented by injury to kernel weight by chemical desiccation, had no significant effect on $intercept_p$.

DISCUSSION

The trials reported here were performed under variable moisture regimes in a Mediterranean climate. Based on the long term average, the rainfall pattern of this climate is described as a typical winter rainy season that begins at about wheat planting time (November-December), develops through mid-winter (January-February) and terminates before wheat harvest in the spring (April-May). However, this climate is also characterized by large variability in rainfall, especially in regions of low total annual rainfall. Variability in total annual rainfall and its seasonal distribution is the greatest within the range of about 250 to 350 mm of total annual rainfall and under these conditions the long-term typical Mediterranean seasonal rainfall is not commonly experienced, as seen in Southern Israel (Dr. N. Seligman, personal communication). The two years sampled in this study were characterized by a mid-season drought stress during February-March in four locations of the lowest rainfall. The results of this study are therefore limited to this type of drought stress, namely at stem elongation and ear formation.

A large proportion of the variation in mean yield among trials (75.7%) was explained by the amount of precipitation. Thus, the water regime, as compared with other possible environmental variables, had the main effect on yield variation among trials. The apparent mean water-use efficiency of precipitation was comparable to 10kg ha^{-1} mm^{-1}, which should indicate that wheat in these trials was largely free of any stress apart from drought stress (French and Schultz, 1984). Under these conditions variations between cultivars is expected to result mainly from variations in their response to the water regime. Undoubtedly, yield in these trials were reduced by drought stress from the maximum level of about 650 g m^{-2}.

An urgent issue in breeding for drought resistance is the understanding and the isolation of the relative effects of a high yield potential and the specific drought adaptive responses in sustaining cultivar yield as drought stress increases (*e.g.* Fischer and Maurer, 1978). Under the conditions of this study cultivars having a large yield potential such as "V652" maintained their relative high yield as long as it was not reduced below about 350 g m^{-2}. A "crossover" in yield of cultivars occurred at yield of about 250 to 350 gr m^{-2}, corresponding to a total precipitation of around 250 to 350 mm. Such a "crossover" has been commonly observed by others for various wheat cultivars, and it may be observed at higher (*e.g.* Sinha *et al.*, 1986) or lower (*e.g.* Laing and Fischer, 1977) mean site grain yield. We suggest that this "crossover" may occur at lower mean yields, if factors other than the water regime are involved with yield reductions, such as low soil fertility. It may also vary with the mean yield of the cultivars tested. Thus, if selection for drought resistance by measuring yield is to be performed independently of the effect of yield potential, drought stress must be severe enough to depress yield below the "crossover" range. Alternatively, if mean yields are not sufficiently depressed by drought stress below the "crossover", the selection for yield will most likely operate mainly on genetic variation for yield potential and not on genetic variation for drought adaptation. A definition of the "crossover" yield level for the target environment and the germplasm concerned is therefore essential before any attempt is made to improve drought resistance by selection for yield under drought stress. The significance of this "crossover" with respect to defined plant traits which may be used in selection is also important. In this study, at least the phenology of the cultivars corresponded with the interaction between yield and drought stress. Early cultivars apparently had a yield advantage only below the "crossover" range of yield.

Where drought stress occurred in these trials it developed for about a month prior to heading, followed by a recovery period during grain filling. Under these conditions, the main yield component associated with yield reduction across trials was ear number. Ear number was reduced mainly as a consequence of increased tiller abortion under drought stress. Cultivars that performed better under these drought stress conditions apparently had a better capacity to compensate for reduced ear number by sustaining a high number of kernels per ear (Table 3). This is already supported by the finding that when ear number is reduced by drought stress, cultivars that sustain a larger kernel number per ear are likely to yield more (Blum *et al.*, 1990). Kernel weight was relatively unimportant in affecting yield variation among cultivars, evidently because grain filling was largely free of drought stress. An advantage for a moderately-tillering or a 'uniculm' plant as an ideotype for semi-arid Mediterranean conditions has been suggested (Islam and Sedgley, 1981), but not necessarily reaffirmed (Whan *et al.*, 1988). While a strictly uniculm wheat was not tested here, there was no evidence in the results to suggest that moderate tillering under these conditions had any advantage. There was no relationship between mean yield or the intercepts of the regressions of yield on precipitation or on trial mean yield across cultivars and the maximum number of tillers or ears per plant. There was also no relationship between the maximum number of tillers and the final number of ears per unit area. What was evidently important for sustaining yield in these trials was the

capacity to sustain kernel number per ear in compensation for the reduction in ear number under stress.

Three physiological parameters were found to be associated with drought resistance in terms of yield as expressed by the intercept of the regression of cultivar yield on the environmental index, whether the index represented mean site yields or precipitation. Apart from canopy temperature, all physiological attributes were estimated in separate experiments from those in which yield was measured. Therefore, any associations between these physiological attributes and yield related parameters across cultivars were largely free of unforeseen environmental covariances and may be considered as primarily genetical. Of these physiological parameters, the capacity for osmotic adjustment had the greatest effect while heat tolerance and canopy temperature were of lesser importance (Table 5). The ability to sustain kernel growth by mobilized stem reserves as estimated by the chemical desiccation test was unimportant, evidently because grain filling was largely free of drought stress. In the absence of environmental stress on transient photosynthesis during grain filling, there is only a limited demand for reserve mobilization and cultivars differences for this capacity would not be expressed.

It was found in this study that heat injury, as estimated by cellular membrane thermostability was negatively related to osmotic adjustment across cultivars (Fig.5). This rather high correlation (r=0.90) tends to support the work of Paleg *et al.* (1985) and others (Blum, 1988) who indicated a role for accumulated solutes in the protection of various cellular functions, including these associated with cellular membranes. While canopy temperature was not found to be related to osmotic adjustment across cultivars, it would be reasonable to assume that if osmotic adjustment plays a role in sustaining leaf turgor and/or in allowing deep soil moisture extraction under drought stress (Morgan and Condon, 1986), this should indeed be reflected in lower canopy temperatures. Thus it appears that in this study both heat tolerance and low canopy temperatures may have depended, at least partly, on osmotic adjustment.

At the very low yield levels, plant earliness was important in sustaining yield. The contribution of early heading under the conditions of a pre-heading drought stress in this study is not clear. The conventions assume an advantage for earliness as an "escape" mechanism when the crop is subjected to a post-heading "terminal" stress. That was not the case here. It was however interesting to find a significant negative correlation across cultivars (r=-0.72) between days to heading and osmotic adjustment, indicating that early cultivars tended to have better osmotic adjustment. Inherent physiological differences between early and late genotypes, which are independent of crop growth duration or aging, have already been suggested for the role of fatty acids in drought resistance (Kuiper and Stuiver, 1972), for recovery from drought stress in soybeans (Cure *et al.*, 1983), for leaf photosynthesis in sorghum (Blum *et al.*, 1989) and maize (Dwyer *et al.*, 1989) and for root growth in sorghum (Blum *et al.*, 1977).

The final conclusion with respect to the physiological parameters evaluated here is that the variations among cultivars in yield under drought stress were associated mainly with osmotic

adjustment as a major physiological attribute. Since stress occurred during the period of ear growth and development, a greater capacity for osmotic adjustment apparently allowed sustained ear growth under drought stress and the maintenance of relatively larger ears in the larger yielding cultivars.

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Table 1. Rainfall and irrigation in 16 wheat trials over 3 major growth periods: October-January (planting to end of tillering); February-March (stem elongation and ear formation) and April-may (grain filling).

Location	Year	Rainfall (+ Irrigation) mm			Total
		October-January	February-March	April-May	(mm)
Bet Dagan	1986	206	114 (+130)	50 (+100)	600
Bet Govrin	1986*	161	47	62	270
Hama	1986	309	161	63	533
Lavie	1986*	141	38	51	230
Nahal-Oz	1986	160	106 (+100)	64 (+50)	480
Ein-Harraziv	1986	116 (+100)	95 (+80)	40 (+80)	511
Nir-Oz	1986*	143	27	65	235
Sarid	1986	227	113	60	400
Bet Govrin	1987	390	101	21	512
Lavie	1987	329	99 (+100)	51 (+100)	679
Moiedet	1987	358	133	10	501
Nahal-Oz	1987	334	86 (+100)	4 (+100)	684
Nir-Oz	1987*	220	43	62	325
Kefar Rupin	1987	237 (+30)	46 (+100)	1 (+100)	514
Sarid	1987	396	124	12	532
Yavor	1987	535	208	12	755

(*) see text.

Table 2. Cultivar mean days to heading, mean yield and results of the stability analysis by the joint linear regression (subscript y) and the linear regression of cultivar yield on site precipitation (subscript p) over 16 trials (values in parenthesis are S.E. of the estimate).

Cultivar	Days to heading	Height (cm)	Intercept (y)	Slope (y)	R^2 (y)	Intercept (p)	Slope (p)	R^2 (p)	Mean yield (gr m^2)
V652	89.1	76	14 (15)	1.08 (0.03)	0.93	151 (27)	0.81 (0.05)	0.72	542 (22.6)
Daniel	104.8	95	-23 (14)	1.11 (0.03)	0.92	117 (23)	0.83 (0.04)	0.71	519 (23.3)
Deganit	89.8	74	7 (17)	1.04 (0.03)	0.92	115 (29)	0.83 (0.06)	0.80	516 (21.9)
Atir	89.5	88	3 (12)	1.04 (0.02)	0.94	118 (23)	0.81 (0.05)	0.79	512 (21.7)
Barkaee	85.3	69	5 (14)	1.02 (0.03)	0.92	120 (26)	0.78 (0.05)	0.76	500 (21.3)
V748	93.1	95	-44 (14)	1.11 (0.03)	0.95	98 (28)	0.82 (0.05)	0.72	497 (22.9)
Shafir	85.7	87	-42 (11)	1.10 (0.02)	0.96	102 (27)	0.81 (0.05)	0.72	494 (22.6)
Bethlehem	85.7	91	47 (16)	.90 (0.03)	0.94	165 (22)	0.66 (0.04)	0.71	486 (21.9)
Lachish	97.3	96	-12 (20)	1.01 (0.04)	0.87	90 (24)	0.81 (0.05)	0.78	481 (21.7)
Bareket	94.0	93	-60 (15)	1.09 (0.03)	0.94	69 (24)	0.83 (0.05)	0.75	470 (21.3)
Miriam	85.8	94	98 (14)	.73 (0.03)	0.88	177 (18)	0.57 (0.04)	0.75	454 (15.7)
Inbar	100.8	86	12 (19)	.86 (0.04)	0.85	104 (22)	0.67 (0.04)	0.85	429 (18.7)

Coefficient of correlation between $intercept_y$ and $intercept_p$ is r=0.89.

Coefficient of correlation between $slope_y$ and $slope_p$ is r=0.97.

Table 3. The relative contribution (sum of squares as percent of total) of the variations in three yield components to the variations in mean grain yield between cultivars. Pooled data over two years. General linear model R^2=0.88.

Source	SS (%)	F Ratio	Probability
Kernels per ear	63.6%	61.44	<0.001
Ears per m^2	31.3%	30.25	<0.001
Kernel weight	5.1%	4.95	0.036
Total sum of squares	68,932		

Table 4. Cultivars mean, minimum, maximum and standard deviation values for five physiological parameters of drought resistance.

Variable	Unit	Mean	Minimum	Maximum	S.D.
Injury by chemical desiccation	%	36.2	19.7	51.2	9.1
Heat Injury	%	77.4	56.3	100.0	13.1
Injury to growth by PEG	%	56.2	12.3	98.4	27.4
Osmotic adjustment	MPa	0.51	0.21	0.75	0.1
Mean canopy temperature	%*	100.3	97.5	103.6	2.0

(*) As perecent of the mean temperature of the block in each trials; data are presented as a mean over three trials.

Table 5. The multiple linear regression of $intercept_p$ (the interecpt of the linear regression of cultivar yield on precipitation, as per Table 1) on osmotic adjustment, heat injury and mean canopy temperature. Model R^2=0.78.

Parameter estimates

Term	Estimate	S.E.	t Ratio
Intercept	568.2	27.6	20.5
Osmotic adjustment	20.1	.376	53.5
Heat injury	-1.02	.045	-22.6
Mean canopy temperature	-6.62	.307	-21.5

Test of effect

Source	SS	SS as % of Total	F Ratio
Osmotic adjustment	587,743	74.6	999
Heat injury	105,120	13.3	512
Mean canopy temperature	94,985	12.1	463

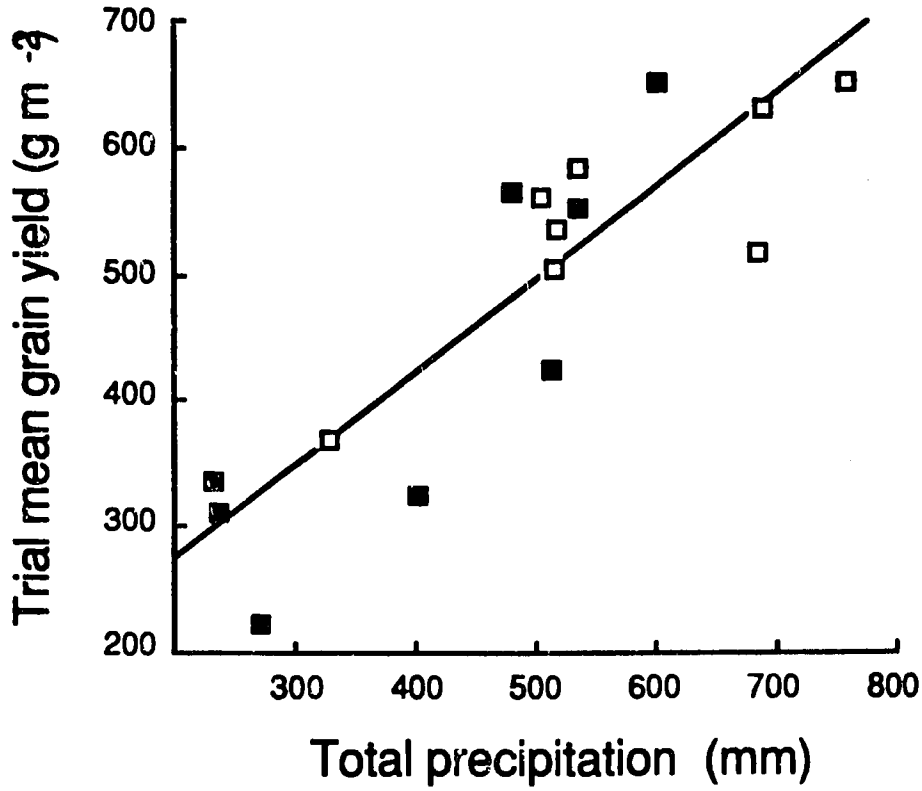

Fig. 1.
The linear regression of mean trial grain yield on trial precipitation. Bold squares: 1986. Open squares: 1987. $y=128.1+0.74x$; $R^2=0.76$.

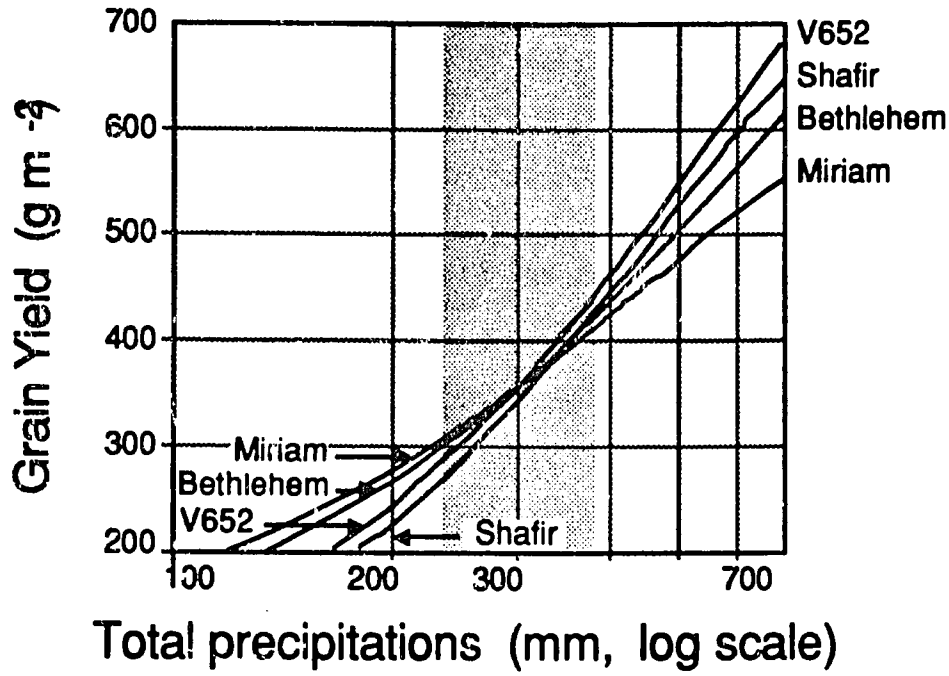

Fig. 2.
The linear regression of cultivar yield on trial precipitation (n=16, as per Table 1) plotted on a log scale of precipitation. The shaded area marks the range of yield "crossover" (see text).

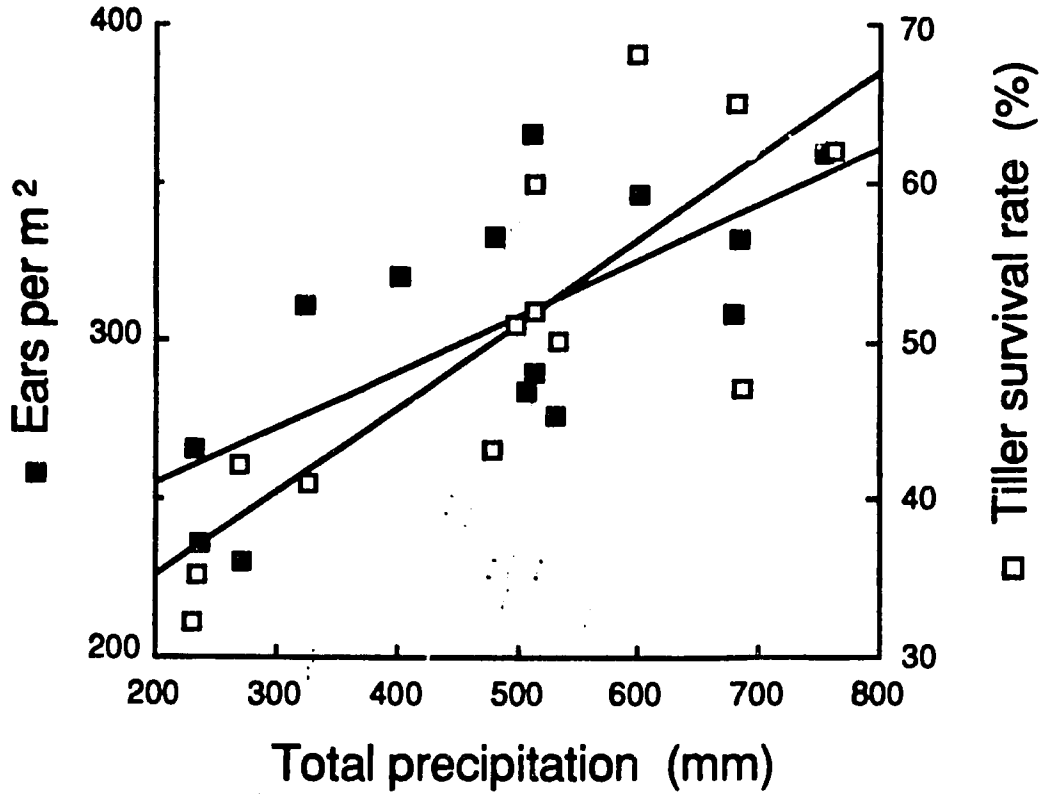

Fig. 3
The linear regressions of mean trial ear number per unit area and mean trial tiller survival rate (the number of ears as percent of the maximum number of stems per unit area) on trial precipitation. Bold squares: ears per m^2; $y = 220.8 + 0.173x$; $R^2 = 0.48$. Open squares: tiller survival rate; $y = -1.24 + 0.023x$; $R^2 = 0.69$.

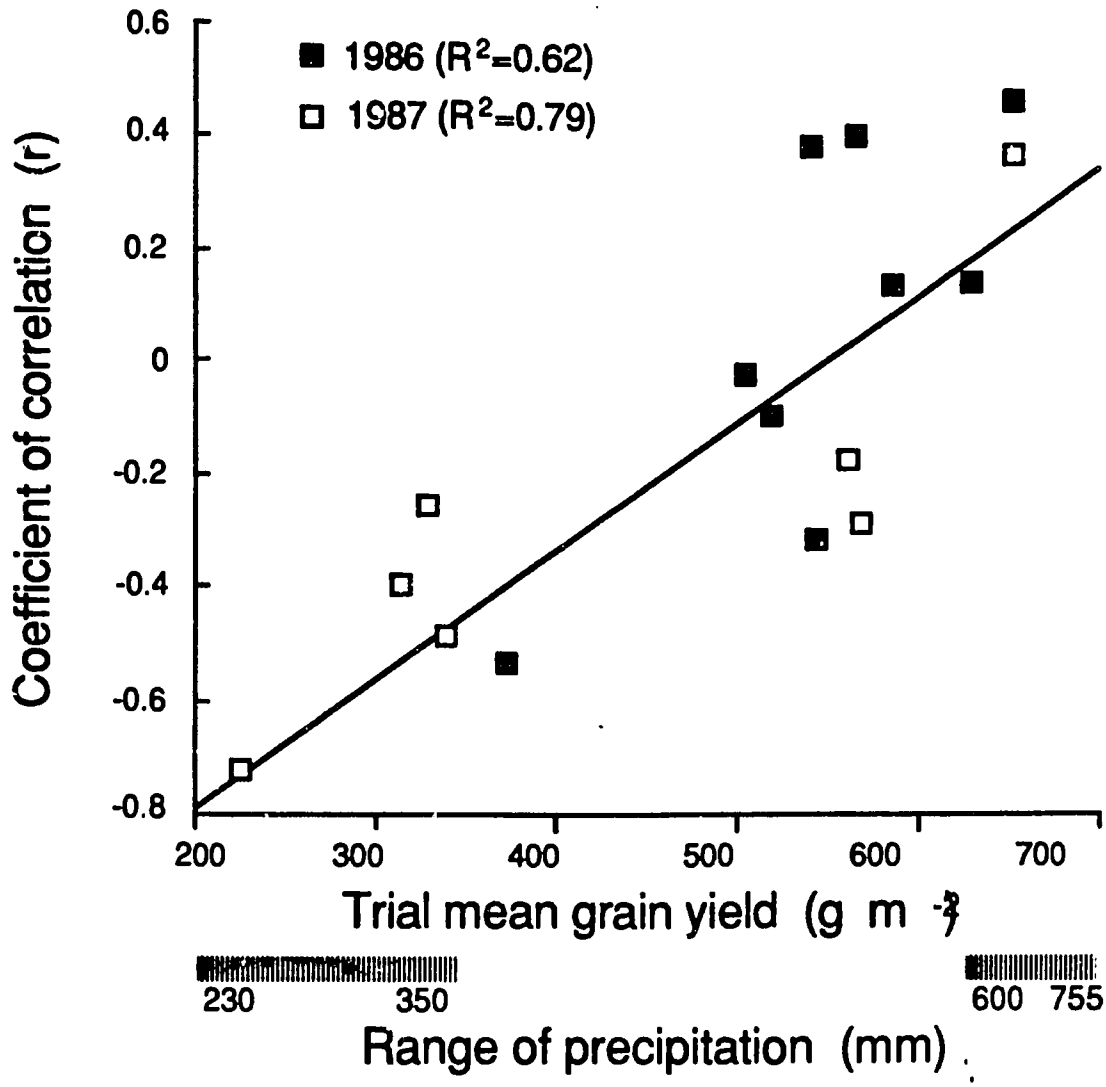

Fig. 4
The relationship between the coefficient of correlation between grain yield and days to heading of cultivars within a trial and mean trial grain yield. The corresponding ranges of trial precipitation are presented as horizontal bars (see text). Bold squares: 1986; open squares: 1987. $y=-1.24+0.023x$; $R^2=0.60$.

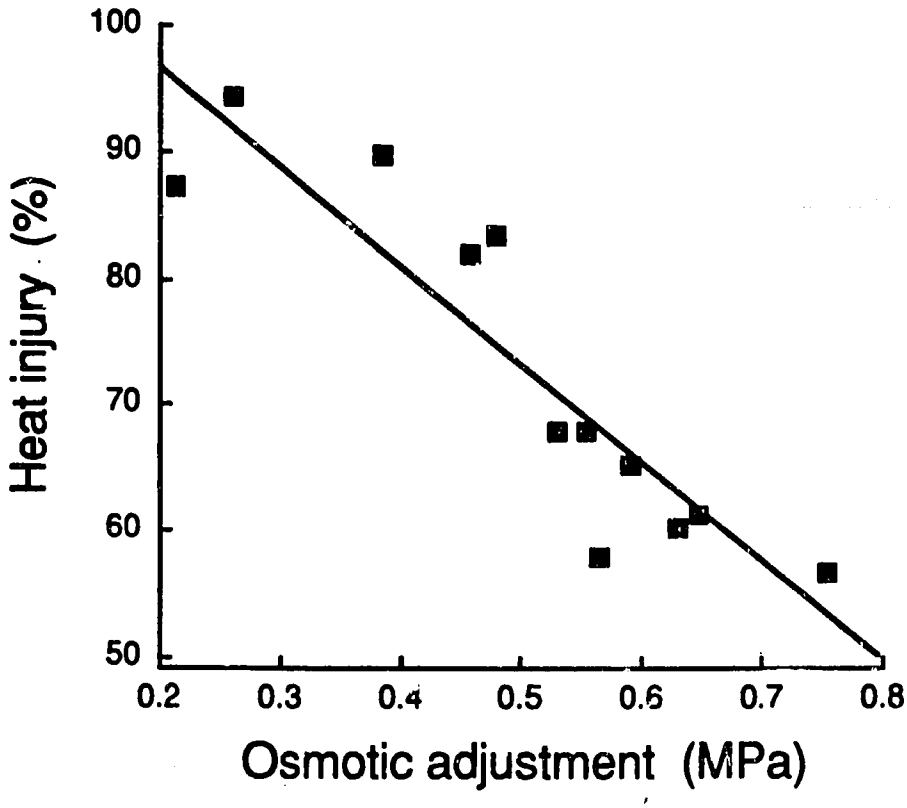

Fig. 5.
The linear regression of percent heat injury on osmotic adjustment across 12 cultivars. $y=112.2-77.8x$; $R^2=0.81$

Variation among wheat cultivars in the response of leaf gas exchange to light.

ABSTRACT

This research was done in order to explore genetic variations in carbon exchange rate (CER) of spring wheat (*Triticum aestivum* L.) leaves in response to variable photosynthetically active radiation (PAR) and to compare old and new Israeli cultivars in this respect. Leaf gas exchange was measured in detached turgid leaves of 17 cultivars in an open system at 25^{0}C when PAR was reduced from *ca.* 1200 to 200 μmol/m^2 per sec. Linear regressions of CER, stomatal conductance, transpiration and leaf internal CO_2 concentration (Ci) on log PAR were fitted for each leaf (regression R^2 was never <0.79) and the regressions were compared among cultivars by analysis of variance.

Genotypes differed signif ly for the slope (b) but not the intercept (a) of the regression of CER on log PAR, indicating that genotypic differences for CER increased with increasing PAR. Photosynthetic capacity, as expressed by the ratio of CER to Ci, differed significantly among cultivars only at high PAR. Stomatal conductance and transpiration increased in a linear or a nonlinear fashion with log PAR and differences among cultivars for both were the greatest at medium to low PAR. Photosynthetic water-use efficiency (WUE) and its variation among cultivars were greatest at the highest PAR. Genotypic variation in CER at high PAR was confirmed by repeated results for 11 cultivars over two independent experiments.

The recently developed high-yielding cultivar V652 had a higher maximum CER, higher photosynthetic capacity and greater WUE at high PAR than older and lower yielding cultivars. The results suggest an upward genetic shift in photosynthetic capacity and in CER at high PAR when selection for yield was performed under the high-irradiation conditions of Israel.

INTRODUCTION

Within-species genotypic variation in leaf photosynthesis is of interest to crop physiologists and breeders on the possible grounds that leaf photosynthesis may serve as an indirect physiological marker for high plant productivity. Genotypic variations in photosynthesis at light saturation (P_{max}) has long been observed in wheat (*e.g.* Evans & Dunstone 1970; Kaul 1974). More recently, such variations were ascribed mainly to variable photosystem II activities which were found to correspond with differences in the ploidy of cultivated and wild wheats (Leech, Leese & Jellings 1985; Austin *et al.* 1988). The modulation of genetic variation in photosynthesis by ploidy has been partly ascribed to the inhibitory effects on photosynthesis of factors on the D genome of wheat (Haour-Lurton & Planchon 1985).

Most of those who have been working in this subject conclude that P_{max} is not associated with plant production, mainly because of the overriding effects of leaf size, leaf longevity, canopy architecture, assimilate partitioning and sink effects on the source. Further studies attempted to avoid the characterization of genotypic leaf CER (carbon exchange rate) by a unique and single measurement, such as P_{max}, while looking for an integrated measure over time or environmental conditions. For example in sorghum, stability in leaf CER over variable environmental conditions is well associated with heterosis in plant production (Blum 1989). In wheat, integrated CER over the life of the flag leaf is well associated with yield per ear in many cultivars (Rawson *et al.* 1983).

Light, as a major determinant of photosynthesis, fluctuates seasonally, daily and hourly during the wheat growing cycle. Photon flux densities below the saturation level for wheat (*ca.* 1500 $\mu mol/m^2$ per sec) are common in many wheat-growing regions. The shape of the apparent light response curve may therefore affect integrated carbon assimilation over time. Although this has been established for species of sun and shade plants (Bjorkman 1981), such information is scarce for cultivars of crop plants. In a unique study, Tu *et al.* (1988) demonstrated that a Chinese rice cultivar adapted to local conditions of low irradiance had an advantage in photosynthesis at low-photon irradiance over American cultivars developed under conditions of high irradiance. Winzeler & Nosberger (1980) found that two German wheat cultivars differed in the light response curve of CER, but the difference was largely a function of a respective difference in flag leaf senescence rate. Day & Chalabi (1988) predicted from their calculations that variations in P_{max} would affect wheat yields only in high-radiation environments, typical of Israel.

It would therefore be interesting to ascertain whether high yielding cultivars selected in Israel are characterized by a large P_{max}. This study evaluated the light response of gas exchange in detached flag leaves of different common wheat cultivars released in Israel over a period of 18 years, and in material from the current wheat breeding programme.

MATERIALS AND METHODS

1988/89 experiment

Seventeen cultivars and selections of common spring wheat (*Triticum aestivum* L.) were tested (Table 1). All material was grown during the normal winter season at Bet Dagan (latitude $34^{0}4'$N). Materials were planted in the field on 2 December 1988, in a randomized blocks design with five replications. Each plot consisted of four rows 5 m long with 30 cm between rows. Plants were grown under conditions prescribed for best growth, including fertilization, irrigation, disease and weed control. Plant development, appearance and colour were excellent. Heading date was noted for all cultivars and spanned 12 days between the earliest and the latest cultivar. At the onset of heading, plants of each cultivar and replicate were pulled out of the wet soil together with a large root clump, placed in a bucket of water, brought to the laboratory and put in a growth chamber at 15^{0}C under 542 $\mu mol/m^2$ per sec of photosynthetic active radiation (PAR).

Flag leaves were sampled for measurement from plants brought to the growth chamber that morning. Flag leaves were taken strictly from main stems from which the ear just emerged, to reduce variations in leaf gas exchange due to leaf age (Winzeler & Nosberger 1980; Rawson *et al.* 1983). Within each cultivar, leaves of the same size were selected to minimize the effect of leaf size on variation in CER (Bhagsari & Brown 1986). The leaf sheath was cut *ca.* 10 cm below the flag leaf lamina and placed in a vial with water under a quartz- iodine light source providing 1200 ± 50 $\mu mol/m^2$ per sec of PAR at the leaf surface. After 15 min, the leaf was used for gas exchange measurements. Preliminary tests had shown that CER at 25^{0}C under 1200 ± 50 $\mu mol/m^2$ per sec of PAR did not change significantly for at least 2 h, the time during which all measurements were performed with any single leaf.

Leaf gas exchange was measured with the ADC system (Analytical Development Co., UK), which has been described elsewhere (Long & Hallgren 1985). The system consisted of a small infrared gas analyser (used in the differential mode), an accurate flow pump and meter unit, a leaf chamber and a data-logger. Gas exchange was measured in the leaf chamber as an open system, so that measurements could proceed for a long time with the chamber attached to the same leaf. Leaf chamber temperature, air humidity, irradiance and air flow rate were monitored continuously. Using these data and the appropriate physical constants and formulae (Long & Hallgren 1985), CER, internal CO_2 concentration, stomatal conductance, transpiration and leaf temperature were recorded every 8 s.

Air was drawn into the system from outside the laboratory at a typical concentration of 335-345 $\mu l/l^{-1}$ of CO_2. Leaf temperature was regulated by directing a hot/cool air blower to the heat-sink at the base of the leaf chamber. By observing the displayed leaf temperature and by manually adjusting the voltage supply to the heater or its distance from the leaf chamber, leaf temperature was controlled to 25 ± 0.1^{0}C, at a room temperature of *ca.* 18^{0}C.

Gas exchange measurements were made as PAR was reduced from 1200±50 $\mu mol/m^2$ per sec in increments of *ca.* 200 $\mu mol/m^2$ per sec. When irradiance was reduced, CER displayed marked oscillations for no more than 10 min, after which it stabilized. Therefore, CER was always recorded twice, 12 and 15 min after reducing irradiance. The two records were then averaged to give one

value for each leaf x PAR combination. Five to eight leaves (replicates) per cultivar were measured. In six additional leaves of the cultivar Lachish, which were subjected to the above measurement procedure, the section above the leaf chamber was cut at the onset of gas exchange measurements, placed in a pressure chamber and its leaf water potential measured. Upon the termination of gas exchange measurements, the water potential of the remainder of its leaf was determined. Mean leaf water potential was high and statistically the same (-0.52±0.08 MPa) before and after gas exchange measurements, indicating stable leaf water status throughout the measurements.

When leaf gas exchange measurements were terminated, leaf area was measured by weighing its print (made with a photocopier machine) against a calibration of paper area on paper weight. The midsection of each leaf (5 cm in length) was then cut, its area measured (as a rectangle) and its total chlorophyll content determined by the N,N-dimethylformamide extraction method (Moran & Porath 1980).

1989/90 experiment

Eleven of the cultivars tested in 1988 were grown in soil-filled pots in a net-house at Bet Dagan. Pots were sown on 11 December 1989 and two plants were established in each and grown under conditions prescribed for best growth, including fertilization, irrigation and disease control. The experimental design was randomized blocks with five replications (pots). When each cultivar headed, pots were brought to the laboratory and intact main-stem flag leaves were measured for gas exchange by attaching the leaf-chamber to the leaf. Measurements were performed at a leaf temperature of 25±0.1^{0}C and leaf irradiance of 1100±25 μmol/m^2 per sec. Two leaves per pot were measured and averaged as a replication. Differences among cultivars in carbon exchange rate were tested by analysis of variance.

RESULTS AND DISCUSSION

The primary consideration in analysing the data was to develop a mathematical treatment of the light response curve of CER that would allow testing for significant genotypic variation by analysis of variance. A typical light response curve for CER in two cultivars over all replications is presented in Fig.1 (inset). The calculation of apparent quantum yield was attempted by fitting a linear regression for CER data at low (≤400 μmol/m^2 per sec) PAR. This analysis was not sensitive enough to reveal significant variation among cultivars, partly because of large variations between leaves, partly because of lack of data at very low PAR and probably also because within-species genotypic variation for quantum yield is most unlikely (Bjorkman 1981).

A simple method for examining genotypic variation in apparent carbon assimilation over a range of PAR, involved plotting CER versus log PAR (Fig.1). A linear regression were fitted for each individual leaf and the R^2 of all regressions was never <0.79. The intercepts and slopes of the regressions were then subjected to analysis of variance.

Significant differences between cultivars were found for the slope (b) but not for the intercept (a) of the linear regression of CER on log PAR (Table 1), indicating that genotypic variation for CER in these cultivars increased with increasing PAR (Fig.1). Genotypes differed significantly ($P \leq 0.05$) in

flag leaf area (data not shown). The correlation across cultivars between flag leaf area and the slope (b) of the regression of CER on log PAR was not significant (R=-0.316, P=0.16, N=17), indicating that leaf area was not an important determinant of genotypic variation for CER. Genotypes differed significantly ($P \leq 0.01$) in chlorophyll content per unit leaf area, which ranged from 37.6 $\mu g/cm^2$ in Seri to 58.8 $\mu g/cm^2$ in V1892-11. Chlorophyll content was not correlated (r=0.04) with the slope of the regression of CER on log PAR across cultivars. Data for leaf gas exchange were also expressed as CER per unit chlorophyll content and regressed on log PAR (results not shown). Genotypes differed significantly ($P \leq 0.05$) in the slope (b) of this linear regression. The slopes of the two regressions (namely CER and CER/unit chlorophyll on log PAR) were well correlated across cultivars (R=0.81, $P \leq 0.01$). Thus, chlorophyll content was not a factor affecting the variation among these cultivars in the apparent light response of CER.

The cultivars Miriam, Lachish, Shafir and V652 are examples of the progress made in the Israeli wheat breeding programmme since 1968 (Table 1). For a clearer representation of the results for these cultivars, only the most recent and highest-yielding release (V652) was compared with one of the older cultivars (Lachish). The other two old cultivars fell between these two or near Lachish in all further comparisons (Figures 1-5).

Cultivar V652 had a significantly greater slope of the regression of CER on log PAR, resulting in an increasing advantage over Lachish in CER as PAR increased (Fig.1). Stomatal conductance increased (linearly or non-linearly) with PAR in all cultivars (data not shown). It was consistently greater in V652 than in Lachish at all values of PAR (Fig.2), especially at the medium and lower irradiance. Stomatal conductance in V652 did not increase with PAR *ca.* >1000 $\mu mol/m^2$ per sec and compared with that in Lachish it appeared to be light saturated at about 1000 to 1200 $\mu mol\ m^{-2}\ sec^{-1}$. Comparison between Figs.1 and 2 indicates that the increasing advantage in CER at high PAR of V652 over Lachish could not be ascribed to a corresponding advantage in stomatal conductance.

Internal CO_2 concentration (Ci), as normalized for external CO_2 concentration (Ca) (C_i/C_a), declined linearly with log PAR in all cultivars (R^2 was never <0.60; data not shown). CER increased linearly with decrease in C_i/C_a (Fig.3, inset). All cultivars differed significantly ($P \leq 0.05$) in the slope (b), but not the intercept (a) of this regression, indicating that cultivars differed in CER, especially when C_i/C_a was low, a situation corresponding with high PAR (Fig.3). Therefore, differences between cultivars in photosynthetic capacity (ratio of CER to Ci/Ca, Fig.3) were the most prominent at the highest irradiance and V652 was significantly superior to Lachish in this respect.

Transpiration increased linearly with log PAR in all cultivars (data not shown). Cultivars differed significantly for both the slope (b) and intercept (a) of this regression (Fig.4). Differences in transpiration between cultivars were generally least at the highest PAR and they increased as PAR decreased. V652 had greater transpiration than Lachish at all values of PAR; the difference between the two cultivars was generally consistent with the respective difference in stomatal conductance (Fig.2).

Photosynthetic water-use efficiency of a single leaf (the ratio of CER to transpiration; WUE) increased linearly with log PAR. All cultivars differed significantly ($P \leq 0.05$) for the slope (b) but not the intercept (a) of the regression (Fig.5) and the differences between cultivars in WUE corresponded to the differences in the relationship between CER (Fig.1) or photosynthetic capacity (Fig.3) and log PAR. A comparison of Fig. 3, 4 and 5 shows that water-use efficiency at high irradiance was greater in V652 than in Lachish (Fig.5) largely because of the greater photosynthetic capacity of V652 at high PAR and in spite of its relatively high transpiration.

The existence of significant genotypic variation in CER at high PAR is supported by data from intact leaves of 11 cultivars measured in 1989/90 (Table 2). Generally, rates of CER at high PAR were similar for detached (Fig.1, 1988/89) and intact (Table 2, 1989/90) leaves taken from plants growing in two different seasons, respectively. A very significant correlation was revealed in the 11 cultivars between CER measured in 1989/90 (Table 1) and the slope of the regression of CER on log PAR (Table 1) ($R=0.82$, $P \leq 0.05$) or CER calculated for PAR of 1100 $\mu mol/m^2$ per sec ($R=0.88$, $P \leq 0.05$). These correlations indicate that genotypic differences in CER at high PAR are real, as these differences held very well over two seasons and irrespective of whether leaves were intact or detached during measurements.

In conclusion, CER, photosynthetic capacity, stomatal conductance and transpiration increased in response to PAR (at constant leaf temperature and leaf water status). Genotypic variation in CER and photosynthetic capacity was greatest and genotypic variations in transpiration were least at the highest PAR used. Genotypic variation in water-use efficiency was greatest at the highest PAR.

The cultivar V652 has a long-standing, proven reputation for producing a high and stable yield over many locations and years in Israel (Table 1). Its successful performance could not be ascribed to an advantage in any single yield component, harvest index or various phenological attributes (A. Blum, unpublished data), so the reasons for its superiour performance remained an open question. The present results indicate that selection of V652 from its source material under Israeli conditions resulted in improved adaptation to high irradiance, as seen in its high maximum CER and photosynthetic capacity. As Day & Chalabi (1988) have pointed out this may be expected under the high irradiation conditions of Israel.

Austin, *et al.* (1980) were among the first to suggest that modern winter wheat cultivars outyielded older ones mainly because of a greater harvest index rather than a greater total biomass, although a slight increase in biomass for modern cultivars was later indicated (Austin, Ford & Morgan 1989). This finding was supported for winter wheat cultivars developed in New York State in the U.S.A (Gent & Kiyomoto 1985), where biomass and photosynthesis were not found to be involved with the yield advantage of modern cultivars. No change in biomass with year of release was detected among American winter wheat cultivars tested in Kansas (Cox *et al.* 1988). On the other hand, work reported for spring wheat in high radiation environments, such as Australia (Siddique *et al.* 1989) and India (Sinha *et al.* 1981) shows genetic improvement in modern cultivars

for biomass and attributes of photosynthesis or photosynthetic capacity. The study reported here also indicates genetic improvement for photosynthetic properties in a spring wheat cultivar recently selected in a high-radiation environment.

The apparent disagreement on whether, in the historical perspective, biomass production and attributes of photosynthesis have been improved is of great importance for the future of wheat breeding and it requires further investigation. Based on the research cited above and on the results reported here, such investigations may consider two explanations for the conflicting results: (a) biomass and photosynthesis are less likely to be improved in winter wheat than in spring wheat; (b) the genetic improvement of photosynthesis can be realized only under high irradiation conditions, as pointed out by Day & Chalabi (1988).

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Table 1. Notes on wheat cultivars used in this study, based on long-term and multilocation testing in Israel, and the slope (b) of the linear regression of carbon exchange rate on log photosynthetically active radiation. Mean yields are from 42 location x year trials.

Genotype	Year of Release	Notes	Mean yield (g/m^2)	Slope (b)
Miriam	1968	Standard cultivar, low yield potential.	453	12.49
Lachish	1971	Standard cultivar, low-medium yield potential.	481	12.12
Shafir	1977	Standard cultivar, medium yield potential.	494	14.20
V652	1986	Consistently the highest yielding cultivar.	542	15.30
V748-74-1S	-	Discarded selection *.		11.80
V1074	-	Discarded selection.		14.77
V1806-11	-	Discarded selection.		14.95
V879	-	Discarded selection.		11.44
V747-16-1	-	Discarded selection.		13.05
V839-9	-	Discarded selection.		14.70
V940-41	-	Discarded selection.		14.83
V979-17-11	-	Discarded selection.		11.98
V1283-7-4	-	Discarded selection.		14.26
V1349	-	Discarded selection.		13.55
V1353	-	Discarded selection.		14.21
V1892-11	-	Discarded selection.		13.90
Seri	-	Medium yielding CIMMYT cultivar.		13.64
S.E. (D.F.=80)				0.71

(*) Selections discarded for different reasons, such as low yield, susceptibility to diseases or poor grain quality.

Table 2. Carbon exchange rate (CER) in intact flag leaves of 11 wheat cultivars, measured at 25^{0}C and photosynthetically active radiation (PAR) of 1100 µmol/m^2 per sec (1989/90 experiment).

Cultivar	CER (µmol/m^2 per sec)
V652	16.6
V940-41	15.1
Shafir	13.6
V747-16-1	13.6
V1074	13.4
V1283-7-4	13.4
Miriam	13.1
Seri	12.8
Lachish	12.5
V748-74-1S	11.3
V979-17-11	9.6
S.E. (D.F.=40)	0.69

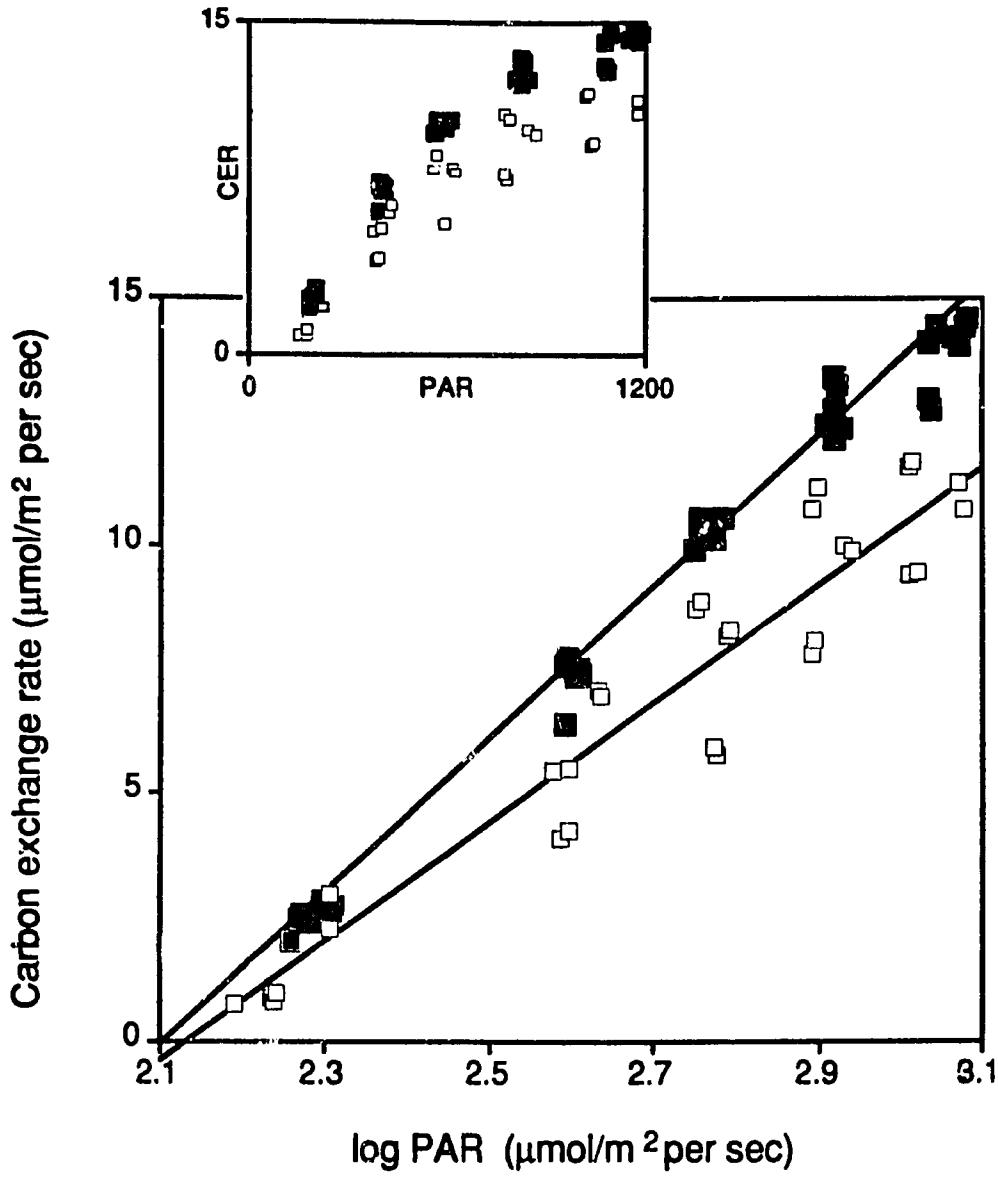

Fig.3.
Ratio of carbon exchange rate (CER) to leaf internal CO2 concentration (Ci) normalized for external CO2 concentration (Ca) (Ci/Ca) in relations to photosynthetically active radiation (PAR, log transformation) in the wheat V652 (■) (y=-43.4+20.1x; R2=0.98) and Lachish (□) (y=-34.0+15.7x; R2=0.77). Inset: V652: y=69.2-69.8x; R2=0.90. Lachish: y=56.7-59.0x; R2=0.86.

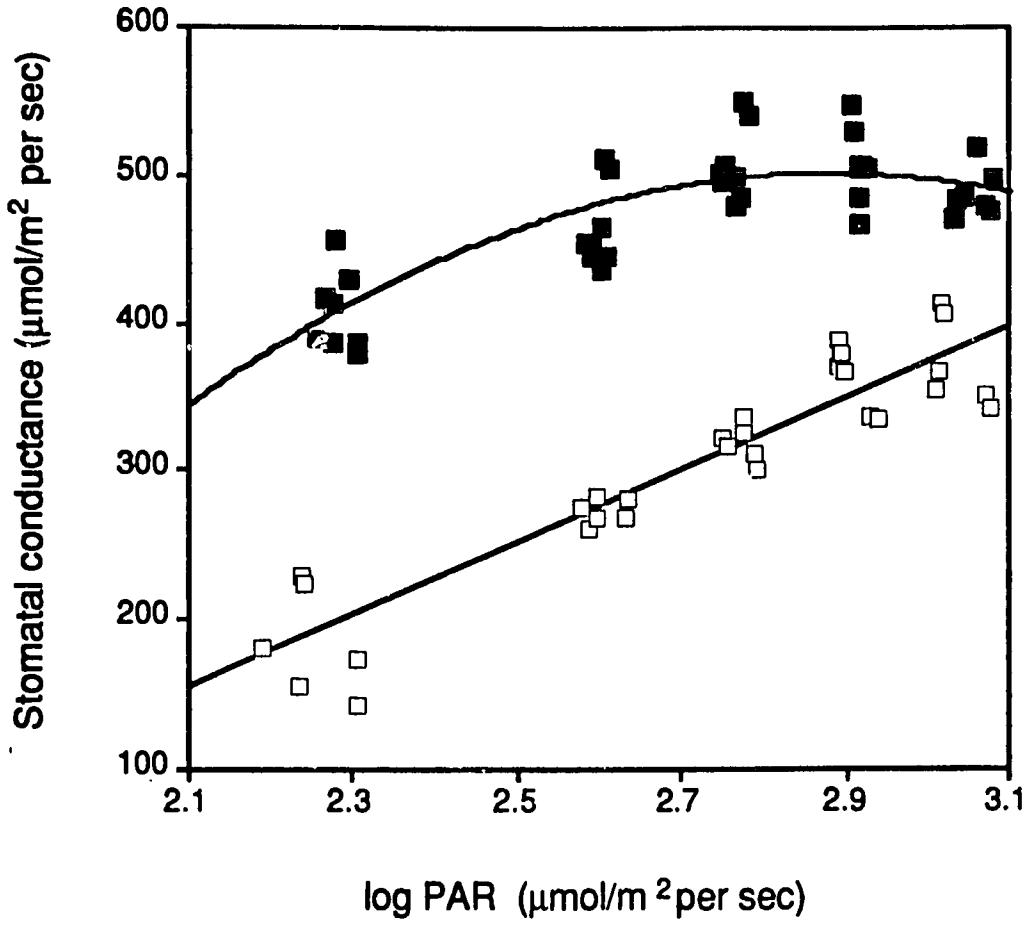

Fig.2. The relationship between stomatal conductance and photosynthetically active radiation (PAR, log transformation) in the wheat V652 (■) (y=-1627+1475x-255x2; R2=0.67); and Lachish (□) (y=-358+244x; R2=0.86).

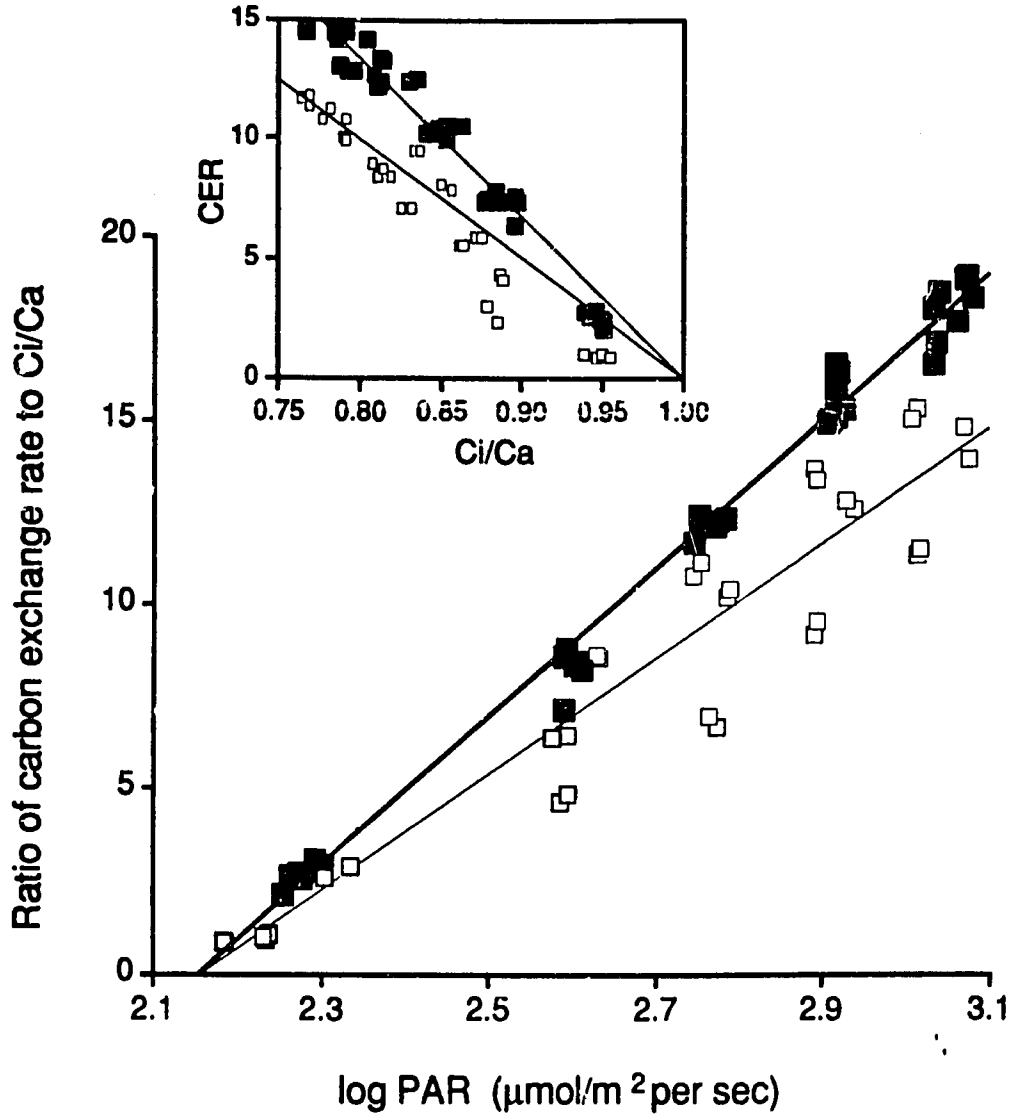

Fig.3.
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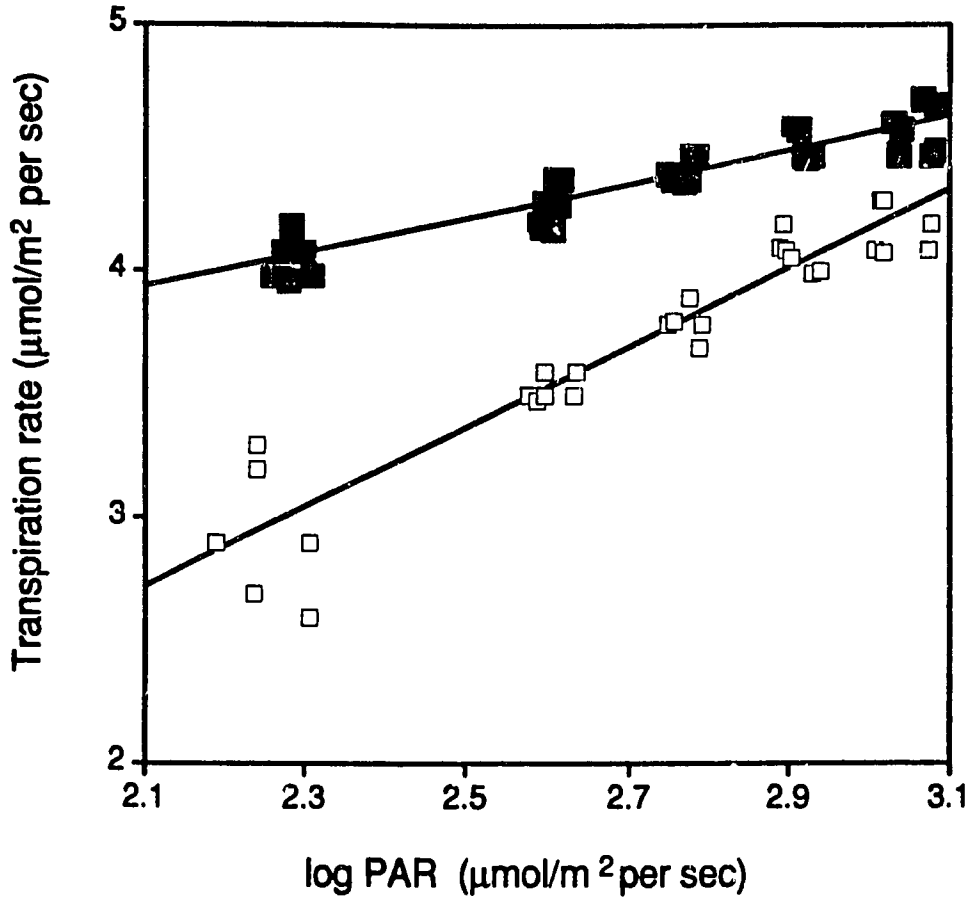

Fig.4.
The relationship between transpiration and photosynthetically active radiation (PAR, log transformation) in the wheat V652 (■) (y=2.46+0.70x; R2=0.88) and Lachish (□) (y=-0.68+16.1x; R2=0.90).

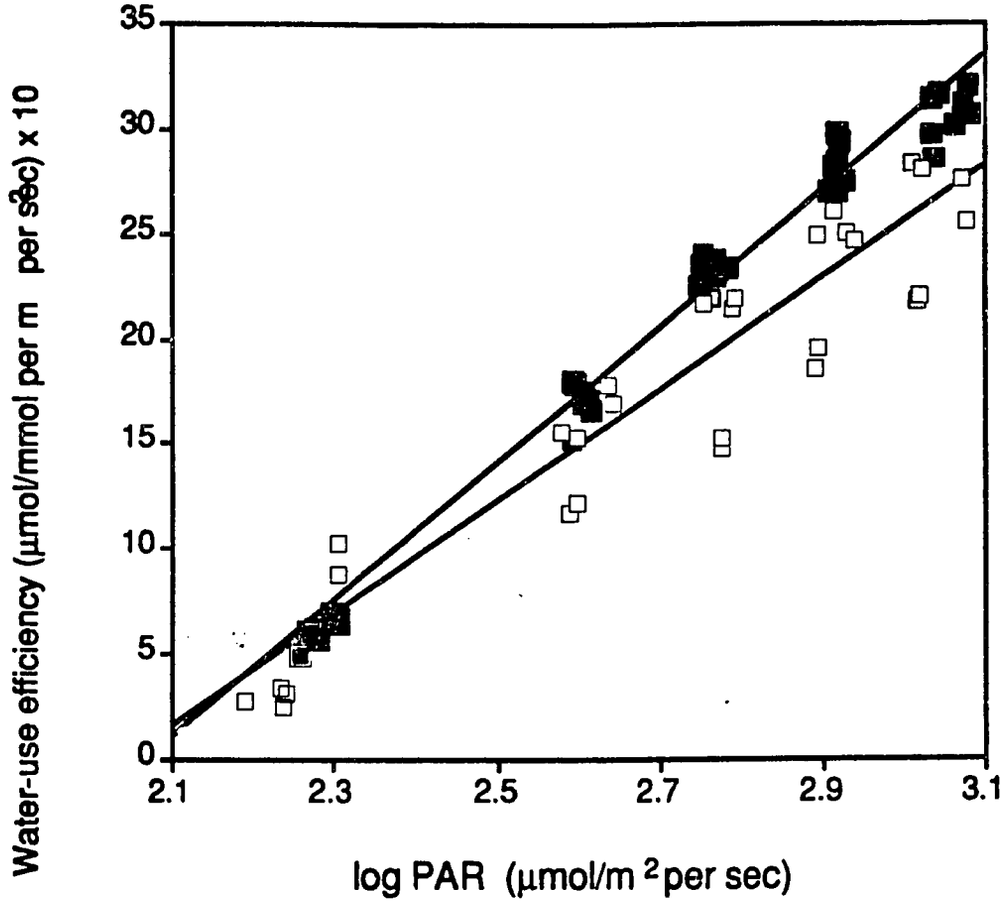

Fig.5.
The relationship between single-leaf water-use efficiency (carbon exchange rate/transpiration rate) and photosynthetically active radiation (PAR, log transformation) in the wheat V652 (■) (y=-0.0067+0.0032x; R2=0.98) and Lachish (□) (y=-0.0055+0.0027x; R2=0.85).

Mass selection for grain filling under chemical desiccation stress

ABSTRACT

Post-anthesis chemical desiccation of plants in the field is a method for evaluating the ability of wheat (*Triticum aestivum* L.) genotypes to utilize stored stem reserves for grain filling, when the transient photosynthetic source is inhibited by environmental stress. This study was performed to reveal if mass selection for large kernel weight under chemical desiccation would result in the improvement of grain filling from stem reserves, in the absence of transient photosynthesis.

Six crosses of common spring wheat where subjected to 3 cycles of mass selection from F_2 through F_4, when selection was performed for high grain weight, with or without post-anthesis chemical desiccation which destroyed the photosynthetic source for grain filling. The resulting 18 bulks were compared with their respective base-F2 populations, when tested with and without chemical desiccation.

Selection for high kernel weight under potential conditions (without chemical desiccation) did not improve kernel weight under potential conditions, evidently because these materials were lacking in genetic variation for kernel weight under potential conditions. Still, selection under chemical desiccation improved kernel weight and test weight under chemical desiccation, depending on the cross and the selection cycle, with no genetic shift in days to heading or plant height. Excessive selection (3rd cycle) for grain weight under potential conditions tended to reduce kernel weight and test weight under chemical desiccation stress in some of the crosses. It was therefore concluded that selection for high kernel weight under potential conditions does not necessarily assure higher kernel weight under chemical desiccation stress, evidently because kernel weight in the two environments depends on different sources of carbon for grain filling, namely transient photosynthesis under potential conditions and stem reserve mobilization under desiccation stress.

INTRODUCTION

The capacity for grain filling under drought stress is a major attribute of drought resistance of wheat in the Mediterranean climate. When sever drought stress occurs during grain filling, leaves desiccate and transient photosynthesis is sharply reduced. Under such conditions, grain filling and consequently yield are highly dependent on mobilized stem reserves (Bidinger et al., 1977; Davidson and Birch, 1978; Hunt, 1979).

Wheat varieties were found to differ in their capacity to support grain filling from mobilized stem reserves (*e.g.* Davidson and Birch, 1978; Hunt, 1979). This capacity can be effectively revealed by the chemical desiccation of plants after anthesis (Blum et al., 1983a, 1983b; Hossein et al., 1990). When plants are chemically desiccated by spraying them with an oxidizing agent such as magnesium chlorate, the plant responds in mobilizing stem reserves into the grain. Thus the capacity of wheat varieties for grain filling from stem reserves in the absence of transient photosynthesis can be revealed by the extent of grain filling under post-anthesis chemical desiccation. It was further found

that the capacity for grain filling under any stress that caused reduction in post-anthesis photosynthesis can be revealed by this method, such as the case was for Septoria leaf blotch disease (Zilberstein et al., 1985). Varieties of superior grain filling under chemical desiccation were found to be also tolerant to the disease, in terms of sustained grain filling under sever infection.

It was therefore assumed that selection for improved grain filling under chemical desiccation should lead to the improvement of grain filling capacity under stress. This work was done to evaluate mass selection under chemical desiccation as a simple means for achieving this purpose.

MATERIALS AND METHODS

Work was performed at Bet Dagan under optimal conditions. Irrigation was provided when needed and diseases were controlled chemically.

Table 1. Parentage of 6 crosses studied

Cross	Parentage
V2013	BTL/Barkaee//V693
V2019	BTL/216//V395/3/LKCRCH/BTL
V2024	BTL/676//V393/3/BTL/216//V395
V2025	BTL/676//V393/293 /3/CV17653/Torchetto//H895/4/Miriam
V2026	BTL/676//V393/3/BTL/LKCRCH
V2050	BTL//676/V393/3/K-3

F_1 populations of 6 original crosses (Table 1) were grown at Bet Dagan to produce enough F_2 seed. From this generation on, part of every harvested bulk seed lot which was used for planting was retained and maintained in cold storage for the final testing stage.

F_2 seed of each cross was split into two lots which were planted in 1985/86. From hereon, the separate lots were submitted to mass selection under two different but parallel programs. One program consisted of selection for grain weight under chemical desiccation while the other consisted of selection for grain weight under potential conditions, without desiccation. Under the chemical desiccation program each plot was sprayed to full wetting with 4% solution of magnesium chlorate, at 15 days after anthesis. Date of anthesis was determined as the anthesis of 80% of the ears in a plot

All F_2 plots were harvested and seed were sieved into three size fractions (small, medium and large) and only the largest was used for planting the next generation in 1986/87. Three such cycles of selection (F_2, F_3 and F_4 generations, planted in 1985/6 through 1987/88) were performed with each cross.

The resulting 36 F_5 bulks (6 crosses by 3 cycles by 2 selection programs) together with the respective 6 base F_2 populations were planted under optimal and disease free conditions at Bet Dagan in 1989/90. Bulks were tested under two treatments, chemical desiccation and controls.

Experimental design was split-plots, with desiccation and controls as main treatments and bulks in sub-treatments, in 5 replicates. Mean heading date in each plot was determined as the time when 80% of the stems produced ears. Plant height was measured to the base of the ear as mean of 20 random stems per plot. Each 'desiccated' plot was sprayed at 15 days after anthesis (see above) with 4% solution of magnesium chlorate. Plots were harvested and grain yield was weighed. Kernel weight and test weight were determined in samples taken from the bulk yield of each plot.

RESULTS

Results of selection for increased kernel weight under chemical desiccation and without desiccation (potential conditions - controls) were evaluated in plots that were either desiccated or not desiccated (controls) (Fig.1-A). Selection under chemical desiccation was effective in increasing kernel weight under chemical desiccation in all crosses, as compared with the base population. However, in some crosses a significant response to selection was seen only in the first cycle of selection while in others it was noted only or also in later cycles. The general trend was an increase in kernel weight from the 1st to the 2nd or the 3rd cycle, which in some crosses was significant and in others it was not.

Selection for increased kernel weight without desiccation (controls) generally caused either a reduction or an increase in kernel weight when materials were tested under chemical desiccation (Fig.1-A). The response depended on the cross and the cycle of selection. Still, in four of the crosses, continued selection pressure (to the 3rd cycle) for increased kernel weight under potential conditions caused a significant reduction in kernel weight when plants were subjected to chemical desiccation.

Selection under chemical desiccation was partly effective in increasing kernel weight in plants tested under potential (no desiccation) conditions (Fig.1-B). In most crosses, a response to selection was seen in the 2nd or 3rd cycles, with exceptions. Surprisingly, selection for increased kernel weight under potential conditions was generally ineffective in increasing kernel weight in plants subjected to potential conditions (Fig.1-B). Only in one cross (V2013), one of the selection cycles was effective in increasing kernel weight. The results for test weight were generally similar to those for kernel weight. Again, selection for increased kernel weight under chemical desiccation was effective in most crosses in increasing test weight in plants evaluated under desiccation (significance of the effect depended on cycle) (Fig. 2-A). Generally, selection under potential conditions either caused an increase or a decrease in test weight under chemical desiccation, depending on cross and cycle. However, continued selection pressure for kernel weight under potential conditions tended to cause a reduction in test weight of certain crosses when plants were grown under desiccation, as seen in the negative responses to the 3rd cycle in crosses V2025 and V2026.

Again, similar to results for kernel weight, selection for kernel weight under chemical desiccation tended to increase test weight also in plants tested without desiccation, depending on cross and cycle (Fig. 2-B). Selection for kernel weight under potential conditions was ineffective in increasing test

weight when tested without desiccation. Thus, all crosses were apparently devoid of genetic variation for test weight under potential conditions or alternatively, selection for kernel weight under potential conditions did not operate on genetic variation for test weight under such conditions.

A strong and significant association (R^2=0.86) between kernel weight and test weight was found for materials selected and tested under chemical desiccation (Fig. 3). These materials generally excelled in both kernel weight and test weight when subjected to chemical desiccation. Materials selected for kernel weight under potential conditions tended to have relatively lower kernel weight and test weight when subjected to chemical desiccation. For these materials, the association between kernel weight and test weight was relatively weak (R^2=0.40). This weak association most likely resulted from the fact that when selection for kernel weight was performed under potential conditions, some response to selection was seen in test weight but not in kernel weight, when evaluated under potential conditions (Fig. 1-B, Fig. 2-B).

Eighty two percent of the variation among in yield under chemical desiccation among bulks selected under chemical desiccation could be ascribed to a corresponding variation in kernel weight under chemical desiccation (Fig. 4). This, however, was not the case for bulks selected under potential conditions, where yield was unrelated to kernel weight.

There was no significant effect of selection for increased kernel weight on days to heading or plant height, in any of the two selection environments (Table 2). For each cross, mean days to heading and mean plant height were statistically the same in all selection cycles and the base population. Therefore, mass selection for increased kernel weight under chemical desiccation did not result in genetic shift in either days to heading or plant height in the materials studied here.

DISCUSSION AND CONCLUSIONS

Chemical desiccation was found to be an effective mass selection pressure for improving stem reserve utilization for grain filling in the absence of transient photosynthesis. Progress in selection under chemical desiccation pressure and the rate of response in each selection cycles depends on the genetic materials used. Some of the materials used here allowed significant improvements in grain filling under chemical desiccation with no genetic shifts in growth duration and plant height. This selection procedure therefore allows to retain the essential phenological features of the base population.

Generally, the lack of effect of selection for kernel weight under potential conditions on kernel weight under potential conditions indicates that the materials evaluated here were largely depleted of genetic variation for kernel weight under potential (stress-free) conditions. Selection for kernel weight under potential conditions was also ineffective in increasing test weight under potential conditions, either because genetic variation for test weight was lacking or because selection for kernel weight under potential conditions did not operate on genetic variation for test weight under these conditions. Taking kernel weight response to selection as an indicator of improved grain filling, it appears that these materials were lacking in genetic variation for factors responsible for

grain filling under stress-free conditions, such as transient photosynthesis or flag leaf longevity (Rawson et al., 1983), while ample genetic variation apparently existed in the capacity to utilize stem reserves for grain filling in the absence of transient photosynthesis. This is indirectly supported also by the fact that selection under potential conditions resulted in some of the crosses in a reduction in kernel weight when bulks were tested under chemical desiccation. In this case, selection for kernel weight under potential conditions may have operated on the transient photosynthesis instead of, or even at the expense of, the capacity for stem reserve utilization, as sources for grain filling. It is therefore suggested that perhaps selection for improved grain filling under potential conditions is not likely to improve grain filling under post-anthesis stress because of the different sources for grain filling under the two different environmental conditions.

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Table 2: Summary of a three-way analysis of variance for days to heading and plant height, as measured in the controls.

Source	Days to heading		Plant height	
	Sum of Squares	F-test	Sum of Squares	F-test
Selection environment (A)	167.5	11.29*	1.2	.05
Cross (B)	1229.9	16.58*	2520.9	20.14*
A x B	145.7	1.96*	75.5	.60
Cycle (C) ‡	6.9	.23	60.2	1.19
A x C	6.4	.21	61.4	1.22
B x C	159.5	1.07	183.7	.73
A x B x C	170.3	1.14	389.0	1.55

* Significant at $p \leq 0.05$

‡ Including base population.

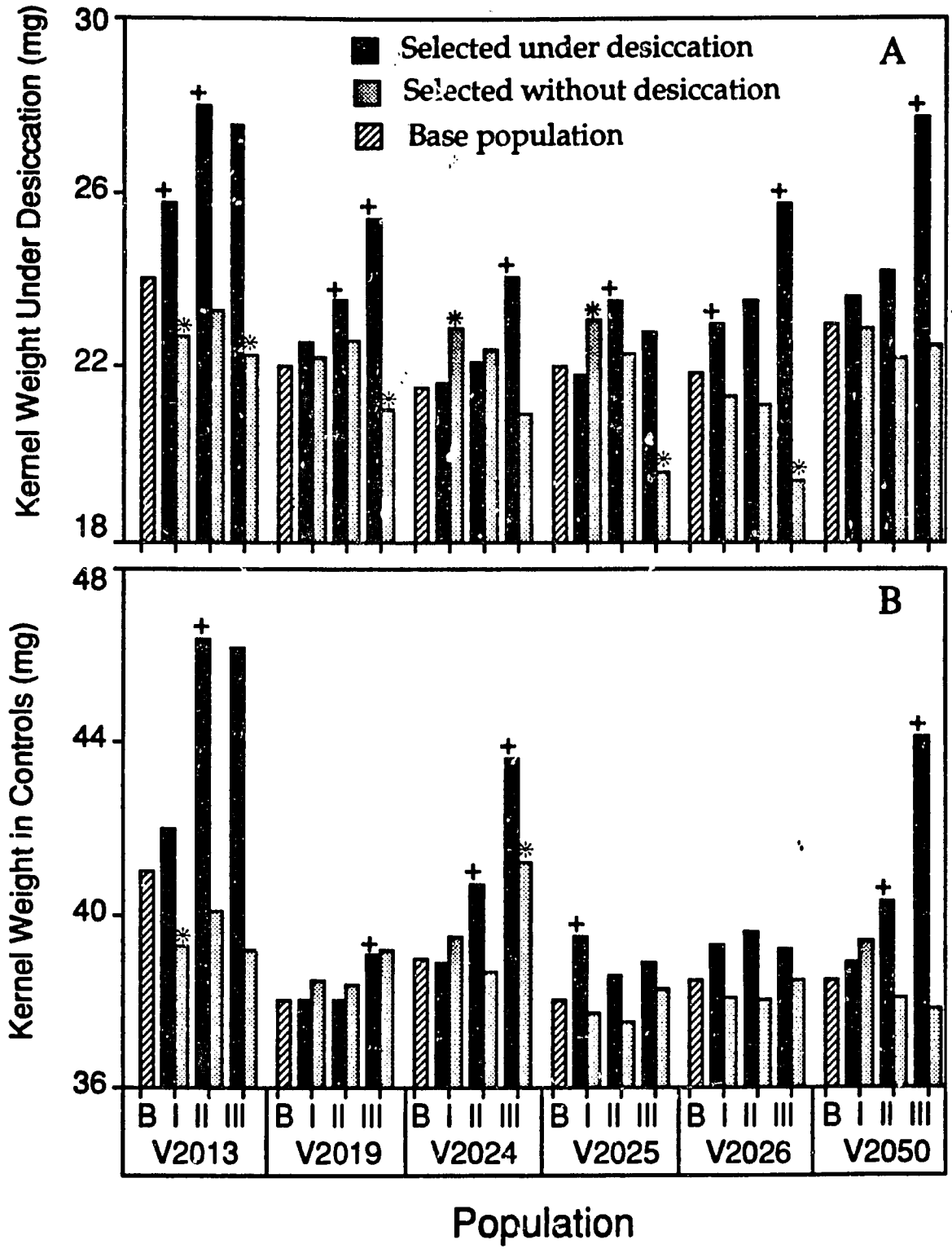

Fig. 1. The effect of three selection cycles in 6 crosses, as performed under chemical desiccation and without chemical desiccation, on kernel weight tested with (A) and without (controls) (B) chemical desiccation. (+ and * denote a significant difference ($p<0.05$) from the base population for bulks selected under desiccation and without desiccation, respectively).

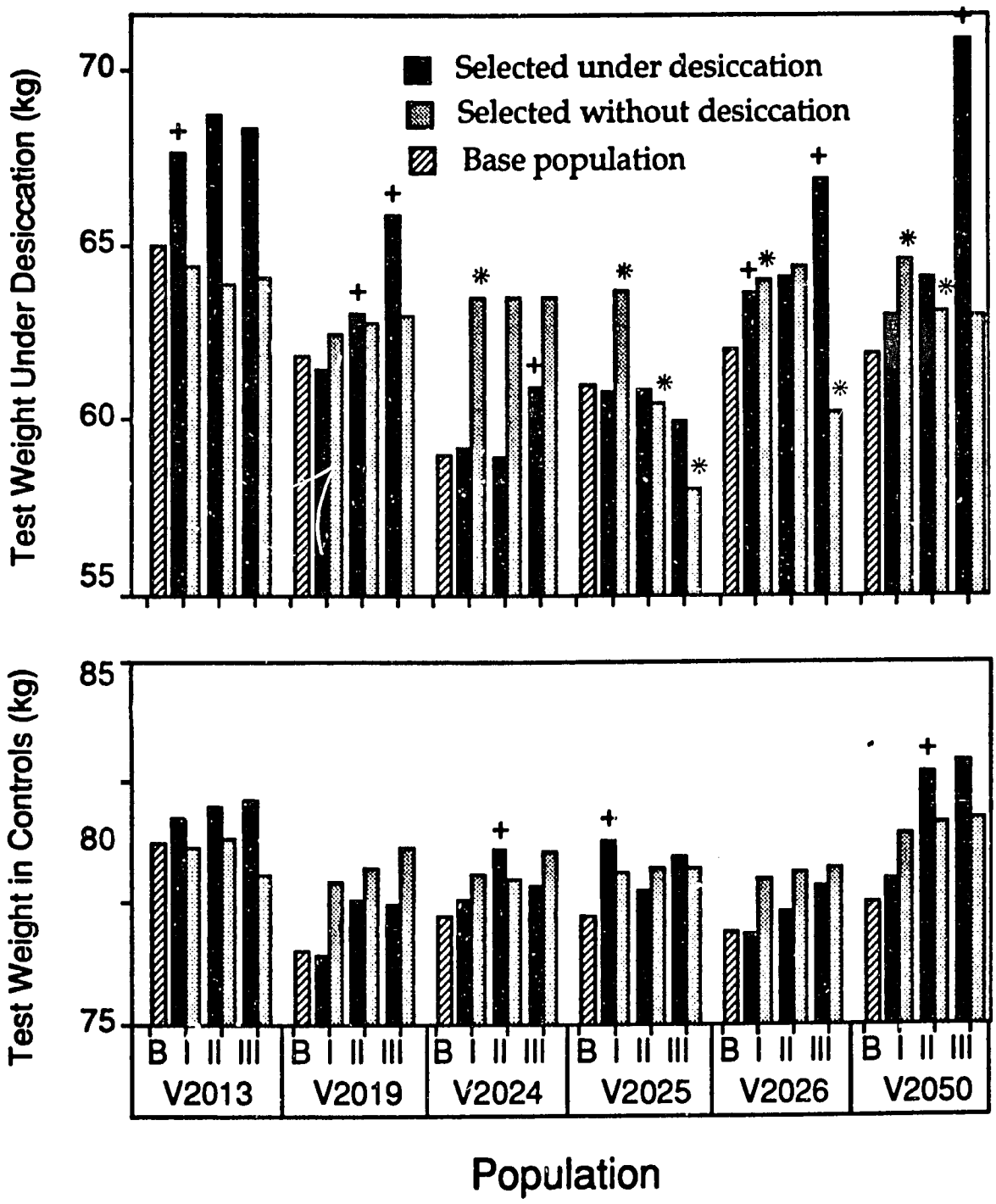

Fig. 2. The effect of three selection cycles in 6 crosses, as performed under chemical desiccation and without chemical desiccation, on test weight evaluated with (A) and without (controls) (B) chemical desiccation. (+ and * denote a significant difference ($p<0.05$) from the base population for bulks selected under desiccation and without desiccation, respectively).

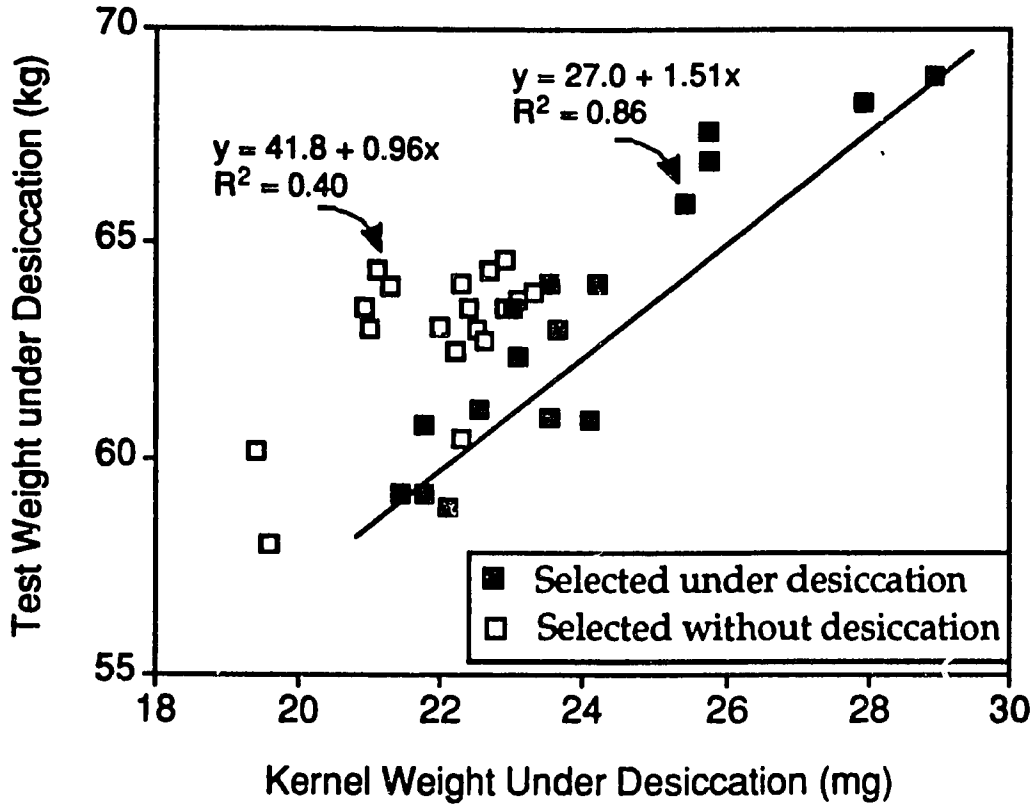

Fig.3. The association between kernel weight and test weight under chemical desiccation for 18 bulks selected with and without chemical desiccation.

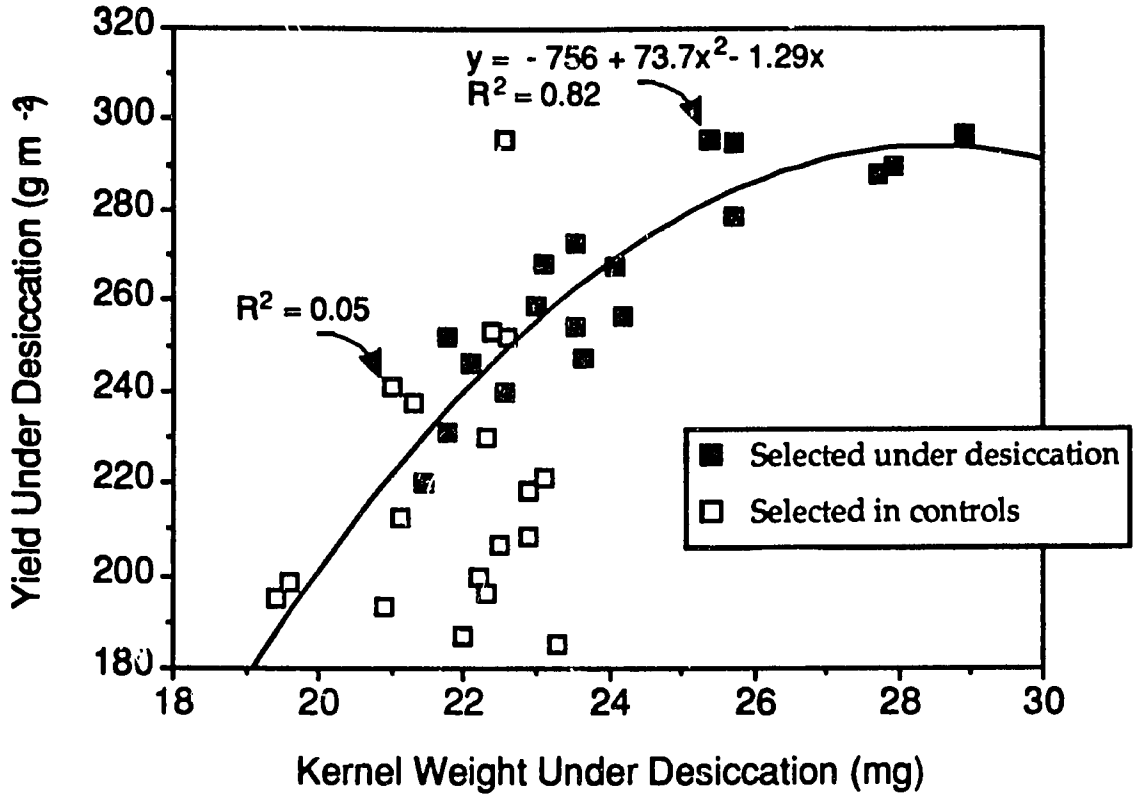

Fig.4. The association between Kernel weight and grain yield under chemical desiccation for 18 bulks selected with and without chemical desiccation.

The evaluation of heat tolerance for yield under field growing conditions.

34 genotypes of wheat were planted at Bet Dagan during the normal winter season of 1988/89 on December, 2 1988. The experimental design was randomized blocks with 4 replications. Each plot consisted of 5 rows, 5m in length at a spacing of 15cm. The trial was fully irrigated and was not subjected to any drought stress. The same materials were planted under the same experimental design during the summer (hot) offseason at Bet Dagan, on July 21, 1990. The trial was irrigated twice a week by sprinklers, in order to avoid the development of soil moisture stress. The mean daily temperature over the whole growing period was 13^0C higher in the summer than in the winter. Thus, the summer trial allowed to evaluate wheat performance under heat stress, as compared with their performance under the non-stress (cool) conditions of the normal winter season. In both trials data were collected on days to heading, plant height, grain yield and its components. Injury (reduction) by heat stress was calculated for each genotype by the reduction in growth duration, plant height and yield from the winter (cool) to the summer (hot) conditions.
On the average, grain yield was 720 g m^{-2} in the winter as compared with 159 g m^{-2} in the summer. Mean grain yield reduction caused by heat stress was therefore 78%. Genotypes differed significantly ($P \leq 0.05$) for percent reduction in yield caused by heat stress (Fig.1). The most susceptible genotypes in this respect were H1102 and H8240, which suffered about 95% yield reduction. The most resistant genotypes were CDN96/87 and C234/87, which suffered only about 55% reduction. The two resistant genotypes had a significantly smaller yield reduction than most other genotypes tested. These two were therefore outstanding in their response to heat stress.

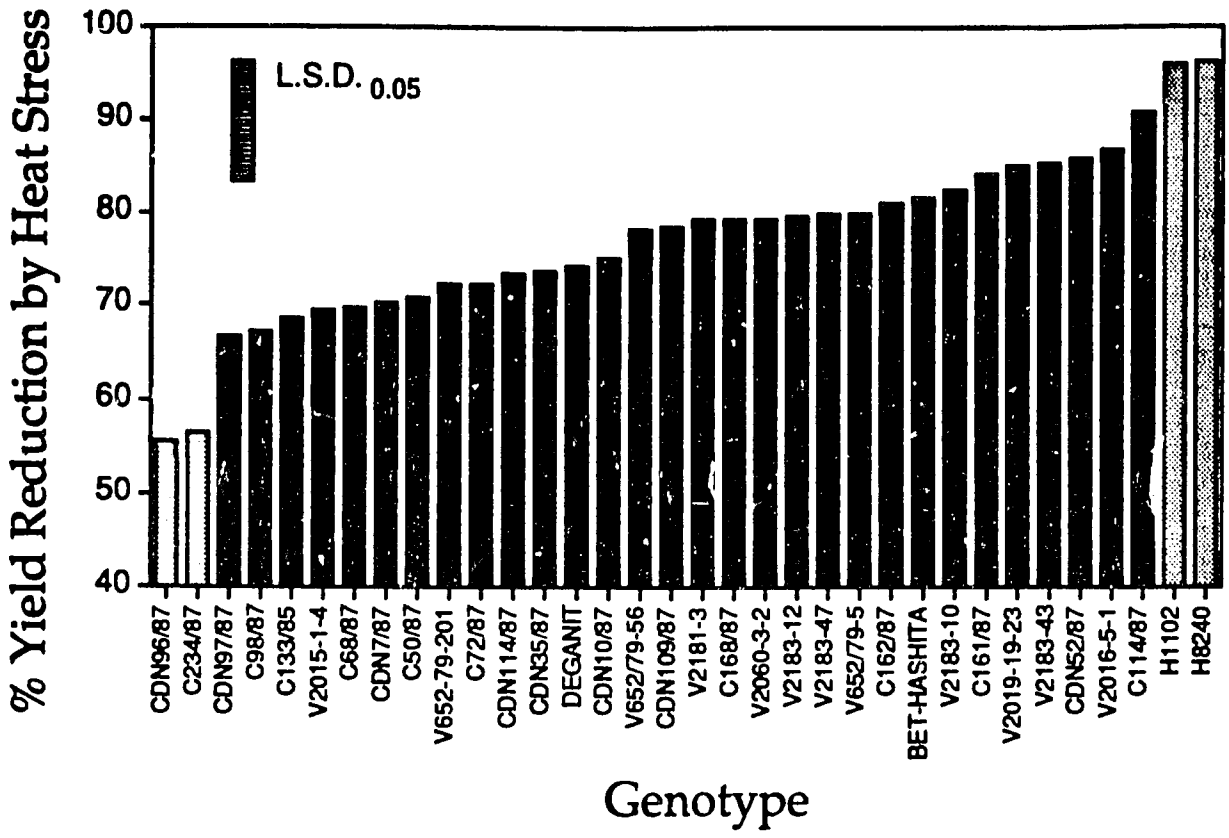

Figure 1. Percent yield reduction during the summer as compared with winter growing conditions, in 34 wheat genotypes.

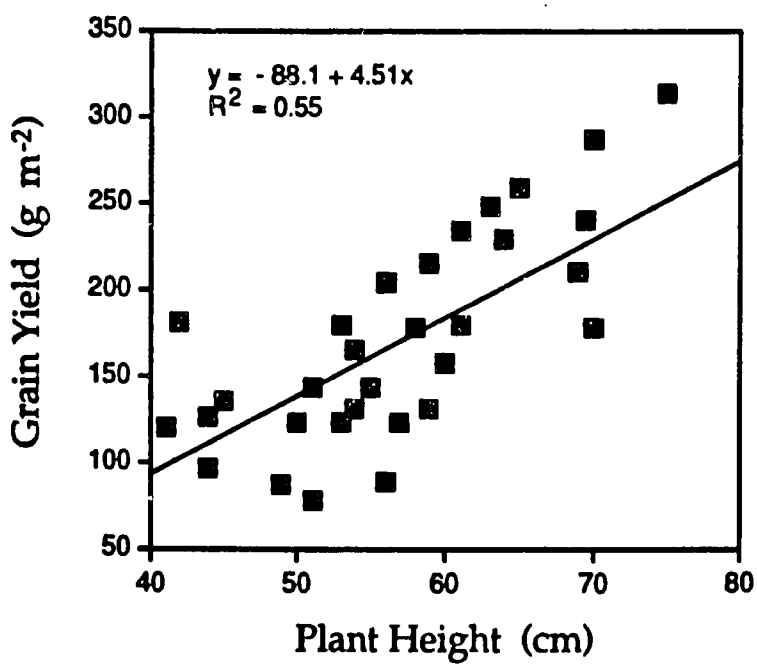

Figure 2. The association between grain yield and plant height during the summer, across various wheat genotypes

Mean (over all genotypes) plant height was reduced under the summer growing conditions to 57.6cm, as compared to 92.6cm in the winter. Few genotypes were of a full dwarf stature (75 to 80cm in the winter) while most genotypes were semi-dwarfs, ranging in height between 85 and 118

cm. There was a positive association across all genotypes between summer yield and summer plant height (Fig.2). Such an association was not seen for data collected from the winter trial. Irrespective of the height genotype, plants that grew better in the summer, as expressed by their final height, also yielded better in the summer. Plant height, as an expression of growth under heat stress during the summer, appears to be a relative and rough estimate of genotype yield under heat stress.

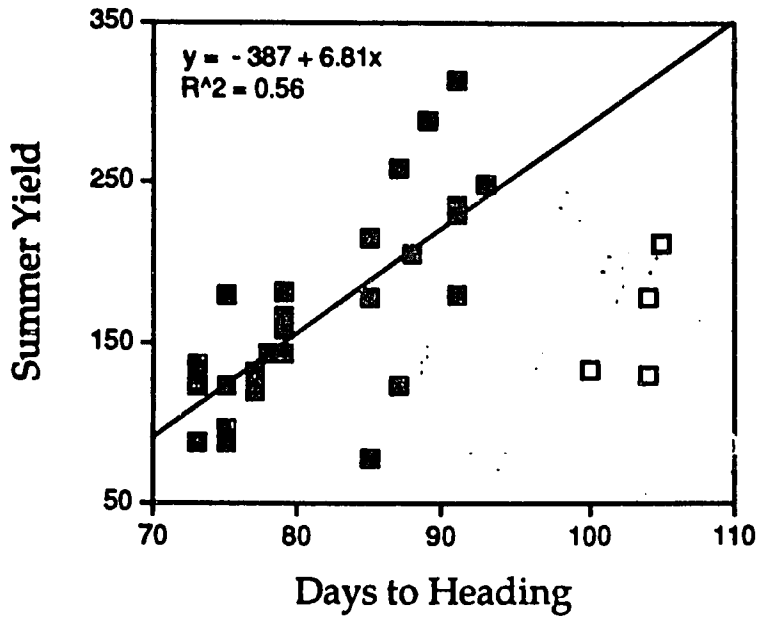

Figure 3: The association between Days to heading and grain yield in the summer (open squares are genotypes not included in the regression).

On the average, days to heading in the summer was reduced by 21% as compared with the winter growing conditions. Excluding the four latest genotypes, there was a positive and significant association between grain yield and growth duration of genotypes during the summer (Fig.3). Apparently, the correlation held only for a maturity range of up to 95 days. The association between summer yield and both plant height (Fig.2) and days to heading (Fig.3) was supported by the significant correlation across genotypes between plant height and days to heading in the summer (r=0.80**). It is unclear whether plant height or growth duration is the operative factor in supporting yield under heat stress. It remains at present that the better yielding genotypes under heat stress tend to be taller and later (though not excessively) in heading.