PB-218 608

THE CASE FOR GENERAL ADAPTATION

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Prepared for:

Agency for International Development

June 1972

BIBLIOGRAPHIC DATA SHEET	1. Report No. 633.11-S352	2.	3. Recipient's Accession No. PB-218608

4. Title and Subtitle

The Case For General Adaptation

5. Report Date June 1972

6.

7. Author(s) J.W. Schmidt, et al

8. Performing Organization Rept. No.

9. Performing Organization Name and Address

University of Nebraska
College of Agriculture
Lincoln, Neb. 68503

10. Project/Task/Work Unit No. 931-17-130-411

11. Contract/Grant No. AID/csd-1208

12. Sponsoring Organization Name and Address

Department of State
Agency for International Development
Washington, D.C. 20523

13. Type of Report & Period Covered Conference Paper

14.

15. Supplementary Notes

16. Abstracts

Some 40 years ago, the U.S. Department of Agriculture and the experiment stations of the Great Plains area recognized the importance of wide adaptation in wheat varieties for that area and initiated a cooperative testing program, to identify high yielding but widely adapted varieties. That program, begun in 1931, is The effectiveness of th/is program can be measured by the success of this cooperative testing venture. Pawnee wheat, identified as a widely adapted variety in these tests, was released in 1942-43 and by 1949 occupied over 11 million of the 86 million acres under wheat production in the United States that year. This is about 13 percent of the acreage. Triumph, Wichita, and Comanche, all tested under this program, at one time reached acreages of 6 million or more. More recently, Scout and /its derivative Scout 66, were identified through this program and in 1972 are estimated to occupy 8-9 million (15-17 Percent) of the 53 million acres in wheat in the United States. Data from the Southern Regional Performance Nursery (Table1) show the step-wise yield increases by the varietal releases identified in this nursery.

17. Key Words and Document Analysis. 17a. Descriptors

17b. Identifiers/Open-Ended Terms

17c. COSATI Field/Group 633

18. Availability Statement	19. Security Class (This Report) UNCLASSIFIED	21. No. of Pages 12
	20. Security Class (This Page) UNCLASSIFIED	22. Price $3.00

FORM NTIS-35 (REV. 3-72) USCOMM-DC 14952-P72

THE CASE FOR GENERAL ADAPTATION

by

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Plant breeders have long recognized the desirability of a variety stable over a range of environments. They have recognized, also, that variations for stability among crop varieties exists. Yet, most breeding programs have been geared toward the breeding of varieties adapted to the particular area in which the breeding center is located. Reich and Atkins (1970) state that this is due largely to the fact that methods for determining general adaptation have not been available. We would add that these should be relatively simple methods if they are to be used widely. However, the methods used in selecting and/or testing of lines have been factors also.

The wide adaptation of many of the spring wheats coming from the CIMMYT program is due in part to selecting the highest yielding segregates successively in different environments (Finlay 1970, Borlaug 1968). Borlaug (1968) credits part of this to the introduction of light insensitivity into this material. Allard and Bradshaw (1964), in their discussion of genotype-environment interaction, suggest that there has been progress in raising average performance in varieties. For example, the average wheat yield in the United States has doubled in the last 20 years (Figure 1).

Genotype-environment interactions have been under study for a long time. However, the recent flurry of papers on this subject was sparked by the research reported by Finlay (1963) and Finlay and Wilkinson (1963). They used regression analyses to determine adaptation. Specifically, they used mean nursery yields to classify the environments from low to high yielding. The response of a variety to these changes in environments was measured by its regression coefficient. Using the regression coefficient and mean yield, they were able to classify lines into those having specific adaptation for either high or low yielding environments, general adaptability to all environments, or poor adaptability to all environments. Finlay (1963) states that varieties having a regression coefficient of 1 would be considered to have average stability, those with values above 1 would be less stable, and those with values close to zero would be highly stable over all environments. He describes, "the ideal variety as having maximum genetic potential in the highest yielding environment and maximum phenotypic stability". This may not be attainable, but new varieties with increased average performance and near average stability are a step in that direction.

Scott (1967) defined average stability as "that showing the least change in relative performance with other varieties in many environments". These varieties would have a regression coefficient near 1. In experiments with corn materials, he found that those F_2's selected as low yielding had the lowest b values and those selected as medium or high yielding had b values above 1. Baker (1969), on the other hand, did not find the regression technique particularly useful in an analysis of Canadian wheat yields. However, diseases were a factor in these experiments, and therefore the yield data were not always a true test of yielding ability. Walton (1968), in discussing similar tests, points out that leaf rust was a confounding factor and that different conclusions were drawn depending on

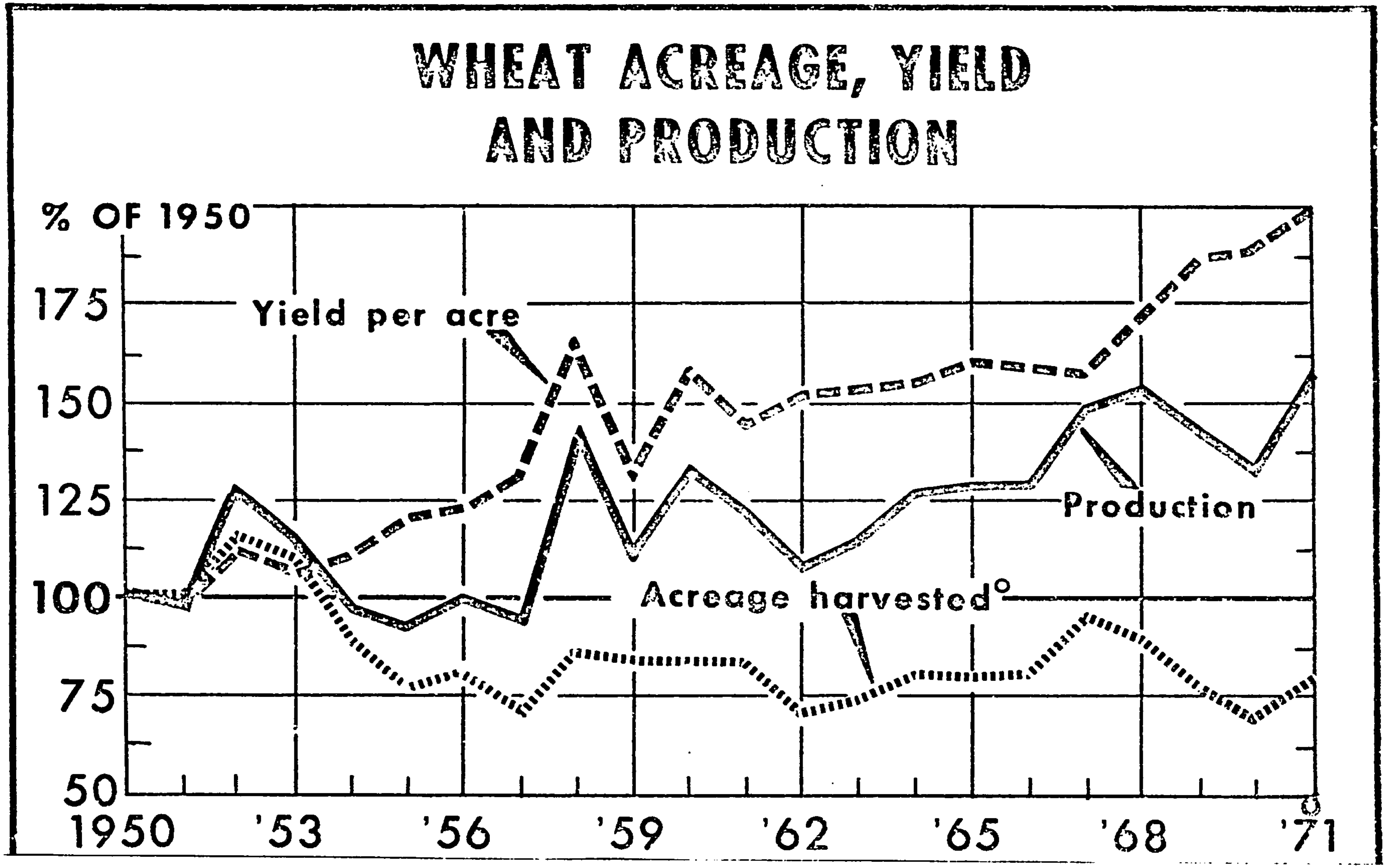

Figure 1. Wheat acreage, yield, and production in the United States, 1950-1971 (based on information from the U. S. Department of Agriculture, Economic Research Service ERS 3967-71(8)).

the exclusion or inclusion of certain tests. Walton concludes that, in general, stability of performance has been sacrificed to yield because phenotypic stability and yield appear to be negatively correlated. Joppa et al. (1971) found the regression method valuable in analyzing uniform regional nursery data. They placed greater emphasis on the mean square deviations from regression ($\bar{s}_d2$). They pointed out that varieties deviating significantly from the slope of the average regression line (b = 1) should be examined carefully for possible deficiencies.

All of the papers reviewed point out that testing over a wide range of environments is essential if widely adapted varieties are to be identified. Russell and Eberhart (1966) suggest that when locations are limited as they usually are during the selection process, "extra locations" at any one site can be produced artificially by differential fertility applications, planting dates, and moisture additions.

The Great Plains of central North America represents an area of extensive wheat production under highly variable and often precarious conditions. The climate is continental and highly variable from year to year and within seasons. Soils are highly variable. Rainfall over the area ranges from about 12 inches to 40 inches, and elevation from about 500 feet to 5,000 feet. In this region is the Hard Red Winter Wheat belt of central North America, the region that Johnson et al. (1968) had in mind when they said that "a variety's capacity for yielding well in a range of environments has importance equal to that of its yield potential". This is the area that cradled the introduction of Turkey hard red winter wheat from southern Russia nearly 100 years ago. The wide adaptation of the Turkey variety is obvious from the fact that by 1919, 21.6 million acres were being grown in the United States. This represented 27 percent of the 80 million acres in wheat production at that time.

Some 40 years ago, the U.S. Department of Agriculture and the experiment stations of the Great Plains area recognized the importance of wide adaptation in wheat varieties for that area and initiated a cooperative testing program to identify high yielding but widely adapted varieties. That program, begun in 1931, is still active today. Two nurseries, the Southern (SRPN) and the Northern Regional Performance Nurseries (NRPN), provide the testing vehicles for this cooperative effort. Testing sites range from about 32° N latitude in central Texas to 50° N latitude in southern Alberta, Canada, and from Illinois in the East to the Rocky Mountains in the West.

The effectiveness of this program can be measured by the success of this cooperative testing venture. Pawnee wheat, identified as a widely adapted variety in these tests, was released in 1942-43 and by 1949 occupied over 11 million of the 86 million acres under wheat production in the United States that year. This is about 13 percent of the acreage. Triumph, Wichita, and Comanche, all tested under this program, at one time reached acreages of 6 million or more. More recently, Scout and its derivative Scout 66, were identified through this program and in 1972 are estimated to occupy 8-9 million (15-17 percent) of the 53 million acres in wheat in the United States. Data from the Southern Regional Performance Nursery (Table 1) show the step-wise yield increases by the varietal releases identified in this nursery.

Table 1. Step-wise yield increases of new winter wheat varieties identified through the testing mechanism of the Southern Regional Performance Nursery, 1931-1971.

Variety	Year Released	Bu/A 1968	1969	1970	1971	Percent Increase
Centurk	1971	45.3	48.1	45.0	50.1	8% over Scout 66
Scout 66	1966	39.1	43.9	43.3	48.8	10% over Comanche
Comanche	1943	36.8	38.5	39.6	44.2	14% over Kharkof
Kharkof	(check)	32.8	33.5	34.2	38.5	

Johnson et al. (1968) used the Finlay and Wilkinson regression analysis method to study varietal performance and stability in such regional nurseries. Sites that were damaged by diseases or winterkill were not used in the analyses. Regression lines (Figure 2) of variety mean yield on nursery mean yield for 3 varieties and the Kharkof check variety were drawn from the regression coefficients calculated from 44 SRPN test sites over a 3-year period. Nursery mean yield was used as a measure of environment. Regression coefficients were: Scout, b = 1.13; Gage, b = 1.08; Triumph, b = 0.92; and Kharkof, b = 0.86. Using these regression coefficients, the expected performances of these three varieties relative to the Kharkof check variety were graphed (Figure 3). If we assume that Kharkof (representative of the Turkey group of wheats) is relatively well adapted in the Great Plains, then we can presume that Scout has maintained that average stability but at a much improved yield level. This greatly improved yield performance of Scout, Gage, and a third variety, Lancer, is evident in Nebraska statewide average yields from 1960 through 1971. These three varieties released in 1963 came into major production in 1966 and have had a dramatic effect on average wheat yields in Nebraska, an area much more restricted than that of the testing region (Table 2). It should be noted that these three varieties are F_3 plant selections, and, therefore, may have a somewhat greater degree of heterogeneity than later-generation selections. Allard and Bradshaw (1964) suggested that heterogeneity could provide populational buffering and provide general adaptation.

Table 2. State average wheat yields in Nebraska, 1960-1971, and annual precipitation, 1959-1970, in the wheat growing districts of Nebraska. Major production of the varieties, Gage, Scout, and Lancer, began in 1966.

Year	Bu/A, yield		Inches Precipitation	
1959			25.27	
1960	28.5		25.02	
1961*	24.5		25.04	6-year av. 23.97
1962*	19.5	6-year av. yield 23.1 bu/a	26.46	
1963	21.5		21.41	
1964*	24.5		20.64	
1965**	20.0		31.97	
1966	35.0		18.96	
1967	26.5		24.14	6-year av. 23.99
1968	32.0	6-year av. yield 34.2 bu/a	23.86	
1969***	31.5		24.85	
1970	38.0		20.26	
1971	42.0			

*Stem rust years
**Winterkilling and stem rust in 1965
***Frost in western Nebraska

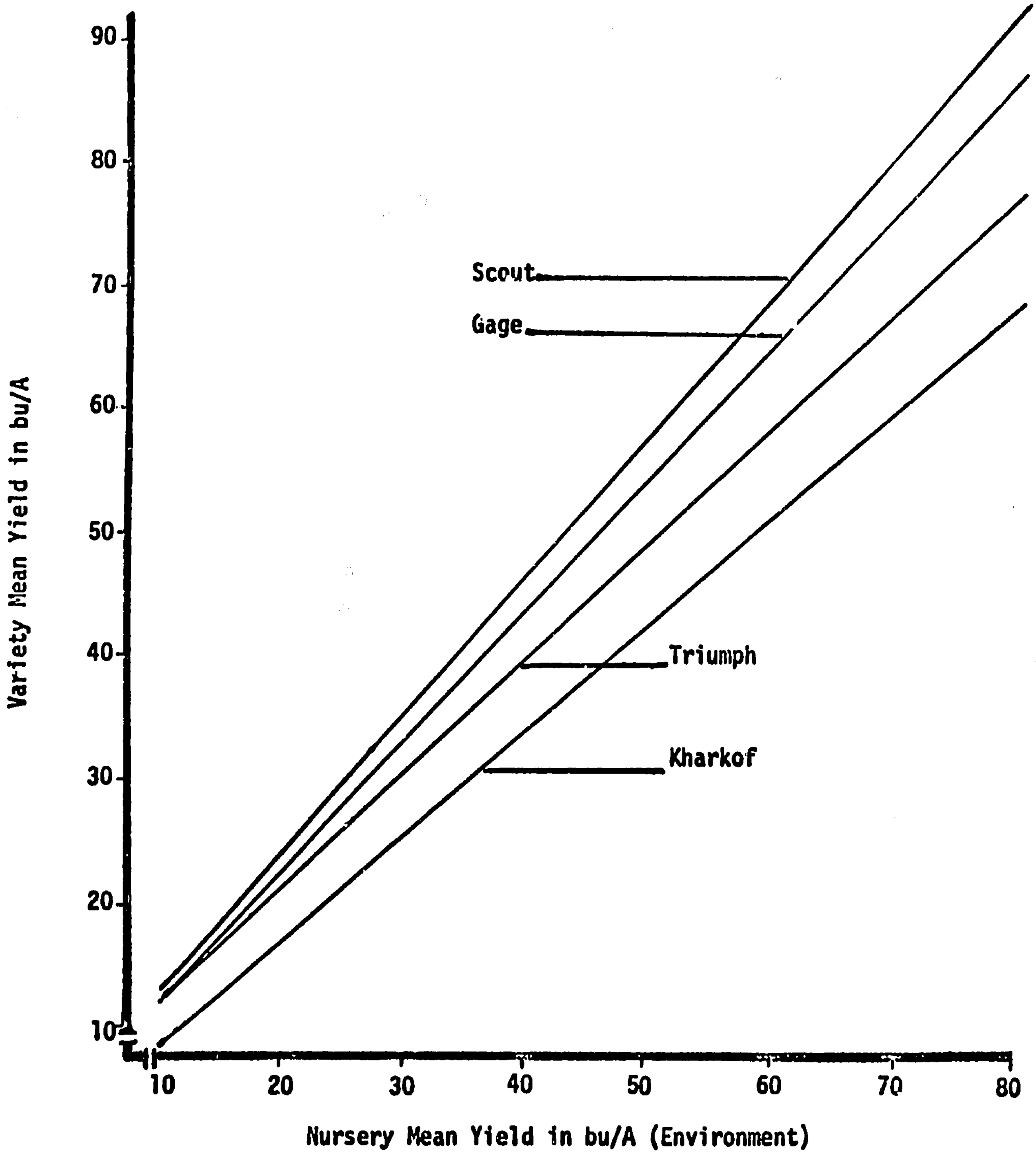

Figure 2. Regressions of the yields of four winter wheat varieties on the nursery mean yield of the southern regional performance nursery during the period 1961 to 1963.

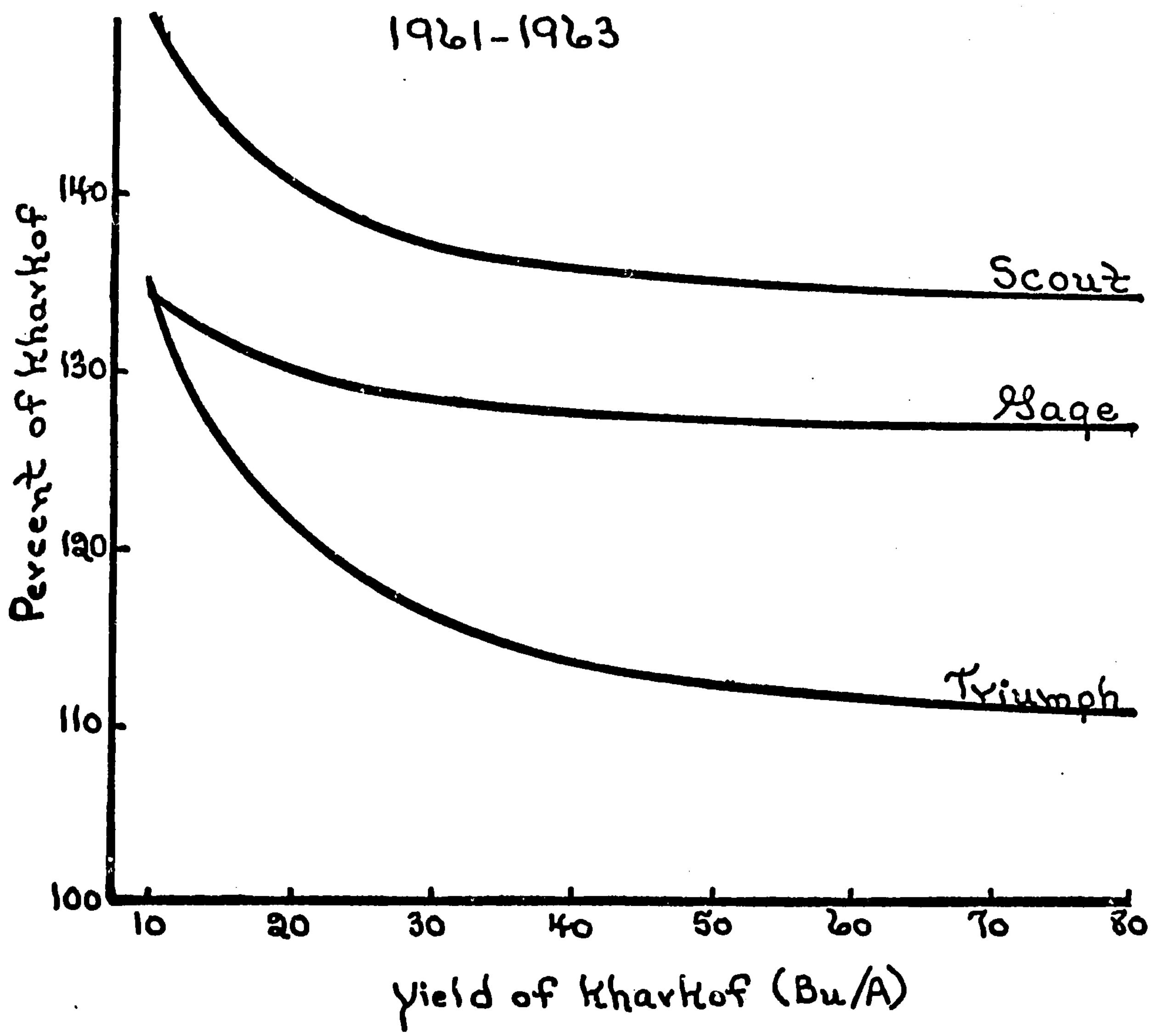

Figure 3. Yield relationship of three winter wheat varieties to Kharkof predicted from the linear regressions of the variety yields on nursery mean yields in the Southern Regional Performance Nursery, 1961-1963.

Regression and correlation analyses were applied to 1971 SRPN data on 32 entries at 24 testing sites. Disease was not a factor at these sites and winter survival was good at all locations. Data are shown in Table 3 only for the top five entries and Scout 66, Bezostaya 1, and the Kharkof check variety. While the average yields of the first seven varieties shown may not differ significantly from each other, the regression coefficients are markedly different. Centurk is the most unstable phenotypically and the most responsive to improved environments. Two of the experimentals behave somewhat similar to Centurk, while the others except Kharkof are near average in stability.

Table 3. Data* for selected entries from the 1971 Southern Regional Performance Nursery (SRPN).

Entry	Yield Bu/a	Yield Rank	Reg. coef. (By.x)	Mean of individual nursery ranks
Experimental A	50.8	1	1.08	12.13 ± 1.83
Experimental B	50.2	2	1.10	12.15 ± 1.44
Experimental C	50.1	3	1.03	11.42 ± 1.73
Centurk	50.1	4	1.16	12.54 ± 1.88
NE68435	49.9	5	1.01	11.17 ± 1.17
Scout 66	48.8	11	1.00	13.13 ± 1.77
Bezostaya 1	48.3	17	.96	14.21 ± 2.09
Kharkof (ck)	38.5	32	.80	27.21 ± 1.42

*Data based on 32 nursery entries at 24 locations

These data are shown graphically relative to the performance of Kharkof in Figure 4. Behavior of Scout 66 relative to Kharkof in 1972 was very similar to its behavior in 1961-63 (Figure 3). This provides a degree of validity to the performance of the other varieties. Joppa et al. (1971) suggested that varieties that had a regression coefficient deviating considerably from 1 could have a serious deficiency. This erratic behavior of Centurk in 1971 may have been due to its tillering ability which was a liability in the very low rainfall test sites. While Centurk's potential yield, partly due to its tillering ability, makes it an attractive variety for growers, it may be expected to be unstable in certain low yield environments. On the other hand, NE68435 appears to have improved yielding ability as compared with Scout 66 and has retained desirable phenotypic stability. Bezostaya 1, which has been superior in both yielding ability and stability in international nurseries, showed stability in this nursery but not superior yielding ability.

Additional information regarding general adaptation on stability can be gained from a simple examination of the average nursery rankings of these entries (Table 3). At Nebraska, average rank has been a key item in the decision of advancing or discarding a line. NE68435, which was fifth in average yield in the 1971 SRPN, had the best average rank and the least variability in rank. On the basis of the 1971 data, this variety appears to have general adaptation combined with above average yield and is an improvement over Scout 66.

1971 Southern Regional Performance Nursery

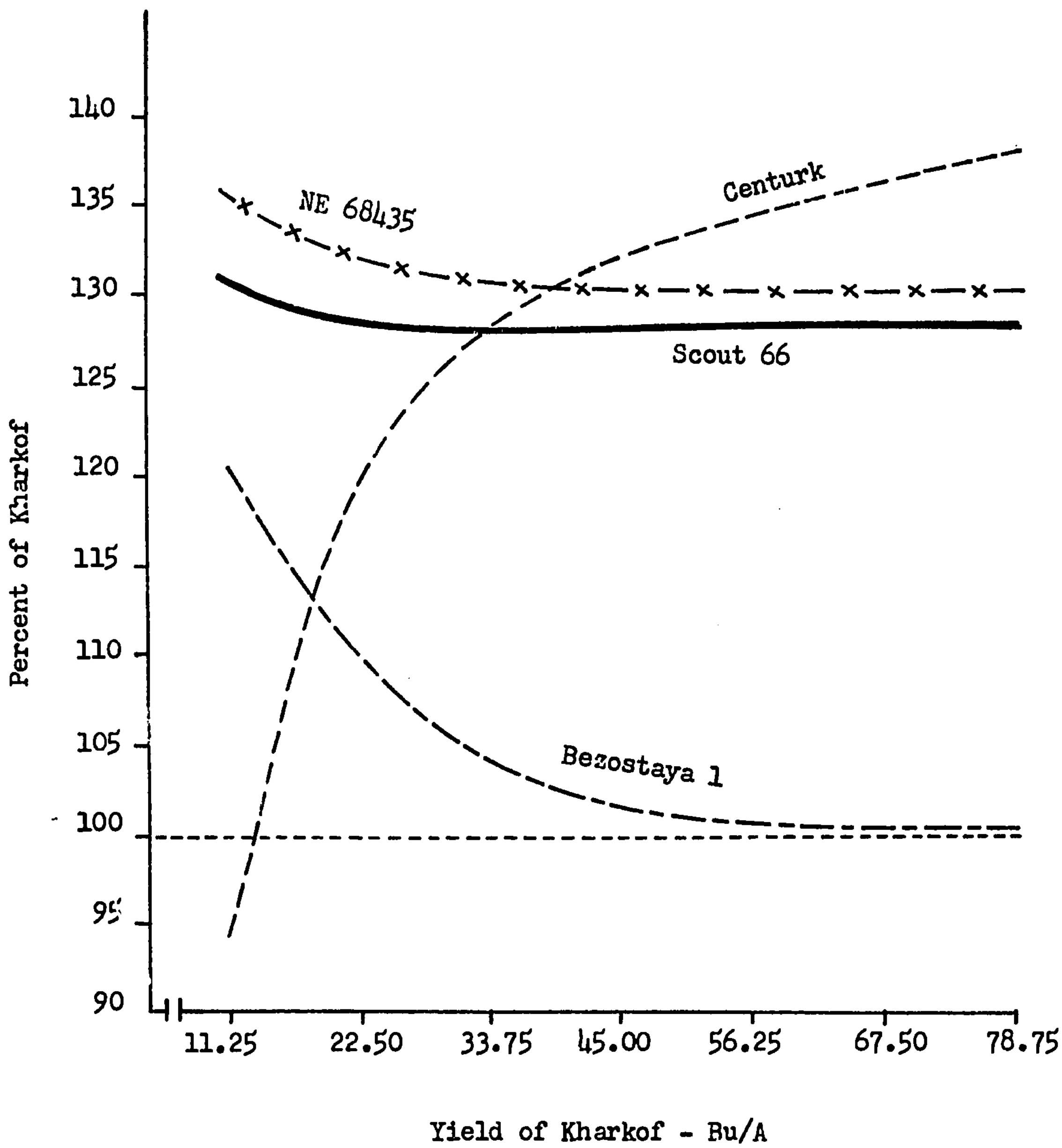

Figure 4. Yield relationship of four winter wheat varieties to Kharkof predicted from the linear regressions of the variety yields on nursery mean yields in the Northern Regional Performance Nursery in 1971.

Wide adaptation need not be at the expense of high yield in more restricted areas. The varieties that performed well in the SRPN also had excellent performance in the more restricted Nebraska state tests in 1970-71 (Table 4). However, it is true that Nebraska shares a climate similar to that of the Great Plains.

Table 4. Yields of promising experimentals and check varieties in Nebraska tests in 1970-71.

	1970 Intrastate Bu/a	1971 Intrastate Bu/a	1971 Nebraska State Tests Bu/a	Average Bu/a
Centurk	54	56	57	55.6
NE68435	55	56	55	55.3
NE68493	52	55	51	52.7
Scout 66	52	53	53	52.7
NE68427	49	55	53	52.3
NE68440	48	54	52	51.3
Lancer	51	53	49	51.1
NE68437	46	53	51	50.0
Turkey (ck)	--	--	41	----

The Northern Regional Performance Nursery (NRPN) is grown from Nebraska northward into Alberta, Canada. Yield advances have been much more difficult to achieve in this region of hard red winter wheat production. In this region, Warrior has been a stable variety but has lacked the ability for outstanding performance under highly favorable environments. In 1971 (Table 5), Centurk had the highest average yield, the highest average rank and consistency of rank, but a very high regression coefficient. NE66403 appears to be quite unstable while NE68427 is stable but lacks outstanding yield performance. Data from the more restricted Nebraska tests would agree with these regional data. The performance of Centurk relative to Kharkof in the NRPN (Figure 5) is similar to its performance in the SRPN but not as extreme in responsiveness to environmental improvement. Warrior behaves as expected and NE68427 is similar to Warrior in response to the environment.

Table 5. Data* for selected entries from the 1971 Northern Regional Performance Nursery (NRPN).

Entry	Yield Bu/a	Yield Rank	Reg. coef. (By.x)	Mean of individual nursery ranks
Centurk	41.9	1	1.21	4.38 ± 1.14
Warrior	40.0	2	.96	7.08 ± 0.98
NE66403	39.4	3	1.25	7.46 ± 1.65
NE68427	39.0	4	.98	8.08 ± 1.14
Winoka	38.7	5	.88	10.38 ± 1.31
Kharkof (ck)	35.7	17	1.00	12.46 ± 1.41

*Data based on 19 nursery entries at 13 locations.

1971 Northern Regional Performance Nursery

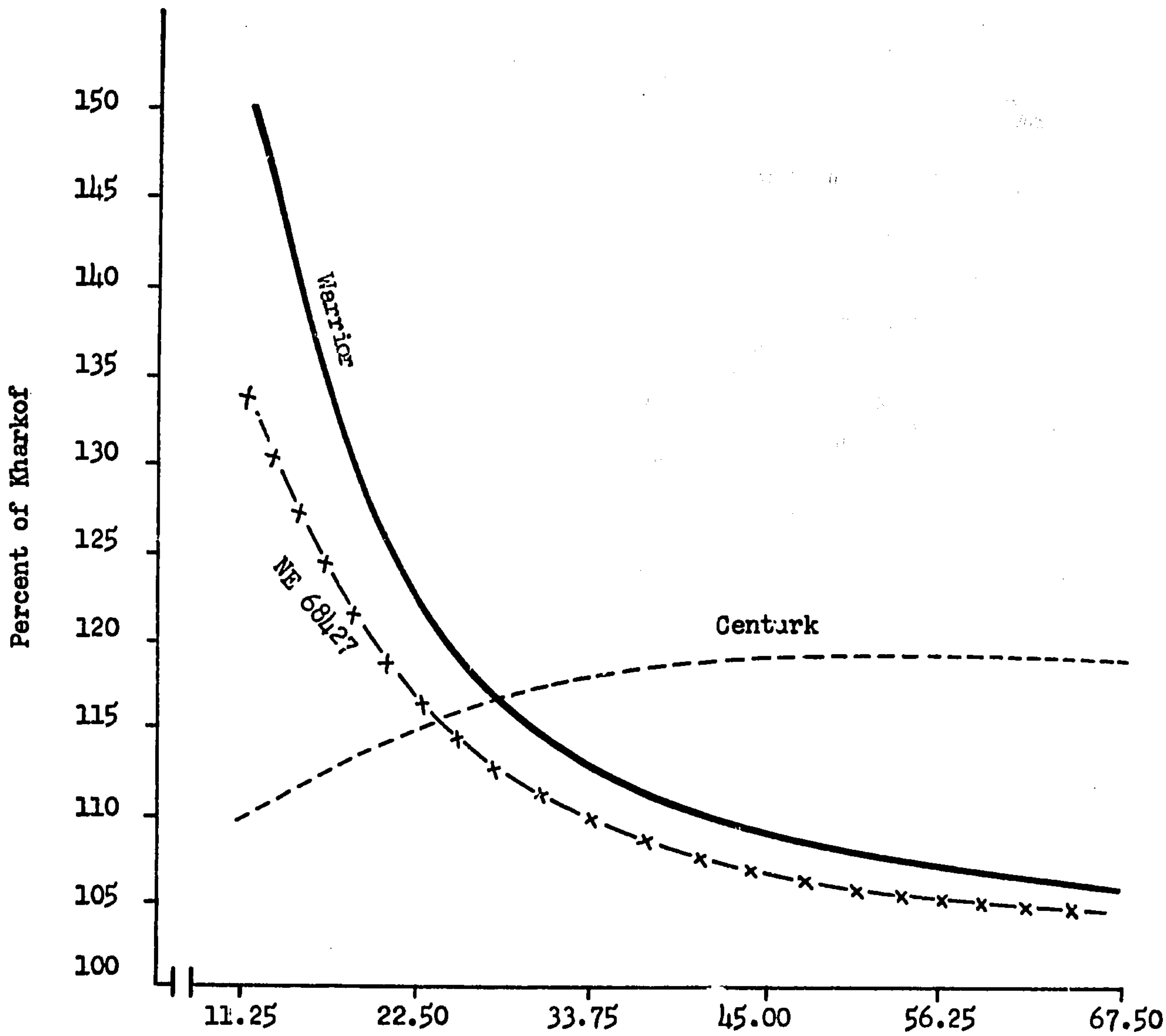

Figure 5. Yield relationship of three winter wheat varieties to Kharkof predicted from linear regressions of the variety yields on nursery mean yields in the Northern Regional Performance Nursery in 1971.

Finally, we would like to look very briefly at data from the 1969 IWWPN (Table 6). These data will be discussed in greater detail in another paper. In general, average yield and average rank agree quite well. In certain instances, however, the average rank and consistency of rank indicates that a variety has greater stability than the varieties that outrank it in yield. These varieties, then, on the average would be better recipient varieties in programs where general adaptation is important than some of those that outrank them in yield. Parker and Gage would be two such varieties. Riley 67, Stadler, and Yorkstar would be poor choices where general adaptation is desired.

Table 6. Yield and yield rank data from the 1969 International Winter Wheat Performance Nursery (IWWPN).

Entry	Yield Bu/a	Yield Rank	Rank Av.	Rank S.E.	Rank of mean rank
Bezostaya 1	63.9	1	6.05	± 1.36	1
Blueboy	60.2	2	7.42	± 1.56	2
Sturdy	57.7	3	8.84	± 1.48	3
Timwin	56.8	4	10.68	± 1.46	7
San Pastore	55.3	5	9.53	± 1.58	4
Benhur	54.9	6	10.95	± 1.12	8
Parker	54.1	7	9.68	± 1.29	5
Fertodi	54.0	8	10.63	± 1.43	6
Scout 66	53.7	9	11.42	± 2.03	9
Arthur	53.2	10	12.90	± 1.89	10
Riley 67	51.3	11	15.21	± 1.44	17
Stadler	51.2	12	15.68	± 1.79	18
Yorkstar	50.6	13	15.16	± 2.29	16
Gage	50.3	14-15	13.84	± 1.20	11
Yung Kwang	50.3	14-15	14.32	± 1.61	12
Triumph 64	50.0	16	14.63	± 2.00	14
Lancer	49.8	17	14.47	± 1.61	13
Shawnee	49.4	18	15.11	± 1.29	15
Bankuti	47.6	19	16.37	± 1.63	20
Heine VII	46.8	20	15.90	± 2.06	19

*19 locations

In summary, we would conclude that there has been considerable improvement in yielding ability in the 40 years of wide scale cooperative testing in the Great Plains of Central North America without a marked loss in stability of performance. Performance over this wide region has not been dissimilar to performance in a smaller area such as the state of Nebraska.

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