

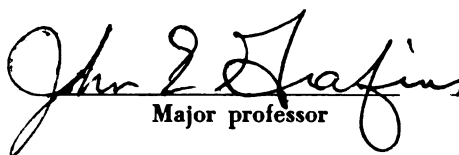
GENOTYPE X ENVIRONMENT INTERACTIONS OF BARLEY
(HORDEUM VULGARE L.)

Thesis for the Degree of Ph. D.
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Virgil Dean Luedders
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This is to certify that the
thesis entitled
GENOTYPE X ENVIRONMENT INTERACTIONS OF BARLEY
(HORDEUM VULGARE L.)

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ABSTRACT

GENOTYPE X ENVIRONMENT INTERACTIONS OF BARLEY (HORDEUM VULGARE L.)

by Virgil Dean Luedders

Parent varieties and crosses of spring barley were planted in the field at early and late planting dates in 1960 and 1962. The parents also were grown at 2 fertility levels in a growth chamber and subjected to several environmental stresses. Photosynthetic and respiratory rates were determined by standard Warburg techniques in modified Warburg flasks.

There were no significant genotype x environment interactions in the field in either 1960 or 1962 or in the growth chamber at the low fertility levels for weight per head, weight per seed or number of seeds per head. However, at the high fertility level, drought stress on seedlings and warm night temperature stress during the heading stage resulted in significant interactions with the genotypes for weight per head.

Physiological studies failed to uncover any real differences in photosynthetic or respiratory rates between

the genotypes or their progeny at the high fertility level. A real difference in leaf size, maturity, and rate of senescence of leaves was found, indicating that they are major factors in the response of these genotypes to stress. At the low fertility level, the photosynthetic rates were significantly different between genotypes and were found to be associated with the weight per head.

The genotype which headed early suffered the least yield reduction due to the late stresses. The late-heading genotype produced the largest head under favorable conditions and early stresses but suffered the greatest yield reductions due to the late stresses.

The midparental values can be used to predict the performance of the progeny for the components of yield and for physiological characteristics.

GENOTYPE X ENVIRONMENT INTERACTIONS OF BARLEY

(HORDEUM VULGARE L.)

By

Virgil Dean Luedders

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INTRODUCTION

Scientists have been trying to explain variation in yield for many years and in many ways. Not all of the research has been fruitful but it has stressed, singly and in combination, such factors as rates of photosynthesis and respiration, the development of the plant, population density, net assimilation rate, leaf area index, pests and pathogens, effects of temperature, photoperiod, water and nutrient supply, chemical constituents and enzymes, and many others.

Barley yield is greatly affected by environmental conditions, especially during its reproductive stage. High night temperature has been shown to affect various genotypes differentially but the exact mechanisms for high or low yield have not been elucidated. Increased respiratory rate at the higher temperatures has been postulated as the reason for lower yields but genotypic differences have not been shown.

This study was aimed at determining whether genotypic differences in respiratory rate exist. It was later expanded to include photosynthetic rates and the development of the plant under several environmental stresses in an

attempt to explain differential yields due to genotypic and environmental differences. The genetic aspects are considered, with special reference to the progeny-midparent comparisons.

REVIEW OF LITERATURE

The adverse effect of high night temperature and its interaction with genotypes has been postulated by Grafius (7). Sarkissian (23) concluded that there was a genotype x night temperature interaction in barley for weight and number of seeds. He employed vector techniques but did not postulate any mechanisms that might be responsible.

Bains (2) showed a genotype x night temperature interaction for barley with a linear relationship between respiratory rate and temperature in the range from 65 to 75°F., with a Q_{10} much greater than 2. Elongation of main shoot was more rapid at the higher night temperature, but the date of heading was earlier so that the final height and weight were less.

More extensive and detailed research has been done on the effect of high temperatures with peas. Lambert and Linck (14) found that high temperature reduced yields: at each temperature, the longer treatments reduced the yield more and for each duration, the higher temperatures resulted in lower yields. Karr, Linck, and Swanson (12) found rather well defined thermal-sensitive periods to both

day and night high temperatures; the high night temperature was more critical. They found that the effect of high day and night temperatures combined tended to be roughly additive.

Watson (32) agreed with his earlier results about leaf growth (area) and further states that it is unlikely that agricultural yield can be improved by increasing the photosynthetic efficiency of the species at present cultivated. However, his measure of photosynthetic efficiency is provided by the rate of increase of dry weight per unit leaf area, i.e., net assimilation rate as defined by Gregory (9). Watson also states that information on the physiological causes of variation in yield is still scanty.

Watson found that variation in nutrient supply over a wide range has little or no effect on net assimilation rate. However Matushima et.al. (18) showed that nitrogen supplied to rice as a top-dressing at the beginning stage of panicle differentiation caused a marked increase in the rate of carbon assimilation per unit leaf area. Drought and shading treatments decreased the rate of carbon assimilation.

Iyama and Murata (11) found that the decrease in photosynthetic rate takes place before the first sign of wilting of the plant and becomes more severe as wilting proceeds. They concluded that soil moisture exerts its

influence on photosynthesis through its effect on the water content in the leaf blade. Murata (20) showed a close correlation between water concentration in the leaf and photosynthetic activity from the middle stage to heading. There was a correlation between photosynthesis and potassium content, with the possibility that potassium was associated with the aging process in the photosynthesis mechanism.

Mooney and Billings (19) conclude that the continued existence of Oxyria digyna throughout a wide range of arctic and alpine conditions is due in large part to differences in metabolic potential among its component populations. The photoperiodic responses of flowering and formation of perennating buds is reflected in latitudinal origin. Nuttonson (21) found that Olli barley from Finland is photosensitive but that Trebi which originated in Turkey is not. Ormrod (22) reported that physiological as well as morphological differences exist between indica and japonica rice varieties.

Kendall and Taylor (13) could find no significant differences in rates of photosynthesis or respiration or the P/R ratio between 3 groups of clones of red clover. Thus, they conclude that rates of photosynthesis and/or respiration per se were probably not decisive factors in determining the longevity of the persistent clones in the

field.

Shibles and MacDonald (24) found similar photosynthetic rates and leaf and cotyledon areas between seedlings of Viking and Empire birdsfoot trefoil. Viking was more vigorous since it utilized more photosynthate for leaf area expansion whereas Empire made more axis growth. Bald (3) recognized the allocation of metabolites as being an important determinant of yield and that maturity time effects and environment were not to be neglected.

Photosynthesis does occur in the head. The estimates of the ear's contribution vary considerably, from 20 to 30% by Watson and Norman (34) and Sugahara et. al. (27) to 40% by Thorne (28) and 50 to 60% by Buttrose (4) although Frey-Wyssling and Buttrose (6) concluded that 76% might be a closer approximation to the true value. Thorne (28) states that separate values of photosynthetic rates for Plumage Archer and Proctor differed by less than 10 per cent; this difference was probably not significant since the standard errors of the original data were more than 10 per cent. She found that the ears of Plumage Archer were slightly larger but concluded that the contribution of ear photosynthesis to yield of grain per acre was greater for Proctor than for Plumage Archer because Proctor had more ears.

Closely related to this is the question of leaf photosynthesis to ear filling. Archbold (1) states that only the top 2 internodes seem to contribute to ear filling; the essential function of leaves is not grain filling but ear formation at the outset. In rice, Ishizuka and Tanaka (10) found that all of the assimilate from the flag leaf moved to the ear but little from the fourth leaf below the flag. There may be a greater transfer of assimilates than is sometimes believed. Labanaukas and Dungan (15) found that foliated oat tillers increased the yield of the main stem from 33 to 58% compared to that of main stems to which defoliated tillers were attached. Foliated main stems increased the yield of tillers from 21 to 58% compared to that of tillers attached to defoliated main stems, and main stems with leaf blades intact gave grain yields which were from 70 to 108% greater than those produced on defoliated main stems.

The means of the progeny can be predicted from the midparental values. This has been shown for the components of yield by Grafius (8) in barley, Luedders (16) in oats, and Whitehouse et. al. (35) in wheat. Working with malting characteristics, Dickson and Grafius (5) got a high correlation between progeny means and midparental values and Smith (26)

states that the progeny means tend to regress towards the mean of the 2 parents.

MATERIALS AND METHODS

Three genotypes, and their crosses, of Manchurian spring barley from the World Collection were planted on April 29 and May 25 in 1960. The seeds were placed at 3-inch intervals in 3-foot rows which were one foot apart. Twelve heads were harvested from each row. In 1962 6 genotypes and their crosses were planted on April 20 and May 17 in hills which were 2 feet apart each way. After emergence the hills were thinned to 10 plants. The hills were harvested as a unit and the number of heads per hill was recorded.

Three genotypes were grown in a growth chamber at 80°F. day and 60°F. night temperatures. The daylength was constant at 16 hours with a light intensity of 2800 foot candles one foot from the source. On November 1 three seeds, one of each genotype, were planted in sand in each of 220, 4-inch clay pots. One half of the pots were kept at a low fertility level to prevent tillering. Nutrient additions were started on November 10, the low fertility set receiving a more dilute solution less frequently than the high fertility set. The high fertility set usually was

given a diluted, acidified, modified Hoaglund's solution to keep the plants from getting too tall.

All of the pots were moved daily to lessen the effects of uneven light intensity and temperature. The light bank and the bench were manipulated to keep the lights approximately one foot above the plants.

At both fertility levels, groups of plants were subjected to moisture and warm night temperature stresses, with one group receiving no stress to serve as a control. Both stresses were imposed on the plants early (to seedlings) and late (during the heading stage). The stress periods were from November 11 until December 5 and from December 11 to January 9 for the early and late stresses, respectively. The water stress was imposed by watering less frequently and less copiously; these plants received the same amount of nutrients as all other plants within the same fertility level. The warm night temperature was maintained near 80°F. by a 500-watt heating cable suspended 6 to 12 inches below and a thermostat above the plants in a plastic covered frame, into which the plants were moved at 11 p.m. The plants were moved back into the chamber at 7 a.m. Due to the extremely cold weather, the night temperature was slightly lower (72-76°F.) during the late stress period.

Metabolic measurements were made by standard Warburg techniques (Umbreit et. al., 30) in modified Warburg flasks. Earlier determinations were attempted in standard 25 ml. Warburg flasks with the centerwell and sidearm. Considerable difficulty was experienced with these flasks. When small pieces of leaves were floated in buffer solution they tended to stick together and jam against the centerwell and the leaves were not in their natural medium.

Therefore, flasks were designed so larger amounts of tissue could be suspended in air. These flasks were calibrated with Brodie solution. Black velveteen was used to make a cover for the bottom and black velveteen and plywood were used to cover the top of the Warburg to keep light out during respiration determinations.

Lanolin was used to seal the flasks. For the respiration determinations 2 ml. of 10% KOH was used to trap the carbon dioxide evolved. During photosynthesis the CO₂ atmosphere was maintained at approximately 15% (calculated) by 3 ml. of 0.8 M potassium bicarbonate saturated sodium borate solution. The photosynthesis determination was made first when both photosynthesis and respiration were determined on the same leaf tissue. The amount of leaf tissue used varied considerably, depending on the size of

the plant and the temperature. More tissue was used for respiration since the respiratory rates were much lower than the photosynthetic rates. Good photosynthesis curves were obtained when using as little as 5 milligrams (dry weight) of leaf tissue from young plants. As the plants became larger the leaves were wider, and more tissue was used. Up to 60 milligrams of tissue were occasionally used for respiration determinations.

RESULTS

The Effect of Temperature and Moisture Stresses

It was not possible to demonstrate genotype x environment interactions in the field in either 1960 or 1962. Table 1 shows significant F-values for the main order effects but there are no significant F-values for interaction for any of the characters measured in either year. However, significant genotype x environment interactions were obtained in the growth chamber, Table 2. There were no significant interactions at the low fertility level but in several cases significant F-values were obtained for interaction at the high fertility level. Each stress was compared with the control to reveal which stresses interacted with the genotypes. The early dry and late warm stresses show a significant genotype x environment interaction for weight per head. The early dry stress also shows a highly significant interaction for the number of seeds per head, which is a yield component that one would expect to be highly sensitive to stress during the early stage of development. Since there were no significant interactions in either 1960 or 1962 in the field, early dry or late warm

Table 1. F-values for environment, genotype, and interaction for weight per head, number of seeds per head, average weight per seed, number of heads per hill, and whole hill weight for parental field data of 1960 and 1962.

	wt./ head	seeds/ heads	wt./ seed	heads/ hill	wt./ hill
1960					
Environment	93.6**	12.2**	141.0**		
Genotype	3.4*	1.7	15.7**		
Interaction	2.0	2.3	1.2		
1962					
Environment	209.3**	302.3**	75.6**	100.4**	141.9**
Genotype	14.6**	3.5**	7.7**	9.5**	8.4**
Interaction	1.2	1.7	1.2	1.6	1.8

Table 2. F-values for environment, genotype, and interaction for weight per head, number of seeds per head, and average weight per seed for the growth chamber data.

	wt./head	seeds/head	wt./seed
Low fertility			
Environment	6.7**	4.4**	20.0**
Genotype	354.6**	292.0**	28.9**
Interaction	0.1	0.1	1.8
High fertility			
Early dry	0.5	42.3**	4.9*
Genotype	31.0**	28.5**	51.4**
Interaction	3.6*	117.4**	1.1
Early warm	1.1	6.0*	2.2
Genotype	44.8**	14.6**	18.5**
Interaction	1.4	0.7	0.1
Late dry	122.5**	68.8**	15.4**
Genotype	19.3**	16.0**	19.5**
Interaction	2.4	0.1	2.0
Late warm	84.6**	22.6**	54.1**
Genotype	13.4**	16.9**	25.1**
Interaction	4.2*	1.1	1.7

night stresses probably were not major factors determining the yield patterns for the early-late plantings in the field in 1960 and 1962.

Table 3 shows the effects of the stresses in the growth chamber on the 3 genotypes grown at the high fertility level. The weight per head of C.I. 4781 was affected more by the early stresses, especially the dry stress, than were the other 2 genotypes. This is more readily seen in the column marked per cent of the control. There is an abrupt drop from 101.9 to 67.9 per cent for the weight per head of C.I. 4527. The weight per head of C.I. 4781 showed the least reduction of any genotype due to the late stresses.

Table 4 gives the weight per head, weight per seed, and the number of seeds per head as the percent of the mean for 1956, 1957, and 1960. The 1962 data also include the weight per hill and the number of heads per hill. Two things are apparent in the table. First, there is no visible interaction between the early and late plantings for any character measured except in 1957. This was demonstrated by Sarkissian for 1956 and 1957 and from the present data in Table 1 for 1960 and 1962. Secondly, there is an apparent difference between the patterns in 1957 for the late planting and all other plantings. Thus 1956 and

Table 3. Growth chamber data showing the effect of the stresses on the weight per head, number of seeds per head, and average weight per seed at the high fertility level expressed as the actual value and as percent of the control.

Character	C.I. 4527		C.I. 4781		C.I. 4562		LSD .05	LSD .01
	actual	%	actual	%	actual	%		
Weight/head, g.							.19	.25
Early dry	2.20	101.9	1.48	84.8	1.83	105.7		
" warm	2.13	98.5	1.61	92.1	1.77	102.2		
Late dry	1.46	67.9	1.33	75.8	1.12	64.9		
" warm	1.49	69.2	1.44	82.3	1.30	75.0		
Control	2.16		1.75		1.73			
Seeds/head, no.							5.21	6.88
Early dry	51.4	98.1	42.1	83.6	42.8	99.6		
" warm	49.2	94.0	45.3	90.1	41.8	97.1		
Late dry	39.7	75.8	39.4	78.3	30.7	71.3		
" warm	43.4	83.3	46.3	92.1	36.3	84.5		
Control	52.3		50.3		43.0			
Weight/seed, mg.							3.02	3.99
Early dry	43.0	103.7	35.0	100.6	42.9	106.6		
" warm	43.2	104.2	35.6	102.6	42.3	105.0		
Late dry	36.9	88.9	33.7	97.0	37.4	92.8		
" warm	34.7	83.7	31.0	89.2	35.6	88.4		
Control	41.5		34.8		40.3			

Table 4. The weight per head, average weight per seed, and number of seeds per head expressed as percent of the mean for 1956, 1957, and 1960.

Year	C.I.	wt./head		wt./seed		seeds/head		wt./hill		heads/hill	
		early	late	early	late	early	late	early	late	early	late
1956											
	4527	112	72	100	87	111	84				
	4810	86	96	94	104	92	93				
	4781	--	--	--	--	--	--				
	4827	102	93	100	97	101	96				
	4274-1	79	120	92	112	86	107				
	4562	121	119	109	100	110	119				
1957											
	4527	75	130	81	115	91	114				
	4810	114	115	107	118	108	98				
	4781	120	90	--	--	--	--				
	4827	116	85	111	84	106	102				
	4274-1	98	78	100	92	98	86				
	4562	97	92	98	101	101	91				
1960											
	4527	100	93	97	92	104	98				
	4781	95	108	94	101	101	107				
	4562	104	101	106	103	99	99				
1962											
	4527	84	88	92	87	91	100	104	122	116	
	4810	95	90	102	101	93	89	105	98	115	
	4781	94	101	95	105	100	97	85	96	84	
	4827	95	85	98	92	96	94	89	114	103	
	4274-1	116	128	105	113	111	113	107	87	84	
	4562	116	109	108	103	108	107	109	97	100	

1960 seem to have been similar years, 1957 shows rather large percent changes for C.I. 4527 and 4781, but 1962 shows only minor changes.

Results from Crosses

The reaction of the parents can be used to predict the reactions of the progeny. Table 5 shows the average heading dates and number of heads per hill for the parents, midparents and the F_3 's of 7 crosses grown in the field in 1962. In general, the F_3 's headed earlier than their respective midparents, which indicates dominance. There is good agreement between the midparent and the means of the F_3 for heads per hill; the correlation coefficients are .781 for the early and .623 for the late planting. The correlation coefficients for the early planting is significant at the 5% level while the coefficient for the late planting is not significant but there are only 5 degrees of freedom. All of the F_3 means show a heterotic effect. The amount varies with the cross and the planting date. The cross C.I. 4527 x 4827 has the most heads per hill in the early planting but drops to third position in the late planting while cross C.I. 4810 x 4562 moves from second lowest to high. This is consistent with the parents' behavior since both C.I. 4527 and 4827 decreased as percent

Table 5. Average heading dates and number of heads per hill for the parents, midparents, and the F_3 's of 7 crosses grown in the field in 1962.

C.I. Cross	Early (April 20)		late (May 17)	
	headed	no. heads	headed	no. heads
Parents				
4527	June	24.0	61.25	July 13.6 41.12
4810	"	24.2	49.25	" 13.6 40.50
4781	"	23.1	43.25	" 10.4 29.50
4827	"	22.9	57.12	" 12.0 36.38
4274-1	"	20.2	43.75	" 8.5 29.50
4562	"	21.6	47.38	" 10.8 34.88
4527 x 4827				
Midparent	June	23.4	59.19	July 12.8 38.75
F_3	"	22.7	74.52	" 13.0 41.25
4810 x 4781				
Midparent	"	23.7	46.25	" 11.9 35.00
F_3	"	20.1	56.58	" 9.7 39.36
4810 x 4274-1				
Midparent	"	22.2	46.50	" 11.0 35.00
F_3	"	20.5	58.20	" 9.8 43.13
4810 x 4562				
Midparent	"	22.9	48.31	" 12.1 37.69
F_3	"	20.3	51.79	" 8.8 43.58
4781 x 4274-1				
Midparent	"	21.7	43.50	" 9.4 29.30
F_3	"	18.7	50.79	" 7.5 39.21
4827 x 4274-1				
Midparent	"	21.6	50.44	" 10.2 32.94
F_3	"	20.0	60.66	" 8.8 34.94
4827 x 4562				
Midparent	"	20.9	52.25	" 9.6 32.19
F_3	"	20.9	53.35	" 8.6 35.59

of the mean from early to late planting, from 122 and 114 percent to 116 and 103 percent, whereas C.I. 4810 and 4562 both increased, from 98 and 94 percent to 115 and 100

percent of the mean, respectively.

Table 6 shows the variances for the number of heads per hill data in Table 5. The genetic variance for the F_3 of C.I. 4527 x 4827 is negative in the late planting due to the abnormally high variances of both parents. These high variances may well be due to sampling error since the parental variances are based on only 8 measurements. A small part of the genetic variance is due to non-additive effects but, in general, the heritability for number of heads per hill will be near 25% which is a satisfactory figure.

The heading dates for the early and late plantings for the F_3 in 1960 and the F_4 in 1962 and for the parents, midparents, and backcrosses are given in Table 7. In 1960, the F_3 's headed earlier than the midparents in the early planting but in the late planting the heading dates of the F_3 coincide with those of the midparents. However, the resulting F_4 's in 1962 headed earlier than their midparents in both plantings.

Table 8 shows the average number of matured heads per hill in 1962 for the midparent, F_4 , and backcrosses of 3 crosses. The F_4 compares favorably with the midparent, as do the backcrosses. The actual values usually are higher (showing heterosis) except in 2 instances which are both in the late planting.

Table 6. Variances of number of heads per hill for the parents and the genetic variances of the F_3 's of 7 crosses where the genetic variance is equal to the variance of the F_3 minus the mean variance of the parents.

C.I. Cross	early	late
Parents		
4527	133.64	90.12
4810	69.36	48.57
4781	85.07	60.00
4827	35.84	80.55
4274-1	87.07	40.86
4562	98.84	28.98
4527 x 4827	182.43	62.86
	<u>84.74</u>	<u>85.34</u>
	97.69	-22.48
4810 x 4781	77.22	54.28
	<u>55.84</u>	<u>50.84</u>
	21.38	3.44
4810 x 4274-1	119.88	69.17
	<u>78.22</u>	<u>44.71</u>
	41.66	24.46
4810 x 4562	84.10	53.17
	<u>59.41</u>	<u>38.78</u>
	24.69	14.39
4781 x 4274-1	102.04	50.43
	<u>86.07</u>	<u>45.41</u>
	15.97	5.02
4827 x 4274-1	61.46	60.70
	<u>60.83</u>	<u>48.60</u>
	.63	12.10
4827 x 4562	67.34	54.76
	<u>52.66</u>	<u>40.68</u>
	14.68	14.08

Table 7. Heading dates for early and late plantings of the F_3 in 1960 and the F_4 in 1962 and for the parents, midparents, and backcrosses.

C.I.	F_3 in 1960		F_4 in 1962	
	early	late	early	late
Parents				
4527	July 7.2	July 25.5	June 24.0	July 13.6
4781	" 3.5	" 18.0	" 23.1	" 10.4
4562	" 4.8	" 22.0	" 21.6	" 10.8
4527 x 4781				
Midparent	July 5.4	July 21.8	June 23.6	July 12.0
F_3 ---- F_4	" 3.6	" 22.0	" 20.9	" 8.2
B.C. to 4527	" 3.9	" 23.4	" 20.8	" 10.2
B.C. to 4781	" 3.3	" 22.1	" 20.3	" 8.3
4527 x 4562				
Midparent	July 6.0	July 23.8	June 22.8	July 12.2
F_3 ---- F_4	" 3.9	" 23.0	" 19.9	" 8.2
B.C. to 4527	" 4.0	" 23.2	" 20.2	" 8.7
B.C. to 4562	" 3.1	" 20.8	" 18.6	" 6.9
4781 x 4562				
Midparent	July 4.1	July 20.0	June 22.4	July 10.4
F_3 ---- F_4	" 2.3	" 21.3	" 18.8	" 7.4
B.C. to 4781	" 0.4	" 19.3	" 18.6	" 7.7
B.C. to 4562	" 1.3	" 20.3	" 19.5	" 7.0

Table 9 shows the weight per head, number of seeds per head and the average weight per seed for the early and late plantings of the F_3 and backcrosses of 3 crosses in 1960. Here again the observed values usually are very close to the expected values. The row variances for the F_3 and the parental data are given in Table 10. The heritabilities again are in the acceptable range, being slightly higher than for the number of heads per hill.

Table 8. The average number of matured heads per hill in 1962 for the midparent, F₄, and backcrosses of 3 crosses.

Generation	4527 x 4781		4527 x 4562		4781 x 4562	
	midparent	progeny	midparent	progeny	midparent	progeny
F ₄	Early	52.25	56.65	54.32	45.32	51.79
	late	35.31	41.08	38.00	32.19	37.35
B.C. to 1st parent	early	56.75	57.96	57.78	44.28	51.56
	late	38.22	35.62	39.56	30.84	29.33
B.C. to 2nd parent	early	47.75	48.31	50.85	46.35	47.97
	late	32.40	32.46	36.44	33.54	36.78

Table 9. The observed and expected values for the weight per head, number of seeds per head, and average weight per seed, for the F_3 and backcrosses of 3 crosses grown in the field in 1960.

Cross C.I.	Early					
	Wt./head		seeds/head		wt./seed	
	exp.	obs.	exp.	obs.	exp.	obs.
4527 x 4781	2.533	2.617	71.35	71.00	35.35	36.77
B.C. to 4527	2.565	2.710	71.78	71.34	35.58	37.88
B.C. to 4781	2.501	2.72	70.92	73.73	35.12	36.71
4527 x 4562	2.642	2.582	70.400	68.88	37.45	37.25
B.C. to 4527	2.619	2.550	71.300	69.13	36.62	36.68
B.C. to 4562	2.663	2.690	69.50	69.15	38.28	38.76
4781 x 4562	2.577	2.544	69.55	68.00	37.00	37.18
B.C. to 4781	2.523	2.571	70.02	69.63	35.95	36.87
B.C. to 4562	2.631	2.511	69.08	67.98	38.05	36.95
	Late					
	Wt./head		seeds/head		wt./seed	
	exp.	obs.	exp.	obs.	exp.	obs.
4527 x 4781	1.956	2.001	68.45	66.47	28.00	29.98
B.C. to 4527	1.880	2.035	66.98	68.54	27.40	29.39
B.C. to 4781	2.032	1.969	69.92	66.84	28.60	29.43
4527 x 4562	1.941	1.939	65.65	67.79	29.18	28.50
B.C. to 4527	1.847	1.991	65.58	70.55	27.58	28.02
B.C. to 4562	1.932	1.928	65.72	68.75	29.12	27.80
4781 x 4562	2.107	2.020	68.60	69.16	29.55	29.28
B.C. to 4781	2.075	1.957	70.00	66.86	29.38	29.02
B.C. to 4562	2.008	2.154	67.20	70.02	29.72	30.10

Table 10. Variances of weight per head, number of seeds per head, and weight per seed for the parents and the genetic variances of the F_3 of 3 crosses grown in the field in 1960; the genetic variance is equal to the variance of the F_3 minus the mean variance of the parents.

C.I. Cross	early			late		
	<u>wt.</u> head	<u>seeds</u> head	<u>wt.</u> seed	<u>wt.</u> head	<u>seeds</u> head	<u>wt.</u> seed
Parents						
4527	.0308	16.400	0.190	.0036	2.290	0.863
4781	.0003	2.010	0.414	.0090	1.750	1.043
4562	.0020	2.170	0.910	.0009	0.107	0.120
4527 x 4781	.0513	14.734	5.045	.0386	17.250	4.994
	<u>.0155</u>	<u>9.205</u>	<u>.302</u>	<u>.0063</u>	<u>2.020</u>	<u>.953</u>
	.0358	5.529	4.743	.0323	15.230	4.041
4527 x 4562	.0362	10.418	2.998	.0413	12.907	5.671
	<u>.0164</u>	<u>9.284</u>	<u>.550</u>	<u>.0022</u>	<u>1.199</u>	<u>.491</u>
	.0198	1.134	2.442	.0391	11.708	5.180
4781 x 4562	.0455	13.315	3.503	.0456	14.864	4.426
	<u>.0012</u>	<u>2.090</u>	<u>.662</u>	<u>.0049</u>	<u>.928</u>	<u>.582</u>
	.0443	11.225	2.841	.0407	13.936	3.844

Physiological and Morphological Considerations

Photosynthetic and respiratory rates were determined in an attempt to explain differences in yield between genotypes. Photosynthetic rates in Q_{O_2} 's (microliters of oxygen per hour per milligram dry weight of leaf tissue) for 3 genotypes assayed at 3 temperatures and 1800 foot candles are given in Table 11. The rates at 20 and 30°C. are about

the same but are much higher than those at 15°C. There is no statistically significant difference between the 3 genotypes at any one temperature, but the seedlings of C.I. 4527 tend to have a slightly higher photosynthetic rate than those of C.I. 4781. The standard deviations are quite high in some cases which indicates considerable variability.

Table 11. Photosynthetic rates in Q_{O_2} 's for 3 genotypes assayed at 3 temperatures 2 and 1800 f.-c.

C.I.	15°C.	20°C.	30°C.
4527	19.0 \pm 0.42	42.8 \pm 4.66	42.6 \pm 1.33
4781	18.8 \pm 0.00	38.4 \pm 3.57	39.1 \pm 3.55
4562	19.7 \pm 1.98	39.3 \pm 4.04	43.1 \pm 0.97

Table 12 shows the respiratory rates in Q_{O_2} 's for 3 genotypes assayed at 2 temperatures. The respiratory rate of C.I. 4781 is the lowest but there is no significant difference between the rates of the genotypes. The respiratory rates at 30°C. are low but were determined with the same seedlings used for photosynthesis in Table 11. Higher respiratory rates were obtained at 30°C. with other seedlings but the relationship between the genotypes was the same. Some of these higher respiratory rates are shown in Table 13; each group of three: e.g., C.I. 4527, 4562, and their F_1 , represents the rates determined in

Table 12. Respiratory rates in Q_{O_2} 's for 3 genotypes assayed at 2 temperatures.

C.I.	15°C.	30°C.
4527	1.13 \pm 0.21	1.93 \pm 0.01
4781	0.99 \pm 0.03	1.73 \pm 0.12
4562	1.12 \pm 0.18	2.18 \pm 0.39

Table 13. Photosynthetic and respiratory rates of 3 genotypes and their F_1 's grown in the growth chamber.

	Photosynthesis	Respiration
4527	46.2 \pm 3.68	3.94 \pm 0.265
4562	42.4 \pm 3.87	3.64 \pm 0.203
F_1	43.1 \pm 2.32	3.91 \pm 0.599
4527	37.5 \pm 0.78	3.75 \pm 1.802
4781	34.0 \pm 4.06	3.71 \pm 0.220
F_1	36.2 \pm 3.60	3.59 \pm 0.297
4781	31.5 \pm 4.17	3.27 \pm 0.093
4562	33.8 \pm 2.89	3.29 \pm 0.232
F_1	29.7 \pm 4.04	3.10 \pm 0.481

one day and the next group of three represents the successive day's determinations. Thus the photosynthetic rate decreases markedly for each days' increase in age of the seedlings. This is one reason why the standard deviations here and elsewhere are quite large. The decrease in respiratory rate seems to be less rapid; this is partially true because the most recently expanded leaf was used for

respiration while the next older leaf was used for photosynthesis. The rates determined on any one day are not significantly different. The F_1 's are neither significantly higher nor lower than their parents.

There apparently is little direct physiological change due to 80 vs. 60°F. night temperatures. The respiratory rates of the plants subjected to warm night temperatures were slightly lower at both 15 and 30°C. whereas the photosynthetic rates were slightly lower at 15 and slightly higher at 30°C. However, none of the rates were significantly different from the rates of the plants under cool night temperatures. There does seem to be a difference in the length of time that the leaves are physiologically active.

Table 14 shows the average photosynthetic rates, the number of leaves used to obtain this average, and the weight of the top leaves of the tillers of plants grown in the growth chamber. Due to its earlier senescence, fewer lower leaves of C.I. 4527 were available and also the photosynthetic rate was lower for the leaves that still had a green portion remaining. More flag leaves were used of C.I. 4527 than of C.I. 4781, 15 vs. 9, because C.I. 4527 had more tillers, most of which were slightly younger than those of C.I. 4781. Even though the flag leaves of C.I. 4527 were

slightly younger, the average photosynthetic rates are about equal. The F-values in Table 14 show that there is a significant difference in the photosynthetic rate only for the second leaf below the flag (flag-2). The weight of the top 2 leaves of the tillers is greater for C.I. 4527, but the weight of the third leaf is about the same. In general, the tillers had fewer leaves than the main culms and the first 2 or 3 leaves were very small.

Table 14. Average photosynthetic rates, the number of leaves used to obtain this average, and the weight of the top leaves of the tillers of plants grown in the growth chamber.

Leaf	C.I. 4527				C.I. 4781				F
	no.	wt.	Q_{O_2}	s	no.	wt.	Q_{O_2}	s	
Flag	15	38.2	31.0	5.85	9	18.4	30.8	3.95	0.44 N.S.
Flag-1	14	44.6	26.1	8.01	9	29.0	29.9	5.35	1.62 "
Flag-2	6	28.4	22.7	4.16	7	30.2	27.9	3.39	6.11*
Flag-3	0	-	-	-	2	-	23.0	-	-

The data in Table 15 for plants grown in the field in 1962 are similar to the preceding results from plants grown in the growth chamber. The average photosynthetic rates are about the same but this is slightly misleading since the averages include several values for the main culm in which the rate for C.I. 4527 is appreciably higher. The higher rates for C.I. 4527 result from using younger plants

Table 15. Average photosynthetic and respiratory rates and leaf weights of main culms and tillers of plants grown in the field.

	C.I. 4527			C.I. 4781		
	no.	Q_{O_2}	s	no.	Q_{O_2}	s
Photosynthesis						
main culms	25	26.2	7.12	23	26.0	5.24
tillers	73	29.5	5.58	70	30.3	6.12
Respiration						
main culms	19	4.00	0.61	19	3.93	0.78
tillers	41	3.89	2.47	31	4.00	3.10
Leaf weights						
main culms	16	110.6	29.58	16	83.9	26.53
tillers	55	145.1	25.39	53	121.3	35.85

earlier in the season (June 11) with 31.0 vs. 26.3 (averages of 5 and 6 leaves). On June 27 comparable leaves (leaf below the flag) were taken from plants planted 1 week apart: the average photosynthetic rates were 24.6 vs. 28.9 for the earlier and 30.3 vs. 22.8 for the later planting for C.I. 4527 vs. 4781. Thus here, too, the photosynthetic rate for C I. 4527 apparently decreases more rapidly with time. The weight of the leaves again is greater for C.I. 4527 than for C.I. 4781: 145 vs. 121 mg. for the tillers and 111 vs. 84 mg. for the main culms. Even though the difference is greater with the main culms, a t-test indicates that the difference in weight is highly significant for the tillers but is not significant for the main culms.

This is due to the smaller number of plants and the large variances.

The same trend was observed in the field with the main culms as with the tillers. Average photosynthetic rates obtained on June 7 and 12 were 33.2 and 26.7 for C.I. 4527 and 4781, respectively, whereas corresponding rates on July 15 to 18 were 22.2 and 25.6. The respiratory rates decreased only slightly during this period, from 4.25 and 4.22 to 3.89 and 3.84 for C.I. 4527 and 4781, respectively. The respiratory rates given in Table 15 are not significantly different. The photosynthetic rates of the tillers are significantly higher than the main culms' because of younger leaves. The respiratory rates are higher than some of the rates obtained in the chamber, partly because the rates were determined at 32.5 instead of 30°C. However, the field plants also were infected with mildew and leaf rust even though frequently dusted with sulfur. Both of these diseases tend to increase the respiratory rate of infected plants.

Photosynthetic and respiratory rates were obtained on F₄ plants in 1962; these data, the leaf weights, and their standard deviations are given in Table 16. There are no significant differences in the photosynthetic rates. The leaf weights of C.I. 4527 is significantly higher than that

Table 16. Photosynthetic and respiratory rates and leaf weights of C.I. 4527 and 4781 and a sample of their F_4 progeny grown in the field in 1962.

	C.I. 4527	C.I. 4781	F_4
Photosynthesis			
no.	48	46	47
Q_{O_2}	27.0	29.6	29.3
s_{O_2}	6.23	5.50	7.70
Respiration			
no.	45	39	40
Q_{O_2}	3.92	4.01	3.38
s_{O_2}	0.23	0.30	0.27
Leaf weight			
no.	48	46	47
mg.	124	92	93
s	24.5	23.7	25.1

of either C I. 4781 or their F_4 . The standard deviations are large, partially because several different leaves were used. The respiratory rate of the F_4 is significantly lower than those of its parents. The F_1 of this cross (C.I. 4527 x 4781 in Table 13) also had a slightly lower respiratory rate but the difference was not significant. The F_4 plants seemed to be physiologically older, and Table 7 showed that the late planted F_4 hills did in fact head earlier than either of the parents. The earlier heading did not result in lower yield since Table 17 shows that the F_4 was more productive than either of its parents. Earlier

genotypes are expected to be more productive under late stress. The lower respiratory rate may be related to age and/or disease but the photosynthetic rate is high and these 2 facts may have contributed to the F_4 's' higher yield.

Table 17. The average weight per head and total weight per hill for C.I. 4527 and 4781 and their progeny for 2 planting dates in 1962.

C.I.	wt./head				wt./hill			
	early		late		early		late	
	exp.	obs.	exp.	obs.	exp.	obs.	exp.	obs.
4527		1.14		.763		70.29		31.57
4781		1.28		.882		54.11		25.68
F_4	1.21	1.28	.88	.96	62.20	72.00	28.62	39.23
B.C.to 4527	1.17	1.29	.79	.81	66.24	74.38	30.10	29.34
B.C.to 4781	1.24	1.62	.85	.76	58.16	77.71	27.15	24.52

In the growth chamber experiment, C.I. 4781 had fewer leaves per plant than C.I. 4527 and 4562 but only its first 2 leaves were slightly heavier. The leaf weight may be taken as an indication of leaf area. Table 18 presents the weights of the top 3 leaves and C.I. 4527 definitely has the heaviest leaves. Apparently none of the stresses had any significant effect on the leaf weights of C.I. 4781 and 4562. However, the plants of C.I. 4527 responded to the early stresses by developing significantly heavier leaves than the control plants; the late dry stress was somewhat less effective than the early stresses but the late warm

night temperature stress had no significant effect on the leaf weight.

Table 18. The response of the weights of the top 3 leaves of 3 genotypes to stresses at the high fertility level.

Leaf C.I.	Control	Dry		Warm nights	
		early	late	early	late
Flag (LSD $.05=7.4$)					
4527	39.2	53.0	49.5	52.9	41.2
4781	31.4	35.3	36.4	34.0	30.8
4562	28.0	37.6	30.6	31.2	23.8
Flag - 1 (LSD $.05=6.0$)					
4527	59.6	70.7	69.5	71.3	59.7
4781	52.0	52.2	59.8	56.6	55.8
4562	47.5	57.2	50.4	50.8	47.5
Flag - 2 (LSD $.05=5.4$)					
4527	63.2	68.2	67.1	72.1	64.2
4781	50.0	52.0	55.9	62.0	54.4
4562	51.1	59.9	55.4	58.4	50.9

The rate of senescence of leaf tissue is another important factor in the performance of a variety. The advantage of the larger top leaves of C.I. 4527 is negated to some extent by its earlier senescence through loss of photosynthetic activity and also loss of leaf area due to physiological discoloration and withering of the leaves, Table 19.

The heading of C.I. 4781 seems to be more responsive to photoperiod than the other 2 genotypes. The planting and

Table 19. Cumulative inches of leaf tip discolored on 29 plants of each of 3 genotypes grown in the growth chamber.

C.I.	3	4	5
4527	63"	58"	17"
4781	33"	26"	4"
4562	29"	39"	10"

heading dates and number of days of heading for 1960, 1962, and for the control plants in the chamber are given in Table 20. In this latitude (about 42.75°N.) the day-length varies from 14.7 hours on May 21 to 15.2 hours on June 21 and then back to 14.7 on July 21. In terms of heading response C.I. 4781 seems to head earlier as the day-length increases while C.I. 4562 consistently heads about 3 days earlier than C.I. 4527. The long (16 hour) photoperiod in the chamber elicits a heading response that is similar to that for the late 1960 planting in the field, in which the plants were exposed to long days earlier in the growth cycle.

The difference in date of heading and development response in the chamber is illustrated graphically in Figure 1. The height measurements are to the top auricle, the dates of heading are indicated by crosses, and the circle is at the (Dec. 20, 60 cm.) coordinate in all cases.

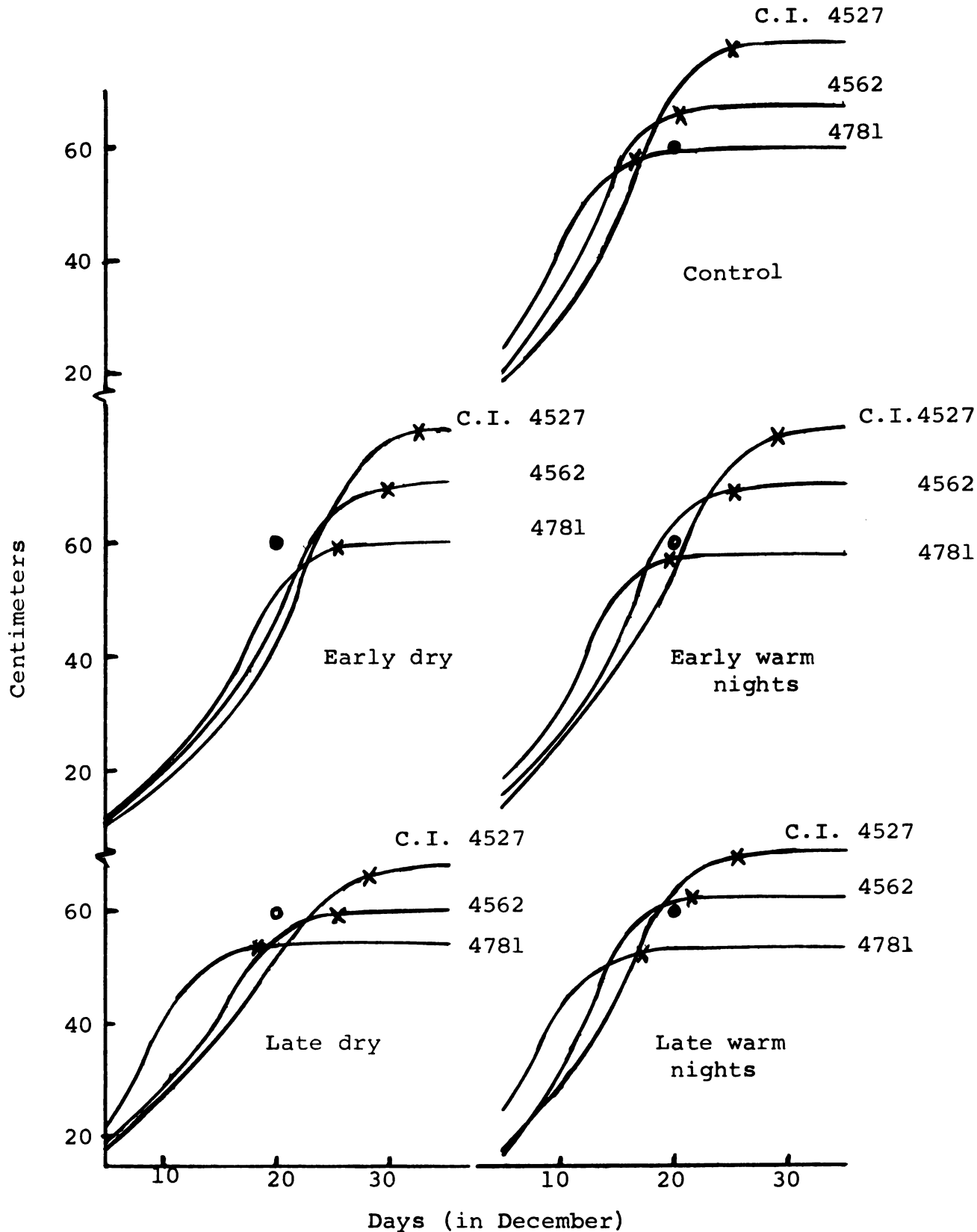


Figure 1. Comparison of growth curves for 3 genotypes for 4 stress situations and the control. The curves are for the height of the flag leaf. Heading dates are indicated by crosses. Circles are at the (Dec. 20, 60 cm.) coordinate.

Table 20. The dates of planting and heading and the number of days till heading for 3 genotypes in 1960, 1962, and in the growth chamber.

Planting dates	C.I. 4527		C.I. 4781		C.I. 4562	
	headed	days	headed	days	headed	days
1960						
April 29	July	7.2 69.2	July	3.5 65.5	July	4.8 66.75
May 25	"	25.5 61.5	"	18.0 54.0	"	22.0 58.0
1962						
April 20	June	24.0 65.0	June	23.1 64.1	June	21.6 62.6
May 17	July	13.6 57.6	July	10.4 54.4	July	10.8 54.8
Chamber						
Nov. 1	Dec.	25.2 55.2	Dec.	17.0 47.0	Dec.	20.9 50.9

The early stresses were applied from November 11 to December 5; therefore, the first points on the figure are at the end of this stress period. The late stress period, December 11 to January 9, is indicated by vertical lines. It is obvious that C.I. 4781 has made most of its growth by the time the late stresses are applied whereas C.I. 4527 still has much of its growth period remaining, C.I. 4562 is in an intermediate position. There is no interaction for either heading date or height due to the stress or the time of stress.

DISCUSSION

The effect of either drought or heat early in the growth period is relatively less severe on C.I. 4527 and 4562 than on C.I. 4781. Conversely these same stresses late in the growth cycle have relatively less effect on C.I. 4781. Although 1957 was quite wet, June was the driest month. The warmest night temperatures, including July, occurred during the middle of June. This period of slightly less moisture and definitely warmer nights affected the early planting during a much later stage of growth than the late planting of June 2. These stresses would give the yield responses that were observed in Table 4 and probably also a significant interaction since the early drought and the late warm night stresses interacted with the genotypes in the chamber.

The preceding argument does not conclusively prove the causal agent(s) responsible for the yield patterns, but only that the early dry and the late warm night stresses resulted in significant genotype x environment interactions in the chamber. Sarkissian reports the degree-nights (cumulative degrees above 60°F.) for 1957 as 88 for the early and 129 for the late planting. Since the heat summation

is less under drought conditions (Nuttonson, 21), the early planting may have been affected more by drought stress than the late planting.

In 1960 the F_3 headed earlier than expected for the early planting but in the late planting it headed on the expected midparental dates, Table 7. The resulting F_4 headed earlier than expected for both planting dates in 1962. The reason for this is not readily apparent. If the environment only were responsible, then the F_3 's in 1962 all should have headed earlier than their midparents but the F_3 's vary from slightly later to over 3 days earlier than their respective midparents (Table 5). If the source of the seed and selection in 1960 were responsible for the F_4 's earlier heading, then all of the F_3 's would have been expected to head on the midparental values.

In general, the agreement between the observed and the expected values is very good. This is true not only for the yield components and the heading dates but also for the metabolic rates. The midparental values can be used to predict the performance of the progeny for all of these characters. Thus detailed physiological studies can be made without the necessity of analyzing all of the possible progeny. In effect this frees the breeder to do more fundamental research since he need make only those crosses

which maximize his chance of success.

The most striking thing about Table 10 was the increase in genetic variance in the late planting. The greatest changes were due to the abnormally high variance of C.I. 4527 for number of seeds per head in the early planting. C.I. 4527 also had high variances for number of heads per hill, Table 6. These large variances may be due to sampling errors or C.I. 4527 may be more sensitive to minor differences in its micro-environment. There is a trend in Table 10 for the variances of the F_3 to increase slightly and the variances of the parents to decrease slightly from the early to the late planting. This shift in the magnitudes of the variances results in higher heritabilities for the late planting.

The yield differences between genotypes cannot be explained on the basis of metabolic rates. The size and number of leaves seems to be relevant. C.I. 4527 has more and heavier leaves but they also senesce sooner. C.I. 4781 has fewer and lighter leaves but they are active longer. The date of heading or maturity seems to be important in determining not only the yield but also the effect of stress on it. C.I. 4527 heads late and also develops the largest head under favorable conditions but under late stresses its head size is reduced much more than C.I. 4781 which heads earlier. C.I. 4781 suffers the least reduction

by avoiding the late stresses but C.I. 4527 and 4562 suffer less from the early stresses than C.I. 4781.

Although the metabolic rates per se could not explain the differences at the high fertility level, they are related to the head sizes at the low fertility. The photosynthetic rates of seedlings grown at the low fertility level were 35.7, 26.8, and 30.7 for C.I. 4527, 4781, and 4562, respectively. The head weights are in the same order as the photosynthetic rates although the weight of C.I. 4562 is slightly less than expected but its respiratory rate is slightly higher. The photosynthetic rates are all significantly different but there are no significant differences between the respiratory rates. The stresses had very little effect on the weight per head at the low fertility level but perhaps this should have been expected. Ulrich (29) got greatly reduced top growth in sugar beets due to nitrogen deficiency, lowering the night temperature decreased the top growth of the high nitrogen plants appreciably but had little effect on the nitrogen deficient plants.

CONCLUSIONS

There were no significant genotype x environment interactions in the field in either 1960 or 1962 for weight per head, number of seeds per head, weight per seed, number of heads per hill or weight per hill. In the growth chamber there were significant interactions for weight per head and number of seeds per head due to the early dry stress and for weight per head due to the late warm night temperature stress. The early warm night temperature and late drought stresses did not interact significantly with the genotypes.

The heritability of approximately 25% for the number of heads per hill is acceptable and effective selection can be made in the F_3 . The heritability for seeds per head and weight per seed apparently increased with stress. The progeny in general tended to head slightly earlier than the midparents. The progeny means can be predicted on the basis of the midparental values for the components and also for physiological characteristics.

Physiological studies failed to uncover any real differences in photosynthetic or respiratory rates between the genotypes or their progeny except for the

progeny except for the respiratory rate of the F_4 of one cross but this was due to the age of the leaves. There seemed to be very little change in rates due to the warm night temperature stresses. However, a real difference in leaf size, maturity, and rate of senescence of leaf tissue was found, indicating that they are major factors in the response of these genotypes to stress. More precise equipment and sampling probably will reveal genotypic differences in metabolic rates at high fertility levels. At the low fertility level the yield was related to the photosynthetic rates but the stresses had very little effect.

C.I. 4527 had the heaviest top leaves in all cases. In the growth chamber C.I. 4781 had fewer leaves than either C.I. 4527 or 4562, but its leaves senesced later. The stresses had no effect on the weights of the top 3 leaves of C.I. 4781 and 4562. Under the early stresses and the late dry stress, C.I. 4527 developed significantly heavier leaves but the late warm night temperature stress had no effect.

C.I. 4781 responded to longer photoperiods by heading earlier. C.I. 4527 headed the latest in all cases. The date of heading or maturity seems to be very important in determining the yield per se and also the response to

stress. C.I. 4527 developed the biggest head under favorable conditions. Early stresses were less detrimental to C.I. 4527 than to C.I. 4781 but the opposite was true under late stresses. C.I. 4781 seemed to avoid the late stresses whereas C.I. 4527 compensated for the early stresses by developing heavier leaves.

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