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Drought Resistance of Inbred and Hybrid Corn Under Artificial and Natural Conditions

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By
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This thesis is approved as a creditable independent investigation by a candidate for the degree, Master of Science, and acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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INTRODUCTION

The term, drought resistance, has been applied to that particular combination of factors which enables certain plants to survive periods of drought with little or no injury. Because of the complexity of this property, workers have found it difficult to study and difficult to incorporate into crop plants.

A tool which has shown promise in studying the effects of controlled drought conditions is the artificial drought chamber.

This investigation was carried on for the purpose of determining the value of such a chamber in the study of drought reactions in corn. This paper is concerned with the development of a technique for studying reactions of inbred lines to artificial drought; with the use of this technique in establishing a correlation between artificial drought reactions and field observations; and with the study of the inheritance of both drought resistance and drought susceptibility in F_1 hybrids.

REVIEW OF LITERATURE

The wealth of scientific data that are available on the subject of drought gives an indication of the interest that this problem has prompted in investigators. It is not the purpose of this paper to review all available material, but several pertinent aspects will be considered.

The drought chamber was an important innovation in the study of plant reactions to conditions of high temperature, low relative humidity, and low soil moisture. Because it is difficult, if not impossible, in most areas to study drought under uncontrolled, natural conditions, this type of special equipment is a necessity for determining the inherent ability of a plant to develop under adverse moisture and heat conditions.

Probably one of the first machines of this type was built by Maximov and described by Aamodt (1), who later constructed a larger and improved chamber, which in turn was modified by Kemmey and Peto (14). Spring wheat varieties tested in the latter two machines reacted similarly to their known behavior under natural drought conditions.

Other workers who have successfully used a drought chamber of one form or another on a variety of plant species are Shirley (22), Mueller and Weaver (19), Coffman (5), McAllister (17), Bayles et al. (2), McCrory (18), Haber (8), Chisholm (4), and Dirks (7). Hunter et al. (11) first described the effects of artificial drought on corn in a study of inbred seedlings. He found that the relative resistance of corn seedlings was essentially the same as was noted for plants in the field.

A significant point to be considered in reviewing the work of these individuals is their conclusion, where correlation studies were undertaken,

that artificial drought tests at the seedling stage reveal results similar to the effects of natural drought. Seedlings which were resistant to wilting were generally resistant to wilting at later stages of growth. The importance of resistance to wilting and leaf firing is brought out by Lonnquist and Jugenheimer (16) who reported that inbred lines of corn, as well as the single crosses among them, which were resistant, set more seed throughout the life of the silks and remained receptive longer than did susceptible lines and crosses.

Only a small portion of the data on drought resistance is concerned with the complex manner in which it is inherited.

Jenkins and Richey (13) crossed Dark Green Lancaster, an inbred line of corn which had shown definite resistant characteristics during the drought of 1930, with ten other inbred lines. Some of the single crosses showed burning of top leaves and only 12.6% showed burned tassels. On the other hand Krug variety, which was the best of 12 commercial varieties, revealed 37% of the plants with burned top leaves and 13.4% with burned tassels. Since some of the lines which were crossed with Dark Green Lancaster were drought susceptible, it indicates that resistance was transmitted as a dominant characteristic.

In a similar study by Jenkins (12), ten crosses of a resistant inbred line, L317B2, were completely free from leaf burning while another line which appeared to be susceptible showed a variability of damage according to the resistance of the other parent. This indicates that in his study resistance acted as a dominant character.

Observations of a group of pure lines of corn and their hybrids by Sayre (21) indicated that lines which were injured by drought transmitted their susceptibility to the hybrids in which they occurred.

A genetic study by Heyne and Brunson (9) showed tolerance of corn to heat and drought to be intermediate to dominant in its inheritance. Also their work indicated that hybrid vigor in itself does not make a cross resistant to drought.

MATERIALS AND METHODS

All artificial drought studies in this study were carried out in the drought chamber described by Chisholm (4). Preliminary tests conducted by the author indicated a high degree of temperature variation within the chamber, and it was modified to eliminate the possibility of error due to this variation. Three turntables were installed, and by placing one replication on each turntable it was possible to eliminate all variation due to temperature within a replication.

After reviewing the work of Hunter, et al. (11), it was decided to test the seedlings at 14 days of age, but the 140°F. temperature which they used was beyond the range of the drought chamber which was used in these investigations. Further preliminary studies indicated that a temperature of approximately 120°F. over a longer period of time would still give a satisfactory degree of wilting.

In order to carry on a technique study for the purpose of obtaining information leading towards the correct treatment of corn seedlings in the drought chamber which would bring about a reaction similar to field conditions of sub-normal moisture and high temperature, it was thought desirable to use three inbred lines — resistant, intermediate, and susceptible to drought. Sixty-three inbred lines were grown for the purpose of selecting three lines which would correspond to those desired for study. Since the capacity of the drought chamber was 36 pots, 12 lines with three replications per line were all that could be tested at one time. Planting dates were staggered in order that the seedlings in each test would be the same age upon entering the drought chamber. One

line, SD26, was used during each test as a check; so that results of separate runs could be compared. Plants were grown in one-pint parafin frozen food containers which are referred to as pots in this paper.

To insure similar growing conditions in all pots, 400 grams of soil were added before planting. After the soil was firmly tamped, five kernels were spaced evenly on the surface, and 200 more grams of soil were used to cover the seeds. One hundred milliliters of water were then added to each pot bringing the total weight to 700 grams. As moisture became limiting during the growing period, each pot was placed on a scale, and water added until the total weight was again 700 grams. In this way soil moisture was maintained approximately the same in all pots. It was found undesirable to measure in equal amounts of water due to the variability of transpiration among lines. The seedlings were germinated and grown under greenhouse conditions. After seedling emergence plants of each pot were thinned to three to further insure similar conditions among pots.

When the seedlings were fourteen days old they were placed in the drought chamber and subjected to a temperature of 120°F. and a relative humidity of 18% for a period of 12 hours. The plants were then given a relative rating according to the degree of heat damage which they showed.

The index to the rating is listed as follows:

Degree of Wilting	Injury Rating
None	0
Slight tip burn	1
One-fourth wilted	3
One-half wilted	6
Three-fourths wilted	9
Over three-fourths wilted	11
Completely wilted	12

Where the degree of injury fell between two ratings as they are listed, the plant was given a rating which was appropriate to its particular degree of injury.

In order that a correlation might be established between artificial and natural drought, observation plantings were made during the spring of 1953 at the Central Substation at Highmore and the Range Field Station at Cottonwood, South Dakota where drought conditions might be expected during most growing seasons. Because the seed of some of the inbreds was limited, not all of the lines were planted at both places. Observations were made and each line was rated on September 9 after a prolonged dry spell had been in effect at the Cottonwood station. A correlation coefficient was calculated between the field and drought chamber results.

The search for a technique which would bring out the inherent differences among inbred lines and hybrids was begun in the fall of 1953 with the use of three lines which had reacted resistant, intermediate, and susceptible to drought, and correlated well in both drought chamber and field results. The study was designed to include three soil moisture treatments, three relative humidity levels, and four temperatures. However, it was found that maintaining a high relative humidity at high temperatures was not possible with the equipment used, therefore that portion of the experiment could not be conducted. Different soil moisture treatments were obtained by watering to field capacity every day, every other day, and every third day. Temperature treatments used were 115°, 120°, 125°, and 130°F. Readings on heat damage in the drought chamber were made every four hours except at the 130°F. temperature in which case they were read every two hours due to the rapidity with which the plants succumbed.

An analysis of variance was applied to the results for each temperature and moisture treatment to determine which treatment resulted in the maximum differences among the three lines.

A test was conducted under the conditions which the previous experiment showed to be the most desirable on all of the lines which had been included in the study at the Cottonwood station. A correlation coefficient was then obtained between field and drought chamber results.

It was noted in preliminary studies that lines seemed to vary a great deal in the amount of water which they transpired, and it was thought possible that a plant might be susceptible because of a high transpiration rate. Haber (8) found that drought susceptible lines of corn transpired more than resistant lines when measured by the method of hygrometric paper. However, when the measurement was figured on the basis of grams of water absorbed by a system involving $CaCl_2$, there was not as great a variation between susceptible and resistant lines as groups as there was among inbreds within a group. Thirty-six hours before they were placed in the drought chamber all pots of corn were watered to field capacity by weight along with three pots which had no corn planted in them. By subtracting the weight of a pot which contained growing plants from the average weight of the pots which contained no growing plants at the end of the 36-hour period the amount of water transpired by the plants in a pot was obtained. A similar method was used for computing the transpiration rate for the 12-hour period in the drought chamber. The correlation coefficients were obtained between drought chamber results and 36-hour transpiration, between drought chamber results and 12-hour transpiration, between field

results and 36-hour transpiration, between field results and 12-hour transpiration, and between 36 and 12-hour transpiration.

Another phase of study was the determination of the role of light on the reaction of seedlings to artificial drought. Three resistant lines and three susceptible lines were planted in pots in the usual manner except that one group was shaded from the direct rays of the sun, and differences in reaction of the plants to drought due to light were recorded.

It was also thought desirable to determine whether or not inherent differences in drought resistance could be measured by reducing the soil moisture on the greenhouse bench; so a similar set was left on the bench and progressive injury due to soil drought was noted for the different lines.

To determine the mode of inheritance of factors involved in drought resistance and susceptibility, a number of inbred lines, previously rated as highly resistant or susceptible, were included in a crossing program. Resistant x resistant, resistant x susceptible, susceptible x resistant, and susceptible x susceptible lines were involved in the production of F_1 hybrids with diversified genetic make-up. Some of these were grown and tested for their reactions to drought. Not all of these crosses were developed to the point where they could be tested at the time of this writing, and for that reason can not be included in this paper.

EXPERIMENTAL RESULTS

I. Drought Chamber Studies Preliminary to Field Trials and Technique Study.

The results of a drought chamber study on 63 inbred lines of corn are listed in Table I in decreasing order of their resistance.

Table I. Means of drought injury ratings for 63 inbred lines of corn when tested under conditions of 120°F. and 18% relative humidity for 12 hours.

	Line	Mean Injury Rating
1	2(5) - 52198-1	4.7
2	2(5) - 52198-2	4.7
3	2(5) - 52201-1	5.3
4	2(5) - 52202-2	5.3
5	W8	5.7
6	52240-2	6.0
7	L317	6.0
8	A322	6.3
9	Oh43	6.3
10	Oh45	6.3
11	Oh56A	6.3
12	5(W8) - 52157-3	6.3
13	52239-1	6.3
14	SD7	6.7
15	W32	6.7
16	1(56A) - 52138-1	6.7
17	2(5) - 52149-1	6.7
18	7(I153)	6.7
19	2(5) - 52204-2	6.7
20	52236-2	6.7
21	SD2	7.0
22	A340	7.0
23	5(51A)	7.0
24	7(W8) - 52186-3	7.0
25	SD26	7.3
26	Oh51	7.3
27	A73	7.3
28	5(420) - 52176-1	7.3
29	7(W8) - 52186-1	7.3
30	52300-2	7.3
31	A188	7.3

	Line	Mean Injury Rating
32	38-11	7.3
33	5(Oh56A)	7.7
34	52242-1	7.7
35	52307-2	7.7
36	SD1	8.0
37	SD5R	8.0
38	A34	8.0
39	R53	8.0
40	52245-1	8.0
41	Rainbow Flint 52399-1	8.0
42	SD5	8.3
43	SD48	8.3
44	W275A	8.3
45	1(Oh56A) - 52141-1	8.3
46	5(Os420) - 52173-1	8.3
47	7(W22) - 52178-1	8.3
48	7(Os420)	8.3
49	A225	8.7
50	A277	8.7
51	W9	8.7
52	B8	8.7
53	7(W22) - 52183-1	8.7
54	7(W22) - 52183-3	8.7
55	B16	9.0
56	W273C	9.0
57	ND230	9.0
58	7(W22) - 52182-1	9.0
59	Rainbow Flint - 52386-2	9.0
60	SD4	9.3
61	SD6	10.0
62	7(W22) - 52181-2	10.0
63	7(W22) - 52179-1	11.0
Mean		7.6

Table II. Analysis of variance of artificial drought injury of 63 inbred lines of corn.

Source of Variation	d. f.	Mean square	F
Lines	62	4.91	6.06**
Replications	2	7.16	
Lines x Replications	124	.81	
Total	188		

**Significant at the one per cent level.

The analysis of variance shows that differences between lines are highly significant.

II. Field Results

A. Central Substation at Highmore

Due to the unusually high rainfall at the Highmore station during the summer of 1953 none of the inbreds planted showed any indication of drought damage; consequently, no data as to the relative resistance of the inbreds was available from this test.

B. Range Field Station at Cottonwood

During the spring and early summer moisture conditions were excellent at this station also, but an extended dry spell subjected the plot to rather severe drought later in the growing season. Observation of the plot and rating of the lines was made on September 9, and the results are listed in Table III.

Table III. Means of drought injury ratings of 44 inbred lines of corn when tested under natural drought conditions at the Range Field Station at Cottonwood, 1953.

Line		Mean Injury Rating
1	WS	1.5
2	52240-2	2.5
3	A227	3.0
4	Oh43	3.0
5	A73	3.0
6	52239-1	3.0
7	A225	3.5
8	Oh45	3.5
9	R53	3.5
10	2(5) - 52149-1	3.5
11	L317	3.5
12	M16	4.0

	Line	Mean Injury Rating
13	A322	4.0
14	W32	4.0
15	Oh51	4.0
16	Oh56A	4.0
17	SD2	4.5
18	SD48	4.5
19	2(5) - 52201-1	4.5
20	2(5) - 52202-2	4.5
21	38-11	4.5
22	SD5R	5.0
23	7(W22) - 52179-1	5.0
24	SD5	5.0
25	B8	6.0
26	7(W22) - 52183-3	6.0
27	2(5) - 52204-2	6.0
28	Rainbow Flint - 52386-2	6.0
29	SD26	6.5
30	A188	6.5
31	Rainbow Flint - 52399-1	6.5
32	SD4	7.0
33	7(W22) - 52183-1	7.5
34	7(W8) - 52186-1	7.5
35	7(Os420)	7.5
36	SD1	8.0
37	SD7	8.0
38	W275A	8.0
39	A340	9.0
40	W273C	9.5
41	SD6	10.0
42	ND230	10.0
43	A34	11.0
Mean		5.5

The analysis of variance listed in Table IV shows a highly significant difference among lines.

Table IV. Analysis of variance of natural drought injury of 44 inbred lines of corn.

Source of Variation	d. f.	Mean square	F
Lines	43	10.37	9.60**
Replications	1	21.50	
Lines x Replications	43	1.07	
Total	87		

**Significant at the one per cent level.

The correlation coefficient between artificial and natural drought injury ratings for 44 inbred lines previously listed was..364. This is significant at the five per cent level.

III. Technique Study

The results of the technique study are listed in figures 1, 2, 3, and 4. Figure 1 shows graphically the progressive injury to three inbred lines in the drought chamber maintained at 115°F., 18% relative humidity, and under three moisture treatments. Figures 2, 3, and 4 present the results obtained on the same lines under similar conditions except that temperatures were maintained at 120°, 125°, and 130°F., respectively.

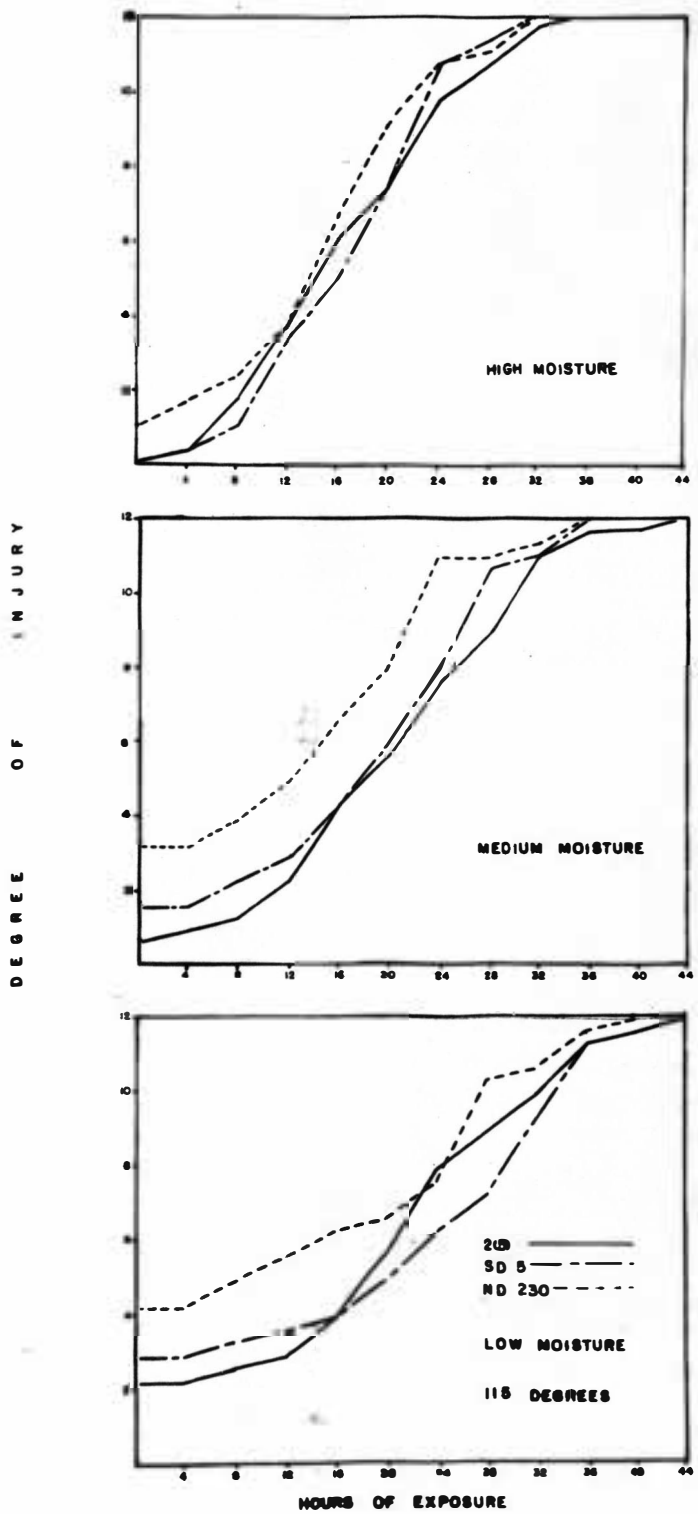

Figure 1. Progressive injury of three inbred lines of corn at 115°F., 18% relative humidity, and at high, medium, and low moisture treatments.

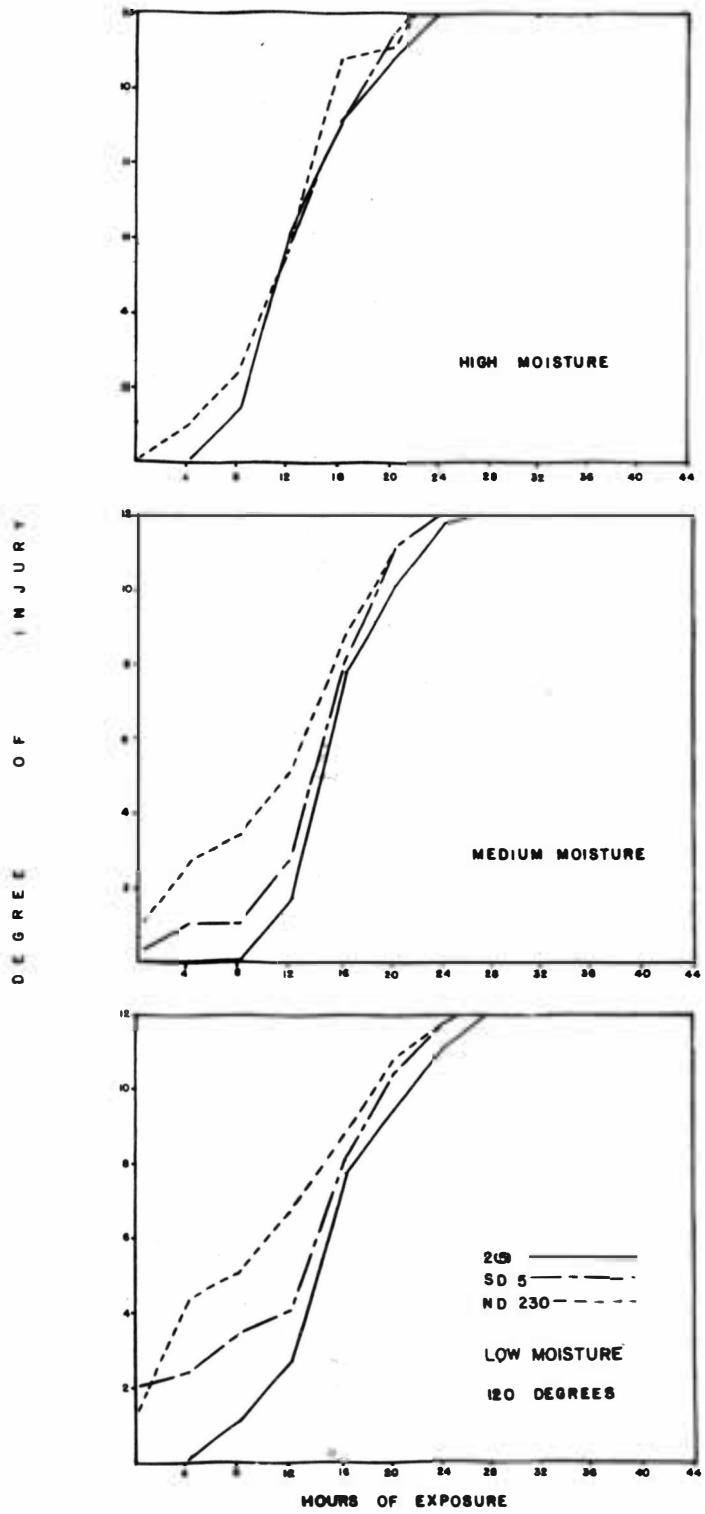

Figure 2. Progressive injury of three inbred lines of corn at 120°F., 18% relative humidity, and at high, medium, and low moisture treatments.

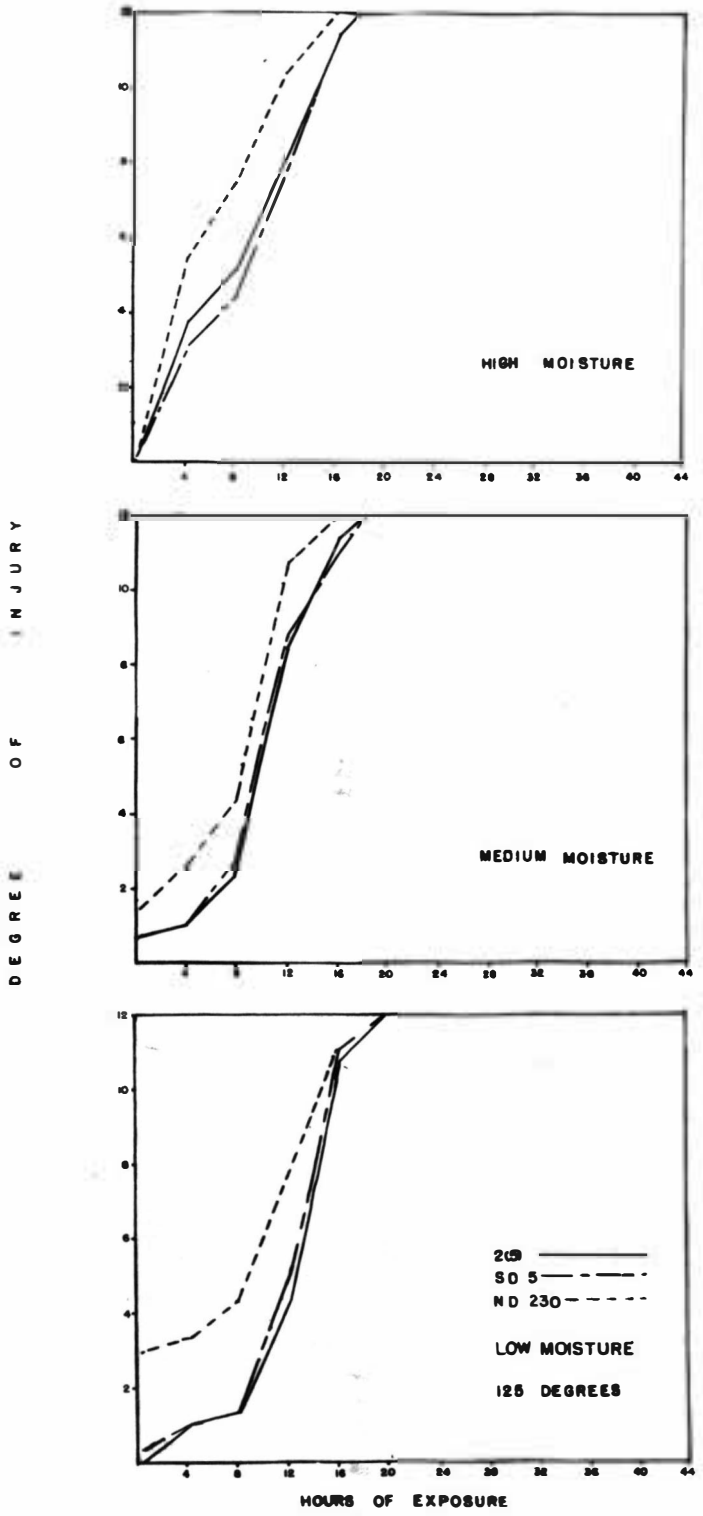

Figure 3. Progressive injury of three inbred lines of corn at 125°F., 18% relative humidity, and at high, medium, and low moisture treatments.

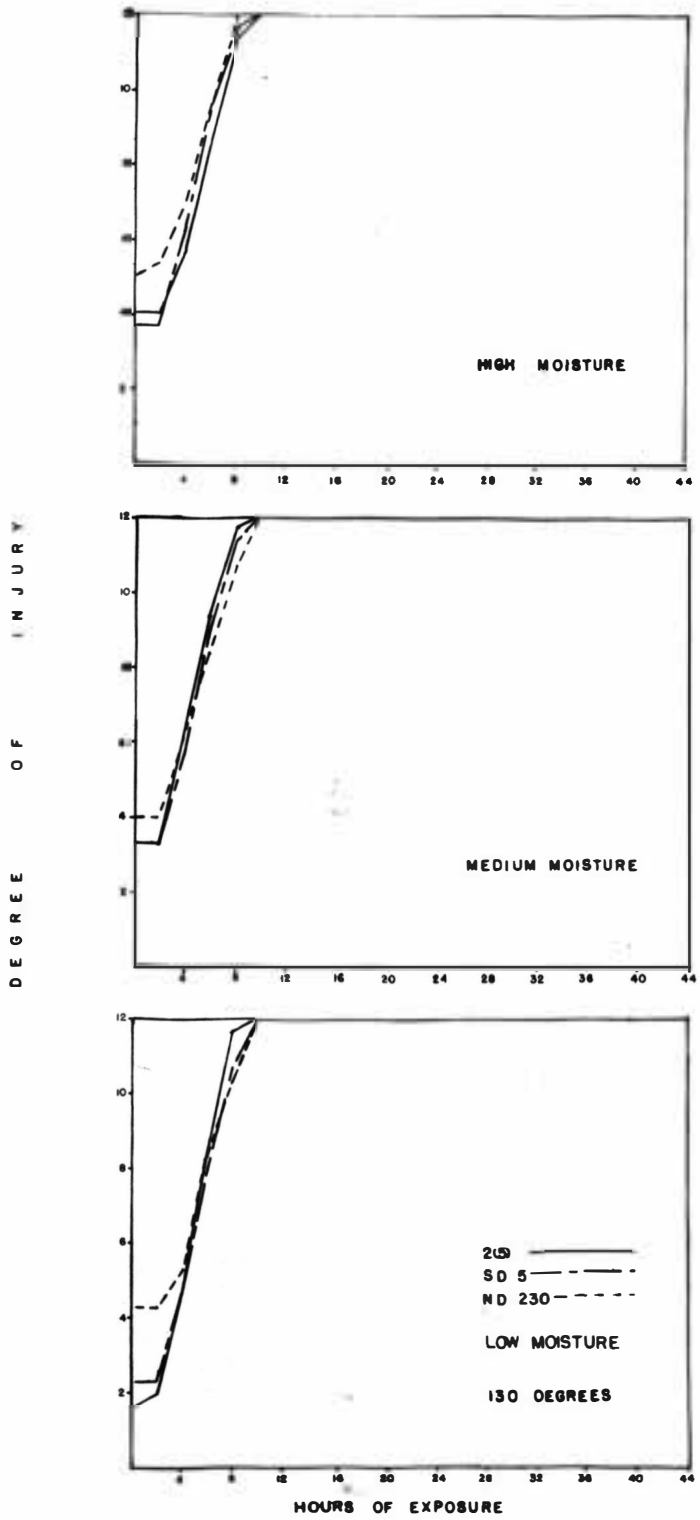

Figure 4. Progressive injury of three inbred lines of corn at 130°F., 18% relative humidity, and at high, medium, and low moisture treatments.

The analysis of variance, which follows in Table V, was applied to injury ratings which were common to all four temperatures used in this study -- namely the ratings at four, eight, and twelve hours of exposure.

Table V. Analysis of variance of the degree of injury of three inbred lines of corn at 115°, 120°, 125°, and 130°F., and at low, medium and high moisture treatments.

Source of Variation	d. f.	Mean square	F
Lines	2	88.45	114.87**
Temperatures	3	871.18	1131.40**
Moistures	2	5.05	6.56**
Hours	2	466.67	606.49**
Replications	2	2.24	2.91
Lines x Temperatures	6	11.96	15.53**
Lines x Moistures	4	4.45	5.78**
Lines x Hours	4	.04	.05
Temperatures x Moistures	6	28.09	36.48**
Temperatures x Hours	6	54.96	71.38**
Moistures x Hours	4	3.48	4.52**
Lines x Replications	4	.35	.45
Temperatures x Replications	6	1.01	1.31
Moistures x Replications	4	.86	1.12
Hours x Replications	4	.41	.53
Error	264	.77	
Total	323		

**Significant at the one per cent level.

The analysis shows that effects due to lines, temperatures, moistures, and hours were highly significant. It also shows a high F value for a number of interactions. The high value for lines x temperatures and lines x moistures indicates that similar differences between lines do not exist at all temperatures and moisture levels, whereas the low value for lines x hours indicates that similar differences did exist between lines at all stages of treatment subjected to analysis. That the relative differences due to temperatures are not maintained through out all

moisture levels and at all hours is signified by the highly significant F values for temperature x moistures and temperature x hours. This is also true for the differences due to moisture at all hours. The absence of significant interactions between the main sources of variation and replications indicate that similar differences due to lines, temperatures, moistures, and hours existed for all replications.

Within each moisture and temperature level an analysis of variance was applied to the drought injury ratings of the three inbred lines. The F values were computed, and the highest F value was assumed to signify that treatment which brought about maximum differences between the three lines tested in their reaction to artificial drought. The results are given in Table VI.

Table VI. F values as computed by analysis of variance on the degree of drought injury of three inbred lines at temperatures of 115°, 120°, 125°, and 130°F. at low, medium, and high moisture treatments.

Moisture Treatment	Temperature			
	115°	120°	125°	130°
LOW	38.24*	234.78**	61.21*	.55
MEDIUM	92.18*	144.88**	72.07*	2.84
HIGH	5.95	5.00	20.99*	6.50

**Significant at the one per cent level.
* Significant at the five per cent level.

The table brings out again the importance of temperature and moisture treatments as they effect corn plants subjected to excessive heat and soil drought. A high degree of significance was shown for only one temperature, 120°, and that at two moisture treatments, whereas in no case did the 130°,

temperature show significance. It is apparent that the differences due to moisture are a result of a similar effect due to low and medium moisture treatments as compared to the high moisture treatment. Low and medium moistures show high significance in one case, significance at the five per cent level in two cases, and no significance in one case. Comparing this to only one case of significence at the five per cent level within the high moisture level, it seems logical to assume that under the conditions of this experiment the effects of low and medium moisture were similar, and that the high moisture level provided the statistically significant differences between moistures as shown in Table V. The highest F value was shown for the treatment which involved low moisture and a temperature of 120°F. All of the experiments which will be reported in the remaining portion of this paper were based upon this technique.

It was purely by chance that the technique used in the study involving 63 inbred lines, which was carried on the previous winter, incorporated the use of the 120°F. temperature. No attempt was made to control the moisture except in the respect that the soil in all pots was maintained equally. They probably received somewhat more water than the medium treatment of the previous experiment.

IV. Correlation Studies Between Natural Drought, Artificial Drought, and Transpiration.

Seed from 42 of the 44 inbred lines, which were grown under field conditions at the Range Substation at Cottonwood in 1953 for observation of their reactions to natural drought, was available for artificial drought testing. The conditions of exposure were 120°F. temperature, low soil moisture treatment, and 18% relative humidity for 12 hours. The

transpiration rate was measured for the 36 hour period previous to exposure and also for the 12 hours time in the drought chamber. The results are listed in Table VII.

Table VII. Degree of injury and grams of water transpired by 42 inbred lines of corn during 12 hour exposure to 120°F. temperature, low moisture treatment, and 16% relative humidity and grams of water transpired during the 36 hour period previous to exposure.

Line		Mean Injury Rating	Transpiration 12 hours	Transpiration 36 hours
1	Oh56A	4.7	15.0	11.3
2	7(W22)52179-1	5.0	12.3	8.3
3	7(W8)52186-3	5.0	11.7	9.1
4	SD1	6.0	9.1	7.6
5	A225	6.0	10.4	5.3
6	L317	6.0	14.1	8.1
7	SD4	6.3	7.0	7.1
8	A34	6.3	13.7	6.7
9	SD7	6.3	10.7	7.3
10	SD26	6.3	13.3	11.4
11	SD5	6.5	13.7	12.4
12	A340	6.7	13.1	8.8
13	A73	6.7	14.0	10.7
14	52240-2	6.7	14.1	9.6
15	Oh43	7.0	12.2	8.3
16	52240-2	7.0	12.7	8.8
17	W8	7.3	12.3	8.8
18	KD230	7.3	16.0	11.2
19	7(W8)52186-1	7.3	11.9	12.7
20	W27R	7.7	11.9	6.8
21	2(5)52204-2	7.7	13.6	12.0
22	SD2	8.0	13.2	7.9
23	SD2R	8.0	13.2	8.3
24	SD48	8.0	13.7	10.8
25	A227	8.0	12.2	6.6
26	2(5)52202-2	8.0	13.8	10.0
27	Oh45	8.0	15.4	12.8
28	Rainbow Flint 52386-2	8.0	15.9	13.1
29	2(5)52201-1	8.0	13.2	13.2
30	7(W22)52183-3	8.0	13.2	10.6
31	SD6	8.3	11.4	7.2

Line		Mean Injury Rating	Transpiration 12 hours	Transpiration 36 hours
32	R16	8.3	13.0	6.6
33	R8	8.3	14.0	11.4
34	A322	8.7	13.9	7.0
35	W32	8.7	12.8	10.4
36	7(Os420)	8.7	15.4	13.2
37	7(W22)52183-1	8.7	12.6	10.7
38	38-11	8.7	11.9	12.8
39	R53	9.0	15.4	9.7
40	Rainbow Flint 52183-1	9.3	15.6	8.3
41	Oh51A	9.3	9.1	8.9
42	W9	9.7	14.8	12.8
Mean		7.5	13.0	9.6

Correlation coefficients between natural drought injury, artificial drought injury and transpiration rates are shown in Table VIII.

Table VIII. Correlation coefficients between natural drought, 1953 and 1954 artificial drought results and transpiration rates for periods of 12 and 36 hours.

	Natural Drought 1953	Artificial Drought 1953	Artificial Drought 1954	Transpiration 12 hour
Artificial Drought 1953	.364*			
Artificial Drought 1954	.014	.043		
Transpiration 12 hour	-.004	-.087	.254	
Transpiration 36 hour	.058	-.147	.191	.559**

**Significant at the one per cent level.
* Significant at the five per cent level.

The data show significance at the five per cent level between field response to drought and the injury received in the 1953 drought chamber test, but no significance was found between the same field results and the 1954 chamber reactions.

No significant correlation was shown between transpiration for either the 12 or 36-hour period and drought reaction in the field or in the drought chamber for either the 1953 or the 1954 results.

There was a highly significant correlation between 12 and 36-hour transpiration.

V. Effects of Limited Light and Soil Drought on Drought Injury.

The effects of shading and of soil drought on the greenhouse bench as compared to the standard treatment as a check on the drought reaction of three resistant and three susceptible lines are shown in Table IX.

Table IX. Drought injury ratings of three resistant and three susceptible lines when subjected to shade and soil drought on the greenhouse bench as compared to an untreated check.

Lines	Treatments			
	Check	Shaded	Soil Drought	Mean
	Resistant			
W8	5.3	10.7	8.0	8.0
2(5)D	5.7	9.0	8.3	7.7
L317	5.3	7.7	5.3	6.1
Mean	5.4	9.1	7.2	7.2
	Susceptible			
SD6	8.3	10.0	10.0	9.4
ND230	8.0	10.0	9.0	9.0
W9	9.3	10.0	9.3	9.5
Mean	8.5	10.0	9.4	9.3

Figures 5 and 6 will help to show the actual differences represented by the data reported in Table IX.

The shade was provided with a heavy grade of brown paper to prevent the plants from being exposed to the direct rays of the sun. Soil drought was brought on merely by failing to water the plants. Readings were taken

each day, and the injury rating reported was observed three days after the plants were last watered when maximum differences between lines occurred.

Figure 5. Effects of artificial drought on a group of resistant lines of corn, W8, 2(5)D, and L317, and a group of susceptible lines, SD6, ND230, and W9.

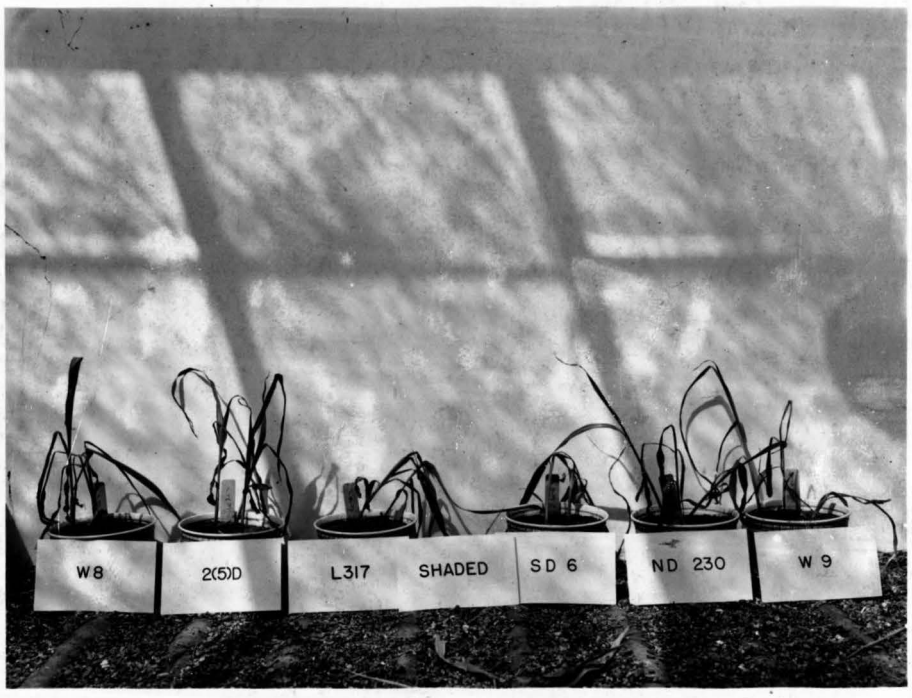

Figure 6. Effect of shading on the relative drought resistance of three resistant lines of corn, W8, 2(5)D, and L317, and three susceptible lines, SD6, ND230, and W9.

A more direct comparison as to the effect of light on the ability of a corn plant to withstand heat and drought is shown in Figure 7. This illustrates the reaction of W8, a resistant line, and SD6, a susceptible line, to three different light treatments. From left to right in each case is the day light check, the shaded plants, and those grown in complete artificial light. The artificial light treatment is probably of relatively low intensity.

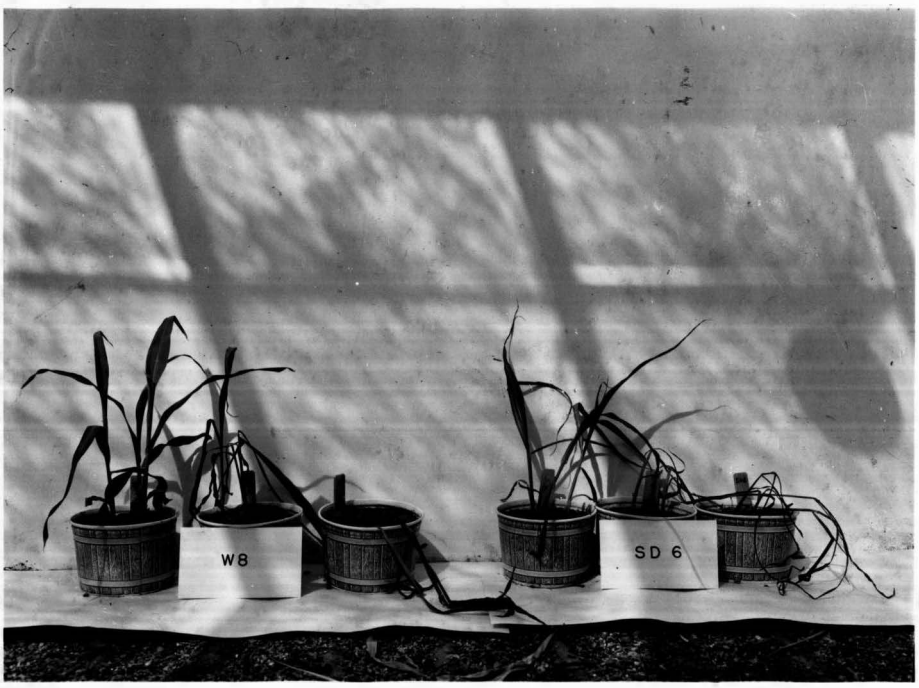

Figure 7. Artificial drought reaction of two inbred lines, W8 and SD6, which are considered drought resistant and susceptible, respectively, to three light treatments, from left to right, untreated check, shade, and artificial light.

The analysis of variance of artificial drought injury reported in Table IX is listed below in Table X.

Table X. Analysis of variance of drought injury ratings of three resistant and three susceptible inbred lines when subjected to shade and soil drought on the greenhouse bench as compared to the unshaded check.

Source of Variation	d. f.	Mean square	F.
Replications	2	.08	.33
Lines	5	15.59	64.96**
Within resistants	2	9.15	38.12**
Within susceptibles	2	.78	3.25
Resistants vs susceptibles	1	58.08	242.00**
Treatments	2	29.41	122.54**
Lines x Treatments	10	2.58	10.75**
Within resistant lines x Treatment	4	2.93	12.21**
Within susceptible lines x Treatment	4	.72	3.00*
(Resistant vs susceptible) x Treatment	2	5.63	23.46**
Error	34	.24	
Total	53		

**Significant at the one per cent level.
* Significant at the five per cent level.

The analysis of variance shows a highly significant difference due to lines. In breaking this down to "within resistants", "within susceptibles" and "resistants versus susceptibles", it can be readily seen that the variation "within resistants" was highly significant and was undoubtedly due to that variation shown among the means of the resistant lines. There was no significant variation due to lines in the susceptible group, and it becomes apparent from the high value for "resistants versus susceptibles" that the greatest variation due to lines was derived from this source. Treatments show a definite effect upon the relative drought resistance, and the high value for lines x treatments signifies that the differences due to lines do

not remain the same for all treatments. The lines x treatments interaction was broken down into its component parts to give added information concerning the source of the high mean square which it showed. The highly significant mean square for "within resistants x treatments" indicates that all lines within the resistant group did not react the same for all treatments. "(Resistants versus susceptibles) x treatments" is also highly significant meaning that the resistant lines as a group and the susceptible lines as a group did not show similar injury for all treatments. Both of these interactions are undoubtedly due in the main to the high degree of variation among the lines within the resistant group shown in the shaded treatment.

VI. Inheritance of Drought Resistance and Susceptibility in F_1 Hybrids.

A number of single crosses were made in the greenhouse during the winter of 1953-54 between lines of known drought reaction bringing together resistance and susceptibility in various ways. Only those which had shown high resistance or susceptibility were used in these crosses. The mean injury rating of these F_1 hybrids when grown in unshaded pots at low moisture and placed in the drought chamber at 120°F. are listed in Table XI.

Table XI. Drought injury ratings of F_1 hybrids made up of inbreds which have shown resistance or susceptibility to drought.

Cross	Mean Injury Rating
Resistant x Resistant	
W8 x B2A158	3.0
2(5)D x W8	4.0
2(5)D x B2A158	2.7
Mean	3.2
Resistant x Susceptible	
W8 x ND230	4.3
B2A158 x W9	7.0
2(5)D x SD6	4.7
2(5)D x W9	5.3
Mean	5.3
Susceptible x Susceptible	
ND230 x W9	7.3
ND230 x SD4	6.0
ND230 x SD6	5.7
SD4 x W273C	4.7
SD4 x SD6	3.7
Mean	5.9

The resistant x resistant crosses as a group showed definite resistance to injury. However, the susceptible lines seemed to have a pronounced effect upon the resistance of the single cross as can be seen by the difference in means. A high degree of variation was shown within the susceptible x susceptible group.

The analysis of variance of the previous experiment is reported in Table XII.

Table XII. Analysis of variance of drought injury ratings of F_1 hybrids made up of inbreds which have shown resistance or susceptibility to drought.

Source of Variation	d. f.	Mean square	F.
Crosses	11	8.69	5.08**
Within res x res	2	1.46	.85
Within res x susc	3	4.22	2.47
Within susc x susc	4	9.77	5.71**
(Res x res) vs (res x susc) + (susc x susc)	1	39.11	22.87**
(Res x susc) vs (susc x susc)	1	1.91	1.12
Replications	2	6.86	4.01*
Replications x Crosses	22	1.71	
Total	35		

**Significant at the one per cent level.
* Significant at the five per cent level.

A highly significant F value for crosses indicates differences in the hybrids. There were no differences within the resistant x resistant or resistant x susceptible groups, but this was not true for the susceptible x susceptible group. However, most of the variation between crosses was derived in a comparison between resistant x resistant crosses as a group with the rest of the test as is shown by the unusually high F value for that comparison -- namely (resistant x resistant) versus (resistant x susceptible) + (susceptible x susceptible).

DISCUSSION

A low correlation was shown between drought chamber results which were obtained in the winter of 1952-53 on inbred lines of corn and results obtained the following winter. This indicates an effect of some environmental factor upon the reaction of corn seedlings to artificial drought.

Cloudy weather for a period of several days previous to artificial drought treatment and natural low light intensity of that season of the year prompted the thought that light differences might have been an important factor in bringing about the variation in results of the two tests. Results in Table IX show increased susceptibility to drought in all cases when light intensity was reduced. However, this increase in susceptibility due to shading was not uniform between lines. It was greatest in the resistant lines, especially in the case of W8 which showed more damage than any of the lines in the susceptible group.

Effect of light upon corn plants has been reported by Heyne and Laude (10) who found that heat resistance of plants kept in the dark for 12 to 18 hours increased by exposure to light for as little as one hour. Shirley (21) in his review of the effects of light intensity on seed plants states that plants developed in the shade are less resistant to drought than those grown in full sunlight. Dexter (6) indicates that photosynthesis is involved in the hardening of plants. He found that winter wheat plants deprived of either light or CO_2 would not harden against cold. Many workers have indicated a close relationship between injury of the plant cell by drought and cold.

Newton and Martin (20) found that bound water content of the press-juice of leaves of wheats and grasses was directly related to their ability to resist drought, and Bartel (3) reported that the order of spring wheat varieties with respect to osmotic pressure and per cent of total solids was the same as their supposed drought resistance.

A high positive correlation was found by Chisholm (4) between the amount of chlorophyl present in leaf tissue and drought resistance of barley varieties which gives evidence that photosynthesis is important in the development of this character. Lauda (15) suggests the photosynthetic production of organic material as an explanation for increased resistance of plants to heat. However, he adds that the amount of material which might be manufactured in the short time that it takes to bring about a marked increase in resistance would probably be insufficient to account for so much change in resistance.

A number of factors which are generally considered as being closely associated with the ability of plants to withstand drought were studied by Haber (8) in inbred lines of sweet and field corn. He found that the classification of pure lines of sweet corn of unknown behavior as resistant or susceptible was not possible on the basis of stomata number or type of root system. He reported significantly larger numbers of vascular bundles per unit area for five resistant lines of field corn as compared to five susceptible lines; but this did not hold true in the case of sweet corn. Transpiration rate was found to be greater in a group of susceptible lines of sweet corn than in a resistant group, but this difference was not great enough to be used as a basis for classification. No definite trends were shown by the transpiration studies reported in this paper.

These facts seem to indicate that probably the most important single factor involved in providing a plant with resistance against drought is that quality of the leaves which provides the power to hold water against the forces of evaporation.

The importance of hardening plants by growing them under limited moisture conditions before drought treatment was brought out in a comparison of F values of injury readings for various treatments in Table VI. Such hardening results in increased photosynthetic products and thus reduced evaporation. High light intensities versus shading would have the same effect.

It is not possible to determine with any certainty the method of inheritance involved in drought resistance or susceptibility with the limited data in this paper. Further study is needed for determining the factors involved, how each factor is inherited, and how these individual factors affect the inheritance of others involved.

The significance of the products of the photosynthetic process in drought resistance has been brought out. In doing this the author does not minimize the importance of other characteristics involved in this trait. The value of an adequate root system and an effective vascular system should not be underestimated. The complexity of the inheritance of drought resistance becomes apparent when we consider that several factors are involved which are probably inherited quantitatively.

The data in Table XII show that the single crosses made up of two drought resistant inbreds were significantly more resistant than the rest of the hybrids tested. This indicates the possibility of producing drought resistant hybrids.

The variation between the reactions of the F_1 hybrids in the resistant x susceptible group can not be adequately explained with the information available, but with the possibility of quantitatively controlled characteristics involved all degrees of resistance would be possible.

As might be expected the damage to single crosses which were made up of susceptible inbreds was generally greater than in the resistant group. However, the range was quite pronounced among the crosses of susceptible lines. SD4 x SD6 showed greater resistance than W8 x B2A158, a resistant single cross. It is not inconceivable, where quantitative inheritance is involved, that two inbreds demonstrating susceptibility to drought could be incorporated into a drought resistant F_1 hybrid because of complementary gene action. This may make it necessary to test all single crosses as well as the inbreds which make them up to prevent discarding valuable germ plasm in corn.

SUMMARY

A study of the effects of artificial drought was carried out on 14 day old corn seedlings. Purposes of the investigation included the development of a technique for studying reactions of corn seedlings to artificial drought, establishing a correlation between artificial and natural drought reactions, and studying inheritance of resistant and susceptible factors.

Three inbred lines which had reacted as resistant, intermediate, and susceptible to drought were exposed in the drought chamber to 115°, 120°, 125°, and 130°F. temperatures. Effects of three soil moisture treatments during the growing period were also observed. Results showed that 120°F. brought about maximum differences among the three lines and also indicated that hardening the plants by limiting moisture during the growing period was important.

An artificial drought test of a large number of inbred lines conducted during the winter of 1952-53 correlated well with field results, but this correlation was not repeated in a drought chamber test the following winter.

No correlation was shown between transpiration and drought resistance.

It was found that shading reduced the resistance to drought in all lines tested. However, lines of the resistant group did not react the same when shaded as they did when exposed to sunlight.

Lines subjected to soil drought on the greenhouse bench did not respond in the same manner as those exposed to artificial drought.

Inheritance studies indicated that resistant hybrids were produced by crossing inbreds of high drought resistance. Single crosses which

contained susceptible inbreds showed a high degree of variation in their response to artificial drought. Factors affecting susceptibility indicated a range from little or no dominance in some crosses to high dominance in others.

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