

DROUGHT RESISTANCE IN RELATION  
TO MORPHOLOGY AND PHYSIOLOGY OF CORN

by

MERVIN DUANE HAGUE

B. S., Iowa State College, 1954



---

A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE  
OF AGRICULTURE AND APPLIED SCIENCE

1955

LD  
2668  
T4  
1955  
H34  
c.2  
Documents.

# TABLE OF CONTENTS

11

INTRODUCTION.....	1
REVIEW OF LITERATURE.....	2
MATERIALS AND METHODS.....	11
Heat Tolerance of Three Strains of Corn at Different Stages of Growth.....	13
Transpiration Rate of Three Strains of Corn Differing in Heat Tolerance.....	13
Root Investigations of Three Strains of Corn Differing in Heat Tolerance.....	14
EXPERIMENTAL RESULTS.....	15
Comparative Ability of Corn to Withstand High Temperatures at Different Stages of Growth.....	15
Transpiration Rate of Corn Differing in Heat Tolerance..	17
Water Loss from Soil as Related to Drought Resistance..	25
Water Required for Each Unit of Plant Material as Related to Drought Resistance.....	30
Comparison of Plant Weights of Corn Grown in Favorable Conditions with Moisture Deficit.....	31
Percentage Normal Growth when Comparing Weights of Plants Grown Under Favorable Conditions with an Increasing Moisture Deficit.....	42
Root-Top Ratios of Corn as Related to Drought Resistance.....	43
Root Development of Corn when Placed in an Increasing Moisture Deficit.....	45
DISCUSSION.....	52
SUMMARY.....	62
ACKNOWLEDGMENTS.....	64
LITERATURE CITED.....	65

## INTRODUCTION

Severe droughts in the midwest have stimulated interest in the problem of drought resistance.

During the period of 1933 to 1936 the region from the Dakotas to Texas and from Nevada to the Atlantic Ocean was scourged with drought. Westbrook (51) estimated the total loss from the 1934 drought in the United States was \$5,000,000,000. Crop yields are a direct reflection of the weather conditions and as such may be roughly predicted from the weather prevailing over a period of time. Since climatic conditions vary from year to year, one can expect both favorable and unfavorable climatic conditions. It sometimes appears that seasons run in cycles but it is virtually impossible to predict from year to year what conditions will prevail.

The midwest, which has often been termed the "bread basket of the world", is frequently subject to weather conditions unfavorable to plant growth. These unfavorable periods are usually due to a number of complex factors involving temperature and water. Drought is usually considered a condition of the soil or atmosphere, or of both, that prevents or curtails the plant in obtaining sufficient water for its metabolic functions. Drought resistance usually includes tolerance to both high temperatures and low available water.

Many measures of tolerance to drought conditions caused either by moisture deficit or high temperature have been studied to find some simple means of determining a plant's drought resistance. No single morphological or physiological characteristic in a variety or within a species has been found to be an accurate means of

detecting drought resistance. Most evidence indicates the ability of a plant to tolerate adverse conditions lies within the protoplasm itself and the physico-chemical makeup that enables it to withstand wide variations in climate. However, the phenomena of drought resistance are still not well understood.

The present investigations included a study of:

- (a) Heat tolerance of corn at different stages of growth.
- (b) Transpiration rates of corn differing in heat tolerance.
- (c) Water requirement of corn differing in heat tolerance when grown under increasing moisture deficit.
- (d) Plant weights of corn differing in heat tolerance when grown with adequate water and with increasing water deficit.
- (e) Root development of corn differing in heat tolerance when grown under increasing water deficit.

#### REVIEW OF LITERATURE

Shirley (41) was one of the first to describe a machine for testing drought resistance in plants under artificial conditions. The length of time each coniferous seedling survived was used as a criterion of drought resistance together with the moisture content of the soil at the depth of the plant.

Shutz and Hayes (42) conducted artificial drought tests using some hay and pasture grasses and legumes in sod and seedling stages of growth. They concluded that artificial tests of drought could be used to indicate those species or varieties which can be expected to succeed best under natural drought conditions. Helgersen and

Blanchard (16) in their laboratory studies of wheat concluded that their results correlated very close with field conditions. They also stated that they hope certain standard conditions may be set up which will enable the plant breeder to test his varieties for drought and heat resistance early in the process of their breeding in order to discard the less promising varieties without having to carry them in field trials for a number of years.

After exposure for 1-15 hours at 110°F with 14 percent relative humidity, and an air velocity of six miles per hour, wheat varieties known to be drought resistant in the field showed less injury from drought than varieties known to be drought susceptible was shown by Aamodt (1) in his machine for testing atmospheric drought.

Aamodt and Johnston (2) concluded in their studies on drought resistance in wheat that by use of an artificially produced drought the most reliable index of susceptibility to atmospheric drought is obtained where percent of leaf loss is estimated in conjunction with percent of dead culms and percent of dead plants.

In laboratory experiments with corn seedlings Heyne and Laude (18) found that 20 day old corn plants subjected to the heat chamber for five hours at 130° F. with a relative humidity ranging from 20-30 percent gave the most satisfactory results for classifying high temperature tolerance of different strains of corn. They concluded that for most inbreds there was a fairly good agreement between field observations from previous years and those of the heat chamber.

Hunter et al. (21) tested 14 day old seedlings in a heat chamber at 140° F. with a relative humidity of 30 percent and found

that it was possible to distinguish among strains with respect to drought resistance. Essentially the same order of relative resistance was obtained with the seedlings as was noted for plants in the field.

Laude (29) concluded that plants have a diurnal cycle of heat resistance. He studied temperature relations in both seedling and mature plants and found that a daily maximum resistance to heat was attained by plants about mid-day and continued during the afternoon. Minimum resistance prevailed early in the morning. He also suggested that the photosynthetic production of organic matter suggested itself as an explanation for the increased resistance of plants to heat.

Wilting coefficient has been thought by investigators as being influential in drought resistance. Briggs and Shantz (9) were among the first to study phases of water relations of plants and concluded that species differ only slightly as regards to the soil-moisture content at which permanent wilting first takes place. They tested a number of species and concluded that the differences exhibited by crop plants in their ability to reduce the moisture content of the soil before wilting occurs are so slight as to be without practical significance in the selection of crops for semi-arid regions. Differences observed were attributed to a more perfect root distribution in one variety as compared with another.

Caldwell (11) found that the moisture content of the normal functioning leaves, taken collectively, at the time of permanent wilting, was found to be approximately constant for all individuals of the same species, at the same stage of development. He con-



cluded that permanent wilting is a definite protoplasmic condition and that loss of turgor in permanent wilting was established throughout the entire plant. Permanent wilting may result from either one or both of two factors; a decrease in the soil moisture content and a loss of water from the plant by transpiration.

Sorghum and corn have been used for many years in comparison of morphological and anatomical differences in association with drought resistance. Miller (35) compared dwarf milo and Blackhull kafir with corn as to several characteristics. The two sorghums have twice as many fibrous roots as the corn at any stage of development. The leaf area of the corn at all stages of growth was approximately twice as great as that of the dwarf milo and never less than 1.5 times that of Blackhull kafir. It was also concluded that the sorghums would have the advantage over the corn plant under any climatic condition which would bring about a loss of water from these plants. This advantage is due, in the first place, to the fact that the two sorghums have only half as much leaf area exposed for evaporation of water as corn, and in the second place, to the fact that they have a root system twice as efficient in the absorption of water from the soil because of the greater number of fibrous roots.

Bound water has been suggested as an index in classifying cultivated crops by Newton and Martin (37) in their experiments with wheat and several other grasses. The percent of bound water increased regularly with colloidal concentration. Both the quality and quantity of the colloids came into the picture of bound water capacity. They concluded that drought resistance is depend-

ent upon three factors, namely: adsorption, transpiration, and wilt endurance.

Bakke (5), Jost (23), and Warming (46) believe that the principal peculiarity of xerophytes is their ability to spend water scantily. Maximov (33) on the contrary, noticed that wild plants which are capable of enduring prolonged drought maintain high transpiration rate as long as the soil moisture is readily available. The high intensity of transpiration exhibited by relatively drought resistant plants, according to Maximov, is not accidental but due to the fact that most of the factors that make for a dry habitat provoke such changes in the body of the plant as enable them to maintain a high transpiration rate.

Experiments of Frey (13), Kokin (27), and Alexandrov (3) showed that foliage developed under conditions of scanty water supply possessed higher intensity of transpiration than developed under condition of liberal water supply. Briggs and Shantz (8) were unable to confirm their original premise of a close association between the water requirement of plants and drought resistance. They found that millet, sorghums, and corn had a lower water requirement than wheat, oats, or barley. The drought resistant grass, agropyron, was found to have a very high water requirement, while rice and buckwheat, relatively drought susceptible species, showed a moderately low water requirement. Maximov (33) also was unable to show water requirement and suitability for arid areas. He did find a tendency for plants that transpired intensively to use the water less efficiently.

Kiesselbach (25) could not establish a definite correlation



between drought resistance and water requirement. Bayles et al (6) observed that the ability to limit transpiration and to carry on the process of photosynthesis and assimilation under conditions conducive to high evaporation was one of the factors to determine the ability of wheat plants to produce grain under drought conditions.

Miller and Coffman (36) concluded that corn and sorghums seem to differ in their transpiration power. They concluded that the corn plant is not capable of supplying its large leaf surface with sufficient amount of water to satisfy the evaporating power of air, as a result its rate of transpiration per unit of leaf surface falls below that which is needed to retain turgor. The sorghums with their small leaf surface are able to supply water in amounts sufficient to satisfy the evaporating power of the air and, their rate of transpiration per unit of leaf surface is higher than that of corn.

Brooks (10) worked on the movement of eosin dye through leaves of resistant and susceptible inbreds and found the most susceptible leaf of a susceptible plant showed a much slower rise of dye than did a comparable leaf from a resistant plant when the leaves were cut below the collar. When these leaves were cut above the collar, the dye rose more rapidly in the leaf of susceptible plants. He concluded that the nature of the vascular tissue in the collar region of susceptible leaves did not permit the rapid conduction of water.

Various phases of drought resistance have been investigated with hope of deriving at some simple and practical method of

determining drought resistance. The relation of root development to drought resistance has been the subject of considerable interest.

Ivanov (22) stressed the importance of the root system in relation to drought resistance. He points out that plants with roots which have high suction power were in the most favorable position to resist drought. He concluded that the denseness of the root hairs was an important characteristic of resistant plants. This character enabled the plant to tap a much greater volume of soil than it would otherwise.

Miller (35) observed that sorghum had twice as many secondary roots as corn and this could partially explain its resistance. The sorghum roots were also found to be more fibrous than corn roots. The greater number of finer roots of sorghum, together with the smaller leaf area, are instrumental in keeping the water supply of the leaves sufficient to retard incipient wilting. Talanov (46) and Aamodt and Johnston (2) believed that one of the important contributory factors to the drought resistance possessed by *Milturum* and *Casidium* lies in the character of their root system. Bales et al. (6) suspected that the ability of wheat plants to produce grain under drought conditions might be due to two distinct phenomena. One of them is the ability of the root systems to take in moisture as fast as or faster than it is transpired. Hubbard (19) found that, under dry conditions, *Ceres* spring wheat generally had a larger number of roots, more root hairs, and a greater weight of roots than *Marquis* or *Hope*. Although many workers have found differences of root systems in relation to drought resistance, Harber (14) found no significant differences between the root

system of drought resistant and susceptible lines of sweet corn.

Theil (47) stated that plants grown in a moist or wet soil show a strikingly small root system in comparison to those grown in a relatively dry soil. He observed that roots growing from a layer of fertile soil into a layer of sand and then again into fertile soil showed a profuse branching in the fertile soil layers, while that part of the root system in the layer of sand was very sparsely branched. Kiesselbach (25) in his transpiration work with the corn plant concluded that in general root development varies inversely as the soil water content. He concluded that plants which have their early growth in dry soil may be expected better to withstand a later period of drought because they would have a great absorbing surface exposed to the soil particles. Harris (15) also found that in general all of the plants produced a proportionately greater root growth in comparison to the aerial parts when grown in low percent of available moisture compared to adequate moisture.

Shantz (40) believes that the roots of some drought-resistant plants are able to penetrate dry soil, but that ordinary crop plants lack this ability. Magistad and Brezeale (30) made extensive studies of the moisture equilibrium between soil and plant and concluded that not only will roots elongate into dry soil, but some plants can absorb water through roots in moist soil, transport the water, and build up the moisture content of a dry soil to the wilting percentage. Hunter and Kelley (20) found that the roots of corn were able to elongate into dry soil and build up the moisture content of the soil but no evidence was obtained for the

absorption of nutrients from dry soil by plants.

Kramer (28) has shown a close relation between absorption and transpiration and concludes that changes in rate of transpiration precede changes in rate of absorption which indicates that under ordinary growing conditions if the plant is under a stress, the rate of water intake probably is determined largely by the rate of water loss. This absorption is primarily controlled by the roots and it is assumed the characteristic of the root system is responsible in the different absorption rates.

Shank (39) and Spencer (44) found there was a marked difference between inbreds and single crosses of corn to number, dry weight, and total length of the main root and length of adventitious roots. Shank (39) concluded that several genetic factors control top-root ratios because the range of inbred ratio means in each test was large with individual lines means being distributed uniformly throughout these ranges.

Cook (12) found two types of roots in his studies of Bromus inermis; one large in diameter and lighter colored, and the other smaller, darker, and more extensively branched. The latter composed the major portion of the drought resistant root systems. Measurements of "large" roots were found to be less reliable index to drought resistance than those of "small" roots. No significant differences were found in lateral spread of roots between the resistant and non-resistant groups. The resistant strains were consistently high in number of both "larger" and "small" roots, and in most cases, possessed significantly greater root depths. Total axial root length was one of the best single

measurements for evaluating root systems but it was incomplete unless supplemented by other measurements. In general, the resistant selections made a more vigorous herbage growth throughout the season than the susceptible strains. The root-top ratios were found to favor the more drought-resistant selections but differences were not of sufficient magnitude to be used as dependable indices.

#### MATERIALS AND METHODS

Ten single cross strains of yellow dent corn were obtained from Kansas State College and Pioneer Seed Corn Company. These strains were selected for resistance or susceptibility to drought and high temperatures previously observed under laboratory and field conditions.

These ten strains were planted in six inch clay pots with three plants per pot and allowed to grow for twenty-eight days. They were then tested in the heat chamber, each variety being replicated fifteen times. The heat chamber had a temperature of 130° F. and a relative humidity of 30-40 percent.

The preliminary investigations indicated wide differences among the strains in ability to recover from high temperatures. Three varieties, including one that was consistently most resistant, one that was intermediate, and one that was susceptible, were chosen for subsequent research. In the remainder of the manuscript the resistant strain will be referred to as number 1, intermediate number 2, and susceptible number 3.

Several methods were used to estimate the amount of damage inflicted to the strains by the high temperature test. The first



measurement was to score the plants on a scale from 0-100, rating each plant for apparent damage.

Secondly, the linear length of the longest leaf of each plant was measured and the percentage of desiccated tissue calculated from a direct measurement.

Thirdly, the tissue above the third node was cut with scissors and separated as to whether dead or live. The tissue was then dried in an oven, weighed, and the percentage that survived the test was calculated on a dry weight basis.

It was apparent that all three measurements gave similar results.

The strain consistently most resistant was K77 x G5, the intermediate was Kys x K201, and the susceptible strain was G33L1 x MY1.

The experiments reported in this thesis were conducted in the greenhouse and laboratory during the winter of 1954-1955. According to Heyne and Laude's (18) studies with corn seedlings there is a close association between laboratory and field results. It was also found by Hunter et al. (21) that essentially the same order of resistance was found in laboratory and field observations in studying resistance to drought injury in lines of maize. The results of the ten strains tested in the laboratory agreed in general with previous field observations.

The various techniques and equipment used in the investigation are described in the following sections.

### Heat Tolerance of Three Strains of Corn at Different Stages of Growth

The three strains chosen for these studies were tested for heat tolerance at three, six, and nine weeks of age.

The three strains were planted in one gallon cans and grown for three and six weeks and in four gallon cans for nine weeks. The plants were thinned to three in each can. Each strain was replicated six times. Soil moisture was brought to field capacity and the pots were rotated at random once each week.

The soil was covered with one inch of sand to check surface evaporation. Six replications of each strain were placed in the heat chamber at each growth interval with temperatures of 130° F. and 30-40 percent relative humidity. The plants were not left in the heat chamber for a predetermined length of time but were removed when observable differences were apparent.

The plants were then removed from the heat chamber and allowed to recover for two weeks. The previously described method of clipping the live and desiccated tissue was found to be most reliable. The tissue from each plant was clipped, dried, and percent recovery was expressed on a dry weight basis.

### Transpiration Rate of Three Strains of Corn Differing in Heat Tolerance

The same varieties were used in transpiration investigations as in the other studies and were tested at three, six, and nine weeks of age.

The three varieties were planted in one gallon cans for the

three and six week intervals and four gallon cans for the nine week interval. The plants were thinned to three plants in each can. Each strain was replicated six times. They were watered once each day and rotated at random once each week.

The cans were covered with a paraffin wax layer to check evaporation from the soil, before they were put in heat chamber at a moderate stress of  $115^{\circ}$  F. During the test the cans were weighed each hour for twelve hours. The cans were then left in the heat chamber for another twelve hours and weighed to determine the total loss due to plant transpiration over a 24 hour period.

The tops were then cut and roots washed and oven dried for dry weight determination.

#### Root Investigations of Three Strains of Corn Differing in Heat Tolerance

The roots of the three varieties were studied after three, six and nine weeks of growth.

The corn was planted in soil from the Ashland Agronomy farm which was air dried, sieved through a mesh screen to separate the trash and wet to field capacity. The field capacity and wilting point of the soil were determined by laboratory method. Equal weights of soil were put in each can, filling them to about four inches from the top. The seeds were planted in one gallon cans for the three and six week intervals and four gallon cans for the nine week interval. Each variety was replicated six times. Three plants were grown in each can. The soil was covered with an inch of sand to check surface evaporation. The cans were weighed at

planting and at the end of three weeks to determine water requirements. Those retained longer in the experiment were weighed after six and nine weeks. No water was added to any of the pots during this experiment. The soil was removed from the roots by washing at the end of the respective intervals.

The fibrous root system has been explained by Miller (35) as being a factor contributing to drought resistance of sorghums. A scheme was devised to determine the extent of the secondary root system which includes the fibrous roots. The method found most satisfactory was to stretch out the primary root and count the number of branching roots at different predetermined distances from the main root. By adding the number of branching roots at each length interval it was possible to determine the characteristic of the fibrous root system.

Other investigations included linear measurements and weights as indicated in the discussion of the results.

#### EXPERIMENTAL RESULTS

##### Comparative Ability of Corn to Withstand High Temperatures at Different Stages of Growth

It was determined from preliminary investigations explained earlier that differences were apparent in the ability of the strains of corn to withstand high temperatures at a young age. It is also desirable to know if the resistance persists with the strain as it matures.

The three strains chosen for experimental study, because of their range in heat tolerance under both field and laboratory

conditions, were tested in the heat chamber, three, six and nine weeks after planting. It is apparent from Table 1 the three week interval showed the greatest differences between the three strains. Two weeks after exposure the percentage recovery was 61, 28, and 20 for strain numbers 1, 2, and 3, respectively. There was a statistically significant difference at a 5 percent level between numbers 1 and 2, and numbers 1 and 3 but there was not a significant difference between number 2 and number 3.

Table 1. Comparative ability of three strains of corn to withstand high temperatures at different stages of growth.

Age of plants	Strains			
	1	2	3	Ave.
3 weeks	61.05	28.26	20.26	36.52
6 weeks	37.26	17.45	7.32	20.68
9 weeks	35.20	14.10	9.89	19.73
Average	44.65	19.94	12.49	

L.S.D. = 18.2

L.S.D. between means = 10.5

The six week interval showed similar results with numbers 1, 2 and 3 recovering 37, 17 and 7 percent respectively. Number 1 was significantly superior to number 2, and number 3, but there was no significant difference between numbers 2 and 3, although number 3 tended to recover much less than number 1 or number 2.

The same order of resistance was found nine weeks after planting with number 1, number 2 and number 3 retaining the same order



of recovery, viz., 35, 14, and 10 percent respectively. There was again a statistically significant difference between number 1 and numbers 2 and 3, but no difference between numbers 2 and 3.

The strain means indicate the relative position between the strains at all intervals with number 1 significantly greater than numbers 2 and 3 but no significant difference between number 2 and number 3.

Plate I shows the range in heat tolerance of the three strains. During the rest of the manuscript the heat tolerant strain will be referred to as number 1, the intermediate as number 2 and the susceptible strain as number 3.

#### Transpiration Rate of Corn Differing in Heat Tolerance

An experiment was conducted to determine the transpiration rates of the three strains of corn differing in heat tolerance. The plants (prepared as explained in Materials and Methods) were weighed hourly for the first 12 hours and at the end of 24 hours to determine the total loss of water. The shoots and roots were then harvested, oven dried, and weighed. Table 2 shows that after three weeks of growth strain number 1 transpired significantly more than numbers 2 or 3 during the first twelve hours of the test, transpiring 30, 21 and 17 grams respectively. Additional twelve hours of transpiration did not seem to change the relative position of the three strains. The total weight transpired during the 24 hours was 43, 33 and 29 grams respectively for numbers 1, 2 and 3.

#### EXPLANATION OF PLATE I

Damage inflicted on three strains of corn when grown for three weeks and placed in the heat chamber with temperatures of  $130^{\circ}$  F. and relative humidity of 30-40 percent.

PLATE I



Table 2. Grams of water for each gram of shoots transpired by three strains of corn differing in heat tolerance.

Age of plants	Hours of transpiration	Strains			L.S.D.
		1	2	3	
3 weeks	12	29.50	20.93	17.34	6.34
	24	42.72	33.42	28.53	11.92
6 weeks	12	11.76	9.75	10.66	--
	24	16.76	14.18	13.44	3.51
9 weeks	12	14.17	8.84	5.95	5.23
	24	18.79	12.75	7.16	5.86

Six weeks after planting indicated no statistically significant differences between the three strains during the first twelve hours of the test. The plants transpired less per gram of shoots than at the three week interval with 12, 10, 11 grams respectively for numbers 1, 2 and 3. During the next twelve hours number 1 had the ability to keep on transpiring at a high rate and was significantly greater than number 2 or number 3 with a total transpiration of 17, 14 and 13 grams of water per gram of shoot for numbers 1, 2 and 3 respectively.

After nine weeks of growth the transpiration rate was similar to that at the six week stage with number 1, number 2 and number 3 transpiring 14, 8 and 6 grams respectively per gram of dry shoots. Number 1 was significantly greater than numbers 2 and 3 but number 2 was not significantly greater than number 3. After 12 more hours

of transpiration the same order of transpiration and significance was maintained with numbers 1, 2 and 3 transpiring 19, 13 and 7 grams respectively.

It is apparent from the data that number 1, which has been designated as resistant, has the ability under a moderate stress to transpire more water for each gram of dry shoots than the intermediate and susceptible strains. The three strains transpired most per unit of dry matter after three weeks of growth and decreased at the six and nine week stages. Numbers 1 and 2 transpired about the same rate per unit of dry matter at the six and nine week stages but number 3 steadily decreased as it matured.

Another method of expressing transpiration rate is the amount of water transpired for each gram of dry roots. Table 3 shows that after three weeks of growth number 1 transpired significantly more water than numbers 2 and 3 but no significant difference was obtained between numbers 2 and 3 for the first twelve hours. The strains transpired 68, 53 and 42 grams for each gram of roots for strains number 1, 2 and 3 respectively. After 12 more hours number 1 had transpired significantly more water than numbers 2 and 3, and number 2 significantly more than number 3 with a total loss of 98, 85 and 69 grams for the three strains.

The six weeks stage showed no statistical significance between the strains in rate of transpiration for the first 12 hours with a total transpiration of 29, 25 and 30 grams respectively for numbers 1, 2 and 3. After twelve more hours of transpiration number 1 had transpired significantly more water than number 2 but not significantly more than number 3. At the end of 24 hours the



strains transpired 41, 37 and 38 grams for numbers 1, 2 and 3 respectively.

Table 3. Grams of water for each gram of roots transpired by three strains of corn differing in heat tolerance.

Age of plants	Hours of transpiration	Strains			L.S.D.
		1	2	3	
3 weeks	12	67.63	53.33	42.11	11.41
	24	97.95	85.17	69.26	12.65
6 weeks	12	29.40	25.21	30.30	--
	24	40.89	36.69	38.20	3.79
9 weeks	12	35.61	25.50	27.14	7.93
	24	47.22	36.77	34.92	9.36

The strains transpired 36, 26 and 27 grams of water for the first 12 hours at the nine week stage. The amount transpired by number 1 was significantly greater than numbers 2 and 3 but number 2 was not significantly greater than number 3. The strains maintained their order of transpiration and significance during the next 12 hours with a total transpiration of 47, 37, 35 grams for numbers 1, 2 and 3 respectively. Plate II shows the three strains after 24 hours of transpiration when nine weeks old.

The transpiration rate is also greater at the three week stage than the six and nine week stages when expressing transpiration per gram of dry roots as well as dry shoots.

EXPLANATION OF PLATE II

Damage inflicted on three strains of corn when nine weeks old after 24 hours of transpiration in the heat chamber with a temperature of 110° F.

## PLATE II



It can also be seen from Figs. 1, 2, and 3 that number 1 was superior at all the growth stages in its ability to transpire more water per unit of dry matter than the other strains but this is most striking at the three and nine week intervals. The susceptible strain often transpired as much as the other strains for the first 12 hours but in most cases fell behind during the next 12 hours.

#### Water Loss from Soil as Related to Drought Resistance

In addition to determining differences in transpiration rates an attempt was made to determine the water requirement of the three strains. The pots were brought to field capacity and weighed when planted and no more water was added. They were weighed again at the respective three week intervals before the root investigations were made. The loss of weight minus the loss of weight of the checks (pots without plants) indicates the water used by the plants in their growth.

It was found from preliminary investigation the raw data did not have homogenous variances at the three stages of growth so the data were transposed to logarithms as shown in parentheses.

It is evident from Table 4 that three weeks after planting number 1 had used significantly less water than numbers 2 or 3 and number 2 was significantly less than number 3, the amounts being 98, 111 and 130 grams respectively.

Six weeks after planting similar results were obtained with number 1 using less water than numbers 2 and 3, the amounts being

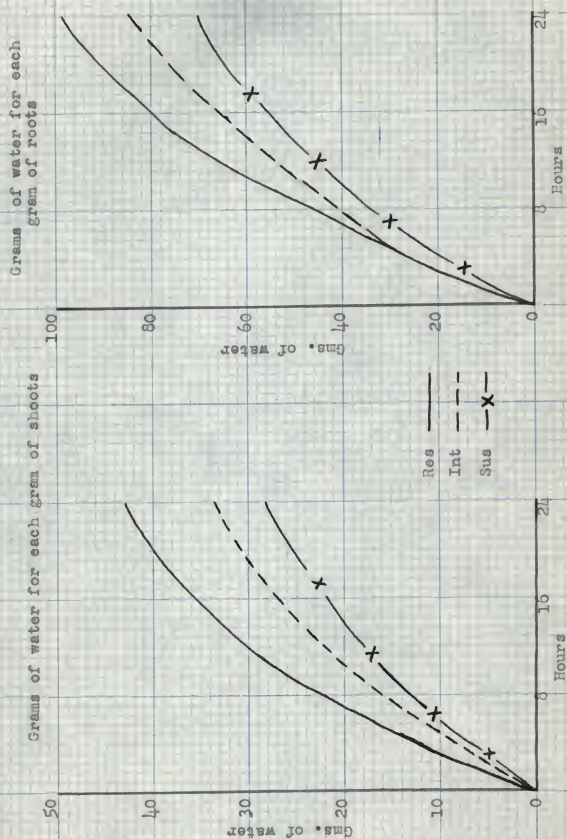


Fig. 1. Transpiration rate of three strains of corn, differing in heat tolerance, when three weeks old.



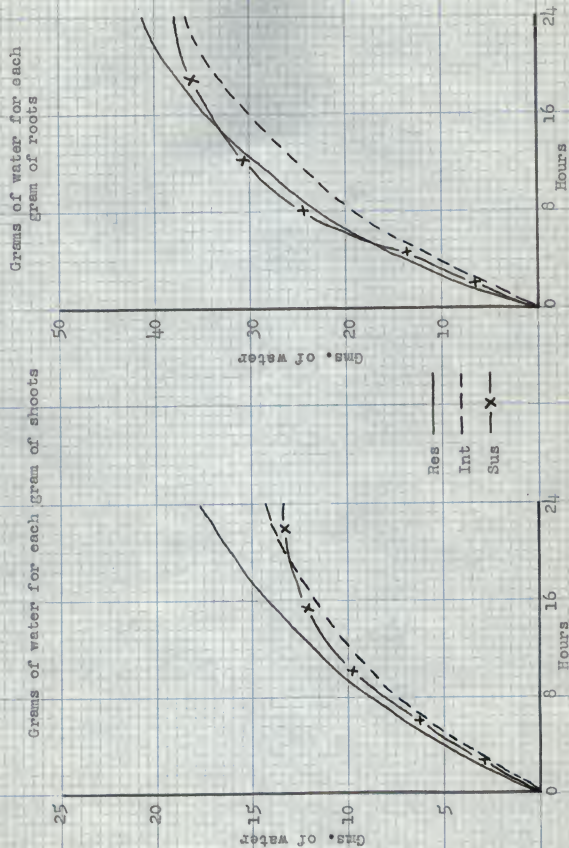


Fig. 2. Transpiration rate of three strains of corn, differing in heat tolerance, when six weeks old.

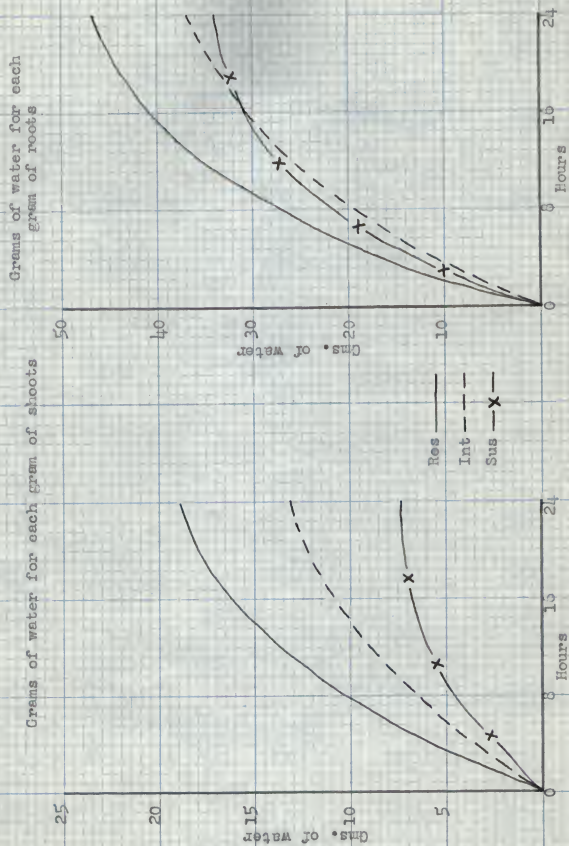


Fig. 3. Transpiration rate of three strains of corn, differing in heat tolerance, when nine weeks old.

Table 4. Grams of water loss from pots planted to corn differing in heat tolerance during periods of increasing moisture deficit.

Age of plants	Strains			Ave.
	1	2	3	
3 weeks	97.5	110.7	130.0	112.73
	(1.987)	(2.042)	(2.113)	(2.047)
6 weeks	268.9	285.0	327.0	293.63
	(2.425)	(2.452)	(2.513)	(2.463)
9 weeks	1238.8	1354.2	1453.3	1348.77
	(3.091)	(3.129)	(3.162)	(3.127)
	535.07	583.30	636.77	
	(2.501)	(2.541)	(2.596)	

L.S.D. = (.053)

L.S.D. between strain means = (.003)

269, 285 and 327 grams respectively. The amount used by number 1 was not significantly less than number 2 but number 1 and number 2 were both significantly less than number 3.

The nine week interval showed a similar trend with numbers 1, 2 and 3 using 1239, 1354 and 1453 grams of water respectively. Number 1 was not significantly less than number 2 and number 2 was not significantly less than number 3 but number 1 was significantly less than number 3.

The strain means show that numbers 1, 2 and 3 used 535, 583 and 637 grams of water respectively. Number 1 was not significantly

less than number 2 but both numbers 1 and 2 were significantly lower than number 3. This illustrates that irrespective of plant vegetation the strains lost water in a consistent manner with the resistant strain losing the least amount of water.

Water Required for Each Unit of Plant Material  
as Related to Drought Resistance

The fact that one group of pots lost more weight than another is not the most important fact but the amount of water used for each gram of dry material produced is most desirable.

Table 5 represents grams of water required to produce one gram of dry plant material in an increasing moisture deficit. It is evident that the three week interval showed no statistically significant difference between the strains although numbers 1, 2 and 3 used 79, 83 and 85 grams of water respectively.

Table 5. Grams of water required for each gram of plant material produced by three strains of corn undergoing an increasing moisture deficit at different stages of growth.

Age of plants	Strains			Ave.
	1	2	3	
3 weeks	78.50	83.47	85.43	82.47
6 weeks	80.72	88.62	109.85	93.06
9 weeks	122.60	150.34	160.26	144.40
Average	93.94	107.48	118.51	

L.S.D. = 11.0

L.S.D. between strain means = 6.3

Data at the six week interval indicate the plants were undergoing a more severe stress and wider differences were evident. Number 1 required 81 grams of water which was not significantly less than number 2 which required 89 grams, but both numbers 1 and 2 used significantly less than number 3 which required 110 grams of water per gram of dry plant material.

As the plants went into a more severe stress, nine weeks after planting, greater differences were evident between the resistant and susceptible strains. Number 1 required significantly less than number 2 or 3 but number 2 was not significantly less water than number 3; using 123, 150 and 160 grams of water per gram of dry plant material respectively.

The strain means of number 1 was significantly less than numbers 2 and 3, and number 2 was significantly less than number 3, the amount used being 94, 107 and 119 grams of water per gram of dry material respectively. It is evident that number 1 used less water to produce one gram of dry plant material than either numbers 2 or 3 when placed in an increasingly severe moisture deficit.

#### Comparison of Plant Weights of Corn Grown in Favorable Conditions with Increasing Moisture Deficit

It is also interesting to note in Table 6 the shoot and root weights of plants which had ample water during growth compared with plants which were undergoing a moisture stress. There was no apparent differences in the way the three strains responded to the moisture treatments at the three week stage. The important fact



Table 6. Grams of dry weight produced by three strains of corn differing in heat tolerance when grown at different stages under conditions of adequate water and increasing water deficit.

		Strains					
		1		2		3	
Age of plants	Portion of plant	Adequate: water	Under-: going a: stress:	Adequate: water	Under-: going a: stress:	Adequate: water	Under-: going a: stress:
3 weeks	tops	1.74	.83	1.52	.99	1.73	1.09
	roots	.76	.44	.50	.43	.71	.45
	total	2.50	1.27	2.12	1.42	2.44	1.54
6 weeks	tops	7.10	2.39	6.28	2.20	8.39	2.18
	roots	3.09	.96	2.43	1.02	2.95	.81
	total	10.19	3.35	8.71	3.22	11.34	2.99
9 weeks	tops	32.23	8.39	33.78	7.17	58.74	7.45
	roots	12.83	2.07	11.72	1.89	12.72	1.78
	total	45.06	10.46	45.50	9.06	71.46	9.23
Average	tops	13.69	3.87	13.86	3.45	22.95	3.57
	roots	5.56	3.47	4.92	1.11	5.46	1.01
	total	19.25	5.03	18.78	4.57	28.41	4.58
						Average	
						: Adequate: Under-: Adequate: Under-: Adequate: Under-:	
						: water : going a: water : going a: water : going a:	
						: stress: : stress: : stress: : stress:	
						: 1.67 : .97	
						: .69 : .44	
						: 2.35 : 1.41	
						: 7.26 : 2.36	
						: 2.84 : .93	
						: 10.08 : 3.15	
						: 41.58 : 7.34	
						: 12.43 : 1.91	
						: 54.01 : 9.58	



is the strains with no water added after planting produced significantly less plant material than the ones which had been watered daily, although the difference was not detectable visually and insipient wilting was not observed. The average dry matter of three plants each of strains 1, 2 and 3 weighed 2.5, 2.1 and 2.4 grams respectively when sufficient water was supplied and 1.3, 1.4 and 1.5 without adequate water. Plate III shows the three strains after three weeks of growth with no water added after planting.

The six week stage showed little differences when comparing root and shoot weights within the treatments. The weight of dry plant material with sufficient water was 10.2, 8.7 and 11.3 grams for strains 1, 2 and 3 respectively. The weight of dry plants undergoing a moisture stress was 3.4, 3.2 and 3.0 grams for strain numbers 1, 2 and 3 respectively. Plate IV shows number 1 after six weeks of growth with adequate water and an increasing moisture deficit.

After nine weeks of growth the strains still differed slightly between treatments as to both shoot and root weights. With sufficient water number 1 made less growth than numbers 2 and 3, weighing 45, 46, and 71 grams respectively. It is apparent that with plenty of water number 3 produced more plant material than the other strains but when placed under a stress it produced less than number 1 and virtually the same as number 2. The plants averaged 10.5, 9.1, and 9.2 grams of dry material for numbers 1, 2 and 3 respectively.

When sufficient water was available the susceptible strain

EXPLANATION OF PLATE III

Growth of three strains of corn differing in heat tolerance when exposed to three weeks of moisture limitation.

## PLATE III



#### EXPLANATION OF PLATE IV

Vegetative growth of the resistant strains of corn after six weeks of growth with different quantities of soil and water. Pots 1 and 3 were supplied with sufficient water throughout the experiment. The soil in pots 2 and 4 was brought to field capacity at planting. No more water was added. Thus the plants were subjected to increasing moisture deficit during the experiment. Pots 1 and 3 differed with respect to amount of soil but were both supplied with adequate water.

PLATE IV



#### EXPLANATION OF PLATE V

Comparative root growths of three strains of corn differing in heat tolerance after six weeks of growth with adequate water.

- FIG. 1. Strain 1 (resistant)
- FIG. 2. Strain 2 (intermediate)
- FIG. 3. Strain 3 (susceptible)



## PLATE V

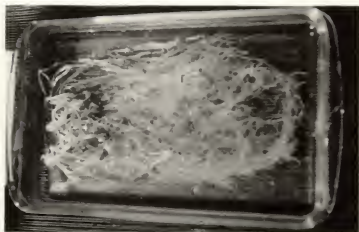


FIG. 1



FIG. 2



FIG. 3

#### EXPLANATION OF PLATE VI

Comparative root growths of three strains of corn differing in heat tolerance after six weeks of growth when undergoing an increasing water deficit.

- Fig. 1. Strain 1 (resistant)
- Fig. 2. Strain 2 (intermediate)
- Fig. 3. Strain 3 (susceptible)

PLATE VI



FIG. 3



FIG. 2



FIG. 1

(number 3) produced more plant material than the other two strains which are thought to be more resistant. When the strains were subjected to moisture deficit which required that the plants rely upon their ability to seek moisture for metabolic activity numbers 1, 2 (the more resistant strains) had the ability to produce more plant material. Plate V compared with Plate VI shows the difference in root growth of the three strains when grown under conditions of favorable moisture and increasing moisture deficit.

Percentage Normal Growth When Comparing Weights of  
Plants Grown Under Favorable Conditions with  
An Increasing Moisture Deficit

It is evident from Table 7 that plants from strain numbers 2 and 3 were capable of producing 67 and 63 percent of normal growth when placed under a moisture stress compared to 51 percent for number 1 for the first three weeks. Numbers 2 and 3 differed significantly from number 1 but number 2 did not differ significantly from number 3.

The six weeks stage showed number 2 still producing greater percentage of normal growth than number 1 or number 3. Strain 2 produced 37.0 percent; 1, 33.1 percent; and 3, 26.0 percent of normal growth. Numbers 1 and 2 were significantly greater than number 3 but number 2 was not significantly greater than number 1.

After the plants had been in an increasing water deficit for nine weeks the strains produced 23.2, 19.9 and 12.4 percent of normal growth for numbers 1, 2 and 3. Number 1 and number 2 had significantly greater percentages than number 3 but number 1 was

not significantly greater than number 2.

It is evident from the data the intermediate and susceptible plants were capable of producing higher percentages of normal growth than the resistant strain when undergoing a slight moisture stress. As the stress continued the resistant and intermediate strains were capable of producing higher percentages of normal growth than the susceptible strain.

Table 7. Percentage plant weight of three strains of corn differing in heat tolerance, at different stages of growth, under conditions of moisture deficit compared with ample moisture.

Age of plants	Strains			L.S.D.
	1	2	3	
3 weeks	50.80	66.98	63.11	8.7
6 weeks	33.14	36.97	26.37	4.9
9 weeks	23.21	19.91	12.42	6.8
Average	35.72	41.27	34.13	

#### Root-top Ratios of Corn as Related to Drought Resistance

There was no statistically significant difference between the root-top ratio (dry basis) after three weeks of growth with ample water. Table 8 shows number 1 had a ratio of .45 which was not significantly greater than numbers 2 and 3, both of which had a ratio of .42.

After six weeks of growth there was no significant difference between the ratios of numbers 1 and 2 or numbers 2 and 3, but

Table 8. Dry root-top ratios of corn differing in heat tolerance when grown at different stages with adequate water.

Age of plants	Strains			Average
	1	2	3	
3 weeks	.448	.420	.421	.430
6 weeks	.457	.387	.345	.396
9 weeks	.411	.349	.252	.337
Average	.439	.385	.339	

L.S.D. = .084

L.S.D. between strain means = .048

but number 1 was significantly greater than number 3. The three strains had a root-top ratio of .46, .39 and .35 respectively for numbers 1, 2, and 3.

Nine weeks after planting wider differences were revealed between the strains with numbers 1, 2 and 3 having root-top ratios of .41, .35 and .25 respectively. The ratios of numbers 1 and 2 were significantly greater than number 3 but number 1 was not significantly greater than number 2.

The mean ratios for the strains showed number 1 significantly greater than numbers 2 and 3 but number 2 was not significantly greater than number 3.

The data indicate that with normal metabolic activity number 1 has the genetic ability to keep producing a high root-top ratio, that is, a large proportion of root in relation to top as it matures, while numbers 2 and 3 do not have this characteristic. Number 1 and number 2 maintained about the same root-top ratio but



number 3 decreased as it grew.

Root Development of Corn When Placed  
in an Increasing Moisture Deficit

Root-top Length Ratio. There was no statistically significant difference at the 5 percent level between the strains when comparing the length of primary root to the length of the longest leaf apparently because of many individual fluctuations. Table 9 shows the strains had a root-top length ratio of .69, .78 and .56 for numbers 1, 2 and 3 respectively after three weeks of growth and ratios of .47, .38 and .57, at the six week stage.

After nine weeks of growth the strains had ratios of .68, .50 and .61 for numbers 1, 2, and 3 respectively.

Table 9. Root-top length ratios, when comparing length of primary root to longest leaf of corn differing in heat tolerance, when grown at different stages with an increasing water deficit.

Age of plants	Strains			Average
	1	2	3	
3 weeks	.686	.777	.556	.673
6 weeks	.466	.381	.571	.473
9 weeks	.676	.499	.614	.596
Average	.609	.552	.580	

No significant difference between strains.

Root-top Ratio (Fresh Basis). The plants were weighed after harvest at the three stages of growth to determine the root-top fresh ratio. Table 10 illustrates that numbers 1, 2 and 3 had

ratios of 1.0, .86, .91, respectively, after three weeks of growth. Number 1 was significantly greater than number 2 but not significantly greater than number 3 and number 3 was not significantly greater than number 2.

Table 10. Root-top ratios (fresh basis) of corn differing in heat tolerance when grown at different stages with an increasing moisture deficit.

Age of plants	Strains			Average
	1	2	3	
3 weeks	.999	.861	.906	.922
6 weeks	1.085	1.018	.871	.991
9 weeks	.653	.529	.488	.557
Average	.912	.803	.755	

L.S.D. = .104

L.S.D. between strain means = .061

After six weeks of growth the strains had a root-top ratio of 1.09, 1.02 and .87 respectively for numbers 1, 2 and 3. Number 1 and number 2 were significantly greater than number 3 but number 1 was not significantly greater than number 2.

At the nine week stage a marked decrease in the root-top ratio was found with numbers 1, 2 and 3 having ratios of .65, .53 and .49 respectively. Number 1 was significantly greater than numbers 2 and 3 but number 2 was not significantly greater than number 3.

The strain means showed number 1 having significantly higher ratio than numbers 2 and 3 but number 2 was not significantly greater than number 3. The mean ratios for the three strains were

.91, .80 and .76 respectively for numbers 1, 2 and 3.

It is evident from the data shown in Table 10 number 1 had the ability to maintain a relatively high fresh root-top ratio for three and six weeks of growth and decreased slightly at the nine week stage when in a moisture stress whereas the ratio of number 3 continually decreased.

Root-top Ratio (Dry Basis). The plants were oven dried and weighed after the various root investigations, previously mentioned, had been made. Table 11 shows that the dry root-top ratios of numbers 1, 2 and 3 were .48, .45 and .42 respectively, at the 3 week interval. There was no statistically significant difference between numbers 1 and 2 or numbers 2 and 3, but number 1 was significantly greater than number 3.

After the plants had been in an increasing moisture deficit for six weeks the strains had root-top ratios of .41, .48 and .38 respectively for numbers 1, 2 and 3. The ratio of number 2 was significantly greater than numbers 1 and 3 and number 1 was significantly greater than number 3.

At nine weeks of age, after exposure to the moisture stress for much of that time, no statistically significant differences were found between the strains. Numbers 1, 2 and 3 had root-top ratios of .26, .28 and .24 respectively.

The strain means indicate number 2 had the best root-top ratio and numbers 1 and 3 next with ratios of .40, .38 and .35 respectively. Numbers 2 and 1 were significantly greater than number 3 but number 2 was not significantly greater than number 1.

Table 11. Root-top ratios (dry basis) of corn differing in heat tolerance, when grown at different stages with an increasing moisture deficit.

Age of plants	Strains			Average
	1	2	3	
3 weeks	.478	.451	.420	.450
6 weeks	.411	.480	.376	.422
9 weeks	.258	.277	.239	.258
Average	.382	.403	.345	

L.S.D. = .051

L.S.D. between strain means = .028

Secondary Root Development. Many investigators have pointed out the main difference between plant roots in relation to drought resistance is their fibrous characteristic. Table 12 shows data collected from the three strains at the three stages of growth. It was found in statistical analysis the three stages did not have homogenous variances when using raw data so the figures were transposed to logarithms as indicated in parenthesis. After three weeks of exposure to a water limitation numbers 1, 2 and 3 produced 613, 469 and 526 cm. of secondary roots respectively. Number 1 produced significantly more than numbers 2 and 3 but number 3 did not produce more than number 2.

The six week stage showed number 1 increasing in length of secondary roots, number 2 maintaining about the same and number 3 decreasing slightly. Numbers 1, 2 and 3 produced 712, 468 and 510 cm. of secondary roots respectively. Again number 1 was significantly greater than numbers 2 and 3 but number 3 was not signifi-

Table 12. Length of secondary root development (cm.) of corn differing in heat tolerance when grown at different stages with an increasing water deficit.

Age of Plants	Strains			Average
	1	2	3	
3 weeks	612.7 (2.782)	469.3 (2.646)	525.9 (2.710)	536.0 (2.713)
6 weeks	712.2 (2.846)	468.0 (2.609)	510.8 (2.694)	563.7 (2.716)
9 weeks	954.1 (2.961)	527.8 (2.709)	416.1 (2.600)	632.7 (2.757)
Average	759.7 (2.863)	488.4 (2.655)	484.3 (2.668)	

L.S.D. = (.098). L.S.D. between strain means = (.056)

cantly greater than number 2. Plate VI shows the fibrous characteristic after six weeks of growth in an increasing moisture deficit.

After nine weeks, during much of which the plants were exposed to a water deficit, numbers 1, 2 and 3 produced 954, 528 and 416 cm. of secondary roots respectively. Numbers 1 and 2 produced significantly more than number 3 and number 1 significantly more than number 2.

It is evident that when placed under a water deficit the drought resistant strains were capable of producing more secondary roots than the susceptible strain, but as the stress continued the susceptible strain did not produce any more fibrous roots. The strain means indicate that number 1 produced 760 cm. of secondary roots compared to 488 and 484 for numbers 2 and 3 respectively.

Seminal Root Development. Some investigators have shown the



seminal roots to be influential in plant response to environmental conditions and physiological activity. Table 13 shows that number 2 produced 63 cms. of seminal roots compared to 26 and 36 cm. respectively for numbers 1 and 3. The length of seminal roots of number 2 was significantly greater than number 1 but not significantly greater than number 3, and number 3 was not significantly greater than number 1.

Table 13. Length of seminal root development (cm.) of corn differing in heat tolerance when grown at different stages with an increasing water deficit.

Age of plants	Strains			Average
	1	2	3	
3 weeks	26.44 (1.345)	63.00 (1.695)	36.47 (1.533)	41.97 (1.524)
6 weeks	37.08 (1.503)	52.83 (1.649)	44.72 (1.566)	44.88 (1.573)
9 weeks	96.97 (1.955)	151.88 (2.144)	95.94 (1.952)	114.26 (2.017)
Average	52.83 (1.601)	89.24 (1.829)	59.04 (1.684)	

L.S.D. = (.208)

L.S.D. between strain means = (.120)

The six weeks stage showed similar results with numbers 1, 2, and 3 producing 37, 53 and 45 cm. of seminal roots respectively. However, there was no statistical significance between any of the strains.

After nine weeks, much of the time under deficient moisture, number 2 still produced more seminal roots than numbers 1 and 3. The strains produced 97, 152 and 96 cm. of seminal roots re-



spectively for numbers 1, 2 and 3.

The strain means indicate number 2 produced significantly greater length of seminal roots than numbers 1 and 3 but number 3 was not significantly greater than number 1.

It is apparent that when placed under moisture deficit the intermediate and susceptible plants were more capable of producing seminal roots than the resistant strain.

Crown Root Development. The crown roots have also been considered as influential in drought resistance of corn because they later comprise most of the root system. Table 14 indicates after growing in moist soil without additional water for three weeks numbers 1, 2 and 3 produced virtually the same amount of crown roots, 51, 52, 51 cm. respectively.

After six weeks of exposure, to an increasing moisture deficit, numbers 1, 2 and 3 produced 75, 77 and 57 cm. of crown roots respectively. Numbers 1 and 2 were significantly greater than number 3 but number 2 was not significantly greater than number 1.

Nine weeks of moisture stress showed number 1 and numbers 2 and 3 producing 220, 230 and 175 cm. of crown roots, respectively. There was no statistically significant difference between the three strains.

The strain means of numbers 1 and 2 were significantly greater than number 3. No significant difference was obtained between numbers 1 and 2.

Table 14. Length of crown root development (cm.) of corn differing in heat tolerance when grown at different stages with an increasing water deficit.

Age of plants	Strains			Average
	1	2	3	
3 weeks	51.11 (1.676)	52.08 (1.671)	50.69 (1.632)	51.29 (1.660)
6 weeks	74.83 (1.850)	77.00 (1.885)	56.81 (1.599)	69.55 (1.778)
9 weeks	220.36 (2.319)	229.97 (2.334)	174.69 (2.201)	208.22 (2.285)
Average	115.43 (1.948)	119.68 (1.963)	94.06 (1.811)	

L.S.D. = (.197)

L.S.D. between strain means = (.114)

#### DISCUSSION

In these studies the strains of corn showed considerable difference in ability to recover from the harmful effects of drought during the subsequent favorable period. In the test it was revealed that single crosses K77 X G5, Kys. X K201 and G33L1 X MY1 recovered in the respective order from high temperatures at each of the three, six and nine week intervals of growth.

The results were in agreement with Hunter et al. (21) and Heyne and Laude (18) in that young plants give the most satisfactory results for classifying high temperature tolerance of different strains of corn. In the present studies, as the corn matured differences became progressively less.

There are several possibilities of changes within the plants

to make them more resistant to high temperatures. The rapid and marked effect of so short an exposure as three to four hours at  $130^{\circ}$  F. suggests that a shock response not correlated with the product of time and temperature of exposure might have induced the resistance. Changes within the plants similar to those reported by Newton and Martin (37) might have increased resistance to high temperatures. Factors suggested by those workers included an increase in the amount of bound water, a change in the osmotic pressure of the plant cells, or the reaction of unidentified physico-chemical properties.

A temperature of  $130^{\circ}$  F. is approximately 55 degrees above the temperature at which plants are normally grown in the greenhouse. The thermal death point of most plants cells lies between  $113$  and  $131^{\circ}$  F. According to Maximov (33) as a temperature of  $110^{\circ}$  F. is approached there is a disturbance in the coordination of the biochemical processes taking place in the cell and poisonous substances of the type of toxin accumulate, for death usually begins at temperatures slightly above  $110^{\circ}$  F. Coagulation of the protein substances of the protoplasm might also begin at this temperature. A by-product of one of these break-down processes might induce heat resistance at  $100^{\circ}$  to  $110^{\circ}$  F. and yet the temperature would not be high enough to kill the cells.

The next problem undertaken in this study was to determine the transpiration rates. It is apparent the strains differ in resistance to high temperatures and it is desirable to know if this difference is due to the ability of the roots to secure water and the vascular system to supply it to the leaf area at sufficient rates

to retain cell turgidity.

The results from this study indicate the strain resistant to high temperatures also had the ability to transpire more water per gram of plant material, i.e. had higher transpiration rates than the intermediate or susceptible strains after three weeks of growth. The strain, classified resistant, used more water than the other two strains per gram of dry shoots and also per gram of dry roots. After six and nine weeks of growth the strain termed resistant also had higher transpiration rates than the other two strains. The six week interval showed the strains had approximately the same transpiration rates for 12 hours of transpiration, but, as the test continued the susceptible strain fell below the resistant strain. After nine weeks of growth the resistant strain had higher transpiration rates at both 12 and 24 hours of evaporation than the other two strains.

Martin (32) reported that sorghum has a lower transpiration than corn under conditions of high evaporation, and Arland (4) stated that there is a good inverse correlation between relative transpiration and hardiness. Kiesselbach (25) found no correlation between transpiration rate and drought resistance but Miller and Coffman (36) concluded that one of the reasons for drought differences between corn and sorghums is the superiority of sorghums in transpiration power. Their results indicated that in most cases a small leaf surface is the most important factor in reducing the loss of water from these plants. The corn plant is not capable of supplying its large extent of leaf surface with sufficient amount of water to satisfy the evaporation power of the surrounding air.

As a result its rate of transpiration per unit of leaf surface falls below what it would be if the needed amount of water were supplied. The sorghums, on the other hand, with their small leaf surface are able to supply water in amounts sufficient to satisfy the evaporating power of the air and, as a result, their rate of transpiration per unit of leaf surface is higher than that of corn. In the present studies there was a significant difference in the water requirement of the strains when the soil was brought to field capacity and the plants were allowed to grow on a given amount of water. The resistant strain required less water than the susceptible strain at all stages of growth.

Some investigators have postulated that water requirement of a plant is related to the available supplies of water in the leaves as determined by the water-gathering power of the roots. Number 1, which has been termed drought resistant, had the best root system and on this basis, water requirement does not seem to be correlated with the root system when growing under an increasing moisture deficit. Research workers in this field found neither much variation in water requirement between varieties nor high correlation between water requirement and drought resistance. Kiesselbach (25) noted that there was no significant difference in the water requirement of drought resistant varieties of corn as compared to non-drought resistant varieties. He further concluded that the sorghum varieties which are recognized for special drought resistance in the Great Plains had no lower water-requirement ratio than corn. Their acknowledged superior drought resistance in comparison with that of corn was not indicated by the water-requirement



ratio, and is doubtlessly due to other physiological differences.

Briggs and Shantz (8) on the other hand, concluded in their studies of relative water requirements that there is a difference among varieties of crops now grown in the dryland region in efficiency of water utilization. Representing the water requirement of proso as one, other crops are as follows: millet 1.06, sorghum 1.10, corn 1.25, teosinte 1.34, wheat 1.76, barley 1.88, buckwheat 1.98, oats 2.04, rye 2.34, rice 2.42, and flax 3.38. It was observed that in general late maturing crops have a comparatively low water requirement and crops maturing during mid-summer have a comparatively high water requirement.

The plant weights were approximately the same for the three strains after three and six weeks of growth with sufficient water supplied. But, the susceptible strain produced significantly more plant material after nine weeks of growth than the other two strains. This would indicate the susceptible strain had the genetic ability, when the environment was favorable, to produce more vegetative growth than the more resistant strains.

A different relationship was observed when the same strains were grown in conditions where moisture deficit became increasingly severe. After three weeks of growth the susceptible strain produced more vegetative growth than the other two strains. No signs of a water deficit could be observed in those plants. After six weeks of growth, in soil which had not been watered after planting, the resistant strain produced more plant material than the other two strains. After nine weeks of growth number 1, the resistant strain, had the ability to keep on drawing moisture from the soil, carry on



metabolic activity and permit plant growth, while number 3, the susceptible strain, fell below the other two strains in this respect.

When comparing the percentage of normal growth between plants in an increasing water deficit and plants growing with plenty of water an interesting relationship was evident. After three weeks of growth, where water deficiency was not evident, the susceptible strain produced 10 percent more growth than the resistant strains. At six weeks the susceptible strain fell below the resistant strain in ability to utilize equal quantities of water. After nine weeks of growth the resistant strain had the ability to secure enough water to promote 23 percent of normal growth while the susceptible strain only produced 12 percent of normal growth.

In view of the findings, it appears that the resistant strain has a root system which is superior to the other two strains because of its ability to continue drawing water in an increasing water deficit. It is important at this point to determine whether the strains differed in ability to promote growth because of genetic differences or environmental influences. The root-top ratios after three weeks of growth with plenty of water showed little differences but after six and nine weeks of growth the resistant strain had significantly higher root-top ratio. This would indicate the resistant strain has a superior genetic ability to produce roots in proportion to the tops with plenty of water for metabolic activity. Weihing (50) found that in general the small varieties have higher dry weight root-top ratios than medium and larger sized varieties. Shank (39) also found heritable differences in root-top ratios, based on dry weights and concluded that

inbred lines differ materially in a number of root characters such as number of main roots per plant, number of branches per unit length of main root and lateral root spread. He also found that the root development in subsequent generations exhibits heterosis, as does top growth and development.

There was evidence that the different strains of corn which differed in heat tolerance, transpiration rates, and root-top ratios with sufficient water for growth also differed in root systems when grown in an increasing water deficit. The strain which had the ability to recover from high temperatures also had the superior root system. In the present studies no difference was found between the strains as to root-top length ratios when measuring the primary root and longest leaf length. In contrast, Parker (38) found evidence that depth of root penetration was a factor affecting survival of certain Rocky Mountain conifers. The resistant strains of Bromus inermis consistently had a larger number of roots, and in most cases significantly greater root depths than the non-resistant strains, as observed by Cook (12).

It was also found the resistant strains had higher root-top ratios when calculated on a fresh or dry weight basis at the three, six and nine week intervals. Number 1 had significantly higher fresh root-top ratios than the other two strains at all of the intervals while number 2 had a little higher root-top ratio than number 1 on a dry weight basis but both were significantly higher than the susceptible strain. Cook (12) also found, in his studies of Bromus inermis, that the resistant plants had more roots in proportion to the top than the susceptible plants.

Weaver (19) stated that grass roots have a primary and secondary root system with the latter eventually comprising the important roots. The seminal roots are those roots arising from the seed and crown roots are formed just below the soil later representing most of the root system.

The resistant strain also had more secondary roots branching from the primary root than the other strains at all three intervals. It is also interesting to note that number 1 increased in amount of secondary root growth in an increasing water deficit while number 3 did not increase. These results are in conformity with Cook (12) who found in his work with bromegrass the drought resistant strains tended to have more smaller, darker and extensively branched roots than susceptible strains. Miller (35) also found, in his studies of sorghum and corn, that the sorghums possessed twice as many fibrous roots as corn at any stage of growth and were consequently twice as efficient in the absorption of water from the soil because of the greater number of branch roots.

No correlation was found between heat tolerance and seminal root development. The resistant strain had the lowest seminal root length for the three and six week intervals while after nine weeks of growth it was virtually the same as the susceptible strain. This is in agreement with Manzelschorf and Goodsell (31) who found no correlation among strains as to seminal root development and yield. Manzelschorf and Goodsell as well as Smith and Walworth (43) concluded that high seminal root production is highly correlated with early seedling vigor.

The present studies showed a correlation between the length of crown roots and resistance to high temperatures. The intermediate strain tended to have slightly more crown roots than the resistant strain but no statistical significance was obtained. The resistant and intermediate strains produced more crown roots than the susceptible strain at the six and nine week interval but not after three weeks of growth. This would suggest the strains which have been termed resistant and intermediate had the ability to keep producing significantly more crown roots after six and nine weeks of growth than the susceptible strain. Spencer (44) found no consistent correlation, among the inbred lines of maize studied, between the development of the seminal roots and the development of the crown roots or the tops but he found marked differences among the strains in regard to number, dry weight, and total length of main roots of the crown root system. The single-cross hybrids exceeded the inbred lines in dry weight of roots, dry weight of tops, diameter of main root, and length of crown and seminal roots.

In view of the author's findings, those strains which had the ability to recover from high temperatures also had in general a superior root system. These findings are in conformity with the results obtained by Aamodt and Johnston (2). Comparing four varieties of wheat, they reported that drought hardy varieties had a capacity to develop better root systems than non-hardy varieties. Talanov (46) has reported that the root system of drought hardy wheat varieties in their ultimate aspect are as characterized by profused branching and great thickness. Stoddart (45), Miller (35), and Martin (32) have concluded that plants with better root systems

are comparatively drought resistant. It could be suggested that the capacity of any variety or strain to develop a root system rapidly in the early stages of growth is quite important. This characteristic is of obvious importance when limited moisture is available at the time of seeding since it allows the plant to establish itself more quickly in the soil. Furthermore, an early and well-developed root system will enable a plant to withstand early periods of drought more successfully. Also, in the latter periods of growth and development the available supply of water in the leaves is determined, in large measure, by the water-gathering power of the roots. The larger and wider areas would be covered by the better-developed root system, and, consequently, the plants can resist drought conditions better. Some workers have concluded that shallow root systems would be particularly unfortunate under conditions where soil dries out during the latter part of the growing season. Also, a plant with a superficial root system is especially susceptible to drought because it lacks roots that penetrate the lower strata of soil and is, therefore, unable to utilize the soil moisture of the lower strata.

In this study no correlation was found between drought resistance and length of primary root but the fibrous characteristic was most evident. Thus, it appears safe to conclude that root development is probably closely associated with drought hardness in many of our agronomic crops.



## SUMMARY

A study of drought resistance in relation to the morphology and physiology of three strains of corn differing in heat tolerance was carried out in the greenhouse from the fall of 1954 to the spring of 1955.

The strain which was most resistant to high temperatures at the seedling stage was also superior to the other strains at the six and nine week intervals when placed in the heat chamber and then allowed a favorable period for recovery. The resistant and intermediate strains were superior in heat tolerance to the susceptible strain at all of the growth periods but as the plants matured the differences became increasingly smaller.

The resistant strain was also found to have higher transpiration rates at each of the three growth intervals than the other two strains. This would indicate the resistant strain was more capable of supplying its leaves with water to maintain cell turgor.

When the three strains were planted in pots of soil brought to field capacity and no more water added the resistant strain required less water per unit of plant material than the other two strains at each of the intervals. Thus, it appears the resistant strain was more efficient in its water utilization than the intermediate and susceptible strains.

When comparing the plant weights of the strains grown in an increasing water deficit and ones grown with plenty of water, the susceptible strain produced more vegetation after three weeks of growth. But, as the stress continued for nine weeks the resistant



strain had the ability to produce 11 percent more vegetation than the susceptible strain.

The resistant strain was superior to the other strains in root-top ratios when grown in favorable or adverse soil moisture conditions. This would indicate the resistant strain not only had the genetic ability to grow more roots in proportion to tops but also had the ability to produce more roots in proportion to tops under increasing moisture deficit.

The root-top length ratios, when comparing the length of the primary root to the longest leaf, showed no significant differences between the strains but the resistant strain tended to be somewhat superior.

No correlation was found between seminal root growth and drought resistance while there was an association between crown root development and heat tolerance.

A high association was obtained between secondary root development (fibrous roots) and drought resistance. The resistant strain had the ability to produce more secondary roots than the other two strains in an increasing water deficit but as the moisture stress continued the susceptible strain did not produce more secondary roots.

In conclusion, it appears from this study that resistance to high temperatures of young corn plants was highly associated with transpiration rates and extent of root development. These two factors combined may partially explain drought resistance in corn.

## ACKNOWLEDGMENTS

To Dr. H. E. Laude, under whose direction the study was made, the author desires to express his sincere appreciation for many suggestions and criticisms throughout the course of this investigation and preparation of the manuscript.

Thanks are also due to Mr. Leo Schneider, Pioneer Hi-Bred Seed Corn Company and Dr. Lloyd Tatum for supplying the seed for this study and many suggestions and help during the progress of the work. Compliments are due to Dr. G. O. Throneberry and Mr. Arland Pauli for their help and suggestions from time to time. Dr. Fryer's assistance in statistical analysis is acknowledged.

## LITERATURE CITED

1. Aamodt, O.S.  
A machine for testing the resistance of plants to injury by atmospheric drought. *Canad. Jour. Res.* 12:788-795. 1935.
2. Aamodt, O. S., and Johnston, W. H.  
Studies on drought resistance in spring wheat. *Canad. Jour. Res.* 14:122-152. 1936.
3. Alexandrov, W.  
Le reginee D'ean de la feuillage d'une mesophyte nomiteu. *Jard. Bot de Tiflio Sec. I, Ser. II, Liver* 1:57-72.  
Original not seen. 1920.
4. Arland, A.  
Krankheit sbefall Anfalligkeit, pflanzene mahrung, und winter jestagkeit in ihren Beziehungen uker due kaltetod der kartoffel, *Beiter. Biol. Pflanz.* 9:215-262. Original not seen. 1931.
5. Bakke, A. D.  
Studies on the transpiring power of plants as indicated by standardized hybrometric paper. *J. Ecology.* 2:145-173. 1914.
6. Bayles, B. B., J. W. Taylor, and A. T. Bartel.  
Rate of water loss in wheat varieties and resistance to artificial drought. *Jour. Amer. Soc. Agron.* 29:40-52. 1937.
7. Briggs, L. J., and H. L. Shantz.  
The water requirement of plants; Investigations in the Great Plains in 1910-1911. *U.S.D.A. Bur. Plant Ind. Bull.* 284. 1913.
8. \_\_\_\_\_.  
Relative water requirements of plants. *Jour. Agric. Res.* 3:1-64. 1912.
9. \_\_\_\_\_.  
The wilting coefficient for different plants and its indirect determination. *U.S.D.A. Bur. Plant Ind. Bull.* 230. 1916.
10. Brooks,  
Anatomical and physiological studies of Maize inbreds and hybrids differing in resistance to top-firing. Master's thesis, K.S.C. 1949.
11. Caldwell, J. S.  
The relation of environmental conditions to the phenomena of permanent wilting in plants. *Physiol. Res.* L:1-56. 1913.

12. Cook, C. W.  
A study of the roots of *bromus inermis* in relation to drought resistance. *Ecology*. 24(2):169-182. 1943.
13. Frey, Lucy.  
The influence of soil moisture on the transpiring power of plants. *Trev. Soc. Natur. De Petrograd*. 33:173-210. 1923.
14. Harber, E. S.  
A study of drought resistance in inbred strains of sweet corn. *Zea Maize Va. Rugosa*. Iowa State Coll. Agr. and Mech. Arts Res. Bull. 243. 1938.
15. Harris, F. S.  
The effect of soil moisture, plant food and age on the ratios of tops to roots in plants. *Jour. Amer. Soc. Agron.* 6:65. 1914.
16. Helgeson, E. A., and K. L. Blanchard  
Heat res. of several spring wheats as shown by lab test. *N. Dak. Agr. Sta. Bimouth Bull.* 3:5-6. Sept. 1940.
17. Heyne, E. G. and A. M. Brunson.  
Genetic studies of heat and drought tolerance in maize. Reprint *Jour. Am. Soc. Agron. Vol.*, 32. No. 10. 1940.
18. Heyne, E. G., and H. H. Laude.  
Resistance of corn seedlings to high temperatures in laboratory test. *Jour. Amer. Soc. Agron.* 32:116-126. 1940.
19. Hubbard, V. C.  
Root studies of four varieties of spring wheat. *Amer. Soc. Agron. Jour.* 30:60-62. 1938.
20. Hunter, A. S., and O. J. Kelley.  
Extension of plant roots into dry soil. *Plant Physiol.* 21:445. 1946.
21. Hunter, J. W., H. H. Laude, and A. M. Brunson.  
A method for studying resistance to drought injury in inbred lines of maize. *Amer. Soc. Agron. Jour.* 28:694-698. 1936.
22. Ivanov, L. A.  
The present state of the question of drought resistance. *Bull. Appl. Bot. Plant Breed.* 13:1-32 (with English summary). 1923.
23. Jost, L.  
Lectures on Plant Physiology. London; Oxford Univ. Press. 1907.

24. Kiesselbach, T. A.  
Transpiration experiment with the corn plant. Nebr. Sta.  
23rd. Ann. Rpt. 125. 1910.
25. \_\_\_\_\_  
Varietal cultural and seasonal effects upon the water re-  
quirements of crops. Proc. Int. Cong. Plant Sci. I.  
Ithaca, New York. 1926.
26. Kiesselbach, T. A., and R. M. Weiking.  
The comparative root development of selfed lines of corn  
and their  $F_1$  and  $F_2$  hybrids. Am. Soc. of Agron. Jour.  
27:538-541. 1935.
27. Kokin, S.  
Zur Frage uber den Einfluss der Bodenfeuchtigkeit auf  
Planzen. Bull. Jard. Bot de Leningrad. Original not seen.  
326:1-19. 1926.
28. Kramer, P. J.  
The relation between rate of transpiration and rate of ab-  
sorption of water in Plants. Amer. Jour. Bot. 24:10-15.  
1937.
29. Laude, H. H.  
Diurnal cycle of heat resistance in plants. Science 89:556-  
557. 1939.
30. Magistad, O. C., and J. F. Brezeale.  
Plant and soil relations at and below the wilting percentage.  
Arizona Agr. Exp. Sta. Tech. Bull. 25:1-36. 1929.
31. Manzelschorf, P. C., and S. F. Goodsell.  
The relation of seminal roots in corn to yield, and various  
seed, ear and plt. characters. Am. Jour. Agron. 21:52.  
1929.
32. Martin, John H.  
Comparative studies of winter hardiness in wheat. Jour.  
Agr. Res. 35(6):493-535. 1927.
33. Maximov, N. A.  
Internal factors of frost and drought resistance in plants.  
Protoplasm 7:259-291. 1929.
34. \_\_\_\_\_  
Plant Physiology. New York. McGraw-Hill. 363 P. 1938.
35. Miller, Edwin C.  
Plant physiology, New York. McGraw-Hill. 1201 p. 1938.

36. Miller, E. C., and W. B. Coffman.  
Comparative transpiration of corn and the sorghums. Jour.  
Agric. Res. 13:579-604. 1918.
37. Newton, R., and W. M. Martin.  
Physico-chemical studies on the nature of drought resistance  
in crop plants. Canad. Jour. Res. 3:336-427. 1930.
38. Parker, T.  
Moisture retention in leaves of conifers of the Northern  
Rocky Mountains. Bot. Gaz. 113:216-271. 1951.
39. Shank, D. B.  
Top Root ratios in inbred and hybrid maize. Am. Soc. Agron.  
Jour. 35:976-987. 1943.
40. Shantz, H. L.  
Drought resistance and soil moisture. Ecology. 8:145-157.  
1927.
41. Shirley, H. L.  
The influence of light intensity and quality upon the growth  
of plants. Amer. Jour. Bot. 15:621-622. 1928.
42. Schultz, H. K., and H. K. Wags.  
Artificial drought tests on some hay and pasture grasses  
and legumes on sod and seedling stage of growth. Amer. Soc.  
Agron. Jour. 30:676-682. 1938.
43. Smith, L. H., and E. W. Walworth.  
Seminal Root development in corn in relation to vigor of  
early growth and yield of crop. Am. Jour. Agron. 18:1113.  
1926.
44. Spencer, J. T.  
Comparative study of seasonal root level of some inbred  
lines and hybrid of maize. Jour. Agr. Res. 61:521. 1940.
45. Stoddart, L. A.  
Osmotic pressure and water content of prairie plants. Plant  
Physiol. 10:661-680. 1935.
46. Talanov, V. V.  
The best varieties of spring wheat. Bull. App. Bot. & Pl.  
Breed. 29:1-231. 1926.
47. Thiel, Hugo.  
De radicum plantarum quarundum ab agricolis praecipue  
culturarum directione et extensione. Diss. Bonn. Original  
not seen. 1865.



48. Warming, E.  
Oecology of plants. London: Oxford Univ. Press. 1909.
49. Weaver, John E.  
Root development of field crops. McGraw-Hill Book Co.  
New York. 1926.
50. Weihing, R. M.  
The comparative root development of regional types of corn.  
Amer. Jour. Agron. 27:576. 1935.
51. Westbrook, Lawrence.  
Drought cut grain crops to a 30-year low. Lit. Digest  
118:5. 1935.



DROUGHT RESISTANCE IN RELATION TO  
MORPHOLOGY AND PHYSIOLOGY OF CORN

by

MERVIN DUANE HAGUE

B. S., Iowa State College, 1954

---

AN ABSTRACT OF A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE  
OF AGRICULTURE AND APPLIED SCIENCE

1955

Severe droughts have created a great deal of interest in finding some simple means of determining resistance of a plant to drought. No characteristic existing in a variety or within a species has yet been found to be definitely and consistently associated with drought resistance. Therefore, no reliable morphological or physiological characteristic can be used to distinguish degrees of hardiness.

In the present study ten single cross strains of yellow dent corn were obtained from Kansas State College and Pioneer Hi-Bred Seed Corn Company. Previous field observations had indicated differences in tolerance to drought. These strains were tested for heat tolerance in the high temperature room with temperature of 130° F. and relative humidity ranging from 30-40 percent. Three strains that differed appreciably in heat hardiness were chosen for this study. The strain found most resistant was K77 x G5, intermediate Kys. x K201, and most susceptible G33L1 x MY1. These strains were then subjected to the following tests after three, six and nine weeks of growth to find:

1. Heat tolerance of corn at different stages of growth.
2. Transpiration rates of corn differing in heat tolerance at different stages of growth.
3. Water requirement of corn differing in heat tolerance when undergoing an increasing moisture deficit.
4. Plant weights of corn differing in heat tolerance when grown in conditions of adequate water and in an increasing water deficit.
5. Root development of corn differing in heat tolerance when grown in an increasing water deficit.

The strain which was most resistant to high temperatures at

the seedling stage was also found to be superior to the other strains at all of the growth intervals.

The resistant strain had higher transpiration rates, when comparing either shoots or roots, at each of the three growth intervals than the other two strains.

The resistant strain had a lower water requirement than the other two strains at all growth intervals.

The susceptible plant was found to be genetically larger under favorable moisture conditions but under an increasing moisture deficit the resistant plant was capable of producing more plant material.

The resistant strain had in general a more fibrous and extensive root system than either of the other two strains when grown under ample moisture conditions as well as with increasing moisture limitation.

It appears from this study that resistance to high temperatures of young corn plants was highly associated with transpiration rates and extent of root development. These two factors combined may partially explain drought resistance of corn.

