

INHERITANCE STUDIES OF HEAT AND
DROUGHT TOLERANCE IN MAIZE

by

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INTRODUCTION

Drought is probably the major factor in limiting crop production in semi-arid regions. These regions have been periodically subjected to droughts and in severe cases complete crop failures have resulted. Previous weather records indicate that high temperatures and low rainfall may occur periodically and as an insurance against such adverse weather conditions the plant breeder must necessarily produce plants that will withstand such conditions.

The westward migration into the Great Plains area resulted in a great change in the natural vegetation. Previously the prairies were in their natural state and over a long period of time a balance in vegetation had been reached. During this long unmolested period, a climax vegetation was established through the weeding out of the non-resistant plants. However, man has plowed many acres of this virgin land and has substituted his own crops, which often have been brought from great distances and lack the necessary resistance to adverse conditions. Nature's balance has been upset and man is now attempting to produce an artificial balance with crops that have not been subjected to the rigor of nature's long-time selection in the Great Plains region.

Corn, although not the most important crop in the Great Plains area, is grown extensively in areas where drought con-

ditions frequently occur. Corn is naturally a subtropical crop and grows during the warmest season of the year when moisture shortage and dry hot weather frequently prevail. Corn possesses characters which seemingly make it adapted to droughty conditions, such as its deep roots extending five to six feet in depth and its relatively low water requirement. Because of its flowering habit it is not well adapted to dry hot regions. Low soil moisture delays silking much more than it does pollen shedding and the tassel often "blasts" when hot winds occur. The flowering period has been shown to be the most critical period of the corn plant by the rather high correlations which exist between July rainfall, especially July 20 to August 10, and high temperatures with the yield of corn in Kansas as shown by Robb (1934) and Hodges (1931).

Corn with its apparent lack of adaptation for semi-arid conditions probably will continue to be grown in areas subject to droughts. As such conditions do prevail it has become necessary to consider the tolerance of various strains of corn to heat and soil drought in a corn improvement program. The task of the plant breeder, then is to produce strains that will be better suited to their environment. Corn improvement methods normally are long and rather costly and testing drought tolerance under field conditions is not very certain because of the weather variations that occur

from year to year. To accelerate the progress of the plant breeder, who is developing crops for use in the drought regions, the perfection of some suitable, simple and reliable methods for determining the comparative resistance of plants in the laboratory is desirable. Adverse weather conditions do not occur regularly and with a suitable system of controlled conditions the plant breeder would not have to depend upon the highly variable climatic factors to test his plants. Such reasonably accurate laboratory methods have been described by Hunter, et. al. (1936) for corn and by Aamodt (1935) for wheat.

Much of the early work done on the drought relationships of plants represents attempts to find some simple index of measuring drought resistance by means of a number of relatively easily observable anatomical characteristics. The xerophytic adaptations and drought resistance of native plants are of small value to the agronomic crops. Dormancy during dry spells and slow growth are characteristics of the perennials while the annuals are often of an ephemeral nature. The ultimate goal of economic crop plants is yield of either grain or forage and this generally cannot be accomplished in early maturing plants, or in plants which remain dormant for extended periods of time, although modifications of these adaptations may be utilized.

The study of drought resistance is complicated by the

fact that the degree of drought resistance is influenced by all the conditions under which the plant develops and that the sensitivity of the plant to drought varies at different periods of growth. Drought resistance in the field is a summation of several factors which under proper laboratory conditions can be separated. Drought generally is associated with low atmospheric moisture and high temperature which causes a very low relative humidity and a high rate of evaporation. Under field conditions it is impossible to separate the effect due to lack of moisture from that due to high temperature, while with controlled conditions the moisture or temperature relations of the plant can be worked out separately. In this study air temperature is the only factor of drought considered.

The physiological basis of drought resistance has been studied extensively but the genetic behavior of drought tolerance has received relatively little attention. These two factors cannot be separated satisfactorily since physiological behavior is the response of the hereditary potentialities of the individual to its surrounding habitat. In studying such a problem as drought tolerance the close association between the physiology and genetics of the plant must be kept in mind.

Since yield depends upon such factors as drought tolerance, winter hardiness, and insect resistance, it is important

that the plant breeder knows something about the mode of inheritance of these characters to carry out a successful breeding program. This paper deals primarily with the problem of determining whether any major genetic factors for drought tolerance are associated with any of the ten linkage groups in maize and only incidently with the mode of inheritance of drought tolerance.

REVIEW OF LITERATURE

Physiological Studies

Drought resistance which is possessed by any group of plants undoubtedly is due to the interaction of a number of factors. A review of the literature shows that although considerable work on drought resistance in plants has been done, primary emphasis has been placed on the attempt to find a simple index to measure drought resistance.

Perhaps the best interpretation is given by Maxsimov (1929) in which he defines drought resistance of crop plants as the capacity of the plants to endure drought and to recover readily after permanent wilting with minimum damage to the plant itself and to the yield produced.

The term "drought" may be considered in several ways. There are at least two readily distinguishable types of drought: (1) atmospheric drought and (2) soil or edaphic drought. Ellis et. al. (1936) have suggested another type as

(3) physiological drought. Atmospheric drought is one caused by a hot dry wind resulting in a low humidity and a high rate of evaporation which causes the plant to wilt but which is usually of a temporary nature. Soil drought is most commonly thought of as the condition in which the soil no longer provides the plant with moisture, causing the plant to wilt permanently. One or the other types of drought may occur and when they occur in combination very adverse conditions for plant growth prevail. Physiological drought is caused by too high a concentration of the soil solution whereby the plant cannot obtain water from the soil. This type is of a very local nature occurring in such areas as alkali spots and sometimes associated with frozen soil. The problem of drought may also be classified as to (1) moisture and (2) temperature relationships that exist in the environment. Each may be subdivided into two parts: (a) soil and (b) air. Thus under moisture, the water available to plants and the relative humidity of the air would be considered, and under temperature, the soil and air temperatures would be considered. Soil temperatures, though not so important, are known to cause damage, especially to flax plants. Kincer (1919), of the United States Weather Bureau, considers a drought to be 30 consecutive days, or more, without 0.25 inch of rainfall in 24 hours for the period from March to September inclusive. This probably is not a satisfactory definition be-

cause it does not take into consideration the effect of temperature.

Earlier it was thought that plants differed in their ability to absorb water from the soil. Briggs and Shantz (1912) did extensive work on the ability of plants to remove moisture from the soil. Plants were allowed to grow in sealed containers until permanently wilted. The moisture content of the soil at this stage was determined and was called the "wilting coefficient." It was found that the wilting coefficient for all plants tested on the same soil was nearly the same, and that no relationship existed between the amount of water a plant could remove from the soil and its relative tolerance to drought.

It was previously thought that plants with xerophytic characteristics adapted to droughty habitats were economical in their use of water. Miller (1931) defines "water requirement" as the ratio of the number of units of water absorbed by the plant during the growing season to the number of units of dry matter produced by the plant during that time. Briggs and Shantz (1913, 1914, 1917) have determined the water requirement of many plants and have concluded that various factors of the environment affect the amount of water used by plants. They at first thought that there would be a close association between the water requirement of plants and drought resistance, but they found that sorghums, millets,

and corn had a low water requirement and certain Agropyrons and Brome grass had high water requirements. Also sorghums often had a higher water requirement than corn although sorghum is recognized to be more drought resistant than corn. They found a wide range in water requirement among the varieties of many crops and encouraged the belief that strains could be obtained which were still more efficient in the use of water than those grown at present in dry-land regions. Dillman (1916) also suggested that the plant breeder should determine the water requirement of his selected strains and if significant differences were found it was one of the best indications of difference in adaptability to drought conditions. Later, (1931), he stated that water requirement probably is not a dependable measure of the adaptation of a variety to conditions of drought.

Plants that are growing under arid conditions differ morphologically from those growing in humid climates. It was thought that xerophytic structures in crop plants would insure drought resistant qualities. Size of cells and number and size of stomata were thought to be a rather definite measure of drought resistance. Kiesselbach (1916) studied correlations between leaf structure and number of stomata and concluded there was no consistent correlation between these histological coefficients and the transpiration rate per unit dry matter or per unit leaf-area of the different varieties

of corn studied. In summarizing the value of xerophilous structures such as small cells, a dense network of veins, numerous (but small) stomata per unit area, a relatively great development of the root system, succulent nature of stem and leaves, and hairy and waxy coverings, Maxsimov (1929) considered them to be only of secondary importance. He placed the most emphasis on the plants ability to withstand wilting without injury and loss in yield.

The extent, type, and amount of the root systems have been studied in considerable detail. Miller (1916) reported that the nature of the root system may have an important part in preventing incipient wilting in the leaves. For any given stage of growth Miller found that corn and sorghum possessed the same number of primary roots and that the general extent of these roots in both a horizontal and vertical direction was the same. Sorghums have about twice as many secondary roots per unit of primary roots as corn and the primary and secondary roots of sorghum are more fibrous than those of the corn plant. Corn ordinarily has from 1.5 to 2.3 times as great a leaf area as sorghum, but sorghum has a main root system as large as corn and furthermore has twice as many secondary and fibrous roots which suggests that the absorbing system of sorghum would be twice as efficient in the absorption of water from the soil as corn. It is a well known fact that sorghum is a better dry-land crop than corn and its ef-

ficient root system may be a partial explanation of this difference. Weaver and Albertson (1936) in studying the changes in prairie vegetation due to the drought of 1934 and 1936, found that all of the native grasses suffered loss, but that the death rate was greater among those with relatively short roots. Andropogon furcatus because of its deeper root system was usually injured least. There apparently exists some correlation between type and extent of root systems and drought resistance, but the procedure necessary to determine the type and extent of roots on a comprehensive scale is out of the question for the average plant breeder.

More recent studies have been made upon the physiology of the protoplasm in relation to drought resistance. Novikov (1931), a Russian worker, determined the amount of bound water in the plants. Bound water is referred to as the water which plants hold in an unfree state. From field records Novikov selected drought resistance and non-drought resistant strains of wheat that had proven qualities over a period of years. In one experiment Novikov grew plants in soil of 40, 60, and 80 percent maximum water content. There was no significant difference in percent of frozen water between plants growing in soil with 60 and 80 percent of maximum moisture content. A significant difference was found, however, in plants which were grown in soil of 40 percent of maximum moisture. The

resistant wheat had 18.6 percent frozen water and the non-resistant wheat had 30 percent frozen water. In a series of tests the drought resistant wheat yielded more than the non-resistant wheat in dry years but showed no advantage in normal years.

Holbert et. al. (1932) made total, free, and bound water determinations on yellow dent corn during a brief drought period. Indications were obtained that the water holding capacity of the leaf tissue in resistant strains of corn increases as heat and drought continue. Total water decreased slightly but bound water increased 35 percent on the dry basis. On the second day following one-half inch of rain another marked shift in bound water and free water equilibrium occurred in the direction of the condition existing prior to the heat and drought period. On the other hand, the water binding capacity of comparable leaf tissues of heat susceptible strains increased very little as heat and drought continued and even in some strains there was a decrease. During the first three days after the stress period had passed susceptible strains made phenomenal growth. Prehardening for heat as well as for cold has been found associated with marked increase in water binding capacity.

More recently studies have been made on the physico-chemical properties of plants in regard to drought tolerance. Newton and Martin (1930) have done a large amount of work in

this field, having studied many plants in relation to known drought adaptations. In determining the osmotic pressure of plants they found that the osmotic pressure of the tissues of many grasses, both cultivated and wild types, varied with the physiological scarcity of water, but they concluded it was not a good index of drought resistance. They also determined the colloidal content of cells. A characteristic property of colloids is the imbibition of water and the holding of this water against a rather high tension. The colloidal content of the cell varied considerably but there apparently was some relation between the amount of colloids present and the drought resisting nature of the plants. Their technique is not simple enough to be used in making many tests. Newton and Martin also determined the bound water content of various plants and found this index to be more dependable. On this basis the cultivated wheats and several grasses have been arranged satisfactorily in the order of their drought resistance.

The principle factors affecting drought resistance in plants were summarized by Newton and Martin (1930) as shown in the following outline on page 14.

- | | | |
|------------------|--------------------------------|--|
| | | (a) Available moisture |
| | | (b) Concentration of soil solution |
| | (1. Soil factors | (c) Toxic substances in solutions |
| | (| (d) Temperature |
| | (| (e) Aeration |
| | (| |
| | (2. Root development | (a) Spread and depth of penetration |
| | (| (b) Intensiveness of branching |
| A. Absorption | (| (c) Number and persistence of root hairs |
| | (| |
| | (| (a) Osmotic pressure of cell sap of root hairs |
| | (3. Physiological adaptations | (b) Imbibition pressure of hydrophilic colloids in cells |
| | (| (c) Mucilaginous secretions in regions of root hairs |
| | | |
| | | (a) Temperature |
| | | (b) Humidity |
| | (1. Atmospheric factors | (c) Air movements |
| | (| (d) Light intensity |
| | (| (e) Atmospheric pressure |
| | (| |
| | (| (a) Ratio of root to leaf |
| | (| (b) Conducting tissue |
| | (| (c) Reduction of leaf surface |
| | (| (d) Rolling, folding, or thickening of leaves |
| | (| (e) Deciduous leaves |
| B. Transpiration | (2. Structural features | (f) Epidermal coverings |
| | (| (g) Diminution of intercellular spaces |
| | (| (h) Sunken stomata |
| | (| (i) Size and number of stomata |
| | (| (j) Stomatal regulation |
| | (| (k) Surface hairs |
| | (| |
| | (3. Physiological adaptations | (a) Osmotic pressure of cell sap |
| | (| (b) Imbibition pressure of hydrophilic colloids in cells |

C. Wilt endurance

Outline showing the principal factors affecting drought resistance in plants. Newton and Martin, 1930.

Quantitative Factors

Inbred lines of maize ("pure lines") and other true breeding varieties of plants breed true not only for such visible characters as color, height, leafiness, strength of stalk and so forth, but also for physiological functions such as disease resistance, insect resistance and drought resistance. East (1936) states that in any given population there are more different alleles present among the genes influencing the physiological efficiency than among the genes influencing the morphological pattern. It is recognized that somatic changes, although genetically determined, may be influenced by the environment in which grown or by the other elements in the genetic composition. In the more simple cases of known genes the epistatic or modifying effect, duplicate, complementary and supplementary behavior of genes has been well worked out. However, with such elusive genes as quantitative factors, very complicated situations occur because of the many more genes present and the lack of knowledge of their exact mode of inheritance.

Quantitative characters often may best be studied by determining whether they are associated with any known, simple qualitative genes. With the rapid cataloguing and classification of chromosomal translocations in maize, another

method besides well known genes, can be used in the study of quantitative factors. This latter method makes it possible to use normal stocks of maize without the probable alteration some of the better known qualitative genes may have on the physiology of the plants. Genetic factors responsible for size (quantitative) characters are unquestionably difficult to analyze and their actual presence in the germinal complex is still largely theoretical. Enough work has been done on the problem of quantitative characters to verify that heritable variations are probably due to a large number of Mendelian factors but more work should be done.

In any such study involving quantitative factors care should be taken that the causes of variability are properly separated. Many size characters are influenced by external conditions and it becomes difficult to distinguish the different genetic possibilities because of the knowledge that these genetic factors can be modified by the environment. Therefore it becomes more important that the response of genes to their environment be more fully understood in order to facilitate the study of complex quantitative characters and further aid in the breeding of better crop plants.

There are relatively few critical studies on quantitative factors in maize. Many of these studies have been on disease resistance, which has been found in some cases, to be due to a single gene.

Emerson and East (1913) reported upon the inheritance of several size factors in maize. The inheritance of the number of rows per ear was studied and in nearly every case the F_1 was intermediate and the parent types were recovered in F_2 and F_3 generations. Ear length studies gave similar results. Earliness of F_1 plants was intermediate while in F_2 and F_3 generations the range between both parents was obtained. In height of plants the F_1 was generally taller (heterosis) than either of the parents. In studying these various size factors it was concluded that certain quantitative relations in maize are the influence of a single factor in the development of two or more characters as well as the influence of several factors in the development of a single character. The multiple-factor hypothesis furnishes a satisfactory interpretation of the behavior of size characters in plants and animals which is based upon the Mendelian principle of segregation and recombination of factors.

Wellhausen (1937) studied the behavior of fifty-six inbred lines of corn to bacterial wilt and selected the most resistant and the two most susceptible lines and made all the possible crosses between them. He concluded that there were at least three dominant factors, independent and supplementary, which were involved in the inheritance to bacterial wilt. Two factors were major in importance and the other minor. The presence of all three factors in heterozygous or homo-

zygous conditions gave a high degree of resistance while the triple recessive was very susceptible. Apparently one of the factors may be located on chromosome I as a loose linkage was noted with the P gene. Resistance also was associated with late maturity and susceptibility with early maturity. Hybrid vigor was exhibited when the two susceptible inbreds were crossed but this vigor did not increase the resistance. Wellhausen suggested that there may be other minor factors besides the three factors he had postulated. This carefully planned experiment shows the difficulty in isolating quantitative factors and assigning them to linkage groups.

Lindstrom (1929, 1931) noted that the number of rows on an ear was governed by multiple factors and was one size character that was influenced relatively little by environment. It was thought that the multiple genes controlling row number (or any other size character) are scattered on many of the chromosomes and if enough characters were analyzed genetically and correlated with row number by appropriate hybridization methods, certain linkages would be demonstrated. Lindstrom used only four well known qualitative factors in his study but found a very significant correlation between cob and pericarp color (P) and row number in a large series of crosses and was inclined to believe that one of the major row number genes is located on the P-br chromosome. He also found rather loose linkage with endosperm texture

(Susu), endosperm color (Yy) and aleurone color (Rr). In such a study as the linkage of quantitative and qualitative genes it is often only through the use of exceedingly large numbers of progeny that certain linkages can be detected.

Jenkins (1931) observed very marked differences in resistance of inbred lines of corn and their single crosses to leaf burning which is common in hot, dry weather. One inbred seemed to carry factors for drought resistance, for in the ten crosses in which it occurred, no injury was noted. Comparable crosses of another inbred were very susceptible to leaf burning. This latter line seemingly carried somewhat dominant factors for susceptibility. Incidentally the crosses involving the resistant line were on the average the most productive. No cross between these two lines was grown in the year the observations were made. The data indicate that much may be accomplished in breeding corn for drought resistance.

Immer (1927) studied the linkage relations between the factors determining smut reaction and one or more known genetic factors in seven of the ten linkage groups in maize. He found that the factor was linked with two groups, the P-br group and the B-lg group. However, he thought that perhaps the morphology of the liguleless factor caused high smut infection. The number of smut infected ears on the liguleless plants was low which further gave evidence that the morpho-

logical character itself may have been of more importance than any linked genes for specific smut behavior. It is of interest to note that smut was not linked with Su su when smut is of such common occurrence in sweet corn. In general, the inheritance of reaction of corn smut in maize was shown to be intermediate, although there were several instances in which there was an apparent dominance of susceptibility.

Hoover (1932) also studied the inheritance of smut in maize. He found that the F_1 was intermediate. He used genetic markers on nine of the ten chromosomes and found linkage of smut reaction with four of these. These four included the factors for "ramosa", "tassel seed", "brachytic" and "liguleless", and each character giving such a morphological change from the normal condition that it might play an important role in the reaction of a plant to smut and not be true linkage relationship. Hoover concluded that in so far as the host is concerned, two sets of genetic factors seemed to control the reaction of any particular strain to smut. One group of factors was considered to be concerned primarily in the control of physiological behavior and the second with the morphology of the plant.

Not all cases of disease resistance are explained on the multiple-factor basis. Rhoades (1935) showed that resistance to race 3 of Puccinia sorghi was due to a single Mendelian factor, which was located on chromosome IX. Her method used

in locating the gene for rust resistance was of interest in that she used irradiated pollen and trisomics, thus escaping the possible direct effect of any marker genes. Mains (1931) also showed that resistance to two forms (1 and 3) of Puccinia sorghi was inherited in a very definite manner obtaining in F_2 a ratio of three resistant to one susceptible plants.

Lindstrom (1926) presented conclusive evidence to demonstrate that genetic linkage occurs between color factors and size factors in the fruit of tomatoes. Two known factors, Yy for skin color and Rr, for flesh color, located on two different chromosomes, were used as simple qualitative factors. Rather definite linkage of the size of fruit occurred with the yellow skin color. Also some linkage with red flesh was noted, but not as striking as in case of yellow skin. Small size tended to be dominant. No complimentary factors were present, at least no transgressive segregation occurred in F_2 . Only two of the 12 chromosomes in tomatoes were tested and it may be possible that there are size factors on all of them.

Yeager (1937) also worked with size inheritance in tomatoes. He found that locule number was associated with size whereas Lindstrom found no such association. Locule number was also associated with the shape of the fruit. Yeager did find that tomatoes with the same locule number differed several hundred percent in size so obviously there are

other size factors present. Since the vegetative vigor of a plant may greatly affect the size of the fruit, Yeager concluded that genes not directly related to size and shape of the fruit but which affect the general vigor of the plant and other plant characteristics have their effect on fruit size.

Griffiee (1925) has shown that resistance and susceptibility of barley to Helminthosporium sativum are due to definite genetic factors. By studying the reaction of F_3 lines to this pathogene in relation to other characters the inference was drawn that at least three factors are concerned. One factor was linked with the factor for 2-rowed heads, one with white glumes and one with rough awn. The linkage of the factor for susceptibility to barley stripe with the factor for earliness was very intense, or else earliness in itself predisposes the plant to attack by the pathogene. Such complications as these make the separation of physiological and genetical factors difficult.

The relation between genes affecting size and color in tobacco was studied by Smith (1937). He found that each color gene studied was linked with genes affecting corolla size. Apparently a large number of size genes of comparable magnitude was involved, none having major effects and all being non-dominant.

In observing the varietal resistance of small grains to

spring frost injury, Harrington (1936) found a relationship between remote ancestry and susceptibility to frost damage. Wheats having winter-hardy Kanred as a parent showed more frost resistance than wheats involving emmer and Indian wheats in their ancestry. This is a striking example in which frost reaction (a quantitative character) is transmitted from the parent to the progeny.

The study of inheritance of winter-hardiness in wheat by Quisenberry (1931) indicated that this character appears to be controlled by several genetic factors, the final expression being greatly influenced by the environment under which the material is grown. Worzella (1935) made a further study of cold tolerance and grew the F_1 , F_2 , and F_3 generations together with their parents, and subjected them to artificially controlled freezing tests. The F_1 was intermediate and the F_2 varied from some more susceptible than the non-hardy parent up to plants as resistant as the hardy parent. F_2 lines which were susceptible carried over into F_3 . The transgressive segregation which occurred was significant. The great increase in the variability between the parents and F_2 generations, the reappearance of the parental types and transgressive variation indicates clearly that segregation of genetic factors had occurred. The number of genetic factors involved could not be determined.

Castle (1929) in studying size inheritance in rabbits

doubted that genes exist which affect the general rate of growth and which influence the size of the organism as a whole. Although size is a highly complicated character, being the resultant of many factors, Castle studied only four factors representing four linkage groups of the twenty-two in rabbits. General body conformation is similar to yield in grain crops in that both are possibly the cumulative result of many factors. At best the linkage test is a difficult and uncertain method of isolating quantitative genes and only by the use of large numbers may certain linkages be detected.

Methods of Studying Drought Resistance

The Russian investigator Novikov (1931) and others have made considerable use of the amount of bound water in plants as a measure of drought or cold resistance and have obtained some rather definite results.

Timofeeva (1933) used a very simple method to determine the drought resistance of various crop plants. Seeds of wheat were germinated on blotters, put into various concentrations of sucrose for certain periods of time and then removed and planted in sand to note recovery. A greater proportion of plants of drought resistant varieties survived than of those which were non-resistant to drought. Aamodt and Johnston (1936) on the other hand found no marked superiority of ker-

nels of drought resistant varieties over non-resistant varieties in their capacity to germinate in more concentrated solutions of common salt, potassium chloride and sucrose.

Shirley (1934) was perhaps the first to build a chamber in which entire plants could be tested under constant conditions of temperature and young spruce trees were placed in an illuminated chamber with a revolving table to expose all plants to the same conditions. Temperature and humidity were controlled by the use of an electric heating element and calcium chloride. The length of time the plants survived was used as the measure of drought resistance.

Bayles et. al. (1937) grew two varieties of wheat in the same pot and allowed the pots to dry and noted the loss of water from the plants. The rate of recovery was also noted when proper growing conditions were reestablished. Plants were also exposed to a current of hot air (92° - 98°) and the amount of injury was observed.

Aamodt (1935) described a machine for testing the resistance of plants to atmospheric drought. The machine consisted of a glass chamber through which air was forced at a constant rate. The temperature was maintained by thermostatically controlled electric heaters and the air current was regulated by dampers and baffles. After exposure for 8-15 hours at 110° F., 14 percent relative humidity and an air velocity of 6 miles per hour, wheat varieties known to

be drought resistant in the field showed less injury than varieties known to be non-drought resistant.

Hunter et. al. (1936) subjected two week old corn plants to artificial heat in a simple chamber with thermostatically controlled electrical units as the source of heat. The plants were exposed for 6.5 hours at 140° F. and relative humidity ranging from 28-32 percent. Almost perfect correlation between survival value of seedlings after treatment and field behavior of inbred strains of maize was obtained.

Zink and Grandfield (1936) constructed a temperature and humidity control chamber to study the set of seed in alfalfa. A double glass chamber was built to allow the plants access to light. Heat was supplied by electric heaters and humidity was controlled by a known concentration of sulfuric acid. A small fan kept the air in constant motion.

All these methods are steps forward in working out the complex problem of drought resistance. The actual treatment of seedling plants to drought conditions has given high correlation with field behavior just as subjecting plants to artificial cold has been very successful in studies of cold resistance. Wide differences between varieties of a single crop and among different crop plants can be shown by these various methods. For determining smaller differences between similar strains these tests should be used in conjunction with a study of the factors that actually exists in the natu-

ral environment under which the crop is to be grown. Waldron (1931) has clearly shown that this is necessary. Kubanka wheat has always been thought to be highly drought resistant. Moreover, the bound water of Kubanka was 7 percent and only 4 percent in Marquis which would lead one to believe Kubanka would be quite superior to Marquis in drought resistance. In a comparison involving 68 crop years which were reasonably droughty and omitting rust years, however, Kubanka yielded only 0.11 ± 0.21 bushels more than Marquis, which is not significant. The final decision as to the best crop or variety should take into account its behavior over a long period of years.

MATERIAL AND METHODS

The drought of 1936 illustrated very clearly the difference in reaction of various strains of maize to drought condition. Some inbred lines in the corn breeding nursery at Manhattan, Kansas, succumbed rather early while others endured the drought to a remarkable degree. Although many strains failed to reach the tasseling stage, some were able to produce a few grains under the very adverse weather conditions that prevailed. Five Kansas inbred lines of maize were selected on the basis of their behavior to drought under actual field conditions. One of the lines selected failed to set seed in 1936 but was chosen because of its

ability to remain erect, green, and apparently uninjured by the drought. These selected lines were used as drought resistant parents in crosses made with susceptible genetic testers in the winter of 1936-37. Descriptions of the five inbred lines are given in Table 1.

Table 1. Description of inbred lines of maize with known behavior to natural and controlled conditions.

=====							
In-	Genera-	Aleurone	Average:	Drought Rank:			
bred:	tions	: and	:height	:Matur-	: in	: in	:Variety
line:	selfed	:endosperm	:inches	:ity	:field:	:lab.	:source
:	:	:constitution:	1937	:	:	:	:

BS1	8	A ₁ A ₂ CRPrSuy	50	Early	5	5	Blue Squaw
PS10	4	A ₁ A ₂ crPrSuy	58	Medium	1	1	Pride of Saline
PS39	5	A ₁ A ₂ CrprSuy	64	Late	4	4	" " "
M1	2	A ₁ A ₂ CrprSuY	85	Late	2	3	Midland
M2	2	A ₁ A ₂ crPrSuY	85	Late	2	2	"

The rank of drought resistance in the field of M1 and M2 was rated the same since they originated from one ear. After one more year of selfing M2 was noticeably better in tolerance to artificial heat than M1. The early inbred BS1 probably is not as much drought enduring as it is drought escaping, being so early that pollination occurs before the most severe conditions are experienced. In addition to the above factorial composition, BS1 carries a gene for brown

midrib (bm) but it is not known which bm factor is involved. PS10 is the outstanding inbred of the group in heat and drought tolerance.

Thirteen translocation stocks of maize involving all ten chromosomes were obtained from Dr. E. G. Anderson, California Institute of Technology, four linkage testers from Dr. A. A. Bryan, Iowa State College, and ten linkage testers from Dr. C. R. Burnham, University of West Virginia. These twenty-seven genetic testers were used in the study as the susceptible parent stocks and as markers for the ten chromosomes in maize. The assumption was made that all these testers were drought susceptible, having been grown under much more favorable conditions than exist in Kansas. Most of these testers did prove to be susceptible to artificial heat but several gave an intermediate reaction.

Besides the strains and testers used, two sweet corn inbreds received from the Minnesota Experiment Station and two inbreds and one single cross sweet corn from the Indiana Experiment Station were used extensively in crosses and outcrosses made during the summer of 1937. These sweet corn strains were very susceptible to artificial heat and early in July 1937 they showed apparent drought susceptibility. However, a timely rain occurred and irrigation was supplied with recently installed equipment so that no further field observations of drought resistance could be made. Several other

inbred lines from various states selected on the basis of their behavior in the 1936 top-cross test at Manhattan were tested.

During the winter of 1936-37 the five selected Kansas inbred lines of maize were crossed with the twenty-seven genetic testers. Three plants each of the translocation stocks were grown and only one each of the ordinary linkage testers. Crosses were made indiscriminately, although approximately equal numbers were made with each line. Crosses could not be planned accurately in advance because the relative flowering dates of the testers used were unknown. Fifty-two crosses between the drought resistant (DR) inbreds and the non-drought resistant (NDR) testers were harvested. The seed matured soon enough so that field plantings were made the first week in May 1937.

These 52 crosses, the parent stocks, 18 inbred lines of varying drought resistance in addition to the five used as DR parents, 15 other linkage testers and three single crosses were planted in the field in 1937. Planting dates were staggered in an attempt to make crosses between early and late maturing strains. A total of 225 rows were planted, each row containing 15 plants spaced 14 inches apart.

Crosses were made between the DR, intermediate and NDR inbreds. Outcrosses to susceptible strains were made with the crosses involving translocations. Backcrosses and a few

self pollinations were made with the crosses involving the ordinary linkage testers.

Three of the translocations used were heterozygous which made it necessary to examine the pollen of the crosses involving these heterozygous stocks. Only the pollen from plants having semi-sterile pollen was used in making the outcrosses so the translocations would be carried on. Over one thousand ears were harvested in the fall of 1937.

During the winter of 1937-38 the progeny of material grown during 1937 was subjected in the seedling stage to artificial heat. A simple heat chamber constructed by Laude and Zink, Kansas State College, with thermostatically controlled electrical heating units was used in making all tests. Twenty-day old seedlings grown in 4-inch clay pots were placed in the heat chamber for 5 hours at 130° F. and a relative humidity of 30 percent.

The soil used throughout the experiment was a good uniform compost. Ten kernels were planted in each pot and later thinned to seven plants per pot. Four or more pots of each strain or cross was planted at one time. The plants were kept at about optimum growing conditions at all times. Before placing the plants in the heat chamber they were well watered so that during the trial the plants always had sufficient water and were subjected only to heat.

The temperature of the soil was recorded in every test and

averaged 102° F. for all tests. The pots in the center of the table generally had a soil temperature several degrees lower than those on the outside. There also was a slight variation in amount of injury that occurred between pots in the middle and those on the outside but this was equalized by the random distribution of the four pots representing each lot of material.

As an index of measure of differential injury the amount of exposed leaf and sheath tissue killed was estimated the third day after treatment. After considerable practice reasonably accurate readings could be made. About the tenth day after treatment the number of plants killed was recorded and notes taken as to the recovery of the plants. Each pot was considered a unit and no attempt was made to record the injury of the individual plants. Plant height and number of plants were recorded before the treatment.

EXPERIMENTAL RESULTS

Method Studies

Before attempting a detailed study of differences between varieties and within segregating populations, several experiments were conducted to determine the best stage of plant growth at which to test corn seedlings to assure the most uniform and consistent results.

In all method studies PS10, an inbred, and Hy x R₄, a single cross, were used. Whenever more than these two were used, strains were chosen that gave a wide range of resistance and had a uniform behavior to artificial heat treatments.

Number of Plants per Pot. Due to differential germination planting a uniform number of kernels per pot did not produce a uniform number of plants. To determine whether the difference in number of plants per pot influenced the results, a series having uniform stands, ranging from one to fifteen plants per pot was treated. On exposure to heat no significant difference in percentage of plant tissue killed was observed with varying numbers of plants except where eleven or more plants were growing in each pot. The pots with the higher numbers of plants showed less injury. This was explained as being due to the protection offered by the large number of plants growing together. When planted at thicker rates, the plants grew faster but were lighter green in color and more spindly than plants sown at a lower rate. Seven plants per pot was chosen as the most representative rate, as this number of plants developed normally within the period before the plants were subjected to the heat treatment.

Type of Container. It was thought that planting the corn in rows in greenhouse flats would be a good method of showing differential injury. With all the plants growing in one container, there probably would be less variation in some

cases than occurs when the plants are grown in four-inch clay pots. Six strains of corn were planted in a greenhouse flat 3 x 12 x 22 inches. A duplicate test was planted in clay pots and all were treated at the same time. The results are shown in Table 2.

Table 2. Comparison of injury to corn seedlings grown in 4-inch clay pots and greenhouse flats when subjected to artificial heat.

	Strains					
	PS10	KYSx38-11	HyxR4	GCB	su42	su51

	Grown in flat					
Percent Injury	5	40	55	60	85	80
Height, Inches	6	8	9	6	9	8

	Grown in pots					
Percent Injury	0	35	45	55	75	90
Height, Inches	8	9	10	9	9	7

The plants made a faster and more uniform growth in the pots than in the flat. The inbred strains were at a disadvantage in direct competition with single crosses in the flats. This competition was shown more strikingly when the plants were treated severely or when they were not hardened. It was also noted that the outside rows of plants were injured more severely than the middle rows. The rank in injury of the strains was nearly the same in both containers. Since inbred lines, F_1 plants, backcrosses, and outcrosses were to

be tested at the same time, the use of pots appeared to be the better method in order to eliminate the competition between vigorous and less vigorous strains growing together.

Age of Seedlings. When twenty day-old seedlings were subjected to the high temperatures (140° F.), at which Hunter et. al (1936) treated them, such severe injury occurred that nearly all plants were killed. Since 14 day-old seedlings were treated in the experiment referred to, it suggested that the age of seedling may have some effect upon the plant's ability to withstand artificial heat. Corn was planted at two-day intervals giving plants ranging from 10 to 28 days in age at the time of treatment. These plants of various ages were all treated at the same time. At each time corn was planted, 30 additional kernels were weighed and planted in large pots filled with sand. When these plants reached the age of 10 to 28 days, the seed was carefully removed from 20 plants in each pot. The dry weight of the seed remaining was determined and the percentage of weight of the original seed was calculated. The results are shown graphically in Figure 1. The seedlings showed the greatest resistance at ten days of age and remained fairly resistant up to the fourteenth day. At the 10-day stage the weight of the seed was only 31 percent of the original weight. A marked decline continued from the tenth to the twelfth day. From the twelfth to the eighteenth day the decline was slight and

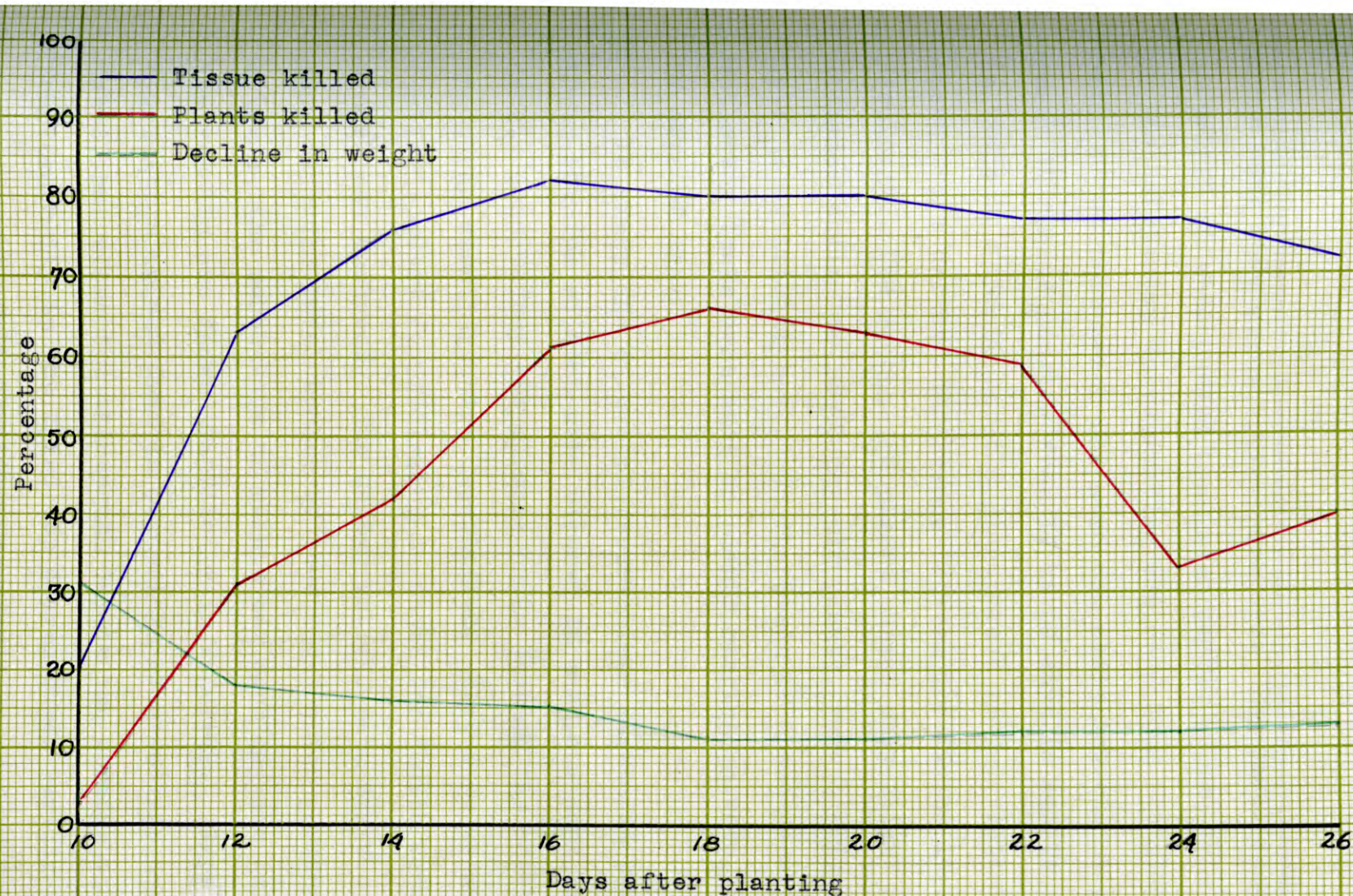


Figure 1. The effect of the age of seedlings on heat tolerance. Tissue killed, plants killed, and weight of seed in percent is shown.

after that time no reduction occurred. The small increase in weight of seed toward the later period is probably due to the difficulty in separating the seed from the plant and soil, as at this stage the seed was badly rotted. A photograph of plants ranging from 12 to 22 days in age is shown in Plate I. The 12 day-old plants were very resistant and there was a decided difference between the 14 and 16 day-old seedlings. The 22 day-old plants showed only slight resistance while the 16-20 day-old plants, were highly susceptible to artificial heat. On the basis of these results all following tests were made on plants ranging between 18 and 22 days of age.

To study the effect of reserve food stored in the seed, three strains of corn were planted in sand and kept in the dark. Just before the plumule broke through the coleoptile, the young seedlings were decapitated. They were treated similarly every day following in which one-fourth inch or more growth had occurred. The number cut off each day was recorded. With the total number of seedlings, which germinated as a basis, the percentage of plants cut each day was calculated. The results are shown graphically in Figure 2. There are some fluctuation up and down in percentage of seedlings decapitated, but after the thirteenth day in two strains and the fourteenth day in the third the decrease was rapidly downward. Eighteen days after planting the seedlings of Hy x R4 failed

Explanation of Plate I

Effect of heat on Hy x R4 seedlings 12 to 22 days old.
The number refers to the age of the seedling from planting
to treatment. Photographed 8 days after treatment.

Plate I



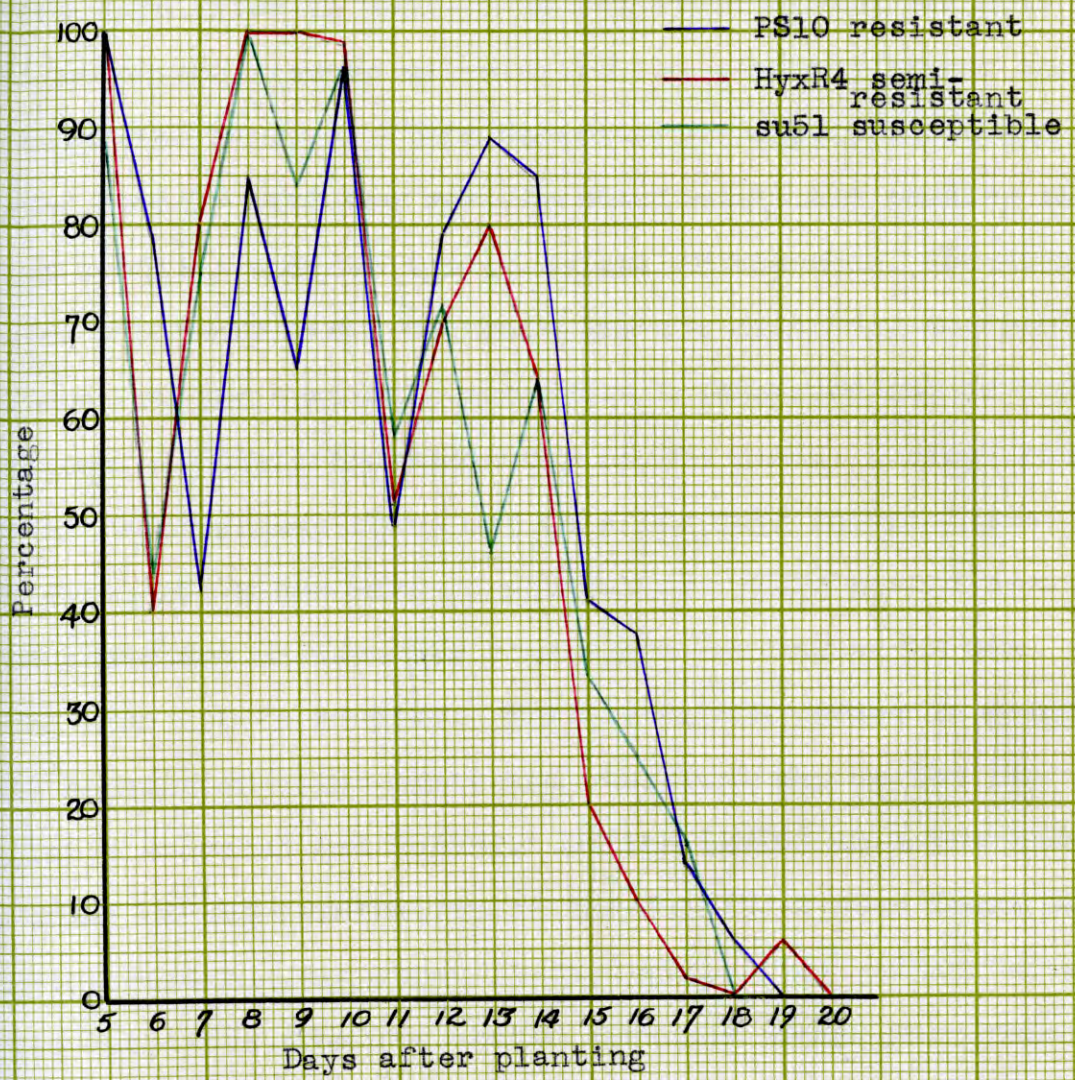


Figure 2. Decapitation of corn seedlings. Three strains representing resistant, semi-resistant, and susceptible, were used.

to send out new growth. This occurred one day later in PS10 and two days later in su51. The resistant strain did not make use of the reserve material in the seed any longer than the other two strains. This decapitation experiment correlates closely with the results obtained in the studies of age of seedling and decline in weight of the seed. Sometime between the tenth and fourteenth day the plant has apparently used most of the available nutrients in the seed and is then establishing itself independently of the seed. During this time of readjustment there may be a few days in which the corn plant has a low rate of metabolism. This period seems to be somewhere between the fourteenth and twentieth day in the corn plants studied. This is also a period in which rapid elongation takes place and the plant may be low in available starches and sugars. Miller (1910) in a physiological study of the germination of the sunflower seed found that when the seedling was about 13 days old, it had exhausted all of the nutrients from the seed. When the plants were kept in air free of carbon dioxide for seven days previous to the end of this period the plants had shown no further growth of their parts. This was to be expected, since the plants, being unable to synthesize their own food, had no material for growth after the reserve material had been consumed. Suneson and Peltier (1934), working with various stages of development of winter wheat plants, found that very young

seedlings, which were presumably still dependent upon the endosperm to a considerable degree, surpassed all other more advanced stage-of-development groups in cold tolerance.

Jones and Huston (1914) in analyzing maize at various stages of its growth found that 19 days after planting, the dry matter in the plant was practically the same as the dry matter in the seed used. The evidence from several tests has indicated that twenty day-old seedlings of any strain were no longer dependent upon material in the endosperm and any resistance the plant had to artificial heat would depend upon its inherited characteristics.

Twenty day-old plants subjected to heat for five hours at 130° F. and relative humidity ranging from 20-30 percent gave the most satisfactory results. If a longer treatment was given, variations occurred in the rate at which the pots dried out. When rather large and vigorous plants were tested, if the pots were well watered before treating, there was still moisture available for the plants at the end of a five hour treatment. Consequently it was not necessary to add water during a five-hour test.

Reaction to Light. It has been known for a long time that various exposures of light markedly affects the growth and physiological response of plants. When corn seedlings were treated early in the morning before they had received any daylight they were noticeably more susceptible to heat

than plants treated in the afternoon under similar conditions.

On observing this difference in reaction, two experiments were set up to study quantitatively the relation of exposure to light and heat tolerance. In the first case, the plants were exposed to various hours of daylight followed by a period of darkness before being placed in the heat chamber. A series of plants receiving the following combinations of light and dark periods was tested.

Group 1 No light

"	2	1 hour daylight followed by 6 hours of darkness							
"	3	2 hours	"	"	"	5	"	"	"
"	4	3	"	"	"	4	"	"	"
"	5	4	"	"	"	3	"	"	"
"	6	5	"	"	"	2	"	"	"
"	7	6	"	"	"	1 hour	"	"	"
"	8	7	"	"	"	0 hours	"	"	"

These groups were treated at the same time so the conditions of heat and humidity were identical. The evidence presented in Figure 3 shows that plants which received no light were the most susceptible to heat. Plants that received more light had a higher resistance to heat. PS10, however, gave a peculiar behavior, in that plants receiving one hour of light followed by six hours of darkness were injured less than those receiving two or three hours of light.

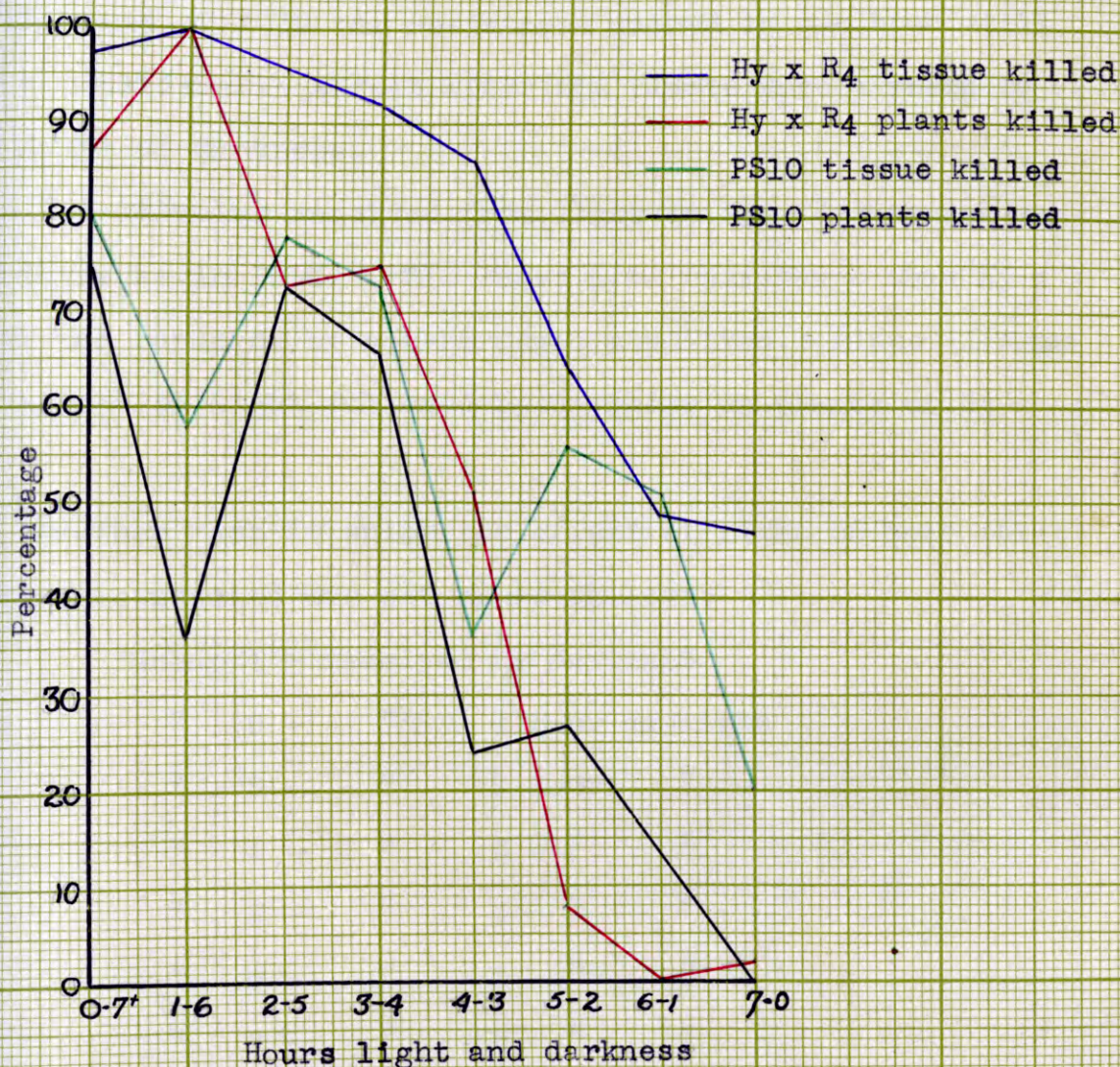


Figure 3. Effect of light on heat tolerance. The first number of each pair on the x-axis refers to the hours of light and the second number to the hours of darkness to which the plants were exposed previous to treatment. The percentage of injury and plants killed are shown. The two strains Hy x R₄ and PS10 give slightly different results.

This same phenomenon occurred in the two tests conducted. In the case of PS10 the resistance gained in one hour still had a considerable effect after the plants were exposed to six hours of darkness.

The stimulus received from light in Hy x R₄ was not so effective as in PS10. PS10 shows more resistance than Hy x R₄ in the hardened or non-hardened condition. Plate II shows the effect of light followed by darkness on plants of Hy x R₄.

Another test in which the effect of light on heat tolerance was studied was set up as follows:

Group 1 - received no daylight

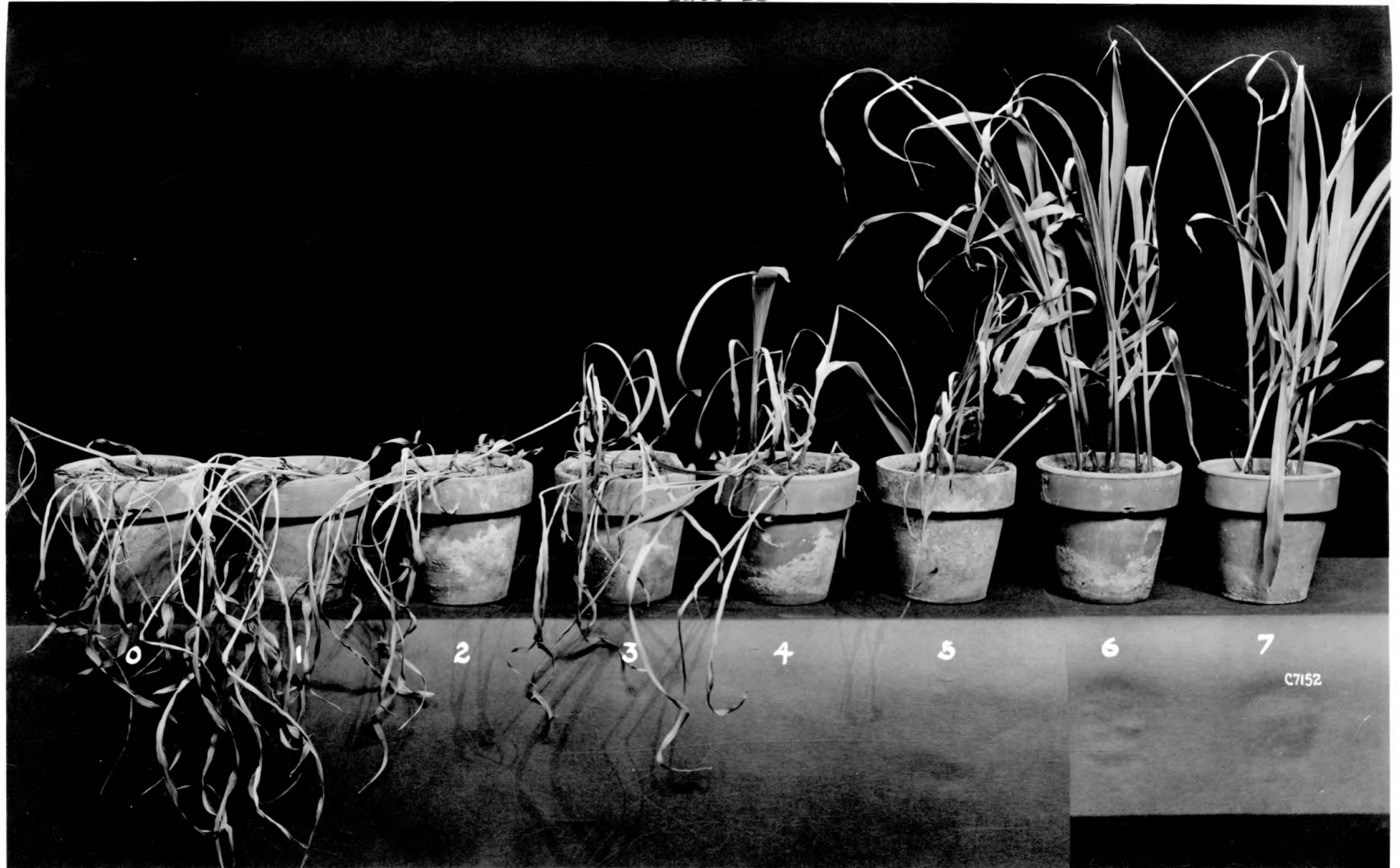
"	2 -	"	1 hour daylight		
"	3 -	"	2 hours	"	
"	4 -	"	3	"	"
"	5 -	"	4	"	"
"	6 -	"	5	"	"
"	7 -	"	6	"	"
"	8 -	"	7	"	"

The plants were tested at 2 p.m. so the last several hours of daylight received were the most intense. Very striking differences were obtained as shown in Plate III. Only four pots of the series of Hy x R₄ and three of PS10 are shown. The response to light by PS10 is more noticeable than in Hy x R₄.

Explanation of Plate II

Effect of light on heat tolerance of Hy x R₄. The first three pots are very susceptible to heat while the other pots show increasing resistance to heat as the period of light is increased and the amount of darkness decreased. The numbers 0, 1, 2, etc. refer to the number of hours of daylight the plants received. Each was followed by a period of darkness varying from 7 to 0 hours, reading from left to right.

Plate II



Plants exposed to periods of less than one hour of light was not attempted. In one case, however, the plants were exposed to light for about 10 minutes when they were transferred from one greenhouse to another before being put into the heat chamber. When these plants were subjected to heat they showed nearly the same resistance as those exposed much longer to light, indicating an almost immediate response to light. To obtain the best results it was found advisable to transfer the plants directly to the heat chamber from the dark box with no light in the chamber during the trial.

This very quick response to light, undoubtedly, has a direct relation to the photosynthetic process which is dependent upon light. Dexter (1933, 1933) has shown that light has a profound influence on hardening winter wheat plants against cold. Plants deprived of carbon dioxide would not harden under any circumstances, which shows that photosynthesis is involved in hardening plants. He concluded that the development and maintenance of a high available carbohydrate supply, with much retarded vegetative growth, is essential before cold-temperature reaction or hardening of plants will occur in an efficient manner. Tysdal (1933) observed that light was an important factor in the hardening process of alfalfa. Plants exposed to 16 hours in the hardening room and 8 hours in a warm greenhouse during daylight developed more hardiness than did

Explanation of Plate III

The response of corn seedlings to light and the effect upon heat tolerance. The four pots to the left are plants of Hy x R₄ receiving 0, 1, 3, and 7 hours of light respectively, and the three pots to the right are plants of PS10 receiving 0, 1, and 7 hours of light respectively.



those subjected to continuous low temperatures in the dark. Duggar (1936) in reviewing the effects of light intensity upon seed plants stated that work had been done which indicated that plants developed in the shade are less resistant to drought than those grown in full sunlight.

Weight of Seeds. Strains of corn vary in size of seed. To determine the effect of the size of seed on heat tolerance the lightest and heaviest kernels of six strains of corn were used. Eighty kernels of each weight group were weighed in grams, and ten kernels were planted in each pot. Later the plants were thinned to seven per pot. The strains used and the comparative weights of seed planted and heights of plant in inches at the time of treatment are shown in Table 3.

Table 3. Relation between weight in grams of kernels and height in inches of seedlings in several strains of corn.

		Strain				KYS x	suPB x
		PS10	G6626	suPB	HyxR4	38-11	G6626
Small kernels	Weight	14.11	15.85	10.80	14.16	13.49	8.89
	Height	5.2	5.7	5.5	8	7.5	5.2
Large kernels	Weight	19.39	21.72	16.88	20.72	16.49	20.32
	Height	5.5	6.5	5.0	9	8.2	6.2

In all cases but one the plants from the heavy seeds were the taller. In most cases no noticeable difference was evident in plants from small seeds and large seeds, except

in height. In Hy x R₄, however, the plants from the small seeds had smaller stems and were slightly lighter green in color.

The percentage injury was recorded and the data obtained were subjected to the analysis of variance using Fisher's (1936) F tables to determine the significance of the results. The analysis of variance in Table 4 shows that difference between strains and weight groups is highly significant. The significant discrepancy in this experiment shows that the effect of different weights of kernels is not always the same, but depends upon the strains which are being tested. These results indicate that it is important either to select seeds within a size group or at random in order to avoid difference in injury due to difference in weight of seed.

Table 4. Analysis of variance of percentage injury by heat in six strains of maize divided into seed weight groups.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Total	95	23,043.5	
Strains	5	16,420.1	3,284.02**
Weight groups	1	436.8	436.8 **
Interaction (subclass discrepancy)	5	939.7	187.94*
Pots in subclass (error)	84	5,246.9	62.46

** Highly significant		* Significant	

Kiesselbach (1924) found that the small seeds of winter and spring wheat and oats when planted in equal numbers yielded 19 percent less than large seeds. He attributed this difference to the immediate advantage of a greater reserve food supply in the larger seed which results in a more vigorous initial growth. It is not known whether the plants from small kernels in corn would be more susceptible to heat in later stages of growth or not but this does not seem to be very probable.

Observation on Inbred Lines

Approximately 50 inbreds were tested for tolerance to artificial heat. The field reaction of most of the lines was known from their behavior to the drought of 1936. Only a few lines were classed as highly drought resistance. Most lines were classed as intermediate and it was difficult to rank them very accurately as to drought resistance. A small percent was classed as non-drought resistant. The small number of susceptible lines can be explained by the fact that most of them have been previously weeded out under Kansas conditions through natural selection.

The heat chamber did not operate at the same level for each test and comparisons were only made between lines tested at the same time. Although the amount of injury varied with each test the ranking between lines remained

very similar. PS10 was used as a check in all tests, which made it possible to make comparison between lines in different tests. As in field behavior, only a few lines were considered highly resistant to artificial heat, the greater portion giving an intermediate resistance to heat.

The inbred lines apparently have definite temperatures at which they become subject to damage by heat. When some lines were subjected to temperatures of 120° F. they were resistant but by raising the temperature slightly they were very susceptible indicating that lines vary in their thermal death point. In some lines the leaves began to curl 15 minutes after the test was started while others would show no apparent injury until near the end of the test and then become injured severely in a short time. A few lines showed dried leaf tissue within one-half hour after the test was started but after this first brief period, they remained unchanged during the remainder of the test.

This sensitivity to small temperature changes was observed in the field in 1937. Two lines susceptible to burning of the top leaves were injured by the hot weather in 1937. The leaves of most lines curled during the midday, but when the temperature went up to 100° F. the top leaves in one line were killed. When the temperature went up to 112° F. the second line was injured. In the first line the top three leaves were killed but the plant was still in a

vigorous growing stage and recovered when a two-inch rain occurred several days later. This injury was evident throughout the entire season. These two lines which were top fired in 1937 were also very susceptible to artificial heat.

The reaction of about ten percent of the lines subjected to artificial heat was not as expected from their known field behavior to drought. Only one of these lines, YS74, varied greatly, being classed as one of the best inbreds in the nursery in 1936. This line was one of the most susceptible lines to artificial heat. This inbred was in the best single crosses in 1935 with respect to drought resistance. As a seedling and young plant this line has yellow striations on the leaves which may be a type of chlorophyll deficiency. The rate of growth is very slow until it becomes a uniform green color and begins to grow vigorously. This unusual seedling behavior may explain its susceptibility to heat in the seedling stage. The other non-conforming lines were rated as better than the average in the field but were below the average when subjected to artificial heat. One of these lines was early and its apparent drought resistance in the field probably was due to its earliness which made it possible to escape the drought.

Mode of Inheritance

Crosses were made between inbred lines of corn that differed in their behavior to drought. The crosses were between resistant lines, resistance x susceptible, and susceptible x susceptible. The results of artificial heat injury to five inbred lines and crosses between them is shown in Table 5. The results are an average of three trials and in each of which the temperature was low enough to cause only moderate injury. The resistant x resistant cross was very resistant. At higher temperatures it was superior to the parents, but in the results in Table 5 it does not appear to be any better than either parent.

Table 5. Comparative injury of inbred lines differing in heat tolerance and crosses between them.

Strain	Drought classification	Percent injury	Percent killed	Notes on recovery
PS10	DR	6	0	Good
YS48	DR	4	0	Good
su39	NDR	39	21	Poor
su51	NDR	48	33	Poor
G6626	NDR	42	13	Live plants recover quickly
PS10 x YS48	DR x DR	5	0	Excellent
PS10 x G6626	DR x NDR	6	0	Fair
PS10 x su39	DR x NDR	15	0	Fair
YS48 x G6626	DR x NDR	25	0	Slow
YS48 x su39	DR x NDR	10	0	Fair
G6626 x su39	NDR x NDR	43	2	Very yellow, slow
su39 x su51	NDR x NDR	50	35	Poor
DR - Drought resistant		NDR - Non-drought resistant		

The F_1 , resistant x susceptible crosses gave varying results but the tendency was for resistance to be semi-dominant. In one of the crosses between susceptible lines there was no difference from the inbred parents in percent of tissue killed but the F_1 plants had a higher survival value. In the cross su39 x su51, the F_1 was more susceptible

to heat than either parent, which shows that heterosis, in itself, does not necessarily make the F_1 seedlings heat tolerant. Not all crosses reacted like those shown in Table 5. For example when G6626 was crossed with lines classified as intermediate to drought resistance the crosses were as susceptible to heat as G6626. PS10 apparently has a number of dominant genes for heat tolerance as shown by its consistent tendency to increase the heat tolerance of the crosses in which it is involved.

The inheritance of heat tolerance also was studied in single and double crosses. Only three single crosses were used, but these had a wide range in heat tolerance. The three possible double crosses were made and all six hybrids tested at the same time. The evidence presented in Table 6 shows that differences between double crosses relative to heat tolerance do occur. The range in percent of injury was small but the survival of crosses differed significantly. The double crosses were intermediate in reaction to heat tolerance.

Table 6. Comparative injury of single crosses differing in heat tolerance and crosses between them.

Strain	Drought classification	Percent injury	Percent killed	Notes on recovery
KYS x 38-11	DR	85	14	Fair
Hy x R4	M	94	23	Good
su39 x su51	NDR	100	88	Poor
(KYS x 38-11) x (Hy x R4)	DR x M	94	24	Good
(KYS x 38-11) x (su39 x su51)	DR x NDR	91	33	Fair
(Hy x R4) x (su39 x su51)	M x NDR	96	45	Fair
DR - Drought resistant M - Intermediate NDR - Non-drought resistant				

A test was made to determine the heat tolerance of seven open-pollinated varieties, four from Kansas and three from other states. The California variety was developed for irrigated land and had the reputed quality of being able to shed viable pollen during hot weather. The varieties have been listed in order of their heat tolerance in Table 7. The percentage injury and plants killed and the recovery notes are shown. The two long season Kansas varieties were outstanding in heat tolerance, which is probably due to the influence of natural selection. The California variety, al-

though burned severely, made an excellent recovery. The two early Kansas varieties, Hays Golden and Freed White, were not as heat tolerant as would be expected since these varieties ordinarily yield better under adverse conditions than later varieties. The varieties usually yield more in dry years probably because they are early and therefore escape the drought, while Pride of Saline is later in maturity, it would necessarily have to endure a drought to produce a crop. The other two varieties were rather susceptible to heat.

Table 7. Comparative injury by heat to seven varieties of corn.

Variety	Origin	Percent injury	Percent killed	Recovery
Pride of Saline	Kansas	75	11	Excellent
Yellow Selection #1	Kansas	79	7	Good
California Yellow	California	98	20	Good
Freed White	Kansas	97	44	Fair
Hays Golden	Kansas	94	59	Fair
Boone County White	Missouri	95	63	Poor
Krug	Iowa	100	63	Poor

Linkage Experiments

Ten linkage groups corresponding to the ten chromosomes in maize are now recognized. Known genes located on all ten

groups have been studied and can be used in tests to determine the linkage relationships of unplaced genes.

In testing for the possible association of drought tolerance with particular chromosomes drought resistant plants were crossed with stocks carrying known recessive genes and then the hybrids backcrossed to the recessive. Drought resistant plants were also crossed to translocation stocks representing all ten chromosomes and the semi-sterile hybrids outcrossed to drought susceptible plants. Only chromosome VIII and X were not fully represented by the translocation stocks.

The translocation behaves as a dominant in crosses and is expressed by the semi-sterile condition of the pollen and ovules. Plants must be grown to the pollen shedding stage before semi-sterility can be determined so no linkage data were obtained by use of translocations. All the outcrosses with translocations were tested as seedlings but if any segregation occurred within a pot it was not observable. Some of the translocations carried known genes that could be separated on the basis of seed color or texture and these were used as ordinary gene testers.

Testers Used. The genetic stocks and translocations used in these experiments are listed in Table 8, according to their respective chromosome groups. All factors used could be identified in the endosperm or in the seedling.

Such factors, however, were not available in chromosome VIII and the attempt to obtain the initial cross involving chromosome III was unsuccessful.

Table 8. Genes and translocations used as testers.

Chromosome and linkage group		Gene and symbol
I	<u>P-br</u>	<u>P</u> , pericarp and cob color; <u>f</u> ₁ , fine stripe; T1-4a; T1-5b.
II	<u>b-lg</u> ₁	<u>lg</u> ₁ , liguleless; <u>gl</u> ₂ , glossv: T2-4b; T2-9a
III	<u>a</u> ₁ - <u>ts</u> ₄	<u>na</u> , nana; <u>ts</u> ₄ , tassel seed; T3-5b.
IV	<u>su</u> ₁ - <u>Tu</u>	<u>su</u> , sugary; <u>gl</u> ₃ , glossy; T2-4b; T4-6a.
V	<u>pr-v</u> ₂	<u>a</u> ₂ , anthocyanin (plant and aleurone color); <u>pr</u> , aleurone color; T3-5b; T5-7.
VI	<u>Y-P</u> ₁	<u>y</u> , endosperm color; <u>P</u> ₁ , plant color; T4-6a; T6-9b.
VII	<u>ra-gl</u> ₁	<u>gl</u> ₁ , glossy; T5-7.
VIII	<u>ms</u> ₈ - <u>j</u> ₁	<u>ms</u> ₈ , male sterile; T8-10b; T8-10c.
IX	<u>c-sh-wx</u>	<u>c</u> , aleurone color; <u>sh</u> , shrunken; T2-9a; T6-9a.
X	<u>r-g</u> ₁	<u>r</u> , aleurone color; T8-10b; T8-10c.

The data obtained by treating the progenies of the backcrosses and outcrosses are shown in Table 9. The dominant member of each pair of alleles was associated with the resistant parent.

Table 9. Summary of results of heat tolerance in relation to genes in eight of the linkage groups in maize. Dominance was associated with the resistant parents.

Genes tested		Percent injury			Percent killed	
X	x	X	x	Significance of	X	x
				difference		
Chromosome I	I					
F ₁	f ₁	88	92		16	50
Chromosome II	II					
Gl ₂	gl ₂	70	46	**	18	9
Chromosome IV	IV					
Su ₁	su ₁	87	95	**	42	72
Chromosome V	V					
A ₂	a ₂	67	72		17	11
Pr	pr	79	88	**	21	33
Chromosome VI	VI					
Y	y	78	83		7	11
Chromosome VII	VII					
Gl ₁	gl ₁	92	73	**	34	24
Chromosome IX	IX					
Sh	sh	62	65		4	11
C	c	87	93	*	53	71
Chromosome X	X					
R	r	90	92		55	61

*Significant

**Highly significant

The significance of the differences in percent injury was determined by analysis of variance from Fisher's (1936) table of F values. The problems were set up to measure whether any significant differences occurred between the genes tested, between the tests, and interactions between

genes and tests. There would be no interactions if all pairs were alike in difference. A significant discrepancy would indicate one of two things: (1) the pairs differ in percentage of injury at various temperature levels and (2) as different parents were used it may show that some lines react differently than others. The percentage of plants killed was not analyzed because it was not as good a measure of difference as percentage of leaf tissue burned.

Tests with Chromosome I. Fine stripe F_1 , f_1 , was the only pair of genes studied in this group. No significant difference was noted in percentage of injury but the fine stripe plants had a lower survival value. This may be explained by the fact that f_1 gives virescent-like seedlings which are deficient in chlorophyll and for this reason probably do not have the ability to recover from heat injury.

Tests with Chromosome II. Two genes, lg_1 and gl_2 , were used to determine whether drought resistance is associated with this chromosome. These two genes were in a coupling series. The double recessive segregates in the backcross were separated from the heterozygous dominant segregates. Although the glossy factor was associated with the susceptible parent the glossy plants were more tolerant to heat than the normal condition as indicated by the highly significant difference. The percentage survival is also in favor of the glossy seedlings which is probably due to less burning of

leaf tissue. The resistant inbred parent, however, was considerably more resistant than the linkage tester lg₂gl₁. The surface of the leaves on the glossy plants may reflect more heat rays than the non-glossy condition keeping the leaves cooler and causing less damage. Shull (1929) found that hairy, smooth, or shiny leaf surfaces were not necessarily correlated with high reflection. Because the surface of the leaves on glossy plants is of a waxy nature the rate of transpiration may be lower. This waxy condition would tend to keep the leaves moist and prevent drying and burning by keeping the transpiration rate low enough so no deficiency of water would occur in the leaves.

Tests with Chromosome III. No testers involving characters that could be distinguished in kernels or seedlings were available for this chromosome. The pair of genes used was Na, na, which causes a dwarf condition of the plant and is difficult to classify in the seedling stage. The back-cross progenies were tested but no evident segregation was observed.

Tests with Chromosome IV. The pair of genes influencing the sugary and starchy texture of the endosperm is located in this linkage group. The sugary gene (su₁) is the factor which is responsible for the endosperm character in sweet corn. Extensive evidence from five segregating progenies in 32 tests shows that the sugary factor is associated with heat

susceptibility. Although only a small difference in percentage of leaf burning is shown in Table 9 the results are highly significant. In backcrosses the seedlings from the sugary kernels had a much lower survival value than the seedlings from the starchy kernels.

Very striking results were obtained when the seedlings from starchy and sugary segregates on the same ear were treated at the same time. Such evidence is shown in Plate IV. The two parents are represented by the first and third pots, M_2 and su su. The F_1 in this case is as resistant as the resistant parent. The segregating progeny are represented by the four pots to the right; the Su su plants came from starchy kernels and the su su plants came from sugary kernels.

Tests were available in which gl₃ and su₁ were in a coupling series. These two genes are about 40 units apart on the chromosome, so frequent crossovers would be expected. Starchy glossy and non-glossy plants, and sugary glossy and non-glossy plants were tested at the same time. There was no significant difference between the starchy glossy plants (crossovers) and the starchy non-glossy plants (non-crossovers) in relation to heat tolerance. The sugary non-glossy plants (crossovers), however, were slightly more resistant to heat than the double recessive condition, su gl₃. This is not in agreement with the results obtained with gl₁ and gl₂. The sugary seedlings in both cases were more susceptible

Explanation of Plate IV

The effect of heat on maize plants segregating for starchy and sugary kernels. The parents are represented by the first and third pots, and the F_1 is between them. The starchy and sugary segregates resulting from a backcross to the su su parent are represented by the Su su and su su plants respectively.

Plate IV



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than the starchy segregates. These results indicate that the sugary condition has more influence on heat tolerance than the glossy factor in the strains of maize studied.

Sweet corn is generally considered to be more susceptible to drought conditions than dent corn. The sweet corn industry is located in the regions near the northern range of the corn belt and in the eastern states where extremes in weather conditions do not frequently occur. As sweet corn seems to be susceptible to drought it suggests that the sugary gene may also be responsible for heat susceptibility. This was indicated rather clearly by growing to the pollen shedding stage some plants involving translocations which included chromosome IV. The translocation, T₁-4a, was heterozygous for sugary (Su su). This was crossed to a resistant inbred (Su Su). The sugary condition was not expressed in the F₁ but half of the plants would carry su, and by outcrossing the F₁ plants to a sugary stock the sugary factor would be expressed in one-half of the ears pollinated. When the sugary and starchy segregates from one of these ears were tested the seedlings from the sugary kernels were the most heat susceptible. The outcross, not involving the su gene, was also planted and subjected to heat. The 16 most resistant plants, from 56 tested, were transplanted and grown until they shed pollen. Only 12 plants lived. If heat susceptibility was located on chromosome IV one would

expect all the plants to be normal, however, seven of the 12 plants were semi-sterile and five normal. Although very small numbers were used it indicates that heat susceptibility is transmitted independently of the semi-sterile condition and that heat tolerance is probably not associated with chromosomes I or IV.

Another translocation, T₄-6a, which was sugary, was crossed with a resistant Su Su inbred and the F₁ outcrossed to a sugary stock. Four plants each from the sugary and starchy kernels were grown to the pollen shedding stage. The four plants from the starchy kernels were normal and the four plants from the sugary kernels were semi-sterile. This was to be expected for the translocation was linked with su. No crossovers were observed as only a very small number of plants were analyzed.

The results with sugary translocations are very similar to those obtained with ordinary sugary testers. The effect of heat on the parents and progenies when a translocation was used is illustrated in Plate V. PS10 and T₄-6a were the parents. The F₁ is not shown but the third pot, su su, represents the stock to which the F₁ was outcrossed. The segregating progenies are illustrated by the four remaining pots. The inbred, PS10, consistently increased the resistance of the crosses in which it occurred. This is shown by the two pots on the right being more resistant than either

Explanation of Plate V

Relative heat tolerance of a starchy inbred and sugary translocation and the resulting progeny when outcrossed to a sugary stock. PS10 is the resistant parent, T₄-6a is the susceptible translocation parent. The third pot from the left, su su is the stock to which the F₁ plants (not shown) were outcrossed. The four pots on the right represent the segregating progeny, the Su su designating plants from the starchy segregates and su su the sugary segregates.

Plate V



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the translocation parent (T₄-6a) or the outcross parent (third from left).

Significant discrepance occurred in this experiment which indicates that lines differed in the reaction to heat. All five resistant inbreds were crossed with sugary testers and when two inbreds were crossed on the same tester and backcrossed or outcrossed to the same stock evident differences occurred in the reaction of the progenies to heat. This difference is illustrated clearly in Plate VI. The plants shown are the segregating plants from sugary (A) kernels and starchy (B) kernels. The original cross in figure 1 was made between PS10 and T₄-6a (su su) and the F₁ was outcrossed to a susceptible sugary tester. Figure 2 represents the same as figure 1 except that BS1 was substituted for PS10. The time of planting and treatment were identical. PS10 transmitted more heat resistance to its progeny than BS1. Even the plants from the sugary kernels show considerable resistance to heat when PS10 was involved, while the plants from sugary kernels were killed when BS1 was used as a parent. The inbred, PS10, shows more resistance to heat than BS1 when subjected to the same conditions. This may be a reason why the plants in figure 1 are more resistant than those in figure 2. These pictures indicate that progress can be made in breeding for drought resistant in lines and hybrids of corn.

Explanation of Plate VI

Effect of different parents on the heat resistance of their progeny. The plants indicated by A were from sugary segregating kernels and the plants B were from starchy segregating kernels. In figure 1 PS10 was used as the resistant parent and in figure 2 BS1 was used as the resistant parent. The susceptible parent and outcross stock were the same in both cases. Plants were planted and treated at the same time. Pictures were taken the same day.



fig. 1



fig. 2

It is probable that the su gene in itself could affect tolerance similar to other genes in maize which are known to have dual effects on unrelated structures or functions of the plant. In the tests conducted no sweet corn lines were found to be resistant to heat. If the su gene is responsible for the lower resistance to heat it will be a limiting factor in the production of a sweet corn possessing as high a degree of resistance as is found in lines of starchy corn.

Both dent and sweet corn have many diseases in common but in nearly all instances their effect is more severe on sweet corn. In studying the inheritance of smut resistance it is of interest to note that Immer (1927) did not find smut to be linked with Su su. Senn (1932), however, found that in artificially inoculated plants the sugary segregates were significantly more susceptible to seedling blight than the starchy segregates. In naturally infected ears the difference was not significant but in favor of the Su kernels. He concluded that the su gene is also a factor responsible for the differential resistance to seedling blight disease exhibited between the two kernel types.

No tests were made with the Su₂su₂ or Su₃su₃ pairs of genes which also cause a sugary condition of the endosperm.

Tests with Chromosome V. The behavior of heat tolerance was determined in relation to two genes in this group, a₂ and pr. The evidence presented in Table 9 indicate that

A₂, a₂ is probably inherited independently of heat tolerance. The a₂ tester used was one of the testers that gave an intermediate reaction to artificial heat. Enough plants were tested so if a linkage did exist the results would have been significant as determined by analysis of variance.

The behavior of heat tolerance with the Pr, pr pair of genes gave highly significant results. In the cases studied Pr was associated with the resistant parents and the purple segregates on the ear resulted in the most resistant seedlings. The survival value is also in favor of the Pr plants.

Stadler⁽¹⁾ suggested that it is possible that the Pr factor may affect the pH value of the cell sap in the plants and that this change may be of such a nature as to make the plants more resistant to heat. The Pr factor intensifies the anthocyanin pigmentation in the corn plants. Purple plants are a darker color if Pr is present instead of pr and red kernels become purple if Pr is present. This color change can be compared with the change of litmus paper from red to blue when the solution is changed from an acid to a base.

Tests with Chromosome VI. The behavior of heat tolerance was studied with reference to only one pair of genes Y₂, y₂, in this chromosome and no significant differences.

(1) Personal conversation with Dr. L. J. Stadler, Bureau of Plant Industry, U. S. Department of Agriculture, University of Missouri, Columbia, Missouri.

were observed. It has been thought by some that white corn is superior to yellow corn in the drier regions just because it is white corn. These tests do not uphold this hypothesis for the plants from kernels with white endosperm were no better than the plants from kernels with yellow endosperms. In fact, although the results are not significant, they are in favor of the yellow corn in percentage of leaf tissue burned and in survival of plants.

Tests with Chromosome VII. As shown in Table 9 gl₁ appears to have an effect on the relative heat tolerance of corn seedlings. The glossy seedlings were more resistant to heat than the non-glossy seedlings. This parallels the case reported in chromosome II, in which the glossy seedlings, due to gl₂ were also the more resistant although the glossy character was associated with the susceptible parent.

As the glossy testers were more susceptible to heat than the resistant inbreds it does not seem possible that in the segregating progenies resulting from backcrosses to the recessive parents that the glossy seedlings should be the most resistant. The reason the glossy seedlings behave this way is not known. Not enough evidence was available to determine whether the glossy factor or genes closely linked with glossy were responsible for this behavior to heat in the seedling stage.

Tests with Chromosome VIII. For linkage group 8 only

two genes have been reported and neither of these affect kernel or seedling characters. Crosses were made involving the Ms_g, ms_g pair of genes but the seedlings tested did not show any observable segregation.

Tests with Chromosome IX. Heat tolerance was studied in relation to two pair of genes, Sh, sh and C, c on this chromosome. The shrunken character causes the endosperm to collapse during the drying stage at maturity and the seedlings are somewhat retarded in early stages of growth. Although the seedlings from shrunken kernels may have been at a disadvantage no significant difference in percentage of heat injury occurred between this pair of genes.

In tests with the C, c pair of genes, which affects aleurone color, a significant difference occurred. The C factor was associated with the resistant parent. The results were only significant (odds 19 to 1) and it may have been only a fortuitous choice of material that caused the differences. The difference in survival, however, is considerably in favor of the C factor that is, in plants from seed having the colored aleurone. One of the temperature tests in which pronounced differences occurred in this pair of genes is illustrated in Plate VII. The cc and Cc plants represent the colorless and colored segregates respectively resulting from a backcross to the recessive parent.

Tests with Chromosome X. The factor pair, R, r, which

Explanation of Plate VII

Differential response of seedlings from colorless (cc) and colored (Cc) kernels to artificial heat due to the C, c pair of genes.



is associated with aleurone color, was the only pair of genes studied in this chromosome to determine the inheritance of heat tolerance. The evidence presented in Table 9 indicates that in the crosses studied heat tolerance is inherited independently of the R, r pair of genes.

DISCUSSION

Emerson (1937) in discussing heredity and environment stressed the fact that he knew of no characteristics of plants, animals or man, that one can be perfectly sure are wholly environmental or wholly hereditary. In fact, usually one is unable to separate these two influences. He further states that characters of all sorts are influenced by genetic factors. Emerson defines "What is inherited", as "the possibility - indeed the necessity - of reacting in a particular internal and external environment."

In relation to heat tolerance some inbred lines of corn are resistant to heat up to a given temperature and then become susceptible when the environment changes i.e. when higher temperatures prevail. The expression of this character is not shown until the proper environment exists. If such an inbred is grown in conditions where high temperatures never prevail this susceptibility would be transmitted from year to year although the character would not be expressed.

Even after growing for several years in favorable conditions, and then being planted where drought conditions prevail, the susceptibility to drought would be expressed.

It is impossible to separate the physiological responses of a plant into two distinct categories and label them as being conditioned exclusively by environment or by heredity. The final expression is the result of a complex interaction of the inherited potentialities of the individual with the environment in which it finds itself. Many genes are so uniformly present within a species that they are not given special attention by many as part of the hereditary make-up of the individuals, unless they are observed to segregate from their very infrequent alleles, when they are at once recognized. Possibly literally thousands of these stable and unknown genes make up the genetic background of a species and form the basis of the more constant physiological responses which many botanists commonly think of as purely environmental. The sum total of the genes present in an individual or species, then determines the final expression of the response of the plant to its habitat.

In addition to these universal or very widely distributed genes, there are others of which one or more alleles are known. Some of these factor pairs produce their typical character responses throughout the range of environmental conditions that we recognize. For example, ears produced on

maize plants carrying \underline{P}^{rr} in the presence of \underline{A}_1 always have red cobs and red pericarp under all known conditions of growth. Other factors require a special environment in order to express themselves and may long pass unnoticed unless the necessary conditions for their expression are present. Sun-red pericarp in corn is an example of this type of behavior. Kernels completely shaded by the husks have a colorless pericarp, but if the husks are pulled back allowing sunlight to fall on the kernels, the pericarp develops a bright red color. These two types of behavior are not contradictory, but merely indicate that in some cases we do not know the entire range of environmental conditions which influence the reaction of certain genes.

As a corollary to this statement, our knowledge of rare genes may often be so limited that we may conclude that a given environment always produces a certain result. This has been the case with certain plant diseases such as flax wilt, or Pythium disease of milo until an exceptional plant containing a gene or genes for resistance is found which reveals a resistant type within a susceptible variety.

In the cooler and more humid sections of the corn belt temperatures of 100° F. are frequently regarded as lethal to the pollen of adapted varieties. Maize is a highly variable species, however, and under natural selection in the southern Great Plains varieties have been developed in which

the pollen will stand temperatures appreciably over 100° F. without injury. Similarly, varieties, and more especially inbred lines, from humid and arid regions differ very markedly in the ability of plants to survive under conditions of high temperatures and deficient moisture. These differences certainly have a hereditary basis, although they could not be recognized or differentiated under a more favorable environment. Studies of problems such as drought resistance can best be solved by a combined attack by plant geneticists and plant physiologists.

Anyone acquainted with agriculture realizes that both environment and heredity play important parts in the production of crops. The factors of the environment can be separated but the effects of these factors upon the plant cannot be clearly analyzed unless the hereditary make-up of the plant is known. There is a close relation between the two and to think clearly on the subject one must consider both major factors.

Considering heredity and environment as the two major factors controlling the responses of plants the outline of Newton and Martin (1930) on page 14 has been revised. The rearranged outline is included in this chapter for reference.

- Drought resistance
- (Environmental factors
 - ((1. Soil factors
 - ((a) Available moisture
 - ((b) Available nutrients
 - ((c) Concentration of soil solution
 - ((d) Toxic substances in solution
 - ((e) Temperature
 - ((f) Aeration
 - ((2. Atmospheric factors
 - ((a) Temperature
 - ((b) Humidity
 - ((c) Air movements
 - ((d) Light quality, intensity, duration and distribution
 - ((e) Atmospheric pressure
 - ((1. Physiological adaptations
 - ((a) Osmotic pressure of cell sap
 - ((b) Imbibition pressure of hydrophilic colloids in cells
 - ((c) Mucilaginous secretions
 - ((d) Stomatal regulation
 - ((e) Rolling and folding of leaves
 - ((f) Percentage of bound water
 - (Heritable factors
 - ((2. Morphological adaptations
 - ((a) Spread and depth of root penetration
 - ((b) Extensiveness of branching of roots
 - ((c) Number and persistence of root hairs
 - ((d) Ratio of roots to leaves
 - ((e) Type of conducting systems
 - ((f) Low leaf surface exposed
 - ((g) Thickness of leaves
 - ((h) Epidermal coverings
 - ((i) Deciduous leaves
 - ((j) Amount of intercellular space
 - ((k) Sunken stomata
 - ((l) Size and number of stomata
 - ((m) Surface hairs
 - ((n) Size of cells

The adaptations listed under morphology are easily shown to be of an inherited nature as the inheritance of structural changes in many plants and animals have been well demonstrated. The physiological adaptations listed as being of a heritable nature may cause considerable discussion. But if one keeps in mind Emerson's definition of what is inherited it can be readily assumed that genes influencing the physiological efficiency of a plant or animal actually exist. Although the environmental factors are independent of the heritable factors many of the heritable factors depend on environmental conditions for their full expression. For example, osmotic pressure of cell sap may be influenced by available moisture, temperature, light, and perhaps other factors, while the spread and depth of root penetration may be affected by the type of soil, the soil temperature, and the amount and distribution of soil moisture. The genotypical responses of the plant due to variations of the environment are then often expressed in the modification of the morphological and physiological features.

The isolation of quantitative genes by linkage tests is often difficult because of the number of genes involved and the relative variations in their importance. The maize experiment reported upon gives some evidence that genes controlling heat tolerance occur on at least three of the eight chromosomes tested and that the glossy character protects

the seedlings from injury to artificial heat.

In addition to using gene markers of known position for determining linkage relations, a new method of locating quantitative genes was attempted. The use of translocation stocks involving parts of two reciprocally interchanged chromosomes was thought to be a better method of locating quantitative genes. Several advantages are evident in the use of chromosomal interchanged stocks of maize. Translocations in the homozygous or heterozygous condition apparently do not affect the normal somatic development of the plant, and in this way normal stocks of maize containing the translocation could be established, avoiding any possible altering effects of known genic testers. The translocation behaves as a dominant. The whole chromosome is involved and no particular emphasis is placed upon one locus on the chromosome.

Only little use could be made of crosses involving translocations in this experiment because relatively few plants could be grown to the pollen shedding stage in the greenhouse. It will be of interest, however, to note whether the linkage associations found by the use of genic testers will be borne out in the field by analyzing the outcross progenies involving translocations now on hand.

SUMMARY AND CONCLUSIONS

The reaction of corn seedlings to artificial heat was studied, approximately 27,000 seedlings being subjected to high temperature conditions. This reaction was found to correlate well with known field behavior in drought years.

Ten to 14-day old seedlings when treated for 5 hours at 130° F., with a relative humidity of 25-30 percent, were more heat tolerant than those at any later stages of development.

Testing 18 to 20-day old seedlings for 5 hours in a chamber controlled at 130° F., with a relative humidity of 25-30 percent and preceded by 12 hours of darkness gave the most satisfactory results.

Decapitation experiments and decline in weight of seeds indicate that after the 14th day the young plant is probably independent of the endosperm for food material.

Corn seedlings respond quickly to light which increases their resistance to heat within one hour's time.

Inheritance of reaction to heat tolerance was studied in varieties and in selfed lines of corn and crosses between them.

Heat tolerance in most cases was dominant but there were crosses in which susceptibility tended to be dominant.

Hybrid vigor, in itself, apparently does not make the

cross resistant to heat in the seedling stage.

Linkage relations were studied between the factors determining heat tolerance and one or more factors in eight of the linkage groups. Close association of heat tolerance with Su₁su₁ and Pr pr and a loose association with C c was observed. Glossy seedlings apparently protect the seedlings from injury by artificial heat.

The su gene is considered to be directly responsible for the differential resistance to heat as shown by the differential behavior of seedlings from sugary and starchy kernels. The equal distribution of the semi-sterile and normal conditions in translocation outcrosses involving chromosome IV strengthens this hypothesis.

If the sugary gene in itself lowers the resistance of the plant to heat it is not likely that a sweet corn will be developed that possesses as high a degree of heat tolerance as dent corn.

The resistance of heat tolerance is conditioned by multiple factors and it is probable that the su gene is one of the major factors that is responsible for a low heat tolerance. The Pr factor may also have a significant effect.

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