

GENETIC STUDIES OF REACTIONS TO DROUGHT
AND HIGH TEMPERATURES IN MAIZE

by

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INTRODUCTION

Corn production in the Great Plains area frequently is limited by periods of extremely high temperatures accompanied by low humidity and deficient soil moisture in midsummer. Frequently, in Kansas, hot dry winds may occur at the time of flowering and cause the silks or pollen to be desiccated to the point they do not function. High temperatures and low humidity at pollinating time, or during the period of rapid growth just prior to this, may cause the withering of the upper or lower leaves. Maximov (1929) and Moliboga (1927) stated that it is during the period of maximum growth in length that the plant requires the most water for its growth. Robb (1934) correlated yield of corn with rainfall over a period of 33 years, and concluded that the time of tasseling was the critical period in corn, where yield was being considered.

The most common firing which occurs is top-firing, which is the withering and subsequent dying of all or portions of the upper leaves of the corn plant. This type of firing may occur any time before flowering but is more common during the period of rapid elongation of the plants just prior to flowering time. Top-firing is the distinctive type of injury which usually occurs in the youngest leaf which has attained its maximum leaf area. This is concluded, Tatum (1949), from the fact that when a leaf is fired on a hot, dry day the upper and younger and the lower and older leaves often do not express any injury. On another hot, dry day leaves which have just reached their maximum area may be fired. Thus, leaves which had already fired and those just fired can be separated by a number of uninjured leaves. This can be attributed to the fact that a number of cool days intervened between the two hot days.

Several types of top-firing can be distinguished. It seems that an inbred line will exhibit a type of top-firing which is characteristic of that line. In the most common type of top-firing some leaves may show firing starting at the tip with a progressive extension downward on the margins, followed by the firing of the portion between the margins. If the conditions continue to be severe the firing in this type may extend until the entire leaf has fired.

Another type frequently found is the firing of the tip and portion of the blade along the midrib before the margins are damaged. Still another may occur also in a belt across the blade. This belt is that portion of the blade which receives the greatest amount of direct sunshine.

Base-firing is the firing of the lower leaves of the corn plant. In this type of firing the lower leaves start to fire at the tip with a progressive extension on the margins, followed by the firing of the portion between the margins. This base-firing was not necessarily accompanied by top-firing. It appeared in the inbred CI₇ and in the material of which this inbred was a parent. Thus it was believed that this kind of firing described as base-firing might be entirely a different character and be due to different genes. There was also the possibility that this character was associated with nitrogen deficiency, although the symptoms were not typical of deficiency of this element.

The relative tolerance to drought and high temperature of various inbred lines and hybrids is an important consideration in corn improvement programs in regions such as Kansas.

Available information indicates that resistance and susceptibility to drought and high temperatures is inherited. Jenkins (1931), and Jenkins and

Richey (1931) observed that inbred lines of corn differed in the transmission to their progenies of reactions to drought and high temperatures. Some seemed to transfer resistance in a dominant manner while others transmitted susceptibility. Heyne and Brunson (1940), under heat chamber conditions, studied the reactions of seedlings of corn and concluded that tolerance to heat and drought was inherited and was in most cases intermediate to dominant.

Genetic studies of the reactions of commonly used inbreds to drought and high temperatures under field conditions should be of much help to the corn breeder. By knowing the mode of the inheritance of this character and the possible location of the genes controlling it, he would be in a position to conduct a breeding program in a more intelligent way. In other words he could find the proper manner of improving inbreds that are susceptible to drought and high temperatures but are otherwise good material. He should thus reach in a shorter time, his aim of releasing better hybrids.

It is recognized that the reactions of inbred lines of corn to drought and high temperatures are inherited in a complicated way due to the nature of the character itself. Thus, for a solution, the problem must be met from different angles, using all available means.

Since there are reasons to expect that the genes controlling tolerance to drought and high temperatures in seedlings under heat chamber conditions might not be the same as those controlling tolerance under field conditions and in more developed stages of growth, field tests should be considered an essential phase of testing for resistance.

The tests being reported in this thesis were conducted under field conditions to determine something of the mode of inheritance of resistance to top-firing. In one phase of the study, chromosome translocations were used as markers to locate genes affecting firing in the susceptible inbreds La⁴⁴

and CI₇. The other phase of the study consisted of F₃ progenies and selfed progenies from backcrosses involving resistant and susceptible inbreds.

REVIEW OF LITERATURE

In studies of water requirement in plants, Kiesselbach (1916) found no difference in the average water requirement per pound of dry matter between varieties of corn acclimated to humid and dry climatic conditions. Also he found no difference in water requirements between drought resistant varieties of corn and other varieties. He concluded that drought resistance of certain crops was not associated with a low water requirement per pound of dry matter.

Briggs and McLane (1912), Miller (1916 and 1923) and Kiesselbach (1926 and 1929) did not find significant differences between drought resistant and drought susceptible plants in water requirement ratios.

Miller and Coffman (1918), Peel (1923) and Haber (1938) concluded that the transpiring power of a plant was not an indication of its drought resistance.

Maximov (1926) described drought resistance as being the capacity of a plant to endure a state of permanent wilting with a minimum of injury. Usually the efforts to classify plants as to their relative drought resistance had been based on the amount of injury sustained when subjected to extreme drought conditions, both soil and atmospheric, produced either artificially or occurring naturally.

Maximov (1929) and Moliboga (1927) showed that cereal plants may be affected differently at different stages of their growth by the same degree of wilting due to moisture deficiency. They concluded also that the stage of rapid elongation of stems and formation of flowers was the most critical,

severe conditions during this stage causing stunting, while the earlier and the following stages of development were less affected by these conditions.

Maximov (1929) suggested that the ability of a plant to withstand permanent wilting could be explained on the basis of conditions within the cells, such as increased osmotic pressure, and modifications in the protoplasm that increase its water holding capacity. External changes (xeromorphism) that could be helpful in conserving water are merely manifestations of these more fundamental inner physiological changes.

Briggs and McLane (1912), Tumanov (1926 and 1929), Shantz (1927) and Kondo (1931) in their studies made with the object of determining whether there was any relationship between the kind of plants and the level to which soil moisture could be utilized, did not find any significant differences. The range in moisture retention exhibited by different soils was larger. Thus the main cause for drought resistance must be found in the plant itself.

Newton and Martin (1930) believed that the inhibitional properties of the cell sap were very important in water retention under drought conditions. They found that the osmotic pressure of the cell sap of crop plants varied with the physiological scarcity of the water but that it was not a reliable index of drought resistance. However, bound water content of the cell sap was much more dependable. They were able to arrange cultivated wheats and several grasses in order of their drought resistance on this basis.

Horikov (1931) was able to classify wheat varieties as to relative drought resistance on the basis of bound water determinations.

Martin (1930) in comparing corn and sorghum found that sorghum had a higher osmotic concentration of the sap in the stalk, crown and roots, but a lower osmotic concentration in the leaf. Sorghum was found also to have a

lower transpiration ratio under conditions of high evaporation and wilted less rapidly.

Holbert and Frye (1933) grew heat resistant and heat susceptible inbred lines of yellow dent corn under conditions of artificial drought. They found that the bound water content of the heat resistant lines increased as the heat and drought continued with temperatures ranging from 95 to 103° F. At the same time the total water content decreased. Heat susceptible strains on the other hand, showed very little if any, increase in amount of bound water under similar conditions, and in some cases the bound water content decreased significantly.

Loomis (1935) found, by removing leaves at the tasseling stage, that the upper leaves were significantly more efficient in grain production than were the lower ones. Since firing occurs more frequently at or near the tasseling stage, corn which top-fires may produce significantly less grain.

Haber (1938), under conditions with less than normal rainfall and with temperatures higher than normal, could classify corn strains into four groups; those which are subject to (a) tassel firing, (b) firing of the top two or three leaves, (c) firing of the lowest three or four leaves, and (d) excessive rolling and wilting of the leaves.

Lonnquist (1942) found that silks of material susceptible to leaf firing grew more rapidly than silks of resistant material for the first two or three days after emergence. However silks of the resistant material did not taper off as rapidly as did that of the susceptible material so that for the subsequent periods they exceeded the susceptible material in rate of growth. Resistance to leaf firing and increased soil moisture appeared to have no effect in prolonging the growth period of silks. The receptiveness of the silk

to pollen remained longer in the resistant lines than in the susceptible lines. Soil moisture had no effect on the length of silk receptivity of inbred lines while for the crosses it did.

More seed set was obtained on single crosses between resistant lines than on single crosses between susceptible lines either grown under dry land or irrigation. A significant positive correlation was obtained between persistence of silk growth and amount of seed set. Individual inbred lines differed significantly in the ability of their pollen to effect fertilization when placed on silks of the single cross WF₉ x 38-11.

Interference with the pollination process has been recognized as one important way in which drought may affect corn plants. Tatum and Kehr (1951) in their studies concerned with the seed setting ability of various inbred lines when they were self-pollinated at different times of the day and under different conditions of temperature and relative humidity found that the success of hand pollinations on dent corn inbreds varied from day to day and for different inbreds. There were no striking indications of a differential response of different inbreds to environmental conditions. There was evidence for a time of day by date interaction. A close relationship was found between success of pollination and the temperature and relative humidity which prevailed at the time the pollinations were made. It was suggested that temperature and relative humidity influences pollination indirectly through their effects on evaporation and transpiration, and in turn, the internal water supply or turgidity of the plants. They found also an indication that lack of sufficient moisture in silks to germinate pollen may be more important in causing poor seed set than is lack of viable pollen.

Brooks (1949) in experiments on the movement of eosin dye through leaves

of resistant and susceptible inbreds observed that during conditions of high evaporation, there was a much greater demand for water than during conditions of lower evaporation. Under conditions of high evaporation it was observed that the most susceptible leaf of a susceptible plant showed a much slower rise of dye than did a comparable leaf from a resistant plant when the leaves were cut below the collar. When these leaves were cut above the collar, the dye rose more rapidly in the leaf of the susceptible plant. Frequently the leaf of a susceptible plant showed dye only in those veins near the midrib or those branched from the midrib. Under conditions of low evaporation he found apparently no difference in the rise of dye through the inner collar region of immature leaves of resistant and susceptible plants. The outer veins of the leaves of susceptible plants were much slower in showing the dye than those of resistant plants under conditions of low evaporation. Under conditions of high evaporation these observations were not made. He concluded that the nature of the vascular tissue in the collar region of susceptible leaves did not permit the rapid conduction of water.

In his histological studies made of the base of the leaf sheath, the collar, and the leaf blade of resistant and susceptible inbreds, significant differences were found in the stage of maturity of the bundles in the base of the leaf sheath. The susceptible inbreds were more mature in this respect. He found that there was no difference in the conducting capacity of the leaf sheath, collar, or blade in resistant and susceptible inbreds by calculating the cross-sectional area of the conducting tissue per units of width, but he stated that his studies of this characteristic should be more extensive. However it was shown that the tracheids in the collar bundles were more mature in resistant inbreds. It was suggested that the differentiation of these

tracheids provided an explanation as to why a leaf is susceptible for a short time and later becomes resistant.

Immer and Christensen (1925) observed differential reaction to drought and high temperatures in parent strains of Minnesota No. 13. Each strain had a different percentage of fired plants. In crosses between strains of different behavior they found a complete absence of dominance. Their F_2 data indicated the action of a single factor pair but they suggested that more than one factor might be involved. They found no linkage between smut and firing.

Jenkins (1931) and Jenkins and Richey (1931) observed that inbred lines of corn as well as their crosses differed in their reaction to the extreme heat and dry weather which prevailed at Ames, Iowa in 1930. One resistant inbred, L317B₂, seemed to carry dominant factors for resistance. Its crosses with the rest of the inbreds and especially with the very susceptible inbred Mc412A₃ were resistant. Another inbred, the susceptible L293A₁, seemed to carry a somewhat dominant factor for susceptibility. Due to the absence from the tests of the cross L293A₁ x L317B₂, in other words the cross between the lines for which was suggested the presence of dominant factors for susceptibility in one and for resistance on the other, results on the reaction of these two dominant factors were not available.

Haber (1936) in his studies included only inbreds exhibiting extreme resistance or susceptibility. The susceptible lines were those exhibiting much leaf firing, either basal or top leaves, and leaves that were extremely rolled with a resultant stunting and high mortality. He found no difference in the rate of transpiration between the resistant and susceptible inbreds. He found also no difference in number of stomata, either when the upper or

the lower surface was examined. Rolling of leaves occurred in both the resistant inbreds and susceptible inbreds. No difference between the resistant and susceptible inbreds was found for the volume of roots and number of nodes below the surface of the soil. The average number of vascular bundles per unit area was not found to differ for the susceptible and resistant sweet corn inbreds. For a limited number of inbred lines of field corn there was a significant difference between the two classes, the susceptible having more bundles per unit area of cross-section.

Shirley (1934) studied drought resistance of white spruce, Picea canadensis, in an illuminated, temperature-controlled chamber. The entering air stream was passed over calcium chloride to dehydrate it. The length of time of survival was used as a measure of the drought resistance of each plant.

Amoldt (1935), by exposing the plants in a wind tunnel to 110° F. and a six mile per hour wind, demonstrated for wheat varieties differential resistance paralleling that observed in the field under conditions of severe drought.

Hunter, Laude and Brunson (1936) included in their tests under heat chamber conditions eight inbred lines of corn differing under field conditions in their reaction to drought and high temperatures over several years. In some susceptible lines in the field, the first indication of injury, designated as "top-firing", was the blasting of the tassel and usually the wilting of the top leaves. Other susceptible lines, in which the injury was referred to as "base-firing", fired progressively from the bottom of the plant upward. In inbred lines known as "resistant", obvious evidence of heat injury was not shown until after the susceptible lines were badly fired. A simple heat chamber with thermostatically controlled electrical heating units was used in

the artificial tests. By testing 14-day-old seedlings for 6.5 hours in the chamber with temperature controlled at 140° F. and with a relative humidity of about 30 per cent they could distinguish among strains with respect to drought tolerance. They found essentially the same order of relative resistance with the seedlings as was noted for the plants in the field. Those lines susceptible to top-firing under field conditions showed marked injury in the testing chamber in three to five hours; those susceptible to base-firing showed injury in four to six hours and the resistant lines showed little or no injury after 6.5 hours. When the exposed plants were returned to growing conditions, the survival of plants was zero per cent in the lines susceptible to base-firing, zero to 25 per cent in those susceptible to top-firing, and 50 to 100 per cent in the resistant lines.

Haber (1938) found that exposure of seedlings to high temperature and low humidity when 15-20 days old was a satisfactory laboratory test for classifying the lines into resistant and susceptible classes. Exposure at 55° C. (131° F.) for five hours caused the death of most of the susceptible seedlings. Some resistant plants of sweet corn survived at a temperature of 55° C. for six hours. Field corn inbred lines, classified as resistant, endured a higher temperature for a longer period of time than resistant sweet corn lines.

Heyne and Laude (1940) found that twenty-day old corn plants subjected to heat in the heat chamber for five hours at 130° F. and relative humidity ranging from 20 to 30 per cent gave the most satisfactory results for classifying high temperature tolerance of different strains of corn. No relation was found between kernel size and heat resistance or susceptibility at the seedling stage of plants. Plants which were subjected to heat early in the

morning before they had received any daylight were more susceptible than those which received light before being exposed to heat. One hour of light seemed to be long enough for the corn plants to acquire considerable resistance. The inbred lines were found to become subject to damage at a definite temperature, some being resistant up to 120° F. but becoming susceptible at slightly higher temperatures. Some were injured shortly after the treatment started and others near the end of the treatment. They concluded that for most inbreds there was a fairly good agreement between field observations from previous years and those of the heat chamber.

Brooks (1949) found also that seedling reaction to high temperatures as indicated by heat chamber results, could be used as a fairly reliable index to drought resistance. He found that resistance to drought was dominant or partially dominant in some crosses and complementary in others, and that one inbred seemed to transmit susceptibility as a dominant factor or group of factors in one of its crosses.

Heyne and Brunson (1940) conducted genetic studies, under heat chamber conditions, for heat and drought tolerance using the Kansas inbreds BS₁, K201A, K201B, K39 and K10. For these studies twenty-seven genetic testers carrying genes marking the ten chromosomes, ten translocation stocks and four sweet corn inbred lines were used as the susceptible inbreds. Four or more pots of each strain with seven twenty-day-old seedlings were exposed for five hours to a temperature of 127° to 130° F. and a relative humidity of 30 per cent. That inbred K10 apparently had a dominant gene or genes for heat tolerance was shown by its consistent tendency to increase the heat tolerance of the crosses in which it was involved. The reaction of double crosses was intermediate between the single crosses from which they were made. Hybrid vigor

in itself, apparently did not make a cross resistant to heat in the seedling stage. Eight of the ten linkage groups were studied. Close associations of heat tolerance with the Su su and Pr pr and a possible association with Cc loci were observed. The effects of gl_1 and gl_2 in the seedling stage apparently protected the corn seedlings from injury by artificial heat, while the factor gl_3 probably did not possess this protective quality. The su gene was considered to be directly responsible for susceptibility to heat injury as shown by the behavior of seedlings from sugary and starchy kernels.

Saboe and Hayes (1941) by the use of chromosome translocation stocks studied a firing susceptible Rustler inbred and found that at least three factor pairs or linked groups of factors seemed to be responsible for the firing character. One of these might be located on the short arm of chromosome 4, another one either in the long arm of chromosome 2 or in the long arm of chromosome 4 and another one probably in the long arm of chromosome 7.

The following papers are reviewed as background information on the use of chromosome translocations to study linkage relations.

Brink (1927) found that the abortion of the pollen grains in semi-sterile corn plants was accompanied also by abortion of the ovules of these same plants, the abortion occurring in 50 per cent of the pollen or ovules. He excluded the explanation that this fact could be attributed to the action of two pairs of factors and he concluded the interchange of portions between non-homologous chromosomes might be the possible explanation. He suggested that those spores receiving the "disjoined" section in duplicate or lacking it altogether are abortive.

Brink and Burnham (1929) explained the semisterility which they had found in certain strains of maize by suggesting chromosomal translocations.

Reciprocal crosses between normal and semisterile maize plants gave equal numbers of normal and semisterile offspring and self pollination of semisterile individuals likewise produced the same two classes in the same proportion.

Muller (1928) found, in the offspring of x-rayed *Drosophila*, that although crossing over sometimes occurred between the translocated chromosomes and their normal homologues it was much disturbed.

Anderson (1935), referring to the use of the method used by Brink and Burnham (1929), stated that when plants heterozygous for an interchange were selfed or crossed to other semisterile plants from the same source, one half of the progeny obtained were semisterile and the other half normal. The normals were two types; ordinary normals and homozygous interchanges. These were not distinguishable in appearance but may be distinguished by outcrossing to known standard stocks.

Burnham (1934), in plants heterozygous for an interchange of a terminal piece of the short arm of chromosome 9 with a small terminal piece of the long arm of chromosome 5, found about two per cent of recombination between the point of interchange and waxy and about eight per cent with shrunken. Tests in plants homozygous for the interchange showed that the order in the short arm is centromere-point of interchange--wx-sh. In plants heterozygous for the interchange, yellow green-2 and shrunken gave 11 per cent crossing over while shrunken and waxy gave six per cent. The values in normal plants were 23 and 20 per cent respectively. Therefore the greatest reduction is in the region nearest to the point of breakage. Cytologically this reduction could be explained by assuming that crossing over occurs only when homologous pairs are together, since this position is one of all those possible.

Burnham and Cartledge (1939) used translocation stocks susceptible to smut as genetic markers to determine linkage relationships for smut resistance. A significant difference in the percentage of smutted plants in the normal and semisterile classes was taken as indication of linkage between either or both interchange points and a gene or genes for smut reaction. Further they stated that since a translocation is an interchange of pieces between two non-homologous chromosomes, the linkage obtained is in each case evidence for the location of smut reaction factors in either or both chromosomes; that is, near either or both loci at which the original interchange occurred. To determine which of these three possibilities is true a test must be made for each of the two loci with an additional translocation involving a break at nearly the same locus in each of the chromosomes, with the other break in this additional translocation being in a third or different chromosome. This latter break locus may need to be checked in the same manner with still another translocation. Negative evidence for association from only the F_1 of translocation x resistant does not eliminate the possibility that the translocation line was carrying the same smut resistance factor or factors in its translocated chromosomes as was the resistant inbred line in its normal homologues. In several cases, a locus that appears to be relatively close on the map to a locus not showing linkage, may be too far away to show linkage with smut reaction. The reason for this is that in chromosome 9 for example, the gene *waxy* is in the short arm, probably near the centromere. The genetic length from the terminal knob to *waxy* corresponding to most of the short arm is 53.5 units. Although this cytogenetic length may not be applicable directly to the other chromosomes, it gives an indication of what physical length may correspond to about 50 genetic units. The genetic length

which a given interchange will test for the presence of smut reaction factors depends on (a) the degree of reduction in crossing-over in the presence of the translocation in the heterozygous condition and (b) the relative amounts of smut shown in the different homozygous and heterozygous genotypes for the different smut factors. In the susceptible inbred which, with its long period of inbreeding, should have been relatively homozygous for smut reaction factors, an average of more than 50 per cent of the plants escaped infection. In a segregating progeny these cannot be distinguished from genotypically resistant plants. The evidence from the linkage tests indicates that several factors must be concerned in smut resistance. If these were all of equal value in their reaction to infection, a case of close linkage should give a greater difference between the percentage of smutted plants in the semisterile and in the normal classes, than should a case of loose linkage. This would be modified if several pairs of smut factors were involved and if they were unequal in smut reaction value; that is, if comparable genotypes for different pairs of alleles differ in their reaction to smut infection. In this case, the "relative differences" in percentages of smut for translocations involving different chromosomes would depend on the particular smut reaction alleles involved as well as in the strength of linkage.

The interchanges were crossed with each of two pure lines which differed in smut reaction, one resistant, the other susceptible. Without previous information on inheritance, semisterile F_1 plants in each of these crosses would then be backcrossed to each of the two smut reaction lines for a study of segregation of smut reaction in relation to semisterility. A more satisfactory method would have been to make the genetic background of all the interchanges being used more comparable by backcrossing each F_1 to the original

inbred smut reaction line for five or six generations. Crosses between susceptible chromosomal interchange lines and a resistant, the Lancaster Surecrop inbred line, were backcrossed to a susceptible, the Leaming, inbred to study segregation for smut reaction in relation to the interchange points.

Anderson (1938) presented data on linkage relations with waxy for 14 translocations involving the long arm of chromosome 9.

Anderson (1939) presented data on linkage relations with msg and j_1 for nine translocations involving chromosome 8, the cytological positions of seven of which have been determined.

The usefulness of chromosome translocations in studying the linkage relations of a particular gene and the distribution of genes controlling a polygenic character is indicated by the above studies.

Genes for qualitative character also may be used as markers in studying quantitative characters but they have the disadvantage that only a small portion of a chromosome is marked because no reduction of crossing over is involved.

Lindstrom (1931) in his studies to determine genetic linkage of the genes for kernel row number, a quantitative character, with other known genes on several of the maize chromosomes, used genes for qualitative characters as markers. Crosses were made in such a manner that in one cross the higher row number with the recessive qualitative character came from the side of one parent and the low row number and the dominant qualitative gene from the second parent and in a second cross the higher row number with the dominant qualitative from one parent and low number with the recessive from the second parent. If genetic linkage existed between row number genes and the qualitative gene, in these crosses, the F_3 and backcross data of first cross should

be different in the distribution from those of the second, otherwise the correlation of these two characters should be attributed to some morphological or physiological association of the character rather than to genetic linkage. To check the difference in the distribution in the two classes of crosses the test of independence was applied. In that way he found linkage between cob color and row number but the results were doubtful for linkage between aleurone color and row number, and sugary and row number as well as for endosperm color and row number.

Heyne and Brunson (1940), in testing for the possible association of major genes for heat and drought tolerance with particular chromosomes, crossed the Kansas drought resistant inbred lines with stocks carrying genetic factors that could be identified by endosperm or seedling characters. The data on the percentages of leaf tissue burned in progenies obtained by back crossing the F_1 plants of susceptible testers x resistant inbreds to the susceptible testers were analyzed. The existence of a difference in the percentages of tissue killed in plants belonging to the two classes of plants, characterized by the dominant and by the recessive respectively qualitative marker genes, was taken as an evidence of linkage. The significance of the difference was determined by comparing the F values computed from the analysis of variance of the data with tabulated F values, Snedecor (1950). The experiment was set up so as to measure any significant differences between the gene pairs tested, between the tests, and in interaction between genes and tests. Close associations of heat tolerance with the $Su\ su$ and $Pr\ pr$ and a possible association with Cc loci were observed.

Another approach to the study of quantitative characters is that of Castle and Wright in which a statistical method is used to estimate the

number of genes involved.

Castle (1921a) took as a basis the original suggestions made by Bateson that blending inheritance was a variety of Mendelism in which dominance was lacking but in which several or many independent factors were involved, and put out his theory for determination of number of genes controlling a quantitative character. He stated that in blending inheritance also, it was the F_2 generation which afforded a clue to how many genetic factors were involved, not by formation of clearly distinguishable types, because there was only one type, but by the amount of the variability of that single type in F_2 as compared with F_1 . His theory was based on the assumption that the parents were completely homozygous and so devoid of genetic variability, the same being true for the F_1 . Any variability shown by these was due to environmental effects. Under like environmental conditions the F_2 would be expected to show a like amount of non-genetic variability. Basically his theory consisted of the isolation of the genetic variability of F_2 by subtracting the observed F_1 variability from the actual variability of F_2 . By comparing the difference of the standard deviations of the F_2 and F_1 , divided by the difference between the parental means and multiplied by 100, with a tabular value, which he gave, the determination of number of genes could be made. His theory was based on the assumption that each factor was equal to every other factor in its influence on the character affected although this was not strictly true. If one factor really has an influence greatly superior to that of other factors, in a case of blending inheritance, this will be seen in the production of asymmetrical or multimodal variation polygons of F_1 and F_2 . If, when adequate numbers are produced, the variation curves of F_1 and F_2 are both smooth it is certain that no genetic factor of predominant influence is

involved in the case, but that several or many factors substantially equal in influence are concerned.

Castle (1921b), following suggestions made by Sewall Wright, agreed that instead of the difference of standard deviations, the difference of the squared standard deviations or in other words of the variances, should be used and suggested the use of the formula

$$n = \frac{D^2}{8 (S_2^2 - S_1^2)}$$

given by Sewall Wright in his "Systems of Mating IV". Wright (1921) in crosses of inbred strains of guinea pigs, used the method to make an estimation of gene number.

These lines were inbred for several generations and they were different in toe formation. For the estimation of number of genes it was assumed that there was no dominance or epistasis. If the effect of a gene is represented by "a", the difference (D) between the extreme plus and minus types is 2na for a number of n genes. The variance of F_2 due to each pair of genes is $a^2/2$ and hence for n genes is $na^2/2$. The observed variance in F_2 is compounded of this genetic variance and the non-genetic variance which is measured by the variance of F_1 or of the parental strains (P). Thus $s^2_{F_2} - s^2_P$ gives the genetic variance F_2 . Eliminating "a" and solving for n gives:

$$n = \frac{D^2}{8 (s^2_{F_2} - s^2_P)}$$

In the backcross progeny, he stated that the variance due to each pair of genes is $(1/4) a^2$ so that the genetic variance should be just half as great as in F_2 . A minimum estimate of the number of genes (ignoring chance variation) can be attained from either of these formula if D is taken as the

difference between the parental strains.

Charles (1943) in determining the number of genes controlling a measurable character by Wright's formula stated that (a) it is assumed that the larger size genes are concentrated in one strain; the small genes in the other (b) the genes involved have equal effects, without dominance or epistasis and (c) no two of the loci are in the same chromosome. If these assumptions do not match the actual conditions in material to which the method is applied, the estimated number of genes distinguishing the two strains will be smaller than the actual number.

The top-firing data obtained in the present study of F_3 progenies and selfed progenies from backcrosses were not suitable for application of the Castle-Wright formula. Graphic analysis such as has been used by Wellhausen (1937), Jenkins, et. al., (1952) and others seems more appropriate.

Wellhausen (1937) in studying the inheritance of resistance to bacterial wilt in corn used histograms showing the frequency distributions of percentages of plants in F_3 progenies and selfed progenies of backcrosses made between inbreds of various degrees of resistance. He could divide roughly the backcross progenies into four equal groups on the basis of resistance and susceptibility. These groups were resistant, moderately resistant, susceptible, and very susceptible. It was assumed that these different degrees of resistance were due to the independent segregation of two supplementary factors, Sw_1 and Sw_2 completely dominant over their recessive alleles respectively. Therefore he concluded that the resistant genotypes contain both Sw_1 and Sw_2 , the moderately resistant contain only Sw_1 , susceptible genotypes possess Sw_2 alone, and the very susceptible the double recessive. In certain of the backcrosses, in tests made under different environmental conditions, it was

evident that each of the four groups was not homogeneous. This was taken as an indication that a third minor supplementary factor Sw_3 was involved and that this factor when alone, produced a degree of resistance only slightly higher than that of the triple recessive and, when in combination with either or both Sw_1 or Sw_2 , modifies their expression by slightly increasing resistance. The results of F_3 and selfed backcross progenies substantiated the above factorial hypothesis as the breaks in their frequency distribution divided the progenies into a number of groups of resistance being in accordance with the number of factors and their potentiality.

Jenkins, et. al., (1952) in their inheritance studies of resistance to Helminthosporium turcicum in corn tested twelve populations of F_3 progenies from six crosses of susceptible and resistant inbred lines. In the experiments each F_3 progeny was represented by only one plot consisting of a single row and containing a maximum of 25 plants. The scoring was made on a progeny basis using 11 classes. But as most of the F_3 progenies still were segregating for blight resistance it was necessary to observe the individual plants rather closely in arriving at a rating for the progeny as a whole. The leaf-blight ratings on each of the twelve groups of F_3 progenies were summarized in the form of frequency distributions on a percentage basis. The number of major genes acting for the expression of the character was determined by the number of modes in the distribution. The relative position of the mode or the modes in relation to each parent or to the midpoint rating was taken as indication of the manner, dominant or recessive, of action of the particular gene or genes coming from the side of that parent. They concluded that resistance to Helminthosporium turcicum leaf blight is controlled by many genes but that some genes have major effects. Some genes show their major effects

only at a low incidence of disease, others show their major effects at high incidence of disease and still others show their effects over a wider range of disease incidence.

PART I. TESTS WITH TRANSLOCATION MATERIAL

Material and Methods

The susceptible to heat and drought inbreds La⁴⁴ and CI7 were used as the recurrent parents in backcrosses with the resistant to these conditions stocks of the translocations.

The translocations used and cytological data made available by Dr. E. G. Anderson are given in Table 1, A. E. Lengley (1950).

Table 1. Chromosomal translocations used, together with cytological data on the position of the break.

Translocation	Position of the break in the chromosome.		Distance of the break in microns from the centromere of the first chromosome.
wxT1-9c	1S.61 ¹	9L.32	20-25
suT1-4a	1L.49	4S.66	15-20
suT4-9a	4L.18	9L.50	5-10
wxT2-9b	2S.12	9L.12	0-5
wxT4-9b	4L.84	9L.34	
wxT9-10b	9S.11	10S.28	0-5
suT2-4(A-29)	2L.78	4L.14	25-30
suT2-4c	2L.77	4S.09	25-30
suT4-6a	4L.33	6L.44	10-15
suT4-8			
wxT1-9a	1S.17	9L.17	5-10
wxT3-9a	3L.19	9L.40	5-10
wxT4-9(F-22)	4S.35	9L.42	5-10
wxT3-9C	3L.15	9S.20	30-35
su4-6x-57-31 ²	4S.60	6L.51	10-15
wx6-9x-25-78	6L.17	9L.22	25-30
su4-10B-45	4S.70	10L.11	15-20
wxT6-9a	6S.79	9L.40	5-10
suT2-4a	2L.29	4L.15	20-25
suT4-5d	4S.21	5L.19	0-5
su1-4B2	1L.27	4L.30	
wx3-9b	3L.48	9L.53	20-25
wx5-9x-7-39	5L.70	9L.40	20-25

¹ 1S.61 means the break in the chromosome is in the short arm S, 0.61 of the distance from the centromere to the end of the short arm.

² To the translocation su4-6x-57-31 has been assigned the permanent symbol 4-6e and to the su1-4B2 that of 1-4d.

The translocations used in this study, and described in Table 1 are distributed in the arms of the chromosomes as shown in Table 2. In this same table is shown also the frequency with which each arm of the chromosomes, involved in the translocations, entered in the backcrosses to the inbreds La⁴⁴ and CI₇.

Table 2. Chromosomes, arms of these chromosomes represented in the translocations used and the frequency with which each arm entered in the backcrosses to the inbreds.

Arms	Chromosomes	Frequency in La ⁴⁴	Frequency in CI ₇
Short	1	2	2
	2	1	1
	4	6	5
	6	1	-
	9	1	2
	10	1	1
Long	1	2	1
	2	3	2
	3	2	2
	4	5	4
	5	2	-
	6	3	3
	9	10	8
	10	1	1
	8 ¹	1	1

¹Information was not available on the translocation suT⁴-8.

Since chromosomes 4 and 9 occurred with the highest frequency in the translocation stocks used, separate tables for these chromosomes are included. In Tables 3 and 4 therefore translocations of chromosomes 4 and 9 have been arranged in a sequence according to the distance of the break locus from the centromere of respective chromosome. Distances from the centromere are those given in microns in Table 1. The center of each table corresponds

to the centromere of the chromosome and upwards and downwards from it are the short and long arms.

Table 3. The distribution of the break loci of chromosome 4 along the arms of this chromosome for those translocations in which chromosome 4 was involved.

	: Translocation :	: Position of the break on the chromosomea. :	: Distance of the break in microns from the centromere of chromosome 4. :
Short arm of Chr. 4	su4-10B-45	4S.70 ¹	10L.11
	suT1-4a	1L.49	4S.66
	su4-6x-57-31	4S.60	6L.51
	suT4-8	4S.54	8L.48
	wxT4-9(F-22)	4S.35	9L.42
	suT4-5d	4S.21	5L.19
	suT2-4c	2L.77	4S.09
centromere			
Long arm of Chr. 4.	suT2-4(A-29)	2L.78	4L.14
	suT2-4a	2L.29	4L.15
	suT4-9a	4L.18	9L.50
	su1-4B-2	1L.29	4L.30
	suT4-6a	4L.33	6L.44
	wxT4-9b	4L.84	9L.34

¹4S.70 means the break in the chromosome 4 is in the short arm (S), 0.70 of the distance from the centromere to the end of the short arm.

The backcrosses of the inbreds to translocation stocks as well as the seed for the F₃, and the selfed backcrossed progenies used in the next part of this study were supplied by the Corn Investigations Project, under Dr. L. A. Tatum.

The original crosses of the two inbreds, La44 and CI₇, with the strains carrying the translocations were made during the summer of 1950 in the field. During the winter of 1950-51 in the greenhouse, plants grown from the seed given by the original crosses were tested for the presence or absence of the translocation. It was expected that those plants heterozygous for the

translocations would have half of their pollen grains aborted. The examination of the pollen was made with a 40x pocket microscope (Taschen Mikroskop). If about half of the pollen grains of a plant were found aborted, this was taken as sufficient proof that the plant was heterozygous for the translocation. The plants heterozygous for the translocation were tagged and were backcrossed by the firing susceptible inbreds.

Table 4. The distribution of the break loci of chromosome 9 along the arms of this chromosome for those translocations in which chromosome 9 was involved.

	Translocation	Position of the break on the chromosomes.	Distance of the break in microns from the centromere of chromosome 9.
Short arm of Chr. 9	wxT3-9c	3L.15	98.20
	wxT9-10b	10S.28	98.11
centromere			
Long arm of Chr. 9	wxT2-9b	2S.12	9L.12
	wxT1-9a	1S.17	9L.17
	wx6-9x-25-78	6L.17	9L.22
	wxT1-9c	1S.61	9L.32
	wxT4-9b	4L.84	9L.34
	wxT3-9a	3L.19	9L.40
	wxT6-9a	6S.79	9L.40
	wx5-9x-7-39	5L.70	9L.40
	wxT4-9 (F-22)	4S.35	9L.42
	suT4-9	4L.18	9L.50
wx3-9b	3L.48	9L.53	

Seed from these backcrosses was planted in the field in the spring of 1951. Each backcross, originated from each translocation with each inbred, occupied one row of fifteen plants, planted in five hills of three plants. The hills were forty-two inches apart. These rows were replicated up to four times for those backcrosses for which sufficient seed was available. Three or four rows of fifteen plants were available in the field for most of

the translocations. In a few cases, as for the inbred La44 with the translocations wxT2-9b, suT2-4 (A-29), su4-6x-57-31 and wx5-9x-7-39, and for the inbred CI₇ with the translocation wxT9-106, only one row was possible. The rows were assigned at random within replications. This arrangement was made in order to give an equal chance for each backcross to grow under any environmental conditions prevailing throughout the experiment and to permit a valid analysis of the data.

In order to verify that half of the backcrossed plants in each row carried the translocation in a heterozygous condition and that half of them were normal, a sample of six plants from each row was examined, around August 10, for pollen sterility. The plants were tagged with the designation of the class to which they belonged. The examination of the pollen was done just as soon as the anthers were ready to dehisce. The time from 9 a.m. until 11 a.m. proved to be the best for classification.

These samples were in approximate accordance with the expected ratio of 50 per cent plants heterozygous for the translocation to 50 per cent of normal plants.

This short cut method was unavoidable, because time did not permit classification of all plants while pollen was available.

The plants which showed firing were marked with tags on which the date and the kind of firing was written. The firing character appeared around August 13.

Pollen samples from each of the fired plants were examined and classified for the presence or absence of aborted pollen to determine whether the plants carried the translocation or were normal. At the end of the period of pollen shedding and the appearance of the firing, the notes on the tags were recorded in the note book.

At harvest time all the plants of each row, those examined and classified at the time when the pollen was shedding, and those not, were classified again into plants with translocation and normal by examination of their ear formation. The plants with the translocation, in heterozygous condition, were expected (Brink, 1927) to have half of the ovules of their ear sterile. Thus the previous classification was checked and the segregation of the plants of each progeny into normal and semisterile classes was verified.

The translocation stocks used in the backcrosses with the susceptible inbreds La44 and CI7 were resistant to firing.

The chromosomes of the backcrossed material of the normal plants, as well as of the plants with the translocation, were expected to come largely from the recurrent parents, the inbreds La44 and CI7. The chromosomes involved in the translocation in the plants carrying the translocation were expected to come to a large extent, especially the area around the point of interchange (Burnham, 1934), from the side of resistant to firing stock of the translocations.

The situation could be explained as follows:

During meiosis in the F_1 plants heterozygous for the translocation crossing-over would be expected between the non sister chromatids of the homologous pairs of chromosomes not involved in the translocation. The only restriction to random crossing-over was due to the influence of the centromere on the area adjacent to it. For the two homologous pairs participating in the translocation, besides the restriction coming from the centromere, the position of the break is a cause of restriction to crossing-over around that area also. This area of reduced crossing-over around the break might be considered not to exceed 40 to 50 genetical units, Saboe and Hayes (1941),

on either side of the break locus. Beyond those points crossing-over could be expected in an amount in proportion to the length of the arms left.

Thus, for chromosomes not participating in the translocation, crossing-over would be expected to give a random interchange and distribution of genes, originally located on the chromosomes of the translocation stock and those of the inbred except in the region of the centromere. For the two pairs of homologues involved in the translocation, this random interchange and distribution of genes between the homologues could not occur in the area 40 to 50 genetical units on either side of the break locus.

For chromosomes not involved in the translocation there was therefore a 50 per cent probability for the genes of each origin to be present in each gamete produced by the F_1 plants. But for those genes located within 40-50 units of the point of interchange on the homologous pairs involved in the translocation, it was expected, because of the limitation of crossing-over in this area, the original translocated chromosome would tend to carry the genes for resistance to firing.

As a result of this situation, the F_1 plant gametes with the translocation would be expected to transmit firing with the same frequency as the normal gametes of these plants, only if the genes responsible for this character were on the homologous pair not involved in the translocation or on the arms of the homologues involved in the translocation but beyond the region of restricted crossing over. If all the genes for resistance to firing were located on the chromosomes involved in the translocation and on the segment adjacent to the break locus, the gametes of the F_1 plants with the translocated chromosomes would not transmit the firing character at all. The opposite would occur; in other words these gametes would transmit the

character, if the translocation stock were susceptible to firing and the major genes or modifiers were located in the segments adjacent to the break.

Saboe and Hayes (1941) found indications in experiments with inbreds originated from Rustler and Minnesota No. 13, that at least three factor pairs or linked groups were responsible for another type of firing.

There had been indications from observations on crosses of La⁴⁴ and CI₇ inbreds in previous years (Tatum, 1949) that the top-firing character was controlled by several pairs of genes.

It was expected therefore that gametes carrying the translocation might transfer the firing character, through genes located on other chromosomes, even though the major genes were located on the chromosomes involved in the translocation. In this case the only difference between the gametes with the translocation and those without it, would be in the degree to which they transmitted susceptibility to firing.

Since F₁ plants heterozygous for the translocation were backcrossed to the inbred, the backcrossed plants included in the test received their chromosomal complement in half from the gametes of the F₁ plants and in half from the gametes of the inbred. One half of the gametes from the F₁ plants should carry the translocation so it was expected that half of the backcrossed plants should carry the translocation in heterozygous condition and half of them should be normal. Since it was known that the inbred was susceptible, fewer fired plants were expected to be found in the class with the translocation than in the normal class if association of the firing character was to be found with the chromosomes involved in the translocation.

In order to determine the association, the chi-square test for independence, as was outlined by Fisher (1950, 11th edition) and Snedecor (1950) was

used. Because the size of the sample of the fired plants in each class was small and there was one degree of freedom, the correction for continuity, Yates (1934), was applied. This correction was made by subtracting 0.5 from the absolute value of the nominator of each term of the chi-square. Values of P smaller than 0.05 were accepted as significant deviations from independent assortment, and therefore as an indication of the association of the firing character with major genes located on the segments around the break of the two chromosomes involved in the translocation.

Environmental conditions in the field were such that only a very small proportion of the plants fired. In the backcrossed progenies of inbred La⁴⁴ there was only an average of about one top-fired plant per plot. The frequency of base-fired plants in the C17 cultures was somewhat greater but still was rather low.

Such being the situation, the test of independence was applied to the totals of all the available replications for each culture by using a four-fold table in which the two rows represented the classes of plants carrying the translocation and the normal, and the two columns the fired and the non fired plants. The following example with su¹-Ba x La⁴⁴2 demonstrates how the test was applied:

		<u>Fired Plants</u>	<u>Non-fired Plants</u>	<u>Total</u>
Plants with translocation	(Actual No.	0	43.5	43.5
	(Expected No.	3.5	40.0	
Normal plants	(Actual No.	7	36.5	43.5
	(Expected No.	3.5	40.0	
TOTAL		7	80.0	87.0

Expected number in the cell first row and first column = $\frac{43.5 \times 7}{87.0} = 3.5$

$$\chi^2 = \frac{(|0-3.5| - 0.5)^2}{3.5} \text{ plus } \frac{(|43.5 - 40| - 0.5)^2}{40} \text{ plus } \frac{(|7-3.5| - 0.5)^2}{3.5} \text{ plus}$$

$$\frac{(|36.5 - 40| - 0.5)^2}{40} = \frac{2 \times 9}{3.5} \text{ plus } \frac{2 \times 9}{40} = 5.5$$

with degrees of freedom equal to one.

This value of chi-square for one degree of freedom corresponds to a P value between 0.02 and 0.01 and therefore is a significant deviation from independence for this case.

Due to the small number of fired plants, the application of the test of independence did not reveal any information when applied to each replication separately.

Experimental Results

Association Between the Top-Firing Character in La44 and the Points of Translocation. The top-firing character was observed in the backcrossed cultures of the inbred La44. The following Table 5 summarizes the number of fired and non-fired plants in each class of plants, the total number of plants in each culture, and gives the values of chi-square and the corresponding values of P.

Table 5. Summary of top-firing data on progenies from crosses of resistant translocations x susceptible inbred La44 and backcrossed to La44, 1951.

Backcross (Translocation)	: Semisterile	: Normal	: Total	: x ²	: P
	:Fired:Non-fired:	Fired:Non-fired:	plants	:value:	value
wxT1-9c x La44 ²	1 41.5	1 41.5	85	0.0	
suT1-4a "	0 43.5	7 36.5	87	5.55	0.02-0.01
wxT2-9b "	1 10.0	0 11.	22	0.0	
wxT4-9b "	1 20.5	2 19.5	43	0.0	
wxT6-9a "	1 30.5	2 29.5	63	1.636	0.30-0.20
wxT9-10b "	2 27.	2 27.	58	0.0	
suT2-4a "	0 30.5	1 29.5	61	0.0	
suT2-4(A-29) "	0 11.5	1 10.5	23	0.0	
suT4-5d "	0 9.5	1 8.5	19	0.0	
suT2-4c "	0 39.5	2 37.5	79	0.513	0.50-0.30
suT4-6a "	1 43.	4 40.	88	0.848	0.50-0.30
suT4-8 "	2 42.5	4 40.5	89	0.178	0.70-0.50
wxT1-9a "	2 43.	2 43.	90	0.0	
wxT3-9a "	0 19.5	1 18.5	39	0.0	
wxT4 (F-22) "	2 31.5	5 28.5	67	0.637	0.50-0.30
su1-4B2 "	0 30.	3 27.	60	1.403	0.30-0.20
wx3-9b "	0 51.	3 48.	102	1.373	0.30-0.20
su4-6x-57-31 "	0 7.5	1 6.5	15	0.0	
wx6-9x-25-78 "	1 25.5	0 23.5	47	0.0	
wx5-9x-7-39 "	0 10.	1 9.	20	0.0	
su4-10B-45 "	0 43.5	4 39.5	87	1.574	0.30-0.20
La44 (the inbred)	0 0.0	18 62.	80		

As is shown in Table 5, significant deviation from independent assortment as indicated by a P value smaller than five per cent, was found in the

case of translocation suTl-4a. This would indicate that a major gene or genes controlling the top-firing character were located either on the long arm of chromosome 1 or on the short arm of chromosome 4, or on both chromosomes. As a significant deviation from independent assortment was not found for any other translocation in which either chromosome 1 or chromosome 4 participated, it is not determined on which of these two chromosomes the genes controlling this character are located.

Haber (1938) and Heyne and Brunson (1940) suggested that the su gene might be responsible for the susceptibility to heat injury. The present results with translocation suTl-4a might indicate that not the sugary (su) gene itself, but genes closely linked to this gene are responsible for the susceptibility. The fact that the point of interchange in translocation suTl-4a is on chromosome 4 very close to the su gene indicates that the su region is involved in top-firing. Plants heterozygous for the translocation should also have been heterozygous for sugary (su Su) while the normal plants should have been homozygous starchy (Su Su). There is thus evidence that the excess of fired plants in the normal class was not due to the sugary gene.

Associations Between the Base-firing Character of CI₇ and the Points of Translocation. Base-firing was observed in the backcrossed cultures of the inbred CI₇, although top-firing was the kind of heat injury that this inbred exhibited in the previous years. The same base-firing character was observed in the crosses of this same inbred included in the tests in the second part of this work. This might be attributed to the conditions prevailing during the summer of 1951. Table 6 summarizes the number of fired and non-fired plants in each class of plants, the total number of plants in each backcross and gives the values of chi-square and the corresponding values of P.

Significant deviation from independent assortment was found for the translocations su4-10B-45 and suT2-4C.

In the case of the translocation su4-10B-45, more fired plants were found in the class of normal plants. Therefore, if it is assumed that the translocation stock was resistant to base-firing, there is an indication that this character was associated with the point of the translocation and the genes for susceptibility in CI₇ were located either on chromosome 4 or chromosome 10.

Table 6. Summary of base-firing data on progenies from crosses of resistant translocation x susceptible inbred CI₇ and backcrossed to susceptible parent, 1951.

Backcross (Translocation)	Semisterile		Normal		Total	χ^2	P
	Fired	Non-fired	Fired	Non-fired	plants	value	value
wxT1-9c x CI ₇ ²	8	33.	14	27.	82	1.5557	0.30-0.20
suT1-4a "	10	33.	11	32.	86	0.0	
suT4-9a "	8	9.5	5	12.5	35	0.488	
wxT2-9b "	6	16.	7	15.	44	0.0	
wxT4-9b "	13	33.	20	26.	92	1.706	0.20-0.10
wxT9-10b "	0	8.	3	5.	16	1.640	0.30-0.20
suT2-4(A-29) "	13	32.	17	28.	90	0.450	0.70-0.50
suT2-4c "	15	19.	6	28.	68	4.408	0.05-0.02
suT4-6a "	9	31.	10	30.	80	0.0	
suT4-8 "	7	36.5	16	27.5	87	3.782	0.10-0.05
wxT1-9a "	4	17.	11	10.	42	3.733	0.10-0.05
wxT3-9a "	8	25.5	9	24.5	67	0.0	
wxT4-9(F-22) "	0	39.5	0	39.5	79	0.0	
wxT3-9c "	0	33.	0	33.	66	0.0	
su4-6x-57-31 "	0	44.	0	44.	88	0.0	
wx6-9x-25-78 "	9	19.5	7	21.5	57	0.086	
su4-10B-45 "	12	27.5	22	17.5	79	4.182	0.05-0.02
CI ₇ (the inbred)			15	35.	50		

In the case of the translocation suT2-4c more base-fired plants were observed in the class of the semisterile plants. Since in the culture of the inbred CI₇, 43 per cent of base-fired plants were observed, indicating a relatively high degree of susceptibility, the fact that more base-fired

plants were observed in the semisterile class could be taken as an indication of the action of additional genes for susceptibility coming from the translocation stock. Therefore either chromosome 2 or 4 or both, coming from the inbred CI₇ carried a gene or genes for resistance to base firing.

As in no other translocations of chromosome 4, 2 and 10 with any other chromosome, was found a significant association, any suggestion cannot be made as for the possible location of the gene or genes on any particular chromosome or chromosomes.

PART II. TESTS WITH THE F_2 AND BACKCROSSED PROGENIES

Materials and Methods

In these tests the susceptible to firing inbreds La⁴⁴ and CI₇, the moderately resistant inbred 33-16 and the resistant inbreds 38-11, K10 and K155 were included.

The cultures in the field during the summer of 1951 included these inbred lines, the F_1 plants from crosses of these inbreds, F_2 progenies originated from selfed F_1 plants, backcrossed progenies, as well as F_3 progenies originated from selfed F_2 plants and selfed backcrossed progenies originated from selfed plants of backcrosses.

Included were the selfed progenies of the following backcrosses:

- 68 progenies of (La⁴⁴ x CI₇) La⁴⁴
- 52 progenies of (La⁴⁴ x CI₇) CI₇
- 59 progenies of (38-11 x CI₇) CI₇
- 59 progenies of (CI₇ x K10) CI₇

and the F_3 progenies of the following crosses:

- 28 progenies of La⁴⁴ x CI₇
- 49 progenies of K155 x CI₇
- 35 progenies of K10 x 33-16

Each of the parent lines and each of the progenies of the crosses and backcrosses were planted in rows of fifteen plants spaced one foot apart. All the material was planted in two replications. In each replication each group of progenies and in each group the progenies were distributed at random.

Notes on firing were taken on August 13 and on the immediately following days. In those cases where the same plant exhibited both top-firing and base-firing it was recorded in both classes of firing.

Any plant which showed clearly fired leaves was recorded as a fired plant. No attempt was made to record the extent or the degree of the firing of the plants, as this would take more time than was available. Therefore the plants of each progeny were classified only to the two distinct classes of non-fired and fired.

In the analysis of the data on the F_2 and selfed backcrossed progenies, histograms were made showing the distribution of the progenies with respect to percentage of fired plants per progeny.

In the attempt to draw conclusions from these histogram distributions of the F_2 and selfed backcrossed progenies the methods used by Wellhausen (1937) and Jenkins, Robert and Findley (1952) were taken as a basis.

Experimental Results

Table 7 shows the top-firing and base-firing data obtained in 1951 on the parent inbreds, the F_1 generation of the crosses, the F_2 generation and the backcrosses.

In the susceptible inbred La⁴⁴ a small percentage of top-fired plants was observed but due to the absence of severe conditions, firing did not occur in the rest of the material.

Such being the situation it was believed that data from previous years would be helpful in showing the relative susceptibility of the parent material. Firing data of previous years were made available by Dr. L. A. Tatum. These data are from the years 1947 and 1949 and are included in Table 7.

From the data of 1949, the inbred La⁴⁴ seemed to be highly susceptible to top-firing. The inbred CI₇ showed susceptibility also but lower than that of La⁴⁴. The single cross of these two inbreds was resistant to top-firing,

indicating that the firing character may be controlled by different factors in each of these two inbreds. The backcross to La⁴⁴ was more susceptible than the backcross to CI₇, indicating that La⁴⁴ was more prepotent than CI₇ in transmitting the character. The inbred 38-11 was more prepotent for resistance than the resistant inbreds K10 and K155 in backcrosses with CI₇ as the recurrent parent.

Table 7. Firing data on inbreds, single crosses and backcrosses tested in 1947, 1949 and 1951.

Kind of corn	Per cent of			Per cent of
	top-fired plants			base-fired plants
	1947	1949	1951	1951
La ⁴⁴	-	100	7(1)	0
CI ₇	97	71	0	0(2)
La ⁴⁴ x CI ₇	16	0	0	0
(La ⁴⁴ x CI ₇) La ⁴⁴	-	71	0	0
(La ⁴⁴ x CI ₇) CI ₇	-	29	0	0
(La ⁴⁴ x CI ₇) F ₂	-	-	0	0
CI ₇	97	71	0	0
38-11	0	0	0	0
(38-11 x CI ₇)	0	0	0	0
(38-11 x CI ₇) CI ₇	0	0	0	0
CI ₇	97	71	0	0
K10	-	0	0	0
(K10 x CI ₇)	0	0	0	0
(K10 x CI ₇) CI ₇	-	16	0	0
CI ₇	97	71	0	0
K155	0	0	0	0
K155 x CI ₇	0	0	0	0
(K155 x CI ₇) CI ₇	-	13	-	-
K10	-	-	0	0
33-16	-	-	0	0
K10 x 33-16	0	-	0	0

- (1) The inbred La⁴⁴ showed 26 per cent top-fired plants in the tests of the translocation material.
- (2) The inbred CI₇ showed 43 per cent base-fired plants in the tests of the translocation material.

In the year 1947, during which not all the material of these studies was included in the tests, the inbred CI₇ was susceptible to firing in a high degree. Again the inbred 38-11 was prepotent in transmitting resistance. Inbreds K10 and K155 expressed their resistance in their single crosses with CI₇.

From the data of 1950, little information was obtained because of the cool, wet growing season. In the tests of that year, F₃ progenies from crosses between resistant and susceptible lines and selfed progenies from backcrosses involving resistant and susceptible parents. In this year also the inbred La⁴⁴ was more prepotent in transmitting susceptibility in comparison to CI₇. From backcross (La⁴⁴ x CI₇) La⁴⁴ there were more progenies with fired plants than from the backcross (La⁴⁴ x CI₇) CI₇. Most of the material tested in the year 1950 was included in the tests of 1951 presented by this study.

From the already mentioned data from the year 1949 and 1947 the suggestion could be made that the inbred 38-11 was dominant in its resistance over the susceptibility of the inbred CI₇. The resistance of the inbreds K10 and K155 was also dominant over the susceptibility of CI₇.

In analysing the data on the F₃ and selfed backcross progenies first follows the analysis of top-firing data.

Analysis of the Data on Top-firing. Nine of the 68 self progenies of the backcross (La⁴⁴ x CI₇) La⁴⁴, (Fig. 1) were resistant to top-firing, the remaining progenies showing from one to 61 per cent of fired plants. In this case it could be said that three breaks were distinguishable in the distribution. The first between the classes zero per cent and one per cent, the

second between 13 and 15 per cent and the third between 28 and 34 per cent. These three breaks divided the whole distribution of the progenies into four classes. The first class included nine entirely resistant progenies, the second 34 progenies showing from one to 13 per cent fired plants, the third 14 progenies showing 15 to 28 per cent fired plants and the fourth class 11 progenies showing 34 to 60 per cent fired plants. In other words the actual distribution as separated by these breaks was 9:34:14:11. This indicates that at least two major pairs of genes are involved. There probably are more as the second class of 34 progenies, if the conditions had been more severe, may have been separated into more classes.

In the case of the backcross (La44 x CI7) CI7, (Fig. 2), 30 progenies out of 52 were resistant. As there were no distinguishable classes of progenies for this backcross, any indication as far as the number of genes was concerned was not available.

In the frequency distribution of percentages of top-fired plants in the progenies of the two backcrosses, a larger proportion of progenies with top-fired plants was found in the backcross (La44 x CI7) La44 than in the backcross (La44 x CI7) CI7. This indicates that the more susceptible inbred La44 is more prepotent in transmitting top-firing than is the less susceptible inbred CI7. The same results were found in the year 1949 from the F₁ of these two backcrosses.

In the distribution of the percentages of top-fired plants, (Fig. 3) in the F₂ progenies of the cross (CI7 x La44), 19 of the 28 progenies were resistant. These data give little indication as to the number of genes and the existence or not of the action of major genes. They give again an indication that the very susceptible inbred La44 transmitted a degree of susceptibility

in the cross with the susceptible inbred CI₇, while this last inbred under the same conditions did not show any firing.

In the backcross (38-11-CI₇) CI₇, (Fig. 4), 45 out of the 59 selfed progenies were resistant. The percentages of fired plants in those progenies which showed top-firing were very low, being from one to seven per cent. The recurrent parent, the susceptible inbred CI₇, contributed a very low rate of susceptibility to the cross with the resistant inbred 38-11 under these conditions.

In the backcross (K10 x CI₇) CI₇, (Fig. 5), 55 out of 59 selfed progenies were resistant. The contribution of the inbred CI₇ to the susceptibility to firing was very small in this case also.

In the cross K155 x CI₇, (Fig. 6), 31 out of the 47 F₃ progenies were resistant.

Thirty one out of 35 F₃ progenies of the cross (K10 x 33-16) (Fig. 7), of the resistant inbred K10 with the moderate resistant 33-16, were resistant. The four progenies which segregated for susceptibility to firing had very low percentages of fired plants.

Conclusions from the Available Data on Top-firing. From the comparison of the data of the selfed progenies of the backcrosses (La⁴⁴ x CI₇) La⁴⁴ and (La⁴⁴ x CI₇) CI₇, as already was stated, the inbred La⁴⁴ was more prepotent than CI₇ in transmitting susceptibility in crosses of these two inbreds.

The distribution of the progenies in the different percentages of fired plants in the backcross (La⁴⁴ x CI₇) La⁴⁴ gave an indication of the action at least of two pairs of genes. Probably an indication for a greater number of genes could be found if conditions were more severe.

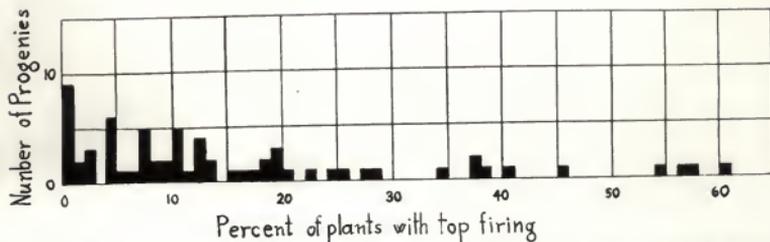


Fig. 1. Frequency distribution of top-firing percentages in 68 selfed progenies from the backcross (La44 x CI7) La44.

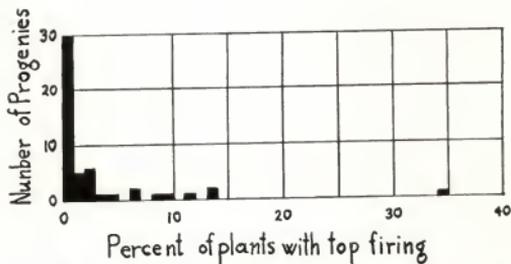


Fig. 2. Frequency distribution of top-firing percentages in 52 selfed progenies from backcross (La44 x CI7) CI7.

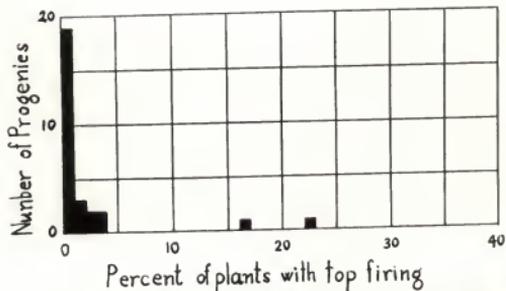


Fig. 3. Frequency distribution of top-firing percentages in 28 F₃ progenies of the cross (CI7 x La44).

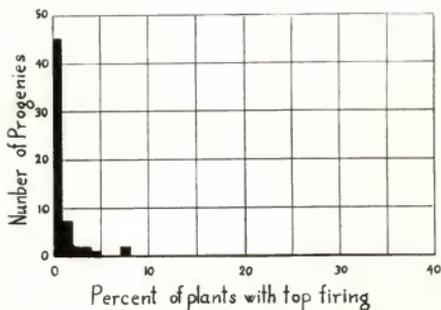


Fig. 4. Frequency distribution of top-firing percentages in 59 selfed progenies from the backcross (38-11 x CI₇) CI₇.

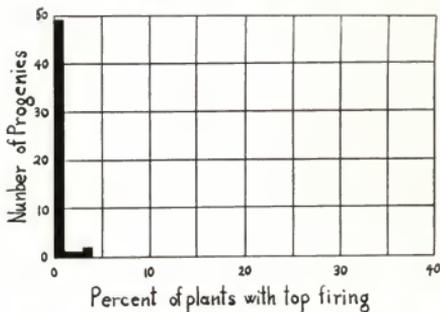


Fig. 5. Frequency distribution of top-firing percentages in 59 selfed progenies from the backcross (CI₇ x K10) CI₇.

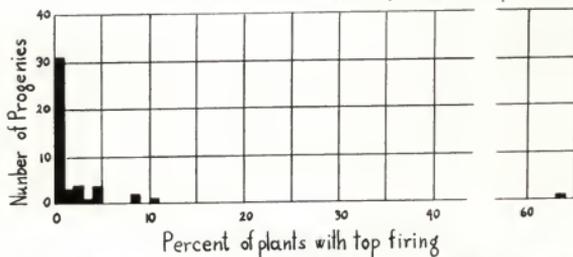


Fig. 6. Frequency distribution of top-firing percentages in 47 F₃ progenies from the cross K155 x CI₇.

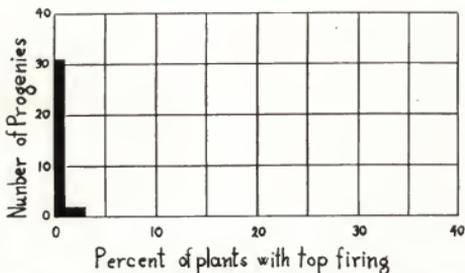


Fig. 7. Frequency distribution of top-firing percentages in 35 F_3 selfed progenies from the cross (K10 x 33-16).

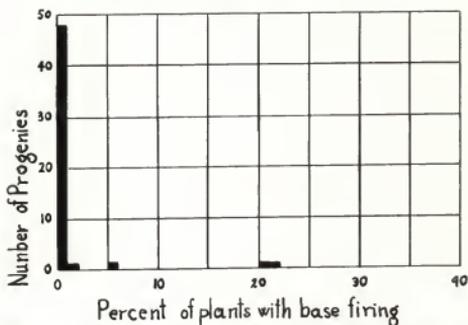


Fig. 8. Frequency distribution of base-firing percentages in 52 selfed progenies from backcross (La44 x CI₇) CI₇.

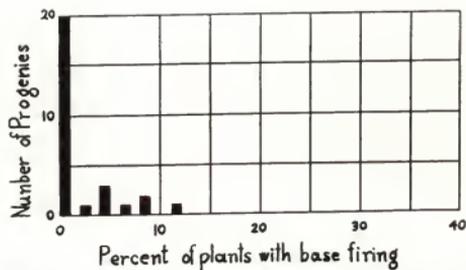


Fig. 9. Frequency distribution of base-firing percentages in 28 F_3 progenies of the cross (CI₇ x La44).

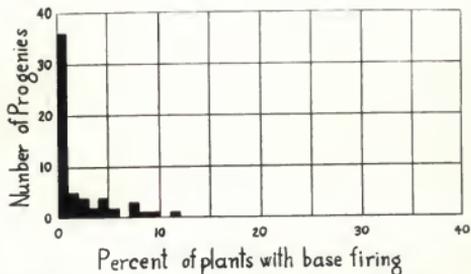


Fig. 10. Frequency distribution of base-firing percentages in 59 selfed progenies from the backcross (38-11 x CI7) CI7.

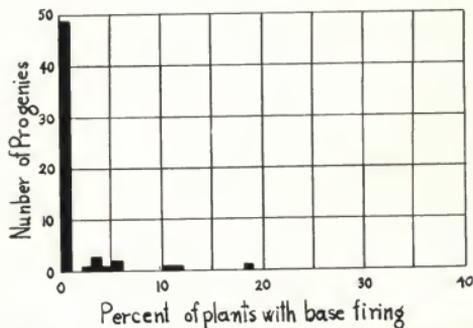


Fig. 11. Frequency distribution of base-firing percentages in 59 selfed progenies from the backcross (CI7 x K10) CI7.

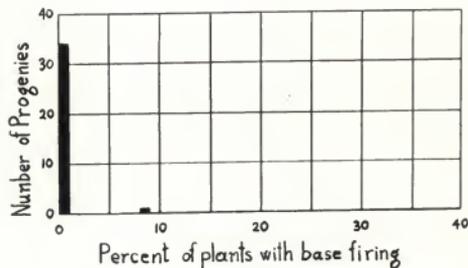


Fig. 12. Frequency distribution of base-firing percentages in 35 F₃ selfed progenies from the cross (K10 x 33-16).

The data made available from the F_3 progenies of the cross (CI7 x La44) would not permit any suggestion of the number of genes involved or for the action of major genes. But the fact that a higher percentage, 30 per cent, of F_3 progenies, than in either inbred, were susceptible, could indicate that different genes in each of these two inbreds were responsible for the character.

The fact that a small number of selfed progenies from (38-11 x CI7) CI7 and (K10 x CI7) CI7 had fired plants, while the susceptible inbred CI7 itself had no firing, could be explained on the basis of K10 and 38-11 carrying genes acting in a complementary manner to those carried by CI7. The same explanation could be given to the fact that a number of F_3 progenies in the cross K155 x CI7 were found with different small percentages of fired plants, as well as for the case of small numbers of F_3 progenies with fired plants in the cross K10 x 33-16.

Analysis of the Data on Base-firing. Four, or seven per cent, of the 59 selfed progenies (Fig. 8) of the backcross (La44 x CI7) CI7 and eight, or 30 per cent, of 28 F_3 progenies (Fig. 9) of the cross (La44 x CI7) exhibited the base-firing character while none of the selfed progenies of the backcross (La44 x CI7) La44 exhibited the character. This fact would be in accordance with the suggestion that the inbred La44 carried genes for resistance to base-firing that were dominant to the genes for susceptibility coming from the CI7 inbred.

In the backcross (38-11 x CI7) CI7 (Fig. 10), 23, or 39 per cent, of the 59 selfed progenies showed different percentages, one to ten, of fired plants. Ten, or 17 per cent, of the 59 selfed progenies (Fig. 11) of the backcross

(K10 x CI₇) CI₇ showed different percentages, 2 to 18, of fired plants. One of the 35 F₃ progenies (Fig. 12) of the cross (K10 x 33-16) had eight per cent of fired plants.

Conclusions from the Available Data on Base-firing. The inbred CI₇ transferred the base-firing character in a variable degree to the progenies when entered as the recurrent parent in backcrosses with the inbred La⁴⁴, 38-11 and K10. The inbred La⁴⁴ seemed to carry genes suppressing the base-firing character.

CONCLUSIONS

From the Backcrossed Cultures of Translocations

Some indication was found that gene or genes affecting the top-firing character in the inbred La⁴⁴ were located either on the long arm of chromosome 1 or on the short arm of chromosome 4, or on both. Indication might be suggested to exist that closely linked genes to sugary (su) gene rather than this gene itself, were responsible for the susceptibility. In that case, chromosome 4 was the chromosome carrying these genes.

The genes affecting the base-firing character in CI7 inbred might be located either on chromosome 2, on chromosome 4, or on chromosome 10, or on two of them, or on all of them.

No definite suggestion could be made regarding which of the above chromosomes was responsible, for in no other translocation in which these chromosomes were involved with other chromosomes, was there a significant association.

From the F₃ and Selfed Backcrossed Progenies

As a recurrent parent in a backcross to (CI7 x La⁴⁴) the inbred La⁴⁴ seemed to be more prepotent than CI7 in transmitting the top-firing character. From the distribution of the selfed progenies to different percentages of fired plants in the backcross (La⁴⁴ x CI7) La⁴⁴, an indication was found for the action of at least two pairs of major genes for susceptibility. The F₃ data of the cross CI7 x La⁴⁴ indicated that these genes might be different in each of these inbreds and might be complementary in their action. Some indication of action of complementary genes for susceptibility was found in the crosses of CI7 with the resistant or moderately resistant inbreds

38-11, K10 and to a lesser extent with K155. The cross of inbreds K10 and 33-16 gave the same indication.

The inbred GI₇ transferred the base-firing character in a variable degree to the progenies of its crosses, when entered as a recurrent parent in backcrosses with the inbreds La⁴⁴, 38-11 and K10. The inbred La⁴⁴ seemed to carry genes suppressing the base-firing character.

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GENETIC STUDIES OF REACTIONS TO DROUGHT
AND HIGH TEMPERATURES IN MAIZE

by

SARANTIS ALEXANDROY ARNAKIS

Diploma in Agriculture, University of Thessaloniki, 1948

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ABSTRACT

It is a common experience that high temperatures and low humidity are limiting factors in corn production. Such climatic conditions occur often in Kansas and in the Great Plains area. These conditions are more likely to occur just before pollination time when rapid growth takes place or during the pollination time and may cause the withering of the upper or lower leaves and the desiccation of the silks or the pollen. Thus stunting of the plants or failure of pollination may result. Both these facts have an immediate effect on production which is greatly reduced if conditions are very severe.

The most common firing is top-firing, which is the withering and subsequent dying of all or portions of the upper leaves of the corn plant. Top-firing is the distinctive type of injury which usually occurs in the youngest leaf which has attained its maximum leaf area. This type of firing may occur any time before flowering but is more common during the period of rapid elongation of the plants just prior to the flowering time. Several other types of top-firing can be distinguished. It seems that an inbred will exhibit a type of top-firing which is characteristic of that line. Base-firing is the firing of the lower leaves of the corn plant.

The relative tolerance to drought and high temperature of various inbred lines and hybrids is an important consideration in corn improvement programs in regions such as Kansas.

Available information indicates that resistance and susceptibility to drought and high temperatures is inherited. Inbred lines of corn differ in the transmission to their progenies of reactions to drought and high temperatures. Some seem to transfer resistance in a dominant manner while others

transmit susceptibility. Therefore genetic studies of the reactions of commonly used inbreds to drought and high temperatures under field conditions should be of much help to the corn breeder.

It is recognized that the reactions of the inbred lines of corn to drought and high temperatures are inherited in a complicated way due to the nature of the character itself.

The tests being reported in this thesis were conducted under field conditions during the summer of 1951 to determine something of the mode of inheritance of resistance to top-firing. In one phase of the study, chromosome translocations were used as markers to determine on which chromosomes and on which arm of these chromosomes are located the genes affecting firing in the susceptible inbreds La⁴⁴ and CI₇. The other phase of the study consisted of F₃ progenies and selfed progenies from backcrosses involving resistant and susceptible inbreds to determine if there are major genes affecting this character or if it is primarily a polygenic character.

Material and Methods

In the 23 translocation stocks used as markers, in the first part of this study, nine of the ten maize chromosomes were involved. Chromosome 7 was that which was not involved. Each chromosome participated either with one of its arms or with both of them in the different translocations. An attempt was made to cross these resistant to firing translocation stocks to both susceptible inbreds La⁴⁴ and CI₇, but seed of some of the crosses was not obtained. The heterozygous for translocation F₁ plants were backcrossed to the susceptible inbred. Backcrossed plants from each of the stocks were grown in plots in the field. The plants were classified for the firing

character into fired and non-fired plants, and for the presence or absence of the translocation. The plants were marked for identification. Since the translocation stocks were resistant to top-firing and the inbred susceptible, if association was to be found with a particular point of interchange more fired plants ought to be found in the normal class of plants than in the semisterile class in the progeny involving that translocation. Therefore a significant deviation from the independent assortment of the fired and non-fired plants in the semisterile and normal classes would indicate the existence of association. The chi-square test for independence was applied to determine whether there was association.

In the second part of this study, the F_3 progenies and the selfed progenies of backcrosses were classified according to the percentages of fired plants. In the histograms of the distribution of these progenies, the relative position of the mode or the modes and the number of modes or the breaks in the distribution were studied to determine the dominance or the recessiveness of firing and the possible number of major genes affecting it.

Conclusions

From the Backcrossed Cultures of Translocations

Some indication was found that gene or genes affecting the top-firing character in the inbred La44 were located either on the long arm of chromosome 1 or on the short arm of chromosome 4, or on both. The possibility was suggested that closely linked genes to the sugary (su) gene, rather than this gene itself, were responsible for the susceptibility if chromosome 4 was the chromosome carrying these genes.

The genes affecting the base-firing character in CI₇ inbred might be located either on chromosome 2, on chromosome 4, or on chromosome 10, or on two of them, or on all of them.

No definite suggestion could be made regarding which of the above chromosomes was responsible, for in no other translocations in which these chromosomes were involved with other chromosomes, was there a significant association.

From the F₃ and Selfed Backcrossed Progenies

The susceptible inbred La⁴⁴ seemed to be more prepotent in transmitting the top-firing than the inbred CI₇ when used as recurrent parents with the single cross La⁴⁴ x CI₇. From the distribution of the selfed progenies to different percentages of fired plants in the backcross (La⁴⁴ x CI₇) La⁴⁴, an indication was found for the action of at least two pairs of major genes for susceptibility. The F₃ data of the cross CI₇ x La⁴⁴ indicated that these genes might be different in each of these inbreds and might be complementary in their action. Some indication of action of complementary genes for susceptibility was found in the crosses of CI₇ with the resistant or moderate resistant inbreds 38-11, K10, and to a lesser extent with K155. The cross of K10 and 33-16 gave the same indication.

The inbred CI₇ transmitted the base-firing character in a variable degree to the progenies of its crosses, when used as a recurrent parent in backcrosses with inbreds La⁴⁴, 38-11 and K10. The inbred La⁴⁴ seemed to carry genes suppressing the base-firing character.