THE PRESENT STATUS OF MAIZE GENETICS[1]

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ADVANTAGES AND DISADVANTAGES OF MAIZE AS GENETIC MATERIAL

As material for genetic studies, *Zea mays* has many advantages and not a few disadvantages. Of first rank among the latter is the long life cycle which makes it impracticable in temperate regions to grow more than one generation a year or, at best with greenhouse facilities, two generations. The relatively large number of chromosomes, ten pairs, with a correspondingly large number of linkage groups, adds to the difficulty of genetic analysis.

The necessity of guarding the pollination of plants even to obtain self-fertilized seed is not an unmixed evil. The technique of pollination is so simple and so many seeds result from a single pollination that it is easily possible to obtain 10,000 seeds from a single hour of work. The wealth of genetic material available in maize is undoubtedly directly related to the cross-fertilization prevailing in this plant. Even relatively weak recessive mutations are long preserved against elimination by natural selection under cover of their dominant normal allelomorphs. No variety of maize not previously inbred fails on self-fertilization to reveal numerous recessive characters. This is in sharp contrast to naturally self-fertilized species.

Maize, being prevailingly diploid, has, for genetic purposes, the further advantage over such polyploid species as common wheat that a recessive mutant gene can manifest itself at once without the necessity of a second identical mutation in a duplicate chromosome. In this connection may be noted the suggestive results of STADLER (1929), showing a much higher rate of X-ray induced mutation in diploid barley, oats and wheat than in polyploid oats and wheat.

A not inconsiderable advantage of maize for genetic analysis is the fact that this plant lends itself readily to cytological examination. The marked differences in size, form, and other morphological features between the several chromosomes of maize are of the greatest advantage in cytogenetic studies.

I cannot refrain from noting here a very real advantage experienced by students of maize genetics, which is in no way related to the peculiar characteristics of the maize plant. I am aware of no other group of investigators who have so freely shared with each other not only their materials but even their unpublished data. The present status of maize genetics, whatever of

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noteworthy significance it presents, is largely to be credited to this somewhat unique, unselfishly cooperative spirit of the considerable group of students of maize genetics. In this connection I want gratefully to acknowledge the help of many persons who have contributed directly or indirectly to this summary statement of the status of maize genetics. Formal credit by means of citations of literature will be given only for the more recent papers.

SIMPLE AND COMPLEX INTERACTION OF GENES

During the past twenty years the mode of inheritance of many characters of maize, involving more than two hundred genes, has been more or less successfully studied. The genes studied influence such diverse characters as color of aleurone, endosperm, plumule, scutellum, pericarp, silks, anthers, and leaves, endosperm composition, chlorophyll abnormalities, plant stature, root development, pollen sterility, sex abnormalities, defective endosperm and embryo, branching of ear and tassel, form of leaves, development of silks, rate of pollen-tube growth, carbohydrate metabolism, disease resistance, and even chromosome behavior during meiosis. Most of these characters are simple recessives, but several of them involve complex relations of duplicate genes, complementary genes, and multiple allelomorphs.

Although most chlorophyll abnormalities of maize are simple recessives, normal chlorophyll development is an outstanding example of genetic complexity. From the fact that some sixty recessive genes are known, any one of which prevents perfectly normal chlorophyll development, it follows that all sixty of the dominant allelomorphs of these genes are essential to the production of normal chlorophyll, and it is highly probable that, as yet, we know only a small part of the story of the genetics of chlorophyll development.

One of the best examples of extreme complexity of complementary interaction of genes, known to the writer, is that afforded by the purple-red series of aleurone and scutellum colors of maize. Since aleurone color ordinarily does not develop except with the genotype $A_1\ A_2\ C\ R\ i$, it is obvious that numerous genetically different types of colorless aleurone may exist. It is equally to be expected that very diverse F_2 ratios of colored to colorless aleurone should be encountered. But when it is recalled that scutellum color develops only with the aleurone color genotype noted above and in addition with S_1 plus any two of the three genes S_2, S_3 and S_4, it will probably be granted that a really complex genetic set-up has been uncovered in scutellum coloration.

Studies of scutellum color (SPRAGUE 1932) have an important bearing

on an earlier idea of the possibly fundamental difference between the interaction of duplicate genes and of complementary genes. Given the aleurone genotype $A_1\ A_1\ A_2\ A_2\ C\ C\ R\ R\ i\ i$ plus the scutellum genes $S_1\ S_1$, the F_2 ratio of colored to colorless scutellum resulting from the heterozygous condition of two of the other three scutellum genes, say $S_2\ s_2\ S_3\ s_3$, is dependent alone on whether the remaining scutellum gene is homozygous dominant, $S_4\ S_4$, or homozygous recessive, $s_4\ s_4$. Thus, $S_2\ s_2\ S_3\ s_3$ gives with $s_4\ s_4$ a 9:7 ratio and with $S_4\ S_4$ a 15:1 ratio. Obviously the particular ratio depends not alone on the interaction of the genes that happen to be heterozygous but rather on their interaction with the residual genetic mass. It follows, therefore, that there may in other cases be no very fundamental difference between so-called duplicate genes giving a 15:1 ratio and complementary genes giving a 9:7 ratio. This scutellum-color situation, moreover, indicates that a 15:1 ratio alone cannot be regarded as critical evidence of duplicated chromosomes.

Examples of multiple allelomorphism in maize have long been known. The more important of these involve the P, R, and A_1 loci. Several combinations of pericarp and cob color are dependent on allelomorphs of P. They present no unusual features, but one of them, P^{wr}, is a convenient tool for use in studies of variegated and mosaic pericarp. The cross variegated pericarp, variegated cob $\times$ white pericarp, red cob, $P^{vv} \times P^{wr}$, produces in F_2 the following genotypes:

$1\ \frac{P^{vv}}{P^{vv}}$ variegated pericarp, variegated cob

$2\ \frac{P^{vv}}{P^{wr}}$ variegated pericarp, red cob

$1\ \frac{P^{wr}}{P^{wr}}$ white pericarp, red cob

It is, therefore, possible to separate the heterozygous from the homozygous variegated ears by reference to the color of the cob without the necessity of growing progenies of the two classes.

The R series of allelomorphs exhibits peculiarities worth noting. R^r is dominant for both aleurone and plant color and r^g is recessive for both; R^g is dominant for aleurone color and recessive for plant color, while r^r is recessive for aleurone and dominant for plant color.

The A_1 allelomorphs (EMERSON and ANDERSON 1932) exhibit no simple

sequence with respect to dominance. Thus, A_1 is dominant to a_1 for aleurone, plant and pericarp colors. A_1^b is like A_1 in its dominance to a_1 with respect to aleurone and plant color but is dominant to A_1 with respect to pericarp color. The allelomorph a^p is similar to a_1 in its relation to plant color, like A_1^b in relation to pericarp color, and has an effect on aleurone color intermediate between the effects of A_1 or A_1^b and of a_1.

Until recently all that could be said about the inheritance of quantitative characters in maize was that the results could be interpreted on the basis of the interaction of numerous genes affecting size, length of growing season, etc. Recently, however, it has been shown (LINDSTROM 1931) that a quantitative character, number of kernel rows, is linked with genes for well-known qualitative characters. This may well be accepted as proof that quantitative characters are inherited just as are other characters. As yet, however, no thorough genetic analysis has been made of any quantitative character in maize. An attempt by the writer to do just this for a relatively simple quantitative character has been under way for ten years. The results to date do not encourage him soon to undertake the genetic analysis of so complex a character as yield of grain or forage. Doubtless, however, by some date well in the future some progress toward this goal will have been made by somebody.

LINKAGE IN MAIZE

Ten linkage groups are now known in maize, corresponding to the ten pairs of chromosomes of the ordinary diploid form of this plant. Somewhat over one hundred genes, or about half of those studied, have been assigned to one or the other of the linkage groups. In some cases the order of the genes and their relative linkage-map distances apart are known. Of other genes the approximate order is known, and of still others our only information at present is that they belong to a particular linkage group. In the accompanying diagram the approximate location of genes is shown for the several linkage groups, those genes not even approximately located being shown below the map line.

With a single exception, all these genes have been placed in their respective groups by purely genetic methods. In general the first indication of linkage is obtained from F_2 cultures. The next step is to examine backcrosses to the double recessive. Since most newly found genes are recessive to their normal allelomorphs, the repulsion phase of linkage is involved in most instances. With such material backcross data are better than F_2 data. If, as often happens, plants with recessive characters are weak and double recessives still weaker, failure to recover the double recessive type in an F_2

culture of moderate numbers affords little evidence of linkage. The standard practice, as soon as double recessives are obtained, is to test the genes in backcrosses and from these to obtain material exhibiting the linkage in coupling phase. In case of lethal or near-lethal recessive genes, backcrosses

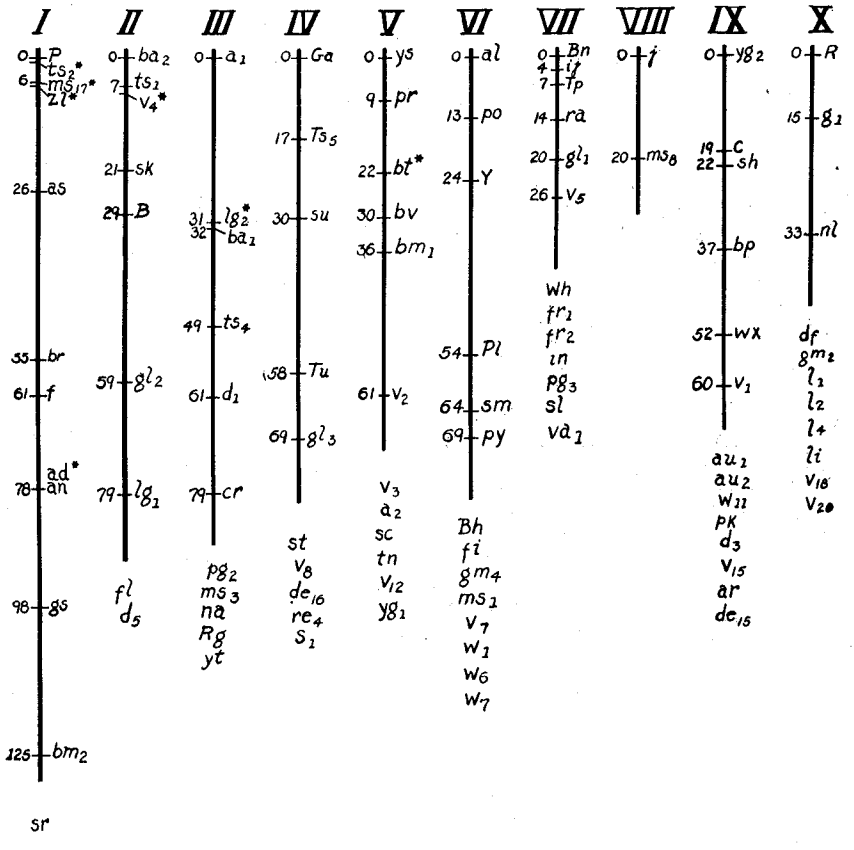

FIGURE 1.—Linkage maps of maize. Genes whose loci are known only approximately are starred. Genes known to belong to a particular group but whose loci are not even approximately known are listed below the appropriate map line. R_s should have been placed near ts_4, chomosome III, and l_1 near R, chromosome X, and starred.

are out of the question. In general, however, close linkage can be determined readily in F_2 progenies; and, with loose linkage, double recessives for backcrosses are easily obtained.

Maize affords numerous illustrations of the difficulty experienced in attempts to determine the linear order of genes when only two pairs are involved in any one culture. The variability of different cultures in percentage

of crossing over is such that, for all but relatively close linkages, three-point tests must be resorted to.

To facilitate the discovery of linkages, maize geneticists have built up sets of linkage testers, each having at least two workable linked genes whose loci are relatively far apart on the linkage map. With such testers there is little chance of failure to locate a new gene in its group at an early stage of the study. And yet only recently two supposedly independent linkage groups have been found, by the discovery of intermediate genes and the use of trisomics, to constitute a single group (BRINK 1931). As linkage groups become better known and linkage testers further developed, such difficulties should disappear. But in any material in which, as in maize, crossing over occurs with approximately equal frequency in both male and female, absolute certainty of the correctness of interpretation by purely genetic methods is scarcely to be expected. In view of such considerations, one should not be unduly disturbed by sporadic reports of more linkage groups than there are chromosomes in this or that organism.

There are now available cytological helps to the determination of linkages. Such materials and methods will be noted later. It is enough at present to say that trisomics, reciprocal translocations, and deficiencies are among the most useful of cytogenetic tools. The available trisomics should prove particularly valuable in determining linkages, but as yet they have not functioned prominently other than as a means of proving with certainty the independence of groups previously assumed on genetic evidence to be independent.

ASSOCIATION OF PARTICULAR LINKAGE GROUPS WITH SPECIFIC CHROMOSOMES

Diploid maize has ten pairs of chromosomes, corresponding to the ten known linkage groups. The importance of determining which linkage group is associated with a particular chromosome is obvious.

Fortunately the chromosomes of maize differ in length and in other morphological features. The longest chromosome is more than twice the length of the shortest. The several chromosomes are given numbers in order of their length, the longest being I and the shortest X. The spindle-fiber attachment point, indicated by a constriction or a non-stainable area, is terminal in no case and in none is it strictly median. In some cases, however, it approaches a median position so that, as in chromosome I, the longer arm is only a little longer than the shorter one. In others, VII for instance, the longer arm is somewhat more than twice the length of the shorter one. Chromosome VI has a satellite which is attached to the major part of the

chromosome by a thread of variable length and which is always associated with the nucleolus. In certain strains of maize the ninth chromosome has a conspicuous accumulation of stainable substance, appearing as a knob, at the end of the short arm. Similar conspicuous bodies occur, usually some distance from the end, in certain other chromosomes. Even in the case of chromosomes of nearly the same length it is possible, therefore, by means of these other morphological features, to identify each of the ten pairs.

Ten linkage groups and ten morphologically different chromosomes having been identified, the next step was obviously to determine which linkage groups are associated with particular chromosomes. This has now been accomplished. For the most part this has been done by the use of trisomics (McCLINTOCK 1931).

Trisomics, 2n + 1 or 21-chromosome plants, were first obtained from a naturally occurring triploid. It is now possible to obtain triploids and consequently trisomics almost at will. A recessive gene, asynaptic, with its locus in the first chromosome (BEADLE 1930), which largely prevents pairing of all chromosomes at diakinesis, gives a high percentage of triploids when the partially sterile plants homozygous for it are crossed by normal diploids. Moreover, it has been shown that tetraploids can be produced in considerable numbers by heat treatment of diploid maize (RANDOLPH 1932). Crosses of tetraploids with diploids give triploids which in turn yield trisomics.

With random distribution of the three chromosomes of a trisomic group, the resulting gametes of a duplex dominant simplex recessive trisomic, *D D d*, should exhibit a 5:1 ratio of dominant to recessive. Similarly a simplex dominant duplex recessive, *D d d*, should give a ratio of 1:1. It has been shown, however, that of functional eggs only about one-third instead of one-half are n + 1 and of functioning sperm less than two percent are n + 1. Approximate ratios of dominant to recessive expected in progenies of duplex dominant and simplex dominant maize trisomics in F_2 and in backcrosses to and by recessive diploids are as follows:

Duplex dominant		Simplex dominant	
D D d selfed —	12.5:1	*D d d* selfed —	1.7:1
D D d × *d d* —	3.5:1	*D d d* × *d d* —	1:1.25
d d × *D D d* —	2:1	*d d* × *D d d* —	1:2

All but one of these ratios (*D d d* × *d d* = 1:1.25) are in sharp contrast to the usual 3:1 and 1:1 ratios encountered in F_2 and backcrosses of heterozygous disomics.

While the identification of trisomic individuals by means of chromosome

counts from seedling root tips presents no serious difficulty, it is often possible to use trisomics as genetic tools without making chromosome counts. Thus, 2n + 1 plants with chromosome V trisomic are easily distinguished from diploids of the same cultures both as seedlings and through later stages of development. Trisomics which cannot be identified phenotypically can, not infrequently, be made use of without constant resort to chromosome counts. This can be done by keeping the trisomic cultures heterozygous for aleurone, endosperm, or seedling characters of the linkage group identified with the chromosome involved in the trisomic. Trisomic individuals can then be distinguished from their diploid sibs by the distorted ratios shown by their seeds or seedlings.

Chromosome deficiencies and deletions, though perhaps not so generally useful as trisomics in identifying a given gene or linkage group with a particular chromosome, not infrequently afford specific information as to the region of a chromosome in which a particular gene has its locus. Thus, if a plant homozygous for a recessive gene or group of genes is crossed with X-rayed pollen from a plant homozygous for the dominant allelomorphs of those genes, a few of the resulting plants may exhibit the recessive character of the seed parent rather than the dominant character of the pollen parent. Some such plants are maternal haploids. Others are 2n -1 individuals due to the loss of an entire chromosome of the chromosome complement of the pollen parent. In other cases, cytological examination reveals the loss of the terminal part of one chromosome or even of a small piece from some other part of a chromosome.

The inference is clear in such cases that the observed deficiency or deletion has resulted in the loss of a dominant gene carried by the pollen parent and that, therefore, the locus of that gene must have been in the lost part of the chromosome. By such studies (McCLINTOCK 1931b) it has been shown that the gene l_g is very near the end of the short arm of chromosome II, gene a_1 near the end of the long arm of chromosome III, P_l probably near the middle of the long arm of chromosome VI, and Y between P_l and the satellite, and that R is in the long arm of chromosome X. Very recently it has been shown (McCLINTOCK unpublished) that j lies near the end of the long arm of chromosome VIII. This is the only case so far of the placement of a gene in a particular linkage group by other than purely genetic methods. Male sterile-8 (BEADLE unpublished) belongs in the same group. Only one other gene, C_h, has been placed even tentatively in this group (ANDERSON and EMERSON 1931). This was done by the process of elimination; C_h shows no linkage with appropriate tester genes in any of the other nine groups. Very recently, however, it has been shown by use

of a trisomic involving chromosome VIII (BURNHAM unpublished) that C_h is not in that chromosome. This illustrates well the difficulty of locating genes with entire assurance by genetic methods alone.

Reciprocal translocations, as well as trisomics and deficiencies, can be used to identify the chromosome carrying the genes of a particular linkage group. By this means it has been shown (BURNHAM 1930) that genes of the *P-br* linkage group are borne by chromosome I. By means of a somewhat unique combination of a trisomic and a reciprocal translocation involving chromosomes VIII and IX (MCCLINTOCK 1931a) it has been found not only that genes of the *C-wx* linkage group are borne by chromosome IX but also that *C* is near the end of the short arm and that the genes of the entire linkage map as now known involve little more than the short arm of that chromosome.

The simple reciprocal translocations, those involving only two nonhomologous chromosomes, so far as they have been identified cytologically, are associated with about 50 percent of pollen and of egg sterility. Such semisterility can be used in linkage studies much as it could be if it occurred as a gene mutation, except that it shows linkage with genes of two linkage groups (BRINK and BURNHAM 1929). The point of breaking and reattachment of the chromosomes involved in a reciprocal translocation can be determined cytologically with respect to knobs, fiber attachment points, etc. Semisterility resulting from reciprocal translocations can be used with two genes in three-point genetic tests as an aid in determining the approximate loci of those genes. The absence of interference to double crossing over between genes on opposite sides of the translocation (RHOADES 1931) is a further aid in fixing the approximate location of the genes included with semisterility in three-point tests.

MUTATIONS IN MAIZE

Little need be said about mutations in maize. Most of the genes studied by geneticists are assumed to have arisen earlier as point mutations. Relatively few of the genes with which we deal are known to have occurred in controlled pedigreed materials. Irradiation has induced, in addition to deficiencies, translocations and other chromosome abnormalities, what appear to be typical gene mutations. Whether or not they are minute deletions is not as yet known. But do we know that naturally occurring point mutations are never such deletions?

The situation with respect to variegated pericarp of maize has been interpreted by the writer as a case of somatic mutation. The variegated type changes somatically to self color with high or low frequency depending

on the strain involved. Self color then behaves as a simple dominant to variegation. Reverse changes from self color to recessive variegation occur but with less frequency in most strains than the change from variegation to self color. The several strains of variegated maize are conceived to differ fundamentally only in respect to the frequency of change to self color. In other words, they are considered as differing only in mutation rate.

Crosses between variegated strains of very low mutation rate and stable colorless races usually exhibit a greatly increased rate of mutation. In F_2 of such crosses high and low mutability are linked with the gene for pericarp color, *P*. Colorless segregates from a heterozygous variegation culture of low mutability, when crossed with homozygous variegates of low mutability, do not increase the rate of mutation in F_1.

The writer is quite unable to interpret these facts on the basis of chromosome non-disjunction or the elimination of chromosome fragments in somatic mitosis.

SEX EXPRESSION IN MAIZE

Normal maize plants are usually monoecious, the terminal inflorescence bearing staminate and the lateral inflorescence bearing pistillate flowers. Numerous genes, mostly recessive, however, influence the expression of sex. Thus, in certain dwarf and semi-dwarf types stamens regularly develop in the flowers of the lateral inflorescence, resulting in an andro-monoecious condition. A few types are, barring infrequent sex reversal, wholly staminate flowered and others are wholly pistillate flowered. Of the former are barren stalk and silkless and of the latter tassel seed-1, -2, and -3.

A dioecious strain has been produced by JONES, involving tassel seed-2 and silkless. The writer has similar strains involving barren stalk-1 and tassel seed-2 and -3. In view of the fact that of some animals—Drosophila, man, and certain fishes—the male is the heterogametic sex, while of others—birds, moths, and certain fishes—the female is heterogametic, the status of dioecious maize is of interest. One of the writer's dioecious strains involves barren stalk-1 and tassel seed-2, both recessives. The male is $ba_1\ ba_1\ Ts_2\ ts_2$, heterogametic, while the female is $ba_1\ ba_1\ ts_2\ ts_2$, homogametic. The other strain involves barren stalk-1 with tassel seed-3, the latter a dominant. Here the male is $ba_1\ ba_1\ ts_3\ ts_3$, homogametic, and the female is $ba_1\ ba_1\ Ts_3\ ts_3$, heterogametic.

It is perhaps worth noting that in these synthetic dioecious strains of maize, the two sexes are differentiated by a single pair of genetic factors whose loci on the chromosomes are known.

MISCELLANEOUS OBSERVATIONS

Complex translocations. Reference was made earlier to simple reciprocal translocations involving two non-homologous chromosomes. These form rings of four chromosomes at diakinesis, as in other materials. By combining different semisterile types, rings of six or more chromosomes or two rings of four each result. Since maize chromosomes are differentiated morphologically and since all the ten pairs of chromosomes carry workable genes which can be used as markers, maize affords excellent material for checking similar situations previously noted in Oenothera and Datura.

Crossing over between chromatids. Maize trisomics have been found useful in determining whether crossing over in plants ever occurs after synaptic chromosomes have split to form four chromatids. RHOADES (1932 and unpublished) has shown by this means that crossing over does occur in the double-strand stage.

Teosinte-maize hybrids. It has been shown (EMERSON and BEADLE 1932) that hybrids of maize with annual teosinte exhibit in general normal crossing over. The only exception to this so far discovered is the entire or almost entire absence of crossing over between chromosome IX, the *C-sh-wx* chromosome, of maize and its homolog in Florida and in Durango teosinte. Normal crossing over occurs between these chromosomes of maize and Chalco teosinte. It has been suggested but not proved that this failure of crossing over may be due to inversions in the region of the ninth chromosome in question.

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