[1] *Jour. Hered.*, **26**, 162 (1935).

[2] *The American Anatomical Memoirs*, No. 17, p. 59 (1939); *Anat. Rec.* **81**, p. 283 (1941).

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EQUILIBRIUM IN GENIC MATERIALS

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Inbred strains of maize, continuously inbred for many generations, are favorable material to show small heritable variations. Changes in cob and silk color, plant and ear size, and in the amount of chlorophyll have been reported (Jones, 1924, 1939; Singleton, 1943). These alterations either have no effect upon vigor and productiveness or clearly reduce the plants in some degree. In addition to these, other heritable changes have been found recently in various inbred material. All of these lessen the ability of the plant to grow and to reproduce itself in some measure. In their total effect upon the inbred plants, they appear to be degenerative changes.

Unexpectedly, it has been found that these apparently degenerate lines, when crossed back with their parental lines, show heterosis. Presumably, they differ by only a single gene. This point remains to be tested. Furthermore, one of these degenerate lines has been shown to give better results, than the parental normal line, in outcrosses. The changes so far noted affect both physiological and morphological characters and are listed as follows:

INBRED LINE	CHARACTERISTIC FEATURE	NATURE OF CHANGE
C14[a]	Late flowering	Tassels and silks appear later
C14	Blotched leaf	Chlorophyll reduced
C30	Reduced plant	Smaller in all parts, blooms earlier
C237	Reduced ear	Ears smaller, stalks taller
Illinois Hy	Dwarf plant	Internodes reduced in length
C.I. 4–8	Narrow leaf	Leaf width and stalk diameter smaller, blooms earlier
C.I. Kr (187-2)	Crooked stalk	Internodes shortened and bent
C.I. Kr (187-2)	Pale top	Chlorophyll reduced

[a] The letter C designates inbreds produced at the Connecticut Agricultural Experiment Station, New Haven, Connecticut. Illinois refers to the Agricultural Experiment Station at Urbana, Illinois, and C.I., the Office of Cereal Investigations, U. S. Department of Agriculture, Washington, D. C.

The reduced plant, C30, has been described by Singleton (1943, 1944). It is a change in the Purdue 39 inbred sweet corn originally found in Idaho. It is used in the production of Connecticut hybrid sweet corn. This single gene mutation gives evidence for increased growth in crosses with unrelated lines as well as a hybrid vigor effect when crossed with the parental line.

Increased growth in crosses of related lines was noted during the 1943 growing season in the narrow leaf line crossed back to the original plants from which it was derived. The narrow leaf condition was found two years previously in one progeny that had been grown from a single self-fertilized ear. When grown the following year in adjoining rows it was seen to be clearly distinct in width of leaf. It was crossed back to the original line to see if it would segregate as a single factor difference. When the original line, the deviating line and their first generation hybrid were all grown in adjoining rows in 1943, differences were clearly noticed.

The originally 4-8 line and the same line from a new source were alike, showing that no visible change had occurred in the parental line. The deviating narrow leaf line was smaller in leaf width and stalk diameter, the same or slightly taller in height of stalk, the same in time of shedding pollen but earlier by seven days in time of silking. Thus it was not a degeneration in all respects as earliness of flowering is a good measure of growth efficiency in maize. Any environmental or inherited condition that favors growth is reflected in a speeding up of the time of flowering.

The first generation hybrid plants resulting from the cross of the deviating narrow leaf line and the original line from which it came was equal to or better than the better parent in all characters. The combined result was a noticeably greener, and more robust plant that was early maturing and more productive of grain. Not enough plants were grown to measure these small differences accurately. The hybrid did not surpass either parent in any single character by a statistically significant margin but the total result was impressive, especially in yield of grain.

Illinois Hy is an inbred that is widely used in the production of hybrid field corn. A dwarf form of this inbred was compared with the original line for two years. It has proved to be typical Hy in all details of color and structure except that the internodes are shorter, and the leaves smaller. The plant is brachytic in type, averaging about half the height of the original line. The dwarf plants flower at the same time as their normal parent and produce smaller ears with smaller kernels and are somewhat less productive in total amount of grain. While the segregation of this character has not been tested, dwarfs of this type have appeared in other lines and are usually due to a single mendelizing recessive gene.

The first generation of the cross of dwarf and normal Hy was grown alongside the normal plants. The crossed plants averaged the same in height but shed pollen two days earlier and silked four days earlier. The plants were noticeably greener and more thrifty in appearance during the growing season and at maturity the ears were larger with brighter and better filled kernels. As the hybrid vigor effect was not anticipated only a few plants were grown and most of the ears were used for hand pollination so that no yield figures are available. The earlier flowering and maturing is a clear indication of heightened growth efficiency.

An inbred line of Leaming, C14, has been continuously self-fertilized for 21 generations. After the first ten generations it was reduced to a high degree of uniformity and constancy. In the 17th generation a conspicuously tall darker green plant, flowering early, was noted in one progeny. This single plant had the appearance of a typical C14 slightly enlarged and invigorated as if it was growing in a particularly fertile spot. It was not large enough to be an outcross such as appear occasionally as a result of contamination with pollen from unrelated plants. This deviating plant was self-fertilized and the resulting ear was larger and better matured than the other self-fertilized ears in the same progeny. The kernels were marked with a faint pericarp stripe not characteristic of any other varieties that had been grown that year or before.

The progeny grown from this ear was noticeably taller, greener and more productive than the other related lines. It was slightly more variable but showed no clear segregation. Several plants were self-fertilized and grown for two successive generations. Some of these now differ from the original line in glume and internode color and in the amount of chlorophyll blotching shown by the leaves late in the season. All progenies have been reduced to the same level of productiveness as the original line or below.

The segregation of color markings indicates that the original plant could have resulted from an outcross with a related back-crossed line that was growing nearby the year before the deviating plant was discovered. It was so considered until the behavior of the other deviating lines was noted. The possibility that this is a mutation originating in the heterozygous condition must now be considered.

One line from this source more heavily blotched than the original is now noticeably less vigorous and productive. Whatever its origin it differs from the original C14 line by only a small germinal alteration. When crossed with the normal line the first generation hybrid plants were taller, greener and more productive. Here again the differences are small and not statistically significant for any one measurable character but all are in the same direction of increased growth efficiency.

The reduced ear size character has been described previously (Jones, 1939) as a change in two directions. The number of kernels on the ear is reduced but the height of plant is increased. Crossed with the original this deviating line showed no increasing effect in either height of stalk or production of grain. The first generation plants were intermediate in both respects.

A single factor mutation in tobacco (Jones, 1921) gives results in the heterozygous condition that are superior in some respects to either parent. In this case the change is from the determinate to the indeterminate habit of growth. The heterozygous plants average several more leaves and more flowers per plant than the determinate parent and produce a larger amount of total plant material than either parent in the same period of growth.

Several other deviating lines in maize have been found but have not yet been compared in crosses with their parental lines. Late flowering plants appeared in another progeny of C14 also in the 17th generation. The seedlings germinate more slowly and the plants are shorter than their normal sibs throughout the growing period. At the end of the season, when the normal plants cease to increase in height, the late flowering plants continue growth for a longer time until they are either as tall or almost as tall as normal when elongation ceases.

In 1942 the normal line averaged 84.0 inches in height to the tip of the tassel and the late flowering line 78.9. In 1943 the heights are 78.2 and 75.9, respectively. In time of flowering in 1943 the two lines compare as follows:

DAYS FROM PLANTING TO	FIRST TASSEL	LAST TASSEL	FIRST SILK	LAST SILK
Late flowering line	63	67	66	78
Normal flowering line	59	65	61	66
Differences	4	2	5	12

The number of days is counted from date of planting to pollen shedding and first appearance of silks. The results are based on an average of four replicated plots in each case. The two lines differ in no morphological character and at the end of the season appear to be alike in every respect.

In 1942 several progenies of C.I. Kr (187-2) were grown from single self-fertilized ears all coming from a single line that had been inbred for many years and grown in Connecticut four generations with continuous self-fertilization. No unusual variations had been noted in previous years. In 1942 several progenies were segregating for an obscure chlorophyll variation. A few plants were noted in the early stages of growth as being shorter and lighter in color at the base of the upper leaves. These plants were marked and self-fertilized. At time of flowering the differences had largely disappeared, the plants were entirely normal in appearance but were usually a few days later in silking. At maturity the plants were so nearly the same as the normal plants in height and productiveness that they could not be noted as deviations.

When grown the following year two progenies were homozygous for this pale top condition, four were segregating and six were free of it. In the homozygous progenies the plants were now noticeably reduced in size throughout the season. The stalks were more slender and shorter at maturity. One homozygous pale top progeny measured 72.8 inches in height compared to six normal progenies that averaged 76.8. The plants flowered later and the ears were smaller and less well matured. Chlorophyll color was a little lighter throughout the season although the plants grew out of the early pale top condition and were not clearly differentiated in this respect after flowering. Only when they were growing together in an entire row were they distinctly different. Nevertheless, the deviating plants appeared to be more differentiated from normal the second year than when they first appeared as segregates from normal. The condition had become progressively worse.

In one of the progenies, segregating for pale top in 1942, one normal green plant was noted as distinctly shorter at maturity. Upon closer examination it was seen that two internodes at the base of the plant were much shortened and bent. The progeny grown from the self-fertilized seed of this plant were all crooked in the same way as the parent, varying in the number of internodes affected from one to five. In some plants alternate internodes are shortened and bent, the intervening internodes being normal.

Out of thirteen progenies grown, six are normal, four are segregating normal and crooked stalk, and three are all crooked. In two of the latter the parental plant was not noted as being abnormal in stalk formation. All of the progenies showing crooked stalks are also either homozygous or heterozygous for pale top and all of the progenies showing pale top are either homozygous or heterozygous for crooked stalk. Apparently the two deviating types originated at the same time. They both behave as mendelian recessives. One progeny is also segregating for flat cobs. Further tests are needed to show whether or not these three conditions are associated in any way and the meaning of the simultaneous appearance of the three degenerate types.

Neither pale top nor crooked stalk have been tested in crosses with normal related or unrelated lines. But there is an indication that the normal plants heterozygous for one or both conditions are taller than homozygous normals. Two progenies segregating for pale top and crooked stalks averaged 80.1 inches in height compared to the six normal progenies which averaged 76.8 in adjacent rows. The segregating progenies had several deviating plants that were clearly shorter than normal and these were included in the measurements. The heterozygous normal plants must be taller than the homozygous normal to more than make up for this difference.

In all cases so far observed the deviating lines originate in heterozygous normal plants that are selected either wittingly or unwittingly for propagation. The larger growth of the heterozygous plants increases the chance that they will be used as the progenitors for the succeeding generations. The maintenance of inbred strains to be used in the production of hybrid corn is a more difficult problem than was at first realized. Even if the reduced lines do give better results in crosses the propagation of the inbred line may become prohibitively costly. This apparently has happened in several widely used inbreds which are now so unproductive as to be difficult to produce in those regions where the hybrids from them are still among the most productive.

The increased growth shown by some and possibly all of these related crosses results in each case from a single allelic difference. This at first sight appears to be a stimulus of heterozygosis as originally postulated by East (1909), East and Hayes (1912) and Shull (1914). This conception was extended by Rasmusson (1934) and by East (1936) as an interaction between alleles. East dismissed these defective genes as having no importance in heterosis. It is now apparent that no clear distinction can be made between normal and degenerate characters since they may have multiple effects, some favorable, some unfavorable. Dunn and Caspari (1942) describe numerous changes in a small section of a mouse chromosome having diverse effects, some lethal, others having degenerate effects. Hybrid combinations of some of these multiple changes promote normal growth.

Deviating lines show a loss in some respects and a gain in others. The earlier flowering of the narrow leaf and reduced plant lines is an indication of increased growth efficiency. There seems to be an equilibrium in genic substances such that a change in one direction may be counter-balanced by a change in another. Whatever the deviating line has lost the original line supplies in their crossbred offspring. What the deviating line has acquired may be added to the sum total of genic action. Along with this there is the accumulation of non-allelic, favorable growth factors that is known to occur.

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