

A REGULAR AND CONTINUING CONVERSION-TYPE PHENOMENON
AT THE B LOCUS IN MAIZE*

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It is extremely difficult to visualize a feasible process by which one molecule might transmute another into a copy of itself. In its original usage¹ the term *conversion* was concerned with changes in genes as abstract units; the assumption that *molecular* conversion was implied has come about with the development of molecular concepts for genic structure. As Goldschmidt points out,² "conversion" has been used to describe phenomena with effects that "do not fit into the classical conception of segregation and crossing over" in recent examples. No particular mechanism is implied in such usage—the term is thus applied in the same way as "position effect," "mutable locus," "crossing over," and "transformation."

This paper presents data on an effect in maize that is evidently of the conversion type, when considered in terms of phenotypic expression.

Materials and Observations.—At the *B* locus on chromosome 2, three known alleles,³ *B*, *B*^w, and *b*, confer, respectively, intense, weak, and no anthocyanin color in the husks, sheaths, culm, and other less conspicuous plant parts. Dominance is in the same order but is not quite complete. This locus has not yet been given an extensive analysis for variability, compoundness, or mutation, but apparently there are other alleles, perhaps more complex in their relationships.

In 1953, two weak-colored plants were observed among approximately 140 in the uniform progeny of a single intense-sun-red (*B B pl pl*) individual. The two exceptions occurred separately, one on each of two selfed ears of one parent plant. Testing was obviously in order, for they were unusual from the first: if mutation of *B* to *B*^w had occurred, these exceptions would have had to be homozygous for *B*^w, but their frequency in the progeny did not suggest a segregation ratio; if a newly-arisen dominant weak (at any locus) had arisen, it would be a previously unobserved type.

The two exceptional plants were self-pollinated and crossed onto intense individuals of the same line. Figure 1 shows the combined results of these and subsequent pollinations. The self-pollinated progenies did not segregate for color but remained uniformly weak in color through three generations of selfing. Outcrosses to intense were all weak and continued to give only weak progeny throughout three generations of outcrossing as male and female to four widely different strains having intense color. Self-pollination of these outcrosses yielded no intense individuals.

Intense plants, *B*, have strong color in the husks, sheaths, culm, glume face, and glume bar; weak plants, designated as *B*^w, have only a flush of color in these parts, occasionally none, except for the dark-colored glume bar at the base of the tassel glumes. *B* and *B*^w are most conspicuously differentiated by husk color. Plants of *b b* constitution have no color in any of these parts, and are most clearly distinguished from *B*^w by the absence of glume bar color.

As indicated in Figure 1, crosses of weak to green (*b b*) gave all weak plants in the

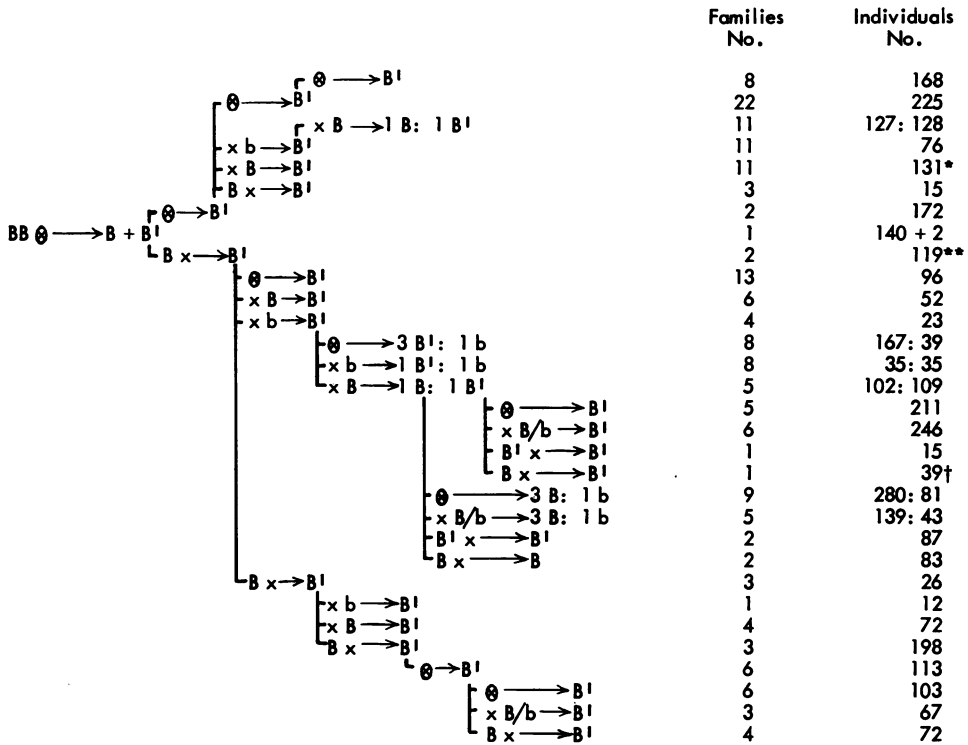


FIG. 1.—Progeny data for two exceptional maize plants with weak color and a continuing conversion-type effect. *B* = intense, *B'* = weak (converter), *b* = green plant color; “⊗” denotes self-pollination, “*B* x” a cross on *B B* egg parent, “x *B*” by *B B* pollen parent, “x *b*” by *b b* pollen parent, etc. The numbers of individuals observed are given at the right for each progeny; the number of families indicates the number of progenies observed (individuals in the previous generation).

* Plus one having intense color but no ear and no pollen.

** One with a definite intense sector.

† Plus two intense (see text).

F₁; when these were selfed or backcrossed to *b* they segregated normally for dominant weak and recessive green. Crosses of the *B' b* F₁ to intense showed a ratio of 1 intense:1 weak; these crosses gave the only segregants having intense color in any progenies derived from *B'* plants. All weak plants of this background, when progeny-tested, showed only the *B'* type; intense plants consistently showed an absence of *B'* and a segregation for *b*. It is significant that chromosome 2 markers (*lg*₁, *gl*₂, *v*₄, *Ch*, inversion 2a) introduced with *b* have segregated normally, appearing as expected in the progenies.

Figure 1 may be summarized as follows: Two exceptional weak-colored individuals arose in a large progeny of intense plants; these exceptions failed to segregate for intense on selfing and continued to confer weak color in backcrosses to intense egg parents through three repetitions and to intense pollen parents in several crosses; crosses of weak plants to the phenotypic null, *b*, when selfed or backcrossed, segregated for *b* and associated markers; *B' b* individuals crossed to intense gave half weak plants, which were *B' B'* by progeny test, and half intense plants, which were *B b*. Other progenies shown in the figure give peripheral information that is entirely confirmatory.

The few exceptions to the pattern presented here are indicated by footnotes in Figure 1. A single intense plant appeared in a progeny from an outcross by *B* but was barren of ear and died without shedding pollen. It is assumed that this individual was intense because of the typical pigment increase in injured or barren plants. The one observed sector for intense, in an outcross progeny, is of considerable interest. This otherwise weak individual had an intense sector including approximately $\frac{1}{8}$ of the circumference of the sheaths, extending from a node near the ground through the internode sheath just above the top ear, but including neither ear nor tassel. Several smaller *possible* sectors have been observed in these progenies, especially from similar crosses, but the manner of expression of sun-red color makes it difficult to distinguish occasional true sectoring from a pattern of pigmentation due to growth and light effects. The rarity or absence of germinal exceptions, which are expected with regularity in unstable systems, suggests that the weak type is stable. Some preliminary observations on purple (*Pl*; alternative to sun-red) plants with the *B'* system indicate that small sectors occur at a low frequency. The only remaining exceptions to the general pattern are two intense plants in one family of 41 in which only *B'* was expected. The family concerned has reduced pollen fertility in several plants, including one of the exceptions. This would suggest a chromosome aberration of some kind. Further study of this family may clarify the origin of these exceptions.

To determine whether plant color in a *B'* background changes on repeated selfing or outcrossing to *B*, husk color grades were estimated in a 1958 planting of these progenies, on an arbitrary scale of 0-6 for increasing color. The grading was objective to the extent that the grader knew neither the backgrounds of the families nor the purpose of the experiment. The grades of *B* and *B'* families did not overlap: *B* plants ranged from 3-6 (mostly 4-5), and *B'* plants ranged from 0-2 (mostly 1). Table 1 shows the grade averages for these progenies. It would appear that no consistent changes occur. However, outcrossing to intense lines may maintain a slightly higher average level of color than does selfing. The outcross progenies show no indication of segregation for grade in the raw data, although distinguishing segregation among grades 0, 1, and 2 is difficult because of their close similarity.

TABLE I
HUSK COLOR GRADES ON REPEATED SELFING AND BACKCROSSING OF WEAK-COLORED LINES

Source	No. Plants	Av. Grade
B comparator	38	4.6
<i>B'</i> (X)	75	1.0
<i>B'</i> (X) (X)	54	1.0
<i>B'</i> (X) (X) (X)	160	0.9
<i>B</i> × <i>B'</i>	51	1.2
<i>B</i> × <i>B</i> / <i>B'</i>	7	1.9
<i>B</i> × <i>B</i> /(<i>B</i> / <i>B'</i>)	46	1.0

New occurrences of *B'* plants are observed occasionally in the original intense sun-red line, in frequencies varying from single exceptions in large families up to one-half or more of the progeny. In one case mutation of the whole family is suspected. Some derivatives of the original line appear to be stable; others seem to have a high potential for mutation to *B'* but do not have conspicuous weak sectors on the intense plants. An "ear map" of one *B'*-carrying progeny, in which the seeds were planted and observed according to their position on the ear, only vaguely

suggests the occurrence of sectors of B' on the ear, with varying sizes of "islands" of B' kernels. Preliminary tests on a few of these weak exceptions indicate properties parallel to those of the original B' individuals.

Discussion.—Segregates from $B' b \times B$ show a correlation of segregation for the weak color effect with segregation at the B locus on chromosome 2. In crosses of B' with B , however, normal segregation fails to occur, even when B' previously has gone through a generation of normal segregation with b . Known systems that can bring about failure of segregation, especially chromosomal transmission irregularities and cytoplasmic inheritance, should be explored.

If exclusive transmission of B' is involved, we must make the broad and improbable assumptions that B' is dominant for weak color, that exclusion of the B -carrying chromosome from the gametes is complete through both male and female, that no sterility occurs in connection with the exclusion, and that no exclusion of b gametes occurs. A simple test is in preparation, using a marked B chromosome to determine whether proper segregation occurs from heterozygotes with the B' chromosome. For the present it appears that a system completely associated with the B locus in which B' can exclude B but not b is very unlikely.

If a cytoplasmic factor is involved, it is rather unusual. It must be transmitted through both male and female with no reciprocal differences, be undiluted by repeated outcrossings as male, and have a remarkable relation to the nuclear genes in transmission—a plant carrying such a factor must produce B' gametes that bear the factor and b gametes that do not. These restrictions are not at all typical for cytoplasmically inherited effects in maize.⁴ A complicated mechanism for chromosomal attachment and detachment of a "cytoplasmic" factor could be constructed but seems superfluous at present.

A comparison of these effects with those recently described⁵ for certain alleles at the R locus in maize should be of interest. A striking similarity exists in the apparent interaction between alleles, and the basis for such interaction may very well be the same in the two cases. The two systems differ strikingly, however, in several ways. Changed R' (that is, R' or R'^{st} or R'^{mb}) is different from R^{st} or R^{mb} ; B' is monotonously constant from change-to-change. R^{st} and R^{mb} are mutable; B' is relatively stable. When made homozygous, R' reverts very nearly to R' ; B' continues unchanged on selfing. Thus in the phenomenon presented here there appears to be a very specific induced change of B to B' —all the properties of B' are conferred upon B . In the R case the change that occurs is specific and may involve allele interactions, but the changed allele has few of the properties of its inducer. Indeed, the parallel relationship of changes in the two components⁶ of this established compound locus indicates a mechanism distinct from the genes themselves, as does the reversibility of the change.⁷

The term *conversion*, originally applied by Winkler¹ to explain crossing over, has come to be discredited with later demonstrations of Mendelian explanations for apparent examples. Notwithstanding these clarifications, the term is useful, when held distinct from any implied mechanisms, in categorizing an unexplained system with apparent interaction between alleles. In view of the phenomena of transformation and transduction in microorganisms, in which introduced hereditary material transfers its properties into the hereditary material of recipient cells, it would seem likely that, within a diploid heterozygous nucleus (carrying two dif-

ferent species of DNA at homologous loci), examples of similar transfer could exist. Goldschmidt⁸ recently applied such an explanation to an interesting case in *Drosophila*; he suggested a separate "transductor locus" to transfer a segment of chromosome from one homolog to the other. A distinct element which would presumably have similar properties was suggested by Brink⁹ for the *R* case in maize. In the absence of indications for separability of such an element from *B'* by crossing over or transposition, or for multiple-locus action, no distinct element is implied in the system presented here. If such an element were invoked, a "transductor" would simply be a repository for the unusual effects at the *B* locus. Certainly a more likely mechanism would be one of enforced copying of *B'* as a property of *B'* itself, carried out at some time or times in the life cycle of *B'/B* plants. This is, of course, one method by which a phenotypic conversion could occur. A clear distinction should be drawn between conversion observed at the level of the whole life cycle of the organism and that observed at the level of replications of single chromosome strands or virus particles. However, conversion-type events observed in any system must be kept distinct from the mechanism^{10, 11} used to explain them.

The striking features of the system presented here are the regularity (or infallibility) of the conversion effect, and the continuity of the effect from one life cycle to the next. Whatever their mechanism, the possibility should not be overlooked that conversion effects may occur, whether as infrequent exceptions for most loci or as the rule for certain loci. Maize should not be unique in this behavior; infrequent natural occurrence might be expected in any organism.

Summary.—An effect on plant color in maize, interpreted as a regular conversion of one allele at the *B* locus by another at some time or times in the life cycle, is reported. The effect is a continuing one in that the "converted" *B*, termed *B'*, is also regularly able to "convert" newly introduced *B*. The phenotypically null allele (*b*) is unaffected by *B'*.

The basic pattern is one of absolute failure of segregation when *B'* plants (weak color) are crossed repeatedly to *B* plants (intense color) as male or female, or when the *B'* individuals from such crosses are self-pollinated. Only when *B'* plants are crossed to *b* (green) and backcrossed to *B* do intense individuals appear. The intense individuals in these segregating progenies have received the chromosome 2 carrying *b*, and segregate *b*; the weak individuals have received the *B'* chromosome, and fail to segregate for *b* or *B*.

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