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An Unstable Locus in Soybeans[1]

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Summary. Investigation of a variegated condition in the soybean variety Lincoln indicates instability at the *Y* locus. Leaf sectors of chlorophyll-less yellow tissue occur in distinct heritable patterns; some leaves have small flecks of yellow tissue (late occurring mutations) and others possess large areas or whole leaflets (early occurring mutations).

There is evidence that this allele, Y^m_{18}, mutates to the wild type, *Y*, which is green and stable and to the recessive, *y*, which is yellow and lethal in the seedling condition. (With an increase in the amount of yellow tissue there is an increase in the frequency of lethals.) However, changes from one type to the other are observed, and patterns of variegation representing different states of the instability are described. These depend upon the time and frequency of mutation events.

Evidence is presented to support the hypothesis that this instability is controlled by a factor that resides at the locus. Such a factor governs the timing of the mutation events and is related to similar elements in maize, which are part of specific mutable systems. Control of variegation of the Y^m_{18} locus is compared with the models proposed for the cases of instability in maize.

Introduction

Variegation in plants has long elicited interest among biologists because of its universal relevance to spontaneous gene mutation. A case of leaf variegation in soybeans, originating spontaneously in the Lincoln variety, possesses distinctive features that resemble cases of variegation in a wide variety of other plants (DEMEREC, 1935). Direction, frequency, and timing of the mutation event are similar; timing suggests the states of mutation that have been so extensively studied in maize (MCCLINTOCK, 1951, 1956a, 1956b; BRINK and NILAN, 1952 and PETERSON, 1960, 1961, 1968a) and also in *Antirrhinum* (HARRISON and FINCHAM, 1964).

In this report, an analysis will be made of the unstable allele Y^m, which controls chlorophyll production, its direction of mutation, and the various derivative patterns. It has been established that the instability resides at the *Y* locus (PETERSON and WEBER 1964) and the unstable allele has been designated Y^m_{18}. Further, a hypothetical depiction of the locus involved will be presented.

Materials and Methods and Description of the Mutant

This case of variegation arose spontaneously in a single plant in the soybean, *Glycine max* L. Merrill, variety Lincoln in 1951. Instability is expressed in the leaflets as yellow areas within green tissue and the size of the mutant tissue ranges from small (Figure 1B–1D) to large sectors (Figure 1E–1G), some of which involve an entire leaflet (Figure 1H) or a whole trifoliate leaf (Figure 2B). Usually a given plant exhibits a uniform variegation pattern. When the yellow area includes a large part of the leaf, mutation has occurred early (Figure 1E–1H). On the other hand, small patches of yellow tissue indicate late occurring events (Figure 1B-1D).

Some progeny of variegated plants are completely devoid of green tissue; these seedlings succumb after the food reserves of the seed have been exhausted and are, therefore, scored as lethals. Plants possessing even a small amount of green tissue are able to survive.

All progenies studied arose from selfing.

(Within this report, *Y* refers to the Y^m_{18} allele).

Results

Description of the variegation

In variegated plants yellow sectors appear within green tissue. As stated before, the size of these sectors varies from that of a pinhead to that of an entire leaf and depends upon the timing of the mutation event; larger sectors result from a mutation that occurs early in the ontogeny of the leaf tissue (Figure 1E–1M); small sectors are a consequence of late-occurring mutations (Figure 1B–1D). Changes from one pattern type to another occur infrequently as exceptional sectors in an otherwise uniformly variegated area (Figure 3B). These particular patterns of expression will be referred to as states, and these are designated early-mutating, Y^{m-e}, and late-mutating, Y^{m-l}.

Light or pale green sectors also occur (Figure 4). These appear pale rather than colorless because of differences in the genotypes of the layered leaf cells. If phenotypically the palisade tissue is green and the spongy tissue is yellow, the combination produces a pale-green coloration.

The unstable allele — Y^m

Plants with the unstable allele are phenotypically green until a mutation occurs. The allele is designated

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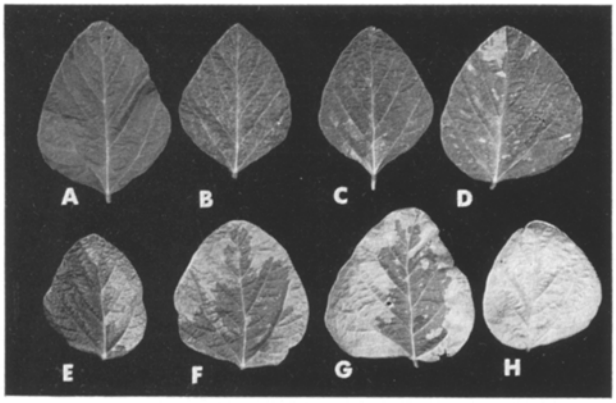

Fig. 1. Normal (A), variegated (B—G) and non green (H) leaflets. — B, C, D — late mutations; E, F, G — early and late mutations; N — all mutant. — Alternatively, B, C and D could represent homozygous plants Y^m/Y^m and E, F, and G, heterozygotes, Y^m/y

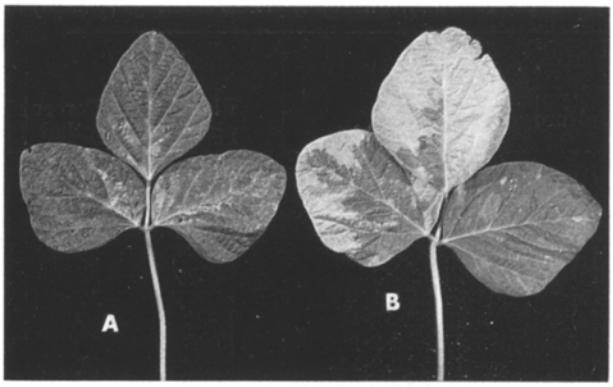

Fig. 3. Leaves from an original late variegation type. — A. Late mutations in all leaflets — parent pattern; B. One leaflet (right) is like those in A (original pattern); other two leaflets have some early mutations and their occurrence indicates a change from late to early-variegation type

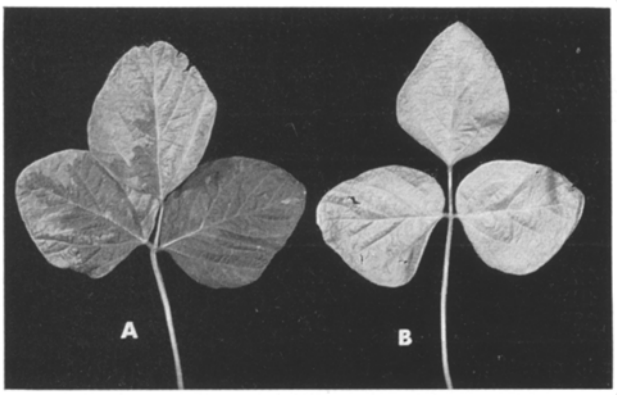

Fig. 2. A type of pattern variegation, — B. Mutant (yellow) seedling leaflets that arose from 2 A type

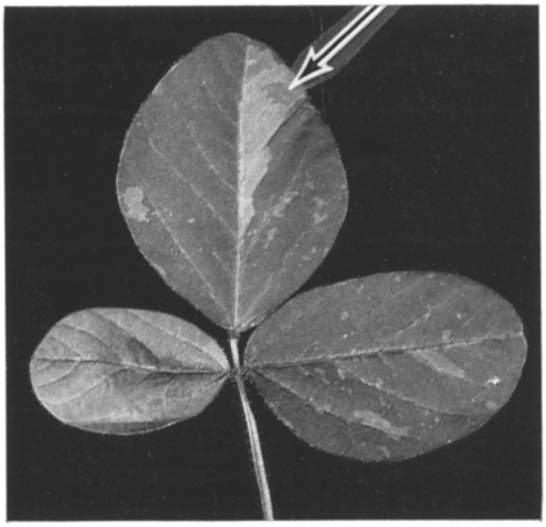

Fig. 4. Notice pale green mutant sectors (arrow) and yellow sectors; the pale green sector is due to differences in the genotype of the layered cells which result from phenotypically green palisade tissue and non-green spongy tissue

Y^m, dominant and unstable (Figures 1, 2, 3). The sectors showing a change are always yellow; in a background of green tissue this indicates that the direction of mutation is from Y^m to y. If the allele were recessive and unstable, one would expect to find green sectors (Y) in a yellow background. These are never found.

The mutation to y

The frequency and size of yellow sectors vary. Within a progeny row appearance of seedlings with excess yellow tissue is correlated with an increased frequency of non green seedlings, which are lethal subsequent to early seedling development in the field. The frequency of yellow seedlings (lethals) arising from the selfs of plants possessing diverse genotypes is shown in Table 1.

The newly arisen y allele is stable. As indicated previously, reversions of y to Y have not been observed. In view of this, the y allele is designated $y^{(nr)}$ (nonreverting) as opposed to a y that could revert. It resembles the non-reverting types in maize that arise from unstable alleles such as $a_1^{m(nr)}$ and $a_2^{m(nr)}$ of the *En* system (PETERSON, 1961, 1968a) and non-responding *bz* of the *Ac-Ds* system (MCCLINTOCK, 1956). Other stable, nonreverting types have been described, g^0 of a mutable flower color gene in china aster (HONDELMANN, 1958) and unspotted white in *Antirrhinum* (HARRISON and FINCHAM, 1964).

In general, the large sectoring types give a higher frequency of yellow seedlings (Table 1, items 6, 9, 12) than the small (low) sectoring types (Table 1, items 7 and 8). The presumed genotypes of each of the parent cultures (S_0 plants) of each of the progenies listed were confirmed by determining the distribution of homozygous (Y^m/Y^m) versus heterozygous (Y^m/y) genotypes among the unstable S_1 plants.

Table 1. *The frequency of yellow seedlings (lethals) arising from the selfs of plants and their presumed genotypes*

Culture	S_0 plants*	Plant phenotype	Percent lethal	Progeny test (S_1) plants Homo Hetero*** Y^m/Y^m 1 : 0 Y/y^s or Y^m/y^s 1 : 2	Presumed genotype original culture**
(1)	263-2-3	normal	27	13 : 17	Y/y^s
(2)	264-21-1	light	4	16 : 7	Y^m/Y
(3)	264-10-2	heavy	33	26 : 11	Y^m/y^s
(4)	264-11-2	heavy	59	1 : 8	Y^m/y^s
(5)	264-54-2	heavy	32	10 : 13	Y^m/y^s
(6)	264-61-1	heavy	37	11 : 13	Y^m/Y^m
(7)	264-10-2-1	light	7	11 : 8	Y^m/Y^m
(8)	264-10-2-7	light	10	11 : 15	Y^m/Y^m
(9)	264-10-2-14	heavy	33	8 : 4	Y^m/Y^m
(10)	264-10-2-28	heavy	28	1 : 10	Y^m/Y^m
(11)	264-11-2-6	heavy	43	0 : 12	Y^m/y^s
(12)	264-11-2-8	heavy	27	4 : 8	Y^m/Y^m

* S_0 plants = single plant selections.

** Based on 3 observations: plant phenotype, % lethality, and distribution of homozygotes-heterozygotes in the progeny tests of the S_0 plants.

*** The designation of the homozygote or heterozygote is based on the percent of yellow seedlings among the S_1 progeny. A value of less than 25% yellow seedlings would designate a homozygote and greater than 25%, a heterozygote.

Table 2. *Frequency of progeny types from plants with different phenotypes, each derived from the initial* 263-2 *variegated plant*

Item		Plant phenotype (parent)	Progeny: Non-lethal	Lethal	Total survived	Variegated	Green non-variegated	Presumed genotype of parent
1	263-2-1	light	43	15	43	29	12	Y^m/Y^m
2	263-2-2	heavy	23	27	18	13	4	Y^m/y^s
3	263-2-3	normal	37	18	38*	1	37	Y^m/y^s

* Excess survivors over non-lethal probably due to error in counting.

Among S_0 plants (table 1) the homozygous Y^m/Y^m types would be expected to give rise only to homozygous types. Of course, the continual mutation of Y^m to y results in a low frequency of y gametes replacing the original Y^m. These would give rise to heterozygotes (Y^m/y). The frequency of y gametes cannot be predicted because of the erratic nature of the mutating event. In any case, the frequency of the class designated as heterozygotes would be less than the frequency expected among the progeny of an original heterozygote Y^m/y. Without mutation of Y^m to y the expected distribution of homozygous (Y^m/Y^m) to heterozygous (Y^m/y) plants among the progeny of a homozygous type would be 1:0, but with heterozygous plants the ratio would be 1:2. However, the occurrence of y-containing gametes following Y^m to y mutation adds some heterozygotes to the progeny of the original homozygote and increases the frequency of heterozygotes among progeny of original heterozygous plants. Because of the highly unpredictable frequency of y containing gametes, it is not possible to absolutely define the phenotypic ratio designating the progeny of a heterozygote. Since the self of a Y^m/y^s plant should result in at least 25% yellow seedlings, a frequency of 25% or greater might indicate a heterozygous condition, and a frequency of less than 25% non-green seedlings would suggest a homozygotic one. A bias is possible here since some homozygotes with a very high frequency of sectoring would yield an abnormally high frequency of non green seedlings (example, Table 1, items 6, 9, and 12). But otherwise, this manner of defining genotypes leads to a fair approximation of the classes.

The green allele, Y, expresses the stable dominant green phenotype in the heterozygote, Y^m/Y. This is confirmed by examining the progeny of numerous normal plants. Two were from heterozygous Y^m/Y plants (Table 3, Part C).

Y^m mutates to Y

Three different types of plants were selected from the progeny of an original variegated plant, 263-2 (Table 2). It is evident from the distribution of the progeny of these three that the original plant, 263-2, was Y^m/Y^m or Y^m/y. Among the progeny of two of the plants (Table 2, items 1 and 2) green, non variegated plants segregated. Further, one of the three original progenies of 263-2 (Table 2, item 3) was green, nonvariegated. The seedling ratio of non

variegated to lethal suggests that the genotype is Y/y^s and indicates that Y (green) is dominant to y^s (yellow). This was confirmed by testing 30 of the surviving 37 green, nonvariegated plants. If the original plant (Table 2, item 3) was Y/y^s 1/3 of the resulting progeny would be expected to be Y/Y, and 2/3 would be expected to be Y/y^s. The genotype, Y/Y, is established by the complete absence of yellow seedlings and Y/y^s is indicated by the segregation of yellow seedlings. Though 25% yellow seedlings would be expected, there was a wide range in their occurrence because of the small size of the progeny. However, the occurrence of any nongreen seedlings would confirm the heterozygous nature of the plant, irrespective of their frequency. The predicted genotype, Y/y^s of the original plant (Table 2, item 3) is confirmed (see chi square analysis, Table 3). These results indicate that the Y^m allele mutates to Y. Further, Y is dominant to y. The high frequency of nongreen seedlings in the heavily variegated plant, 263-2-2 (Table 2, item 2), suggests that the excess numbers of yellow seedlings arose from the mutation of Y^m to y. Additional proof will be presented later.

It should also be pointed out that this Y allele arose from an original Y^m allele by mutation of Y^m to Y. Among the progeny of the original normal plant (Table 3, part B) only one questionable variegated seedling appeared among the 432 seedlings, which attests to the stability of the newly originated Y alleles derived from Y^m.

Table 3. *Distribution of progeny phenotypes of designated plants*

	Plant Type (parent)	Progeny					Genotype parent
		Non lethal	Lethal**	Total	Variegated	Normal	
A. Initial heterozygote Y/y^s-263-2-3							
263-2-3	green stable	37	18	38*	1	37	Y/y^s
B. Progeny test of green plants from 263-2-3							
263-2-3- 1	green stable	14	7	12	0	12	Y/y^s
- 2	green stable	24	0	23	0	23	Y/Y
- 3	green stable	13	0	12	0	12	Y/Y
- 4	green stable	27	3	25	1	24	Y/y^s
- 5	green stable	25	3	21	0	21	Y/y^s
- 6	green stable	31	0	28	0	28	Y/Y
- 7	green stable	33	0	33	0	33	Y/Y
- 8	green stable	12	2	12	0	12	Y/y^s
- 9	green stable	41	4	40	0	40	Y/y^s
-10	green stable	25	4	23	0	23	Y/y^s
-11	green stable	13	4	11	0	11	Y/y^s
-12	green stable	16	0	13	0	13	Y/Y
-13	green stable	35	0	30	0	30	Y/Y
-14	green stable	15	10	15	0	15	Y/y^s
-15	green stable	11	3	9	0	9	Y/y^s
-16	green stable	12	4	11	0	11	Y/y^s
-17	green stable	5	0	5	0	5	Y/Y
-18	green stable	13	0	15	0	15	Y/Y
-19	green stable	22	6	18	0	18	Y/y^s
-20	green stable	5	2	5	0	5	Y/y^s
-21	green stable	13	3	12	0	12	Y/y^s
-22	green stable	9	1	9	0	9	Y/y^s
-23	green stable	3	0	3	0	3	Y/Y
-24	green stable	9	0	8	0	8	Y/Y
-25	green stable	8	0	8	0	8	Y/Y
-26	green stable	11	1	9	0	9	Y/y^s
-27	green stable	5	0	5	0	5	Y/y^s
-28	green stable	7	0	7	0	7	Y/Y
-29	green stable	4	1	3	0	3	Y/y^s
-30	green stable	7	2	7	0	7	Y/y^s
C. Progeny test of two green stable types							
265-2-3	green stable	66	1	66	7	59	Y/Y^m
265-10-3	green stable	54	0	53	19	34	Y/Y^m

D. Chi square analysis of the distribution of genotypes among the progeny of 263-2-3

263-2-3	1-30	Y/Y	Y/y^s
observed	13	17	
expected	10	20	
χ^2	1.35		

* Excess survivors over non lethal due to original miscount.
** The low frequency probably due to differential survival.

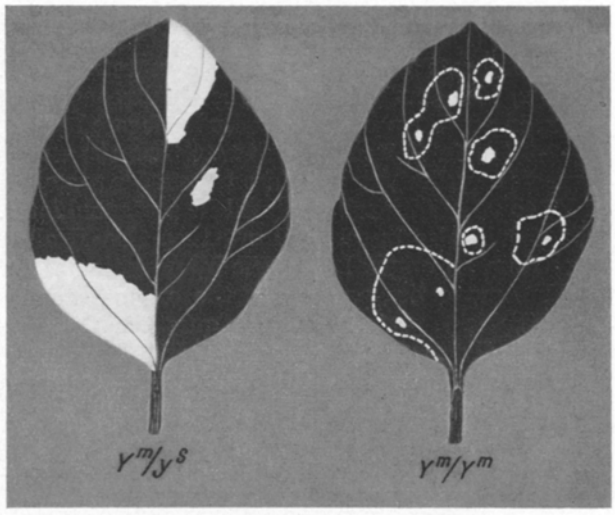

Fig. 5. A graphic representation of the expression of mutation in leaves of plants with the designated genotypes. In B, the broken dash outline in the Y^m/Y^m leaf indicates the size of sectors of the original mutation event that is not expressed until the second Y^m allele mutates — In A, each mutation of Y^m to y is expressed

The states of Y^m

Different patterns of variegation distinguish Y^m. Two explanations are possible, light versus dense types may be due to heterozygosity versus homozygosity or to late versus early timing of the mutation event. For example, early Y^{m-e} mutation leads to heavy sectoring in the leaves (Figures 1, E—H) and probable inclusion in gametic tissue. As indicated in a previous section, the early mutation of Y^m to y results in a high frequency of lethal types (Table 1, items 6, 9, 12). A late state (Y^{m-l}) is distinguished by small sectors (Figures 1, B—D, 3A). The lateness of the event in Y^{m-l} reduces the possibility of the inclusion of the newly originated sector in gamete-forming tissue and consequently the production of y gametes in plants containing the Y^{m-l} allele.

The timing of the mutation event is critical and affects the frequency of appearance of mutant sectors. States that control early mutations produce fewer individual mutations than late states.

Proof for heritability of states is confounded by the difficulty in determining genotypes from the phenotypic appearance of individual plants. In a heterozygous plant, Y^m/y^s, any mutation in the leaf would be immediately expressed (graphically illustrated in Figure 5A). This gives the appearance of heavy sectoring. In the homozygote, (Y^m/Y^m), however, two simultaneous mutations are necessary for the expression of a yellow sector. This is due to the dominance of the non-mutated, Y^m, which masks the expression of the mutated allele until the second Y^m allele also mutates (dash lines in Figure 5B). Thus, it is evident that homozygosity can mask the true state of the allele. A heterozygote possessing a late-state allele, Y^{m-l}/y^s, would mimic the homozygote of an early state, Y^{m-e}. An attempt can be made to distinguish between the possibilities by examining the progeny of plants originating from a single isolated allele.

Among a group of mutant plants characterized by medium to heavy variegation, light variegated plants were selected. After two generations of further selection to analyze the particular light type, the progeny of one plant, light variegated, was tested. Seedling counts (i.e., green vs. non green) were made of the progeny of 32 individual plants to determine the distribution of genotypes. From the analysis of the distribution of genotypes it is evident that the selected plant originally considered to be light variegated was green and therefore the Y allele arose from Y^m to Y mutation. Nine of the 32 S_1 plants were Y/Y. The remaining 23 Y/Y^m or Y^m/Y^m. In Figure 6A, the distribution of lethals in these segregating plants (1/3 of those in 6A are expected to be Y^m/Y^m) is presented. The distribution of this light type can be compared with another selection characterized by a medium variegation. As with the previous light type, this medium type was isolated to analyze the heritability pattern, and seedling counts were made of the progenies of individual S_1 plants. The progeny of the medium type (similar to the leaf in Figure 1B) arose from an S_0 plant that produced 18.1% lethals. Since this is less than 25% (expected if the genotype is Y^m/y) and the mutation is characterized by a medium level of variegation, one would hypothesize that the original S_0 plant was Y^m/Y^m. The distribution of lethal frequencies among the 41 S_1 plants (Figure 6B) supports this supposition. There were 26 S_1 plants with more than 45% lethals. This represents a y gamete frequency of approximately .7 among these plants. Fifteen of the S_1 plants had lethal frequencies of less than 45%. The first group

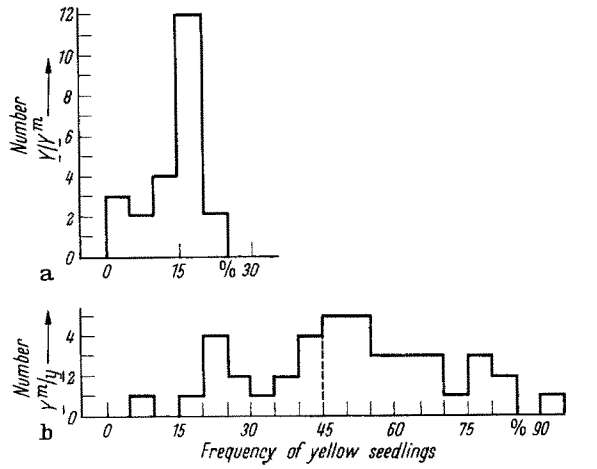

Fig. 6. Distribution of frequencies of yellow seedlings among the progeny of plants with the designated genotypes. — A. Y^m/Y — phenotypically green; B. Y^m/y — phenotypically variegated

(above 45%) probably includes heterozygotes, Y^m/y, with a base value of 25% lethals; the additional lethals would originate from Y^m to y mutation. The group below 45% probably includes Y^m/Y^m plants and the high frequency of lethals arises from a high rate of Y^m changes to y.

If it is assumed that the S_0 plant containing the medium variegated Y^m allele in this series was a heterozygote, approximately 26 of the S_1 plants would be expected to be heterozygotes. The remaining 15 plants would then be homozygotes. It is evident that some of the homozygous plants have a high frequency of lethals. A comparison of the distribution of the two types (Figure 6A and B) shows that there is a difference in the frequency of lethals arising from variegated plants of light versus medium states.

In addition to the above differentiated states, changes from one pattern to another are observed within individual leaves. Further, initial S_0 plants of a specific pattern type give rise to distinctly different patterns among the progeny. For example, late types have been isolated from an original early pattern type. In addition, a wide variety of pattern types have been isolated from an original variegated plant containing only one variegated allele. Though the presence of particular selected types does not exclude genetic modifiers (highly unlikely since the whole population is nearly isogenic having descended from a single plant of a relatively uniform variety, Lincoln) as a basis for the distinctiveness of the phenotypic patterns of variegation, the changes in pattern type within an individual leaf support the concept of early and late states of the allele.

More conclusive proof could be obtained by outcrossing a series of putatively designated states. An analysis of the subsequent progenies with their accompanying patterns would aid in further distinguishing between these alternatives.

Discussion

Model for variegation of the Y^m allele

Observation of the phenotypic pattern, yellow sectors within green areas and the absence of green sectors within non-green tissue, supports the hypothesis that the unstable allele Y^m is a dominant green allele that mutates to stable green and recessive yellow. The rate of occurrence of y from a particular Y^m allele is very high (Table 1: some Y^m/Y^m plants have a 60% frequency of y gametes). Less frequently the change is to the stable green allele, Y. The direction of change and the accompanying phenotypes of each of the alleles are shown in Figure 7.

This case, therefore, where a dominant allele frequently reverts to a recessive form, is in contrast to those cases of instability extensively investigated in maize, where generally the direction of change is from the recessive to the dominant form.

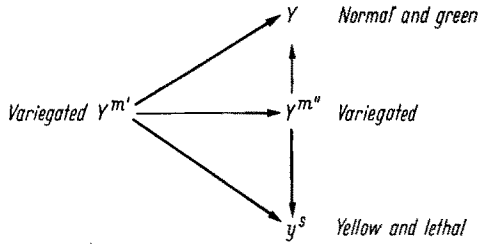

Fig. 7. Direction of change and plant types associated with the unstable Y^m complex; $Y^{m'}$ and $Y^{m''}$ — medium and light variegated, respectively

The maize cases of instability are ascribed to a suppression of the dominant allele that results in the recessive phenotype. It has been demonstrated in several systems (McCLINTOCK, 1951, 1956a, 1956b); BRINK and NILAN 1952; PETERSON, 1960, 1961, 1968b) that change from recessive to dominant is accompanied by the removal of a suppressing element from the locus involved. This leads to full expression of the dominant allele.

With the Y^m allele mutating in the reverse direction, it is difficult to hypothesize element insertion which would result in suppression of Y since one would expect an occasional loss of the element within a yellow sector. This would lead to the appearance of green sectors within yellow tissue. As was pointed out in the results, none were found. Proof for the presence of suppressing elements requires an extensive crossing program and the availability of a tester allele (such as $a_1^{m(r)}$ in the *En* system — PETERSON 1961); it has not been possible in this material.

One of the clues for the presence of elements causing variegation is the appearance of instability at other loci. As has been demonstrated in the case of instability in maize, elements of a system such as *Ac—Ds* or *En—I* are transposed from one locus to another causing instability at the new sites (McCLINTOCK, 1953; PETERSON, 1963, 1968a). Further, the insertion of an element at a locus can result in the origin of novel variation, a type that is not apparent in natural populations (PETERSON, 1966a). Such variation might be useful in a breeding program.

The different patterns that have been considered as states of the allele represent a universal feature characteristic of unstable genes. States of high and low instability observed in *Antirrhinum* (HARRISON and FINCHAM, 1964) are examples of extreme differences. A series representing a continuous spectrum is found in maize (McCLINTOCK 1951, 1956b; PETERSON, 1960, 1961, 1966b), in *Pharbitis* (IMAI and TABUCHI, 1938) and in many other plants (reviewed by DEMEREC, 1935). Since indications are that timing of the mutation event is critical, the mechanism of timing control should be investigated further.

Zusammenfassung

Die Untersuchung eines variegaten Zustandes bei der Sojabohnensorte 'Lincoln' führte zum Nachweis einer Instabilität des *Y*-Locus. Blattsektoren mit chlorophyllfreiem gelbem Gewebe traten in bestimmten erblichen Mustern auf. Einige Blätter wiesen kleine Flecken gelben Gewebes auf (spät eingetretene Mutationen), während andere große Flächen oder vollständig gelbe Blättchen besaßen (früh eingetretene Mutationen).

Es gibt Beweise dafür, daß das entsprechende Allel Y^m_{18} sowohl zum stabilen Wildtypallel *Y*, mit grünem Phänotyp, als auch zum rezessiv gelben *y*, das im Sämlingsstadium letal wirkt, mutiert. (Eine Zunahme der Menge gelben Gewebes ist mit einer Zunahme der Letalfrequenz verbunden.) Umwandlungen eines Typs zu einem anderen werden beobachtet und Variegationsmuster beschrieben, die unterschiedliche Stadien der Instabilität verkörpern. Diese hängen von dem Zeitpunkt und der Frequenz der Mutationsereignisse ab.

Es werden Beweise vorgelegt, die die Hypothese stützen, daß diese Instabilität durch einen Faktor kontrolliert wird, der sich am Locus befindet. Ein Faktor dieser Art kontrolliert das zeitliche Auftreten der Mutationsereignisse. Er ist mit ähnlichen Elementen des Maises verwandt, die Teile eines spezifisch mutablen Systems sind. Die Kontrolle der Variegation durch den Y^m_{18}-Locus wird mit den Modellen verglichen, die für die Fälle der Instabilität beim Mais vorgeschlagen wurden.

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