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Agronomy Department, University of California, Davis

An Additional Gametophyte Factor in the Lima Bean[1]

By **R. W. ALLARD**

Introduction

Assays have been conducted periodically during the past 15 years to determine the frequencies of homozygotes and heterozygotes at a number of loci governing conspicuous color and morphological differences in several mass-propagated lima bean populations. In these assays the segregation ratios observed in the progenies of heterozygous individuals have usually conformed to expected Mendelian ratios for each of 8 loci which have been studied extensively, but significant deviations from Mendelian expectations were observed in a small proportion of families in each generation. Presumably most of these deviant ratios were due to random sampling errors. However, certain aberrancies occurred so persistently as to suggest that they were not to be dismissed as mere chance events, but represented real deviations from expectations. The present report is concerned with the analysis of one of these persistent aberrancies, namely, cases of disturbed ratios in families heterozygous for *P/p*, a gene which governs purple (*P/P* or *P/p*) vs. red (*p/p*) seed-coat color (ALLARD, 1953).

Experimental Materials

The experimental materials used in the study of aberrant purple: red ratios were selfed progenies derived from 5 F_1 plants obtained by crossing a single individual of a highly inbred accession line, designated L20 (*p/p*), with a single individual of another highly inbred accession line, designated L76 (*P/P*). These two accessions had also been the parents of one of the mass-propagated populations in which purple aberrant ratios had been observed. When disturbances of similar magnitude were observed in 2 among the 5 F_2 progenies of the above cross, it was assumed that the aberrancies observed in the population and in these two progenies resulted from the same cause.

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The F_2 Generation

The segregation ratios observed in the F_2 progenies obtained by selfing the 5 original F_1 plants are given in Table 1. Chi-square tests indicate that: (1) relative to the expected 3:1 ratio there is significant deficiency of purple plants for the pooled data of the 5 families; (2) significant heterogeneity exists between families; (3) families No. 1, No. 2, and No. 4 are homogeneous in supporting a 3:1 ratio and families No. 3 and No. 5 are homogeneous in deficiency of purple individuals. It is therefore clear that either the L20 or L76 parental individual was heterozygous for a gene (or genes) which affects the functioning or viability of gametes or zygotes.

Table 1. *Segregation in F_2 families derived from hybridization between single individuals of accessions L20×L76.*

Family	Purple	Red	Ratio (purple:red)	χ^2 (3:1)
1	65	27	2.41:1	0.928
2	67	21	3.19:1	0.013
3	76	52	1.46:1	16.667*
4	104	36	2.89:1	0.104
5	96	69	1.39:1	24.890*

* Probability less than 0.001.

Several easily tested one- and two-gene hypotheses which might explain the F_2 results (e.g. heterozygosity of one of the parental individuals for isoalleles producing indistinguishable seed-coat color, but with differential effect on penetrance, or viability; segregation of complementary genes) were eliminated on the basis of the F_2 data alone, or on the basis of simple progeny tests. Among various remaining possibilities the F_2 results seemed to be best explained on the basis that F_1 plants No. 3 and No. 5 were of genotype *P ga/p Ga*, and plants No. 1, No. 2, and No. 4 were of genotype *P ga/p ga* or *P Ga/P Ga*, where *Ga/ga* is a lethal or semilethal gene affecting only the male gametophyte. The previous description and analysis of "gametophyte factors" in maize (e.g., EMERSON,

Table 2. *Genetic expectations* among progeny derived by selfing plants of genotype P ga/p Ga.*

F_2 Genotypes	F_3 Segregation	Observed Numbers	Expected proportions (× 4)		
			Ga	*ga*	*Ga* + *ga*
P Ga/P Ga and *P ga/P ga*	True-breeding purple	a	π	$\varkappa(1-\pi)$	$\pi + \varkappa(1-\pi)$
P Ga/p ga	Purple-excess	b	π^2	$\varkappa\pi^2$	$\pi^2 + \varkappa\pi^2$
P Ga/p Ga *P Ga/p ga*	3 purple: 1 red	c	$2\pi(1-\pi)$	$2\varkappa\pi(1-\pi)$	$2\pi(1-\pi) + 2\varkappa\pi(1-\pi)$
P ga/p Ga	Purple-deficient	d	$(1-\pi)^2$	$\varkappa(1-\pi)^2$	$(1-\pi)^2 + \varkappa(1-\pi)^2$
p Ga/p Ga and *p ga/p ga*	True-breeding red	e	$1-\pi$	$\varkappa\pi$	$(1-\pi) + \varkappa\pi$

* Expectations for the coupling phase double heterozygote, *P Ga/p ga*, can be obtained by substituting $1-\pi$ for π.

1934; SCHWARTZ, 1950) made it attractive to postulate similar action for this gene. It was therefore decided to test in detail the hypothesis that *ga* pollen grains function irrespective of stylar genotype in the absence of *Ga* pollen grains, but that they are at a disadvantage when in competition with *Ga* pollen grains on *Ga/Ga* or *Ga/ga* stylar tissue. Under this hypothesis the genotypes *P ga/p Ga* and *P Ga/p ga*, respectively, are expected to produce purple-deficient and purple-excess progenies. The extent of the deficiency or excess (assuming normal meiosis, complete manifestation, equal viability in zygotic stages and no other complications) depends on π and $\varkappa$, where π is the recombination fraction between *P* and *Ga* and $\varkappa$ is a measure of the competition between *Ga* and *ga* pollen on *Ga/ga* styles. If *Ga* and *ga* pollen grains produce fertilization in the ratio $1:\varkappa$, $0 \lessgtr \varkappa > 1$. Expectations in terms of $\varkappa$ and π for self-pollinated progeny of F_1 plants of genotype *P ga/p Ga* (F_1 plants No. 3 and No. 5) are given in Table 2. It is apparent that F_2 data alone do not provide sufficient degrees of freedom to estimate these parameters simultaneously but that they can be estimated from F_3 data.

F_3-Type Data

The information required to estimate π and $\varkappa$ was obtained by growing 433 families derived from purple-seeded plants of the previous generation. The F_3 generation consisted of 50 progenies whose parents were randomly chosen purple plants of F_2 family No. 5. The subsequent plantings represented F_4 through F_8 generation families obtained by selfing randomly chosen individuals from either purple-deficient (repulsion) of from purple-excess (coupling) families of the previous generation. Mean family size was approximately 40 individuals.

Assignment of each family to one of the four classes predicted in the second column of Table 2 was on the basis of ambiguous ratios. In computing the ambiguous ratios use was made of data from F_2 families No. 3 and No. 5 (Table 1) and from 7 large F_3 families (Table 3) grown for the purpose of determining ratios of purple: red in repulsion and in coupling phase families. The observed ratios in these large families were 7.6780:1 (purple-excess) and 1.5565:1 (purple-deficient). The observed segregation ratio which gives equal χ^2s for the 7.6780:1 vs. the 3:1 ratio is 4.799:1 and that for the 3:1 vs. the 1.5565:1 ratio is 2.161:1. Hence, all segregating families in which the observed ratio (purple:red) exceeded 4.799:1 were assigned to the purple-excess class, families with ratio between 4.799:1 and 2.161:1 were assigned to the 3:1 class, and families with ratio less than 2.161:1 to the purple-deficient class. Since family size was rather small it is probable that a few families were classified incorrectly.

Table 3. *Observed segregation ratios within large F_3 families.*

Family	Observed number of:		Ratio (purple:red)	Presumed Genotype of F_2 parent
	Purple	Red		
11	183	101	1.81:1	*P ga/p Ga*
14	168	90	1.87:1	*P ga/p Ga*
18	193	127	1.52:1	*P ga/p Ga*
35	205	127	1.61:1	*P ga/p Ga*
43	181	142	1.27:1	*P ga/p Ga*
Total	930	587	1.5843:1*	
27	226	26	8.69:1	*P Ga/p ga*
31	227	33	6.88:1	*P Ga/p ga*
Total	453	59	7.6780:1	

* Pooled F_2 and F_3 data give 1.5565:1.

The results of the classification of 357 progenies derived from purple-seeded plants taken at random from purple-deficient (repulsion) and 76 progenies derived from randomly chosen purple-seeded plants from purple-excess (coupling) families of the previous generation are given in Table 4. Maximum-likelihood

Table 4. *Classification of families derived from purple-deficient (repulsion) or purple-excess (coupling) families of the previous generation.*

Class	F_3	F_4	F_5	F_6	F_7	F_8	Total
Repulsion							
True-breeding purple	10	28	3	6	6	16	a = 69
Purple-excess	3	8	0	2	2	3	b = 18
3:1	15	38	5	9	10	26	c = 103
Purple-deficient	22	46	12	12	24	51	d = 167
Total	50	120	20	29	42	96	357
Coupling							
True-breeding purple		15	17				a = 32
Purple-excess		10	13				b = 23
3:1		9	9				c = 18
Purple-deficient		2	1				d = 3
Total		36	40				76

estimates of π and $\varkappa$ for the repulsion data are given by

$$\frac{\partial \log L}{\partial \pi} = \frac{a(1-\varkappa)}{\pi + \varkappa(1-\pi)} + \frac{2b}{\pi} + \frac{c(1-2\pi)}{\pi(1-\pi)} + \frac{-2d}{1-\pi} + \frac{-(a+b+c+d)(1-\varkappa)}{1+\pi+2\varkappa-\varkappa\pi} = 0 \quad (1)$$

and,

$$\frac{\partial \log L}{\partial \varkappa} = \frac{a(1-\pi)}{\pi + \varkappa(1-\pi)} + \frac{b+c+d}{1+\varkappa} + \frac{-(a+b+c+d)(2-\pi)}{1+\pi+2\varkappa-\varkappa\pi} = 0\,. \quad (2)$$

Explicit solutions for these equations do not appear to exist. However, they are readily solved by iteration, making use of the fact that the variances and covariances of π and $\varkappa$ are given essentially by the elements of the inverse of the matrix of expected values of the second partial derivatives. The inverse is

$$\begin{bmatrix} \frac{I_{\varkappa\varkappa}}{D} & -\frac{I_{\pi\varkappa}}{D} \\ -\frac{I_{\pi\varkappa}}{D} & \frac{I_{\pi\pi}}{D} \end{bmatrix} \quad (3)$$

where

$$I_{\pi\pi} = \frac{\partial^2 \log L}{\partial \pi^2} = \frac{-a(1-\varkappa)^2}{[\pi+\varkappa(1-\pi)]^2} + \frac{-2b}{\pi^2} + \frac{-2c}{\pi(1-\pi)} + \frac{-c(1-2\pi)^2}{[\pi(1-\pi)]^2} + \frac{-2d}{(1-\pi)^2} + \frac{(a+b+c+d)(1-\varkappa)^2}{(1+\pi+2\varkappa-\varkappa\pi)^2}\,, \quad (4)$$

$$I_{\varkappa\varkappa} = \frac{\partial^2 \log L}{\partial \varkappa^2} = \frac{-a(1-\pi)^2}{[\pi+\varkappa(1-\pi)]^2} + \frac{-(b+c+d)}{(1+\varkappa)^2} + \frac{(a+b+c+d)(2-\pi)^2}{(1+\pi+2\varkappa-\varkappa\pi)^2}\,, \quad (5)$$

$$I_{\pi\varkappa} = \frac{\partial^2 \log L}{\partial \pi\, \partial \varkappa} = \frac{-a}{[\pi+\varkappa(1-\pi)]^2} + \frac{3(a+b+c+d)}{[1+\pi+2\varkappa-\varkappa\pi]^2}\,, \quad (6)$$

and

$$D = (I_{\pi\pi})(I_{\varkappa\varkappa}) - (I_{\pi\varkappa})^2\,. \quad (7)$$

Standard errors of π and $\varkappa$ are given by $(I_{\varkappa\varkappa}/D)^{1/2}$ and $(I_{\pi\pi}/D)^{1/2}$. A digital computer was used to facilitate the computations giving,

repulsion: $\hat{\pi} = 0.241 \pm 0.019$ $\hat{\varkappa} = -0.003 - 0.072$
coupling: $\hat{\pi} = 0.271 \pm 0.044$ $\hat{\varkappa} = 0.0007 \pm 0.342$
joint: $\hat{\pi} = 0.244 \pm 0.017$ $\hat{\varkappa} = -0.003 \pm 0.070$.

$\chi^2[7]$ heterogeneity tests show that the estimates of π and $\varkappa$ given by the 8 sets of data of Table 4 are homogeneous (for π, $\chi^2 = 11.58$, $P = 0.10-0.20$; for $\varkappa$, $\chi^2 = 4.31$, $P = 0.70-0.80$).

It can be seen from Table 2 that π and $\varkappa$ enter the expectations in the same way for both *Ga* and *ga* pollen with respect to plants which are genotypically *P/p*. Hence, as pointed out by EMERSON (1934), an estimate of π independent of $\varkappa$ can be obtained from the proportions of purple-excess, 3:1, and purple-deficient families. The maximum-likelihood estimator of π (repulsion) is

$$\frac{\partial \log L}{\partial \pi} = \frac{2b}{\pi} + \frac{c(1-2\pi)}{\pi(1-\pi)} + \frac{-2d}{1-\pi} = 0\,. \quad (8)$$

The standard error of π is given by $(I_\pi^{-1})^{1/2}$ where

$$I_\pi = \frac{\partial^2 \log L}{\partial \pi^2} = \frac{-2b}{\pi^2} + \frac{-2c}{\pi(1-\pi)} + \frac{-c(1-2\pi)^2}{[\pi(1-\pi)]^2} + \frac{2d}{(1-\pi)^2}\,. \quad (9)$$

As expected, both $\frac{\partial \log L}{\partial \varkappa}$ and $\frac{\partial^2 \log L}{\partial \varkappa^2} = 0$, indicating that families of these types give no information about $\varkappa$. The estimated values of π from the data of Table 4 are

repulsion: $\hat{\pi} = 0.241 \pm 0.022$
coupling: $\hat{\pi} = 0.272 \pm 0.074$
joint: $\hat{\pi} = 0.244 \pm 0.021$,

which are nearly identical to the estimates obtained from the 4-class data.

In the estimation of $\varkappa$ from the 4-class data only one class (homozygous purple) contributes information about $\varkappa$ and the estimate of $\varkappa$ obtained consequently has high standard error. However, since an estimate of π is available, F_2-type data can also be made to yield an estimate of $\varkappa$. The maximum-likelihood estimator of $\varkappa$ (repulsion) is

$$\frac{d \log L}{d\varkappa} = \frac{(a+b+c+d)(2-\pi)}{1+2\varkappa+\pi-\varkappa\pi} + \frac{e\pi}{1-\pi+\varkappa\pi} + \frac{-(a+b+c+d+e)}{1+\varkappa} = 0 \quad (10)$$

with standard error $= (I_\varkappa^{-1})^{1/2}$ where

$$I_\varkappa = \frac{d^2 \log L}{d\varkappa^2} = \frac{-(a+b+c+d)(2-\pi)^2}{[1+2\varkappa+\pi-\varkappa\pi]^2} + \frac{-e\pi^2}{[1-\pi+\varkappa\pi]^2} + \frac{-(a+b+c+d+e)}{(1+\varkappa)^2}\,. \quad (11)$$

The estimated values of $\varkappa$ from the data of Tables 1 and 3, taking $\pi = 0.244$, are

repulsion: $\hat{\varkappa} = -0.049 \pm 0.022$
coupling: $\hat{\varkappa} = -0.022 \pm 0.027$
joint: $\hat{\varkappa} = -0.043 \pm 0.0128$

Taking zero as the most reasonable value of $\varkappa$, a heterogeneity test gives $\chi^2[8] = 1.75$, $P = 0.98 - 0.99$. Apparently *ga* pollen grains rarely if ever function when in competition with *Ga* pollen grains on *Ga/ga* styles.

Test of the Gametophyte Factor Hypothesis

The hypothesis that the observed purple:red segregations result from linkage between *P/p* and *Ga/ga* (recombination fraction = 0.244) and that *ga* pollen grains fail to function in competition with *Ga* pollen grains on *Ga/ga* styles ($\varkappa = 0$) was tested by comparing observed numbers with expected numbers for all the sets of data available (Tables 1, 3, 4). "Goodness of fit" tests indicated good agreement ($P > 0.05$) between observation and expectation in 16 of the 17 tests which could be made ($P = 0.02 - 0.05$ for family 43, Table 3), and thus provide support for the hypothesis advanced. It is proposed that the *Ga/ga* gene described by BEMIS (1959) be denoted Ga_1 and the present gene be denoted Ga_2.

Map Location of Ga_2

The purple (*P/p*) gene has been assigned tentatively to linkage group I by ALLARD and CLEMENT

(1959) at a location 45.9 map units to the left of R. The only other group I gene segregating in the present materials was *D*, which is located 39.3 map units to the right of *R*. Data at hand are therefore inadequate to distinguish between order Ga_2-P-R and $P-Ga_2-R$. The gametophyte factor (Ga_1) described by BEMIS (1959) is also located in group I, but 39.4 map units to the right of *D*. Hence the positions of Ga_1 and Ga_2 with respect to the main marker genes of group I are either: (a) $Ga_2-P-R-D-Ga_1$ or (b) $P-Ga_2-R-D-Ga_1$. Map distances in the 4 intervals (left to right) are approximately 25, 46, 39, 39 if (a) is the correct order, or 25, 21, 39, 39, if order (b) is correct.

Discussion

Gametophyte factors and the self-incompatibility genes found in cross-fertilized plants such as *Nicotiana, Oenothera* and *Trifolium* are comparable in the sense that interaction occurs between the haploid male gametophyte and diploid stylar tissue. However, the form of the interaction is not the same in the two cases. With incompatibility systems the growth of the male gametophyte is usually inhibited on styles that carry the same allele as the male gametophyte; self-fertilization is therefore normally prohibited and heterozygosity is the usual state at such loci. With gametophyte factors, on the other hand, selfing is not prohibited. Thus BEMIS (1959), working with lima beans, had evidence the *ga* pollen grains function on *ga/ga* styles; *ga* pollen grains were also functional on *Ga/Ga* and *Ga/ga* styles so long as there was no competition from *Ga* pollen grains. TABATA (1961) found that *Ga* and *ga* pollen grains were equally competitive on *ga/ga* styles but *Ga* pollen grains had great advantage over *ga* pollen grains on *Ga/Ga* or *Ga/ga* styles. The same situation apparently applies in the present case and in an unpublished case in barley (JAIN, et al.). Similar patterns have generally been observed with gametophyte factors in maize. However, SCHWARTZ (1950) found a third allele, Ga^s of the gametophyte factor on chromosome 4 which prevents the functioning of *ga* pollen on Ga^s silks even in the absence of competition with *Ga* or Ga^s pollen and a case described by DEMEREC (1929) appears to be analogous to the Ga^s allele of SCHWARTZ. Thus, in general, gametophyte factors permit self-fertilization whereas incompatibility genes are highly effective in preventing selfing.

These differences between gametophyte factors and incompatibility systems lead to very unlike genetic expectations. The minimum number of self-incompatibility alleles possible is, of course, three; and if there are n such alleles, the equilibrium value is 1/n (WRIGHT, 1939). In contrast, the *Ga* allele at a locus is tremendously favored relative to the *ga* allele because *Ga* pollen grains function on any style whereas *ga* pollen grains are competitive only on *ga/ga* styles. It follows (other things being equal) that the *ga* allele will be eliminated rapidly from populations polymorphic for *Ga/ga*. It also follows that *ga/ga* populations cannot persist unless they are strictly isolated from populations containing *Ga* alleles. This deduction is supported by the observation that most gametophytic factors have been discovered in crosses between previously isolated populations (for example, crosses between dent and sweet corns; intervarietal crosses in predominantly self-pollinated species).

Once *Ga* is introduced into a *ga/ga* population, either by mutation $ga \rightarrow Ga$ or by migration, the spread of *Ga* is expected to be a function of the mating system. Under complete selfing, spread of *Ga* would occur only within affected families. However, should any outcrossing occur, the *ga* allele must ultimately be replaced in the entire population by *Ga*, unless selection against *ga* in the gametophytic stage is countered by strong opposing forces, such as great reproductive advantage of *ga/ga* or *Ga/ga* in sporophytic stages.

It is commonly accepted that inbreeding plants have evolved from outbreeding ancestors and further, that intensification of inbreeding is likely to occur under domestication. MATHER and DE WINTON (1941) and MATHER (1943) have shown that the incompatibility systems of *Primula sinensis* and *Petunia violacea* are under the control of numerous genes in addition to those directly responsible for mating type and that self-fruitfulness can be increased, without change in the primary system, by altering the assemblage of genes governing the relationship between pollen and style. Gradual imposition of inbreeding on an incompatibility system might therefore lead to greater self-compatibility, which is the main difference between gametophyte factors and incompatibility genes. This suggests that gametophyte factors may be relic incompatibility genes whose expression has been modified to fit the circumstances of altered mating habits. A difficulty with this hypothesis is that incompatibility systems are usually under the control of a single locus, or sometimes two loci, whereas at least three *Ga* loci are known in maize and two are known in each barley and lima beans. Should additional gametophyte factors be discovered, which seems likely when additional known cases of disturbed ratios have been analyzed, the difficulty in accounting for all of them on the basis of descent from incompatibility loci will be compounded. The excess of gametophyte factors therefore suggests that not all of them are relic incompatibility genes but that at least certain ones have arisen by mutation independent of incompatibility genes.

There is, however, also a difficulty with this hypothesis. According to MATHER (1943) the interaction system between pollen and style in incompatibility systems is governed by many genes; it is presumably a highly complicated end-product of a series of developmental processes and hence must have arisen gradually. There is no reason to believe that the interactions between pollen and style which characterize gametophyte factors are any less intricate than those characterizing incompatibility systems. Hence, following MATHER'S argument, they are no less difficult to reconcile with sudden development by a single mutational event than incompatibility systems.

If, however, gametophyte factors can in fact arise by mutation independent of incompatibility genes, the properties of the gametophyte factors indicate that these mutations are likely to have been $ga \rightarrow Ga$, since a *ga* allele arising by mutation is effectively a

lethal in the absence of *ga/ga* styles. The following case can be made that the present *Ga* allele arose in this fashion, i.e. by mutation $ga_2 \rightarrow Ga_2$.

The mass-propagated population in which Ga_2 was first noted was synthesized by blending seeds from 10 F_1 plants tracing back to several L20 and several L76 parental individuals. In early generations following synthesis of this population, families giving purple-deficient ratios were infrequent, making up 5 percent or less of the total, and families giving purple-excess ratios were not observed. It can therefore be deduced that few, perhaps only one or two of the 10 F_1 parents of these populations were genotypically $P\ ga_2/p\ Ga_2$ and that none of the F_1 parents were $P\ Ga_2/p\ ga_2$. It can also be deduced that parent line L76 is uniformly $P\ ga_2/P\ ga_2$ whereas parent line L20 consists primarily of $p\ ga_2/p\ ga_2$ homozygotes but includes a small proportion of $p\ Ga_2/p\ Ga_2$ and $p\ Ga_2/p\ ga_2$ individuals.

The sequence of events leading to the postulated polymorphism for Ga_2/ga_2 in L20 might have occurred as follows: (1) a mutation $ga \rightarrow Ga_2$ occurred, probably in a single plant of L20; (2) interaction between male gametophyte and style resulted in rapid increase in frequency of Ga_2 in progeny derived from the Ga_2/ga_2 tissue; (3) occasional outcrossing (1 to 2 percent in lima beans) permitted sporadic migrations of Ga_2 into other familial lines, in which Ga_2 in turn rapidly replaced ga_2; (4) at the time (1947) when L20 was hybridized with L76 to produce the mass-propagated populations and the 5 F_1 plants upon which the present study was based, this process had not proceeded very far and L20 still consisted primarily of ga_2ga_2 homozygotes. Hence most hybrids between L20 and L76 are expected to be $P\ ga_2/p\ ga_2$ and only a few are expected to be $P\ ga_2/p\ Ga_2$. The single plant of L20 which was the parent of the families reported in Table 1 was presumably one of the infrequent $p\ Ga_2/p\ ga_2$ heterozygotes postulated to occur in L20.

Summary

A second gametophyte factor (Ga_2) is described in lima beans. This gene produces an interaction between the male gametophyte and style such that: (a) Ga_2 pollen functions irrespective of stylar genotype; (b) ga_2 pollen is functional on *ga/ga* styles but is unable to compete with Ga_2 pollen on Ga_2/Ga_2 or Ga_2/ga_2 styles. Ga_2/ga_2 is linked with the *P/p* locus (recombination fraction = 0.244 ± .017); it is therefore probably located in linkage group I.

Some similarities and differences between gametophyte factors and incompatibility systems and some factors which might influence the establishment and maintenance of *ga* alleles in populations are discussed. Evidence is presented that the Ga_2 allele arose as a recent mutation $ga_2 \rightarrow Ga_2$ in one of the pure-line parents of the families studied.

Zusammenfassung

An Limabohnen-Familien, die für das Gen *P/p* für Samenschalenfarbe heterozygot sind, wurden persistente Spaltungsabweichungen analysiert.

Ein zweiter gametophytischer Faktor (Ga_2) wird beschrieben. Dieses Gen bewirkt eine Interaktion zwischen dem männlichen Gametophyten und dem Griffel in der Form, daß a) Ga_2-Pollen unabhängig von dem Genotyp des Griffels funktionsfähig ist, b) ga_2-Pollen zwar *ga/ga*-Griffel befruchten, aber auf Ga_2/Ga_2 -Griffeln oder Ga_2/ga_2-Griffeln mit Ga_2-Pollen nicht konkurrieren kann. Ga_2/ga_2 ist mit dem Locus *P/p* gekoppelt (Rekombinationswert 0,244 ± 0,017) und daher wahrscheinlich in Koppelungsgruppe I lokalisiert.

Ähnlichkeiten und Unterschiede zwischen gametophytischen Faktoren und Inkompatibilitätssystemen sowie Faktoren, die das Auftreten und die Ausbreitung von *ga*-Allelen in Populationen beeinflussen können, werden diskutiert. Es wird der Beweis erbracht, daß das Ga_2-Allel in einer der reinen Elternlinien der untersuchten Familien als eine neue Mutation $ga_2 \rightarrow Ga_2$ entstanden ist.

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