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Provocation of Mutability in the Level of Mutation Expressed at the *Pal-rec* Gene in *Antirrhinum majus*

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Summary. The *pallida* gene of *Antirrhinum majus* governs anthocyanin production. The nature of the mutability displayed by its unstable allele *pal-rec* was dramatically altered following crosses between two *pal-rec pal-rec* lines with certain separately maintained lines. In both cases a minority of progeny in F_1 or F_2 revealed unprecedented infrequent mutability termed 'Low mutability'. These Low plants and their sibs showed many areas of contrasting mutability superimposed on their initial mutability level. This frequent 'shifting' and Low mutability persisted through several generations of offspring obtained by both selfing and crossing to a non-mutable tester line. Evidence is presented to suggest a hypothesis that the two features of altered mutability are two aspects of the same phenomenon caused by joint action of two independent factors *J* and *k*, one contributed by each parental line at the outcross.

A separate gene, *eosinea*, governs anthocyanin type, *eos eos* plants having pelargonin in place of wild-type magenta cyanin. In addition to the previously known simple depression of *pal-rec* to *Pal* mutation frequency in *eos eos* plants, *eos* also influences the action of *J* and *k* when heterozygous (i.e. *Eos eos*), thus contributing a basal and a third tier of control influencing mutability of *pal-rec*.

Three levels of control are thus identified, the middle tier being governed by the partnership of *J* and *k* producing not a simple change but a complex mutability of mutability.

Key words: Mutability – Regulation of mutability – Anthocyanin – *Antirrhinum majus*

1 Introduction

The *pal-rec* gene in *Antirrhinum majus* mutates frequently during development of the plant so that flowers are characterized by pigmented *Pal* spots on a recessive background (*pal*) of anthocyaninless tissue. The level of mutability exhibited by *pal-rec* in plants grown under uniform conditions can vary widely. Within a plant the level may shift during development giving adjacent areas of contrasting mutability. Usually more noticeable however is the difference between sister plants of predominant mutability level, which forms the background against which areas of contrasting level or 'shifts' would appear.

The number of *Pal* spots on one of the larger corolla lobes may range in one family from 600 to about 9000, but by selfing and selection lines of more uniform mutability have been established where the mutability range is 9000 – 9400 (a highly mutable line) or 600 – 1050 (low – mutable).

On two separate occasions plants showing heritable, abnormally low mutability have appeared with fewer than 100 spots per lobe and representing a discrete class in an otherwise continuous range. One such case has been investigated by Sastry (1976), Aslam (1979) and Sastry et al. (1980). The present investigation deals with the second.

Pal plants doubly recessive at the *eosinea* locus show the pink pigmentation of pelargonin in place of the wild type magenta cyanin produced in the presence of *Eos*. Also, frequency of mutation at *pal-rec* is reduced in *eos eos* plants (Harrison and Fincham 1963). The present investigation developed from a test of hypothesis that this lowering of mutability was due to an *eos*-linked modifier. No such simple modifier was found, but a striking and separate effect on the behaviour of *pal-rec* occurred which is here described.

2 Materials and Methods

Four lines were principally used of which the relevant parts of the genotypes and phenotypes are given in Table 1. Lines b and d are termed 'Leeds stock', having been maintained in the Genetics department of the University of Leeds since 1968, when the stocks from which they were derived were brought to Leeds from the John Innes Institute. Lines a and c are termed 'John Innes stock'

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Table 1. Description of lines used[a]

	Genotype	Description
Line a	*eos eos pal-rec pal-rec*	A family showing rather low, though normal mutability of fairly narrow range; pink spots on acyanic background. Average of 2 shifts per inflorescence of more than 8 flowers
Line b	*Eos Eos pal-tub pal-tub*	An inbred line homozygous for the non mutable recessive allele *pal-tub*; acyanic flowers except for magenta ring at the base of corolla tube
Line c	*eos eos Pal Pal*	Solidly coloured pink flowers
Line d	*Eos Eos pal-rec pal-rec*	A uniformly high mutable line obtained from more heterogeneous mutable families. Average of less than 2 shifts per inflorescence of more than 8 flowers

[a] None of the lines carry the known modifier of *pal-rec*, 'Stabiliser' (*St*), which reduces the mutability level (Harrison and Fincham 1968)

and were donated by Mr. Brian Harrison of the John Innes Institute in 1970.

The heritable, abnormally low mutability mentioned in the Introduction is henceforth referred to as 'Low' mutability and defined in *Eos* – *pal-rec* – plants as exhibiting 100 spots per lobe or less; in a few exceptional cases plants with 500 spots were classed as Low if their sister plants were all unusually highly mutable.

'Low plants' have a striking appearance if *Eos* –, having Low as the predominant mutability level of the main inflorescence, and only superimposed shifts to normal mutability exhibiting any appreciable spot density. The few *eos eos* plants recognized as Low had less than 10 spots per lobe and all their *eos eos pal-rec*-sister plants showed 600 or more. Low mutable *eos eos pal-rec* plants may be mistaken for the non-mutable genotype *pal-tub pal-tub* since the pink spots are pale and often very small. Quantitative investigation was largely confined to the *Eos* genotype. All non-Low levels are referred to as 'normal mutability'. Mutability level was scored according to a scale from 0 (colourless) to 7 (entirely *Pal*), the intermediate range being distributed between classes 1–6, which were recognizable by eye. Scoring was, however, checked regularly by complete spot counts of representative classes with the aid of a microscope. The score of a plant on this scale referred to its predominant mutability level which could be Low, or a normal level.

Uniformity of mutability refers to the frequency of shifts on this predomiant background. 'Normal' does not imply 'uniform'.

3 Results

3.1 *Origin of Altered Mutability*

The first Low plants appeared in the F_2 of reciprocal crosses between a *eos eos* mutable line and the Leeds stock nonmutable tester line: Line a (*eos eos pal-rec pal-rec*) × Line b (*Eos Eos pal-tub pal-tub*).

All 72 plants in the seven F_1 families showed a moderate mutability level, higher than in the mutable parent line, demonstrating that the low (but normal) mutability of Line a was not caused by a dominant modifier. Mutability level of F_1 plants was not noticeably less uniform than that of Line a or Line d (*Eos Eos pal-rec pal-rec*).

F_2 families were raised from 14 F_1 plants; of 231 mutable F_2 plants, 220 showed normal mutability similar to that of the F_1. Eleven, however, were Low plants, being *Eos pal-rec* but with strikingly few *Pal* spots. At least seven of them proved to be *Eos eos*. The immediate hypothesis was that an *eos* linked modifier had recombined to give very low mutability of *pal-rec* on an *Eos* background.

The observed low level was actually clearly lower than that of parental Line a. However, (i) Some of the Low plants produced secondary inflorescences with normal mutability as illustrated in Fig. 1. (ii) The F_3 from all Low plants tested included a large proportion of normally mutable plants (Table 2) showing that the Low phenotype is not caused by interaction of a homozygous recessive modifier with *pal-rec*. (iii) Backcrosses of F_2 Low plants to Line b included Low plants (Table 2). A recessive Mendelian modifier is thus ruled out, and the normally mutable F_1 had already demonstrated the absence of a dominant modifier.

As had been expected, the *eos eos pal-rec* segregants were found to fall in general at the lower end of the mutability range in any family. Selfed and backcrossed offspring of the highest and lowest normally mutable *eos eos pal-rec* plants revealed no Mendelian modifier of mutability separable from *eos*, displaying instead the wide and continuous range of mutability level typical of non-inbred families. It is evident that the alteration of behaviour of *pal-rec* typified by Low mutability must be examined in broader terms than any simple relationship with recessive *eos*.

3.2 *Shifting of Mutability Level*

Several of the F_2 plants showed frequent shifts to contrasting mutability levels superimposed upon their predominant level. Of 16 branches on three of the Low plants, 11 had normal mutability (see Fig. 1.) Five Low plants had striking shifts to high mutability in the main inflorescence and many of their normally mutable sibs displayed

Fig. 1. Side inflorescences on an almost colourless plant found in the selfed progeny from *Eos eos pal-rec pal-tub* hybrid

areas of contrasting mutability of various levels including Low.

Interpretation of these phenomena as any sort of simple chimera consequent upon somatic origin of an altered genotype was strongly opposed by the complexity and random pattern of shift-distribution and the variety of levels displayed. Equal prevalence of Low upon normal and normal upon low, and occasional superimposition on a shift of another to a third mutability level within one flower, would necessitate an unlikely frequency and flexibility of genetic change during development. Such frequent shifting was not apparent in the parent mutable plants of Line a, nor in the F_1 but in the F_2 and subsequent generations, both selfed and backcrossed to Line b, it was frequent in all types of mutable plant.

This enhanced shifting was not always reliably recognisable in an individual plant. Parental and enhanced frequencies of shifting are adjacent sections of a continuum as opposed to forming clearly separate frequencies. Assessed on a family basis,

Table 2. Offspring of F2 Low plants from Line a × Line b crosses

	Low parent	Total *Eos-pal-rec* plants	Number of Low plants	% Low plants
(i) F3 i.e. selfed progeny	343- 6	11	2	18
	342-23	11	1	9
	337- 9	14	3	21
	337-21	14	2	14
	339-15	47	4	9
	502- 4	10	8	80
(ii) Progeny of back-cross to Line b	343- 6	11	0	< 9
	343-23	8	0	< 13
	337- 9	12	3	25
	337-21	31	3	10
	502- 4	14	6	43

however, enhanced shifting was clearly present in nearly all post-F_1 families, both selfed and backcrossed to Line b. In fact, the backcrossed families displayed more shifting on average than the selfed offspring.

Plants of Line a had displayed on average only two shifts per inflorescence, an infloresence being defined as a branch bearing more than 8 flowers. Such uniformity of mutability level was rarely approached in descendants of the Line a × Line b cross, and was surpassed only once, in a selfed family consisting nevertheless entirely of Low plants so as to leave no doubt regarding the alteration of the expression of its *pal-rec*. Thus enhanced shifting was recognisable in all except one of the families termed 'Low families' descended from the first 11 Low plants which were part of the F_2 of the Lines a and b cross.

The extremely infrequent mutability of Low plants among the descendants of the a × b cross, and the prevalence of somatic shifting among them and their normally mutable sibs, clearly distinguished them from mutable families in either Leeds or John Innes stocks.

Since a single modifier cannot explain the above results, it is hypothesized that two factors are necessary for the observed alteration of the behaviour of *pal-rec*, one factor carried by each of the Leeds and John Innes stocks. It is proposed that the effect is caused by a combined action of a dominant factor *J* carried in the John Innes stock, Lines a and c, and a recessive factor *k* carried by the Leeds stocks, Lines b and d. This concept is outlined in Table 3. The hypothesis allows for expression of enhanced shifting at the observed prevalence as well as appearance of Low plants among backcrossed families. The effective genotype, *J – k k*, produces an enhancement of shifting frequency relative to that in the parent mutable line which in a proportion of plants is accompanied by a predominant mutability level classified as Low. It is these Low plants which first identified the phenomenon and which are most clearly diagnostic of the effect by operation. But it must be emphasised that they are not a necessary, nor the most frequent, result of the *J – k k* genotype.

Further crosses were made in which the combination of factors from each of the parental genomes gave rise to altered behaviour of *pal-rec*. Line c (*eos eos Pal Pal*) was crossed and backcrossed twice to Line b and then selfed, to minimise segregation among offspring at loci other than *eosinea* and *pallida*. Segregants that carried *pal-tub pal-tub* and were *eos eos* or *Eos Eos* were crossed to the inbred, uniformly mutable Line d (*Eos Eos pal-rec pal-rec*). Of the 125 mutable plants in the twelve F_1 families two plants were Low, both occurring in one family where the non-mutable parent was *eos eos*.

For the twelve families as a whole shifting was moderately enhanced. An F_2 of 173 mutable plants in nine families was raised from F_1 families where the non-mutable parent was *Eos Eos*. All were normally mutable but showed enhanced shifting.

It is evident that the *pal-rec* allele maintained in Leeds stock is as susceptible to alteration of its behaviour as is the *pal-rec* allele in the John Innes Line a which first demonstrated the effect. It is equally clear that Line c bears an effective component with which that in the Leeds stock co-operates, as did Line a in the first outcross (a × b). In contrast to the first outcross, the (c × d) cross yielded two Low plants in the F_1, which may be accounted for in terms of the hypothesis outlined in Table 3 since the initial crossing of (c × b) and the two backcrosses would have eliminated most of the *K* as well as *J* alleles derived from Line c, hence occasional *J j k k* plants in the F_1.

For further comparison with the cross (a × b) two mutable lines, Line d (*Eos Eos pal-rec pal-rec*) and Line a (*eos eos pal-rec pal-rec*) were crossed. Thirty families resulted from this cross, representing F_1 – F_4 and one F_5 family.

They included 53 Low plants of which two appeared in the F_1 and shifting was frequent throughout. The two Low plants in the F_1 demonstrated simultaneous alteration of behaviour of *pal-rec* alleles from both stocks since Low mutability is not detectable in the presence of normal *pal-rec* mutability. Their appearance weakens the hypothesis of Table 3 since it cannot account for their apparent lack of Line a-derived, dominant allele *K*. Direct demonstration is nevertheless furnished that the effect is due to two differing components since this outcross (d × a) is an immediate combination of two genomes both of which were at the time of crossing permitting only normal mutability of their respective *pal-rec* alleles.

It is reasonable to suppose, the two *pal-rec* alleles in question being from a common origin, that they are not themselves a component of influence each upon the other, but that two other genetic entities (*J* and *k*) must be combined in the same genome to produce an effect to which either *pal-rec* is susceptible.

Table 3. Hypothesis offering simple Mendelian interpretation of the observed incidence of altered mutability at *pal-rec* as recognised by enhanced shifting and/or Low mutability. Two factors are proposed, *J* and *k*, the genetic constitution which gives rise to the effect on *pal-rec* being *J – k k*

Generation Outcross	Genotypes Line a × Line b	Appearance of effect	
		Predicted	Observed
F1	*J J K K* × *j j k k* *J j K k*	Normal, uniform mutability	Normal, uniform mutability
F2	3/16 *J – k k* 1/3 of these *J J k k*	Enhanced shifting and Low plants in a minority of families	Low plants in 5 out of 14 families. Precise measure of shifting available for only 6 families. Of these: 4 lacked Low plants of which 1 showed enhanced shifting. 2 included Low plants of which both showed enhanced shifting
F3 from F2 Low plants	1/3 families entirely *J J k k* 2/3 families have *J/j* segregating	Enhanced shifting and Low plants in more than 75% families	8 out of 9 families contained Low plants. All 9 displayed enhanced shifting
F2 Low plants backcrossed to Line b	*J – k k* × *j j k k*	At least 50% families should show enhanced shifting and/or Low plants	4 out of 6 families contained Low plants 5 displayed clear shifting. One family (lacking Low plants) displayed marginally enhanced shifting

3.3 Transmission of Low Mutability by Non-mutable Segregants

If the Low mutability and associated shifting of the *pal-rec* gene described in the previous sections was caused by two factors *J* and *k* as suggested in Table 3, then most or all of the non-mutable *pal-tub pal-tub* segregants in the Low families should be *J – k k*. To test this assumption 11 *pal-tub pal-tub* plants from the F_5 Low families (Table 4) were crossed with members of Line d.

Mutability was affected in all 11 families as shown by enhanced shifting. In addition, four plants in two crosses displayed Low predominant mutability. F_2 progeny were raised from 18 normally mutable but shifting plants and 6 of the resultant progeny – families included Low plants as well as enhanced shifting. In contrast to these instances of altered mutability many crosses between Line d and Line b made over a period of 10 years have produced neither enhanced shifting nor Low plants. All 11 *pal-tub pal-tub* segregants were therefore able to transmit altered mutability to the highly mutable uniform Line d. The cause of Low mutability can thus exist in a genome unable to express its effect, and following its introduction by crossing can then exert that effect on a susceptible *pal-rec* allele. In the terminology of Table 3 the 11 *pal-tub pal-tub J – k k* segregants in the F_5 of the (a × b) cross obtained their *pal-tub pal-tub* from Line b but their *J* from Line a. *J* is therefore separable from the pallida locus at such a frequency as to rule out close linkage.

3.4 Relationship Between Shifting and Low Mutability

A more detailed investigation was made of the characteristics of altered mutability as revealed by descendants of the first type of cross (a × b).

Table 4. Proportion of Low plants in successive generations of Low families

Generation	Number of families	Normally mutable plants	Low plants	% Low plants
F 1	7	72	0	0
F 2	14	193	11	5
F 3	9	110	34	24
F 4	16	116	80	43
F 5	12	39	113	74
F 6	1	5	5	50
F 2 backcross[a]	6	65	19	23
F 3 backcross	6	47	11	19
F 4 backcross	8	80	18	18

[a] Backcrossed to Line b, *Eos Eos pal-tub pal-tub*

A total of 77 families were raised following the Line a X Line b crosses representing generations F_1 – F_6 and backcrosses of members of the F_2, F_3 and F_4 to Line b. Of the post – F_2 families all had a low-mutable parent except three families which were selfed offspring of normally mutable sibs of Low plants.

The proportion of Low plants tended to rise with successive generations of selfed families, remaining at a moderate level in backcrossed families (Table 4).

For each of the 77 families the following five characteristics, A – H, were recorded and quantified, and correlations were sought between pairs of characteristics.

A: Proportion in a family of mutable plants with a Low-mutable inflorescence.

G: The measurement of A for the family to which the Low parent of the family under consideration belonged. A and G are arranged in classes 1 – 6, which in practice covered the percentages:

class:	1	2	3	4	5	6
%:	0-10	12-23	25-34	38-62	68-82	100

Families containing more than 9 plants were allotted to classes 1 – 6, but those with fewer than 9 plants to classes 2 – 5, incorporating 1 in 2 and 6 in 5.

E: Amount of shifting in a single parent plant was recorded as number of shifts per inflorescence of eight or more flowers, and allotted empirically to classes 1 – 6 where class 1 represented almost completely uniform mutability (i.e. no shifts) whereas class 6 was a patchwork of different mutability levels. Line a plants fell into class 1.

D: This is a measurement of shifting in a whole family, using the same data as for E, adjusted empirically to cover a numerical range of −2 to +2, almost completely uniform families falling near −2 and very frequently shifting families approaching +2. The value of D for the parent mutable Line a was about −1.5. Only one of the Low families had a D value less than −1.5, and most exceeded + 1.0.

H: The measurement of D for the family to which the Low parent of the family in question belonged.

Characteristics A and G describe the proportion of Low plants in a family; characteristics E, D and H describe the amount of shifting. These two aspects of the altered behaviour of *pal-rec* were found to vary inversely in the extent to which they were expressed, and to display inheritance of that extent in succeeding generations. Lineages characterised by a very high proportion of Low plants and relatively infrequent shifting are said to display 'Strong' expression of the effect, and the converse extreme has been termed 'Weak' expression, the bulk of families forming a continuous range between the two.

Families which were backcrossed to Line b tended to show a Weaker effect than the majority of families under examination, which were selfed offspring of Low plants. 'Backcrossed' families did not, however, actually depart from the trends observed for the total families, and were included in the statistical examination.

Significant correlations found between pairs of the characteristics A, G, E, D and H are set out in Table 5.

Further investigations threw light on the relationship of constitution at the *eosinea* locus to the effect on *pal-rec*. Of 31 *Eos* – Low plants examined, nine proved to be *Eos Eos* establishing that the alteration of mutability is not dependent on the presence of recessive *eos*.

However, comparison of constitution at *eosinea* with two of the characteristics defined above suggested association of heterozygosity at *eos* with a Strong mode of expression of the effect on *pal-rec*.

(i) Comparison of the proportion of Low plants in each family (Characteristic A) with the number of generations for which that family's lineage had carried recessive *eos* gave a significant positive correlation ($r = + 0.58$, $P < 0.001$).

(ii) Comparison was made of the amount of shifting in each family (Characteristic D) and the family's constitution at *eosinea*. The distribution is summarized in Table 6. The numbers of families falling into each category, though too small for a meaningful statistical analysis, suggest that families with relatively little shifting tend to be confined to the segregating families, *Eos Eos* families being nearly all very highly shifting.

From the above comparisons, it is apparent that the two aspects of altered behaviour of *pal-rec*, though separable from *eos*, appear to bear some relationship to it. Prolonged experience of *eos* in the same genome correlates positively with the proportion of Low plants, and current heterozygosity appears to permit relatively uniform mutability within the range of enhancement of shifting provoked at *pal-rec*. The relationships suggest promotion

Table 5. Correlation between pairs of characteristics in Low families

Pair of characteristics[a]	Correlation coefficient	Significance	Indicates
A G	+ 0.62	P 0.001	Inheritance of proportion of Low plants
D H	+ 0.46	$0.001 < P < 0.01$	Inheritance of amount of shifting
D E	+ 0.34	$0.001 < P < 0.01$	
E H	+ 0.66	$P < 0.001$	
A E	− 0.28	$0.02 < P < 0.05$	Inverse relationship
A D	− 0.31	$0.01 < P < 0.02$	between them

[a] See Section 3.4 for definition

Table 6. Comparison of amount of shifting with family's constitution at *eosinea*

	Uniform[a]				Extremely frequent shifting
D value: –	−2 to −1	−1 to −0.5	−0.5 to +0.5	+0.5 to +1	+1 to +2
Segregating families: –	5	3	7	4	20
EosEos families: –	0	0	1	0	14

[a] Scale of shifting frequency on which the parental Line a gave a value of −1.5. See Section 3.4 for detailed definition

by recessive *eos* of a Strong rather than a Weak mode of expression of the effect on mutability of *pal-rec*.

4 Discussion

Operation of the mutable allele *pal-rec* accords with the definition of an 'autonomous' or 'one element system', in which both the function blocking normal *Pal* activity and that which releases this activity in some cell lineages, reside at or near to the *pallida* locus (Fincham 1973). There has, however, been no demonstration as yet of transposition of a controlling element accompanying release of *Pal* activity as is frequent in the maize systems for which the definition was originally devised (Fincham and Sastry 1974). Suggestive of such transposition was the appearance de novo of unstable *delila* and *eluta* alleles in stocks carrying *pal-rec* (Harrison 1965).

From its first appearance the strikingly infrequent mutability of the 'Low' plants described here was accompanied by the more widespread phenomenon of frequent shifting of mutability level. These two aspects of the effect on the behaviour of *pal-rec* were jointly investigated.

Observed segregation of the effect ruled out a single Mendelian modifier as its cause, whether dominant or recessive. The entity responsible for the effect consists of two factors, suggested to be a dominant allele *J* carried by the John Innes lines and homozygous recessive alleles *k k* of a second gene carried by Leeds stock (Table 3). This hypothesis accords with observations except for the F_1 Low plants from the cross Line a × Line d. The dominant *J* is demonstrated to be recombinationally separable from the *pal* locus.

A number of mutable systems have been reported where separate loci affect mutability of an unstable allele. The *speckled* allele of *Pharbitis nil* mutates less frequently and at a later stage of flower development in the presence of the *speckled-reduced* (Imai 1931). The *p** allele of *Delphinium ajacis* is dependent for full mutability on the 'activator' gene (Dawson 1955). For the *pal-rec* allele itself the semi-dominant unlinked modifier *Stabiliser* has been well characterised. It reduces the mutation frequency, and has been associated with enhanced shifting which was, however, ascribed to a proposed mutability of *St* itself (Harrison and Fincham 1968, Fincham 1970, Harrison and Carpenter 1973).

The complex and well-documented controlling element systems of maize yield two instances. Modifier of the controlling element *Spm* is an unlinked transposable dominant entity which enhances mutability of 'weak' isolates of *Spm* having no effect on a fully active *Spm* (McClintock 1965).

M^{st}, a linked transposable modifier of R^{st}, raises the 'stippled' mutability from a level termed 'Light R^{st}' to the 'Standard R^{st}' frequency, while not affecting paramutagenicity of R^{st} (Ashman 1960).

An unlinked modifier, Fleck-timer, *Flt-3*, in *Nicotiana* hybrids delays the mutation of unstable *v* alleles, but promotes their germinal mutation to the dominant solidly coloured *V* concurrently with its own loss, which suggests transposition as well as constituting a uniquely qualitative effect on mutability, since *V* does not arise germinally in the absence of *Flt-3* (Sand 1976). The origin of the unstable *v* alleles themselves is unique in that they arise somatically de novo in a small proportion of hybrid plants following interspecific crosses (Sand 1969). Contributions from two different parental lines are evidently necessary, but after its isolation *v* behaves as a single ordinary recessive Mendelian unit irrespective of genetic background.

Frequent changes in mutability level of unstable genes can be envisaged as shifts between different modes of insertion of the controlling element, consequent upon intralocus transpositions (Fincham and Sastry 1974). The shifting of mutability level of *pal-rec* central to the current observations can then be suggested to illustrate a series of insertion positions, giving equal repression of *Pal* activity but individual frequencies of release of activity by long-range transposition of the element away from the *pallida* locus. Promotion of shifting by the two factors under investigation can be envisaged possibly as an influence on the topology of the *pallida* region of the chromosome. The 'Weak' and 'Strong' modes of expression of this effect confer emphasis respectively on the frequent shifting of insertion position by the controlling element of *pal-rec*, and its achievement early in development of a position giving an

infrequency of mutability unprecedented in the stocks used. The latter aspect of the effect, seen as Low plants, is proposed to be merely a special case of the former and the Weak-Strong range as suggestive of a range of forms or configurations available to the $J - k\ k$ partnership. This would hint at the possibility of these alleles themselves constituting a two-part controlling system, as is more positively suggested in maize for *Mod-Spm* and M^{st} by their transposability. Besides its similarities to other modified mutable systems, the one under consideration displays a unique mutability of mutability, as opposed to its alteration in a particular, predictable way.

This influence on *pal-rec* having been demonstrated, economy requires that the new and relatively uncharacterised factors be held responsible only for those occurrences necessary to account for observations which cannot be allotted elsewhere. Thus the modifying entity is envisaged as having the capability of a range of modes of expression from 'Strong' to 'Weak', the mode tending to remain constant after adoption within lineages. The many different frequencies of mutation *pal-rec* to *Pal* exhibited during shifting is thought most probably under the control of the autonomous controlling element resident at *pallida*. The relationship between the short-range transpositions postulated as the cause of shifting and the long-range transpositions of the controlling element away from *pal-rec* so that *Pal* expression is restored, may not be one of simple proportion, since predominantly highly mutable inflorescences have not on average shown the most frequent shifting. Developmental stage clearly influences frequency of intra-locus transpositions since timing of shifts is uneven, a predominant background mutability level being clear in nearly all inflorescences, and the areas covered by tissue of contrasting shifted mutability level being usually smaller than one flower.

The system becomes even more complex upon consideration of the role of recessive *eos*, which is unlinked to *pal-rec* whose mutability it depresses when homozygous. Its influence when heterozygous though evident from its progressive reinforcement of the 'Strong' mode of influence of *J* and *k k* on *pal-rec*, does not extend to its presence being necessary for any aspect of the alteration in mutability of *pal-rec* to occur.

Thus the influence of *eos* partially imitates a modifier like M^{st} (Ashman 1960) of a classic mutable system R^{st} (Kermicle 1973) where mutability of a locus is influenced only via its controlling element: and partially resembles paramutation as elucidated by Brink in maize (Brink 1973) and by Hagemann in tomato (Hagemann and Berg 1978) where continuation in the same genome of both perpetrator and recipient progressively promotes the effect. It differs from the latter in that *eos* is a locus independent of the two factors *J* and *k* as well as being unlinked to *pallida*, whereas paramutation classically requires perpetrator and effector to be alleles. It differs from the former in that besides causing the familiar effect of *pal-rec* mutability depression, *eos* has a function that bears on the normal function of *pallida*, the locus by which these effects are detected.

This raises the possibility that the situation represents an intermediate condition between the two classical phenomena, whereby mutability level in general is affected, and existence in the same genome allows a progressive influence of one function upon another without necessity for an allelic relationship between the two.

The system as here described reveals that there are four sources of influence on mutability of *pal-rec*: the known simple mutability depressors *Stabilizer* and *eos*, and the newly proposed *J* and *k*. These four sources constitute three tiers of control, with *eos* acting at a basal level as does *St*, but also as the third tier superimposed on the middle-tier influence of *J* plus *k*. The intermediate-level control constituted by the partnership of *J* plus *k* is unique in causing instead of a single predictable alteration in behaviour of *pal-rec*, a mutability of its mutability.

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Book Reviews

Steele, E.J.: Somatic Selection and Adaptive Evolution on the inheritance of acquired characters. London: Croom Helm 1980. 91 pag., 6 figs., 3 tabs. Hard bound £ 8.95.

In this interesting and provocative book the author has reopened the discussion about the mechanisms of the evolutionary process. After a consideration of contemporary ideas in immunology, virology and molecular biology he wants to revive Lamarck's much discredited theory on the inheritance of acquired characters. In his opinion some essential paradoxes in immunology and virology can only be satisfactorily resolved by the rejection of Weismann's doctrine of the isolation of the soma from the germline. This leads to the acceptance of a Neo-Lamarckian view of inheritance, i.e. the somatic selection hypothesis, which is experimentally testable by endogenous mammalian RNA viruses carrying somatic genes to the germline.

The biochemical details of this theory are necessarily technical and much attention is given to many specific facts from immunology, virology and molecular biology. But all these numerous facts will be omitted from the following discussion, because the review of this book will concentrate on the basic concepts and principles and the theory and consequences developed from these assumptions.

First, we will give some references to the classification and content of the book, which has been divided into six chapters and an appendix. Chapter 1, 'The problem and the purpose', contains an introduction and some general considerations on the author's thesis that in many multicellular sexually reproducing organisms Lamarckian modes of inheritance exist, which provide an element of 'directional' progress in the evolution of biological complexity.

Chapter 2, 'Lamarck in perspective', gives an historical account of Lamarckism, followed in chapter 3, entitled 'The central paradox of immunology', by a discussion of some topics from modern immunology, virology and molecular biology. Here the author puts aside the usual consideration of natural selection acting on populations of organisms and the discussion has been focussed on natural selection operating on cell populations within the body of an individual. Chapter 4, 'The somatic selection hypothesis', contains the most essential part of the book, namely a Neo-Lamarckian model of a possible mechanism for the transmission of acquired characters, in the sense that somatic gene mutations can be genetically inherited. In chapter 5, 'Implications and conclusions', it is shown how the somatic selection hypothesis provides solutions and predictions to the theory and practice in many areas of modern biology. The final chapter 6, 'Speculations on man, mind and matter', deals with the philosophical implications of this theory; for example, contributions to the perennial nature-nurture debate, and an approach to the mind-body problem. It concludes with a speculation on how man may shape his own evolution. An appendix 'On the relevance of the RNA tumor viruses to the somatic selection hypothesis' describes some further biochemical and virological details. Additionally, all chapters are followed by extensive Notes, which include supplementary comments, literature and explanations.

The author's main ideas can be summarized as follows. One difficulty with Darwinism arises from the fact that it provides no satisfactory explanation for the intuitive belief of 'directional' progress in the evolution of biological complexity. The reasons lie not in Darwin's concept of selective survival but in the two assumptions that 1) the locus of all meaningful phylogenetic changes (in multicellular organisms) occurs only in the germline genes of the gonads and 2) that the genes in the gonads are resistant to most direct influences of the contemporary environment. One problem of the hereditary phylogenetic adaption process is that one important change can be expressed usefully in the organism only if additional harmonious adjustments are also made in other parts of the organism. Conventional Darwinian theory requires no concept of simultaneity by assuming that a sufficient time interval exists for all these evolutionary changes. The author's rejection of this concept is based upon a discussion of spontaneous mutation rates.

All these difficulties can be simply solved by altering our views on where the Darwinian process of chance mutation and natural selection first takes place. The author's hypothesis stresses that this locus is not so much the genes in the germ cells but rather those genes carried in that large, constantly changing differentiated cell population of the soma. If these new somatic gene mutations can be incorporated into the hereditary DNA of the gonads this mechanism makes it possible that adaptive solutions to contemporary environmental pressures achieved by the parental generation can be passed on to their offspring via the hereditary genes of the gonads.

The author's argument makes use of the properties of the immune system, which responds to the unexpected, because a given organism can produce antibodies specific for almost any chosen antigen, naturally occuring or artificially made by man. In the author's view it would be most improbable and most unbiological to expect all these possible organism adaptions to their antigenic environment to be codified by the hereditary DNA of the gonads, because it would be difficult to see how such an enormous gene array can be maintained in the face of random genetic drift.