6. The mutable pale green locus

The mutable pale green phenotype was found in material provided by Dr. E. G. Anderson which had been exposed to irradiation from the Bikini atom bomb.

Two distinct seedling phenotypes are associated with the pg complex; a stable-type (pg^s) characterized by its uniform "pale green" color with occasional sectors of green stripes and a variegated-type (pg^m) containing numerous dark green stripes on a pale green background. There is experimental proof that these green stripes represent mutations of pg to the normal allele, Pg.

These two phenotypes appear, together with the normal green plants, in three characteristic ratios in the F_2 progenies. (1) 3:1 for green to stable pg - the s class; (2) 12:3:1 for green to mutable pg to stable pg - the m & s class; and (3) 3:1 for green to mutable with a low and variable fraction of stables - the m class.

There are various lines of evidence to show that the m & s class is due to the presence of an independently segregating factor, En, increasing mutability at the pg locus. Such a factor acting on pg is suggestive of the Dt influence on a_1 and of the Ac effect on Ds-controlled loci. When mutable plants homozygous for independent En (pg En) are outcrossed to various agronomic lines, the following results are obtained:

	Classes of F_2 progenies			
Pollen parent	G	s	m & s	m
1950 43-54	4	0	22	2
1950 43-57	15	0	29	2
Total	19	0	51	4

When pg plants from the unexpected m type progenies are further tested in the F_3, they behave like members of the m class.

The mutability of the m class is autonomously controlled -- i.e. En is located adjacent to the pg locus (pgEn). When pollen parents containing homozygous pgEn are outcrossed to lines, the following results are obtained:

	Classes of progenies			
Pollen parent	G	s	m & s	m
1950 66-108	11	3	10	54
1950 40-37	1	1	5	17
1951 388.1	0	0	2	7
1951 647-3	24	1	11	12
1951 283-1	21	2	3	20

In addition to the m-type F2 progenies, two unexpected classes -- the m & s and s -- also appear. Their frequency is interpreted as indicative of a high rate of change from pgEn (m class) to pgEn (m & s) and pg (s class). Transposition of En from its position adjacent to the pg locus results in its appearance at another position in the chromosome complement. Plants from the

newly-arisen m & s type behave as if En were independently segregating and those in the s class lack En.

Tests show that En is not present in 20 agronomic lines examined.

Rate and direction of mutation. - pg^s mutates to pg^m in a low frequency (1/420). The occurrence of pg^m seedlings in pg^s stocks is correlated with the sectors of mutability observed in pg^s seedling leaves. This is indicative of the appearance of En in somatic tissue. The isolation of one B-type progeny from the outcross of pg^s indicates that this new En lies adjacent to the locus.

pg^m mutates to pg^s at the rate of approximately 2.5% - 4% in the gametes of pgEn P_1 pollen parents.In the F_1 plants, the rate is approximately 17%. A number of explanations, such as different rates of mutation in homozygotes versus heterozygotes and the presence of non-specific modifiers in the P_1 plants reducing mutation rate, may account for this difference.

The autonomous and independent En differ in their phenotypic expression and in their relative stability in that the latter is characterized by a pattern of later occurring mutations and has not been found to mutate.

In addition to the location of En adjacent to the locus and on an independently segregating chromosome, En was found in one instance to be linked with pg at a distance of approximately 36 cross-over units. This third location of En is further evidence that it undergoes transposition.

A hypothetical representation of the pg complex is diagrammed below:

pg^s	=	Pg(I)	-stable type seedlings
pg^m	=	Pg(I)En	-mutable seedlings: the autonomous location of En.
	=	Pg(I) En	- mutable seedlings: the independent location of En.
Green	=	Pg	- Normal wild allele of all lines.

According to this scheme, the mutable locus represents the association of an inhibitor (I) with the normal dominant allele Pg resulting in a pale green phenotype. The loss of (I) under the influence of En is manifested in the mutation of pg to Pg. This scheme fits McClintock's concept which considers that mutation of unstable genes represents the removal of an inhibitory locus adjacent to the dominant allele.

Two new mutables (a_1^m and wx^m) arose in pg^m families containing the dominant alleles A_1 and Wx.

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