## THE SEGREGATION OF MUTANT GENES

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A clear 3:1 segregation in the progenies of monohybrid plants can be expected only if three conditions are satisfied:

- The frequency of gametes with the dominant and the recessive allele must be approximately equal.
- The two categories of gametes must have equal chances of participating in fertilization.
- The three genotypes AA, Aa, and aa in the F2 or M2 families must have approximately equal chances of survival during the earliest stages of ontogenetic development.

The first condition is usually fulfilled because meiosis is a very reliable process. In the large group of lethal mutants, the third condition is not fulfilled in all those cases in which the mutant gene is effective during seed germination or immediately afterwards, resulting in a deficit of mutants.

In the second and most interesting group, the growth rate of the pollen tubes containing the mutant recessive allele often is lower than that of the tubes containing the non-mutant dominant allele. This phenomenon, called zertation, necessarily leads to a deficit of mutants in the segregating families, the extent of the deficit depending on the differences in the growth rates between A and a/a tubes.

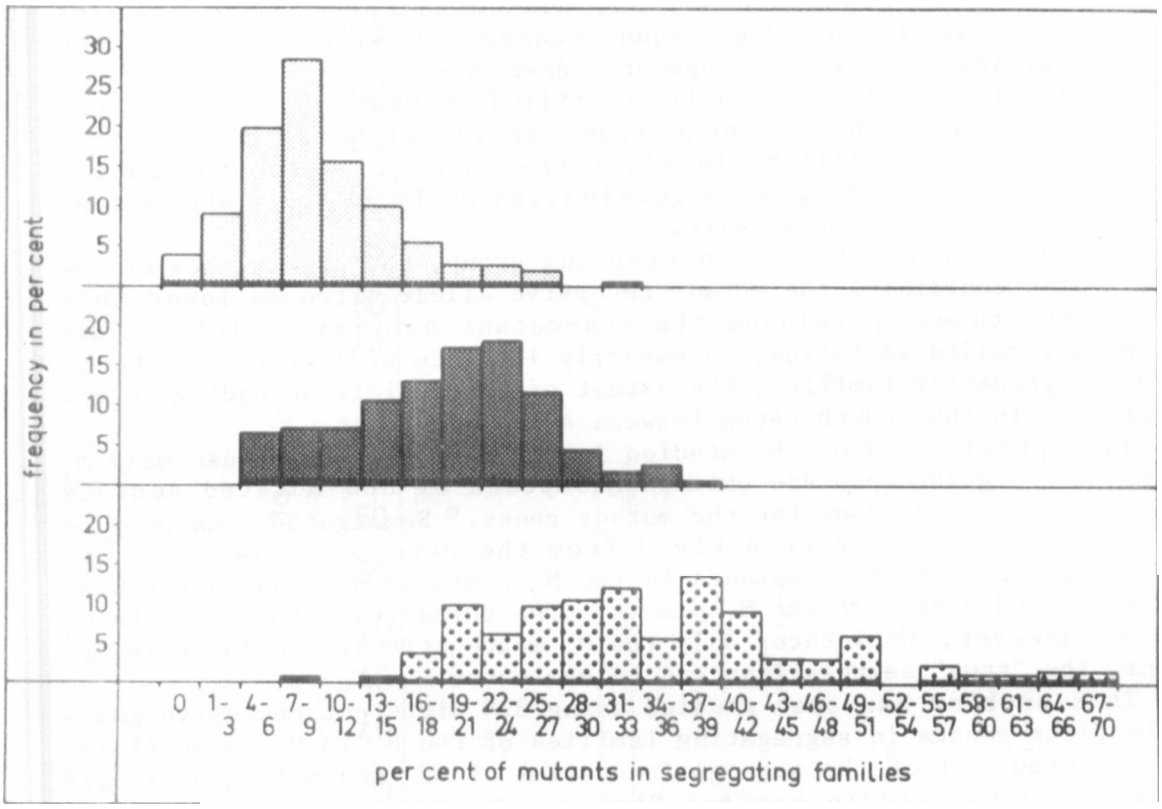
This problem cannot be studied in the M2 families because many M1 plants of the garden pea are chimeras composed of non-mutated sectors and sectors heterozygous for the mutant genes. Segregation can only be expected in the offspring derived from the heterozygous sectors. Therefore, the deficit of mutants in the M2 families depends on the size of the mutated sector of the M1 plants. The chimerical status of the M1 plants, however, influences only the M2 segregations. In later generations, the "true" segregations can be evaluated.

This problem has been studied using 324 different recessive genes of the Pisum genome in segregating families of the M3 to M6 generations. The distribution of the segregation ratios of 320 genes is graphically presented in the middle part of Fig. 1, showing a clear deficit of mutants. In many cases, the deviation from a 3:I segregation was statistically not significant, due to the small number of plants in some families. If, however, we consider the whole material evaluated, comprising 3,523 segregating families, the trend toward a deficit of mutants becomes clear.

A particularly strong deviation was found in mutants 60A, 168 and 1206A (upper part of Fig. 1). Genotypes 168 and I206A are fertile chlorophyll mutants; 60A is a tiny, long-living lethal mutant. The deficit of mutants, it must be emphasized, was not due to an ontogenetically early death of some of the mutant plants. Similar deficits were found in subsequent generations, not only In these 3 genotypes, but also in many mutants belonging to the middle group of the graph. Furthermore, they were observed in F2 to F4 generations following hybridizations between the mutants and the mother variety, demonstrating thereby that these deviations are characteristic peculiarities of the respective genes.

The negative selection value, well known for the majority of mutants, is already evident in the haplophase. This implies that the pollen tubes with the mutant genes are not as competitive as those with the non-mutant alleles in many different mutants.

The only case in our large collection that a mutant gene showed a considerable surplus of recessives in segregating families was mutant 142 B, homozygous for dgl. This mutant causes degeneration of leaflets and stipules during ontogenesis. Segregation of this gene was studied in M3 to M9 in 133 families (lower part of the figure). The causes of this unusual behavior are not yet known.




Pig. 1. The segregation ratios of 324 mutant genes in M3 and in latter generations. Upper part: Mutants 60A, 168, 1206A (167 families). Middle part: 320 different mutants (3,523 families). Lower part: Mutant 142B (133 families).