

SELECTION AGAINST THE VARIEGATED GENOTYPE IN *BARBAREA VULGARIS*

R. A. E. TILNEY-BASSETT
Botany School, Oxford

Received 26.viii.63

1. INTRODUCTION

The variegated leaves of *Barbarea vulgaris* consist of a mixture of pure green areas and yellowish-white areas speckled with green flecks. The pure green areas may be whole leaves, sectorial leaves green on one side of the midrib and variegated on the other, or isolated sectors of the leaf blade. In mature plants the leaves frequently have a characteristic pattern somewhat like a periclinal chimera with a yellowish-white, speckled margin and a green centre.

The breeding experiments of Dahlgren (1921) and Andersson (1924) showed that variegation was caused by a recessive gene or genes, but beyond this their results were inconclusive.

2. BREEDING AND DEVELOPMENT

Reciprocal crosses between true-breeding green and variegated stock plants gave 371 green offspring, and a selection of these, when selfed, segregated into green and variegated seedlings. The F_3 generation contained one class of variegated families, true-breeding, and two classes of green families, one consisting of 11 pure green and the other of 18 segregating green families, which is in good agreement with the proportion expected from a 3 : 1 F_2 segregation of one homozygous green : 2 heterozygous green F_2 families. The F_2 and F_3 segregations both showed a significant deviation from the monohybrid 3 : 1 ratio owing to a deficit of variegated seedlings (table 1). The slight heterogeneity between individual F_2 and F_3 families though statistically significant, is of no great moment.

Seeds germinated in J.I. Seed Compost at 20° C. and a 15-hr. day gave the following results for all the F_3 families; each contained 200 or 400 seeds: (1) Ten true-breeding variegated families produced 2598 seedlings. Mean germination 68.37 per cent.; range 49.00-88.50 per cent. (2) Eleven true-breeding green families produced 3446 seedlings. Mean germination 82.05 per cent.; range 72.50-90.25 per cent. (3) Eighteen segregating families produced 4854 seedlings. Mean germination 71.38 per cent.; range 57.50-86.00 per cent.

These results show that seed is less viable from the average variegated family than from a green family. Consequently, the less viable variegated seeds depress the germination of the segregating families. This is confirmed by the mean germination of the segregating families which lies between the values for the true-breeding families. The poorer germination of variegated seeds explains the deviation from the 3 : 1 segregation. Furthermore, the segregating F_3 families produced not more, but somewhat fewer green seedlings than expected from a 3 : 1 ratio and 82.05 per cent germination. Hence there can have been no selective elimination of variegated seed before harvesting, but only during germination.

TABLE 1

Total offspring from segregating families of the F_2 and F_3 generations showing a significant deviation from the 3 : 1 ratio owing to a deficit of variegateds

Nos. families and offspring				Significance tests			
Families	G	V	T		χ^2	d.f.	P
<i>F_2 generation</i>							
9	3206	763	3969	Total χ^2 . . .	84.2	9	v. small 0.10
				Deviation χ^2 . . .	70.6	1	
				Heterogeneity χ^2 . . .	13.6	8	
<i>F_3 generation</i>							
18	3961	893	4854	Total χ^2 . . .	144.8	18	v. small 0.015
				Deviation χ^2 . . .	112.8	1	
				Heterogeneity χ^2 . . .	32.0	17	
$F_2 + F_3$ combined heterogeneity χ^2 . . .				45.6	25		0.007

Individual seedlings differ in the stage of growth at which variegation first appears (table 2). Thereafter, it does not necessarily develop in each leaf but, generally speaking, the later the initiation of variegation the lower its frequency during subsequent development. Mature plants therefore

TABLE 2

Relationship between the stage of leaf development and the first appearance of variegation in 373 seedlings from six segregating families of the F_3 generation

First appearance leaf stage	Seedlings	
	Nos.	%
Cotyledons . . .	250	67.02
1st pair . . .	104	27.88
2nd pair . . .	17	4.53
3rd pair . . .	2	0.54

show a wide variation in the phenotypic expression of variegation, which is presumably controlled by modifying genes.

The growth of green and variegated plants was compared by measuring their fresh weights under different light conditions (table 3). The fresh weight of young green plants was always greater than the variegated especially at the lowest light level. This result agrees with the growth in the garden where the green is always more vigorous than the variegated.

TABLE 3

Comparison of the fresh weights of green and variegated plants grown for 122 days at 18° C. under varying light intensities, five plants at each level

Light level	Mean fresh weight per plant	
	G	V
High . . .	18.5 gms.	18.0 gms.
Medium . . .	5.5 gms.	4.5 gms.
Low . . .	2.5 gms.	1.7 gms.

3. SELECTION AGAINST VARIEGATED PLANTS

The breeding results show that variegation is controlled by the action of a recessive gene. But owing to the reduced viability of seeds with the homozygous recessive genotype, there is a marked deviation from the expected 3 : 1 ratio. The reduced viability of the variegated seeds is followed by the poorer growth of the variegated seedlings. Hence there is a selection pressure against the variegated genotype throughout development from the immature seed to the mature plant, a selection pressure which would be quite sufficient to reduce the variegated plants in the wild to a very low frequency maintained by the pressure of mutation.

Acknowledgments.—I would like to thank Professor C. D. Darlington for his invaluable supervision, and the Christopher Welch Trustees for a Scholarship which enabled me to prepare this account while studying for a D.Phil. degree in the University of Oxford.

4. REFERENCES

ANDERSSON, I. 1924. Structural mosaics and inheritance of variegation in *Barbarea vulgaris*. *J. Genet.*, 14, 185-195.
 DAHLGREN, K. V. O. 1921. Vererbungsversuche mit einer buntblättrigen *Barbarea vulgaris*. *Hereditas*, Lund, 2, 88-98.