

ON THE FREQUENCY OF INTROGRESSION OF THE RADIATE ( $T_r$ )  
ALLELE FROM *SENECIO SQUALIDUS* L. INTO *SENECIO*  
*VULGARIS* L.

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THE origin and maintenance of the rayed gene polymorphism in *Senecio vulgaris* L. within Britain has been the subject of much recent discussion (see Stace, 1977, and Ingram *et al.*, 1980, for details). Plants homozygous for the normal allele ( $T_n$ ) produce capitula bearing only tubular, hermaphrodite disc florets, while plants homozygous for the radiate allele ( $T_r$ ) possess 8-13 marginal ray florets in addition to the disc florets of the normal type. Dominance is incomplete, and the heterozygote ( $T_r T_n$ ) has short, stubby ray florets. A body of circumstantial evidence has led to the hypothesis that the  $T_r$  allele originated in *S. vulgaris* as the result of introgression, following the hybridisation of non-radiate *S. vulgaris* (var *vulgaris*),  $2n = 40$ , with the naturalised alien *S. squalidus*,  $2n = 20$  (Crisp and Jones, 1972). This hypothesis has been reinforced by the recent work of Ingram *et al.* (1980), in which the triploid hybrid *S. vulgaris* var *vulgaris*  $\times$  *S. squalidus*,  $2n = 30$ , was synthesised, and fertile tetraploid radiate individuals ( $2n = 40$ ) were obtained by selfing the product of the backcross to *S. vulgaris* var *vulgaris*. These synthesised radiate plants bore a marked resemblance in gross morphology to radiate groundsel (var *hibernicus*) from natural populations.

Hull (1976), from a study of the distribution of the  $T_r$  allele in Central Scotland, has argued that introgressive gene flow from *S. squalidus* into *S. vulgaris* is common and plays a major role in determining the frequency of the  $T_r$  allele in *S. vulgaris* populations. This suggestion has, however, aroused some controversy (Stace, 1977). If correct, we should expect the triploid hybrid to be frequent in areas such as East Central Scotland (see Hull, 1974) where *S. squalidus* is often found at high densities in the same habitats as, and in intimate association with, polymorphic populations of *S. vulgaris*. However, Ingram *et al.* (1980) found only three hybrids judged to be of the type *S. vulgaris* var *vulgaris*  $\times$  *S. squalidus* during an investigation of three large sites in East Central Scotland. Moreover, Stace (1977) has concluded from many searches throughout Britain that the triploid hybrid is rarely encountered in the wild. To obtain information on the amount of hybridisation that occurs in the wild we have screened large numbers of progenies of both radiate and non-radiate *S. vulgaris* for the occurrence of the triploid hybrid. Seed progenies of *S. squalidus* have not been screened as the triploid hybrid only appears to be produced when *S. squalidus* acts as the pollen parent (Ingram *et al.*, 1980).

Four sites (table 1) were investigated, each containing several thousand plants of *S. squalidus* together with both the radiate and non-radiate forms

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TABLE 1

The number of hybrids found on sites and among the progenies of radiate and non-radiate plants sampled from each site

Site	No. of hybrids on site*	No. of hybrids recovered from radiate parents†	No. of hybrids recovered from non-radiate parents†
Edinburgh (i)	5 (13,859)	0 (4522)	0 (2951)
Edinburgh (ii)	2 (7490)	1 (2784)	0 (1237)
Leeds	0 (1047)	0 (1168)	0 (1150)
Cardiff	1 (7597)	0 (995)	1 (1054)
Total	8 (29,993)	1 (9469)	1 (6392)

\* No. in parentheses represents *S. vulgaris* plants counted on site.

† No. in parentheses represents progeny scored.

of *S. vulgaris*. The two Edinburgh sites were visited on several occasions during 1978, while the sites at Leeds and Cardiff were visited once in June 1979, when both species were judged to be at their peak of flowering. At each visit, a thorough search was made for the triploid hybrid, *S. vulgaris* × *S. squalidus*, and a count was made of the total numbers of individuals of *S. vulgaris* present on the site. Subsequently, seed for progeny testing was collected from each of 50 radiate and 50 non-radiate, open pollinated plants randomly sampled from the site. Progenies were screened for the presence of the triploid hybrid after being raised to the flowering stage under glass. Hybrids were recognised by their distinctive morphology (Ingram, 1977; Ingram *et al.*, 1980) and by chromosome counts made on root tip preparations.

The results obtained from both the field survey and the progeny tests (table 1) clearly show that hybridisation between *S. vulgaris* and *S. squalidus* is a rare event in the wild. The few hybrids which were found were all highly sterile. Any seeds formed on the hybrids under open pollinated conditions are likely to be the result of backcrosses to *S. vulgaris* and such plants will have a lower fertility than wild type *S. vulgaris* (Ingram *et al.*, 1980).

From a consideration of the combined effects of the demonstrated low frequency of hybridisation (table 1) together with the low fertility of the hybrids and their backcross progeny, we conclude that, although the  $T_r$  allele is likely to have originated in *S. vulgaris* as a result of introgression from *S. squalidus* (Ingram *et al.*, 1980), introgressive gene flow occurs only at very low frequencies under natural conditions. We therefore reject the suggestion by Hull (1976) that introgressive gene flow plays a major role in the maintenance of the  $T_r$  allele in *S. vulgaris* populations.

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