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# Selection and hybridisation as possible causes of changes in the frequency of alleles controlling capitulum-type in *Senecio vulgaris* L.

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## ABSTRACT

In 1973 samples of 50–500 plants of *Senecio vulgaris* L. were again classified from 27 populations in central Scotland, in which the relative frequency of the two alleles at the *T* locus, controlling capitulum-type, had been determined in 1972. A significant increase in the frequency of the $T_r$ allele occurred in one group of populations in an area where plants of *Senecio squalidus* L. were growing in large numbers. No significant increase occurred in another group of populations in an area where *S. squalidus* is rare. It is suggested that the radiate capitulum characteristic is being introduced passively into the *S. vulgaris* population as a result of hybridisation with *S. squalidus*. The possibility that radiate $T_rT_r$ *S. vulgaris* plants might have, at least under some circumstances, a higher reproductive fitness than the typical (i.e. rayless) $T_nT_n$ plants, and that the frequency of the $T_r$ allele is being increased by natural selection within the *S. vulgaris* populations, cannot, however, be ruled out.

## INTRODUCTION

*Senecio vulgaris* L. grows in abundance throughout the British Isles where soil conditions are suitable. In some areas it can be a troublesome weed, competing for light, nutrients and water with crop plants. It is particularly common as a first colonist of recently disturbed earth. In successive years plants of *S. vulgaris*, an annual species, will continue to grow from seed until replaced by other, more persistent species, such as *Tussilago farfara* L., *Agropyron repens* (L.) Beauv. or *Epilobium angustifolium* L. Data from numerous sources (e.g. Trow 1912, Crisp 1972, Hull 1974a) indicate that the radiate (*R*) phenotype of *S. vulgaris*, whose capitula have 8 or 9 long ray florets, is homozygous for the $T_r$ allele; the intermediate (*I*) form, with 8 or 9 very short, stubby ray florets is $T_rT_n$; while the typical rayless (*N*) form is $T_nT_n$.

A distribution map of locations where the radiate form of *S. vulgaris* grows in the British Isles (Perring & Sell 1968) shows that these coincide, to a large extent, with localities where *Senecio squalidus* L. has been found (Perring & Walters 1962); the latter is an alien species, probably first introduced in the late 18th century, which has since spread through much of the British Isles, including Scotland (Kent 1966). Usually the appearance of the radiate form of *S. vulgaris* in an area is preceded by the appearance of *S. squalidus*, although there are areas, such as those in Northern Ireland, where the radiate form of *S. vulgaris* occurs apparently in the absence of *S. squalidus*.

There is evidence (Lousley 1955, Rosser 1955) that hybridisation between *S. vulgaris* ($2n = 40$) and *S. squalidus* ($2n = 20$) can give rise, by polyploidy, to the fertile hybrid *S. cambrensis* Rosser ($2n = 60$). A natural tetraploid hybrid between *S. vulgaris* and *S. squalidus* has been reported (Crisp & Jones 1970). Some of the progeny of this latter plant were fertile when crossed with *S. vulgaris*, but were of greater vigour. It was suggested that introgression is occurring, with chromosome loss among the hybrids (Crisp 1972). This would allow the entry of genes (including those controlling capitulum-type) from *S. squalidus* to *S. vulgaris*. However, none of the expected triploid hybrids have been found.

Further evidence of continued interspecific hybridisation, with gene flow from *S. squalidus* to *S. vulgaris*, was provided by a study of the distribution of esterase isozymes of different electrophoretic mobility (located by acrylamide gel electrophoresis), in different populations of plants of the genus *Senecio* in central Scotland (Hull 1974b).

Samples of *S. vulgaris*, (each consisting of 50 to 500 plants), were taken from 45 populations, chiefly in central Scotland, in 1972. From these a distribution map of the $T_r$ allele was built up (Hull 1974a). In the present study, by sampling the same populations again in 1973 in which the frequency of the $T_r$ allele had previously been estimated, it was hoped to decide whether the frequency of the $T_r$ allele was altering in these populations and, if so, to determine the nature of the selective forces responsible.

## METHODS OF SAMPLING

Samples of plants were taken in 1973 from 27 populations which had previously been sampled in 1972 (Hull 1974a). In addition, 14 samples were taken from populations not previously examined. Depending on the total number of plants growing in an area, from 50 to 500 plants were classified as radiate ($R$), intermediate ($I$) or rayless ($N$). The area was marked out into a series of rectangles, each $12 \cdot 5 \times 4$ m, whose positions were carefully noted with reference to some fixed point so that plants growing in exactly the same rectangular areas of ground should be counted in the two years. This subdivision of the populations proved to be important in five cases, where part of the area had been rendered unsuitable for plant growth in 1973, for example by building on the land; under these circumstances the sample for 1972 was adjusted to include only plants in those rectangles which could be sampled again in 1973. These data are presented in Table 1. Only populations where at least 50 plants could be found in both years are included in the analysis. The frequency of the $T_r$ allele and the change in allelic frequency $\Delta f(T_r)$ are given for each area, identified by its national grid reference.

There appears to be a decline of 12% in the total number of plants counted in 1973 in the 27 areas sampled in both years. (This, however, excludes 18 areas sampled in 1972 for which, for a variety of reasons, a large enough sample could not be obtained in 1973). This could indicate that 1973 was less favourable climatically than 1972, but it is more probable that all areas became less suitable for the growth of *S. vulgaris* as the soil surface became more compacted and more persistent competitors colonised the areas.

## ANALYSIS OF RESULTS

In Fig. 1 the frequency of the $T_r$ allele is indicated by the extent of shading in the circles representing the 41 areas sampled in 1973: open circles for any population indicate that only the typical rayless form was found. In addition, the changes in frequency of the $T_r$ allele are given beside the appropriate symbol for all eighteen populations where these changes could be calculated. The 10 km

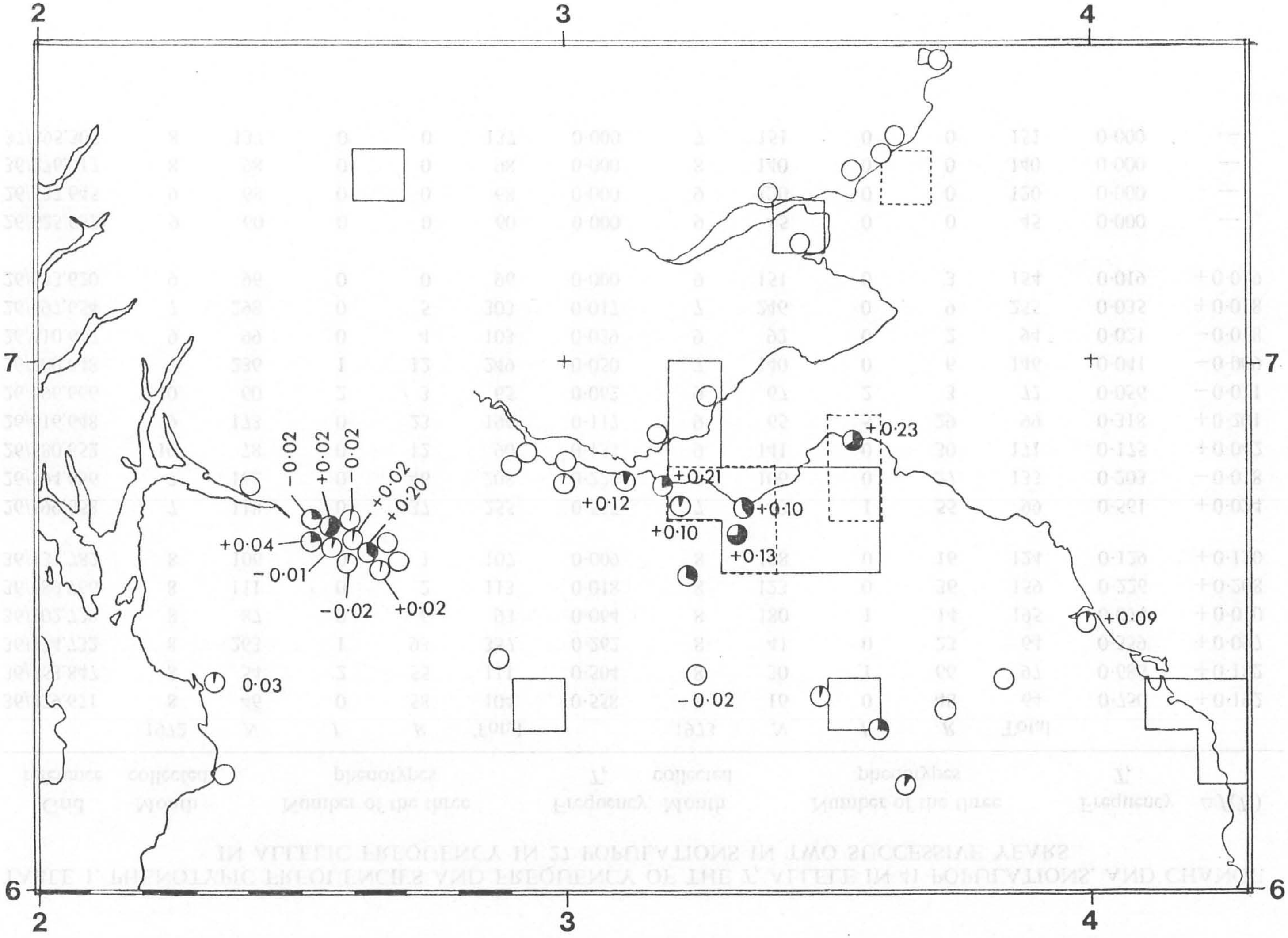

FIGURE 1. Map showing the frequency of the radiate allele ($T_r$) in the 41 populations in central Scotland sampled in 1973, together with changes from the previous year. See text for sources of data and meaning of symbols. The values of +0·23 and +0·13 are wrong; the correct values are +0·18 and +0·19 respectively.

TABLE 1. PHENOTYPIC FREQUENCIES AND FREQUENCY OF THE $T_r$ ALLELE IN 41 POPULATIONS, AND CHANGE IN ALLELIC FREQUENCY IN 27 POPULATIONS IN TWO SUCCESSIVE YEARS

| Grid reference | Month collected | Number of the three phenotypes | | | | Frequency $T_r$ | Month collected | Number of the three phenotypes | | | | Frequency $T_r$ | $\Delta f(T_r)$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1972 | *N* | *I* | *R* | Total | | 1973 | *N* | *I* | *R* | Total | | |
| 36/329.671 | 8 | 46 | 0 | 58 | 104 | 0·558 | 8 | 16 | 0 | 48 | 64 | 0·750 | +0·192 |
| 36/553.847 | 8 | 54 | 2 | 55 | 111 | 0·504 | 8 | 30 | 1 | 66 | 97 | 0·686 | +0·182 |
| 36/334.732 | 8 | 263 | 1 | 93 | 357 | 0·262 | 8 | 41 | 0 | 23 | 64 | 0·359 | +0·097 |
| 36/202.728 | 8 | 87 | 0 | 6 | 93 | 0·064 | 8 | 180 | 1 | 14 | 195 | 0·074 | +0·010 |
| 36/189.766 | 8 | 111 | 0 | 2 | 113 | 0·018 | 8 | 123 | 0 | 36 | 159 | 0·226 | +0·208 |
| 36/131.782 | 8 | 106 | 0 | 1 | 107 | 0·009 | 8 | 108 | 0 | 16 | 124 | 0·129 | +0·120 |
| 26/599.658 | 7 | 118 | 0 | 137 | 255 | 0·537 | 7 | 43 | 1 | 55 | 99 | 0·561 | +0·024 |
| 26/594.656 | 7 | 162 | 0 | 46 | 208 | 0·221 | 7 | 106 | 0 | 27 | 133 | 0·203 | −0·018 |
| 26/580.652 | 10 | 78 | 0 | 12 | 90 | 0·133 | 9 | 141 | 0 | 30 | 171 | 0·175 | +0·042 |
| 26/616.648 | 9 | 173 | 0 | 23 | 196 | 0·117 | 9 | 65 | 5 | 29 | 99 | 0·318 | +0·201 |
| 26/596.666 | 10 | 60 | 2 | 3 | 65 | 0·062 | 9 | 67 | 2 | 3 | 72 | 0·056 | −0·021 |
| 26/600.648 | 7 | 236 | 1 | 12 | 249 | 0·050 | 7 | 140 | 0 | 6 | 146 | 0·041 | −0·009 |
| 26/610.647 | 9 | 99 | 0 | 4 | 103 | 0·039 | 9 | 92 | 0 | 2 | 94 | 0·021 | −0·018 |
| 26/597.654 | 7 | 298 | 0 | 5 | 303 | 0·017 | 7 | 246 | 0 | 9 | 255 | 0·035 | +0·018 |
| 26/633.620 | 9 | 96 | 0 | 0 | 96 | 0·000 | 9 | 151 | 0 | 3 | 154 | 0·019 | +0·019 |
| 26/625.652 | 9 | 60 | 0 | 0 | 60 | 0·000 | 9 | 45 | 0 | 0 | 45 | 0·000 | — |
| 26/637.645 | 9 | 68 | 0 | 0 | 68 | 0·000 | 9 | 120 | 0 | 0 | 120 | 0·000 | — |
| 36/276.917 | 8 | 98 | 0 | 0 | 98 | 0·000 | 8 | 140 | 0 | 0 | 140 | 0·000 | — |
| 37/395.305 | 8 | 137 | 0 | 0 | 137 | 0·000 | 7 | 151 | 0 | 0 | 151 | 0·000 | — |

TABLE 1. *continued*

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 36/190.850 | 8 | 91 | 0 | 0 | 91 | 0·000 | 7 | 116 | 0 | 0 | 116 | 0·000 | — |
| 36/840.396 | 10 | 278 | 0 | 0 | 278 | 0·000 | 10 | 209 | 0 | 0 | 209 | 0·000 | — |
| 26/888.797 | 8 | 350 | 0 | 0 | 350 | 0·000 | 8 | 194 | 0 | 0 | 194 | 0·000 | — |
| 26/888.435 | 9 | 59 | 0 | 0 | 59 | 0·000 | 10 | 59 | 0 | 0 | 59 | 0·000 | — |
| 26/340.215 | 10 | 88 | 0 | 0 | 88 | 0·000 | 11 | 111 | 0 | 0 | 111 | 0·000 | — |
| 36/995.518 | 10 | 229 | 0 | 4 | 233 | 0·017 | 10 | 75 | 0 | 9 | 84 | 0·107 | +0·090 |
| 26/318.385 | 10 | 269 | 1 | 17 | 287 | 0·061 | 11 | 399 | 2 | 11 | 412 | 0·029 | −0·032 |
| 36/251.405 | 9 | 59 | 0 | 1 | 60 | 0·017 | 10 | 169 | 0 | 0 | 169 | 0·000 | −0·017 |
| 36/237.612 | — | — | — | — | — | — | 10 | 48 | 0 | 21 | 69 | 0·304 | — |
| 36/485.363 | — | — | — | — | — | — | 10 | 137 | 1 | 9 | 147 | 0·065 | — |
| 36/578.317 | — | — | — | — | — | — | 10 | 48 | 0 | 18 | 66 | 0·273 | — |
| 36/652.203 | — | — | — | — | — | — | 10 | 121 | 0 | 14 | 135 | 0·104 | — |
| 36/732.336 | — | — | — | — | — | — | 10 | 78 | 0 | 0 | 78 | 0·000 | — |
| 37/718.574 | — | — | — | — | — | — | 7 | 254 | 0 | 0 | 254 | 0·000 | — |
| 37/644.404 | — | — | — | — | — | — | 7 | 363 | 0 | 0 | 363 | 0·000 | — |
| 37/620.395 | — | — | — | — | — | — | 7 | 448 | 0 | 0 | 448 | 0·000 | — |
| 37/566.344 | — | — | — | — | — | — | 7 | 182 | 0 | 0 | 182 | 0·000 | — |
| 37/453.213 | — | — | — | — | — | — | 7 | 320 | 0 | 0 | 320 | 0·000 | — |
| 26/394.756 | — | — | — | — | — | — | 11 | 173 | 0 | 0 | 173 | 0·000 | — |
| 36/003.773 | — | — | — | — | — | — | 8 | 333 | 0 | 5 | 338 | 0·015 | — |
| 26/923.826 | — | — | — | — | — | — | 8 | 407 | 0 | 0 | 407 | 0·000 | — |
| 26/996.815 | — | — | — | — | — | — | 8 | 125 | 0 | 0 | 125 | 0·000 | — |

squares where *S. squalidus* had been found (Perring & Walters 1962) are marked by a continuous outline, and those in which the radiate form of *S. vulgaris* had been found, prior to 1968 (Perring & Sell 1968), by a dotted outline.

An inspection of Fig. 1 indicate that there are three types of populations in the area covered by the map:

a) populations where the radiate allele is absent,
b) populations in an area in the east, roughly coinciding with the area where *S. squalidus* has been found, (first six entries in Table 1), where the frequency of the $T_r$ allele appears to be increasing. The unweighted mean allelic frequency of these six populations in 1972 was 0·236, and in 1973, 0·370, an increase of 0·134.
c) populations in the west with a lower allelic frequency (next nine entries in Table 1), where the frequency of the $T_r$ allele appears to be increasing slowly, if at all. The unweighted mean frequency of the $T_r$ allele of these nine populations in 1972 was 0·130, and in 1973, 0·159, an increase of 0·029.

An analysis of variance was therefore performed to test whether the mean increase in frequency of the $T_r$ allele in the eastern group of six populations was significantly different from that in the western group of nine populations (Table 2). Each allelic frequency was transformed to the angle whose sine is the square root of the individual proportion, so as to equalise the variance among the smaller binomial proportions to that among the larger.

From Table 2, it appears that within the eastern group there is a highly significant difference in allelic frequency among the six populations, and a highly significant increase in frequency of the $T_r$ allele from 1972 to 1973. However, in the western group of nine populations, although there is again a highly significant difference in frequency of the $T_r$ allele between populations, the difference in allelic frequency between years is not significant. If we consider both years and populations as fixed effects (there being thus no component of variance due to year or population group within the group × year interaction) and pool together the residual within-group variance ($F^5_8 = 22{\cdot}55/15{\cdot}00 = 1{\cdot}5$; $p > 0{\cdot}25$), it is found that the interaction of mean allelic frequency of groups with year is significant.

TABLE 2. ANALYSIS OF VARIANCE OF FREQUENCIES OF THE RADIATE ALLELE $T_r$

| Within eastern group | d.f. | M.S. | *F* | *p* |
|---|---|---|---|---|
| Between populations | 5 | 660·06 | 29·27 | <0·002 |
| Between years | 1 | 476·28 | 21·12 | <0·01 |
| Residual | 5 | 22·55 | | |
| Within western group | | | | |
| Between populations | 8 | 364·49 | 24·30 | <0·001 |
| Between years | 1 | 32·00 | 2·13 | >0·10 |
| Residual | 8 | 15·00 | | |
| Between eastern and western groups | | | | |
| Between groups | 1 | 809·84 | | |
| Between years | 1 | 330·67 | | |
| Group × year | 1 | 177·61 | 8·40 | <0·025 |
| Pooled residual | 11 | 21·14 | | |

## DISCUSSION

A significant increase in the frequency of the radiate allele has occurred in the group of populations of *S. vulgaris* in the eastern area, but the increase, if any, in the western group is not significant.

Because of the high degree of inbreeding taking place in this species, very few heterozygous ($I$) plants are produced. It has, in fact, been estimated that only 1% of the ovules producing seed did so as a result of cross-fertilisation: of the plants classified in the populations where the radiate allele was present in 1972, only 0·49% were heterozygous (Hull 1974a).

If selection were taking place in a set of completely isolated populations, the relative reproductive fitnesses of plants with the different capitulum-types being dependent only on their phenotypes and not on the area where they were growing nor on their relative frequencies, then the expected change in frequency of the more favoured allele in a population, plotted against generation, would follow a sigmoid curve, the increase in allelic frequency per generation being lower at low frequency, highest when $f(T_r) = f(T_n) = 0{\cdot}5$, and falling off as the more favoured allele approaches fixation.

This being so, it is possible to interpret the difference in increase in frequency of the $T_r$ allele between the western and eastern groups as being solely due to the fact that frequencies are initially higher on the average in the eastern populations, and to conclude that the simple set of assumptions of the nature of the selective forces initially stated (isolated subpopulations with genotypic selection only, uniform in intensity in all populations) is sufficient to explain the observed differences in the change of allelic frequency between the two groups of populations.

It remains possible that the reproductive fitness of the radiate plants is greater in the east than in the west, because of some important environmental difference. Under these circumstances genotypic selection could cause the differential change in allelic frequency in the two areas.

An alternative, and perhaps more probable, hypothesis is that the frequency of the radiate allele in a population is directly related to the number of *S. squalidus* plants in the area in which the population is growing. *S. squalidus* is known to be common in the east and rare in the west (Fig. 1). It has been shown that there is a cline in esterase isozyme types from a population in the west of Scotland, where there had been no record of *S. squalidus* growing, nor of the occurrence of radiate *S. vulgaris*, through one western and one eastern population of *S. vulgaris*, picked from those whose $T_r$ frequency had been determined, to *S. squalidus* itself (Hull 1974b).

The invasion of $T_r$ alleles from *S. squalidus* could be due to any one of a number of possible causes. For example, preferential fertilisation of *S. vulgaris* ovules by pollen derived directly or indirectly from *S. squalidus*, or the reciprocal pollination, may take place (even though a high degree of self-fertilisation normally takes place in *S. vulgaris*; *S. squalidus* is self-incompatible). On the other hand, it may be that the reproductive fitness of the hybrid plants is much greater than the average for *S. vulgaris* and thus the $T_r$ allele is being transferred passively into the *S. vulgaris* gene pool.

To decide between the relative importance of selection and introgression in altering the frequencies of the radiate allele in these populations, data are required concerning the relative reproductive fitness of the different genotypes in the natural environment.

Although *S. vulgaris* is an annual plant, fruits could persist in the soil for more than one year. However, the work of Roberts & Feast (1972) on the germination of fruits of *S. vulgaris* sown in 2·5 cm of cultivated soil indicates that in this species 85% of fruits would germinate within one year, and all before five years had elapsed. It would thus seem likely that most of the plants germinating in an undisturbed area would be the progeny of plants growing there in the previous year, rather than being derived from fruits dormant in the soil.

In no population in the areas sampled was the $T_n$ allele completely replaced by the $T_r$ allele—the highest frequency of $T_r$ recorded was 0·75. The large reservoir of $T_n$ alleles in the native population would slow down the fixation of the $T_r$ allele, even if some selective force was tending to cause this. By obtaining estimates of changes in allelic frequency from *S. vulgaris* populations where the hybridisation process has been taking place for a longer time, it would be possible to investigate the likelihood that some non-heterotic balance might become established for these two alleles.

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