THE INFLUENCES OF DIFFERENT DEGREES OF INTERSPECIFIC HYBRIDISATION WITH *SENECIO* *SQUALIDUS* ON THE FREQUENCY OF TWO MORPHS OF *SENECIO VULGARIS*

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SUMMARY

In 3 successive years samples of *Senecio vulgaris* L., from different populations were classified according to their capitulum type. Two areas in Central Scotland were chosen, six populations being taken from an area where *Senecio squalidus* L. grows in relative abundance and nine from an area where plants of this species are rarely found. This allowed the investigation of changes in the relative frequency of the alleles T_r and T_n controlling capitulum type in these polymorphic populations. The possibility that the T_r allele is being introduced into the populations of *S. vulgaris* by hybridisation with *S. squalidus* is investigated. It is concluded that this is a more probable explanation than the alternative possibility that the observed changes in allelic frequency are due to differences between the fitnesses of the radiate, intermediate and non-radiate capitulum morphs which are found in the populations.

1. INTRODUCTION

The evidence that the occurrence of the plants of the radiate ($T_r T_r$) capitulum type in populations of *Senecio vulgaris* L. (chromosome number, $2n = 40$) may be a result of limited interspecific hybridisation with *Senecio squalidus* L. ($2n = 20$), followed by backcrossing, has been discussed in several papers (e.g. Hull, 1974a, 1975; Richards, 1975). Several species of *Senecio* found in the British Isles are capable of hybridisation (Gibbs, 1971), and the occurrence of a natural hybrid of *S. vulgaris* and *S. squalidus*, producing many offspring with chromosome number $2n = 40$, has been reported (Crisp and Jones, 1970).

Sterile interspecific hybrids between *S. squalidus* and *S. vulgaris* (Harland, 1955), self-fertile hybrids, $2n = 60$ (Lousley, 1955; Rosser, 1955) and backcrosses to *S. squalidus* (Gibbs, 1971), have been produced experimentally.

The facts that *S. squalidus* is extending its range in the British Isles and that the radiate morph of *S. vulgaris* tends to appear in an area only after *S. squalidus* has become established, have been noted by a number of authors, comparing the published distribution maps of *S. squalidus* (Perring and Walters, 1962) with that of radiate morph of *S. vulgaris* (Perring and Sell, 1968).

Evidence of gene flow, due to interspecific hybridisation, from *S. squalidus* to *S. vulgaris* based on observed clines in phenotypic characters is available from two sources. In the first, the distribution of esterase isozymes of different electrophoretic mobility (located by acrylamide gel electrophoresis) has been studied in several populations of plants of the genus *Senecio* in Central Scotland (Hull, 1974b). The distribution of enzymes from plants of

S. vulgaris collected from an area where *S. squalidus* is common (Kent, 1965), showed more resemblance to that within the local population of *S. squalidus* than did the distribution of enzymes from a sample of *S. vulgaris* plants from an area where *S. squalidus* is very rare. Moreover, within both areas, the enzyme pattern from a sample of radiate plants more closely resembled that of the sample of *S. squalidus* plants than did that of the non-radiate plants from the same area.

In the second study (Monaghan and Hull, 1975), similar clines in leaf length, leaf breadth and leaf shape in plants collected from the same areas provided further data which could be interpreted as evidence of gene flow from *S. squalidus* to *S. vulgaris*.

In order to investigate the possibility that, for any given population of *S. vulgaris*, the frequency of the radiate morph might be directly dependent on the amount of interspecific hybridisation and thus on the number of *S. squalidus* plants growing at that location, it was decided to compare the changes in frequency of the T_r allele in polymorphic populations of *S. vulgaris* taken from two areas, one in and around Edinburgh, where *S. squalidus* had earlier been reported as growing in eight identifiable locations (Kent, 1965), the other in Glasgow where *S. squalidus* was rare; that is, no colonies of *S. squalidus* had previously been noted (Kent, 1965), but occasional individual plants were found by the author in 1972 and subsequently. This comparison was made by taking a sample of plants from several uniform populations within each area (six in the case of the Edinburgh area, nine in the case of the Glasgow area) in 1972, 1973 and 1974, and comparing the rate of change of the T_r allele between the two areas.

2. METHODS OF SAMPLING, RESULTS AND ANALYSIS

Samples of plants were taken from the 15 populations by marking out the chosen area of ground into a series of rectangles, 12.5×4 metres and classi-

FIG. 1.—Approximate location of polymorphic populations (black circles) of *Senecio vulgaris*; populations consisting of the non-radiate morph only (open circles) and populations of *S. squalidus* (triangles).

fying the plants according to their capitulum types as *R* (radiate, $T_r T_r$); *I* (intermediate, $T_r T_n$) or *N* (non-radiate, $T_n T_n$). The genetic control of capitulum type in this species by a single, incompletely dominant locus, the *T* locus, has been established by data from several breeding experiments (e.g. Trow, 1912). A sketch map showing the approximate location of the 15 polymorphic populations, as black circles, other, non-polymorphic populations of *S. vulgaris* (Hull, 1974a, 1975) as open circles and the sites where *S. squalidus* was found (Kent, 1965) as triangles, is given in fig. 1. The exact methods of sampling used have been detailed previously (Hull, 1974a). The frequency of the T_r allele was then calculated for each population in each year; these frequencies are plotted in fig. 2 together with the total number of plants in each sample. An unweighted analysis of covariance of allelic frequency on year was then carried out as summarised in table 1, where again each population is identified by an eight-figure national grid

FIG. 2.—Mean frequencies of the T_r allele in the 15 populations in the 3 successive years.

TABLE 1

Comparison of regression of frequency of the T_r allele on year between populations, within areas, and between the Edinburgh and Glasgow areas

Edinburgh Population	$b_{Y.X}$	Due to regression		Deviations from regression	
		d.f.	S.S.	d.f.	S.S.
36/329 671	+0.109	1	0.023 762	1	0.004 593
553 847	+0.093	1	0.017 113	1	0.005 221
334 732	+0.064	1	0.008 192	1	0.000 726
202 728	+0.044	1	0.003 872	1	0.000 817
189 766	+0.090	1	0.016 025	1	0.009 361
131 782	+0.061	1	0.007 321	1	0.002 360
Total		6	0.076 285	6	0.023 078
Source of variation		d.f.	S.S.	M.S.	F ratio
Separate regression lines		6	0.076 285	0.012 714	—
Joint regression slope		1	0.070 395	0.070 395	$F_6^1 = 18.30$
Difference in slopes		5	0.005 901	0.001 180	$F_6^5 < 1$
Residual		6	0.023 078	0.003 846	—

Glasgow Population	$b_{X.Y}$	Due to regression		Deviations from regression	
		d.f.	S.S.	d.f.	S.S.
26/599 658	+0.029	1	0.001 682	1	0.000 017
594 658	-0.002	1	0.000 008	1	0.000 171
580 652	+0.017	1	0.000 578	1	0.000 417
616 648	+0.062	1	0.007 688	1	0.012 881
596 666	-0.031	1	0.001 922	1	0.000 417
594 656	-0.005	1	0.000 045	1	0.000 014
610 647	+0.032	1	0.002 048	1	0.001 667
597 654	+0.010	1	0.000 200	1	0.000 043
633 620	+0.000	1	0.000 000	1	0.000 241
Total		9	0.014 171	9	0.015 868
Source of variation		d.f.	S.S.	M.S.	F ratio
Separate regression line		9	0.014 171	0.001 575	—
Joint regression slope		1	0.002 813	0.002 813	$F_9^1 = 1.59$
Difference in slopes		8	0.011 358	0.001 419	$F_9^8 < 1$
Residual		9	0.015 868	0.001 763	—

reference. It will be seen that the differences between slope of the six different populations within the Edinburgh area are not significant ($F_6^5 = 0.307$). Similarly, the regression of allelic frequency on years in the nine populations in the Glasgow area are also homogeneous ($F_9^8 = 0.805$). It is therefore possible to calculate a joint regression of gene frequency on year for the six Edinburgh regions and this is found to have a significant positive gradient ($F_6^1 = 18.30$; 1% $F_6^1 = 12.25$). On the other hand, the joint regression for the nine Glasgow regions has a slope not significantly different from zero ($F_9^1 = 1.59$; 5% $F_9^1 = 5.12$).

3. DISCUSSION

The fact that the increase in the frequency of the T_r allele is very much greater in the Edinburgh area than in the Glasgow area (see fig. 2 and

table 1) might be due either to the fact that the fitnesses of the three genotypes are different in the two areas, or that hybridisation with *S. squalidus* is taking place to a greater extent in the Edinburgh area, with consequent gene flow and an expected increase in frequency of all alleles (including the T_r allele), derived from *S. squalidus*.

There is in fact a remarkable stability in allelic frequency within the populations from year to year (fig. 2). The samples taken may be part of much larger populations in each case, or seeds may persist in the soil for more than 1 year, thus smoothing out any fluctuations in allelic frequency.

Evidence has been presented (Monaghan and Hull, 1975) that continued hybridisation of *S. squalidus* with *S. vulgaris* has resulted in an alteration of leaf shape of plants of *S. vulgaris* in these two areas in Central Scotland, so that these plants now show a greater resemblance to *S. squalidus* in this characteristic. Further than this, it was suggested that mean leaf size may eventually show an increase in these populations of *S. vulgaris* as a result of gene flow from *S. squalidus*, which has larger leaves than *S. vulgaris*, but that the initial result of hybridisation is a reduction of both mean leaf length and mean leaf breadth in hybrid populations, perhaps due to chromosomal imbalance in the immediate hybrids. This conclusion was based on a comparison of leaf characters of radiate and non-radiate plants, within populations, the radiate plants being smaller.

Other measurements of vegetative and reproductive vigour of the radiate and non-radiate morphs of *S. vulgaris* have been made under conditions of controlled plant growth (Richards, 1975). He confirms the lack of vegetative vigour of radiate plants; studying leaf size it was found that the leaves of non-radiate plants grew to a greater size in a shorter period of time than did those of radiate plants. Plants with capitula of the intermediate type had the smallest and slowest growing leaves of all. Furthermore, non-radiate plants reached their maximum height in less than half the time required by radiate plants. Intermediate plants were not only much smaller at flowering, but their overall growth rate was again slowest of all. It also appeared that a greater proportion of non-radiate seed germinated than radiate or intermediate and that its germination was more rapid. Similarly, non-radiate plants flowered earlier, and a greater percentage of the total non-radiate plants finally produced flowers than that of the radiate or intermediate plants.

Against all these findings of the general superiority of non-radiate plants is the suggestion (Richards, 1975), from a preliminary experiment, that under conditions of very high density of growth (one plant to 4 cm²), non-radiate plants developed on average one capitulum per plant whilst radiate plants developed an average of six fertile capitula. It might be thought that plants growing naturally under such conditions of extreme overcrowding and producing so few seeds per plant would make only a small contribution to the total quantity of seed produced by the *S. vulgaris* populations.

The radiate plants appear, from a variety of data, to be smaller and to show slower development for almost all components of vegetative vigour and reproductive fitness which have been examined. There is no evidence of heterosis in fitness or vegetative characteristics of plants of intermediate capitulum type. Also, for all the vegetative characteristics examined there appear to be clines in the population means from the *S. squalidus* population through the hybridised *S. vulgaris* populations to the unhybridised populations of *S. vulgaris*. It appears unlikely that all these characteristics would be

affected by natural selection, due to environmental differences between the Edinburgh and Glasgow areas, or that all are closely linked to some characteristic that is so influenced. Thus it appears that the factor most likely to have influenced the present distribution of all the vegetative and floral characteristics studied in *S. vulgaris* populations in Central Scotland is greater interspecific hybridisation with the related species, *S. squalidus* in the Edinburgh area than in the Glasgow area, rather than selection in favour of radiate plants in the Edinburgh area, because of some undefined environmental difference between the two areas.

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