

Life history variation associated with the polymorphism for capitulum type and outcrossing rate in *Senecio vulgaris* L.

Richard J. Abbott

Department of Plant Biology and Ecology, University of St. Andrews, St. Andrews, Fife, KY16 9th, U.K.

A comparison between the non-radiate and radiate morphs of *Senecio vulgaris* for several life history characteristics was made within samples from four geographically separated populations in Britain. For most traits investigated, differences between morph means were common. However, only differences in seed germination behaviour were consistent over all populations. It was also evident that for most characters the non-radiate morph exhibited a similar or greater amount of variation both between and within families than the radiate morph. Possible causes and effects of variation in life history differences between morphs over populations are discussed and considered in relation to the maintenance of the polymorphism for capitulum type and outcrossing rate in natural populations of *S. vulgaris*.

INTRODUCTION

Inland populations of *Senecio vulgaris* L. (Compositae) in Britain are frequently polymorphic for capitulum type. Three morphs are recognised: a non-radiate morph which produces capitula containing only hermaphroditic disc florets, a radiate morph that bears capitula which in addition to a complement of hermaphroditic disc florets contain an outer ring of 8-13 pistillate ray florets (lacking anthers), and an intermediate morph which is distinguished by the possession of capitula with short, stubby ray florets. The polymorphism is under the genetic control of the "ray floret" locus, with non-radiate plants homozygous for the T_n allele, radiate plants homozygous for the T_r allele and the intermediate morph heterozygous for both alleles at the locus (Trow, 1912; Hull, 1974). By using the alleles at the ray floret locus as markers, Marshall and Abbott (1982; 1984a) have demonstrated that in wild polymorphic populations of *S. vulgaris*, non-radiate (hermaphrodite) plants normally outcross at very low frequencies (≤ 1 per cent), whereas radiate (gynomonoecious) plants always show much greater outcrossing levels (15-35 per cent). The cause of this difference seems due, in large part, to ray florets outcrossing at significantly greater levels than disc florets (Marshall and Abbott, 1984b).

The findings of Marshall and Abbott (1982; 1984a) show that the polymorphism for capitulum

type in *S. vulgaris* functions as a polymorphism for outcrossing frequency. This is of particular importance as differential outcrossing of the genotypes at the ray floret locus will have a direct effect on the maintenance of the polymorphism in wild populations. Single gene theory developed by Fisher (1941), Moran (1962), Nagylaki (1976), Charlesworth and Charlesworth (1978), Lloyd (1979), Wells (1979) and others shows that an allele which promotes high levels of selfing is at a selective advantage compared with an allele which promotes outcrossing provided both high and low outcrossing alleles are present in the outcrossed pollen pool. Such selection of a "selfing" allele is a form of "autoselection"—a term used by Jain (1976) and Bell (1982) to distinguish selection that results simply from the mode of transmission of a gene from other forms of selection. A consequence of the autoselective advantage of a selfing allele is that for an outcrossing allele to be maintained in a population, in the presence of a selfing allele, it must be associated with an additional selective advantage.

Several factors have been identified that can override the inherent disadvantage or cost of outcrossing in a population. They are: (i) inbreeding depression due to selection acting against the products of selfing, irrespective of their genotype (Maynard-Smith, 1978; Charlesworth,

1980; Lloyd, 1980; Holsinger, Feldman and Christiansen, 1984; Lande and Schemske, 1985); (ii) heterozygote advantage or overdominance at the locus which controls variation in outcrossing rate (Jain, 1961; Ross and Weir, 1975; Marshall, 1982); and (iii) a lower fitness of the selfing genotype relative to the outcrossing genotype due to reduced viability and/or fertility (Lewis, 1941; Charlesworth and Charlesworth, 1978; Marshall, 1982).

Though field evidence is lacking, the results of experiments conducted under glass and in controlled environments indicate that neither inbreeding depression nor overdominance at the ray floret locus are factors of importance in affecting the evolution and maintenance of the polymorphism for outcrossing frequency in *S. vulgaris* (Abbott, 1985). However, there is evidence of differences between the non-radiate and radiate morphs for various life history traits which may affect their relative fitness in the field and, in turn, the maintenance of the polymorphism. Richards (1975) working with material sampled from a Durham population, found that seed of the non-radiate morph germinated considerably earlier and in much greater numbers than seed of the radiate morph. The non-radiate morph was also quicker to flower, but had a lower seed output than the radiate morph when mixtures of the two morphs were raised at high densities. In a follow up study, Oxford and Andrews (1977) measured mean capitula numbers and seed per capitulum in several British polymorphic populations of *S. vulgaris*. In six out of eight populations surveyed, radiate plants produced greater numbers of capitula than non-radiate plants and only in one population was the opposite result significant. Furthermore, in all six populations subjected to analysis, radiate plants produced significantly more seed per capitulum than non-radiate plants. More recently, Kadereit and Briggs (1985) found that within samples from two Cambridgeshire populations, raised under glass, non-radiate plants were again earlier to flower than radiate plants though the difference was in terms of a few days rather than weeks as had been reported previously by Richards (1975) with Durham material. However, in contrast to what others had found, Kadereit and Briggs (1985) detected no significant differences between morphs in reproductive capacity.

To examine further the life history differences that occur between the radiate and non-radiate morphs of *S. vulgaris* and to determine whether such variation is consistent within the species, a study was made of differences between morphs

within a sample from an Edinburgh population. This was followed by an analysis of morph differences within samples from four different populations, one of which was the Durham population previously investigated by Richards (1975). Attention was principally focused on life history characters associated with germination and development through to first flowering. The results make clear that only differences in germination behaviour are consistently associated with the polymorphism for capitulum type in *S. vulgaris*.

MATERIALS AND METHODS

Experiment 1

Seed was collected in early October 1975 from each of 100 randomly chosen non-radiate and 100 randomly chosen radiate plants that grew amidst a large polymorphic population of *S. vulgaris* occurring on wasteground at Newhaven Road, Edinburgh. The sample was taken at a time when nearly all individuals within the population were fruiting. Details of the site and population at Newhaven Road, Edinburgh, including number of flowering plants, genotype and gene frequencies at the ray floret locus and outcrossing rates of the radiate and non-radiate morphs, recorded on various occasions between 1978–1980 are given in Marshall and Abbott (1982; 1984a).

On June 4, 1976, following storage under laboratory conditions, seed of each individual was sown 10 per pot in each of two 8 cm pots containing a peat based compost. One pot per individual was placed in each of two replicate blocks in an unheated glasshouse. Pots were completely randomised within blocks. Fourteen days from sowing, pots were thinned to one plant per pot, with the seedling that germinated first being retained. Plants were grown to flowering and harvested 14 days after they had begun to flower. Several life history characters were recorded during the course of the experiment as listed in table 1.

Experiment 2

Seed from each of 20 non-radiate and 20 radiate plants were collected from four large polymorphic populations: the same Edinburgh population as in Experiment 1 (sampled October, 1975), open ground in a park at Anstruther, Fife, Scotland (sampled June, 1976), Richards' (1975) site near the Department of Botany, University of Durham (sampled September, 1975) and from the University Campus, Coleraine, N. Ireland (sampled May, 1976).

Table 1 Life history characters recorded on the non-radiate and radiate morphs of *Senecio vulgaris* in Experiments 1 and 2

Character	Symbol
Days from sowing to first germination*†	DTG
Number of seeds to germinate 14* or 21* days from sowing	NG
Plant height (mm) (28, 42 days after germination and at flowering)*	H28, H42, HF
(40, 54 and 68 days after germination)†	H40, H54, H68
Leaf number (28, 42 days after germination and at flowering)*	LN28, LN42, LNF
(54, 68 days after germination)†	LN54, LN68
Days to first flowering from germination*†	DTF
Length of longest leaf (mm) 2 weeks after first flowering*†	LL
Breadth of longest Leaf (mm) 2 weeks after first flowering*†	LB
Length/breadth ratio of longest leaf 2 weeks after first flowering*†	L/B
Shoot dry weight 2 weeks after first flowering*† (mg in expt. 1, cg in expt. 2)	DW

* Recorded in Experiment 1, † Recorded in Experiment 2

The experimental procedure was similar to that of Experiment 1 with the following exceptions. On 28 November 1976, 10 seed per individual was sown in each of six 8 cm pots. Three pots per individual were placed in each of two blocks set out in a heated glasshouse with supplementary lighting provided by mercury vapour lamps. Photoperiod was set at 16 hours and temperature was maintained at 20°C. Twenty-one days after sowing, pots were thinned to one per pot. The life history characters recorded throughout the experiment are listed in table 1.

Statistical analysis

Analysis of variance for differences between morph means assumed a mixed model with morphs considered as a fixed effect and blocks, families (plus populations in Experiment 2) as random effects. Tests of homogeneity of variances using the suite of tests (HOMVAR) in the CSIRO MACRO library of the statistical package GENSTAT (1982 Lewes Agricultural Trust, Rothamsted Expt. Station, Numerical Algorithms Ltd.) showed that for some characters in both experiments when the variances within the two morphs were compared with each other they appeared heterogeneous. A log transformation failed to stabilise these variances and the ANOVA was performed on untransformed values except where transformation was

required to improve the normality of data. Violation of the assumption of homogeneity of variances was not judged as important as the analysis of variance is considered to be robust to the type and magnitude of departure from homogeneity of variances that were present in the data here (see Underwood, 1981, for a discussion of this problem).

RESULTS

Morph means

Experiment 1 Seed of non-radiate plants germinated earlier and in greater numbers than seed of radiate plants (table 2). After germination, both morphs took the same amount of time to flower (7 weeks); however, through development to flowering the non-radiate morph was taller than the radiate morph, although no differences were recorded for leaf number. Length of the longest leaf was the same for both morphs, but radiate plants bore broader leaves which, in turn, caused them to have a lower mean leaf length/breadth ratio. Two weeks after flowering, shoot dry weight of the radiate morph was significantly greater than that of the non-radiate morph though the difference between morphs was small.

Experiment 2 The differences and similarities between morphs recorded in Experiment 1 for Edinburgh material were, in general, present again in the sample of the same material investigated in Experiment 2 (table 3). However, differences in leaf breadth, dry weight and leaf length/breadth ratio were not judged as significant. The major discrepancy between the results of the two experiments for the Edinburgh samples was for height. No difference between morphs was evident for this character in the second experiment.

Analysis of differences between morph means over all four populations (table 3) showed that for most characters recorded there was a significant morph × population interaction. Only for the two germination characters DTG and NG, and the leaf characters, LN54 and LB, was a similar relative performance of morphs maintained over all populations. With regard to germination characters, it was evident that in all the material studied seed of the non-radiate morph germinated slightly earlier and in greater overall numbers than seed of radiate plants.

For characters where a significant morph × population interaction was present, differences in relative performance of morphs over populations

Table 2 Means (\bar{x}), total phenotypic variances (σ^2p) and the between family (σ_b^2) and within family (σ_w^2) variance components, for the non-radiate (T_nT_n) and radiate (T_rT_r) morphs in an Edinburgh population of *Senecio vulgaris*

	\bar{x}			σ_p^2			σ_b^2		σ_w^2	
	T_nT_n	T_rT_r	<i>P</i>	T_nT_n	T_rT_r	<i>F</i>	T_nT_n	T_rT_r	T_nT_n	T_rT_r
DTG	5.77	6.18	*	4.66	4.05	1.15	1.85***	1.47**	2.72	2.52
NG	6.60	5.92	*	4.22	4.36	1.03	2.18***	1.94***	2.02	2.40
H28 mm	72.50	59.24	***	188.12	163.96	1.15	81.70***	66.51***	106.40	96.09
H42 mm	187.61	159.81	***	2130.27	1561.95	1.36	1110.82***	0	981.62	1289.01
HF mm	426.63	393.72	***	6607.13	3881.46	1.70	2731.07***	0	3815.0	3281.0
LN28	5.79	5.74	N.S.	0.92	1.24	1.34	0.21*	0.32*	0.72	0.91
LN42	13.16	13.60	N.S.	4.18	4.88	1.17	1.02**	1.04*	2.72	3.75
LNF	36.32	36.70	N.S.	107.04	49.86	2.15	34.67**	9.11*	71.59	40.43
DTF	49.40	49.51	N.S.	35.66	22.08	1.61	17.49***	7.87**	17.88	13.94
LL mm	121.43	123.20	N.S.	401.93	140.38	2.86	235.25***	0	161.41	126.53
LB mm	47.83	53.41	***	56.06	33.20	1.69	28.90***	7.05*	26.51	25.90
DW mg	972.42	1060.63	***	97832.90	40871.72	2.39	63660.51**	15100.01**	32742.03	25251.10
L/B	2.56	2.32	***	0.16	0.05	2.89	0.05***	0	0.10	0.01

† Where *F* is ≥ 1.34 , differences between phenotypic variances are significant at the 0.05 probability level (based on a two-tailed test). N.B. Alongside between family variances are given the levels of significance for differences between families. Where the difference is not significant, σ_b^2 has been taken to be 0.

* *P* = 0.05, ** *P* = 0.01, *** *P* = 0.001, N.S. = Not significant.

were often striking. For example, for days to flowering (DTF) there was no significant difference between morphs in the Edinburgh sample. In contrast, in the Anstruther and Durham samples, radiate plants took approximately a week longer to flower following germination than non-radiate plants, while in the Coleraine sample the reverse was true. Similarly, whereas radiate plants in the Anstruther and Durham samples grew to produce a much larger shoot dry weight than plants of the non-radiate morph, the opposite was true in the Coleraine sample.

Morph variances

Estimates of phenotypic variance and the variance components due to differences between (σ_b^2) and within (σ_w^2) families were computed for each morph in each population by means of an analysis of variance. As in each analysis each morph has its own appropriate error variance, estimation of variance components on a per morph, per population basis is unaffected by any variance heterogeneity over morphs.

Experiment 1 Comparisons of total phenotypic variances (table 2) show that for several characters, *i.e.*, DTG, NG, H28, LN28 and LN42, similar amounts of phenotypic variation were present within each morph of the Edinburgh sample. Examination of the between and within family variances for these characters also revealed that similar amounts of variance occur for each of these

two components within both morphs. In all instances the between family variation was significant and thus of genetic origin. In contrast, for other characters recorded, *i.e.*, H42, HF, LNF, DTF, LL, LB, L/B and DW, total phenotypic variance was greater in the non-radiate morph than the radiate variant as was, in most instances, the variance both between and within families. For four characters—H42, HF, LL and L/B—no significant genetic variation at all was detected between families within the radiate morph.

Experiment 2 With regard to the relative amounts of phenotypic variation within each morph, the findings of Experiment 1 tended to be confirmed by the results of Experiment 2 (table 4). That is, in general, the amount of total phenotypic variance recorded for characters in all four samples was the same or significantly greater in the non-radiate than the radiate morph. Only for DTG and DW in the Anstruther sample, DTG and LL in the Durham sample and DTG and L/B in the Coleraine sample was there more phenotypic variation within the radiate morph. In the Edinburgh sample some of the characters for which a difference between morphs in phenotypic variance was evident in Experiment 1, *i.e.*, DTF and DW, were not different in Experiment 2. However, the trend remained the same in both experiments with the non-radiate variant showing considerably more phenotypic variation for height and leaf size characters.

Table 3 Character Means of the non-radiate (T_n, T_n) and radiate (T_r, T_r) morphs (m) within four populations (p) of *Senecio vulgaris*

Population	Morphs																	
	T_n, T_n DTG	T_r, T_r	P	T_n, T_n NG	T_r, T_r	P	T_n, T_n H40	T_r, T_r	P	T_n, T_n H54	T_r, T_r	P	T_n, T_n H68	T_r, T_r	P	T_n, T_n LN54	T_r, T_r	P
Edinburgh	5.13	6.50	—	6.05	4.76	—	20.43	20.73	N.S.	45.41	45.10	N.S.	123.10	133.30	N.S.	20.42	19.54	—
Anstruther	2.82	4.28	—	7.87	7.50	—	19.21	19.53	N.S.	49.21	45.21	N.S.	132.70	130.10	N.S.	22.91	19.81	—
Durham	4.75	5.52	—	8.10	7.90	—	37.80	31.54	*	95.69	71.32	**	223.10	174.80	*	18.65	18.31	—
Coleraine	4.32	5.14	—	8.23	7.50	—	23.58	18.25	N.S.	53.34	49.11	N.S.	134.70	152.40	N.S.	18.37	21.04	—
m × p	N.S.†			N.S.			*			**			**			N.S.		
m	†			*			—			—			—			N.S.		
	LN68			DTF			LL			LB			DW			L/B		
Edinburgh	40.94	43.59	N.S.	71.88	70.57	N.S.†	125.46	124.40	N.S.	50.53	53.30	—	338.40	381.80	N.S.	2.54	2.35	N.S.
Anstruther	41.78	39.81	N.S.	65.57	71.03	***	118.34	119.65	N.S.	48.89	53.21	—	220.60	361.90	***	2.44	2.67	N.S.
Durham	38.40	37.85	N.S.	64.72	72.29	**	100.80	102.72	N.S.	47.02	47.37	—	226.90	342.20	*	2.17	2.19	N.S.
Coleraine	34.21	45.65	***	70.62	63.86	***	96.98	100.19	***	48.15	44.32	—	266.30	187.00	**	2.05	2.56	**
m × p	***			***†			**			N.S.			***			**		
m	—			—			—			N.S.			—			—		

† Analysis conducted on \log_e transformed data.

Table 4 Total phenotypic variance of the non-radiate ($T_n T_n$) and radiate ($T_r T_r$) morphs within four populations of *Senecio vulgaris*. Significance levels were based on a two-tailed F test

Population	$T_n T_n$		$T_r T_r$		Morphs		$T_n T_n$		$T_r T_r$		$T_n T_n$		$T_r T_r$		L/B		
	DTG	$T_r T_r$	P	$T_n T_n$	NG	$T_r T_r$	P	H40	$T_r T_r$	P	H54	$T_r T_r$	P	H68		LN54	
Edinburgh	6.89	10.41	N.S.	5.12	5.88	92.04	41.43	***	797.56	291.25	***	5542.83	2769.83	***	43.91	31.44	N.S.
Anstruther	1.91	4.84	***	4.24	3.72	40.87	20.32	***	477.33	174.78	***	2018.83	1764.99	N.S.	39.85	25.16	*
Durham	4.85	9.29	**	2.12	3.00	164.03	103.98	*	1353.67	647.82	***	5346.33	2694.50	***	37.56	33.53	N.S.
Coleraine	7.7.3	12.63	**	2.42	3.08	146.03	22.38	***	834.35	485.99	**	4119.66	2546.17	**	62.65	40.15	*
	LN68			DTF		LL			LB		DW						
Edinburgh	181.37	154.60	N.S.	77.54	62.14	452.14	200.72	***	67.32	41.98	*	18535.17	27420.67	N.S.	0.347	0.074	***
Anstruther	132.12	117.09	N.S.	54.88	61.54	257.30	143.72	**	36.29	48.89	N.S.	15415.50	26221.50	**	0.161	0.054	***
Durham	151.99	174.79	N.S.	111.41	75.31	198.60	383.32	**	44.67	61.47	N.S.	19223.00	20402.83	N.S.	0.104	0.125	N.S.
Coleraine	217.59	198.78	N.S.	130.03	49.18	291.05	177.97	*	100.17	62.52	*	16400.83	9549.50	**	0.148	0.326	***

For days to first germination (DTG) in both morphs and days to flowering (DFF) in the radiate morph none of the total phenotypic variance recorded was due to significant differences between families (table 5). However, for all other characters significant genetic variation between families occurred within one or the other morph in at least one of the four samples investigated. There was a tendency for such variation to be more common and extensive in the non-radiate morph particularly in the Edinburgh, Anstruther and Coleraine samples where the between family variance (table 6) of the non-radiate variant was equal to or larger than the radiate morph for most characters. Comparisons of the within family variances between morphs (table 6) also suggested that for most characters a similar or greater amount of variation was present in the non-radiate morph than in the radiate variant except in the Coleraine sample where differences and similarities over all characters were more evenly distributed between morphs. Only for days to first germination (DTG) was more within family variation present in the radiate morph in all four samples examined.

DISCUSSION

The chief objective of the studies reported here was to determine whether differences between the non-radiate and radiate morphs of *S. vulgaris* occur for a selection of life history traits and whether any differences are maintained over a sample of polymorphic populations drawn from widely separated locations in Britain. The results show that of the traits that were investigated, although differences between morphs were com-

mon, only differences in seed germination behaviour were consistent over populations.

Examination of morph means for days to first germination (DTG) and number of seed germinated (NG) revealed that seed produced by the non-radiate morph tended to germinate more quickly and in greater over all numbers than seed of the radiate morph. This difference in germination behaviour is further illustrated by plotting the cumulative percentage germination for each morph in each sample against time from sowing (fig. 1). The difference between morphs that is seen confirms what was previously reported by Richards (1975) from a study of Durham material. However, whereas the differences between morphs found by Richards (1975) were large, here they were relatively small, particularly in the sample from the Durham population.

Examination of morph means within the Edinburgh sample raised in Experiment 1 provided clear evidence that differences between morphs established by Richards (1975) for several life history traits in a Durham population do not occur in all polymorphic populations of the species. In contrast with what Richards had found, no differences were recorded for leaf number throughout development (LN54, LN68), days to flowering (DTF) or leaf length (LL) in the Edinburgh material investigated. Some caution is needed when making comparisons between Richards' results and those obtained in Experiment 1 as plants were raised under different conditions and there is the possibility of a significant morph \times environment interaction. However, differences between the Edinburgh and Durham samples in the relative performance of morphs were confirmed in Experiment 2 by direct comparison. It was

Table 5 Significance levels for differences between families of the non-radiate ($T_n T_n$) and radiate ($Tr Tr$) morphs in four populations of *Senecio vulgaris*

POPULATION	Morphs											
	$T_n T_n$ DTG	$Tr Tr$	$T_n T_n$ NG	$Tr Tr$	$T_n T_n$ H40	$Tr Tr$	$T_n T_n$ H54	$Tr Tr$	$T_n T_n$ H68	$Tr Tr$	$T_n T_n$ LN54	$Tr Tr$
Edinburgh	N.S.	N.S.	*	***	***	*	***	**	**	*	N.S.	*
Anstruther	N.S.	N.S.	***	N.S.	**	N.S.	**	N.S.	N.S.	N.S.	**	*
Durham	N.S.	N.S.	N.S.	**	***	*	**	N.S.	*	N.S.	*	N.S.
Coleraine	N.S.	N.S.	N.S.	*	***	*	***	N.S.	***	N.S.	***	*

POPULATION	Morphs											
	LN68	DTF		LL		LB		DW		L/B		
Edinburgh	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	***	N.S.	*	N.S.	*	N.S.
Anstruther	**	N.S.	**	N.S.	**	***	**	*	***	**	***	N.S.
Durham	***	N.S.	N.S.	N.S.	N.S.	***	N.S.	*	N.S.	**	N.S.	**
Coleraine	***	*	**	N.S.	**	***	***	***	***	N.S.	N.S.	***

Table 6 Between (σ_b^2) and Within (σ_w^2) family variance components for the non-radiate ($T_n T_n$) and radiate ($T_r T_r$) morphs within four populations of *Senecio vulgaris*

Populations	Morphs													
	$T_n T_n$ DTG	$T_r T_r$	$T_n T_n$ NG	$T_r T_r$	$T_n T_n$ H40	$T_r T_r$	$T_n T_n$ H54	$T_r T_r$	$T_n T_n$ H68	$T_r T_r$	$T_n T_n$ LN54	$T_r T_r$	$T_n T_n$ LN54	
Edinburgh	0	0	1.22	2.94	43.87	8.50	409.33	70.12	1650.83	431.83	0	6.42		
	5.84	10.18	3.02	3.28	33.26	30.43	282.70	186.20	3798.00	2301.00	29.24	21.17		
Anstruther	0	0	2.92	0	5.51	0	40.33	0	0	0	12.60	2.69		
	1.78	4.66	1.12	0.40	31.98	15.93	430.40	134.90	2032.00	1211.00	25.46	22.84		
Durham	0	0	0	0.84	38.93	19.5	273.67	0	1166.00	0	5.63	0		
	4.83	7.74	2.26	2.18	124.10	74.7	1081.00	438.00	3589.00	1547.00	32.25	24.58		
Coleraine	0	0	0	0.88	99.79	4.34	524.55	0	2128.33	0	40.45	5.29		
	7.57	9.42	2.16	2.06	28.51	15.53	194.20	399.60	1533.00	2166.00	22.96	35.68		
	LN68	DTF	LL	LB	DW	L/B								
Edinburgh	0	0	0	0	18.35	31.97	0	2347.17	0	0.105	0	0		
	180.00	149.60	61.20	56.00	240.30	150.80	23.89	42.69	16314.00	26745.00	0.080	0.070		
Anstruther	45.98	0	7.42	0	69.92	30.02	9.00	10.67	4073.50	5912.50	0.090	0		
	78.27	104.60	47.40	35.25	157.50	122.70	26.59	36.90	11274.00	21202.00	0.073	0.047		
Durham	55.02	0	0	0	160.32	0	13.41	0	4084.83	0	0.030	0		
	97.80	164.60	96.26	61.34	172.10	179.80	44.95	39.12	14182.00	17084.00	0.102	0.094		
Coleraine	103.06	43.15	37.57	0	69.15	41.27	23.08	7691.83	0	0	0.171	0		
	84.70	139.50	76.27	41.20	223.20	142.20	59.70	36.95	8219.00	7419.00	0.154	0.133		

Where the difference between families was not significant σ_b^2 has been taken to be 0.

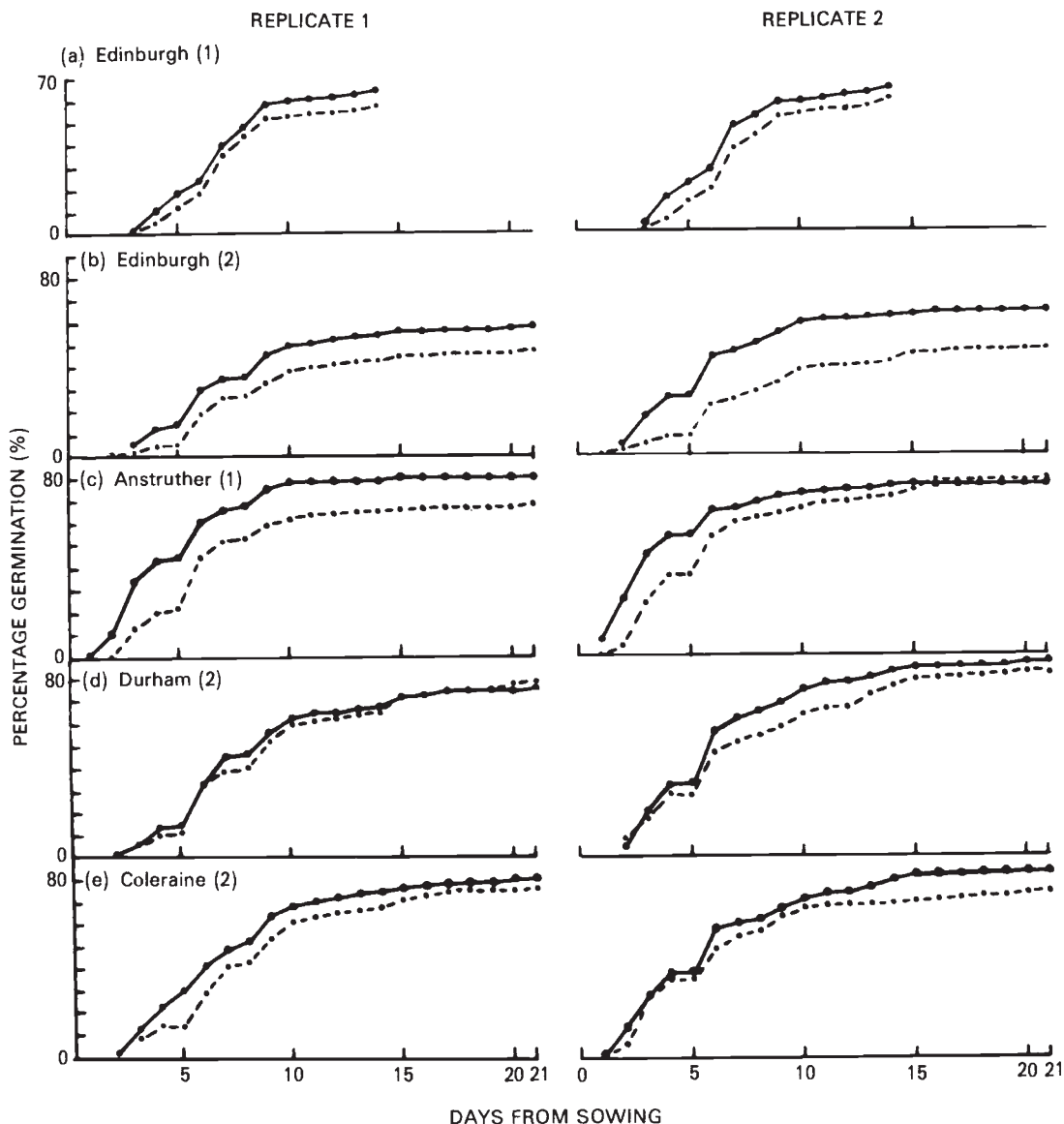


Figure 1 Cumulative percentage germination of the non-radiate (●—●) and radiate (●--●) morphs in samples from four populations of *Senecio vulgaris* raised in experiments (1) and (2).

established that whereas the non-radiate morph was taller throughout the early phase of development and flowered earlier in the Durham sample, as reported by Richards (1975), no differences were apparent for the same characters within the Edinburgh sample. The fact that life history differences between morphs are not generally consistent over all polymorphic populations of the species was made more apparent by the analysis of all four populations investigated in Experiment 2. It emerged that, except for the characters LN54

and LB (for which no differences occurred in all samples) and the germination characters, there was a significant morph \times population interaction for all other traits. For days to flowering (DTF), shoot dry weight (DW) and leaf length/breadth ratio (L/B) the interaction was particularly striking with the relative performance of morphs in certain populations being the very opposite to that found in other populations.

In addition to the differences between morph means, morph differences in the degree of variation

expressed for each character were also present. In both experiments, it was general for the non-radiate morph to exhibit a similar or greater amount of variation than the radiate morph for most characters recorded. This was the case for variation both between and within families. The latter finding is somewhat surprising in view of the known greater female outcrossing shown by the radiate morph in polymorphic populations (Marshall and Abbott, 1982; 1984a). Gouyon and Vernet (1982) have demonstrated that within a polymorphic population, an outcrossing morph is expected to contain greater levels of heterozygosity and genetic variation than a selfing morph. This is of importance in that any selection that favours heterozygotes or the production of genetically varied offspring (see Antonovics and Ellstrand, 1984; Ellstrand and Antonovics, 1985) would be expected to favour the outcrossing morph and offset the cost of outcrossing that it incurs during reproduction. The fact that less phenotypic variation was found within families of the radiate morph does not in itself preclude the possibility that they were more heterozygous, given that increased heterozygosity might improve phenotypic buffering (Lerner, 1954; Vrijenhoek and Lerman, 1982). Clearly, direct estimates of genetic variation within families will be necessary to settle this issue. What is certain, however, is that within the non-radiate morph considerably more genetic variation is maintained between families, providing much potential for future evolution that will counter, to a certain extent, any advantage which the radiate morph would gain from its expected ability to generate a greater within family genetic variance.

In conclusion, it is necessary to consider the cause and effects of the various life history differences that are found between the radiate and non-radiate morphs of *S. vulgaris* and why, with the exception of germination characters, such differences are not consistent over populations. The radiate morph is of recent origin in *S. vulgaris* and there is good evidence that it evolved following introgression between non-radiate *S. vulgaris* var. *vulgaris* and the related introduced species *Senecio squalidus* L. (Ingram, Weir and Abbott, 1980). Along with the *T_r* allele, other genes are likely to have been introgressed from *S. squalidus* into *S. vulgaris* causing differences to occur between the two morphs in a range of characters. Although the frequency of introgression between the species is considered to be low (Marshall and Abbott, 1980), it is not inconceivable that it has occurred several times involving different parental stocks of

S. vulgaris var. *vulgaris* and *S. squalidus*. The net result would be that in different populations the radiate morph is associated with different combinations of life history and other traits. In time, such combinations may break down following outcrossing and recombination, and in large stable polymorphic populations both the non-radiate and radiate morph might eventually exhibit very similar life histories. However, in a weedy, colonising species such as *S. vulgaris* large, stable populations seldom occur and due to the founder effect, various morph differences might be present over a sample of populations without the establishment of a consistent pattern. An association between a particular morph and a (life history) character that is present in all polymorphic populations would indicate either conservation by selection, tight linkage or developmental constraints. It is feasible that the consistent association between seed germination behaviour and capitulum type found in the current study results from a developmental constraint imposed by the pleiotropic action of the alleles at the ray floret locus. An alteration of capitulum type, due to allelic substitution, causing presence or absence of ray florets might also affect the germination behaviour of seed produced by the different florets. It has been established in other Compositae that seed of ray florets often differ in germination behaviour from seed produced by disc florets (Burt, 1977; Venable and Levin, 1985). This might also be the case in radiate *S. vulgaris* and account for the observed differences in germination behaviour between the radiate and non-radiate morphs. This possibility is currently being investigated.

The consistent difference in seed germination behaviour observed between the radiate and non-radiate morph is likely to have an important effect on the demographic genetics and maintenance of the capitulum polymorphism in wild populations of *S. vulgaris*. Particularly so, since recent work (Abbott, in preparation) has shown that in the Edinburgh population, the difference between morphs occurs under field conditions often to a greater extent than was found in the current study. However, the fact that other life history differences are also common, yet in an inconsistent manner over populations, is likely to prevent the determination of a general mechanism of maintenance of the polymorphism in the species. It would seem that future investigations of maintenance will need to be restricted to individual populations. Knowing this, it could be argued that the polymorphism for capitulum type and outcrossing rate in *S. vulgaris* is another one of those polymorphisms which

poses problems of maintenance for which there are, to quote Jones, Leith and Rawlings (1977), "... too many solutions".

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