Germination behaviour of the radiate and non-radiate morphs of groundsel, *Senecio vulgaris* L.

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Comparisons of the germination behaviour of seeds of the radiate and non-radiate morphs of *Senecio vulgaris* produced in spring and autumn were made in controlled environments and in the field. Fresh seeds of the non-radiate morph frequently germinated more readily than fresh seeds of the radiate morph during the first flush of germination after sowing. In two field experiments in which germination of freshly produced autumn seeds was tested over an extended period, an initial flush of germination occurred before winter set in, during which more non-radiate than radiate seeds germinated; there then followed a long dormant phase that spanned the winter months before germination resumed in early spring. Over spring more radiate than non-radiate seeds germinated and the net effect was that by mid-spring there was no difference between the cumulative percentage germination of seeds of the two morphs. It is concluded that whereas fresh non-radiate seeds of *S. vulgaris* tend to show a pattern of germination skewed towards early germination, radiate seeds, produced in autumn, often show a pattern skewed towards late germination. The importance of this difference is briefly discussed in relation to the maintenance of the polymorphism for capitulum type in British populations of *S. vulgaris*.

INTRODUCTION

The evolution of the polymorphism for capitulum type and associated outcrossing rate in British populations of *Senecio vulgaris* has been the subject of several recent studies (Ingram, Weir and Abbott, 1980; Marshall and Abbott, 1982; 1984*a, b*; Abbott, 1985). For a description of the polymorphism and its genetic control see Trow (1912). A recent investigation of life history differences between the non-radiate and radiate morphs sampled from four polymorphic populations in Britain (Abbott, 1986) showed that for many traits differences between morphs were common; however, only differences in seed germination behaviour were consistent over populations. In each sample, seed of non-radiate plants tended to germinate more quickly and in greater overall numbers than seed of the radiate morph over the first 3 weeks from sowing. This difference in morph germination behaviour confirmed a previously reported finding by Richards (1975) based on a study of material from a Durham population.

The results of Richards (1975) and Abbott (1986) were of a preliminary nature in that comparisons were made in growth cabinets or green-

houses, over relatively short periods of time after sowing, and on seed that had been stored at laboratory temperatures for at least 5 months. In view of the likely importance of differences in germination behaviour between morphs on their relative survival and fecundity in wild populations, a further series of experiments has been conducted in which germination of freshly ripened seed of each morph was compared under field and controlled conditions. The aims of these studies were: (a) to establish that differences between morphs in germination behaviour are maintained over a broad range of day/night temperatures; (b) to determine what proportion of seed that fails to germinate in the field during the initial phase after sowing is dormant rather than dead; and (c) to examine the relative germination behaviours of the morphs over an extended period in the field.

MATERIALS AND METHODS

Seeds were collected from radiate and non-radiate plants sampled either from large polymorphic populations located on waste sites in Edinburgh or, where stated, from cultivated material derived

from these populations. Samples were collected in spring and autumn of the years 1982, 1983 and 1984 to coincide with the two peak periods of seed production that occur each year in natural populations in Edinburgh. At each sampling time seeds from several capitula from each of at least 50 plants per morph, were bulked and mixed within morphs before use.

Germination in controlled environments

On 24 June, 1982, 1 month after collection, 50 seeds of either the radiate or non-radiate morphs were sown in 6.3 cm square plastic pots on a mix of washed sand and fine gravel in controlled environment chambers at the Duke University Phytotron, N. Carolina, U.S.A. Seeds came from plants of a population occurring on wasteground at Newhaven Road, Edinburgh (Grid Ref. NT258758). Six replicate pots per morph were placed in each of three chambers over which a day/night temperature range of 25/21, 19/15, 16/12°C was established. Pots within chambers were completely randomised and sprayed to saturation point every morning with 1/30 full strength Hoagland's solution (see Downs and Bonaminio, 1976, p. 17, for composition) and each afternoon with demineralised water. Photoperiod was set at 16 hours with light supplied by a combination of fluorescent and incandescent lamps to give an average quantum flux density of $325 \text{ mol m}^{-2} \text{ s}^{-1}$ (PAR) at pot level. Over a period of 28 days from sowing a daily record was taken of the number of seeds to germinate in each pot. Seeds were removed from pots as they germinated. At 16 and 23 days from sowing, following short periods during which few seeds germinated, the surface of the sand/grit mix in each pot was loosened to a depth of 1 cm with the points of a pair of fine forceps in an attempt to stimulate further germination.

Germination under field conditions

In slide mounts

Samples of 50 seeds, either of the radiate or non-radiate morph were placed in plastic photographic slide mounts. The windows of the slide mounts were replaced with a lower layer of fine nylon mesh and a top layer of tissue paper. The mesh retained the seeds while allowing contact with the soil. The tissue paper provided protection in the early stages of an experiment. Slide mounts were randomised and pinned to the surface of a prepared plot in St. Andrews that had been cleared of vegetation and

covered with sterilised soil to a depth of 5 cm. Each week, germinated seeds were recorded and removed from the slide mounts. After a period in the field (see below), non-germinated seeds were removed from slide mounts, placed on filter paper in petri dishes exposed to daylight, and treated with distilled water in the laboratory. Seeds were removed on germination. After 2 weeks, seeds that had failed to germinate were treated with a solution of 1 mM GA₃ (giberellic acid) for 2 weeks to test their viability. (Treatment with GA₃ serves as an effective test of seed viability in *S. vulgaris* (see Popay and Roberts, 1970a).)

Three experiments were conducted. Experiment 1 tested seeds collected in September, 1982 and ran from 26 November 1982 to April 9 1983 (19 weeks) before slide mounts were removed to the laboratory. Experiment 2 ran from 1 June 1983 to 12 October 1983 (19 weeks) using seeds collected in May 1983. Experiment 3 ran from 1 November 1983 to 6 February 1984 (14 weeks) using seeds collected in October 1983. In each experiment, seeds came from plants of a population located on wasteground at Salamander Street, Edinburgh (Grid Ref. NT278763). Replication was 20-fold in experiment 1 and 10-fold in experiments 2 and 3.

In pipes

Seeds were collected from radiate and non-radiate plants raised in pure stands on the experimental plot at the University of St. Andrews Botanic Garden. Pure stands of each morph consisted of 500 plants (10 progeny plants of each of 50 parent plants originally sampled from the Newhaven Road polymorphic population in Edinburgh). Plants within each pure stand were randomised at 0.5 m intervals and grown so as to flower and set open pollinated seeds in May or September of a given year. Stands were separated by a distance of 30 m to minimise outcrossing between morphs.

At intervals of 1 m, 30 open ended PVC drainage pipes, each 15 cm diameter and 25 cm in length, were sunk vertically into an experimental plot within a nursery area of the Royal Botanic Garden, Edinburgh. The rims were kept approximately 5 cm above ground level. The bottom of each pipe was netted to exclude potential soil borne seed predators. Sterilised soil was added to pipes so that after settling the level was the same as ground level. Twelve replicates of 500 seeds of the radiate and non-radiate morphs were sown as pure stands on the soil surface within pipes. Replicates were completely randomised over pipes. Six pipes that were not sown acted as controls.

After sowing, pipes were netted to exclude birds and thereafter the experimental plot and surrounding area was regularly weeded to prevent seed immigration into pipes. Experiments were initiated in Autumn 1983, early Summer 1984 and Autumn 1984 and ran for between 16 to 32 weeks. At weekly intervals emerging seedlings were recorded and removed. Controls remained clear of germinated seedlings throughout the experimental periods.

Weather records

Records of daily maximum and minimum air temperatures and rainfall for St. Andrews and the Royal Botanic Garden throughout the relevant experimental periods were obtained from the Meteorological Office, Edinburgh. From these records weekly means and totals were calculated.

Statistical analysis

In all experiments the significance of a difference between morphs in cumulative germination percentage was determined by a t-test after transforming percentages into angles using the arcsin transformation.

RESULTS

Germination in controlled environments

At each of the three day/night temperatures the cumulative germination percentage of the non-radiate morph was significantly greater than that of the radiate morph throughout the period that germination was recorded (fig. 1). For both morphs, at all temperatures, germination levelled off after about two weeks although there was a further flush of germination following the "cultivation" treatment on day 16 and to a lesser extent after the "cultivation" given on day 23. There was a trend for the difference between morphs in cumulative germination percentage to increase as the day/night temperature decreased. By the end of the experiment the differences between morphs in germination at 25/21, 19/15 and 16/12°C were respectively 31.7, 35.7 and 45.3 per cent.

Germination under field conditions

In slide mounts

For seeds sown in autumn 1982 and early summer 1983, there was a delay before germination started (fig. 2). This was particularly marked with the

Figure 1 Cumulative percentage germination of seeds of the non-radiate (■) and radiate (□) morphs of *Senecio vulgaris* at three day/night temperatures. Arrows mark the time of cultivations. Differences between morph means within treatments are significant ($P < 0.05$) at all recording dates except for day 4 at 19/15°C and days 5 and 6 at 16/12°C.

summer sown seeds which after the first week from sowing experienced a prolonged drought until the end of August 1983 (fig. 2(b)). Following an increase in rainfall there was an immediate flush in the germination of seeds of both morphs. Delayed germination after sowing was much less marked among seeds sown in autumn 1983 (fig. 2(c)).

For seeds collected in spring and autumn 1983 it was evident that fresh radiate seeds germinated less readily than non-radiate seeds (fig. 2). In contrast there was no difference between morphs in the germination behaviour of fresh seeds collected

Figure 2 Cumulative percentage germination of seeds of the non-radiate (■) and radiate (□) morphs of *Senecio vulgaris* in slide mounts at St. Andrews (—) and in petri dishes following removal from slide mounts (---). Treatments in petri dishes were (W) distilled water, and (G) millimolar gibberellic acid. Seeds used in experiments were collected in (a) September 1982, (b) May 1983, (c) October 1983. (▼) marks date of sowing and (*) where differences between means are significant ($P < 0.05$). The weekly rainfall values and weekly mean maximum and minimum air temperatures for St. Andrews throughout the experimental periods are presented.

in autumn 1982. After the initial flush of germination, there followed a period in all tests during which very little further germination took place. At the stage when slide mounts were removed from the field approximately 50 per cent of non-radiate seeds and between 20–40 per cent of radiate seeds had germinated. Most seeds that failed to germinate in the field were not dead. Many germinated when treated with distilled water in petri dishes (fig. 2) and for the autumn 1983 seeds this was sufficient to reduce the difference between morphs in total germination percentage to a non-significant amount. Further germination of seeds followed treatment with 1 mM GA₃ and by the time each test was terminated there were no significant differences between morphs in final percentage germination within any seed batch. At this stage between 75–85 per cent of seeds sown had germinated and the seeds that remained were presumed to be dead.

In pipes

For seeds collected and sown in autumn 1983 and 1984 more seed of the non-radiate morph than the radiate morph germinated during the first flush of

germination (fig. 3(a, c)). This initial flush occurred over a period of 4–5 weeks and was followed by a period during which very little seed of either morph germinated. With autumn 1983 sown seed, further flushes of germination of seeds of the radiate morph occurred during February and early April 1984 over periods when comparatively few seeds of the non-radiate morph germinated (fig. 3(a)). These flushes followed periods of heavy rainfall but no marked change in maximum and minimum temperature. With autumn 1984 sown seed, major flushes in germination of radiate seed occurred in late February/early March and again in early April 1985 (fig. 3(c)). Each flush followed an increase in weekly mean maximum air temperature (up to 10°C) after a previous fall in temperature (down to 2°C and 6°C respectively) and in April the flush occurred during a 3-week period of heavy rainfall. By the end of the spring flushes in both experiments the cumulative percentage germination of radiate seeds approximated that of non-radiate seeds and no further differences between morphs in germination percentage were recorded. On terminating the experiments between 65–75 per cent of the seeds originally sown had germinated.

Figure 3 Cumulative percentage germination of seeds of the non-radiate (■) and radiate (□) morphs of *Senecio vulgaris* at Edinburgh. Seeds tested were collected in (a) September 1983, (b) May 1984, (c) October 1984. (▼) marks sowing date and (*) where differences between means were significant ($P < 0.05$). Also presented are the weekly rainfall values and weekly mean maximum and minimum air temperatures recorded at The Royal Botanic Garden Edinburgh throughout the experimental periods.

In contrast to what was found for autumn sown seeds, no difference in germination behaviour was recorded between morphs for seeds collected and sown in spring 1984 (fig. 3(b)). Within this batch there was a delay in germination of seeds of both morphs until week 8 after sowing (early August); after a week in which 11 mm of rain fell, seeds rapidly germinated over a 2-week period producing a total cumulative percentage germination for each morph of approximately 80–85 per cent. Almost no further germination took place over the next 7 weeks despite favourable temperatures and rainfall.

DISCUSSION

The results show that during the first flush of germination that follows sowing, fresh seeds of the non-radiate morph of *S. vulgaris* frequently germinate more readily than fresh seeds of the radiate morph. On occasion, however, both morphs exhibit a similar pattern of germination over the initial period. In a previous study of germination of non-radiate seeds of *S. vulgaris*, Popay and Roberts (1970b) found that the dormancy of fresh seeds varied according to the date when seeds were collected from a population. In another study, Roberts and Feast (1973) reported that after sowing seeds outside in late July, the emergence of seedlings of the non-radiate morph before 31

December of the same year, varied greatly between years. Such variation may be due to differences between years in soil conditions after sowing and/or variation in the degree of dormancy in seed samples that had ripened under different conditions. It seems possible therefore, that in any season the conditions experienced by seed during formation and ripening on the mother plant, and then after sowing, may affect whether a difference in germination behaviour is exhibited between the radiate and non-radiate morphs. Nevertheless, the findings of the present study indicate that a difference frequently occurs and that this difference becomes greater with a decrease in temperature (fig. 1).

In all experiments it was evident that after the initial flush of germination there was a lengthy period during which very little germination of seeds of either morph took place. Based on the results from the "slide mount" experiment (fig. 2) it is clear that most seeds which fail to germinate during the first flush are viable and capable of germination. Not surprisingly, therefore, in two of three tests in which seed germination of the radiate and non-radiate morphs was investigated over an extended period in the field, further episodes of germination eventually occurred (fig. 3). In both instances, autumn-produced seed was tested and the further flushes of germination occurred in spring with many more radiate than non-radiate

seed germinating (fig. 3(a, c)). As a consequence there was a sharp increase in the cumulative percentage germination of radiate seeds, and by early April in each year there were no significant differences between morphs in percentage germination. In the third test of the same series, conducted on seed collected and sown in spring (fig. 3(b)), no difference in germination behaviour was recorded between morphs. Instead, a high percentage of seeds of both morphs germinated during the initial germination phase. From the germination patterns recorded for autumn seed we might predict that on occasions when more non-radiate than radiate seed germinate following production and sowing in spring (as occurred in 1983, fig. 2(b)), the cumulative percentage germination of the radiate morph may eventually come to equal that of the non-radiate morph as the length of the test period is extended.

Taken overall, it is apparent that fresh seed of non-radiate groundsel often shows a pattern of germination that is skewed towards early germination, while the pattern of germination of autumn-produced seeds of the radiate morph, is frequently skewed towards late germination. Such a difference between morphs in germination behaviour is likely to have important consequences on the relative frequencies of the two morphs in polymorphic populations of *S. vulgaris*. It is recognised in many plant species that time of seed germination after dispersal can affect both seedling survival and the reproductive output of survivors (Rathcke and Lacey, 1985). In several studies, survival of early germinated seedlings is reported to be much lower than that of later germinated seedlings. However, early germinated survivors tend to capitalise on a longer growing season to produce adult plants with high fecundities (Arthur, Gale and Lawrence, 1973; Baskin and Baskin, 1972; Marks and Prince, 1981; Venable, 1984). This has led Rathcke and Lacey (1985, p. 181) to suggest that within many species "... time of germination reflects a trade-off between selection for high seed set and selection for high survivorship". In the present study survivorship of seedlings was not investigated, nevertheless, it seems feasible that the difference in seed germination behaviour between the radiate and non-radiate morphs of *S. vulgaris* will have a direct effect on relative morph survivorship and seed set and, in turn, the demographic genetics and maintenance of the polymorphism for capitulum type in the wild. This possibility, together with the cause of the difference in germination behaviour between morphs, is currently under investigation.

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