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Spatial variation in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment

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Summary

1. Patches of *Primula vulgaris* occur across a range of light conditions within forests. To understand how light affects the stages of the life cycle involved in reproduction and recruitment, several fecundity-related variables (flower and capsule production, seed set, seed germination and seedling establishment) were studied in eight populations across a range of light conditions.

2. The mean number of seeds per plant varied greatly, from seven to 136, and the percentage of seedling establishment varied from 0.4 to 17.2%. These variables, as well as the number of flowers per plant and fecundity, were positively correlated with the light conditions.

3. *Primula vulgaris* populations establish in newly opened gaps. How this species colonizes new clearings was investigated by looking at seed survival in the soil and seed removal by potential dispersers, in particular rodents and ants.

4. After 14 months in the greenhouse, only three *P. vulgaris* seedlings were observed germinating from 200 soil samples taken from two populations. Germination of retrieved seeds from buried samples was generally lower than 10%. This suggests that only a small number of seeds remain viable in the soil for long periods of time.

5. Seed removal was high in the populations studied (more than 70% in 10 days). Rodents harvested a greater proportion of seeds than ants. Seed dispersal by ants is known to occur within short distances but rodents may be long-distance dispersers, which may be important for the long-term persistence of *P. vulgaris* in a site because it allows seeds to reach newly opened gaps.

Key-words: Fecundity, seed pool, seed removal

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Introduction

Primula vulgaris Huds. is a common element of the ground flora of ancient woodlands in Britain and northern Europe (Richards 1989). Although it is a shade-tolerant species, growth and reproduction are favoured by relatively open conditions such as canopy gaps (Keith-Lucas 1968). The forest canopy is a dynamic system in which gaps are constantly opening owing to natural disturbances like branch or tree falls (Runkle & Yetter 1987). Many woodland herbs colonize these clearings but the changing light conditions as the canopy closes strongly affect their demography (Collins, Dunne & Pickett 1985). Their populations decrease as gaps close and thus their long-term persistence in a forest depends on the creation of new

gaps in the canopy (Bierzychudek 1982; Horvitz & Schemske 1986; Cipollini, Whigham & O'Neil 1993).

To understand how forest herbs persist in such dynamic conditions we need information about ecological processes at two different spatial scales: (1) demographic information at the scale of local populations occupying individual gaps and (2) metapopulation information at the scale of the forest as a whole. In this paper we address the first of these questions in respect of the seed ecology of *Primula vulgaris*. The seed phase of the life cycle is especially important because seeds may be the means by which new gaps are colonized (by dispersal or from the seed bank) and because seed production may limit population growth.

Although the demography of temperate woodland herbs has been much studied (Bierzychudek 1982; Collins *et al.* 1985; Kawano *et al.* 1987; Barkham 1992a), relatively little research has focused on the fates of flowers and seeds in natural conditions. Moreover, most studies have ignored the fact that

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environmental conditions change as the canopy closes. The effect these changes have on the demography of herb populations is unknown, in particular, the way in which different phases of their life cycle are affected as canopy closure proceeds.

Considering the general lack of information concerning the seed ecology of temperate forest herbs, *P. vulgaris* is a relatively well-documented species. Studies on germination and growth have demonstrated that light has a strong effect on these processes under controlled conditions (Keith-Lucas 1968; Helliwell 1980). Flower, capsule and seed production in natural populations vary greatly from season to season and seed set depends on the availability of pollinators (Piper, Charlesworth & Charlesworth 1984; Boyd, Silvertown & Tucker 1990). However, natural populations of *P. vulgaris* occur in a wide range of light conditions and no information is available on the effect of canopy dynamics on the reproductive variables of this species, nor on seed germination and seedling emergence across the range of natural light conditions.

The primary aim of this study was to determine how varying light conditions affect the different phases involved in reproduction and recruitment in *P. vulgaris*, which in turn affect the dynamics of populations in the various successional stages of the canopy regeneration cycle. To such end, flower and capsule production, seed set, seed germination and seedling establishment were studied in eight populations of *P. vulgaris* across a range of different light conditions.

Other aspects of the seed ecology of *P. vulgaris* that have been little studied are seed longevity and seed dispersal. These are particularly relevant when considering spatially structured populations, because they may affect the colonization of new patches. Some authors have suggested that long-term buried seed pools are primarily responsible for the colonization of newly opened gaps by understorey herbs (Brown & Oosterhuis 1981; Brown & Warr 1992). However, the importance of both seedling banks and long-distance seed dispersal as potential sources of colonization has been stressed for some gap-dependent species (Alvarez-Buylla & García-Barrios 1991; Beatty 1991). In this study we addressed the question of colonization strategy of *P. vulgaris* by examining the buried seed pool in two populations, seed survival in the soil and seed removal rates by potential dispersers, in particular ants and small mammals.

Materials and methods

Field work was conducted at Dancers End Nature Reserve, in Buckinghamshire, UK (Grid Reference SP902096). This area is mainly a forest of *Fagus sylvatica* (Beech) and *Fraxinus excelsior* (Ash) on a chalky soil (National Vegetation Classification: W8, *Fraxinus excelsior*-*Acer campestre*-*Mercurialis perennis* woodland, with some stands closer to W12,

Fagus sylvatica-*Mercurialis perennis* woodland, Rodwell 1991). It has traditionally been managed through coppice cycles of 5 to 10 years, the coppiced species being mainly Hazel (*Corylus avellana*) and Hawthorn (*Crataegus monogyna*). Important elements of the ground flora are *Primula vulgaris*, *Mercurialis perennis*, *Rubus fruticosus* and *Hyacinthoides non-scripta*. Within the forest *P. vulgaris* has a patchy distribution. Six populations in different light conditions were chosen for study.

Two additional populations were studied: one in Woburn Wood, a *Quercus robur* (Oak) and *Castanea sativa* (Chestnut) forest in Bedfordshire (Grid Reference SP927325) and another one in Salcey Forest, a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (Grid Reference SP814508).

LIGHT MEASUREMENT

The diffuse site factor, which is a way of measuring diffuse light, was used to describe the light environment of each population (Mitchell & Whitmore 1993). It was evaluated through the computer image analysis of hemispherical photographs taken during summer 1993. Photographs were analysed using the program Solarcalc 5.41, which calculates diffuse light as a percentage of open sky in the hemispherical photograph (Chazdon & Field 1987). The mean diffuse light of seven to 15 photographs was used to characterize the light environment of each population.

1. SEED PRODUCTION

In May 1993, the flowers of 20 reproductive plants chosen at random were marked in each population. The resulting capsules were collected and their seeds counted.

Fecundity was calculated using two approaches: the 'mechanistic' and the 'empirical' (Menges 1990). Mechanistic fecundity was given by

$$(\text{mean no. of seeds per plant}) \times \frac{(\% \text{ of seedling emergence})}{100} \quad \text{eqn 1}$$

Seedling emergence was calculated as described in section 2b.

The empirical approach considers the number of reproductive individuals and the number of seedlings emerging in a population the following year. Empirical fecundity was calculated as

$$\frac{(\text{no. of seedlings at } t+1)}{(\text{no. of reproductive plants at } t)} \quad \text{eqn 2}$$

'Empirical' fecundities were calculated in the eight populations studied by counting the number of reproductive individuals and emerging seedlings in areas of 8 to 25 m² (depending on plant density) for two consecutive years.

2. SEED GERMINATION IN THE GREENHOUSE AND
SEEDLING EMERGENCE IN THE FIELD(a) *Seed germination*

Seeds were collected in seven populations during July 1993. Four replicates of 25 seeds per population were set in Petri dishes with wet filter paper in a greenhouse. Four other replicates of 25 seeds per population were subjected to a cold pretreatment (4 °C) for 8 weeks in damp conditions before placing them in the greenhouse. Seeds were watered as required. Germination was recorded every month for a year, from July 1993 to July 1994.

(b) *Seedling emergence*

Ten 10×10 cm quadrats were marked on the ground evenly spaced along a transect in seven populations. In each of five quadrats, 50 seeds were scattered on the ground in July 1993. No seeds were sown in the other five quadrats. The number of seedlings per quadrat was recorded in May 1994. The number of seedlings in the control quadrats was subtracted from the number of seedlings in the seeded quadrats before calculating the percentage of seedling emergence.

3. SEED SURVIVAL IN THE SOIL

Ten replicates of 50 seeds were buried 5 cm deep in nylon bags (c. 0.03 mm mesh) in each of four populations in late July 1993 (DE1, DE2, DE3 and WW). Five bags were retrieved in late April 1994 and the other five in April 1995. Immediately after retrieval seeds were put in Petri dishes with filter paper to test for germination in the greenhouse. If only seed coats were found in the bags it was impossible to tell whether they had died or germinated before retrieval. However, this distinction was not important for the purpose of this experiment as, either way, they would not become part of the buried seed pool.

A further viability test was carried out on the seed batch retrieved in April 1995: after retrieved seeds had been in the greenhouse for 1 month and when no further germination was being recorded, a subsample of 40 seeds per population was taken at random from the seeds left to test for potential viability using tetrazolium dye.

In order to examine the seed pool, 100 soil samples were taken in each of two populations at Dancers End (DE2 and DE6, a gap and a closed-canopy population respectively). Samples were collected in early June 1993, before seed shed, to ensure that seeds in soil were produced the previous year or earlier. Five-centimetre deep samples were taken with a bulb planter (5 cm in diameter) evenly spaced along 10 parallel transects of 10 m each.

Immediately after collection samples were spread out in plastic trays in a greenhouse. Trays were kept moist from beneath using capillary matting, the edges

of which were immersed in water. The soil was disturbed every 3 months. Seedlings emerging were identified and removed from trays every month for 14 months.

4. SEED REMOVAL

(a) *The effect of deer*

Ten metal mesh cages (50×50×50 cm, 5×5 cm mesh) were set in Woburn Wood to protect *P. vulgaris* capsules from deer in April 1993. Ten control cages were also set without their lids. The number of flowers per cage was counted at the beginning and the number of capsules recorded at the end of the experiment, in July 1993. Plots were chosen at random.

(b) *The effect of small mammals*

Small cages (30×30×30 cm, 0.5×0.5 cm metal mesh) were used in Woburn Wood to test the effect of small mammals. In late May 1994, 15 cages were set at random into the ground around *P. vulgaris* plants. Another 15 cages were elevated 5 cm above the ground with sticks, excluding only larger seed foragers like deer or birds. Capsules on other non-caged plants were also marked and followed as controls. Capsules were counted at the beginning of the experiment and re-counted in mid-June and finally in mid-July.

(c) *The effect of ants*

Primula vulgaris seeds possess an elaiosome and are harvested by a number of ant species directly from the capsule (Richards 1989). At Dancers End we have observed *Myrmica rubra* harvesting *P. vulgaris* seeds. This ant is abundant in grasslands and only occasionally present in forest. Rodents and other small mammals also harvest *P. vulgaris*. Rodents remove whole capsules leaving only the stalks and occasional capsule remains on the ground; ants harvest the seeds one by one leaving empty capsules.

Thirty open capsules were marked in each of two sites at Dancers End in July 1994: (1) a population in grassland (DE1) and (2) a population under a large gap in the canopy (DE2). All seeds were removed from capsules and 20 seeds were then replaced in each. Capsules were kept vertical through a stick to prevent the seeds from falling. The number of seeds per capsule was recorded every other day for a week and finally 2 weeks later.

In order to determine the amount of seed dispersal taking place through means other than ants or small mammals, we followed the seed removal and replacement procedure outlined above for another 20 capsules in the same two populations but in this case we covered the capsule stalks with tangle-foot (a non-setting glue that traps insects). In previous observations we noted that tangle-foot repelled both ants and small

mammals, so this treatment made seeds unavailable to both types of seed foragers.

Additionally, an 8 m long transect was set in a population in the grassland at Dancers End. By noting the state of the capsules (e.g. open, closed, empty, damaged, etc.) of every plant along the transect, we were able to estimate the proportion of seeds following different fates.

Results

1. SEED PRODUCTION

Table 1 summarizes the production of flowers, capsules and seeds by plants from different populations. There was wide variation in all variables. The mean number of flowers produced by plants ranged from 3.7 to 15.1 and the percentage that became capsules ranged from 16.8% to 46.7%. The mean number of seeds per plant (seven to 137) represented almost a 20-fold variation.

The number of flowers per plant was not correlated with the light conditions at each site. However, both the percentage of flowers that produced capsules and number of seeds per plant showed a significant correlation with diffuse light (Table 1).

The mean number of seeds that each plant produced was significantly correlated with its initial number of flowers (data not shown), though the correlation was not very strong (both variables Log transformed, $R^2 = 0.24$, $P < 0.0001$, $df = 138$). None of the variables presented in Table 1 shows any significant difference between pin and thrum flower morphs (according to paired t -tests, data not shown).

The 'empirical' fecundity estimates (Table 1) differ widely for the two periods analysed. For the period 1993–1994, fecundity was also calculated using the 'mechanistic' approach. This resulted in consistently greater estimates of fecundity than with the 'empirical' approach. However, regardless of the calculation method, fecundity and light conditions were positively correlated.

2. SEED GERMINATION IN THE GREENHOUSE AND SEEDLING EMERGENCE IN THE FIELD

Table 2 summarizes seed germination in the greenhouse after 14 months in all seven populations. Seeds germinated at an approximately constant rate, although there was a slight peak around February 1994, the time when seedling emergence occurs in natural conditions. Final germination was similar in both non-pretreated and cold-treated seeds.

Germination velocity was measured by the variable t_{50} , the time needed to achieve 50% germination (Grime *et al.* 1981). A MANOVA was performed to test the effect of pretreatment and of individual population conditions on the two variables (final germination, arcsin transformed for linearity, and t_{50}). The results

Table 1. Mean (\pm SD) flower, capsule and seed production by plants from eight populations of *Primula vulgaris* in three forests. Mean 'mechanistic' and 'empirical' fecundities are also reported. The bottom row refers to the results of the correlations of each variable with diffuse light, given in the first column (% canopy openness). DE1 population was excluded from these analyses because of its different environmental conditions. Percentages were arcsin transformed for normality

Population	Diffuse light	Flowers per plant	Capsules per plant	% Flowers producing capsules	No. of seeds per capsule	No. of seeds per plant	% Seedling emergence in the field	'Mechanistic' fecundity (1993–1994)	'Empirical' fecundity (1992–1993)	'Empirical' fecundity (1993–1994)
DE1	93.5	8.8 \pm 4.4	4.5 \pm 3.7	46.7 \pm 16.9	37.4 \pm 18.9	136.6 \pm 123.4	4.8	6.6	7.2	2.1
DE2	9.1	8.7 \pm 4.8	3.1 \pm 3.0	38.1 \pm 29.2	35.6 \pm 20.8	112.1 \pm 129.5	17.2	19.3	26.9	8.0
DE5	4.9	7.3 \pm 5.4	1.8 \pm 1.7	26.3 \pm 21.4	35.0 \pm 17.8	63.0 \pm 75.4	6.0	3.8	10.8	0.7
WW	4.8	3.8 \pm 2.6	0.8 \pm 0.8	21.8 \pm 26.5	41.7 \pm 18.3	31.2 \pm 35.4	2.8	0.9	0.3	0.3
SF	3.1	15.1 \pm 11.7	2.7 \pm 3.6	16.8 \pm 16.9	24.4 \pm 23.6	65.5 \pm 98.8	0.4	0.3	0.1	0.2
DE4	1.9	—	—	—	—	—	2.0	—	0.8	0.2
DE3	1.9	5.0 \pm 2.8	1.0 \pm 1.1	24.8 \pm 23.8	34.9 \pm 27.8	36.8 \pm 54.0	2.8	1.0	0.3	0.5
DE6	1.6	4.2 \pm 2.6	0.7 \pm 0.8	19.5 \pm 21.2	9.5 \pm 10.4	7.5 \pm 12.5	—	—	0.5	—
Results of the correlations		$R^2 = 0.03$ $P = 0.76$	$R^2 = 0.43$ $P = 0.15$	$R^2 = 0.71$ $P = 0.03$	$R^2 = 0.29$ $P = 0.27$	$R^2 = 0.72$ $P = 0.03$	$R^2 = 0.84$ $P = 0.01$	$R^2 = 0.83$ $P = 0.01$	$R^2 = 0.83$ $P = 0.004$	$R^2 = 0.78$ $P = 0.02$

indicated that final germination was significantly affected by population ($F=20.95$, $P<0.0001$) but not by pretreatment ($F=1.64$, $P=0.206$). However, both pretreatment and population significantly affected germination velocity ($F=26.23$, $P<0.0001$ and $F=11.88$, $P<0.0001$ respectively). Seeds subjected to the cold pretreatment germinated faster than non-pretreated seeds and seeds from Salcey Forest showed a significantly lower final germination than the other populations.

Seedling emergence was positively correlated with diffuse light, varying from 0.4% in a population under the canopy, to 17.2% in the population in a gap (see Table 1).

3. SEED SURVIVAL IN THE SOIL

When we retrieved the buried seed bags, we found a varying number of empty seed coats suggesting that germination (or death) occurred long before retrieval. In both years little germination was recorded when seeds were put in the greenhouse after the period of burial (Table 3). Germination percentage after retrieval exceeded 10% only in two

cases. Seeds that germinated did so during the month following retrieval.

The results of the tetrazolium test and observations on seed germination after retrieval, as well as on the number of retrieved seeds that appeared sound, indicated that, from the total number of seeds originally buried in July 1993, only 9.8%, 19.8%, 25% and 13.6% (for DE1, DE2, DE3 and WW, respectively) were still alive after 21 months.

Only three *P. vulgaris* seedlings were observed (during April 1994) germinating from the buried seed pool in the two populations at Dancers End. All of them were in the soil samples collected from the population in the gap, where plant density is much higher. Germination conditions were good, as seeds of other species germinated in the samples during the course of the experiment.

4. SEED REMOVAL

(a) The effect of deer

Of all the flowers counted inside the cages at the beginning of the experiment, 3.25% survived as capsules in control cages and 5.97% in deer exclusion cages. The number of capsules that survived in both treatments was not significantly different according to a *G* test performed on capsule counts ($G=3.81$, $P>0.05$, $df=1$).

(b) The effect of small mammals

The effect of the three treatments (large and small mammals excluded, only large mammals excluded and controls) was analysed through a multiple *G* test (Table 4), which indicated that the treatments had a significant effect on the number of capsules removed ($G=6.62$, $P<0.05$, $df=2$).

Figure 1 shows the capsule removal rate in this experiment. After 12 days the proportions of capsules missing in both the large mammals exclusions and the control plants, were already higher than in the total exclusion treatment, though not significantly different from it. After 36 days the number of missing capsules was significantly higher in the large mammals exclusions and in the control plants than in the total exclusions (Table 4). Rotting was responsible for some capsule loss, which also explains the high proportion of capsule loss in the total exclusions.

(c) The effect of ants

Figure 2 shows seed removal rate from populations DE2 and DE1. Only around 10% of the seeds were left after 9 and 15 days respectively. As ants leave empty capsules and rodents harvest the whole capsule leaving only the stalks, we were able to estimate seed removal by both ants and rodents. Most seed loss was due to rodent activity in both populations and seeds

Table 2. Final germination percentage after 1 year and germination velocity (measured by the variable t_{50}) for *Primula vulgaris* seeds from seven populations. Values sharing the same letter do not differ significantly within columns according to a Tukey–Kramer test performed after a MANOVA

Population	% Final germination (non-pretreated)	t_{50} (non-pretreated)	% Final germination (cold pretreatment)	t_{50} (cold pretreatment)
DE1	95 a	164.25 b	99 a	87.7 b
DE2	97 a	154.0 bc	84 a	123.5 ab
DE3	92 a	105.0 ac	87 a	99.5 bc
DE5	90 a	112.75 ac	91 a	94.2 b
DE7	93 a	102.0 a	87 a	86.0 b
WW	90 a	186.0 b	90 a	133.5 ac
SF	58 b	170.67 b	58 b	156.3 a

Table 3. Mean (\pm SD) number of seeds germinated in the seed burial/retrieval experiment. Figures were obtained as averages of seed germination from five samples of 50 seeds buried in each population

Population	Mean no. of seeds germinating after retrieval (\pm SD)	% Germination after retrieval
Seeds retrieved in May, 1994		
DE1	0.25 \pm 0.5	0.5
DE2	1.25 \pm 0.96	2.5
WW	11.50 \pm 4.43	23
DE3	3.25 \pm 0.96	6.5
Seeds retrieved in May, 1995		
DE1	1.33 \pm 0.58	2.7
DE2	4.25 \pm 2.63	8.5
WW	5.00 \pm 8.66	10
DE3	6.60 \pm 5.45	13.2

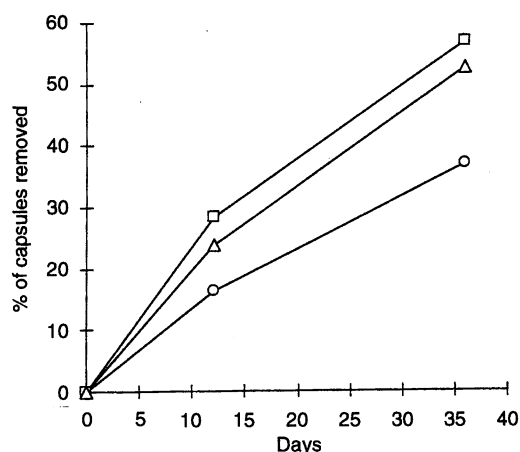


Fig. 1. Capsule removal rate at Woburn Wood during June/July 1994. Circles, total exclusions; squares, only large mammals excluded; triangles, controls (no exclusions).

were removed at a faster rate in the population in the grassland as compared with the population in the gap.

However, in the experiment where the capsule stalks were covered with tangle-foot we found that 41.3% (after 15 days in DE1) and 36.7% (after 9 days in DE2) of the seeds were lost from capsules, regardless of the tangle-foot and of the fact that they were kept in a vertical position. This suggests that seed removal was overestimated in the previous experiment, especially regarding ant activity, as capsules can be found empty as a result of seed removal by ants and/or random seed dispersal.

From a sample of 173 capsules recorded along an 8 m transect in the population at the grassland, 59.8% had signs of rodent activity, while only 17.4% had signs of ant activity or dispersal at random (undamaged capsules were found empty or semi-empty). Other capsules were still closed and only 7.5% of them appeared open but still untouched. These results are similar to the proportions of ant-removed, rodent-removed and non-removed seeds shown in both graphs in Fig. 2.

Discussion

Although *P. vulgaris* has been characterized as a shade-tolerator (Keith-Lucas 1968), our results have

shown that most measures of reproductive output were enhanced under brighter conditions. This must have a dramatic effect on the demography of populations established in patches with varying light availability. As a matter of fact, population growth rates are positive in canopy gaps and negative under closed canopy (T. Valverde, unpublished data). This has also been observed for other gap-dependent woodland herbs, such as *Cynoglossum virginianum* (Cipollini *et al.* 1993) and *Calathea ovandensis* (Horvitz & Schemske 1986). The demographic change caused by canopy closure in these species was the result of a decrease in fecundity-related parameters, as seems to be the case for *P. vulgaris*.

The comparison between the reproductive variables measured in two of the studied populations in contrasting light environments provides detail regarding the specific transitions that may be affected during the process of canopy closure (Fig. 3). Although the number of flowers per plant was similar in both populations the final fecundities differed more than 15-fold. Most of the variation in final fecundity values was caused by a dramatic decrease in the percentage of flowers producing capsules and in seedling emergence under darker conditions. As capsule production in this species appears to be related to pollinator availability (Piper *et al.* 1984; Boyd *et al.* 1990), the spatial variation in capsule production between populations suggests that there might be light-related differences in pollinator abundance in different forest patches.

With regard to the variation in seedling emergence, our results suggest that recruitment is high during the

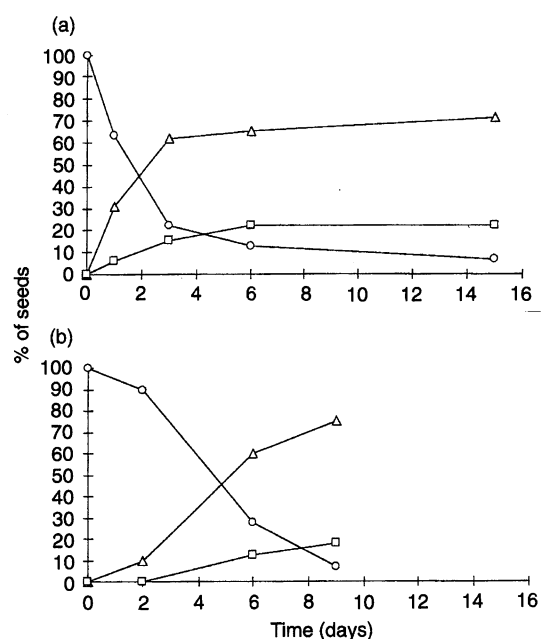


Fig. 2. Removal of *Primula vulgaris* seeds by ants and rodents in a population in (a) a grassland and (b) a gap at Dancers End Reserve during summer 1994. Circles, seeds left; triangles, seeds removed by rodents; squares, seeds removed by ants.

Table 4. Capsule removal in Woburn Wood. Values sharing the same letter in the last column do not differ significantly according to paired *G* tests

Treatment	No. of capsules remaining	No. of capsules removed	Proportion removed
Large and small mammals excluded	46	27	0.369a
Only large mammals excluded	38	50	0.568b
Control (no exclusion)	18	20	0.526b

establishment of populations following the opening of gaps but very low after canopy closure. This raises the question of how *P. vulgaris* persists through forest regeneration cycle. New populations may colonize canopy gaps in three ways: (1) through the reinitiation of population growth from old individuals that have survived for long periods under a closed canopy, (2) through seed germination from a long-term seed pool or (3) through seeds reaching gaps by means of seed dispersal. The results presented in this paper allow us to evaluate the likelihood of (2) and (3) as mechanisms of population re-establishment.

It appears that the majority of *P. vulgaris* seedlings recruited in a population during a given season come from the previous year's seed production rather than from a long-lived seed pool. We found only a small number of *P. vulgaris* seedlings in the soil samples

that we analysed, which coincides with what other studies have reported for this species (Brown & Oosterhuis 1981; Brown & Warr 1992; Warr, Kent & Thompson 1994). Furthermore, we obtained generally low germination percentages in seeds that had been buried for 9 and 21 months, which is in agreement with the results of Boyd *et al.* (1990), who observed that most *P. vulgaris* seeds found in the soil failed to germinate in greenhouse conditions.

Germination in seed samples within the bags buried in the soil in our experiment (as shown by the presence of empty seed coats) followed an almost 'all-or-nothing' pattern, which might have been related to relative humidity or other local microenvironmental conditions at the burial site. This suggests that there is no long-term seed dormancy, which is also supported by the high germination percentages we obtained in the greenhouse. Keith-Lucas (1968) and Helliwell (1980) found that *P. vulgaris* seeds lose their viability after 9 months of dry storage. Although our results show that this does not occur in natural conditions, because the tetrazolium test indicated that between 10 and 25% of the seeds buried can actually remain alive for at least 21 months, the germination capacity of older seeds does seem to be limited.

With regard to seed dispersal as a mechanism for colonization of newly opened gaps, our results suggest that ants harvested only a small proportion of seeds. Moreover, they generally disperse *P. vulgaris* seeds within centimetres from the source (Keith-Lucas 1968). In a study of genetic neighbourhood size Cahalan & Gliddon (1985) reported that in the absence of ant dispersal, most seeds landed a few centimetres away from the capsule.

The arrival of dispersed seed in gaps must occur through exceptional long-distance dispersal by ants or through other dispersal vectors, among which rodents are probably the most important. Richards (1989) reported that *P. vulgaris* seedlings are common outside the burrows of mice and voles, which suggests that these animals may act as seed dispersers as well as seen consumers. Some rodents from temperate habitats have been reported to store between one third and one fifth of their harvest (Price & Jenkins 1986). Nevertheless, rodent foraging and feeding behaviour may vary greatly in space and time with seed density, rodent abundance, weather conditions and the availability of other food sources (Hulme 1994). Long-term estimates of their effect as seed consumers/dispersers are unavailable.

The comparison between 'mechanistic' and 'empirical' fecundities offered a further estimate of seed loss in the populations studied. 'Mechanistic' fecundities were consistently higher than 'empirical' fecundities (Table 1). To calculate the former, we considered the percentage of emerging seedlings from a sample of seeds sown in the field, together with the data on seed production. The difference between the two estimates may be explained by seed removal, that was avoided to some extent in the 'mechanistic' method by sowing

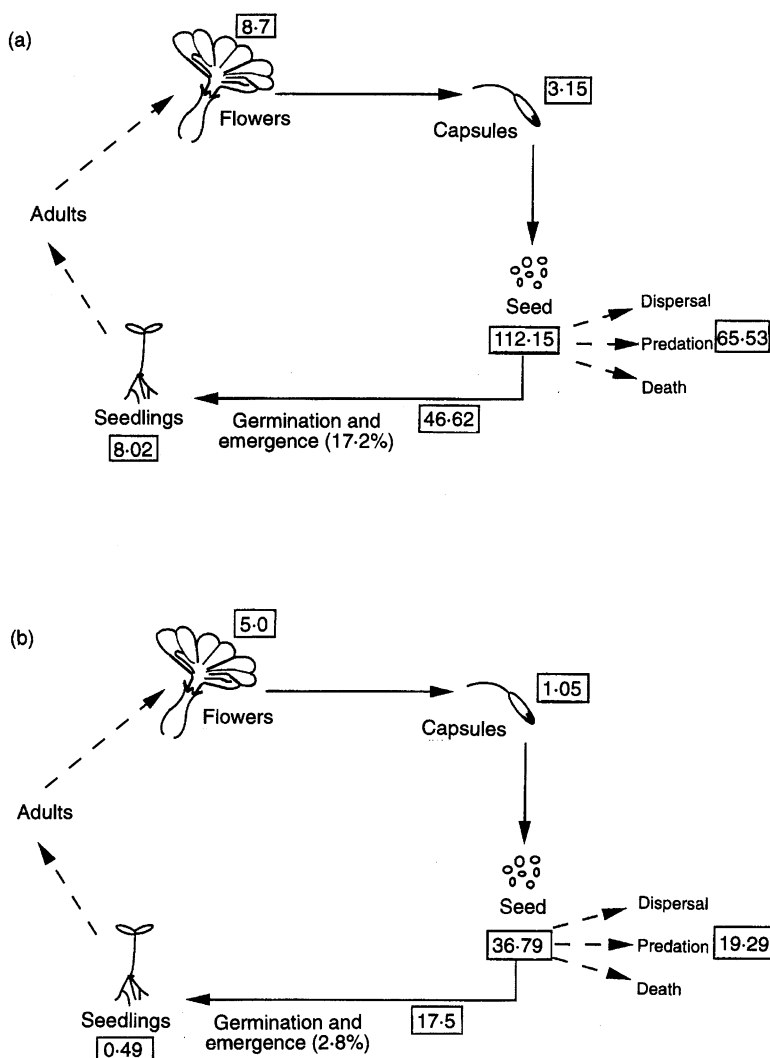


Fig. 3. Different phases of the reproductive cycle of *Primula vulgaris* in (a) a population in a gap (DE2) and (b) a population under closed canopy conditions (DE3). The figures in the squares are the per plant averages as reported in Table 1. The number of seedlings is given by the 'empirical' fecundities for 1993–1994. The number of seeds leaving the population (through dispersal, predation or death) was calculated using other measured and reported variables (empirical fecundity, % of seedling emergence and number of seeds per plant; see text).

the seeds directly into the soil, but was implicit in the results of the 'empirical' fecundities.

Figure 3 illustrates different phases of the reproductive cycle of *P. vulgaris* with the average numbers per plant entering each phase in two populations for the period 1993–1994. 'Empirical' fecundities were used as a measure of the number of seedlings emerging in 1994 per reproductive plant in 1993. The number of seeds leaving each population as a result of either long distance dispersal, predation or death was calculated as:

$$\text{Seeds leaving} = (\text{No. of seeds/plant}) - \frac{(\text{Empirical fecundity}) \times 100}{\% \text{ of seedling emergence}}$$

According to these calculations, 58% (65 out of 112 seeds per plant) and 52% (19 out of 37 seeds per plant) of the seeds produced in populations DE2 and DE3, respectively, were lost. These percentages are strikingly similar, despite the differences in environmental conditions, plant density and seed abundance between the two populations. Our other observations on seed removal (as described in Fig. 1 and the transect results in section 4c) also gave very similar estimates. These data indicate that seed removal plays a major role in decreasing seedling recruitment in natural populations under various light conditions. The fate of those seeds and their role in colonizing newly open gaps remain to be investigated.

The long-term persistence of *P. vulgaris* at a site depends on the opening of areas for potential colonization through either natural disturbances or coppicing. After gap formation new populations may potentially become established from isolated scattered individuals within the forest or less likely from seeds buried in the soil. Besides this, gap colonization through seed dispersal from adjacent populations may also play a critical role. Local extinction could occur if seed dispersal sources (i.e. forest patches occupied by *P. vulgaris* populations) are scarce and isolated. This has important implications for forest management, particularly if dispersal is important. The gradual loss of traditional coppicing practices in a great number of ancient woodlands in Britain could lead to a decrease in the species abundance by reducing the number of colonizable patches (Barkham 1992b).

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