

# Selection on floral display in insect-pollinated *Primula farinosa*: effects of vegetation height and litter accumulation

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**Abstract** Grazing reduces litter thickness and vegetation height and may thereby indirectly affect reproductive success and selection on floral characters in plants with prostrate growth. Reductions in litter thickness and vegetation height should influence both the resource status of plants with leaves positioned close to the ground and the significance of inflorescence height for interactions with pollinators and seed predators. We experimentally examined how simulated grazing of surrounding vegetation affected pollen limitation, fruit predation and fecundity of short-scaped and long-scaped *Primula farinosa*, which differ markedly in floral display and therefore in expected attractiveness to pollinators. Litter removal and pruning of surrounding vegetation increased fruit and seed production per plant in the year of the treatment and the probability of flowering in the following year. Pollen limitation of fruit and seed production was stronger in the short-scaped morph than in the long-scaped morph, but was not significantly affected by litter removal and simu-

lated grazing of surrounding vegetation. Supplemental hand-pollination reduced seed size in the year of the treatment and flowering probability in the second year, and these effects did not differ among scape morphs or grazing treatments. The results suggest that grazing indirectly favours seed production in *P. farinosa*, mainly because it increases the resource status of plants that escape damage. Contrary to expectation, there was no strong evidence that litter accumulation and tall vegetation increase the severity of pollen limitation or reduce the relative performance of the short-scaped morph.

**Keywords** Biotic interactions · Herbivory · Pollination · *Primula farinosa* · Seed production

## Introduction

Plant reproductive success and the evolution of floral display are affected by interactions with both mutualists and antagonists, and these effects are not necessarily additive. The production of a prominent floral display, in terms of many and large flowers, may increase attractiveness to pollinators and pollination success (e.g. Galen 1989; Schemske and Ågren 1995; Campbell 1996; Shykoff et al. 1997; Vaughton and Ramsey 1998), but may also increase the risk of damage from grazers (Ehrlén 1997), seed predators (Galen and Cuba 2001; Leimu et al. 2002; Cariveau et al. 2004) and pollinator-transmitted fungal pathogens (Collin et al. 2002; Giles et al. 2006). The outcome of multiple interactions should depend on their respective strengths, and whether they are additive or nonadditive (cf. Herrera 2000; Gómez 2003). Thus, to assess the

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consequences of a given biotic interaction for variation in plant reproductive success, both direct and indirect effects should be considered.

Grazers can affect plant reproductive success and selection on floral display both directly through selective damage to floral parts and indirectly by their effects on resource availability and the context of interactions with mutualists and antagonists. For example, grazing may favour plants with a leaf-rossette or a short inflorescence because such plants have both a higher chance of escaping grazing damage (Lavorel et al. 1997; Diaz et al. 2001; Louault et al. 2005), and may experience a higher resource availability and increased pollination success in grazed habitats compared to ungrazed habitats. Grazing reduces vegetation height and litter accumulation. It will thus increase light levels close to the ground and may also indirectly increase nutrient availability to ungrazed plants. Moreover, a reduction in vegetation height and litter accumulation should increase their visibility to pollinators and may reduce the pollen limitation of plants with a short inflorescence (cf. O'Connell and Johnston 1998; Ehrlén et al. 2002). However, little is known about the importance of such indirect effects of grazing on plant reproductive success and selection on floral traits.

To assess the context-dependence of seed output and trait selection in perennial plants, it is essential to consider not only effects on current seed production, but also potential demographic costs associated with increases in seed formation (Obeso 2002; Ashman and Morgan 2004). The effects of an increase in seed production on future survival and reproduction should depend on whether it is due to a change in pollination intensity or a change in resource availability. An increase in reproductive output caused by higher pollen deposition might draw upon resources for future reproductive events and result in a reproduction cost (e.g. Montalvo and Ackerman 1987; Primack and Hall 1990; Ehrlén 1992). In contrast, an increase in reproductive output caused by greater resource availability is not likely to reduce future survival or reproduction.

We examined indirect effects of grazing on reproductive output and selection on inflorescence height in the rosette-forming, perennial herb *Primula farinosa* by experimentally simulating grazing of surrounding vegetation. *P. farinosa* is a small distylous, self-incompatible, insect-pollinated herb with a basal leaf-rossette. In semi-natural grasslands on the large island of Öland, southeast Sweden, *P. farinosa* occurs in two distinct scape morphs. In the long-scaped morph, the inflorescence is displayed well above the soil surface, while in the short-scaped morph it is positioned very close to the ground. This difference in floral display influences

the risk of grazing damage. In a survey of 52 populations, the frequency of plants whose inflorescence was damaged by grazers was markedly higher among long-scaped plants than among short scaped plants (means  $\pm$  SE based on population means,  $17.1 \pm 3.2\%$  vs.  $3.5 \pm 1.0\%$ ; J. Ågren and J. Ehrlén, unpublished data). Scape length also influences pollination success and seed predation (Ehrlén et al. 2002; Toräng et al. 2006; Vanhoenacker et al. 2006). The importance of a tall inflorescence for attractiveness to pollinators should increase with litter accumulation and increasing height of the surrounding vegetation. In a previous study, the short-scaped morph was more pollen-limited than the long-scaped morph, and this difference was larger in tall than in short vegetation (Ehrlén et al. 2002). Vegetation height and thickness of the litter layer should also influence the amount of light that reaches the leaf rosette, but this effect is not likely to differ between scape morphs.

We combined litter removal and cutting of surrounding vegetation with supplemental hand-pollination of long-scaped and short-scaped *P. farinosa* in order to examine the following hypotheses: (1) litter removal and cutting of surrounding vegetation increase resource availability and result in an increased seed output, at least in plants receiving full pollination; (2) litter removal and cutting of surrounding vegetation reduce pollen limitation and increase seed predation, and these effects are stronger in short-scaped plants than in long-scaped plants, and; (3) an increase in seed production caused by augmented pollination is associated with a demographic cost, while an increase in seed production caused by an increase in resource availability is not discounted by reduced future reproduction.

## Materials and methods

### Study species

*Primula farinosa* (Primulaceae), Bird's-eye Primrose, is a hermaphroditic, self-incompatible, distylous, perennial herb found primarily on lime-rich moist meadows (Hamblen and Dixon 2003). It is distributed in Europe from central Sweden and Scotland to central Spain and Bulgaria (Tutin et al. 1972). In Sweden, *P. farinosa* is most abundant on the large Baltic island of Öland (Ekstam et al. 1984), where it is usually found in *Sesleria caerulea* and *Carex hostiana* meadows (Sterner 1986). The persistence of *P. farinosa* populations is favoured by grazing and mowing, and the occurrence of *P. farinosa* has declined over the last

century because of changes in land use (Ekstam et al. 1984; Sterner 1986; Lindborg and Ehrlén 2002).

*Primula farinosa* produces leaves in a basal rosette and 3–12 pink flowers in a single umbel. The number of inflorescences per basal rosette is normally one, but occasionally rises up to three. In the study area, scape length is clearly bimodally distributed (Ehrlén et al. 2002). Plants are either long-scaped with a 2–20 cm-long, slender scape, or short-scaped with a 0–3 cm-long, relatively thick striate scape. Crossing experiments suggest a simple Mendelian inheritance of scape morphology, with a dominant allele for short scape (J. Ågren and J. Ehrlén, unpublished data).

*Primula farinosa* flowers in May and early June. In the study area, *P. farinosa* is pollinated mainly by butterflies (especially *Pyrgus malvae*) and solitary bees (especially *Osmia bicolor*). The fruit is a multiseeded capsule, which matures in early- to mid-July. Entire inflorescences can be consumed or damaged because of trampling by domesticated grazers (cattle, sheep and horses). Flowers and fruits can be damaged by molluscs, and initiated fruits are often attacked by the larvae of the moth *Falseuncaria ruficiliana* (Lepidoptera: Tortricidae). Fruits may also be infected by the smut fungus *Urocystis primulicola*.

#### Study area

The field experiment was conducted at Norra Bäck, just north of Stora Alvaret on southern Öland, Sweden, in 2003. The site is characterised by relatively thick soils on limestone rock and has a sparse shrub layer that consists mainly of *Juniperus communis*. The site is grazed, although the intensity of grazing has been relatively low in recent years, allowing a build-up of litter. The study population consisted of several thousand flowering individuals and had a relatively even ratio of short-scaped to long-scaped plants.

#### Field experiment

To examine the three hypotheses, a factorial design including scape morph (long versus short), litter removal and cutting (litter removed and vegetation cut around the focal plant versus control) and pollination (supplemental hand-pollination versus open-pollinated control) was used. A total of 416 plants, 208 short-scaped and 208 long-scaped, were marked with green numbered plastic sticks stuck in the ground. Only long-styled plants were used, as short-styled plants are difficult to pollinate by hand without damaging the flowers. Fecundity did not differ between style morphs in a previous study (Ehrlén et al. 2002).

Moreover, only plants with a single inflorescence were included in the experiment. We took particular care to achieve equal spatial and phenological distributions of the two scape-morphs. The position of each plant was recorded on a map. Plants of respective scape morphs were randomly assigned to one of the four pollination-by-litter-removal-and-cutting treatments, resulting in eight scape-morph-by-treatment combinations with 52 replicates per group.

In the litter removal and cutting treatment, all litter was removed within 10 cm of the focal plant, and within the same area the vegetation was cut to about 1 cm above the ground every second week from flowering to fruit maturation. In the hand-pollination treatment, experimental plants were pollinated by brushing dehiscing anthers across the receptive stigmas. Compatible pollen (i.e. from short-styled plants of both scape morphs) was collected within a radius of 15 m from the focal plant. Each flower received supplemental hand-pollination once during the period of stigma receptivity. For treatments including hand-pollination, but not litter removal and cutting, care was taken to leave the litter layer intact.

#### Data collection and analyses

During flowering, we recorded the number of flowers produced by each plant included in the experiment. Damage to flowers and fruits by slugs was recorded weekly during flowering and thereafter every two weeks up to fruit maturation. At the time of fruit maturation (July), all inflorescences were collected and the number of intact fruits as well as those damaged by seed predators were counted in the laboratory. In up to three intact fruits per individual, we counted the number of fully developed seeds and weighed them. In the year following the experiment, all experimental plants were checked during the flowering period, and the flowering state (flowering or nonflowering) and the number of flowers produced by flowering individuals were recorded.

For each plant, we calculated the mean number of seeds in the intact mature fruits collected. Total seed production per plant was estimated as the product of number of intact fruits and mean number of seeds per fruit. For each fruit, the mean seed mass was calculated as the total seed mass divided by the number of seeds. Mean seed mass of an individual was calculated as the grand mean of fruit mean seed mass.

We used full factorial general linear models to analyse the effects of scape morph, pollination treatment and litter removal and cutting treatment on number of fruits (intact mature fruits and damaged fruits),

number of seeds per fruit and per plant, mean seed mass, total seed mass per plant, and number of flowers in the year following the experiment. Because the number of flowers varied between scape morph  $\times$  treatment combinations, it was included as a covariate in all analyses. Effects on the proportion of plants flowering in the following year were analysed with an analogous generalized linear model with a binomial error distribution and logit link. Number of flowers, fruits and seeds per plant in the year of the experiment and number of flowers in the following year were square-root transformed prior to analysis. The statistical analyses were performed using the SAS statistical package (SAS 2002).

## Results

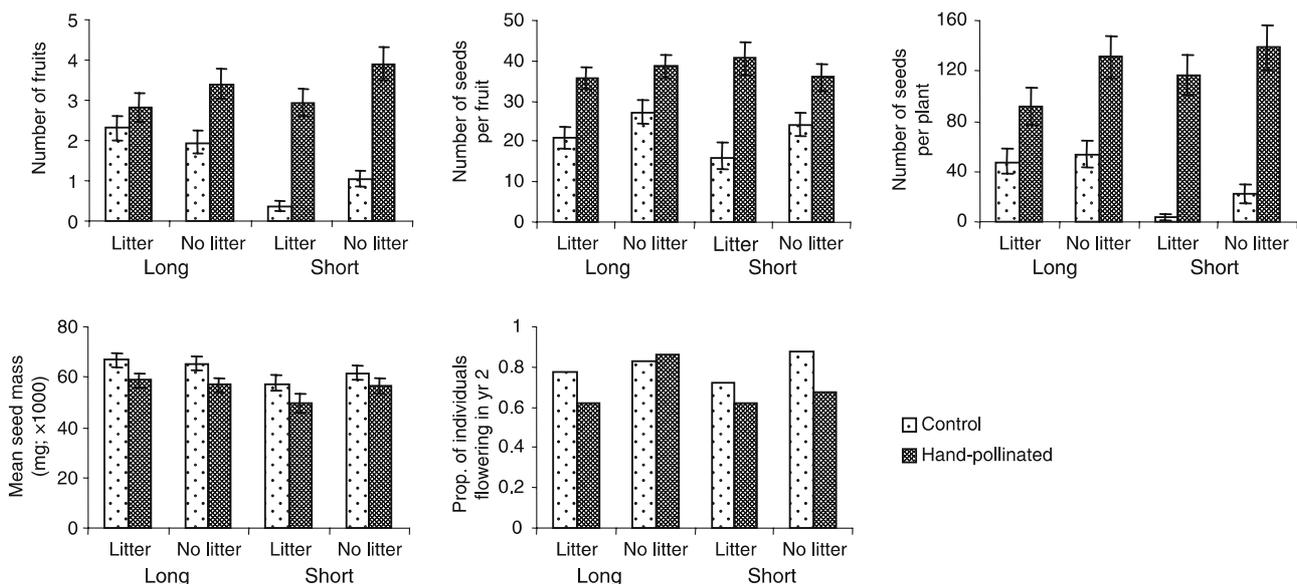
### Components of seed production

Both the grazing treatment and supplemental hand-pollination increased fruit production, and hand-pollination increased also number of seeds per undamaged fruit (Table 1, Fig. 1). The effect of supplemental hand-pollination on fruit production was markedly stronger in the short-scaped than in the long-scaped morph (significant scape morph  $\times$  pollination interaction in the ANCOVA; Table 1, Fig. 1). Seed number per fruit was 1.7 times higher among plants receiving supplemental hand-pollination compared to controls (least-square mean  $\pm$  SE,  $37.7 \pm 1.4$  vs.  $22.0 \pm 1.6$ ; Fig. 1, Table 2).

Floral herbivory and seed predation were low and varied little among experimental treatments. Among long-scaped plants, about 0.8% (range 0–3.1%) of the flowers were consumed by slugs and about 7.4% (5.5–9.3%) of the fruits were attacked by the seed predator *Falceuncaria ruficiliana* (means and ranges based on treatment means). The corresponding figures for short-scaped plants were 1.6% (0.7–2.3%) of flowers and 1.3% (0–3.0%) of fruits. The proportion of fruit-producing plants attacked by *F. ruficiliana* was higher in the long-scaped morph (9%) than in the short-scaped morph (3%;  $\chi^2 = 7.9$ ,  $df = 1$ ,  $P = 0.005$ , in the logistic model which also included number of flowers as an independent variable).

### Total seed production

Litter removal and simulated grazing of surrounding vegetation increased total seed production per plant, but did not strongly influence pollen limitation, which was more severe in the short-scaped morph than in the long-scaped morph. Seed output per plant was about 1.5 times higher in the grazing treatment than in intact vegetation (back-transformed least-square means [95% confidence interval], control 52.7 [42.9–63.6], grazing treatment 77.3 [65.3–90.4]). Pollen-limitation of seed production was markedly more severe in the short-scaped than in the long-scaped morph (Table 1, Fig. 1), but was not strongly affected by the grazing treatment (the scape morph  $\times$  litter  $\times$  pollination interaction only approached statistical significance



**Fig. 1** Fruit production, number of seeds per undamaged fruit and per plant, mean seed mass and proportion of plants flowering in the second year in a field experiment examining the indirect effects of simulated grazing (control versus litter removal and cut-

ting of vegetation), pollination regime (open-pollinated control versus supplemental hand-pollination), and scape morph (long versus short scape) in *Primula farinosa*. Back-transformed least-square means  $\pm$  SE are given ( $n = 26$ –52)

[ $F_{(1,407)} = 2.6, P = 0.10$ ], and the litter  $\times$  pollination interaction was far from significant; Table 1, Fig. 1). In the short-scaped morph, seed output per plant was 12.1 times higher after supplemental hand-pollination, whereas in the long-scaped morph seed output per plant increased by 2.2 times after supplemental hand-pollination (back-transformed least-square means, Fig. 1). Among open-pollinated plants, short-scaped plants produced fewer seeds than long-scaped plants (contrast short-scaped versus long-scaped plants,  $t = 5.2, P < 0.0001$ ), while among plants receiving supplemental hand-pollination no such difference was recorded ( $t = 1.1, P = 0.29$ ).

Seed size

Seed size differed between scape morphs, was reduced by supplemental hand-pollination, but was not affected by

the simulated grazing (Table 2, Fig. 1). Short-scaped plants produced 9% smaller seeds than long-scaped plants, and supplemental hand-pollination reduced mean seed size by about 12% (Fig. 1). The reduction in mean seed mass following supplemental pollination did not balance the positive effect on number of seeds produced. Plants receiving supplemental hand-pollination produced a larger total mass of seeds than open-pollinated plants, and this difference was particularly strong among short-scaped plants (significant scape morph  $\times$  pollination interaction in the ANOVA; Table 2).

Flower production in the year following experimental treatments

Both the grazing treatment and hand-pollination increased seed output in the first year of the experiment, but their effects on the probability of flowering

**Table 1** Effects of scape morph (long versus short), litter removal and cutting of vegetation, and supplemental hand-pollination on fruit production and number of seeds per fruit and per plant,

analysed with ANCOVA models which included square-root number of flowers as covariate

Source of variation	df	Number of fruits <sup>a</sup>		Seeds per fruit		Seeds per plant <sup>a</sup>	
		MS	F	MS	F	MS	F
Sqrt (number of flowers)	1	106.87	232.2***	2,300	6.5*	3,628.0	132.0***
Scape morph	1	14.49	31.5***	162	0.5	230.2	8.4**
Litter removal and cutting	1	5.06	11.0**	765	2.1	243.9	8.9**
Hand-pollination	1	48.27	104.9***	18,783	52.7***	3,350.7	121.9***
Scape $\times$ litter	1	2.75	6.0*	158	0.4	15.6	0.6
Scape $\times$ hand-pollination	1	12.36	26.9***	511	1.4	556.5	20.2***
Litter $\times$ hand-pollination	1	0.03	0.1	1,225	3.4****	1.0	0.04
Scape $\times$ litter $\times$ pollination	1	1.81	2.6	446	1.3	72.8	2.6

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$

\*\*\*\* $P = 0.06$

<sup>a</sup> Square-root transformed prior to analysis

**Table 2** Effects of scape morph (long versus short), litter removal and cutting of vegetation, and supplemental hand pollination on mean seed mass and seed mass per plant, analysed with ANCOVA models which included square-root number of flowers as covariate

Source of variation	df	Mean seed mass		Seed mass per plant	
		MS $\times 10^6$	F	MS	F
Sqrt (number of flowers)	1	64.6	0.2	6,290.9	167.7**
Scape morph	1	2,356.8	6.6*	216.2	5.8*
Litter removal	1	311.3	0.9	556.2	14.8**
Hand-pollination	1	4,046.2	11.3**	2,653.8	70.7**
Scape $\times$ litter	1	1,070.3	3.0	14.2	0.4
Scape $\times$ hand-pollination	1	87.1	0.2	484.6	12.9**
Litter $\times$ hand-pollination	1	15.1	0.04	7.7	0.2
Scape $\times$ litter $\times$ pollination	1	35.9	0.1	9.5	0.3

\* $P < 0.05$

\*\* $P < 0.001$

the following year differed (Table 3, Fig. 1). The proportion of plants producing flowers in the second year increased after litter removal and simulated grazing, but decreased after supplemental hand-pollination. Inspection of the graph indicates that the response to grazing treatment and hand-pollination was not totally consistent among scape morphs, but the scape morph  $\times$  litter  $\times$  pollination interaction only approached statistical significance (Wald  $\chi^2 = 3.2$ ,  $P = 0.07$ ). The number of flowers produced by plants flowering in the second year was positively related to the number of flowers produced in the first year, but was not affected by the grazing treatment or hand-pollination (Table 3).

## Discussion

Grazing reduces litter thickness and vegetation height, and the present study has shown that this translates into increased seed production in the rosette-forming herb *P. farinosa*, which is dimorphic for scape length. Experimental litter removal and pruning of surrounding vegetation increased both seed output in the first year and probability of flowering in the second year. Contrary to expectation, litter removal and cutting of surrounding vegetation did not strongly affect the severity of pollen limitation or selection on scape length. The results suggest that indirect effects of grazing may be important for the viability of *P. farinosa* populations, but that direct effects in terms of differential grazing damage to short- and long-scaped plants

are likely to be more important for selection on scape length and the maintenance of the scape length polymorphism.

Apparently, the simulated grazing of surrounding vegetation increased seed output of *P. farinosa* mainly through increased resource availability. The grazing treatment did not significantly affect the severity of pollen limitation, but increased seed production among both open-pollinated plants and plants receiving supplemental pollination. Moreover, both seed predation and slug damage to fruits were very low and varied little among experimental treatments. Matsumoto et al. (2000) showed that shading by the surrounding vegetation reduced light availability and whole plant carbon gains in the rosette herb *Aster kantoensis*. However, we know of no previous study that has explored the influence of litter accumulation and vegetation height on both resource status and pollination intensity.

The relative reproductive success of long-scaped and short-scaped *P. farinosa* is influenced by several biotic interactions. As expected, pollen limitation of fruit production was stronger in the short-scaped morph than in the long-scaped morph. This is consistent with previous studies of *P. farinosa* (Ehrlén et al. 2002; Vanhoenacker et al. 2006), and with studies of other species that have found indices of pollination success to be positively related to inflorescence height (e.g. Peakall and Handel 1993; Donnelly et al. 1998; O'Connell and Johnston 1998; Totland 2001). Also, seed predation may increase with plant stature (Hainsworth et al. 1984; Traveset 1995; Ehrlén et al. 2002; Cariveau et al. 2004; Toräng et al. 2006). In the present study, the

**Table 3** Effects of scape morph (long versus short), litter removal and cutting of vegetation, and supplemental hand pollination on proportion of plants flowering and the number of flowers produced by flowering plants in the year following the experiment,

Source of variation	df	Proportion flowering in the second year Wald $\chi^2$	Number of flowers in the second year <sup>a</sup>	
			MS	F
Sqrt (number of flowers)	1	0.01	18.433	22.6***
Scape morph	1	0.8	0.514	0.6
Litter removal	1	8.6**	0.536	0.7
Hand-pollination	1	5.0*	2.876	3.5****
Scape $\times$ litter	1	0.2	0.130	0.2
Scape $\times$ hand-pollination	1	1.5	0.031	0.04
Litter $\times$ hand-pollination	1	0.1	0.011	0.01
Scape $\times$ litter $\times$ pollination	1	3.2	0.048	0.06

\* $P < 0.05$

\*\* $P < 0.01$

\*\*\* $P < 0.001$

\*\*\*\* $P = 0.06$

<sup>a</sup> Square-root transformed prior to analysis

analysed with a generalized linear model and an ANCOVA model which included square-root number of flowers in the year of the experiment as covariate

proportion of plants attacked by the seed predator was higher in the long-scaped morph than in the short-scaped morph, but seed predation was very low overall and the higher pollination success of long-scaped plants was not counteracted by the higher probability of fruit predation. Instead, the morph-specific difference in pollen limitation translated into a higher seed production in long-scaped plants.

A previous study demonstrated that the magnitude of the difference in pollen limitation between long- and short-scaped plants of *P. farinosa* can be context-dependent. In that study, which was based on a comparison of two microhabitats in a spatially heterogeneous population, the difference in pollen limitation of fruit initiation between long- and short-scaped *P. farinosa* was significantly larger in tall than in low vegetation (Ehrlén et al. 2002). In the present study, the morph-specific difference in pollen limitation tended to be larger in intact vegetation than when litter had been removed and the surrounding vegetation cut, but this difference only approached statistical significance. The results suggest that the difference in pollination environment between plants in the two grazing treatments was not as large as between plants in low and tall vegetation in the previous study. One reason for this could be that the experimental treatment of the present study created variation in vegetation height at a smaller spatial scale than the natural variation exploited in the study conducted by Ehrlén et al. (2002). Pollinator visitation to plants partly hidden by tall vegetation and litter is likely to be positively affected by the presence of exposed plants close by.

Supplemental hand-pollination increased seed production in the first year, but resulted in reduced seed size and decreased probability of flowering in the second year. This indicates that seed production is associated with a cost, and that an evaluation of the fitness consequences of an increase in pollination intensity needs to take into account both the effects on offspring performance and the relative value of current and future reproduction (cf. Ehrlén and Eriksson 1995). However, the results also suggest that the relative seed output in a single year may be a reasonable estimate of the relative female fecundity of short- and long-scaped plants. First, the flowering propensity in the second year did not differ between scape morphs. Second, seed production was more strongly pollen-limited in the short-scaped morph, but the negative effects of supplemental hand-pollination on mean seed mass and flowering propensity in the following year did not differ significantly between scape morphs.

The grazing treatment increased the seed output of plants receiving supplemental hand-pollination, indicating

that litter removal and pruning of surrounding vegetation increases the pool of resources available for seed development. This increase in seed production did not occur at the expense of future reproduction. Instead, plants in the grazing treatment also had a higher probability of flowering in the second year. The results suggest that the increase in seed production in the grazing treatment was more than balanced by an increase in resource acquisition. Van Noordwijk and de Jong (1986) showed that if variation in available resources is large relative to variation in allocation to reproduction, then this may mask underlying negative correlations and result in a positive relationship between current and future reproduction. Our results imply that if variation in seed production in natural populations of *P. farinosa* is a consequence of variation in pollen deposition, then high seed output should be associated with reduced probability of flowering the following year. In contrast, if variation in seed production is mainly an effect of variation in resource status, no correlation or a positive phenotypic correlation between seed output and flowering propensity in the following year can be expected.

The positive effect of simulated grazing on the reproductive output of *P. farinosa* is consistent with observations that the persistence of local *P. farinosa* populations is favoured by grazing and mowing (Ekstam et al. 1984; Sterner 1986; Lindborg and Ehrlén 2002). Grazing may positively affect population growth in *P. farinosa* for at least a couple of reasons. First, as indicated by the present study, grazing of surrounding vegetation should increase resources available for reproduction. Second, both reduced vegetation height (Lindborg and Ehrlén 2002) and the local disturbance caused by trampling should facilitate seedling establishment.

Grazing should promote the maintenance of the short-scaped morph in *P. farinosa* because short-scaped plants escape grazing damage to a greater extent than long-scaped plants, and because in low vegetation short-scaped plants are also easily detected by pollinators. The results from the present study suggest that positive indirect effects of grazing on the relative performance of the short-scaped morph via decreased litter accumulation and vegetation height are relatively weak. Instead, grazers are likely to influence the relative fitness of the short-scaped morph mainly because of the differential grazing damage to short- and long-scaped plants.

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