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FACILITATION IN AN INSECT-POLLINATED HERB WITH A FLORAL DISPLAY DIMORPHISM

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Abstract. Population context should influence pollination success and selection on floral display in animal-pollinated plants because attraction of pollinators depends not only on the characteristics of individual plants, but also on the attractiveness of co-occurring conspecifics. The insect-pollinated herb *Primula farinosa* is polymorphic for inflorescence height. Natural populations may include both long-scaped plants, which present their flowers well above the soil surface, and short-scaped plants, with their flowers positioned close to the ground. We experimentally tested whether seed production in short-scaped *P. farinosa* varied with local morph frequency and surrounding vegetation height. In tall vegetation, short-scaped plants in polymorphic populations produced more fruit and tended to produce more seeds than short-scaped plants did in monomorphic populations. In low vegetation, population composition did not significantly affect fruit and seed output of short-scaped plants. The results suggest that long-scaped plants facilitate short-scaped plants in terms of pollinator attraction and that the facilitation effect is contingent on the height of the surrounding vegetation. The documented facilitation should contribute to the maintenance of the scape length polymorphism in ungrazed areas where litter accumulates and vegetation grows tall.

Key words: alternative reproductive strategies; facilitation; floral display; plant height; pollination; positive interactions; predation; Primula farinosa.

Introduction

In plants, the production of a large floral display may increase attractiveness to pollinators, but also increase the risk of damage from seed predators (Molau et al. 1989, Galen and Cuba 2001, Leimu et al. 2002), fungal pathogens (Elmqvist et al. 1993), and grazers (Ehrlén 1997). Under conflicting selection pressures, alternative reproductive strategies may develop, and such alternative strategies can be maintained by frequency-dependent (Subramaniam and Rausher 2000) or environment-dependent selection (Ellner and Hairston 1994). For example, risk-taking strategies and safe strategies can coexist in the presence of sexually transmitted diseases (Boots and Knell 2002).

Many pollinators and antagonists are attracted by visual cues; the number, size, and arrangement of flowers are important for attractiveness both to pollinators and seed predators. Visitation rates of pollinators (Hainsworth et al. 1984, Peakall and Handel 1993, Donnelly et al. 1998, O'Connell and Johnston 1998, Lortie and Aarssen 1999) and seed predators (Ehrlén et al. 2002, Cariveau et al. 2004) have been found to be positively related to plant stature. The importance of plant stature for attraction of pollinators and seed predators should depend on the height of the surrounding vegetation. In low vegetation, even very short plants are easily detected, whereas the same plants can be expected to have low visitation rates in areas with tall vegetation.

Neighboring plants may either compete with or facilitate each other in terms of pollinator services (Callaway 1995). Empirical studies have documented both negative (Chittka and Shürkens 2001, Brown et al. 2002) and positive interspecific interactions (Thompson 1978, Laverty 1992, Alexandersson and Ågren 1996, Johnson et al. 2003, Moeller 2004). Studies of intraspecific interactions have often focused on effects of population size and density on pollination success (Sih and Baltus 1987, Ågren 1996, Kunin 1997, Ehlers et al. 2002, Waites and Ågren 2004), while studies considering characteristics of neighboring plants and population

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composition are scarce (but see Gigord et al. 2001 for an example of frequency-dependent selection on flower color mediated by pollinators). However, both within and between species, tall conspicuous plants could act as beacons (Fægri and van der Pijl 1979) that attract pollinators and seed predators, and thus influence the reproductive success of shorter, less conspicuous neighbors. If positive interactions dominate, then this may promote the maintenance of variation in plant stature and attractiveness to pollinators.

We examined whether the stature of neighboring conspecific plants affects the reproductive success of short-scaped individuals in *Primula farinosa* L. growing in low and tall vegetation. This plant is polymorphic for scape length. Individual plants produce either a regular 2–20 cm long scape or a markedly thicker and striate 0–3 cm short scape. As a result, the umbel-like inflorescence is either displayed well above the soil surface or very close to the ground. This difference in floral display can be expected to influence attractiveness to pollinators that forage with the aid of visual cues; however, it may also influence the attractiveness to seed predators and the risk of damage from grazers. Moreover, differences between the two scape morphs in the attractiveness to pollinators and seed predators should be greater in tall than in low vegetation (Ehrlén et al. 2002).

We manipulated the local scape morph frequency and determined the effect on fruit and seed production in short-scaped *P. farinosa*. More specifically, we tested the predictions that (1) short-scaped plants in polymorphic populations, i.e., with long-scaped neighbors, have greater fruit and seed set than short-scaped plants in monomorphic populations, i.e., with short-scaped neighbors only, and (2) that this difference is more pronounced in tall than in low vegetation. We also examined whether (3) short-scaped plants in polymorphic populations experience a higher risk of seed predation than short-scaped plants in monomorphic populations.

Methods

Study species

Primula farinosa L. (Primulaceae) is a hermaphroditic, self-incompatible, perennial herb (Hambler and Dixon 2003). Like many other *Primula* species, it is distylous, i.e., flowers are either long-styled (pin morph) or short-styled (thrum morph). Populations on the islands Öland and Gotland, off the southeast coast of Sweden, also harbor a scape-length polymorphism. These populations include both regular, long-scaped plants and a short-scaped morph local to the island (Lagerberg 1948). *Primula farinosa* occurs in moist meadow vegetation on calcareous ground and its persistence at a given site is favored by grazing (Sterner 1986, Lindborg and Ehrlén 2002). Flowers are arranged in an umbel at the top of a scape, and flowering takes place in May. In the study area, a pasture near the Ecological Field Station of Uppsala University on Öland (56°37′ N, 16°29′ E), butterflies (especially *Pyrgus malvae*) and solitary bees (especially *Osmia bicolor*) are the main pollinators. The fruit is a multi-seeded capsule that matures in July. Initiated fruits are often attacked by larvae of the small tortricid moth *Falseuncaria ruficiliana*, and the entire inflorescence is sometimes eaten by domesticated grazers (cattle, sheep, and horses).

Experimental setup

We manipulated vegetation height and population composition of 40 experimental populations consisting of 8 plants each. In early May, prior to flowering, plants were dug up from natural populations and kept in pots. When the plants began to flower, they were allocated to one of the experimental populations. Populations were distributed randomly at nodes in a rectangular grid that contained 100 nodes separated by 30 m in the pasture near the Ecological Field Station. Each experimental population included four focal short-scaped plants (two pin and two thrum) in a quadratic array with plants spread 0.4 m apart, and was subjected to one of four treatment combinations. To manipulate population composition, we added either four short- or four long-scaped plants interspersed with the four focal short-scaped plants in each population. Scape lengths ranged from 0 to 3 cm for short plants and from 6 to 15 cm for long plants, i.e., well within the range observed in natural populations. The style-morph ratio was even in all experimental populations. In half of the populations, the surrounding vegetation was kept low throughout the experiment by clipping every three to four days; in half of the populations, vegetation was left intact and litter initially added. Vegetation height was <2 cm in low vegetation populations and >6 cm in tall vegetation populations. In natural populations, mean vegetation height varies from 2 to 18 cm during flowering ($N = 72$ populations on Öland). The low vegetation and tall vegetation treatments simulated intense grazing and absence of grazing, respectively. Each treatment combination (population composition $\times$ vegetation height) was replicated ten times. During flowering, we recorded the number of flowers produced by each plant. In mid-July, when fruits were almost fully developed, the entire inflorescence was harvested and brought to the laboratory. For each focal short-scaped plant, and for each of the long-scaped plants in polymorphic populations, we recorded the number of mature fruits (including fruits damaged by seed predators) and total seed production. Twenty-four plants were damaged by drought or by grazing or trampling by cows and were removed from further analyses.

Statistical analyses

We examined the effects of vegetation height (low vs. tall) and population composition (monomorphic vs.

TABLE 1. Effects of number of flowers, vegetation height (low vs. tall), and population composition (monomorphic vs. polymorphic populations) on fruit and seed numbers in the short-scaped morph of *Primula farinosa* in a field experiment on the island Öland, Sweden.

Source of variation	Fruits per plant		Seeds per fruit		Seeds per plant	
	MS	$F_{1,34}$	MS	$F_{1,31}$	MS	$F_{1,34}$
Number of flowers	1.79	5.78*	0.40	0.89	14.1	6.38*
Vegetation height	4.34	14.0***	2.71	6.07*	18.5	8.35**
Population composition	0.30	0.98	0.00	0.01	0.14	0.06
Vegetation height × population composition	1.32	4.28*	0.02	0.05	12.3	5.56*

Notes: Effects were tested with ANCOVA on mean values per population. Fruits per plant, seeds per undamaged fruit, seeds per plant, and number of flowers were $\log_e$-transformed prior to analysis. Nonsignificant interactions terms ($P > 0.1$) were sequentially removed from a full model. Mean square and F values corresponding to statistically significant effects are indicated by asterisks.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

polymorphic) on mean fruit production, mean number of seeds per undamaged fruit, and mean number of seeds per plant among focal short-scaped plants. We also examined the effects of scape morph (short vs. long) and vegetation height (low vs. tall) on the same response variables in polymorphic populations. Plants had more flowers in low (mean = 9.4 flowers) than in tall (mean = 7.7 flowers) vegetation, and flower number was therefore included as covariate in all analyses. A full model was fitted to the data and then stepwise simplified to a minimal adequate model by sequentially removing nonsignificant ($P > 0.1$ in all cases) interactions involving the covariate from the full model, starting from the highest order interaction terms (Crawley 2002). Number of flowers, number of fruits, and number of seeds per fruit and per plant were $\log_e$-transformed prior to analysis.

We used Fisher's exact test to examine whether the proportion of short-scaped plants attacked by seed predators differed between monomorphic and polymorphic populations. We also tested whether the proportion of attacked plants differed between scape morphs in polymorphic populations and between low and tall vegetation for short-scaped and long-scaped plants, respectively. Statistical analyses were performed with Statistica software (StatSoft 2005).

RESULTS

Fruit and seed production of short-scaped plants was affected by population composition in tall, but not in low, vegetation. In tall vegetation, short-scaped plants produced more fruits and tended to produce more seeds in polymorphic populations than in monomorphic populations (significant vegetation height × population composition interactions in ANCOVA; see Table 1). Results of contrasts between polymorphic and monomorphic populations in tall vegetation were as follows: $\log_e$(number of fruits), 0.92 ± 0.18 vs. 0.36 ± 0.19 (least-square mean ± SE), $F_{1,34} = 4.69$, $P < 0.05$; $\log_e$(number of seeds), $F_{1,34} = 3.45$, $P < 0.08$ (see Fig. 1). In contrast, in low vegetation, population composition did not affect fruit or seed production of short-scaped plants ($P > 0.1$). Short-scaped plants produced more seeds per undamaged fruit in low than in tall vegetation ($\log_e$[number of seeds per fruit] was 3.39 ± 0.15 vs. 2.81 ± 0.17; Table 1), but seed output per undamaged fruit did not differ between monomorphic and polymorphic populations. Seed predation was low among short-scaped plants and did not differ between monomorphic (7% of plants attacked, $N = 76$ plants) and polymorphic (5%, $N = 74$) populations (Fisher's exact test, $P = 1.0$).

In polymorphic populations, the long-scaped morph tended to produce more fruits than the short-scaped morph (ANCOVA, $\log_e$[number of fruits] was 1.39 ± 0.12 vs. 1.06 ± 0.12, $F_{1,35} = 3.54$, $P < 0.07$), but it was also subject to more intense seed predation, and seed output per plant did not differ significantly between scape morphs. In polymorphic populations, the percentage of plants attacked by seed predators was five times higher among long-scaped plants (25%, $N = 67$) than among short-scaped (5%, $N = 74$) plants (Fisher's exact test, $P = 0.005$). Long-scaped plants were attacked to a similar extent in low and tall vegetation (Fisher's exact test, $P = 0.15$), whereas all attacked short-scaped plants grew in low vegetation (Fisher's exact test, $P = 0.003$). Most seeds on attacked plants were consumed by the seed predators.

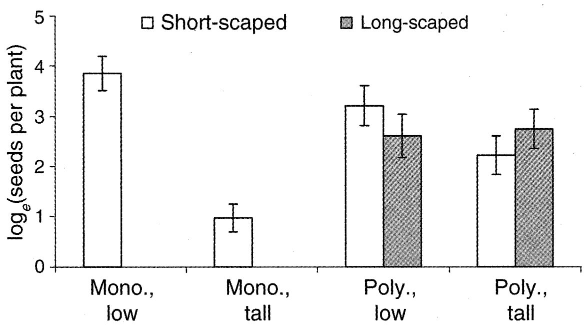

FIG. 1. Effects of vegetation height (low vs. tall) and population composition (monomorphic vs. polymorphic) on the number of seeds ($\log_e$-transformed) produced by short-scaped (open bars) and long-scaped (filled bars) *Primula farinosa* in a field experiment on the island Öland, Sweden. Means are based on population means. Error bars indicate standard errors ($N = 9$–10).

Overall, the number of seeds per undamaged fruit and the number of seeds per plant did not differ between scape morphs (ANCOVA, $\log_e$[number of seeds per undamaged fruit] was 2.78 ± 0.35 vs. 2.57 ± 0.35, $F_{1,33} = 0.52$, $P > 0.1$; $\log_e$[number of seeds per plant] was 3.29 ± 0.18 vs. 3.07 ± 0.18, $F_{1,35} = 0.17$, $P > 0.1$; Fig. 1). Apparently, higher fruit initiation in the long-scaped morph was balanced by higher risk of seed predation. Among undamaged plants, the long-scaped morph produced more seeds than the short-scaped morph, both in low and tall vegetation ($F_{1,34} = 4.46$, $P < 0.05$).

Discussion

The results of the present study suggest that tall plants facilitate short plants in terms of pollinator attraction, and that the facilitation effect is contingent on the height of the surrounding vegetation. More specifically, they indicate that in tall vegetation, the reproductive success of short-scaped *P. farinosa* is higher in polymorphic than in monomorphic populations. The presence of long-scaped plants should thus promote the persistence of short-scaped plants in ungrazed areas, where litter accumulates and vegetation grows tall.

The facilitation provided by long-scaped plants was probably due to effects on pollinator visitation. Previous studies have shown that seed production is more strongly pollen-limited in short-scaped plants compared to long-scaped plants (Ehrlén et al. 2002, Vanhoenacker et al. 2006). Moreover, in the present study, seed abortion was very low and did not vary between treatments (data not shown), suggesting that variation in pollination intensity, rather than in resource availability, caused the observed differences in fruit and seed production. Short-scaped plants are highly exposed in short vegetation but concealed in tall vegetation, whereas long-scaped plants are usually easy to detect regardless of vegetation height. Our results are consistent with the notion that long-scaped plants attract pollinators to polymorphic populations, while, to a large extent, monomorphic short-scaped populations in tall vegetation remain undetected by pollinators.

Pre-dispersal seed predators can be attracted to plants by the same visual cues as pollinators. Seed predators attacked short-scaped plants only in low vegetation, whereas long-scaped plants were attacked regardless of vegetation height. Long-scaped plants were much more likely to be attacked than short, but the population composition did not influence the percentage of short-scaped plants attacked.

Our results suggest that the positive effects of long-scaped plants' increased attractiveness to pollinators are counteracted by the negative effects of increased seed predation, which is in agreement with a previous study conducted on a natural *P. farinosa* population (Ehrlén et al. 2002). Seed output did not differ between scape morphs in polymorphic populations.

The reproductive strategy of the short-scaped morph shows similarities with the "sneaky" mating strategy described for some animals (e.g., Gross 1996). Short-scaped plants avoid costs associated with the production of a tall, attractive inflorescence, such as a high risk of grazing and seed predation, and apparently they do not suffer much from pollen limitation when they grow next to long-scaped neighbors. Moreover, similar to "sneaky" animals, the strategy is not fixed in natural populations; the present study suggests that the reproductive success of short-scaped plants is negatively frequency dependent. However, in contrast to "sneaky" animals, such as satellite male field crickets that choose to interfere with females close to calling males (Cade 1979, Walker and Cade 2003), plants cannot choose their location.

The relative reproductive success of long-scaped and short-scaped plants is likely to be context dependent. The short-scaped morph of *P. farinosa* can be expected to produce more seeds than the long-scaped morph in well-grazed pastures because, under these conditions, it is visible to pollinators, and tall inflorescences are frequently eaten. In contrast, in less intensively grazed areas, the long-scaped morph may have a higher seed output because seed production in the short-scaped morph is more strongly pollen-limited in tall vegetation, and the risk of grazing damage is reduced. In a landscape changing over time, the optimal strategy will vary. The positive, indirect interaction documented in the present study suggests that intraspecific scape morph diversity can be important for the long-term survival of populations. In periods with low grazing intensities, the presence of long-scaped plants may enhance pollinator visitation to the short-scaped morph, which should promote the maintenance of the scape-length polymorphism.

In most plant species, stature is not a discrete character, as in *P. farinosa*, but a continuous trait. However, short plants may generally benefit from the presence of tall, conspicuous neighbors, especially in tall vegetation. Facilitation and the frequency and environmental dependence of the relationship between plant height and reproductive success are readily testable in natural plant populations. Positive interactions may promote coexistence of alternative reproductive strategies in many systems with both discrete and continuous trait variation.

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Literature Cited

Ågren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology **77**:1779–1790.

Alexandersson, R., and J. Ågren. 1996. Population size, pollinator visitation and fruit production in the deceptive orchid *Calypso bulbosa*. Oecologia **107**:533–540.

Boots, M., and R. J. Knell. 2002. The evolution of risky behaviour in the presence of a sexually transmitted disease. Proceedings of the Royal Society B **269**:585–589.

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology **83**:2328–2336.

Cade, W. 1979. The evolution of alternative male reproductive strategies in field crickets. Pages 343–379 *in* M. S. Blum and N. A. Blum, editors. Sexual selection and reproductive competition in insects. Academic Press, New York, New York, USA.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review **61**:306–349.

Cariveau, D., R. E. Irwin, A. K. Brody, L. S. Garcia-Mayeya, and A. von der Ohe. 2004. Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. Oikos **104**:15–26.

Chittka, L., and S. Shürkens. 2001. Successful invasion of a floral market. Nature **411**:653.

Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-plus. Wiley, Chichester, UK.

Donnelly, S. E., C. J. Lortie, and L. W. Aarssen. 1998. Pollination in *Verbascum thapsus* (Scrophulariaceae): the advantage of being tall. American Journal of Botany **85**: 1618–1625.

Ehlers, B. K., J. M. Olesen, and J. Ågren. 2002. Floral morphology and reproductive success in the orchid *Epipactis helleborine*: regional and local across-habitat variation. Plant Systematics and Evolution **236**:19–32.

Ehrlén, J. 1997. Risk of grazing and flower number in a perennial plant. Oikos **80**:428–434.

Ehrlén, J., S. Käck, and J. Ågren. 2002. Pollen limitation, seed predation and scape length in *Primula farinosa*. Oikos **97**:45–51.

Ellner, S., and N. G. Hairston. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. American Naturalist **143**:403–417.

Elmqvist, T., D. Liu, U. Carlsson, and B. E. Giles. 1993. Anther-smut infection in *Silene dioica*: variation in floral morphology and patterns of spore deposition. Oikos **68**:207–216.

Fægri, K., and L. van der Pijl. 1979. The principles of pollination ecology. Third edition. Pergamon Press, Oxford, UK.

Galen, C., and J. Cuba. 2001. Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. Evolution **55**:1963–1971.

Gigord, L. D., M. R. Macnair, and A. Smithson. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soò. Evolution **98**:6253–6255.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution **11**:92–98.

Hainsworth, F. R., L. L. Wolf, and T. Mercier. 1984. Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. Oecologia **63**:405–409.

Hambler, D. J., and J. M. Dixon. 2003. *Primula farinosa* L. Journal of Ecology **91**:694–705.

Johnson, S. D., C. I. Peter, L. A. Nilsson, and J. Ågren. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. Ecology **84**:2919–2927.

Kunin, W. E. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology **85**:225–234.

Lagerberg, T. 1948. Vilda växter i Norden. Second edition. Natur och Kultur, Stockholm, Sweden.

Laverty, T. M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia **89**:502–508.

Leimu, R., K. Syrjänen, J. Ehrlén, and K. Lehtilä. 2002. Pre-dispersal seed predation in *Primula veris*: among-population variation in damage intensity and selection on flower number. Oecologia **133**:510–516.

Lindborg, R., and J. Ehrlén. 2002. Evaluating the extinction risk of a perennial herb: demographic data versus historical records. Conservation Biology **16**:683–690.

Lortie, C. J., and L. W. Aarssen. 1999. The advantage of being tall: higher flowers receive more pollen in *Verbascum thapsus* L. (Scrophulariaceae). Ecoscience **6**:68–71.

Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. Ecology **85**:3289–3301.

Molau, U., B. Eriksen, and J. T. Knudsen. 1989. Predispersal seed predation in *Bartsia alpina*. Oecologia **81**:181–185.

O'Connell, L. M., and M. O. Johnston. 1998. Male and female pollination success in a deceptive orchid, a selection study. Ecology **79**:1246–1260.

Peakall, R., and S. N. Handel. 1993. Pollinators discriminate among floral heights of a sexually deceptive orchid: implications for selection. Evolution **47**:1681–1687.

Sih, A., and M. S. Baltus. 1987. Patch size, pollinator behaviour, and pollinator limitation in catnip. Ecology **68**: 1679–1690.

StatSoft. 2005. STATISTICA (data analysis software system), version 7.1. ⟨www.statsoft.com⟩

Sterner, R. 1986. Ölands kärlväxtflora. Second edition. Forskningsrådens förlagstjänst, Stockholm, Sweden.

Subramaniam, B., and M. Rausher. 2000. Balancing selection on a floral polymorphism. Evolution **54**:691–695.

Thomson, J. D. 1978. Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. American Midland Naturalist **100**:431–440.

Vanhoenacker, D., J. Ågren, and J. Ehrlén. 2006. Spatio-temporal variation in pollen limitation and reproductive success of two scape morphs in *Primula farinosa*. New Phytologist **169**:615–621.

Waites, A. R., and J. Ågren. 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in *Lythrum salicaria*. Journal of Ecology **92**:512–526.

Walker, S. E., and W. H. Cade. 2003. A simulation model of the effects of frequency dependence, density dependence and parasitoid flies on the fitness of male field crickets. Ecological Modeling **169**:119–130.