POLLINATION BIOLOGY OF *SILENE SPALDINGII*

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Summary

Silene spaldingii is a partially self-compatible perennial plant found in the Palouse region of Washington, Idaho and Oregon and disjunct in northwest Montana. It is listed as threatened or endangered in all four states in which it occurs. We observed pollinators of *S. spaldingii* for ≥20 hrs at each of five sites throughout the range of the species. A bumblebee, *Bombus fervidus*, accounted for ≥83% of pollination bouts at all sites. Eleven of 13 *B. fervidus* collected bore pollen of *S. spaldingii*. The mean number of visits per flower per day varied from 0.3 to 21.2. The mean proportion of aborted fruits varied between 0.08 and 0.31, and there was a significant negative correlation between the rate of flower visitation and the rate of abortion ($r=0.39$, $P<0.001$). There was a tendency for pollinator constancy and visitation rates to be lower at sites with larger displays of flowers that compete for *B. fervidus* service. The exotic weed, *Hypericum perforatum* was an important competitor at one site. Our results suggest that small, isolated populations of *S. spaldingii* may not persist, while most larger populations are not threatened by pollinator limitation assuming *B. fervidus* is protected from pesticide application and high fire frequencies.

Introduction

Many species of obligate outcrossing plants require pollination by insects for sexual reproduction (Faegri and van der Pijl 1971, Richards 1986). Although many outcrossing species are capable of self-fertilization (facultative self-compatibility), selfing often results in lower fecundity and suboptimal progeny due to inbreeding depression (Schemske and Lande 1985).

Thus, pollinators are important for maintaining the health of many populations of outcrossing plants (Lesica 1993, Macior 1982).

Silene spaldingii is a partially self-compatible perennial endemic to the Palouse region of southeast Washington and adjacent Oregon and Idaho and is disjunct in northwest Montana (Hitchcock and Maguire 1947). Much of the habitat of *S. spaldingii* has been lost to agricultural development. Although once widespread in the Palouse region, *S. spaldingii* is now known from mainly isolated sites on the periphery of its former range. Most remaining populations are small and threatened by exotic weed encroachment, livestock grazing, and herbicide treatment (Gamon 1991, Lorain 1991, Schassberger 1988). *Silene spaldingii* is listed as threatened or endangered in all four states in which it occurs (Lesica and Shelly 1991). The purpose of this study is to determine the principal pollinator(s) of *S. spaldingii* throughout its geographic range and assess the likelihood and effects of pollinator limitation.

Species description

Silene spaldingii Wats. (Caryophyllaceae) is a partially self-compatible, hermaphroditic, perennial taprooted herb, 20-40 cm tall. Rhizomes or other means of vegetative propagation are lacking (Hitchcock and Maguire 1947, Lesica observation); reproduction is apparently by seed only. The perfect flowers are 1-2 cm long with white petals that are mostly concealed by the green calyx. Three to twenty flowers are borne at the top of the stem in a sparingly branched, terminal, cymose inflorescence. Flowers are held horizontally in flower, but become erect as the fruit matures. Fruits are dehiscent capsules containing up to 150 seeds. Seeds require stratification, so germination occurs mainly in the spring. Rosettes are formed the first year, and

flowering may occur during or after the second season. Examination of numerous flowers over the course of many years indicates that *Silene spaldingii* is protandrous. Anthers mature and dehisce pollen first. During this time, the styles are unexpanded, and the unexposed stigmatic surfaces are held well below the level of the anthers. After anthers have shed most of their pollen, they shrivel and fall from the filaments. At this time the three styles expand in length, and the stigmas spread apart and become receptive. Each open flower persists for two to several days, and two or more flowers may be in bloom on the same plant, so geitonogamous pollination is possible. This system promotes outcrossing while allowing the possibility of selfing (Lesica 1993).

Study sites

We observed *Silene spaldingii* pollination at the five sites described below.

Dancing Prairie Preserve is 6 km north of Eureka in Lincoln Co., Montana. Elevation is 825 m; mean January and July temperatures are -6.8 and 17.7° C respectively; and mean annual precipitation is 438 mm (Fortine). The population of *S. spaldingii* is estimated to be greater than 10,000 plants over ca. 100 ha. Grasslands are dominated by *Festuca scabrella, F. idahoensis* and *Agropyron spicatum*. Flowering forbs visited by bumblebees at the time of the study include *Calochortus macrocarpus, Campanula rotundifolia, Cirsium undulatum, Hieracium cynoglossoides, Monarda fistulosa*, and *Geranium viscosissimum*. Most of these species were in flower and common in the study area. Observations at this site were part of a study on the relationship between pollination and fitness in *S. spaldingii* (Lesica 1993).

Sprague is 3 km southwest of Sprague in Lincoln Co., Washington. Elevation is 600 m; mean January and July temperatures are -3.1 and 20.4° C respectively; and mean annual precipitation is 375 mm (Sprague). The population of *S. spaldingii* is ca. 100 plants occurring in scattered colonies over ca. 100 ha. Grasslands are dominated by *Festuca idahoensis* and *Agropyron spicatum*. Flowering forbs visited by bumblebees at the time of the study include *Haplopappus carthamoides, Hieracium albertinum*, and *Lupinus leucophyllus*. These species were uncommon or mostly done flowering at the time of the study.

Lamona is 17 km southwest of Harrington in Lincoln Co., Washington. Elevation is 580 m, and climate is similar to Sprague. The population of *S. spaldingii* is 500-1,000 plants in 10 colonies over ca. 150 ha. Grasslands are dominated by *Festuca idahoensis, Agropyron spicatum* and scattered *Artemisia tripartita*. There were no flowering forbs visited by bumblebees at the time of the study.

Garden Creek Preserve is 37 km south of Lewiston in Nez Perce Co., Idaho. Elevation is 800 m; mean January and July temperatures are 0.1 and 23.3° C respectively; and mean annual precipitation is 325 mm (Lewiston). There are ca. 200 *S. spaldingii* plants in at least two colonies over ca. 150 ha. Grasslands are dominated by *Festuca idahoensis* and *Agropyron spicatum*. Flowering forbs visited by bumblebees at the time of the study include *Achillea millefolium, Symphoricarpos occidentalis, Cichorium intybus, Orthocarpus tenuifolius, Centaurea solstiatilis, Hypericum perforatum*, and *Perideridea gairdneri*. Flowers of the latter three species were common at the time of the study.

Clear Lake Ridge Preserve is 25 km east of Enterprise in Wallowa Co., Oregon. Elevation is 1525 m; mean January and July temperatures are -4.3 and 17.2° C respectively; and

mean annual precipitation is 332 mm (Enterprise). There are ca. 200 *S. spaldingii* plants in two main subpopulations separated by 0.5 km. *Festuca idahoensis* and *Stipa columbiana* dominate the grasslands. Flowering forbs visited by bumblebees at the time of the study include *Achillea millefolium, Agoseris glauca, Hieracium albertinum, Linum lewisii, Orthocarpus tenuifolius* and *Sonchus arvensis*. Flowering among these species was uncommon at the time of the study.

Methods

Field methods

At each site we located 1-3 patches of *Silene spaldingii* with 12-50 flowering stems clearly visible from a single observation point. We made observations on pollinators for one- or two-hour periods throughout the day, including around dusk and dawn when light was dim. Observations were conducted during peak bloom: 29 July 29 - 7 August, 1995 at the Washington, Oregon and Idaho (Palouse) sites, and 12-14 July 1988 and 9-12 July 1990 at Dancing Prairie. At the Palouse sites, individual pollinators were followed throughout pollination bouts for 17-20 hours per site over two days. Partial bouts (2-3 sequential visits) were observed for an additional 20 hours at each site. These additional data were used to estimate the importance of the various pollinators and pollinator fidelity. Individual pollinators were followed throughout pollination bouts for 65 hours over six days at the Montana site.

During observation periods we followed the activities of pollinators within the patch and recorded the duration to the nearest 0.5 min and the number of *S. spaldingii* flowers and plants visited in each pollination bout. A visit entails the pollinator entering into the mouth of the *S.*

spaldingii corolla. A bout is an uninterrupted sequence of visits within the observation patch. We also recorded when a bout ended with the pollinator switching to a different host species.

We examined 2-3 specimens of *Bombus fervidus* for pollen from each study site to ascertain the ability of this bee to be an effective pollinator of *Silene spaldingii*. Pollen was brushed from the head and thorax of each bee onto a microscope slide with anilin blue in lactophenol (Radford et al. 1974). These were compared to slides prepared from anthers of *S. spaldingii*. Density of pollen was placed into one of three classes: low, medium and high.

Data analysis

We estimated the proportion of aborted fruits by counting the number of erect (>2 day post-bloom) fruits that contained swollen, capsules with maturing ovules and unswollen capsules with aborted ovules. Twenty randomly selected plants with ≥5 erect fruits were examined at each site except Sprague where few fruits had begun to develop.

We estimated the total number of *S. spaldingii* flowers visited per day at each observation site as follows. We calculated the mean number of flowers visited in each 1-hour period (i.e., 0800-0900, 0900-1000 etc.) and interpolated values for which we had no data (There were never more than two consecutive 1-hour periods without data). We summed all the 1-hour values to obtain an estimate of the total.

The effect of site on the proportion of aborted fruits was assessed using analysis of variance (ANOVA) followed by contrast tests. Simple regression analysis was used to determine the degree of correlation between the rates of flower visitation and abortion. Proportion of aborted fruits was arcsine-transformed before analysis to conform to the assumptions of the tests.

Results

A bumblebee, *Bombus fervidus*, was the only common visitor to *Silene spaldingii* flowers at the five sites. *Bombus fervidus* was responsible for ≥83% of the pollination bouts at the five sites (Table 1). A previous report of visitations by *B. nevadensis* at Dancing Prairie (Lesica 1993) were based on misidentified specimens.

Twelve of thirteen specimens of *B. fervidus* examined bore pollen of *S. spaldingii* on their head and/or thorax (Table 2). Densities of pollen were highest at Lamona and Clear Lake Ridge and lowest at Garden Creek. Density was not recorded for Dancing Prairie specimens. Specimens of *B. fervidus* from Garden Creek got wet during transport, and this may have caused the low densities of *S. spaldingii* pollen on some of the bees from this site.

Halictine bees (*Lasioglossum ovaliceps, Halictus tripartitus, Dienoplus rugulosis, Lasioglossum* spp.) were also observed visiting flowers of *S. spaldingii* at the Lamona site, accounting for 17% of the pollination bouts (Table 1). Halictine bees visited only 2-5 flowers per bout (n=3). We did not examine Halictine bees for pollen. However, these bees are likely to be less efficient pollen vectors because they are much smaller and may not always contact anthers and stigma as they crawl to the nectaries. Furthermore, they are not as hairy as bumblebees and probably carry smaller pollen loads. Small moths (Noctuidae) were observed visiting *S. spaldingii* flowers at Clear Lake Ridge, but these visits were uncommon (Table 1).

Bombus fervidus pollination of *S. spaldingii* began between 0700 and 0900 and generally continued until 1900 on most days. Peak activity occurred between 0900 and 1800. Visits to *S. spaldingii* by Halictine bees at Lamona also occurred throughout the day.

The mean number of *Silene spaldingii* flowers open at each observation site during the study and the estimated total number of flower visits per day are given in Table 3. The mean number of visits per flower per day varied from 0.3 at Dancing Prairie to 21.2 at Clear Lake Ridge (Table 3). The mean proportion of aborted fruits varied between 0.08 at Clear lake and 0.31 at Dancing Prairie. Clear Lake had significantly fewer aborted fruits than either Garden Creek or Dancing Prairie, and Dancing Prairie had significantly more abortions than Lamona or Clear lake ($P<0.05$, Fig. 1). There was a significant negative correlation between the rate of flower visitation and the rate of abortion ($r=0.39$, $P<0.001$; Fig. 1).

Bombus fervidus was observed switching from *Silene spaldingii* to alternate hosts at Sprague, Clear Lake and Garden Creek, but switching was common only at Garden Creek (Table 3). One-third of the *S. spaldingii* pollination bouts at Garden Creek ended by *B. fervidus* switching to an alternate host, significantly more than for the other sites (chi-square test, $P<0.001$). *Bombus fervidus* switched to *Hieracium albertinum* (6 times) and *Lupinus leucophyllus* (4) at Sprague; *Hypericum perforatum* (5), *Perideridea gairdneri* (1) and *Orthocarpus tenuifolius* (1) at Garden Creek; and *Sonchus arvensis* (2), *Hieracium albertinum* (1), *Cirsium brevifolium* (1), and *Aster campestris* (1) at Clear lake Ridge.

Discussion

The bumblebee, *Bombus fervidus*, appears to be the only significant pollination vector for *Silene spaldingii* throughout its range, accounting for at least 83% of all pollination bouts at five sites. *Bombus fervidus* is common throughout most of temperate North America (Plath 1934,

Stephen 1957). It is found in grasslands and meadows where it builds nests on or near the surface of the ground (Hobbs 1966).

There was a tendency for pollination visitation rates and pollinator constancy to be lower at sites with large populations of flowering plants that compete with *S. spaldingii* for pollinators. The only possible exception to this rule was Clear Lake Ridge where visitation and pollinator constancy were high in spite of moderate densities of other flowering species that were occasionally used by *B. fervidus*. Optimum foraging theory predicts that a pollinator's constancy to a particular species will be influenced by the magnitude of reward presented by other competing species and the ease with which it can be obtained (Heinrich 1979, Waddington 1983). The presence of heterospecific flowers may increase pollination by attracting more pollinators to the area (pollination facilitation reviewed by Rathcke 1983) or decrease pollination by competing for pollinator service (Feinsinger et al. 1991, Kunin 1993). Our results are consistent with pollinator competition.

Lower visitation rates and pollinator constancy were associated with reduced fruit set in *Silene spaldingii*, probably due to less efficient pollination (Feinsinger et al. 1991, Kunin 1993) caused by fewer compatible pollen grains reaching the surface of the stigma (Feinsinger 1987). Similar pollination limitation has been reported for many other species (Bierzychudek 1981).

Decreased pollination also results in a higher proportion of inbred progeny in a self-compatible species such as *S. spaldingii* (Karron et al. 1995, Lesica 1993). The effects of inbreeding depression on population growth rate are often small if fecundity is high (Lesica and Allendorf 1992). However, pollinator limitation can cause lower fruit and seed set as well as lowered fitness of the progeny. In this case, population growth can decline. This problem will

be most severe in small populations where there is less chance of matings between unrelated individuals. Thus, our study suggests that heterospecific competition for pollinators and the concomitant reduction in visitation and pollinator constancy (pollinator limitation) have the potential for adversely affecting both fecundity and individual fitness in *S. spaldingii* under some circumstances.

The Sprague, Lamona and Clear Lake Ridge *Silene spaldingii* populations had flowers that received at least 12 visits per day. Since each flower is open for two days or more, the average flower will receive at least 24 visits, certainly enough to set fruit. Pollination limitation is not likely to be a problem at these sites.

On the other hand, the Dancing Prairie and Garden Creek populations had estimated visitation rates of less than 2; however, even these low rates may be adequate to allow persistence of *S. spaldingii*. Results presented here and observations made during other studies over the past nine years (Lesica 1995a, 1995b) suggest that the Dancing Prairie population of *S. spaldingii* suffers chronic low levels of pollinator visitation. Nonetheless, results of monitoring studies suggest that the population has become larger over the past nine years (Lesica 1995a). The Dancing Prairie population of *S. spaldingii* is large (>10,000 plants, Schassberger 1988). In a population this large, even limited pollination service may result in sufficient outcrossing to prevent population decline from inbreeding. Smaller populations with fewer genotypes may not fare so well.

At Garden Creek, where pollinator constancy was highest, *B. fervidus* switched most often to *Hypericum perforatum*, an exotic weed. Without these switches to *H. perforatum*, the rate of pollinator constancy at Garden Creek would have been 14%, not significantly different

from the other sites. Competition for water nutrients and light is clearly the main threat to *S. spaldingii* populations posed by exotics (Gamon 1991, Lorain 1991). Nonetheless, competition for pollinators may also have adverse effects.

Implications for management

Colonies of *Bombus fervidus* and their habitat in proximity to populations of *Silene spaldingii* should be protected. Insecticide use must be curtailed and other agricultural chemicals should be used with care (Johansen et al. 1983, Tepedino 1979). Many colonies of *B. fervidus* occur near the surface of the ground. Thus, fire should be used as a management tool with caution (Panzer 1988). Populations of *S. spaldingii* that occupy small areas and are surrounded by large expanses of habitat that will not support bumblebee colonies (e.g., crop lands) are not likely to persist over the long term and should not be given conservation priority. Exotics, such as *Hypericum perforatum*, that compete with *Silene spaldingii* for pollination service should be controlled, at least in the area where *S. spaldingii* occurs.

Most large populations of *S. spaldingii* occur in areas of native vegetation capable of supporting colonies of *B. fervidus*. Results of our study suggest that pollination limitation is not likely to threaten these populations.

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Table 1. Number (and percent) of pollination bouts by various pollinators at five study sites.

	Dancing Prairie	Sprague	Lamona	Garden Creek	Clear Lake
Total # bouts	6	108	172	21	201
B. fervidus bouts	6(100%)	107(99%)	143(83%)	21(100%)	200(99%)
Halictine bouts	0	0	22(17%)	0	0
Vespid bouts	0	1(1%)	0	0	0
Noctuid bouts	0	0	0	0	4(2%)

Table 2. Collected specimens of *Bombus fervidus* classified by density of *Silene spaldingii* pollen collected from them. Density was not measured for the two bees from Dancing Prairie.

	Density			
	None	Low	Medium	High
Sprague	0	2	1	0
Lamona	0	0	1	1
Garden Creek	1	1	1	0
Clear Lake Ridge	0	0	1	2

Table 3. Mean number of *Silene spaldingii* flowers open at each observation site during the study, estimated per flower visitation rate, and percent of *B. fervidus* pollination bouts that ended with host switching.

	Total flowers	Visitation (visit/fl/day)	Switching (% bouts)
Dancing Prairie	24	0.3	0
Sprague	51	12.0	9%
Lamona	36	17.2	0
Garden Creek	32	1.4	33%
Clear Lake	33	21.2	3%

Figure 1. Mean proportion (±SE) of aborted fruits and estimated visitation rate for *Silene spaldingii* at four study sites. Sites with different letters have significantly different abortion rates as determined by ANOVA followed by contrast tests ($P<0.05$).