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Reproductive ecology of the western silvery aster *Symphyotrichum sericeum* in Canada

D. Bizecki Robson*

The Manitoba Museum, 190 Rupert Avenue, Winnipeg, Manitoba R3B 0N2, Canada

ABSTRACT: Previous studies suggest that low seed production due to pollinator competition and seed predation may negatively affect the reproduction of the rare forb western silvery aster *Symphyotrichum sericeum* in Canada. Research was conducted to determine normal flower and seed production and the impact of seed predation, and to ascertain whether clipping surrounding vegetation and/or fertilizing with nitrogen stimulates flower and seed production in *S. sericeum*. Only 41% of all stems observed produced capitula, and less than 40% of the seeds in each capitulum were filled. Flower production was negatively correlated with percentage vascular plant cover and positively correlated with percentage cryptogamic cover. The main seed predator was a weevil (*Anthonomus* sp.) that destroyed about one-third of all capitula produced. None of the treatments applied (e.g. clipped, fertilized and clipped × fertilized) significantly increased stem height, the percentage of flowering stems or seed production over the control; clipping actually decreased stem height. Fertilizing was the only treatment that showed some promise as it increased the number of capitula per flowering stem. Flower and seed production in *S. sericeum* may be facilitated by the presence of other species that modify the microenvironment. Low flower and seed production of plants in Canada is likely due to limited soil resources and pollen, and seed predation.

KEY WORDS: Population ecology · Predation · Production · Competition · Life history traits · Conservation · Endangered species

INTRODUCTION

Habitat loss and fragmentation and changes in the natural disturbance regime are responsible for the endangerment of many ecosystems (Primack 2008). In Canada, one of the ecosystems most impacted by these factors is the tallgrass prairie; less than 1% remains, largely due to cultivation (Rodger 1998). The low population sizes of rare plants in endangered ecosystems make them particularly vulnerable, as reproductive difficulties such as low flower and seed production (Zimmerman & Pyke 1988, Watson et al. 1994, Kéry et al. 2000, Fenner & Thompson 2005) and seed predation (Evans et al. 1989, Louda et al. 1990, Hegazy & Eesa 1991, Bevill et al. 1999, Kéry et al. 2001, Vickery 2002, Young et al. 2007) tend to occur.

Symphyotrichum sericeum (Asteraceae) is a nationally rare species in Canada (COSEWIC in press) that is found only in the tallgrass prairies of southern Manitoba and southwestern Ontario. This perennial species occurs on sandy–gravelly soils, which are being mined in some areas for use in road building and construction, resulting in habitat loss and fragmentation. One factor that negatively affects reproduction in *S. sericeum* is competitive exclusion. Competition with other co-flowering plants for pollinating insects reduces the seed set of early blooming *S. sericeum* capitula (Robson 2010). Competition with other plants for soil resources and light may also be negatively affecting flower and seed production in *S. sericeum*. Periodic disturbances, such as fire, encourage flower production in rare species of forbs that are negatively affected by competition with grasses (Watson et al. 1994, Kirkman et al. 1998, Pendergrass et al. 1999, Heather 2004). Increased flowering after a fire may be due to the nutrient flush that occurs, increase in light

*Email: drobson@manitobamuseum.ca

availability or a combination of these factors (Jones 1978, Gibson & Hulbert 1987, Pendergrass et al. 1999). Mowing combined with the addition of nitrogen fertilizer has been used instead of fire to increase flowering in some rare plants (Lamont & Runciman 1993, Heather 2004). A second factor that may be affecting *S. sericeum* is seed predation. Pre-dispersal seed predation reduces seed production in *S. sericeum* more than in the other species with which it shares its habitat, namely *S. novae-angliae* and *S. ericoides* var. *ericoides* (Newman 1999). To date, *S. sericeum* has not been studied sufficiently to determine the relative influence of the various factors that affect its reproduction; this lack of knowledge impedes the development of conservation plans for its recovery.

The purpose of the present study was to document the normal production of flowers and seeds in *Symphyotrichum sericeum* and quantify the impact of predators on seed production. As competition with grasses was hypothesized to affect the reproduction of *S. sericeum*, an experiment was conducted to determine whether applying nitrogen fertilizer and/or clipping competing vegetation to simulate a spring burn would increase flower and seed production.

MATERIALS AND METHODS

Species description. *Symphyotrichum sericeum* is a perennial herb that produces one to several caespitose stems from woody corm-like rootstocks that may be interconnected by short horizontal rhizomes (COSEWIC in press). The pink capitula are arranged in open, diffuse panicles. *S. sericeum* is a semi-obligate outbreeder pollinated by a variety of insects, including bumblebees, Halictid bees, and Syrphid and bee flies (Jones 1978, Semple et al. 1996, Robson 2010). In Manitoba, *S. sericeum* flowers from mid-August to mid-September, and produces ripe cypselae, hereafter referred to as 'seeds', by early October. *S. sericeum* is a nationally rare species in Canada protected by the federal Species-at-Risk Act 2003, Manitoba's Endangered Species Act 1990, and Ontario's Endangered Species Act 2007. A research and collecting permit to study this plant was obtained from Manitoba Conservation. After examination, all seeds of *S. sericeum* that were harvested were released back into the park.

Study site. Birds Hill Provincial Park, located north of Winnipeg, Manitoba, Canada (50° 01′ N, 96° 53′ W), is a 35 km^2 protected area that contains a variety of plant communities including tallgrass prairie and oak savannah. It is one of the only areas in Canada that contains populations of *Symphyotrichum sericeum*. The population in the park is estimated to consist of over 4400 individuals (COSEWIC in press). Soils where *S. sericeum* occurs are sandy–gravelly, well-drained and calcareous, being derived from glaciolacustrine shoreline deposits (COSEWIC in press).

Vegetation and soils. In 2008, sixteen 2.5 m^2 plots at least 5 m apart that contained *Symphyotrichum sericeum* plants were established. The number of stems, flowering stems and capitula were recorded in each plot, and densities were calculated by dividing the values by the plot area (6.25 m^2). The absolute ground cover of all vascular plants, cryptogams, and bare ground in each plot was visually estimated using the mean percent cover for the 7 Braun-Blanquet cover classes (Mueller-Dombois & Ellenberg 1974). To calculate the relative cover, the value of each cover type was divided by the total cover in the plot.

To determine the fertility of the soils, samples were collected to a depth of 10 cm from the 16 plots in the park and analyzed for pH, electrical conductivity, and quantity of nitrogen, potassium, phosphorus and sulphur (Excova).

Seed production and predation. To assess the normal seed production and predation, 40 random *Symphyotrichum sericeum* plants from each of 4 subpopulations were examined in late September 2008. Plants were selected by establishing a central point in the subpopulation, then randomly choosing 20 directions (i.e. a random heading between 1° and 360°) and 20 distances (i.e. random number between 1 and 25 m). The flowering *S. sericeum* plants closest to the end points were examined, and the number of intact and damaged capitula on each stem were counted. Capitula that had been damaged by seed predators had blackened puncture marks on the involucres, produced very little ripe seed and had a larva or adult insect present where the seeds would normally grow. Both juvenile and adult specimens of the seed predators were collected and sent to Patrice Bouchard at Agriculture Canada, Ottawa, for identification. When the capitula were intact, they were harvested and examined in the lab.

Clipping and fertilizing experiment. One of the *Symphyotrichum sericeum* subpopulations with high vascular plant cover was selected as the location for this experiment, which took place in the summer of 2009. A randomized complete block design with 4 replicate blocks was used. Each block was 2.5 m^2 in size and consisted of four 1 m^2 plots with a 0.5 m buffer between them. Each plot contained 4 to 33 *S. sericeum* stems from which an average value was obtained. One of 4 treatments was applied to each plot: control, clipped, fertilized, or clipped × fertilized. In mid-June, the litter from half the plots was clipped and removed to simulate the effect of a spring burn. Fertilized plots received a surface application of nitrogen (NH_4N0_3) at a rate of 10 g N m^{-2}, the same quantity used to compare the impact of mowing and fertilizing to fire at the

Konza Prairie Long-term Ecological Research site (Collins et al. 1998). Light levels and soil temperatures were recorded from 4 locations in all the plots once a month for 4 mo using a light meter and temperature probe, respectively. Soil samples were collected to a depth of 10 cm from each plot in late August and analyzed for nitrogen (Excova). *S. sericeum* stems were counted and measured in each plot in mid-September to determine density and height. All capitula in the plots were tallied and then harvested in early October for examination in the lab.

Seed examination. To discriminate filled from unfilled seeds, each seed was viewed under a dissecting microscope (10×) and pressed with a metal probe. Filled seeds were firm and approximately 1 mm thick at the widest part and unfilled seeds were soft and flat. The number of filled and unfilled seeds per capitula was counted.

Data analysis. Regression analysis was used to test the relationship between the percentage flowering stems and relative vascular plant and cryptogamic cover among the 16 study plots. ANOVA with significance of $p \leq 0.05$ and least significant difference (LSD) multiple contrast analysis were used to test for differences between treatment plots with respect to stem height, percentage flowering stems, number of capitula per flowering stem, total number of seeds per stem, and soil nitrogen. Repeated measures ANOVA was used to test for differences in soil temperature and light between the treatment plots. These data were log-transformed prior to analysis due to slight skewness of the data. Statistical tests were performed using Analyze-It® (Analyze-It Software).

RESULTS

Vegetation and soils

The 16 plots contained 35 vascular plant species and at least 4 species of cryptogams, including the nitrogen-fixing blue green algae *Nostoc*, growing together in a biological soil crust (Table 1). *Andropogon gerardii* was the most abundant grass in the plots, comprising over 45% of the cover. The most abundant forbs in the plots were *Solidago nemoralis* followed by *Symphyotrichum sericeum*; together these 2 species produced 95% of all insect-pollinated flowers in the plots. Only 41% of the *S. sericeum* stems produced capitula; the average was 1.6 ± 0.5 capitula per flowering stem (Table 2). Regression analysis indicated that the percentage of *S. sericeum* stems that flowered was negatively correlated with the relative cover of vascular plants ($y = -0.6365x + 87.06$, $R^2 = 0.3452$, $p = 0.017$) and positively correlated with the relative cover of cryptogams ($y = -0.433x + 5.316$, $R^2 = 0.238$, $p = 0.05$).

Table 1. Relative cover of dominant species associated with *Symphyotrichum sericeum* in 16 plots located in Birds Hill Provincial Park, Manitoba, Canada. N/A: not applicable

Species	% relative cover (mean ± SE)
Bare ground	
N/A	7.07 ± 3.4
Non-vascular species	
Selaginella densa	13.1 ± 6.6
Peltigera spp.	
Cladonia spp.	
Nostoc spp.	
Vascular plant species	
Andropogon gerardii	45.3 ± 16.5
Festuca trachyphylla	8.34 ± 8.7
Hesperostipa curtiseta	6.94 ± 3.7
Poa pratensis ssp. *pratensis*	4.79 ± 0.1
Solidago nemoralis var. *longipetiolata*	2.43 ± 1.7
Symphyotrichum sericeum	2.18 ± 0.1
Juniperus horizontalis	1.30 ± 0.8
Artemisia campestris var. *borealis*	1.20 ± 0.1
Equisetum laevigatum	1.20 ± 0.1
Populus tremuloides	1.17 ± 1.8
Symphoricarpos sp.	0.73 ± 0.1
Dalea purpurea var. *purpurea*	0.53 ± 0.2
Dalea candida var. *candida*	0.45 ± 0.3
Artemisia frigida	0.42 ± 0.1
Populus balsamifera ssp. *balsamifera*	0.42 ± 0.1
Ambrosia psilostachya var. *coronopifolia*	0.42 ± 0.1
Other species (19 taxa)	2.15

Table 2. *Symphyotrichum sericeum*. Summary of reproductive data on western silvery aster plants in Birds Hill Provincial Park, Manitoba, Canada

Character	Mean ± SE	Sample size (n)
Stems (no. m^{-2})	7.0 ± 0.9	100
Flowering stems (no. m^{-2})	2.9 ± 0.6	100
Total capitula (no. m^{-2})	4.7 ± 0.1	100
Capitula (no. flowering per stem)	1.6 ± 0.5	287
Capitula predated (%)	37.0 ± 0.0	256
Seeds (no. per capitula)	30.4 ± 1.7	161
Filled seeds (% per capitula)	38.9 ± 3.2	161
Unfilled seeds (% per capitula)	61.1 ± 3.2	161

The soil analyses indicate that the soils were slightly alkaline to neutral (pH = 7.41) with low electrical conductivity (0.16 dS m^{-1}). Low levels of nitrogen (1.86 ppm), phosphorus (5.44 ppm), potassium (39.33 ppm) and sulphur (3.06 ppm) indicate that these soils are highly infertile.

Seed production and predation

Of the 256 capitula examined, 37% had been damaged by insect seed predators (Table 2). The seeds of *Symphyotrichum sericeum* were preyed upon by a species of *Anthonomus* weevil that lays an egg at the base of the capitulum shortly before or at bloom. The emerging larva destroys virtually every seed in the capitulum where it grows. Both larvae and adult weevils were observed cocooned in capitula. Of the undamaged capitula, the average number of seeds produced was 30 but slightly less than 40 % of them were filled.

Impact of clipping and fertilizing on reproduction

Stem height was significantly lower in the clipped and clipped × fertilized plots compared to the control and fertilized plots (Table 3). None of the treatments significantly increased the percentage of flowering stems compared to the control. Plants in the fertilized plots produced significantly more capitula per flowering stem than in the other plots. Fertilized plants produced more seeds per stem than those in clipped and clipped × fertilized plots, but not more than the control plants. Light was significantly higher in the clipped plots than in the others. Nitrogen was significantly higher in the fertilized plots than in the control and clipped plots but not the clipped × fertilized plots. Soil temperature was not significantly different among the plots.

DISCUSSION

In a previous study, hand pollination was found to increase seed set in *Symphyotrichum sericeum*, but only by an additional 10 % (Robson 2010), suggesting that both pollen and resources are limiting. Genetic problems such as inbreeding depression are a documented cause of low seed set in some species (Ellstrand & Elam 1993) and may be affecting *S. sericeum*; however, this was not examined in the present study. Stem and flowering stem density of *S. sericeum* was lowest at the sites with the highest vascular plant cover. I hypothesized that competition with other plants for nutrients was responsible for the low flower production observed. Evidence supporting this hypothesis is the observation that prescribed burning increases *S. sericeum* relative cover in Kansas, USA, due to an increase in light and/or nitrogen (Gibson & Hulbert 1987). However, as prescribed burning is not always practical to conduct, an alternative strategy to stimulate flower production is desirable in some areas. Clipping and fertilizing with nitrogen had an impact comparable to fire on flower production in several rare plant species (Lamont & Runciman 1993, Heather 2004), and for this reason was selected as a potential treatment. However, in the present study, June clipping and clipping × fertilizing did not increase flower or seed production in *S. sericeum*; in fact, a negative effect of clipping and litter removal on stem height was observed. As light was significantly higher in the clipped plots, this variable does not seem to be limiting flower production in *S. sericeum*. The presence of litter and other vascular plants may have a facilitative effect on the growth and reproduction of *S. sericeum*, possibly by increasing the organic matter content of the soil and/or decreasing water stress by providing shade and altering wind speeds (Holmgren et al. 1997). Given the high sand content of the soils where *S. sericeum* grows and the fact that adding supplemental nitrogen to clipped plots did not improve growth or seed set, moisture may be more limiting than nitrogen. Thus, mowing is not a recommended treatment in Canada as loss of co-occurring vegetation appears to hinder growth of *S. sericeum*; fire may have a similar negative effect.

The higher flower production of *Symphyotrichum sericeum* plants at sites with low vascular plant cover and high cryptogamic cover may be due to another facilitative effect between species. The cryptogamic cover at the study site consisted of both free-living and lichenized (in *Peltigera* spp.) *Nostoc*, a nitrogen-fixing blue-green algae (Brodo et al. 2001). Studies reviewed in Belnap et al. (2001) show that 5 to 88 % of nitrogen fixed by *Nostoc* leaks into the substrate, and that plants growing in soils

Table 3. *Symphyotrichum sericeum*. Summary of mean values for 4 treatments in plots containing western silvery aster located in Birds Hill Provincial Park, Manitoba, Canada. Data are presented as means ± SE. Values followed by a different letter are significantly different at the 5 % confidence level (ANOVA and least significant difference [LSD] multiple contrast analysis)

Plot value	Treatment			
	Control	Fertilized	Clipped	Clipped × fertilized
Stem height (cm)	27.2 ± 1.1[a]	29.1 ± 1.9[a]	17.8 ± 1.3[b]	19.5 ± 1.5[b]
Flowering stems (%)	40.6 ± 15.8	59.0 ± 17.7	21.9 ± 7.3	28.1 ± 8.2
Capitula (no. flowering per stem)	2.0 ± 0.7[a]	3.5 ± 0.4[b]	1.4 ± 0.3[a]	1.4 ± 0.3[a]
Seeds (no. flowering per stem)	34.7 ± 19.5[ab]	65.9 ± 22.9[a]	9.4 ± 4.4[b]	13.5 ± 6.2[b]
Soil nitrogen content (ppm)	5.5 ± 3.5[a]	14.0 ± 1.5[b]	5.25 ± 1.3[a]	8.75 ± 3.5[ab]
Light (lux)	293.3 ± 33.8[a]	260.4 ± 30.8[a]	534.5 ± 59.9[b]	498.7 ± 61.9[b]
Soil temperature (°C)	15.36 ± 0.6	15.57 ± 0.6	15.7 ± 0.7	15.4 ± 0.7

with a cryptogamic crust possess higher concentrations of nutrients than plants not growing in crusted soils (Belnap et al. 2001). In addition to improving soil fertility, cryptogamic crusts may improve water infiltration rates, particularly on sandy soils, although this is not known conclusively (Belnap et al. 2001).

The slight increase in the number of capitula per flowering stem in the fertilized plots over the control suggests that nitrogen may be limiting reproduction in *Symphyotrichum sericeum* somewhat. However, fertilization did not stimulate significantly more vegetative growth or seed production over the control; there are several possible explanations for this modest response. First, the nitrogen applied may have been utilized largely by earlier growing, more competitive species, such as *Andropogon gerardii*. Second, the growth of *S. sericeum*, like that of many plants, may be limited by 2 or more resources simultaneously (Chapin et al. 1987, Haig & Westoby 1988). Low availability of water, phosphorus, potassium and sulphur may have prevented the *S. sericeum* plants from fully utilizing the nitrogen added as per Liebig's Law of the Minimum (Taylor 1934). Another possible reason for the poor response is that *S. sericeum* cannot exploit an abundance of nutrients for growth and flower production due to a stress-tolerant habit. Species from infertile soils are noted to absorb considerably fewer nutrients under high nutrient conditions than plants adapted to more fertile soils (Chapin 1980). *S. sericeum* possesses a number of traits that are characteristic of stress-tolerant plants including its production of perennial corms and rhizomes, small leaf size, slow growth and sparse litter production (Grime 2001). Stress-tolerant plants tend to be conservative, saving nutrients and energy in storage organs for use in times of scarcity rather than reproduction (Grime 2001). Although the application of fertilizer may not improve seed production in *S. sericeum* the year it is applied, it may improve the survival of adult plants and potential seed production in the following year (Chapin 1980).

Low population sizes combined with high seed predation is one of the reasons behind the low reproduction rates of some rare plants (Evans et al. 1989, Gisler & Meinke 1997, Kolb et al. 2007). Seed predation is one factor affecting *Symphyotrichum sericeum*, as *Anthonomus* weevils destroyed more than one-third of all capitula that were examined. Although seed predation has been noted to vary widely from year to year in some species (Fenner & Thompson 2005), the percentage of predated capitula observed in the present study is comparable to that in earlier reports: 30 to 34% (Newman 1999, COSEWIC in press). Fenner et al. (2002) noted that there was a positive correlation between mean capitulum size and infestation by seed-eating larvae. *S. sericeum* suffers larger seed losses than co-flowering species with smaller capitula, namely *S. ericoides* and *S. novae-angliae* (Newman 1999). Nonetheless, predation losses in *S. sericeum* are not as high as in many other species; losses of 50 to 90% of all seeds are not unheard of (Fenner & Thompson 2005).

The factors limiting seed production in *Symphyotrichum sericeum* are the same ones affecting other species: pollen availability limits fruit initiation, resource availability limits seed maturation and predation limits seed set (Ehrlén 1992). Applying conservation measures that affect several different aspects of reproduction would likely be more successful than measures that target only one. For example, reducing both resource competition and seed herbivory was found to increase recruitment and density by more than the sum of both single-factor effects (Louda et al. 1990, Friedli & Bacher 2001). Hand pollination of early flowering *S. sericeum* is one potential technique to improve seed set (Robson 2010). Increasing resource availability by applying a fertilizer containing all soil macronutrients and/or water may be helpful in increasing seed set even further, although the efficacy and appropriate rates still needs to be assessed. As stress-tolerant plants perform better than competitive species when fertilizer is applied in short pulses (Grime 2001), over-fertilization should be avoided as it may encourage the growth of more competitive species, potentially negatively affecting *S. sericeum* (Grime 2001). Controlling seed predator population is another possible treatment, although one fraught with uncertainties. Pesticides have been used successfully to increase seed set in plant species affected by seed predators (Louda 1982, Ehrlén 1992, Louda & Potvin 1995). However, the use of pesticides on *S. sericeum* may be undesirable due to potential side effects on pollinating insects. Physical barriers, such as netting, are impractical and of questionable use, as weevils were observed to chew through nylon netting to reach capitula. Prescribed burning is another possible treatment, as seed predator populations were reduced, at least temporarily, using fire in several studies (Mejeur 1998, Vickery 2002). However, Camper (2007) found that burning increased seed predation by weevils in the rare plant *Sidalcea malachroides*. As the wintering habits and specificity of the weevil species that predates *S. sericeum* are unknown, and as litter removal had a negative effect on plant growth, the impact of fire should be studied carefully before it is used as a management tool.

Hulme & Benkman (2002) note that the population size of specialist seed predators is often positively correlated with the size of the crop in the preceding year, rather than the density of seeds in the current year. Thus, one of the potential consequences of applying treatments to increase the flower density of *Symphyotrichum sericeum* may be a higher predator population the following year. If conservation treatments that increase *S. sericeum* flower density are not sustained from year to year, and no measures are taken to control predator populations, the percentage of seeds predated may increase dramatically in some years, potentially offsetting the positive effect of any treatments. It may be better to focus conservation efforts on restoring *S. sericeum* to abandoned sand and gravel pits by raising plants *ex situ* and transplanting them, rather than attempting to alter wild seed production.

In summary, *Symphyotrichum sericeum* exhibits stress-tolerant characteristics that make it capable of growing in low nutrient soils. Flower and seed production in *S. sericeum* appear to be inhibited by competition with other plants for pollinators during part of the year, the presence of a weevil seed predato, and the low availability of soil resources. Both cryptogamic species and neighbouring vascular plants appear to have a facilitative effect on *S. sericeum*. Cryptogamic species may increase soil nutrients and, possibly, water availability (Belnap et al. 2001). Although other vascular plants may be competing with *S. sericeum* for some nutrients, the competition appears to be largely offset by the positive effects they have on the availability of other resources (Holmgren et al. 1997). The facilitative effect of the cryptogams is likely greater than that of the vascular plants given the higher flower production on plots with high cryptogamic cover. Additional research is needed to confirm these potential facilitative effects and determine the degree to which water and other nutrients affect growth and reproduction in *S. sericeum*, as this species appears to be limited by multiple environmental factors. To date, the only treatment known for certain to increase seed production in *S. sericeum* is hand pollination. Combining hand pollination with other treatments to address resource limitations may be even more successful.

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