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Original article

Mating strategies and pollen limitation in a globally threatened perennial *Polemonium vanbruntiae*

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ABSTRACT

Knowledge of the factors that limit reproduction is critical to an understanding of plant ecology, and is particularly important for predicting population viability for threatened species. Here, we investigated the pollination biology of a globally threatened plant, *Polemonium vanbruntiae*, using hand-pollination experiments in four natural populations to determine the degree of pollen limitation. In addition, we investigated the mating system and extent to which plants can self-fertilize by comparing geitonogamously and autonomously self-fertilized plants with purely outcrossed and open-pollinated plants. In contrast to several of the more common species of *Polemonium*, we found no pollen limitation in any of the four populations of *P. vanbruntiae* over two years. The lack of pollen limitation was best explained by the capacity for *P. vanbruntiae* to both geitonogamously and autonomously self-fertilize, unlike some of its more common congeners. Geitonogamously selfed flowers set equivalent numbers of seeds when compared to purely outcrossed and open-pollinated flowers. However, autonomously selfed flowers produced significantly fewer seeds, demonstrating that pollinators play an important role as inter- and intra-plant pollen vectors in this system. Our results support the reproductive assurance hypothesis, whereby the ability to self assures fertilization for plants in small populations. Self-compatibility in *Polemonium vanbruntiae* may decrease extinction risk of isolated populations experiencing a stochastic pollinator pool within a restricted geographic range. In addition, a mixed-mating strategy, including the ability for clonal reproduction, may explain the ability for this rare species to persist in small, fragmented populations.

1. Introduction

Plants that exist in small populations and rely on animals to vector pollen are at an inherent disadvantage, because pollinators often bypass small, relatively unrewarding plant populations for larger and more resource-rich populations (Charnov, 1982; Sih and Baltus, 1987; Waites and Ågren, 2004). Thus, these plants are likely to be pollen limited. Rare plants may be especially prone to pollen limitation as they often occur in fragmented landscapes where pollination is disrupted (McKey, 1989; Rathcke and Jules, 1993; Aizen and Feinsinger, 1994), and pollen quality or quantity may be insufficient for maximal seed set (Ashman et al., 2004). When plants persist in small, fragmented habitats, and conspecifics

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are patchy throughout the landscape, pollen is often wasted due to failure to reach conspecific stigmas (Koenig and Ashley, 2003). The result is higher amounts of heterospecific pollen receipt and a subsequent reduction in quality of the pollen pool (Rathcke, 1983). In addition, animal-pollinated, self-incompatible species existing in a rare state are likely to be especially susceptible to pollen limitation when pollinators are in short supply (Larson and Barrett, 2000). These factors may greatly limit the success of many rare plant species.

Over the long term, the potentially negative fitness effects of sessile organisms persisting in a small population may be partially ameliorated through the ability to self-fertilize. Selfing taxa often occupy habitats with low pollinator services, such as those occurring in a restricted geographic range (Lloyd, 1980). Natural selection may favor self-compatible individuals in the face of low pollinator service, even at a cost of reduced heterozygosity and/or lower offspring quality or quantity, if it provides the plant with reproductive assurance (''reproductive assurance hypothesis'' sensu Baker, 1955; Stebbins, 1957; also see Charnov, 1982). However, populations with increased rates of self-fertilization may be prone to inbreeding depression, which may result in lower seed set and fitness when compared to populations receiving large amounts of outcross pollen (Jennersten, 1988a; Lamont et al., 1993; Ågren, 1996; Fischer and Matthies, 1998). Inbreeding depression may, in turn, have potentially serious negative consequences for population persistence (Oostermeijer, 2000) as genetic diversity and fitness is reduced over time (Ellstrand and Elam, 1993). Despite the risks selfing imposes through a reduction in genetic variation and offspring vigor, it can provide a means for persistence when pollinators are scarce.

Here, we examined the degree of pollen limitation and compatibility system for a rare herbaceous perennial, *Polemonium vanbruntiae* Britton. Although the genus is well-studied, the pollination biology, reproductive strategies and mating system of *Polemonium vanbruntiae* were unknown. Because plant mating systems affect population genetic diversity (Hamrick and Godt, 1989), and potentially population persistence, an initial step in the development of an effective management plan for rare plants should be an understanding of the taxon's reproductive biology (Hamrick et al., 1991). Indeed, the lack of data on rare species biology is repeatedly cited as a shortcoming of threatened and endangered species' recovery plans (Schemske et al., 1994; Clark et al., 2002).

The genus *Polemonium* contains about 35 taxa (Porter and Johnson, 2000) characterized by a diverse assemblage of floral structures, mating systems, and pollinators (Grant and Grant, 1965). Self-incompatibility and self-compatibility both exist within the genus *Polemonium*. It is posited that *P. pulcherrimum* may have partial self-compatibility (Grant and Grant, 1965), but *P. viscosum* and *P. foliosissimum* are entirely self-incompatible (Galen, 1985; Zimmerman, 1980). *Polemonium vanbruntiae* is in the same clade as the European *P. caeruleum* (A.C. Worley, personal communication), and *P. caeruleum*'s mating system has been characterized as facultatively xenogamous and autogamous (Ostenfeld, 1923; Plitmann, 1994). *Polemonium vanbruntiae* was reported self-incompatible (Popp, 1990), but without an experimental test of this assumption.

Overall, we were interested in elucidating the mating system of *P. vanbruntiae* and determining whether insufficient levels of pollen receipt may be one of several factors contributing to rarity. Given the small, fragmented nature of *P. vanbruntiae* populations, we hypothesized that populations would be pollen-limited and increased levels of outcrossing would result in an increase in female reproductive success. In particular, we sought to: (1) characterize the mating system of *P. vanbruntiae*; (2) examine the degree of pollen limitation both spatially and temporally; and (3) determine the effect of geitonogamous and autonomous self-fertilization on female reproductive success when compared to purely outcrossed and open-pollinated plants. Our study provides critical data on the reproductive biology and possible factors limiting the persistence of *P. vanbruntiae*, which can inform further studies on the life history and population dynamics of this globally threatened species.

2. Materials and methods

2.1. Study system

Polemonium vanbruntiae is listed as a globally threatened perennial plant species which is extirpated from New Brunswick (NatureServe, 2005), but small populations persist in southern Quebec, eastern Maine, Vermont, and New York, south to Maryland and West Virginia (Fernald, 1950; Gleason and Cronquist, 1991; Crow and Helquist, 2000). *Polemonium vanbruntiae* occurs in wetland habitats, including shrub swamps, marshes, wooded floodplains, forested swamps, and moist roadsides, at elevations generally above 330 m in the northeastern US. The species has a global conservation rank of G3 (''vulnerable to extirpation or extinction;''; NatureServe, 2005), and fewer than 100 populations remain worldwide.

Polemonium vanbruntiae flowers are protandrous and herkogamous, which may signify a reliance on pollinators to transfer gametes. The stamens become functionally mature prior to maturation of the pistil and, as the corolla opens, the unreceptive stigma is exserted beyond the stamens, surpassing the corolla by 5–7 mm (Gleason and Cronquist, 1991; Fig. 1). Upon fertilization, flowers mature into fruits comprised of a capsule with three locules containing 1–10 seeds per locule (Thompson, 1991). The capsule is surrounded by the calyx, which becomes papery as it matures. Seeds require a period of winter dormancy in order to germinate successfully (Brumback, 1989). Seeds are passively dispersed around the parent plant and may be dispersed long distances by winter winds and spring floodwaters (Sabourin, 2002). *Polemonium vanbruntiae* can also reproduce vegetatively via rhizomes and may be capable of forming large, interconnected clones (Deller, 2002), although the degree of clonal diversity in natural populations has yet to be assessed.

2.2. Study sites

In 2004, we conducted pollen limitation studies in three Vermont populations: Blue Banks (BB), Abbey Pond (AP), and Forest Road 233 (FR). In 2005, we conducted pollen limitation and self-compatibility experiments in a single Vermont population in Camel's Hump State Forest (CHSF). The farthest sites