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Original article

Effects of pollination timing and distance on seed production in a dioecious weed *Silene latifolia*

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ABSTRACT

Silene latifolia Poir. (white cockle or white campion) is an important invasive weed in North American agriculture. It exhibits dioecy, therefore, both male and female plants are required in order for seed production to occur. However, dioecious species being invasive is not common because of their limitations in pollination and subsequent seed production. The objective of this study is to determine the effect of pollination timing and distance on seed production of *Silene latifolia*. A series of experiments including pollination exclusion, timing and pollination distance were conducted in 2009 and 2010 at or around Saskatoon, Saskatchewan. For pollination exclusion, exclosures were built around the natural female plants for exclosure, sham-exclosure, and male and female combined treatments. Pollination timing was studied by applying exclosure, non-exclosure, night-exclosure, and day-exclosure treatments to individual female plants. Female plants were transplanted along a linear interval at six different distances from the pollen source to study the effect of pollination distance. *S. latifolia* was exclusively insect-pollinated and pollination occurred both day and night; however, in one year, pollination occurred mainly at night. Female plants that were in the range of 0–4 m from a compatible pollen source experienced no limitation to pollination. However, when the distance was increased further up to 128 m, pollination levels and subsequent seed production were declined. Moreover, there were differences in seed production between years suggesting that pollination was affected by the environmental conditions during pollination and the crop that white cockle was grown in. These experiments indicate that seed production in *S. latifolia* is limited by insect-pollination. Although there was pollination limitation for seed production at greater distances from a pollen source, the high fecundity rate (3000–18000 seeds per plant) resulted in a large seed output. Thus, we believe that a dioecious species may require characteristics that compensate the pollination limitation for a successful invasion.

1. Introduction

Plant invasions are an important consideration in weed management (Booth et al., 2003; Dekker, 2005; Radosevich et al., 2007). They can cause significant ecological and economic losses (Booth et al., 2003). However, the invasiveness of a species may be somewhat limited by its breeding system (Allard, 1965). It is generally believed that self-compatible species are likely to be more successful invaders than self-incompatible congeners (Baker, 1955; Hao et al., 2011; Rambuda and Johnson, 2004). Self-compatibility was found to be the common character of all annuals and most biennial weeds of Canada (Mulligan and Findlay, 1970). The invasiveness of self-incompatible plant species may be limited due to pollination restrictions (Petanidou et al., 2012).

Pollen limitation occurs when plants produce less seed than they would if sufficient pollen quantity were deposited on receptive stigmas (Knight et al., 2005; Ashman et al., 2004). Pollination limitation may hinder seed production, and as a result slow population growth rate (Davis et al., 2004). Pollination limitation has been reported in dioecious species because both male and female plants, as well as their pollinators, must live within relatively close proximity in space and time (Baker, 1955). Pollen limitation was observed in four dioecious plant species dependent on insect pollination (de Jong et al., 2005). Kay et al. (1984) obtained similar results in the dioecious species, *Silene dioica*. They concluded that the occurrence of pollination decreased when the distance

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between male and female plants increased. However, the furthest distance between females and the pollen source in all these studies was 15 m (de Jong et al., 2005). Few studies exist that consider the effects of distance on pollen limitation in potentially invasive dioecious weed species *Silene latifolia*.

Silene latifolia (Poir.) also known as white cockle or white campion, is an important dioecious weed across prairie regions of southern Canada and the northern United States (Royer and Dickinson, 1999). It is native to Eurasia and was introduced to North America in the early 1800s (McNeill, 1977). *S. latifolia* can be found in a variety of cropping systems and is a concern on no-till farms and forage pastures in the prairie provinces of Canada. Considerable damage can occur when establishing forage crops, as the fast-growing white cockle out-competes forage seedlings, resulting in poor forage stands. It is particularly problematic in areas where grain and forage are in rotation because of its biennial to short-lived perennial nature (McNeill, 1977). It has been found that North American populations have evolved to become considerably more aggressive than their European ancestors (Blair and Wolfe, 2004). Furthermore, it was suggested that a possible greater resource allocation to growth and reproduction when compared to its defense mechanisms in the non-native populations (Blair and Wolfe, 2004).

Young (2002) determined that noctuid moths were the most effective pollinator of *S. latifolia* in Colorado. However, little is known of the distance-dependent pollen limitation in this species or in dioecious plants in general. Characterizing the pollination ecology of *S. latifolia* may provide a model for other dioecious plants and help to evaluate the effect of dioecy on pollination limitation and its potential to affect invasiveness. The hypothesis of this study is that *S. latifolia* is pollen limited due to the dioecious nature of the species. The primary objective of this study is to determine the effect of pollination timing and distance on seed production of *S. latifolia*.

2. Materials and methods

A series of experiments (Pollinator exclusion, Pollination timing and Pollination distance) were conducted during 2009 and 2010 in central Saskatchewan.

2.1. Pollinator exclusion trial

2.1.1. Experiment design and location

This experiment was conducted in 2009 and 2010 near Meath Park, SK (53°18′36.53″ N, 105°20′17.74″ W). Treatments were set up in a randomized complete block design and were replicated eight times in 2009 and four times in 2010. Insect exclusion treatments including exclosure, non-exclosure and sham-exclosure were applied to single female plants. In 2010, a fourth treatment was added where single male and female plants were excluded from insect visits together. Male and female plants in this experiment were part of a naturally occurring *S. latifolia* population within a farmer's field where *Pisum sativum* L. (peas) and *Brassica napus* L. (canola) were grown in 2009 and 2010, respectively.

2.1.2. Experimental procedures

To examine the role of insects in pollination, we isolated naturally occurring female plants using different exclosure treatments. . Then, any open flowers were removed before treatments were applied in order to ensure that no pollination occurred before treatment application.

Exclosures were constructed using four wooden stakes, measuring 125 cm (height) by 4 cm (width) by 4 cm (width), as the frame. Stakes were forced approximately 30 cm into the ground to form a 100 cm (height) by 50 cm (width) by 50 cm (width) wooden frame centered on individual female plants.

For the exclosure treatment, female plants were fully surrounded by black fiberglass insect screening (mesh size 0.51 × 0.67 mm) to exclude possible insect pollinators. For the sham-exclosure treatment, the north facing side of the exclosure was left uncovered. The sham exclosures were designed to expose plants to insect pollinators, while partially controlling for shading as a limiting factor in seed production. In addition, sham-exclosures could eliminate the physical presence of the exclosure as a possible deterrent for pollinators. For the non-exclosure treatment, female plants were left fully exposed. On July 9th, 2010, between 14:00 and 16:00 h, incident light was measured using a Quantum Meter® at all experimental sites both under the fiberglass screen (where applicable) and in direct sunlight.

2.1.3. Data collection

In 2009, exclosures were constructed on June 24th and plants were harvested on August 27th. In 2010, treatment exposure commenced on June 25th and plants were harvested August 24th. Following the treatment period, both ripe and immature seed bearing capsules were removed, air-dried and seeds were separated from respective capsules, weighed and counted by hand. Following removal of capsules, entire plants were removed at the soil surface, oven-dried at 70 °C, within 3 h of harvest, for approximately 48 h. Following drying, whole dried plants were weighed for biomass readings.

2.2. Pollination timing trial

2.2.1. Experiment design and location

This experiment was conducted in 2009 and 2010 in Saskatoon, SK (52°06′31.36″ N, 106°42′25.11″ W). Treatments were arranged in a randomized complete block design replicated four times. Exclosure treatments were applied to individual female plants. Treatments were exclosure, non-exclosure, night-exclosure, and day-exclosure (Fig. 1). The experimental site was a grassy area composed partly of a naturally occurring population of both male and female *S. latifolia* plants. Male plants served as the pollen source during treatment application. Female plants for the experimental treatments were transplanted approximately 2 m from the pollen source.

2.2.2. Experimental procedures

Un-pollinated female plants were grown in a controlled growth environment prior to introduction to the experimental location. These female plants were grown from seed obtained from a naturally growing population of *S. latifolia* Poir. located near Meath Park, SK (53°18′36.53″ N, 105°20′17.74″ W) in 2009. The plants were allowed to reach flowering so identification of sex could be made prior to introduction. Each female plant was grown in a single 15 × 18 cm pot using No. 4 Sunshine® Potting Mix. Plants were grown under 18 h of light at 22 °C and 6 h of dark at 16 °C for approximately 35 days. Light intensity was 1185 μmol m^{-2} s^{-1} in the chamber and was measured using a Quantum Meter® at the top of the plant canopy. The plants were then transplanted. Plants for the exclosure treatment had the exclosures built (similar to pollination exclusion trial) at the time of transplanting. Plants for the day-exclosure treatment were introduced then covered with moveable exclosures. Four moveable exclosures were built for this experiment for day-exclosure and night-exclosure treatments. The moveable exclosures prevented insect visits during the day (day-exclosure) and during the night (night-exclosure). These treatments required twice-daily moving of the exclosures just prior to twilight and 1 h prior to sunrise (Dreisig, 1986). Moveable