



## 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, enclosures were built around the natural female plants for enclosure, sham-enclosure, and male and female combined treatments. Pollination timing was studied by applying enclosure, non-enclosure, night-enclosure, and day-enclosure 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.

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## 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 enclosure, non-enclosure and sham-enclosure 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 enclosure treatments. Then, any open flowers were removed before treatments were applied in order to ensure that no pollination occurred before treatment application.

Enclosures 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 enclosure 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-enclosure treatment, the north facing side of the enclosure was left uncovered. The sham enclosures were designed to expose plants to insect pollinators, while partially controlling for shading as a limiting factor in seed production. In addition, sham-enclosures could eliminate the physical presence of the enclosure as a possible deterrent for pollinators. For the non-enclosure 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<sup>®</sup> at all experimental sites both under the fiberglass screen (where applicable) and in direct sunlight.

### 2.1.3. Data collection

In 2009, enclosures 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.

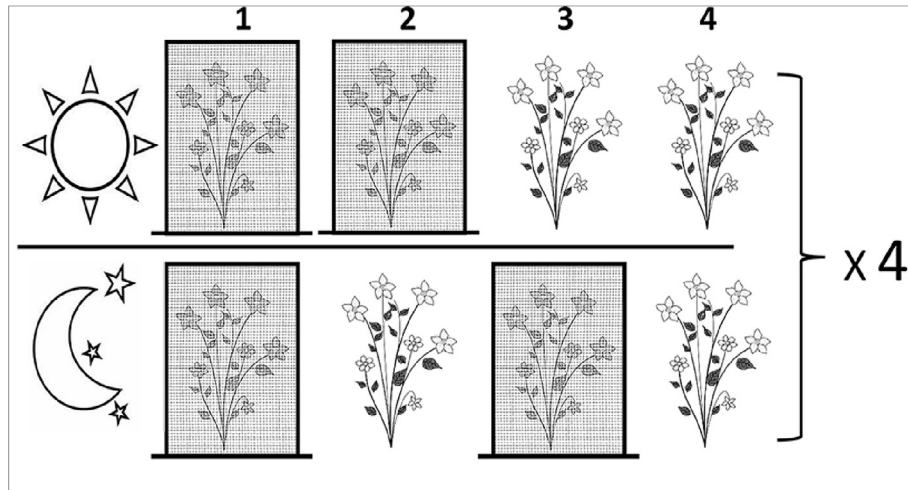
## 2.2. Pollination timing trial

### 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. Enclosure treatments were applied to individual female plants. Treatments were enclosure, non-enclosure, night-enclosure, and day-enclosure (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<sup>®</sup> 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<sup>-2</sup> s<sup>-1</sup> in the chamber and was measured using a Quantum Meter<sup>®</sup> at the top of the plant canopy. The plants were then transplanted. Plants for the enclosure treatment had the enclosures built (similar to pollination exclusion trial) at the time of transplanting. Plants for the day-enclosure treatment were introduced then covered with moveable enclosures. Four moveable enclosures were built for this experiment for day-enclosure and night-enclosure treatments. The moveable enclosures prevented insect visits during the day (day-enclosure) and during the night (night-enclosure). These treatments required twice-daily moving of the enclosures just prior to twilight and 1 h prior to sunrise (Dreisig, 1986). Moveable



**Fig. 1.** Pollination timing trial design: Depiction of pollination timing trial treatments. Plants to the right of the sun are female plants during the day and plants right to the crescent moon are female plants during the night. Plants vertically adjacent to each other (separated by the long horizontally line) represent the same plant at different times (day or night). Boxes drawn surrounding plants represent exclusion structure designed to exclude insect visitors. Moving from left to right are (1) exclusion, (2) day-exclusion, (3) night-exclusion, and (4) non-exclusion treatments.

exlosures that covered female plants during the day were moved in the evening to cover female plants during the night plants and vice-versa to uncover the opposing treatment. Following the treatment application period, exclusions were built around the non-exclosure and night-exclosure treatments to discontinue pollinator visitations to pistillate flowers and allow ripening to occur. Prior to enclosure construction, all open flowers exposed were tagged to facilitate identification during capsule harvest. Flowers were left to ripen until visual indications of physiological maturity were present i.e. capsule hardening and subsequent color change.

### 2.2.3. Data collection

In 2009, treatments were applied commencing July 10th and all plants were fully excluded on July 22nd and in 2010, on July 9th and July 24th, respectively which allowed adequate time for pollination to occur. Flowers and entire plants were harvested following the maturation period. In addition, seed count and biomass data were recorded as previously described.

## 2.3. Pollination distance trial

### 2.3.1. Experiment design and location

This experiment was conducted during the 2009 and 2010 growing seasons near Prince Albert, SK at the Conservation Learning Centre (53°01'43.17" N, 105°45'53.12" W). There were six distance treatments for this experiment. Distance treatments were the distance between females and the pollen source (males). Distances were measured along a linear interval at 4 m, 8 m, 16 m, 32 m, 64 m, and 128 m along a transect. The linear interval was measured running directly south in a commercial annual grain crop field. The linear interval began at the edge of a perennial forage crop, which consisted partly of a dense natural population of male and female *S. latifolia* plants. The natural population served as both a reference point and pollen source for the trial.

### 2.3.2. Experimental procedures

The 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. Thirty female plants were introduced into this site from the controlled growth

environment as previously described. In 2009, 2010, female plants were transplanted into canola and *Avena sativa* L. (oat) crops, respectively. Five female plants were transplanted at each of the six distance transects. Transplants at each distance were spaced 1 m apart and arranged in a single file row perpendicular to the linear interval. This design was used in order to maintain accurate distance from the pollen source at each distance. In both years, a 60 cm area surrounding each transplant was cleared by uprooting the canola or crop to reduce interspecific competition. Furthermore, the annual cropping area was surveyed weekly to ensure no other pollen source was present (i.e. other *Silene* species). This surveying procedure ensured pollen traveling to respective distances was from the designated pollen source.

### 2.3.3. Data collection

In 2009, female plants were transplanted on July 8th and plants were harvested August 22nd. In 2010, female plants were transplanted on June 23rd and plants were harvested August 26th. This protocol allowed sufficient time for pollinators to pollinate given the experimental conditions. Once capsules started ripening, they were removed weekly to prevent seed loss. Following the treatment period, both ripe and immature seed bearing capsules were removed. Entire plants were also harvested for biomass determination. Methodology for data collection was the same as described earlier in the pollinator exclusion trial. In 2009, data was not obtained for 128 m treatment as the transplants didn't survive.

## 2.4. Statistical analysis

Analysis for both the pollinator exclusion trial and the pollination timing trial was very similar. Seed counts were log transformed to equalize variance. Analysis was performed using Analysis of Variance (ANOVA) using SAS Proc Mixed (SAS Institute, 2008). All enclosure treatments were considered fixed in the analysis, whereas block and year were considered random factors. For the pollinator exclusion trial, 2009 and 2010 were analyzed separately because a fourth treatment was added in 2010; therefore, years could not be combined. The pollination timing trial was analyzed by year due to differences in the environment (Table 1).

Data for the pollination distance trial was tested for significance by year using nonlinear regression analysis of curves and model

**Table 1**  
Weather data table: 1971–2000 data obtained from Environment Canada (2010).

Location	Month	Rainfall			Temperature		
		2009	2010	30-yr Average	2009	2010	30 yr-Average
		mm			°C		
Saskatoon	April	2.8	72.6	15	2.9	6.9	4.7
	May	6.9	128.5	41.5	8.7	9.7	11.8
	June	75.5	169.0	60.5	14.8	15.3	16.0
	July	50.3	46.0	57.3	15.8	17.6	18.3
	August	82.4	43.7	35.4	15.9	16.2	17.6
	Total	215.1	387.2	194.7	–	–	–
Prince Albert	April	2.8	105.2	16.6	2.0	6.0	3.1
	May	37.7	81.2	44.3	7.9	9.6	10.5
	June	70.4	128.0	72.5	14.6	15.7	15.2
	July	92.4	92.2	76.8	16.3	18.0	17.5
	August	67.8	26.4	58.0	15.8	16.5	16.3
	Total	268.3	327.8	251.6	–	–	–

parameters using the *multdrc* and *compParm* extension packages in R (Version 2.6.1). In this analysis, global regression and parameters were compared to individual years for each variable tested. This analysis was done by combining years for each variable and then comparing years individually to the global values. The relationship between variables and distance was fit using the 2-parameter power relationship shown:

$$y = a\chi^b$$

In this equation,  $y$  is the dependent variable (seed number or capsule number),  $a$  is the  $y$ -intercept,  $\chi$  is the independent variable (distance), and  $b$  indicates the slope of the line (negative in this case). Where no difference was observed between years for the variable tested, years were combined. A line of best fit was then calculated using parameters from the global model to predicted values to describe both years of data.

### 3. Results and discussion

#### 3.1. Pollinator exclusion

In both years, there was no seed production when pollinators were excluded (Fig. 2A–F). In contrast, all other treatments resulted in seed production and differed from the enclosure treatment ( $P < 0.05$ ). This finding establishes that *S. latifolia* relies on insects to carry pollen from staminate flowers to pistillate flowers and supports findings by Young (2002) who found that in Colorado, *S. latifolia* is pollinated by insects.

Combined-exclosure treatment (male and female combined) resulted in fewer seeds per plant and per capsule than sham-exclosure and non-exclosure treatments, but similar capsule number per plant as the sham-exclosure treatment (Fig. 2B, D, and F). In 2010, when male and female plants were in the same enclosure, some pollination occurred and seed set differed significantly from the enclosure treatment. It was assumed that any seed production that occurred in the combined-exclosure treatment was the result of wind pollination. The incidence of wind pollination was minimal and therefore the number of capsules pollinated per plant in the combined-exclosure treatment was lower than the number of capsules pollinated in the non-exclosure treatment, where insect visitation to flowers was permitted.

The sham-exclosure treatment reduced seed number per plant and seed number per capsule compared to the non-exclosure treatment in 2009 only (Fig. 2A and C). Furthermore, the sham-exclosure treatment did not significantly reduce the number of flowers pollinated per plant compared to the non-exclosure

treatment (Fig. 2E and F). It is possible that this treatment may have partially impeded pollinators, as only the north facing sides of sham-exlosures were open. If pollinators approached from all directions, sham-exlosures may have obstructed three-quarters of pollinator visits.

Reduced seed production per flower between sham-exclosure and non-exclosure treatments in 2009 may be an indication of reduced deposition of pollen by pollinators (Wilcock and Neiland, 2002). A pollinator must effectively remove, transfer, and deposit pollen onto a receptive stigma in order for pollination and subsequent ovule fertilization to occur (Faegri and Van der Pijl, 1971). With bees, the frequency and duration of floral visits may determine how much pollen is removed (Davis, 1997) or in this case deposited. Fewer pollen grains deposited would result in fewer seeds produced per flower. This finding was otherwise undetectable by analyzing differences in seed number per plant between enclosure treatments alone. In general, this result agrees with seed produced per plant, as higher or lower seed production per flower would increase or decrease total seed production per plant, respectively.

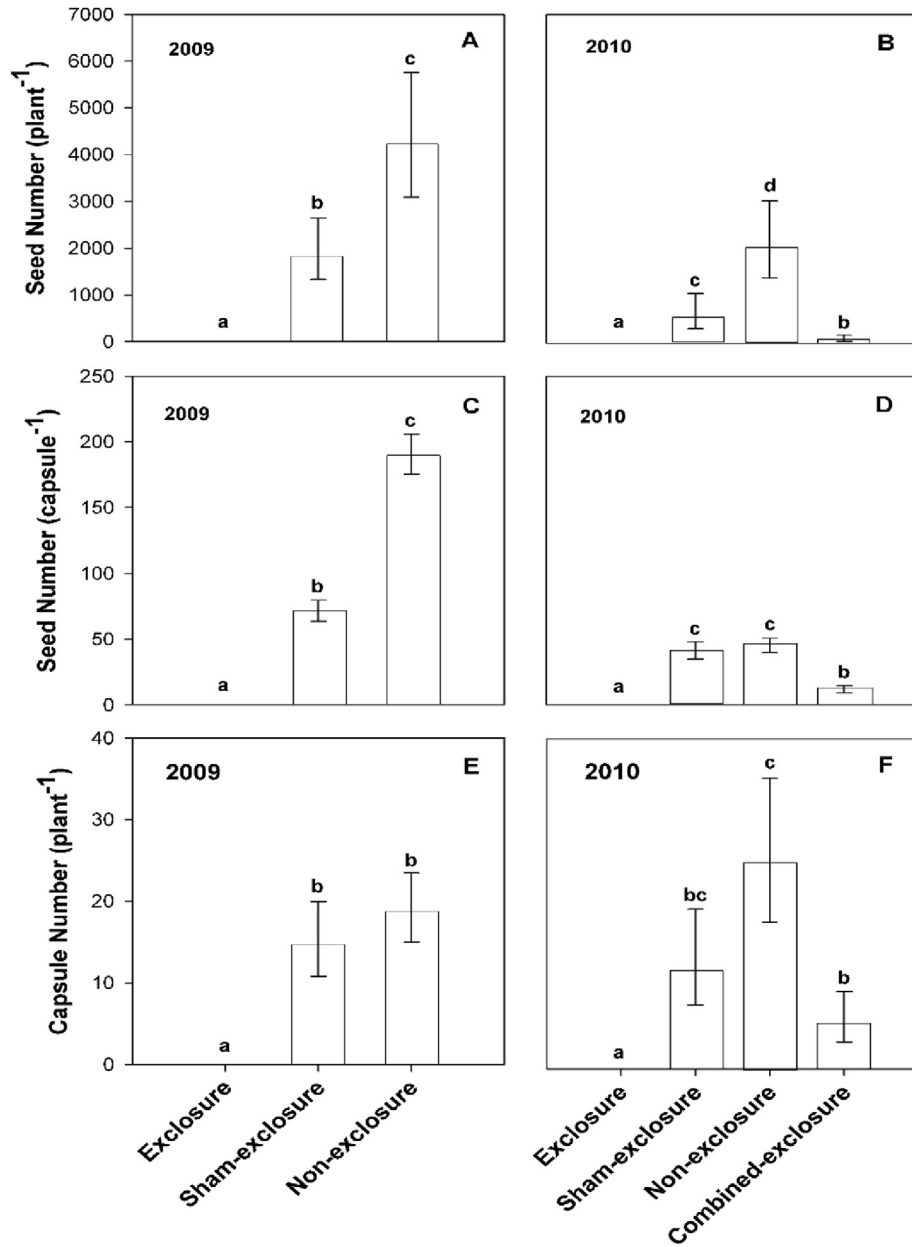
Capsule number per plant was comparable between years; however, there was less seed production per plant and per flower in 2010 when compared to 2009. This reduction in seed production may be due to the heavy rainfall that occurred in 2010 that may have reduced pollinator activity and effectiveness (Table 1).

#### 3.2. Pollination timing

Pollination timing affected the number of seeds produced per plant, and per capsule, and capsule number per plant ( $P = < 0.001$ ; Fig. 3). As observed in the previously described pollinator exclusion trial, there was no seed production in either year when pollinators were excluded. In 2009, the enclosure treatment differed from all other treatments whereas in 2010, the enclosure treatment differed from all other treatments except the night-exclosure treatment.

Excluding pollinators during the day did not affect seed production compared to non-exclosed plants in both years (Fig. 3). The timing of pollinator exclusion affected seed production in 2010 where almost no seeds were produced in the night pollination enclosure treatment. In contrast, seed production in the day-exclosure treatment did not differ from the non-exclosure treatments in 2009 and 2010 for all variables tested indicating that night pollination occurred almost exclusively (Fig. 3). This suggests night pollinators were responsible for the majority of pollination in 2010 only.

In 2009, seed production per capsule was significantly lower in the night-exclosure treatment compared to the non-exclosure



**Fig. 2.** Pollinator exclusion trial: Seed number per plant, seed number per capsule, and capsule number per plant produced by each exclosure treatment in 2009 and 2010 (left to right respectively). Means followed by the same letter are not significantly different at  $P < 0.05$ .

treatment (Fig. 3C). This outcome may indicate lower pollinator efficiency in only night-exclosure treatments (i.e. day-pollinated flowers). This result supports findings by Young (2002) who concluded that nocturnal moths to be the most effective pollinators of *S. latifolia* compared to diurnal bees and flies.

In 2009, more seed was produced per plant and per capsule but from fewer capsules when compared to 2010 (Fig. 3A and C). Therefore, pollinators in 2009 may have visited flowers more frequently and for longer periods of time when compared to 2010 (Davis, 1997). Excessive precipitation in 2010 may have reduced pollinator effectiveness, thereby reducing pollination and seed production. In 2010, total rainfall was more than double the average and during the treatment period (July 9th – July 24th) rain or severe thunderstorms were observed on 50% of the days (Table 1). Excess rainfall may have restricted the activity of daytime pollinators (Corbet, 1990), as there was a considerable reduction in seed

production for night-exclosure plants (i.e. day-exposed). Rainfall can cause irreparable damage to anthers and pollen thereby negatively affecting pollen removal, deposition, or germination (Corbet, 1990). Furthermore, dilution of nectar by free water may interfere with important plant–insect interactions. However, given that seed production was reduced only in the night-exclosure (i.e. day-exposed) treatment, reduced daytime pollinator activity probably caused reduced seed production.

Overall, the results from this study suggests that *S. latifolia* is both day and night pollinated, however, nocturnal pollinators are found to be more efficient than diurnal pollinators.

### 3.3. Pollination distance

In both years, seeds per female plant declined with distance from the pollen source patch (Fig. 4A). However, the decline in seed



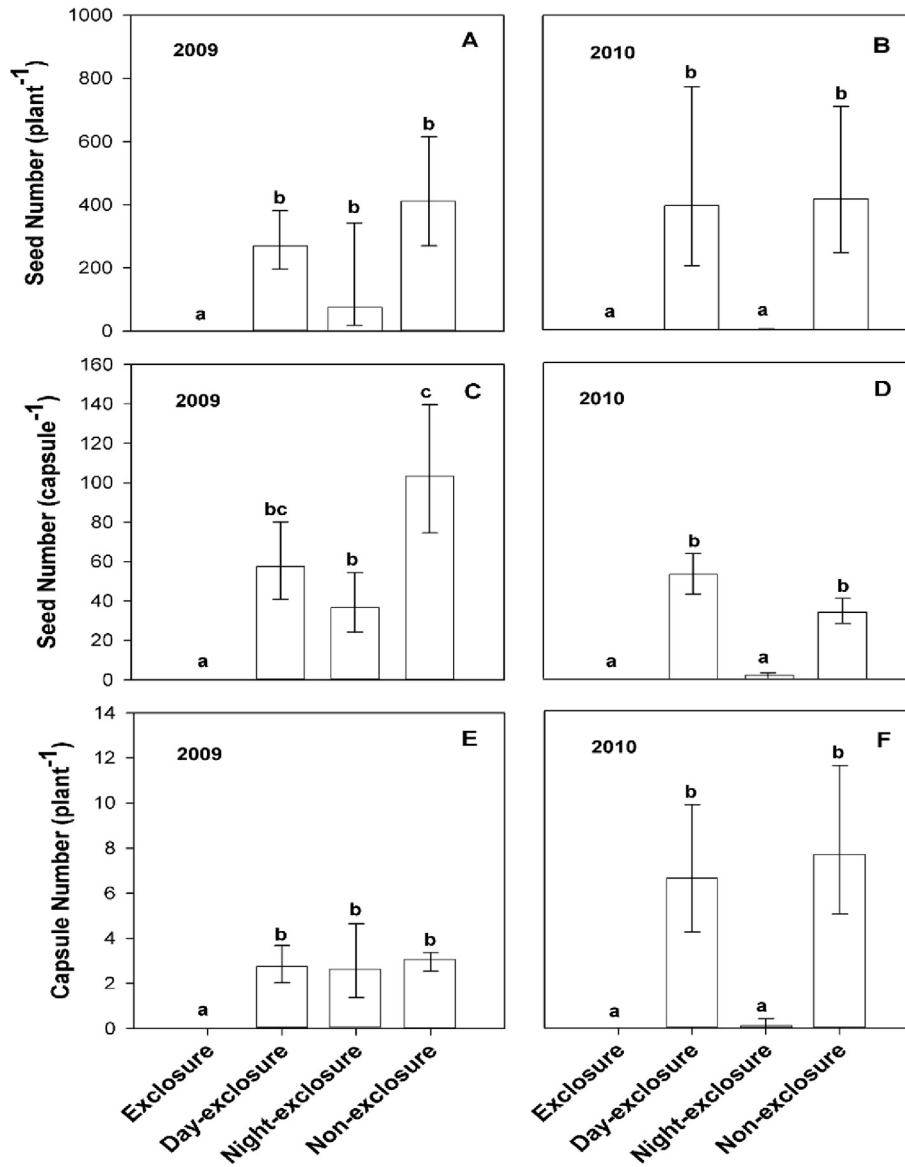


Fig. 3. Pollination timing trial: Seed number per plant, seed number per flower, and capsule number produced per plant produced according to each exclusion treatment in 2009 and 2010 (left to right respectively). Means followed by the same letter are not significantly different at  $P < 0.05$ .

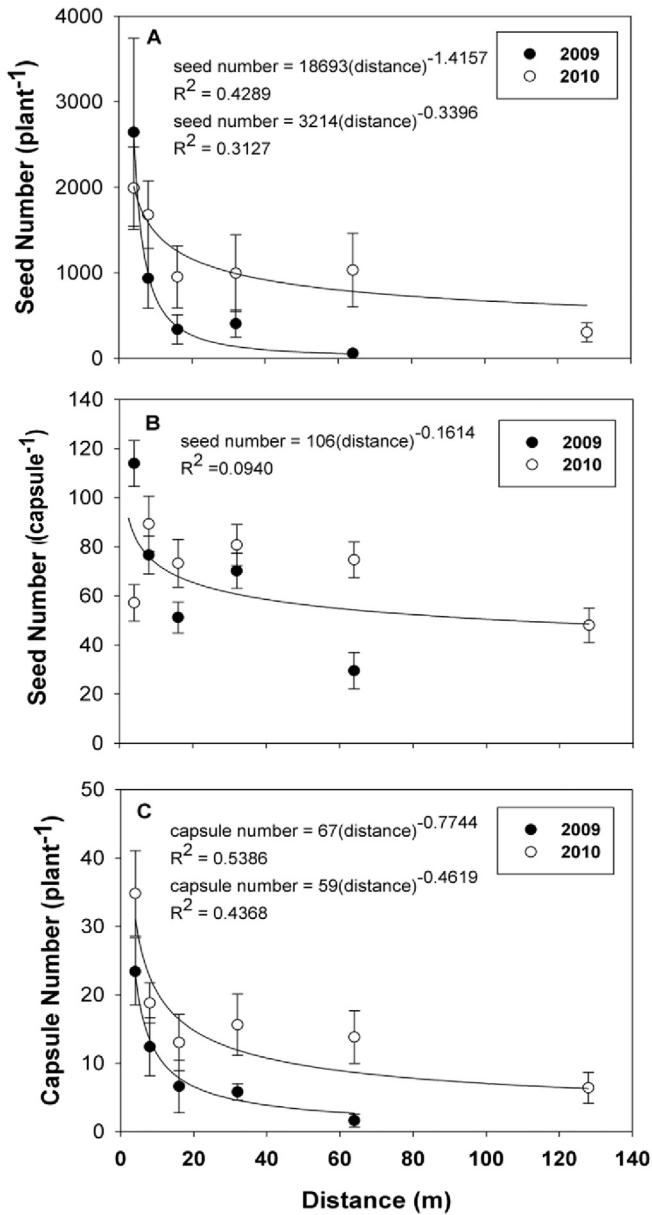
production as affected by distance differed between the years (Table 2 and Fig. 4A). The model predicted that in 2009 and 2010 plants at 0 m would produce 18,693 and 3214 seeds, respectively (Fig. 4A). However, when the distance was increased further up to 128 m, seed production were declined, suggesting that insects were less likely to carry pollen great distances from staminate to pistillate flowers. Distance-dependent pollination limitation has also been reported in the other dioecious plants, *Valeriana dioica*, *Salix repens*, *Asperagus officinale*, and *Bryonia dioica* (de Jong et al., 2005). In that study, when female plants were placed from 0 m up to 25 m from a compatible pollen source; pollination was found to be limited in all species at increasing distance from the pollen source.

The number of seeds produced per capsule did not differ between years ( $P = 0.1338$ , Fig. 4B). The number of seeds per capsule declined slightly with distance from the pollen source (Fig. 4B). The lack of difference between years for number of seeds produced per capsule may indicate that pollinators were equally effective at all distances and in both years. As there was a decline in the number of seeds produced per capsule with distance, seeds produced per

capsule may not have been affected by pollinator competition. Thus, once *S. latifolia* flowers had been located by pollinators, duration of visit would be independent of distance or crop. This result suggests that pollinators deposited equal quantities of pollen at each distance regardless of other factors (such as crop). One way this outcome could have been accomplished is by comparable visit duration of insect pollinators (Davis, 1997) at each distance (i.e. the act of landing versus hovering moths). Therefore, night-flying, settling moths, may be what is important here.

The number of capsules per plant was lower in 2009 than in 2010 and declined with distance at a greater rate ( $P = 0.0078$ ; Fig. 4C). Thus, the number of flowers pollinated per plant resulted in differences between the years in seed number per plant because seed number per capsule did not differ.

The different crops present in 2009 and 2010 may explain the difference between years for seed number per plant and capsule number per plant. In 2009, the crop surrounding the experimental female plants of *S. latifolia* was canola, which flowers indeterminately and is primarily pollinated by honeybees (Sabbahi et al.,



**Fig. 4.** Pollination distance trial: Distance-dependent effects on pollination in *S. latifolia*. (A) Seed number per plant, (B) Seed number per capsule, and (C) Capsule number per plant produced at each distance in 2009 and 2010.

2005). The presence of canola co-flowering insect-pollinated species, could have created pollinator competition in 2009 (Campbell, 1985; Knight et al., 2005). In contrast, in 2010 the crop was oat, a self-pollinated cereal crop lacking conspicuous flowers and floral rewards, there should have been no pollinator competition in 2010.

In 2009, co-flowering competition likely occurred during the day because flowering of *S. latifolia* and canola was observed to overlap. Furthermore, honeybees are diurnal insect pollinators and have previously been observed to be mainly responsible for day-pollination of *S. latifolia* (Young, 2002). The previously described pollination timing trial found no difference between seed production in day- and night-exposed plants. Therefore, having a co-flowering insect-pollinated species present may have decreased pollination of *S. latifolia* overall during the day. There are no reports of nocturnal pollination of canola flowers, so pollinator competition may not have occurred at night.

Overall, it is possible that diurnal pollinators neglected *S. latifolia* in the presence of numerous canola flowers causing less seed production in *S. latifolia* at further distances from the pollen source. A similar process of preferential selection of flowers by insects were also reported in two dioecious species; *Stellaria pubera* and *Claytonia virginica* (Campbell, 1985). When both species were flowered together, *S. pubera* showed a decreased seed production; and when flowers of *C. virginica* were removed, seed production in *S. pubera* has increased; this suggests that *S. pubera* suffers pollination limitation due to the presence of more preferred co-flowering species.

Lower seed production per plant in 2009 may also be explained by pollination failure due to the presence of hetero-specific pollen from the canola crop. Hetero-specific pollen can reduce fertilization and seed production because of chemical or physical inhibitors present during pollen germination (Wilcock and Neiland, 2002) and such transfer also reduces the efficiency of the donor plants because of loss of pollen to foreign stigmas.

**4. Conclusions**

*S. latifolia* is pollen limited due to the dioecious nature of the species. It is mainly insect pollinated with only minimal occurrence of wind pollination when males and females are in very close proximity. *S. latifolia* is mostly dependent on night pollination but it can be pollinated during the day. Finally, female plants at further distances from the pollen source produce less seed compared with female plants closer to the pollen source probably because insects were less likely to carry pollen further distances. Due to the self-incompatible nature of the species, seed production depends on the relative proximity of male, female plants and their pollinators. In a natural setting, where males and females are separated by distances greater than 8 m, seed production can be reduced because of limited pollination.

However, some scientists believe that species may become successful invaders regardless of their self-incompatibility status (Petanidou et al., 2012). Moreover, several studies have shown other traits such as a fast relative growth rate (Grotkopp et al., 2002), a higher specific leaf area (Feng et al., 2008; van Kleunen et al., 2010) and a higher N allocation to photosynthesis (Feng et al., 2008) as associated with invasiveness. A previous study by Blair and Wolfe (2004) also found that introduced *Silene* populations are more invasive because of their early emergence, higher growth rate and greater reproductive ability when compared to the

**Table 2**

P-values from non-linear regression ANOVA in R. Site year data compared to global data for each variable. Equation  $y = a \chi^b$ .

Variable	Model compared	Parameters compared	
		Intercept (a)	Slope (b)
	Site-year: Global	Site-year: Global	Site-year: Global
Seed number (plant <sup>-1</sup> )	0.0044	0.0016	0.0036
Seed number (capsule <sup>-1</sup> )	0.1338	0.0558	0.1154
Capsule number (plant <sup>-1</sup> )	0.0078	0.2122	0.8023

native populations. From the results of these experiments it seems evident that the dioecious nature of *S. latifolia* may limit its invasibility. However, with the amount seed produced by a single plant (3000–18000 seeds plant<sup>-1</sup>), even a limited pollination will result in significant seed output. Overall, it is possible to believe that a dioecious species may require characteristics such as high fecundity that compensate the pollination limitation for a successful invasion.

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