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The contribution of epigean insects to commercial cranberry pollination

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ABSTRACT

Flowering plants rely on a wide range of vectors to move pollen among flowers. Cranberry (*Vaccinium macrocarpon* Aiton (Ericaceae)) appears to be mostly pollinated by flying insects, in particular bees, but as a prostrate plant, it is easily accessible to epigean, i.e., crawling, insects. To separate the contributions of flying and epigean insects, metrics related to fruit yield were assessed under three treatments: no insect access, epigean insect access, and all insect access. As expected in a plant with limited self-pollination, the all insect access treatment produced the highest fruit set, number of seeds per fruit, and fruit weight. There was no difference in any of the measures between the two exclusion treatments. This was likely due to the methods of exclusion used, which may have increased mechanical agitation in the no insect access treatment, or failed to exclude tiny insects, like thrips (Thysanoptera). However, non-bee vectors (either mechanical agitation or insects) were responsible for 49% of fruit set. Although bees are generally necessary for commercially viable cranberry yields, other vectors contribute a larger proportion of pollination services than previously thought.

RÉSUMÉ

Les plantes à fleurs dépendent d'une grande variété de facteurs pour déplacer le pollen parmi les fleurs. La canneberge (*Vaccinium macrocarpon* Aiton (Ericaceae)) semble être largement pollinisée par des insectes volants, en particulier par les abeilles, mais en tant que plante retombant et s'étendant vers la terre, elle est aussi facilement accessible aux insectes epigeans, c'est-à-dire aux insectes rampants. Pour séparer la contribution des insectes volants et des insectes epigeans, des mesures du rendement en fruits ont été prises sous trois différentes conditions: pas d'accès pour les insectes, accès pour les insectes epigeans seulement, accès pour tous les insectes. Tel que prévu pour une plante qui a peu d'auto pollinisation, le traitement donnant accès à tous les insectes a produit le plus grand nombre de fruits, nombre de graines par fruit et poids du fruit. Il n'y a pas eu de différence dans aucune des mesures pour les deux traitements ayant des exclusions. Cela est probablement dû aux méthodes d'exclusion utilisées, qui ont pu créer une augmentation de l'agitation mécanique dans le traitement sans insecte ou être incapable de bloquer les tous petits insectes, tels que les thysanoptères (Thysanoptera). Cependant, les facteurs non liés aux abeilles (soit agitation mécanique ou insectes) étaient responsables pour 49% du nombre de fruit. Bien que les abeilles soient généralement nécessaires pour une culture commerciale viable des canneberges, d'autres facteurs contribuent à la pollinisation d'une manière plus importante qu'on aurait pu le penser.

INTRODUCTION

Most flowering plants require some kind of vector to move pollen among flowers, with around 87.5% of angiosperms relying on animals for this service (Ollerton et al. 2011). Insects are by far the most common pollinators, and are thought to have played a key role in the radiation of modern flowering plants (Regal 1977). Among insects, bees, in particular the social bees, are by far the most important pollinators (Potts et al. 2010). As a result, pollinator research has tended to focus on bees or other flying insects. Much less attention has been paid to epigean, i.e., crawling insects.

Cranberry (*Vaccinium macrocarpon* Aiton (Ericaceae)) is a perennial plant with a prostrate, vining habit that sends up flowering shoots, called "uprights". Each upright produces up to eight flowers, which open sequentially from bottom to top

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over the course of several weeks (Eck 1990). The flowers are protandrous (Rigby and Dana 1972), which, along with the sequential blooming of flowers on an individual upright, makes self-pollination unlikely. When self-pollination does occur, fruit production is lower (Sarracino and Vorsa 1991). As a result, pollination by insect vectors is required for maximum fruit yield. The main pollinators are bees, with bumble bees (*Bombus* spp. Latreille (Hymenoptera: Apidae)) generally performing best. Although honey bees (*Apis mellifera* Linnaeus (Hymenoptera: Apidae)) are often used for supplemental pollination, there is mixed evidence of their efficacy in cranberry (Kevan et al. 1983; Mohr and Kevan 1987; MacKenzie 1994; Ratti et al. 2008; Evans and Spivak 2006; Broussard et al. 2011). This is due to the plant's poricidal anthers, which require buzz pollination to effectively remove pollen. Bumble bees buzz pollinate, while honey bees do not, although it is argued that honey bees make up for less efficient pollination through greater numbers of foraging bees (Evans and Spivak 2006).

Efforts to maximize pollination rates in commercial cranberry operations have focused on bees because of their known effectiveness as cranberry pollinators (Mohr and Kevan 1987; Cane and Schiffhauer 2003). Other types of insect pollinators have been little studied in this crop (Gaines-Day and Gratton 2015). Recent work suggests that both agitation by wind and the activities of non-hymenopteran insects such as thrips (Thysanoptera) contribute to cranberry pollination (Gaines-Day and Gratton 2015). There is also evidence that in the related lowbush blueberry (*Vaccinium angustifolium* Aiton (Ericaceae)), nocturnal pollinators such as moths and mosquitoes may contribute to pollination success (Cutler et al. 2012). Cranberry grows as a low, sprawling mat, which raises the possibility that epigean pollinators could also access flowers. It was estimated recently that ~30% of extant arthropods regularly visit flowers (Wardhaugh 2015). This might involve activities such as florivory, predation, or collection of nectar or pollen, most of which could result in pollen movement at least on a small scale. Casual observations during research on bees in commercial cranberry fields in Newfoundland suggested that epigean pollinators could be contributing to fruit yield. There appeared to be higher fruit production under large aerial pollinator exclusion frames than would be expected by self-pollination (personal observation, 2013). This suggested that epigean insects may contribute significantly to yield in commercial cranberry crops. Given the pollination biology of cranberry, I predicted that if epigean insects do contribute to pollination, then the fruit set, number of seeds per fruit, and fruit weight would be lowest from completely isolated flowers, intermediate from those accessible by epigean insects, and highest from flowers with full insect access.

METHODS

Cranberry farms

This work was carried out at four commercial cranberry farms on the Island of Newfoundland, Canada. The native bee fauna is relatively small, with only 76 recorded species (Sellars and Hicks 2015), compared to over 200 species in mainland Atlantic Canada (Sheffield et al. 2003; 2008; 2009). Farm 1 (elevation 28 m) and Farm 2 (elevation 50 m) are located in western Newfoundland, near Stephenville, NL (48°33'N, 58°34'W). Farm 3 (elevation 74 m) and Farm 4 (elevation 99 m) are located in central Newfoundland, near Grand Falls-Windsor, NL (48°57'N, 55°40'W). The local climates in western and central Newfoundland are fairly similar, with average annual temperatures of 5 °C and 4.5 °C, and average annual precipitation of 1340 mm and 1099 mm, for Stephenville and Grand Falls respectively.

Fruit set, fruit weight and seed number

Two beds at each farm were selected; all planted with the Pilgrim variety of cranberry. In each bed, 25 points were selected, separated by at least 5 metres, avoiding areas with sparse vine growth. At each point, three groups of unopened flowers (7—24, average 12) were selected and the number of flowers recorded. Each group was made up of one to three flowering uprights, most often two, generally on the same vine. One group was covered with an open-bottom cage held to the ground with a metal skewer (epigean insect access). Cages were 10 cm diameter and 15 cm deep, made of fibreglass window screen (1.6 mm openings) reinforced with a popsicle stick along the seam and the rims of two 455 ml plastic cups at the top and bottom of the cylinder, with screen over one end. This prevented access by flying insects, but crawling insects could enter. Another group was placed in a nylon tulle bag (1.2 mm openings) to exclude all insects (no insect access). The upright stems and bottom of the mesh bag were gathered together around a wooden skewer and secured with floral tape. The third group was labelled and left accessible to all pollinators to assess normal fruit set (all insect access). Any resulting berries were collected in late September, when they were mature but not fully ripened to avoid losses due to fruit dropping or being eaten by wildlife. These were refrigerated in sealed bags to reduce water loss, and processed within one week of collection.

For each group of flowers, fruit were counted, and fruit set was calculated as the proportion of flowers that produced mature fruit. Fruit were weighed on an analytical balance (0.1 mg accuracy), and dissected to count mature seeds (>2 mm long, >1 mm thick, well pigmented).

Statistical analyses

The effect of pollinator treatment (all insect vs. epigean insect vs. no insect access) on the proportion of flowers setting fruit and the number of seeds per fruit was assessed using generalized linear mixed models with site, i.e., individual beds, as a random effect and appropriate error distribution (binomial for fruit set, Poisson for seed count). Fruit set was weighted for the number of observations. Fruit weight was assessed using a random slope linear mixed effects model with site as a random effect. Significance was assessed using a Likelihood Ratio Test comparing the full model with one omitting the predictor variable. Post-hoc multiple comparisons of means for all analyses were performed using Tukey contrasts.

All statistical analyses were performed using R software version 3.1.0 (R Core Team 2014). Linear models were produced using procedures glmer and lmer in the package lme4 (Bates et al. 2013) and post-hoc tests were performed using the glht function in the package multcomp (Hothorn et al. 2008).

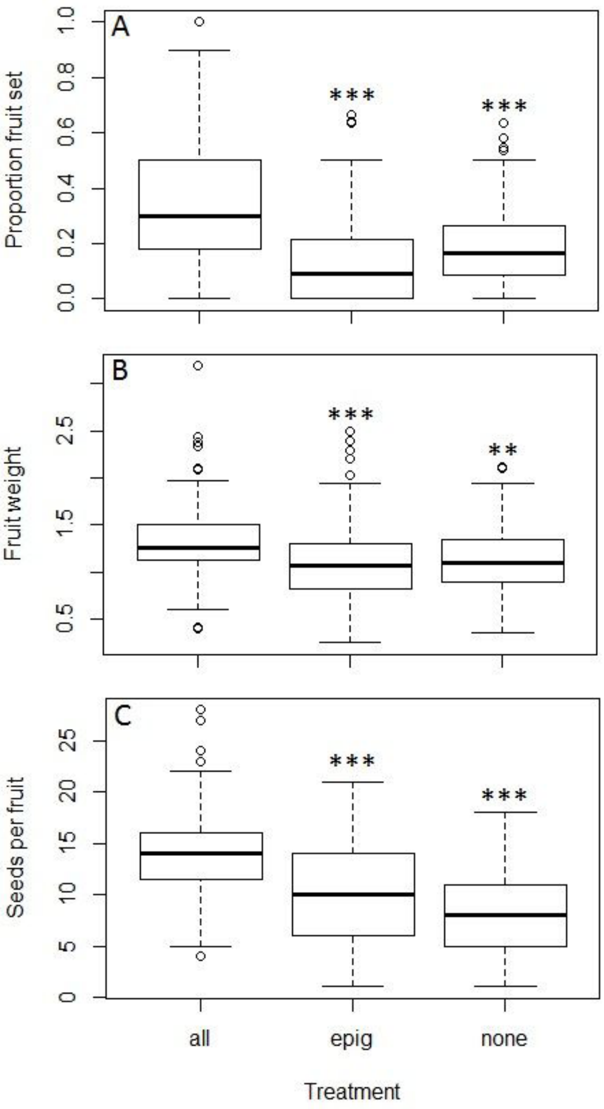
RESULTS AND DISCUSSION

Fruit set was low, as expected in cranberry, which aborts a high percentage of pollinated flowers as a bet-hedging strategy (Brown and McNeil 2006). Flowers pollinated later in the season act as insurance against poor early-season conditions, and are generally aborted if the earlier pollinated flowers develop fruit. In the all insect access treatment, 32.9 ± 1.4% (mean ± 1 SE) of flowers produced fruit, which was significantly more than the two exclusion treatments (Likelihood Ratio Test $\chi^2(2) = 12.573$, *P* = 0.002). Fruit set was 18.4 ± 1.0% with all insects excluded, and 14.3 ± 1.1% with epigean access only.

Similar patterns were seen in the other measures related to yield (Figure 1). Fruit weight ($\chi^2(2) = 9.079$, P = 0.011) was 1.32 ± 0.03 g with full insect access, 1.11 ± 0.03 g in the absence of all insects, and 1.10 ± 0.03 g with epigean insect access. The number of seeds per fruit ($\chi^2(2) = 22.157$, P < 0.001) was also highest with full insect access (13.7 ± 0.3 seeds/fruit), and similar in the two exclusion treatments (8.2 ± 0.3 and 9.9 ± 0.5 seeds/fruit with no insects and epigean access, respectively). There were no differences in any measure between the two exclusion treatments.

There are two possible explanations for the unexpected lack of difference between exclusion treatments. First, to firmly attach the mesh bags to exclude all insects, several flowering uprights were grouped together around a supporting bamboo skewer, covered with a fine mesh bag, and secured with floral tape. The mesh was fairly close to the flowers. The open-bottom exclusion cages for flying insects allowed the flowers to maintain a more natural position

Figure 1. Proportion of flowers setting fruit (A), mean fruit weight (B), and mean number of seeds per fruit (C) under three pollinator access treatments: full pollinator access (all), epigean pollinators only (epig), and no pollinator access (none) on commercial cranberry farms in Newfoundland. Asterisks indicate significant differences from full pollinator access: *** *P*<0.001, ** *P* = 0.001. Exclusion treatments did not differ significantly from one another.



further from the mesh. In the mesh bags, there may have been increased transfer of pollen among the more tightly grouped flowers, and insects may have attempted to access the flowers through the mesh, thereby dislodging pollen that could reach adjacent flowers. Mechanical agitation can successfully pollinate cranberry flowers (Gaines-Day and Gratton 2015), which could result in elevated pollination in mesh bags relative to exclusion cages. This may have confounded the effects of epigean insects and wind. If the flowers in the bags experienced higher mechanical agitation than those in the open-bottom cages, this may have compensated for any difference in epigean insect activity.

A second possibility is that a key epigean pollinator was not successfully excluded by the mesh bags. Gaines-Day and Gratton (2015) suggest that thrips may contribute to cranberry pollination. In cages that excluded insects and prevented wind agitation, yield was higher in cranberry fields than under greenhouse conditions. Thrips were present in the field and were able to pass through the mesh used in the exclusion cages, but were absent from the greenhouse (Gaines-Day and Gratton 2015). Although thrips were not collected in the current study, they were observed in large numbers on occasion (personal observation 2013, 2014). The mesh used in the bags, with 1.2 mm openings, could readily admit thrips. Gaines-Day and Gratton (2015) documented thrips inside exclusion cages with mesh having 1 mm openings. Thus the similar levels of pollination in the two exclusion treatments could be due to thrips activity.

Thrips are pollen-feeders, and have been shown to contribute to pollination of a range of plants (Baker and Cruden 1991, Ananathakrishnan 1993, Momose et al. 1998, Moog et al. 2002), including ericaceous plants (Hagerup and Hagerup 1953, García-Fayo and Goldarazena 2008). Other small insects that could contribute to pollination have been documented visiting flowers, such as springtails (Collembola) (Kevan 1978) and aphids (Hemiptera) (Baker and Cruden 1991); the latter being observed carrying and transferring pollen. Relatively little is known about the anthophilous communities of most plants (Dicks et al. 2013; Wardhaugh 2015), and although most flower visitors are unlikely to contribute significantly to pollination, this represents a considerable gap in knowledge. A full understanding of pollination ecology is necessary to design effective pollinator management strategies.

It is clear that cranberry requires some type of pollen vector, either biotic or abiotic, and that although bees are typically required to obtain commercially viable yields, a considerable amount of pollination takes place through other means. In Wisconsin, bees were responsible for 41% of total yield, while non-bee insects contributed 30%, and mechanical agitation contributed 29% (Gaines-Day and Gratton 2015). This is consistent with the current study, in which 49% of fruit set can be attributed to non-bee vectors, i.e., 16.2% of flowers setting fruit across both exclusion treatments compared with 32.9% in the full insect access treatment, which included all vectors.

There is growing recognition that pollination is carried out by a complex community, and that understanding the full range of pollinators is key to maintaining pollination services in both managed and natural ecosystems (Mayer et al. 2011; Dicks et al. 2013). Although it was not possible to confirm that epigean insects were involved, this study does demonstrate that vectors other than bees contribute significantly to cranberry pollination.

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