

BIOTIC AND ABIOTIC FACTORS CONTRIBUTE TO CRANBERRY POLLINATION

Hannah R. Gaines-Day* and Claudio Gratton

University of Wisconsin-Madison, Department of Entomology, 237 Russell Labs, 1630 Linden Dr., Madison, WI 53706, USA

Abstract—As bee populations continue to decline, farmers face possible crop failures due to insufficient pollination. Crops, however, vary in the degree to which they depend on pollinators, suggesting that some crops may not be as sensitive to variation in pollinator availability and/or abundance as others. The objective of this study was to determine the contribution of biotic and abiotic factors to cranberry pollination. We performed field and greenhouse experiments to compare the effect of biotic (i.e., bee or hand pollination) and abiotic (i.e., wind, agitation) factors on yield. We found that even in the absence of bees, cranberry is able to produce a significant yield. In the field, plants in the abiotic treatments produced higher yields (wind 230 bbl/ac [barrels per acre], agitation 200 bbl/ac) than the closed control treatment (108 bbl/ac), although these yields were not as high as the open, biotic treatment (367 bbl/ac). This corresponds to a contribution of 41% by bees, 30% by non-bee insects, and 29% by mechanical agitation. In the greenhouse, the agitation treatment had, on average, higher berry weight per upright (0.6 g/upright) than the undisturbed control treatment (0.04 g/upright), but again, not as high as the biotic treatment (3.0 g/upright). This confirmed that cranberry does not autogamously self-pollinate indicating that all yields are due to biotic or abiotic vectors moving pollen between flowers. Although bees clearly contribute to cranberry pollination, previous studies have understated the contribution of alternative mechanisms by which cranberry pollen can move between flowers.

Keywords: *Vaccinium macrocarpon*, *pollinator decline*, *physical factors*, *agitation*, *wind pollination*

INTRODUCTION

Insect pollination is an important ecosystem service required by or benefitting two-thirds of global crops (Klein et al. 2007). These crops, however, vary in the degree to which they depend on pollinators, suggesting that not all crops are equally susceptible to variability in the abundance of pollinators. In the absence of pollinators, some plants produce no fruit (e.g., watermelon, Delaplane & Mayer 2000), while others produce misshapen (e.g., strawberries, Free 1968; Jaycox 1970) or small fruit (e.g., cherry tomato, Greenleaf & Kremen 2006). Determining the role of insect and non-insect factors in the pollination of specific crops will provide a better understanding of how the decline of pollinators may affect crop production.

Cranberry (*Vaccinium macrocarpon*) is one crop that is considered pollinator-dependent (reviewed by McGregor 1976; Eck 1986, 1990; Free 1993; Delaplane & Mayer 2000). Although the flowers are self-compatible (Reader 1977; Dana et al. 1989; Sarracino & Vorsa 1991), pollen is released before the stigma is receptive making self-pollination unlikely (Rigby & Dana 1972). Bees are effective pollinators of cranberry (Mohr & Kevan 1987), depositing enough pollen to produce a full-sized fruit in one or two visits (Cane & Schiffhauer 2003). As a result, individual cranberry growers spend thousands of dollars each year on

honey bee rentals to ensure sufficient pollination (USDA NASS WASS 2006).

However, despite over one hundred years of research on cranberry pollination and the widespread use of honey bees, the degree to which cranberry depends on pollinators remains unclear. Previous studies have estimated that 30% to 100% of the cranberry crop would be lost in the absence of bees (Southwick & Southwick 1992; Williams 1994; reviewed by Delaplane & Mayer 2000). At the lower end of this range, pollinator decline would have a minimal effect on cranberry yield, while at the upper end, complete dependence on pollinators would suggest crop failure in their absence. The high variability in these crop-loss estimates may suggest that other, non-bee, factors such as wind or mechanical agitation also contribute to cranberry pollination. If non-bee factors provide significant pollination, cranberry growers may not need to stock as many hives of honey bees as they currently use.

Few studies, however, have considered the role of non-bee factors in cranberry pollination. Of those that do, the results are conflicting. For example, despite the claim that wind is of minor importance to cranberry pollination (e.g., Filmer 1949), Papke et al. (1980) demonstrated that there is enough cranberry pollen being carried in the wind to provide a significant contribution to pollination. Moreover, there is some evidence that manually agitated cranberry plants could set fruit in the absence of bees (Roberts & Struckmeyer 1942). In contrast, several studies found contrary evidence and concluded that wind or the manual agitation of plants does not contribute to cranberry pollination (Filmer 1949;

Received 11 March 2014, accepted 09 February 2015

*Corresponding author; email: hgaines@gmail.com

MacKenzie 1994). The variability among these studies may be partly due to methodological differences in the agitation treatments, differences between cultivars, or variation between growing regions where the studies were conducted. In sum, the paucity of research investigating non-bee mechanisms of pollination, and the inconsistencies in findings between the studies that do, suggest that we still lack a clear understanding of the factors contributing to cranberry pollination.

The goal of this study was to understand the relative importance of biotic and abiotic factors to cranberry pollination. We established field and greenhouse experiments in which we manipulated biotic (i.e., bees) and abiotic (i.e., wind, manual agitation) factors that could contribute to cranberry pollination. Pollination success was measured using yield, berry weight, berries per upright, and seeds per berry since these are measurements relevant to agricultural production.

MATERIALS AND METHODS

Cranberry (Ericaceae: *Vaccinium macrocarpon* Aiton) is a perennial fruit crop native to North America. It is grown commercially in artificially created marshes with sandy, acidic soil. The main production region, where the field component of this study was conducted, is Wood County in central Wisconsin, USA (44.30 °N, 90.11 °W). This region is characterized by sandy soil and flat open terrain (Dott & Attig 2004). The area is heavily agricultural and produces most of the states' cranberry and potato crops. The mean annual temperature is 7°C (mean low -9°C, mean high 20°C) with average summer temperatures of 20°C, and mean summer precipitation of 290 mm (Wisconsin State Climatology Office), which is augmented with irrigation in production areas. Cranberry grows as a vine along the ground and sends up vegetative and flowering shoots ("uprights"). Each flowering upright produces up to 8 flowers that bloom sequentially from the bottom of the upright upwards over the course of several weeks in late June and early July (Eck 1990). Honey bees are commonly brought to commercial marshes for the duration of bloom (Delaplane & Mayer 2000).

Field experiment

To assess the influence of biotic and abiotic factors on cranberry yield in a field setting, we established a cage study in a commercial cranberry marsh in Wood County, WI (USA). Four treatments were established in a single bed of the "Stevens" cultivar: (1) "open", which allowed both insect visitation and movement of plants by wind, (2) "wind", which blocked insect visitation with a fine nylon mesh (bridal veil) but allowed wind to agitate the plants or move pollen, (3) "closed", which prevented insect visitation and wind using floating row cover (Agribon+ AG-15 Insect Barrier, Johnny's Selected Seeds, Fairfield, Maine) and a corrugated plastic wind block surrounding each cage. And (4), an "agitation" treatment was established which used the same cage design as the "closed" treatment but received manual agitation twice per week during bloom. Each agitation consisted of lifting the row cover material and

brushing a PVC tube (30 cm × 2 cm diameter) 20 times across the top of the cranberry uprights. Each treatment was replicated 10 times. Cage frames used in treatments 2 through 4 measured ~45 × 45 cm by ~40 cm tall (for further information on construction see Appendix I).

In order to account for possible differences in local growing conditions (e.g., upright density, soil moisture) as a function of location within the cranberry bed, cages were arranged in a grid and treatments were assigned using a modified Latin Square design with each treatment occurring once per column and twice per row. Cages were set up before cranberry bloom (May 25, 2012) and removed after bloom was complete (July 9, 2012). All berries from within a 30 cm × 30 cm (0.09 m²) plot in the centre of each cage were harvested (September 20, 2012), counted and weighed (wet) to estimate yield. This is a standard method for estimating pre-harvest cranberry yields (e.g., Pozdnyakova et al. 2005). Wet weight was used as this can be easily converted to yield units used by cranberry growers (1 barrel [bbl] = 100 lbs = 45 kg; thus 1 barrel/acre = 111 kg/ha). In order to understand the level of pollination received in each treatment, the number of fully formed seeds from 20 berries from each plot were counted. The number of seeds is proportional to the amount of pollen deposited on the stigma and therefore represents an indication of pollination success (Cane & Schiffhauer 2003).

To test for cage effects we measured several environmental variables both inside and outside of the cages. An additional 15 treatment plots (5 each "open", "wind", and "closed", treatments as described above) were established and within each of these plots, we measured temperature, light intensity, soil moisture, and insect abundance. Temperature and light intensity were measured every 30 minutes for the duration of the cage study using HOBO data loggers (Onset Computer Corporation, Bourne, Massachusetts) hung inside inverted Styrofoam cups as sun shields. Percent soil moisture content was measured using a TDR 300 soil moisture meter (Spectrum Technologies, Aurora, Illinois) twice during the growing season (June 14 and July 9, 2012). Four measurements were taken per cage. The insect community within each treatment type (i.e., "open", "wind", and "closed") was measured continuously during bloom (May 29 - June 28, 2012) using one yellow sticky strip (10 × 15 cm, Great Lakes IPM 025-SS-35) per treatment plot replaced three times during bloom and three pan traps (blue, yellow, and white, ACE Brand Fluorescent paint) per treatment plot containing soapy water (Dawn™ blue dish soap).

To examine differences among treatments for yield, weight per berry, and berries per plot we used a one-way mixed model ANOVA with row and column locations as random effects. After fitting ANOVA models to the field data, a visual examination of the residuals determined that the assumptions of normality were met and no transformations were required. Differences among treatments were determined using Tukey's Honestly Significant Difference (HSD) test (Hsu 1996). Statistical analyses were performed using JMP Pro 10 (SAS Institute Inc. 2007).

Greenhouse experiment

Sixty dormant cranberry plants with visible buds, thirty individuals each of the “HyRed” and “Stevens” cultivars, were dug from a commercial cranberry marsh in late March of 2012. “Stevens” was chosen because it is the most commonly grown cultivar in Wisconsin and “HyRed” is a recently developed hybrid that has an earlier bloom and harvest time than “Stevens”. Plants were rinsed thoroughly to remove all sand and possible pests from the roots and planted into 15 cm pots of moist peat moss. Pots were arranged randomly in a greenhouse set at 22°C with a 16 hour photoperiod. Approximately one month after potting, uprights were thinned to 5-6 flowering uprights per pot in order to reduce the total number of flowers and make hand pollination manageable. All but the first four flowers to bloom per upright were trimmed off as they opened since cranberry plants are more likely to set fruit on the lower, earlier flowers than the upper, later flowers (Birrenkott & Stang 1989).

Three treatments were established in the greenhouse: (1) “hand” pollination, which represents the biotic movement of pollen between flowers (mimicking bee visitation), (2) “agitation”, which represents the physical movement of plants by wind, and (3) an undisturbed control, which provided a measure of autogamous self-pollination. To assess the potential for biotic pollination, flowers with a receptive stigma (i.e., those that were moist and protruding from the stamens) were hand pollinated daily during bloom by gently dipping the stigma into a small accumulation of pollen that had been collected from younger flowers into the cap of a micro-centrifuge tube. To assess the potential for abiotic pollination, plants in the “agitation” treatment were gently jostled daily during bloom by moving the palm of the hand across the vegetative top of the uprights for approximately 3 seconds, causing the plants to bump against each other. This action simulated the physical movement of plants as may be caused by wind while excluding the possibility of wind pollination *per se* in which pollen is moved through the air. Plants in the control treatment were left undisturbed throughout the study to assess whether fruit would be produced in the absence of either biotic or abiotic factors (i.e., autogamous self-pollination). For each treatment we established 10 replicates (i.e., pots) per cultivar. Pots were placed in two parallel rows ~0.2 m apart and spanning 3 - 3.5 m on both sides of a single aisle of greenhouse tables (one cultivar per side). Experimental treatments were initiated as soon as bloom began (April 24) and were continued daily until all flowers were done blooming (June 1). Berries were harvested approximately two months after the start of bloom when fruits began to turn red (June 20). The number of berries per upright were counted and each berry was weighed (wet weight, g). The product of these two variables (i.e., berry weight per upright) was used as a proxy for yield. Although the number of berries per area is an important variable in determining yield (Devetter 2013), the area in our experiment was limited by pot size and was therefore not included in our calculation of yield. The number of fully formed seeds was counted for each berry as a proxy for the amount of pollen reaching the stigma. Averages

of berry weight, berries per upright, and seeds per berry were taken for each pot for a total of 10 replicates per treatment.

To examine differences among experimental treatments (“hand pollination”, “agitation”, undisturbed control) and cultivar (“Stevens”, “HyRed”), we used a fully factorial two-way analysis of variance (ANOVA) to compare yield (berry weight per upright), berries per upright, and weight per berry. After fitting ANOVA models to the greenhouse data, a visual examination of the residuals suggested that a transformation ($\log x+1$) was necessary to meet linearity assumptions for berry weight per upright and berries per upright. Each of these response variables indicates some form of pollination success. Differences among treatments by cultivar were determined using Tukey’s HSD test. Statistical analyses were performed using JMP Pro 10 (SAS Institute Inc. 2007).

RESULTS

Field experiment

The field cages successfully excluded bees while maintaining comparable environmental conditions within each cage type (Appendix II). The cages blocked out all but the tiniest insects: the majority of those that made it into the cages were thrips (Thysanoptera). No bees at all were found in either cage type. The bridal veil mesh used in the “wind” treatment did not result in any difference in average daytime (09:00 - 15:00) temperature as compared to open plots. The floating row cover used in the “closed” and “agitation” treatments resulted in an 8% (3°C) increase in average daytime temperature as compared to the open plots ($F_{2,211.5} = 14.5$, $P < 0.0001$). The bridal veil resulted in decreased average daytime light levels of 7% ($F_{2,276.3} = 4.7$, $P < 0.0103$) in the “wind” treatment. Soil moisture did not vary among treatments (15.3 ± 0.6 , $F_{2,23} = 0.17$, $P = 0.84$). Although some statistically significant differences in light levels and temperature were found, this variation is unlikely to be biologically relevant as light levels from all cage types were well within the range of average daylight intensity (10,000-25,000 lum/m²) and temperatures were within the normal growing range for cranberries (Roper 2006).

In the field, cranberry yields in the “open” treatments where highest (mean 367 bbl/ac), followed by “wind” (230 bbl/ac) and “agitation” (200 bbl/ac) and lowest for the “closed” treatment (108 bbl/ac, $F_{3,23.1} = 70.5$, $P < 0.0001$, Fig. 1A). Thus, yields in the treatments from which bees alone were excluded (i.e., “wind”, “agitation”) were on average about 59% that of the fully open plots, but double those of plots from which wind, agitation and bees were excluded. The variation in yield observed across treatments was the result of differences in both berry weight (Fig. 1B) and total number of berries produced per area (Fig. 1C). Weight per berry was significantly different among treatments with the heaviest berries in the “open” plots, followed by “agitation”, and lowest in the “wind” treatment and “closed” control ($F_{3,24.2} = 36.6$, $P < 0.0001$, Fig. 1B). The total number of berries per plot also varied significantly among treatments with the most berries produced in the “open” and “wind” plots, followed equally by “agitation”

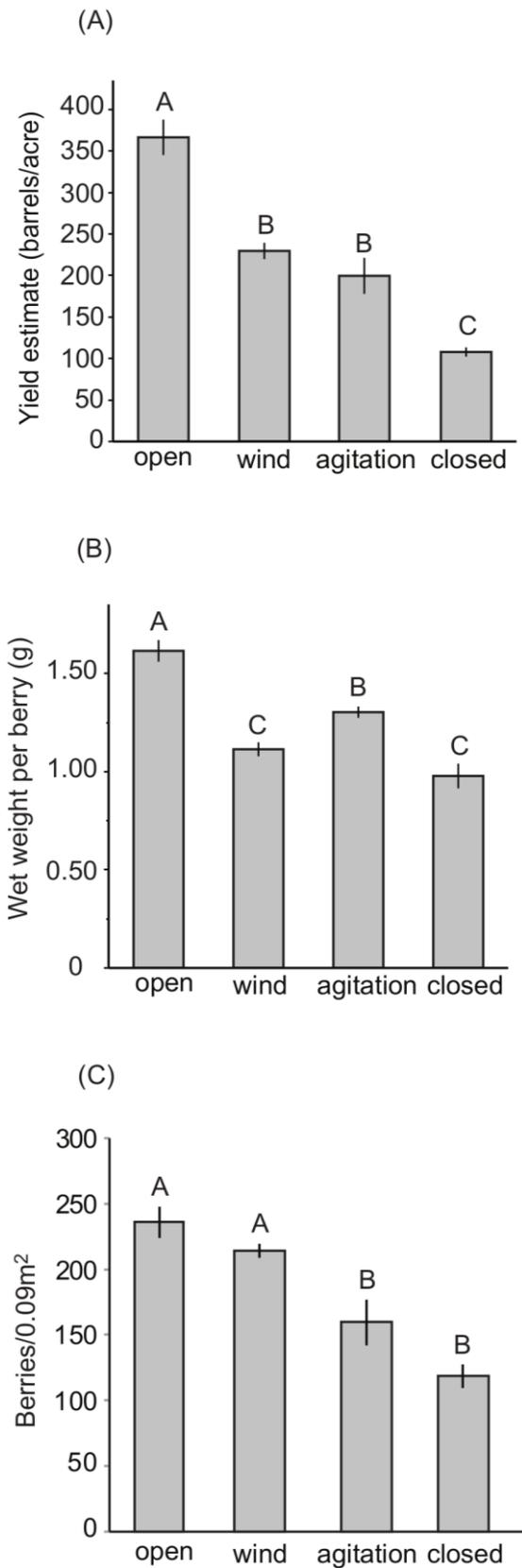


FIGURE 1: Metrics of pollination success for the cranberry cultivar "Stevens" as measured in the field: (A) yield estimate (mean \pm SE), (B) wet weight per berry (mean \pm SE), and (C) number of berries per 0.09 m² plot (mean \pm SE). Letters represent significant differences ($P < 0.05$) between treatments. Note that 1 barrel/acre = 111 kg/ha.

and the "closed" control (treatment, $F_{3,23.03} = 23.5$, $P < 0.0001$, Fig. 1C).

Greenhouse experiment

In the greenhouse, considerable fruit set occurred on plants in both the biotic ("hand") and abiotic ("agitation") treatments but not in the undisturbed control. Ninety-eight percent of "HyRed" and 92% of "Stevens" uprights in the "hand" pollination treatment produced fruit and 52% of the "HyRed" and 30% of the "Stevens" uprights in the "agitation" treatment produced fruit. In contrast, only 2% of "HyRed" and 5% of "Stevens" uprights in the undisturbed control produced fruit.

Yield (represented as the product of weight per berry \times berries per upright) was higher in the "hand" pollination treatment than in either of the other treatments and higher in the "agitation" treatment than the undisturbed control (treatment, $F_{2,58} = 203.8$, $P < 0.0001$, Fig. 2A). The number of berries per upright varied significantly among treatments in both cultivars (treatment, $F_{2,58} = 282.0$, $P < 0.0001$, Fig. 2B). More berries per upright were produced in the "hand" pollination treatment than in the "agitation" treatment, and more in the "agitation" treatment than in the undisturbed control. However, the difference in berries per upright between treatments was greater for "HyRed" than "Stevens" (treatment \times cultivar, $F_{2,58} = 3.3$, $P = 0.046$). Berry weight did not vary across treatments ($F_{2,41} = 2.4$, $P = 0.11$, Fig. 2C) or cultivar ($F_{1,41} = 0.0021$, $P = 0.96$).

Furthermore, we found a relationship between berry weight and seeds per berry for "Stevens" in both the greenhouse ($R^2 = 0.42$, $P = 0.0011$, Fig. 3A) and the field ($R^2 = 0.83$, $P < 0.0001$, Fig. 3A) but not for "HyRed" (greenhouse only, $R^2 = 0.04$, $P = 0.39$, Fig. 3B).

DISCUSSION

Previous research on cranberry pollination has generally concluded that bees are required to produce fruit (Hutson 1925; Farrar & Bain 1946; Marucci 1966; Marucci & Moulter 1977). However, most of these studies did not consider vectors other than bees that could contribute to pollination. In fact, in over one hundred years of research, only four studies have considered the contribution of non-bee factors including wind and mechanical agitation to cranberry pollination (Roberts & Struckmeyer 1942; Filmer 1949; Papke et al. 1980; MacKenzie 1994), with the results providing mixed evidence that non-bee factors are relevant. In this study, we demonstrate that in the absence of bees, cranberry is still able to produce fruit. We found that plants from which bees alone were excluded but which were physically disturbed (i.e., by agitation, wind), produced a greater overall yield than plants from which both bees and disturbance were blocked. This result, combined with agitation treatments showing that physical movement of plants was sufficient to transfer enough pollen to produce full-sized, marketable fruit, challenges the notion that bees are the only way for cranberry plants to achieve fruit set, and suggests that both biotic and abiotic factors contribute to cranberry pollination.

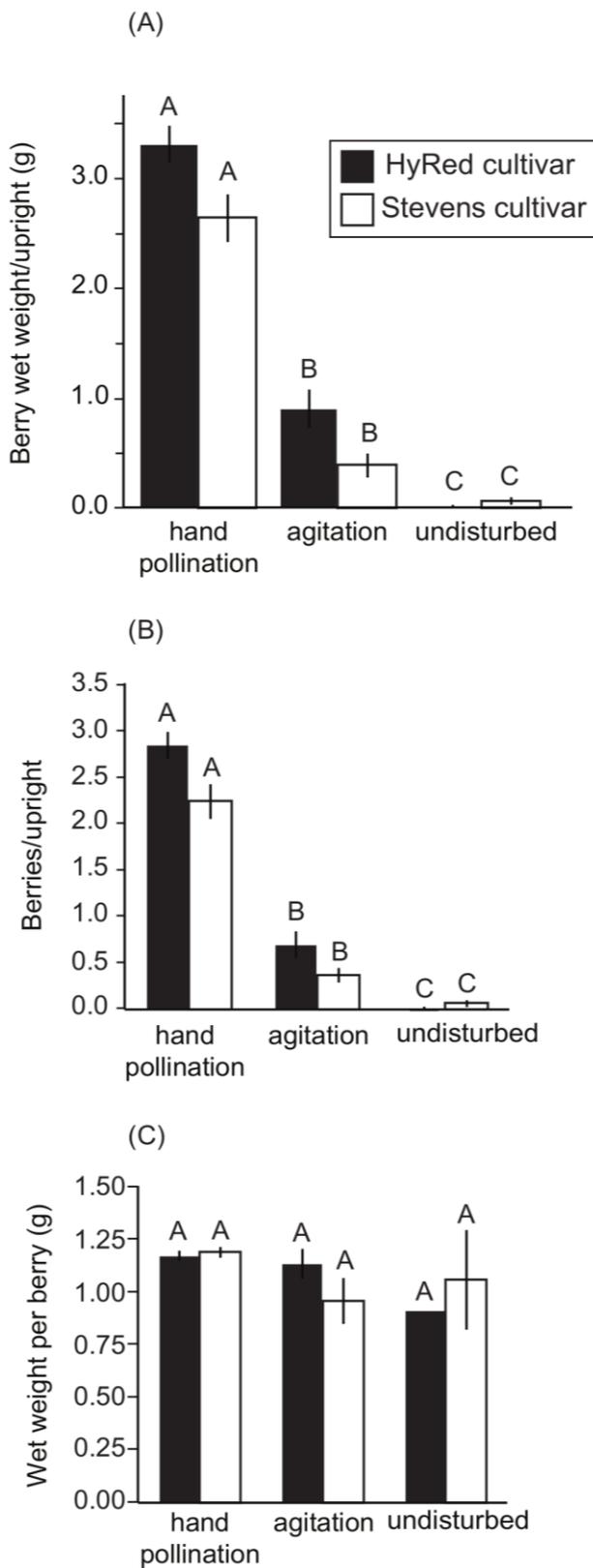


FIGURE 2: Metrics of pollination success for the cranberry cultivar “HyRed” (black bars) and “Stevens” (white bars) as measured in the greenhouse: (A) yield estimate (mean wet weight per upright \pm SE), (B) number of berries per upright (mean \pm SE), and (C) wet weight per berry (mean \pm SE). Letters represent significant differences ($P < 0.05$) between treatments.

One possible reason that our results differ from previous studies on cranberry pollination may be differences in study design and scope. Often, studies that examine the importance of pollinators to fruit production in cranberry are designed only to test the importance of bees for pollination (e.g., Kevan et al. 1983; Cane & Schiffhauer 2003; Phillips 2011). In many of these experiments individual cranberry flowers are either isolated, testing their capacity to self-pollinate, or exposed to bees, demonstrating the effectiveness of bees to pollinate cranberry. Under normal growing conditions, however, flowers are not isolated and pollen may move between flowers through multiple mechanisms. Interestingly, several studies that used field cages to exclude bees from cranberry plants found that berries were produced within their cages, although at lower levels than open plots (Hutson 1925; Farrar & Bain 1946; Phillips 2011). These authors either provide no explanation of how berries formed without bees or interpret their findings as being the result of faulty cages that must have allowed bees to enter, rather than considering alternative mechanisms of pollination. In our study, careful cage construction (e.g., weighing down cage material to ground level, Appendix I) and insect monitoring within cages (Appendix II) makes us confident that bees were not contributing to pollination within the field cages and that other mechanisms are indeed contributing to cranberry pollination.

Differences in the relative contribution of biotic and abiotic factors between field and greenhouse results are likely due to uncontrolled factors in the field that were absent in the greenhouse. The greenhouse experiment suggests that cranberries do not autogamously self-pollinate as there was only ~1% fruit production in the undisturbed controls compared to the hand pollination treatment. In the field, the treatment with fully closed cages was meant to mimic the greenhouse undisturbed control. Yet, under field conditions, plots had yields about 30% (108 bbl/ac) that of open field conditions (367 bbl/ac). One possible explanation for this difference is the presence of non-bee insects contributing to pollination. Specifically, thrips (Thysanoptera) were found in all treatments in the field (Appendix II) but not observed in the greenhouse. These tiny pollen-eating insects have been shown to be effective pollinators in other systems, including ericaceous plants which are in the same family as cranberry (Hagerup & Hagerup 1953; Kirk 1988; Baker & Cruden 1991; Ananthakrishnan 1993). It is notable that although thrips are ubiquitous and abundant in cranberry marshes, their potential influence on cranberry pollination remains a hypothesis to be critically examined (but see Gaines-Day 2013). Differences between the agitation treatment in the field and greenhouse may also be due to differences in density of flowering uprights. In the greenhouse, flowering uprights were thinned to a low density (equivalent to about 279 flowering uprights m^{-2}), whereas in the field, flowering uprights were on average six times as dense (1,705 flowering uprights m^{-2}). We hypothesize that the higher relative effects of agitation in the field (107 bbl/ac greater than “closed”, or 29% that of open plots) compared to the greenhouse (20% of hand pollination) is at least partly due to a higher density of flowering uprights, where pollen is more abundant, flowers are closer together, and there is a higher likelihood

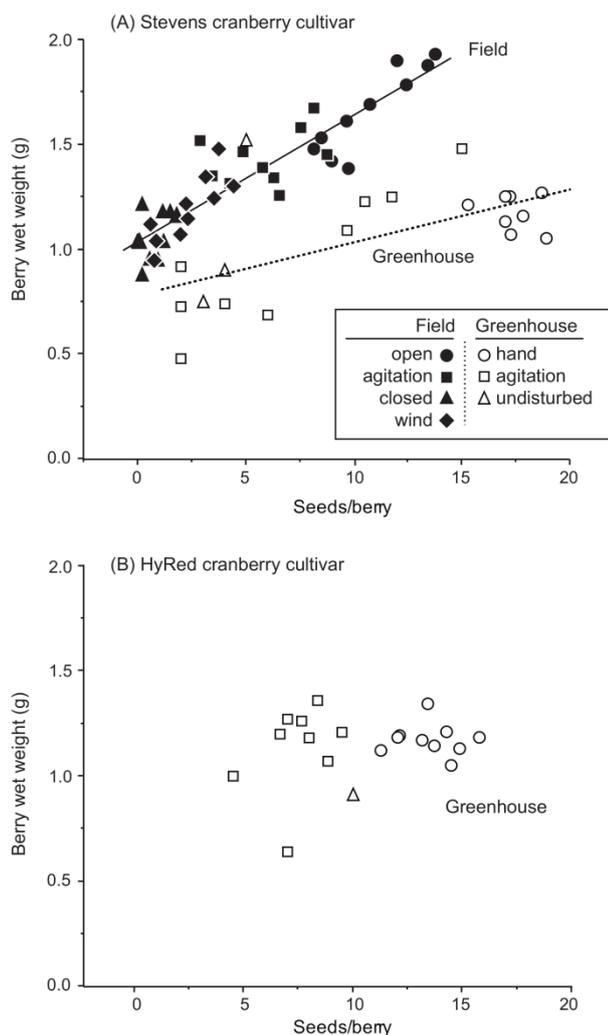


FIGURE 3: Relationship between berry weight (g wet weight) and seeds per berry for the cranberry cultivars (A) "Stevens" and (B) "HyRed", for field (solid symbols) and greenhouse (hollow symbols) experiments.

that pollen could be transferred between flowers with even slight movement. Upright density may also be one factor explaining differences between this study and Filmer (1949) which found no effect of manual agitation on yield in a field setting; in that study upright density was about 2.5 times lower (646 flowering uprights/ m²) than our field densities. Finally, another aspect that could have also contributed to differences in yield among treatments is the proportion of flowers setting fruit. This component was not evaluated in this study but could give additional information on pollination success across the treatments.

The increase in seed number and berry weight in the Stevens cultivar as treatments go from the most undisturbed (undisturbed and closed) to those with progressively more potential for pollen movement (manual agitation and wind) suggests that the amount of pollen deposited onto the stigma is also increasing. Previous studies have also found a strong correlation between seed number and berry weight (Hall & Aalders 1965; Rigby & Dana 1971). Although the berries with the most seeds were found in the hand pollination

treatment in the greenhouse, the heaviest berries were found in the open treatment in the field. Thus, other factors, such as water and nutrient availability, likely play a role in berry weight. Cane and Schiffhauer (2003) found that in the Stevens cultivar, a berry reaches a maximum weight when the flower receives 8 tetrads of pollen resulting in about 15 seeds - a level we achieved in the hand-pollinated treatments but not in the field. In the field, the seed number per berry never reached 15 suggesting that even with bees and abiotic factors contributing to pollination, pollen may be limiting. The lack of relationship between berry weight and seed number in the HyRed cultivar provides evidence that differences also exist among cultivars in their response to pollen availability.

Our study was specifically designed to test the co-occurrence of pollination mechanisms including bees (presence/absence), wind, mechanical action, and autogamous self-pollination. We found that mechanical agitation, by wind or by hand can move pollen between cranberry flowers resulting in significantly greater yields than when these factors are absent. In small plots that were caged with fine mesh and obstructed to prevent wind, yields were 30% (108 bbl/ac) that of plots which received open pollination (367 bbl/ac). The addition of wind or physical agitation resulted in nearly a 100% increase in yield (+107 bbl/ac) contributing an additional 29% of yield (59% of open/bee pollination). The difference between open plots and caged plots suggests that bees alone are responsible for 41% of cranberry yield. This number is consistent with, but on the low end of the range of those reviewed in Delaplane and Mayer (2000). Furthermore, the estimated yield due to non-bee factors (215 bbl/ac) is comparable with average yields observed in commercial operations across North America. For example average cranberry yields in 2012 for Wisconsin were 245 bbl/ac, but yields were lower in other parts of the country, ranging from 81-140 bbl/ac on the west coast of the USA (Washington and Oregon) to 163-183 bbl/ac on the east coast (Massachusetts and New Jersey, USDA 2012 Fruit Summary). If the conditions created in our small experimental plots are similar to those observed at farm field scales (i.e., comparable wind or physical agitation regimes, flowering upright densities, minute insects), then farmers may be realizing more than half of their crop yield from non-bee factors. Whether non-bee related pollination by itself is sufficient for a farmer to achieve an economically viable yield however will depend on additional economic factors such as the market price of the commodity and additional input costs. Although bees clearly contribute to cranberry pollination, results from prior studies may have understated other pathways of pollination (movement of pollen by abiotic factors or tiny insects) that could also result in viable fruit production.

ACKNOWLEDGEMENTS

We thank C.J. Searles Cranberry Inc. for allowing us to conduct our field cage study on their marsh and Gaynor Cranberry for providing plant material for the greenhouse study. We thank Eric Zeldin for his assistance digging plant material and providing guidance on establishing the plants in the greenhouse. We also thank the field and lab technicians who assisted with the project:

Rachel Mallinger, Amanda Rudie, Collin Schwantes, Eric Wiesman, Christopher Watson, Sacha Horn, and Scott Lee. Shawn Steffan, Neal Williams, and Dan Cariveau reviewed earlier versions of this manuscript. Funding for this research was provided by a University of Wisconsin Formula Fund Hatch Grant (WIS01415).

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Cage construction.

Appendix II. Environmental data collected within field cages.

REFERENCES

- Ananthakrishnan TN (1993) The role of thrips in pollination. *Current Science* 65:262-264.
- Baker JD, Cruden RW (1991) Thrips-mediated self-pollination of two facultatively xenogamous wetland species. *American Journal of Botany* 78:959-963.
- Birrenkott BA, Stang EJ (1989) Pollination and pollen tube growth in relation to cranberry fruit development. *Journal of the American Society for Horticultural Science* 114:733-737.
- Cane JH, Schiffhauer D (2003) Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). *American Journal of Botany* 90:1425-1432.
- Dana MN, Steinmann S, Goben L (1989) Pollen source and fruit set of cranberry. *Cranberries* 53:10-14.
- Delaplane KS, Mayer DF (2000) *Crop pollination by bees*. CABI Publishing, New York.
- Devetter LW (2013) Understanding yield of cranberry: Bud development, carbohydrate allocation, and yield component analysis. (Doctoral Dissertation). University of Wisconsin, Madison.
- Dott RH, Attig JW (2004) *Roadside Geology of Wisconsin*, 1st edition. Mountain Press, Missoula, Mont.
- Eck P (1986) Cranberry. In: Monselise, SP (ed) *CRC handbook of fruit set and development*. CRC Press, Boca Raton, FL, pp 109-117.
- Eck P (1990) *The American cranberry*. Rutgers University Press, New Brunswick, NJ.
- Farrar CL, Bain HF (1946) Honeybees as pollinators of the cranberry. *American Bee Journal* 86:503-504.
- Filmer RS (1949) Cranberry pollination studies. In: *Proceedings of the 80th Annual Meeting of the American Cranberry Growers Association*. pp 14-22.
- Free JB (1968) The pollination of strawberries by honey-bees. *Journal of Horticultural Science* 48:107-111.
- Free JB (1993) *Insect pollination of crops*, 2nd edn. Academic Press Inc., London.
- Gaines-Day H (2013) Do bees matter to cranberry? The effect of bees, landscape, and local management on cranberry yield. (Doctoral Dissertation). University of Wisconsin, Madison.
- Greenleaf SS, Kremen C (2006) Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81-87.
- Hagerup E, Hagerup O (1953) Thrips pollination of *Erica tetralix*. *New Phytologist* 52:1-7.
- Hall IV, Aalders LE (1965) The relation between seed number and berry weight in the cranberry. *Canadian Journal of Plant Science* 45:292.
- Hsu JC (1996) *Multiple comparisons: theory and methods*. Chapman & Hall, London.
- Hutson R (1925) The honey bee as an agent in the pollination of pears, apples and cranberries. *Journal of Economic Entomology* 18:387-391.
- Jaycox ER (1970) Pollination of strawberries. *American Bee Journal*:176-177.
- Kevan P, Gadawski R, Kevan S, Gadawski S (1983) Pollination of cranberries, *Vaccinium macrocarpon*, on cultivated marshes. *Proceedings of the Entomological Society of Ontario* 114:45-53.
- Kirk WDJ (1988) Thrips and pollination biology. In: Ananthakrishnan, T.N., Raman, A. (eds) *Dynamics of insect-plant interaction: Recent advances and future trends*. Oxford & IBH Publishing Company, New Delhi, pp 129-135.
- Klein A-M, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences* 274:303-313.
- MacKenzie KE (1994) The foraging behaviour of honey bees (*Apis mellifera* L.) and bumble bees (*Bombus spp*) on cranberry (*Vaccinium macrocarpon* Ait). *Apidologie* 25:375-383.
- Marucci PE (1966) Cranberry pollination. *Cranberries* 30:11-13.
- Marucci PE, Moulter HJ (1977) Cranberry pollination in New Jersey. *Acta Horticulturae (ISHS)* 61:217-222.
- McGregor SE (1976) *Insect pollination of cultivated crop plants*. Agriculture Handbook No. 496. Agricultural Research Service, US Department of Agriculture, Washington, D.C.
- Mohr NA, Kevan PG (1987) Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lingonberry (*V. vitis-idaea* L.). *Proceedings of the Entomological Society of Ontario* 118:149-154.
- Papke AM, Eaton GW, Bowen PA (1980) Airborne pollen above a cranberry bog. *HortScience* 15:756.
- Phillips KN (2011) A comparison of bumble bees (*Bombus spp.*) and honey bees (*Apis mellifera*) for the pollination of Oregon cranberries (Ericaceae: *Vaccinium macrocarpon*). (Master's Thesis). Oregon State University, Corvallis, OR
- Pozdnyakova L, Giménez D, Oudemans PV (2005) Spatial Analysis of Cranberry Yield at Three Scales. *Agronomy Journal* 97:49-57.
- Reader RJ (1977) Bog ericad flowers: self-compatibility and relative attractiveness to bees. *Canadian Journal of Botany* 55:2279-2287.
- Rigby B, Dana MN (1971) Seed number and berry volume in cranberry. *HortScience* 6:495-496.
- Rigby B, Dana MN (1972) Flower opening, pollen shedding, stigma receptivity, and pollen tube growth in the cranberry. *HortScience* 7:84-85.
- Roberts RH, Struckmeyer BE (1942) Growth and fruiting of the cranberry. *Proceedings of the American Society for Horticultural Science* 40:373-379.
- Roper, TR (2006) The physiology of cranberry yield. *Wisconsin Cranberry Crop Management Newsletter*, Volume XIX, Madison, WI.
- Sarracino JM, Vorsa N (1991) Self and cross fertility in cranberry. *Euphytica* 58:129-136.

SAS Institute Inc. (2007) JMP Pro 10. Cary, NC.

Southwick EE, Southwick L (1992) Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology* 85:621-633.

USDA NASS (2013) Wisconsin - 2012 Fruit Summary. Madison, WI.

USDA NASS WASS (2006) 2005 Cranberry production and pollination survey. Madison, WI

Williams I (1994) The dependence of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews* 6:229-257.

Wisconsin State Climatology Office [online] URL: <http://www.aos.wisc.edu/~sco/seasons/summer.html> (accessed 27 September 2014).