Weather During Bloom Affects Pollination and Yield of Highbush Blueberry

JULIANNA K. TUELL[1] AND RUFUS ISAACS

Department of Entomology, Michigan State University, East Lansing, MI 48824

J. Econ. Entomol. 103(3): 557–562 (2010); DOI: 10.1603/EC09387

ABSTRACT Weather plays an important role in spring-blooming fruit crops due to the combined effects on bee activity, flower opening, pollen germination, and fertilization. To determine the effects of weather on highbush blueberry, *Vaccinium corymbosum* L., productivity, we monitored bee activity and compared fruit set, weight, and seed number in a field stocked with honey bees, *Apis mellifera* L., and common eastern bumble bees, *Bombus impatiens* (Cresson). Flowers were subjected to one of five treatments during bloom: enclosed, open, open during poor weather only, open during good weather only, or open during poor and good weather. Fewer bees of all types were observed foraging and fewer pollen foragers returned to colonies during poor weather than during good weather. There were also changes in foraging community composition: honey bees dominated during good weather, whereas bumble bees dominated during poor weather. Berries from flowers exposed only during poor weather had higher fruit set in 1 yr and higher berry weight in the other year compared with enclosed clusters. In both years, clusters exposed only during good weather had >5 times as many mature seeds, weighed twice as much, and had double the fruit set of those not exposed. No significant increase over flowers exposed during good weather was observed when clusters were exposed during good and poor weather. Our results are discussed in terms of the role of weather during bloom on the contribution of bees adapted to foraging during cool conditions.

KEY WORDS *Apis mellifera*, *Bombus impatiens*, *Vaccinium corymbosum*, climate, alternative pollinator

Highbush blueberry, *Vaccinium corymbosum* L., is a native North American ericaceous plant that is now grown throughout the world for fruit production. Although some cultivars have a high degree of parthenocarpy (Eck 1988), this crop requires bee-mediated pollination for optimal yields (MacGregor 1976, Delaplane and Mayer 2000). Flowers receiving sufficient pollen deposition on the stigma produce larger, more evenly, and faster ripening fruit (Eck 1988, Dogterom et al. 2000, Ratti et al. 2008). The full potential productivity of highbush blueberry, in terms of yield and return on investments in land, plants, and crop management inputs, cannot be realized without sufficient pollen deposition provided by adequate activity of pollinating bees during bloom.

Highbush blueberry bloom within a given cultivar may last 2–3 wk, depending on weather. After a blueberry flower opens, it remains receptive to pollination for ≈4 d, but this is also weather dependent, as is pollen germination, pollen tube growth, and ovule fertilization, given sufficient pollen deposition (Stephenson et al. 1992). Commercial growers typically plant a variety of cultivars that have staggered bloom periods; thus, the entire bloom period for this crop can last up to 4–6 wk, typically between early May to mid-June in the primary production regions of Michigan.

Pollination of commercially produced blueberry is primarily performed by honey bee, *Apis mellifera* L., colonies brought to fields by bee keepers or raised by growers. However, flight activity of this species begins at temperatures between 12 and 14°C and decreases with increasing wind speed (Winston 1987), resulting in periods of low activity during cool spring weather conditions common in temperate climates during the bloom period of highbush blueberry. Native bees also may contribute to pollination of this crop, but population levels vary and are generally much lower than honey bees in intensively managed farms (Tuell et al. 2009, Isaacs and Kirk 2010).

Native bumble bee queens are active throughout blueberry bloom in this region, with workers appearing toward the very end (J.K.T., unpublished data). However, it has long been known that resident bumble bee populations are insufficient to support full pollination in commercial blueberry plantings (Martin 1966, Marucci and Moulter 1977, Winston and Graf 1982). One strategy to address this limitation is to purchase commercially raised bumble bees that can be placed in fields early in the season when resident

[1] Corresponding author, e-mail: tuelljul@msu.edu.

0022-0493/10/0557–0562$04.00/0 © 2010 Entomological Society of America

colonies have not yet had sufficient time to produce workers. This provides an alternative pollinator that is more active under cool spring weather conditions (Heinrich 2004), handles more flowers per minute (Javorek et al. 2002), and deposits more pollen per flower visit (Javorek et al. 2002). Unlike honey bees and many other pollinators, bumble bees are well adapted to interact with the flower morphology of *Vaccinium* flowers and can efficiently release pollen from the poricidal anthers by vibrating the flowers (Buchmann 1983). Thus, bumble bees are potential alternative pollinators for blueberry and may have a particularly good fit for use in regions of production with cool spring weather (Stubbs and Drummond 2001). In addition, investment in bumble bees by growers may provide pollination insurance for fruit producers that need to maintain pollen deposition during periods when honey bees have low activity.

In many regions of the world where perennial fruit crops are grown, weather conditions during bloom are unpredictable and may be suboptimal for both bee activity and fertilization (Free 1993, Vicens and Bosch 2000). Understanding how weather affects pollination and the activity of pollinators can help with designing pollination strategies to optimize fruit set and yield in the face of suboptimal weather conditions, but this is challenging to investigate under controlled conditions. We measured pollination of highbush blueberry under varying weather conditions by exposing flowers to pollinators when the weather was suitable or not suitable for honey bee flight. Unsuitable conditions for honey bee flight were expected to bias the pollinator community toward other pollinators to enable measurement of their contribution to blueberry pollination. This 2-yr study was conducted at a site stocked with both honey bees and bumble bees to allow measurement of the response of both types of pollinators to weather conditions and to compare crop pollination during the two weather extremes. We predicted that honey bees would provide the majority of pollination during warm weather, whereas managed bumble bees would be the dominant pollinators during cool spring weather conditions.

Materials and Methods

This study was conducted at a 1.6-ha (4-acre) highbush blueberry research planting at the Trevor Nichols Research Complex near Fennville, MI (42° 36′12.33″ N 86° 09′12.98″ W) between 10 and 31 May 2007 and 14 May and 4 June 2008. The research planting was comprised of three large blocks of 'Bluecrop', 'Jersey', and 'Rubel' blueberries, and a small mixed cultivar trial. In both years the planting was stocked at the beginning of bloom with two honey bee colonies and 16 commercially reared bumble bee colonies (Koppert Biological Systems, Romulus, MI) to ensure activity of both types of bees. Throughout bloom each year, predicted weather conditions for the following day were determined using local forecasts and then periods were selected for bee observations and flower exposure during either good or poor weather. Exposure periods exceeded 3 h within single days, and we attempted to equalize the duration and time of day of exposure across treatments and years. Observations and flower exposures were made during conditions defined as being good for bee activity and pollination when ambient temperature was >15°C and wind speed was <16 km h^{-1}, and poor when ambient temperature was between 10 and 15°C. All treatment exposures and observations ceased when wind speed exceeded 16 km h^{-1}. Weather conditions at the research site were measured hourly using a Campbell Scientific weather station, positioned <1 km from the blueberry field (www.enviroweather.msu.edu), allowing subsequent calculation of average ambient temperature (°C), wind speed (m s^{-1}), solar radiation (kJ m^{-2}), and humidity (%) during each period of bee observation and flower exposure.

To determine bee activity during good and poor weather conditions, two observers walked through randomly selected areas of the whole field at a slow to moderate pace for 20 min during each exposure period and recorded the number of honey bees, bumble bees, and other bees visiting blueberry flowers. The proportion of bees in each category was calculated to compare the pollinator community composition on poor and good weather days, and a chi-square analysis was conducted to determine whether these frequencies were significantly different.

In 2008, bees returning to their colonies were counted during both good and poor weather conditions to quantify differences in the number of pollen and nectar foragers for each managed pollinator type. Observers sat near enough to be able to see whether bees were carrying pollen and recorded how many bees out of 30 returning to the colonies carried pollen or not during good and poor exposure treatments. Chi-square analyses were conducted to determine whether foraging activity differed significantly under different weather conditions for each bee type.

To measure pollination, 20 bushes of Bluecrop blueberries were selected that had uniform branching and flower clusters. Five branches on each bush were assigned one of five treatments: 1) open to pollination throughout bloom (open), 2) covered with mesh to exclude pollinators throughout bloom (enclosed), 3) exposed to pollinators only during good conditions, 4) exposed to pollinators only during poor conditions, or 5) exposed to pollinators only when either treatments three or four were exposed (good + poor). Within each selected branch, the three distal clusters of flowers were selected, comprising 20–30 flowers per experimental unit.

The selected bushes bloomed from 10 to 31 May in 2007 (during which air temperature was between 10 and 15°C for 76 h, between 15.5 and 26°C for 156 h, and between 26.7 and 31.6°C for 50 h) and 14 May to 4 June in 2008 (during which air temperature was between 10 and 15°C for 115 h and between 15.5 and 26°C for 134 h). The clusters designated for the poor treatments were exposed for a total of 23 h in 2007 and 18.5 h in 2008. The clusters assigned to the good treatments were exposed for a total of 27 h in 2007 and

Table 1. Average weather conditions (± SE) in 2007 and 2008 during good and poor weather conditions when blueberry flowers were exposed and bees were observed

Weather parameter	2007		2008	
	Good	Poor	Good	Poor
Ambient temp (°C)	20.4 ± 0.9	11.1 ± 0.9	19.5 ± 0.4	12.0 ± 0.3
Wind speed (m s^{-1})	1.8 ± 0.1	2.8 ± 0.2	1.4 ± 0.1	2.1 ± 0.1
Solar radiation (kJ m^{-2})	2295 ± 144	1415 ± 209	2302 ± 125	2522 ± 126
Humidity (%)	51.8 ± 3.0	66.3 ± 3.4	50.0 ± 2.2	53.7 ± 2.2

22.5 h in 2008. The clusters in the poor + good treatment were exposed for the sum of the hours of the poor and good treatments each year. Average weather conditions during these flower exposure treatments are presented in Table 1.

Fruit set was calculated based on the proportion of the flowers in the distal three clusters that developed into berries, and these values were arcsine transformed before analysis. Blueberry fruit clusters were all harvested when at least 50% of the berries in the open-pollinated clusters were ripe. This method provides berries in which all the seeds have been set, avoids loss of overripe berries to predation or disease, and provides similar fruit weight data compared with harvesting each berry as it ripens (J.K.T., unpublished data). Fruit were weighed, counted, and the number of mature seeds counted (Brewer and Dobson 1969) in the three largest berries from each cluster. Yield values (kg/ha) were estimated for each treatment by multiplying the average berry weight by the number of berries harvested per cluster and the estimated number of clusters per hectare of a mature highbush blueberry field. We assumed a standard 1,250 bushes per hectare, 21 canes per bush, and 85 clusters per cane (R.I. and A. K. Kirk, unpublished data). A mixed model analysis of variance (ANOVA) (PROC MIXED, SAS 9.1, SAS Institute, Cary, NC) was used to determine the effect of exposure treatment on fruit parameters, including estimated yield, after assumptions of normality (Shapiro–Wilk test) and equal variance (LeVene's test) were met.

Results

Bee Abundance and Activity. In both years of this study, bees were far more common on flowers during good weather than poor weather. In 2007, we observed 288 bees in total during good weather and eight bees during poor weather, whereas in 2008 we observed a 147 bees in total during good weather and 73 bees during poor weather (2007: $\chi^2 = 258$, df = 1, $P < 0.0001$; and 2008: $\chi^2 = 24.2$, df = 1, $P < 0.0001$). The composition of the flower-visiting community at this site was markedly different between good and poor weather conditions. Honey bees dominated during good weather, whereas bumble bees dominated during poor weather in both years (Fig. 1) (2007: $\chi^2 = 57$, df = 2, $P < 0.0001$; and 2008: $\chi^2 = 142$, df = 2, $P < 0.0001$). The ratio of pollen to nectar foragers was greater for bumble bees than in honey bees, regardless of weather conditions ($\chi^2 = 5.11$, df = 1, $P = 0.02$) (Fig. 2). However, fewer bumble bee foragers returned with pollen during poor weather than during good weather compared with honey bees ($\chi^2 = 0.35$, df = 1, $P = 0.55$) (Fig. 2).

Berry Parameters and Yield. Fruit set was significantly lower in the enclosed control treatment than all the other treatments, but only in 2007 ($F_{4,94} = 9.59$; $P < 0.0001$) (Fig. 3). However, the proportion fruit set was similar across all the other treatments within both years, with a trend toward lower fruit set in treatments with less exposure to bees (Fig. 3). The weights of berries in the open treatment was significantly greater than all other treatments in both years, with all of the exposure treatments intermediate between this and the enclosed treatment (Fig. 3) (Tukey's honestly significant difference [HSD] test, $P < 0.05$). We also found in both years that average berry weights were higher in berries from flowers exposed only during good weather than those that were enclosed. In 2007, but not 2008, these berries were also significantly larger than berries from flowers exposed only during

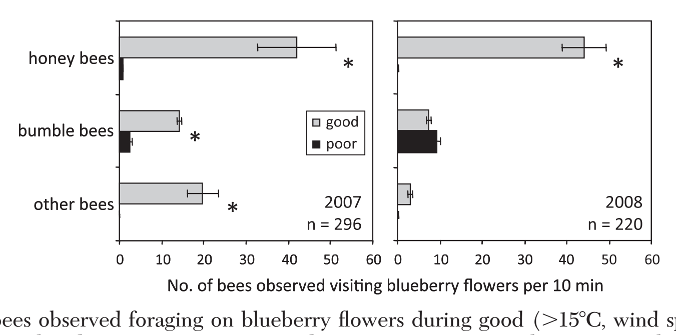

Fig. 1. Number of bees observed foraging on blueberry flowers during good (>15°C, wind speed <10 mph) or poor (between 10 and 15°C) weather during 10–31 May 2007 and 14 May–4 June 2008 at the Trevor Nichols Research Center, near Fennville, MI. Asterisks to the right of each pair of bars indicate that means are significantly different ($P < 0.05$).

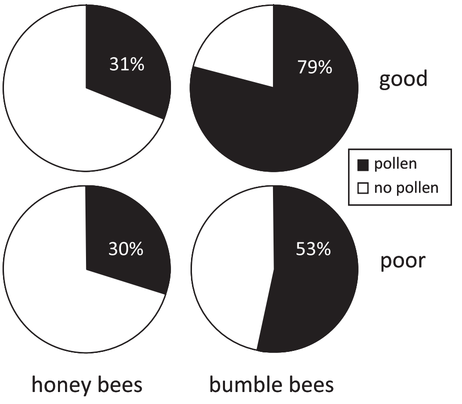

Fig. 2. Proportion of honey bee and bumble bee workers with and without pollen that were observed returning to colonies placed in a blueberry field at the Trevor Nichols Research Center, near Fennville, MI. Data are presented separately for observations conducted during good and poor weather conditions in 14 May–4 June 2008. Honey bees carried pollen with the same frequency regardless of weather, whereas bumble bees carried significantly more pollen during good than during poor weather ($P < 0.05$). However, bumble bees were more likely to return with pollen than honey bees regardless of weather ($P < 0.05$).

poor weather. The production of mature seeds varied significantly by treatment with the berries from open, poor + good, and good treatments all greater than the poor and enclosed treatments (Fig. 3) ($P < 0.05$; Tukey's HSD test). Berries from flowers that were exposed during good weather had more mature seeds in both years of this study than those from flowers that were exposed during poor weather. An important contrast that was planned a priori was to compare data for the treatments exposed during good weather with those exposed during poor + good weather. For all berry parameters measured, there was no significant difference between these two treatments (Fig. 3).

Estimated yields calculated from the values for fruit set and average berry weight showed a similar pattern to those described above; the enclosed treatment had the lowest yield, the open treatment had the highest yield, and the weather exposure treatments had yields intermediate to the open and enclosed treatments in both years of this study (Table 2) ($P < 0.05$; Tukey's HSD test). Clusters exposed only during good weather had a 101% increase in estimated yield compared with clusters exposed only during poor weather, and this difference was statistically significant. Although there was a 38% increase in yield between these treatments in 2008, the treatments were not significantly different. As seen with the fruit set, berry weight, and mature seed counts, there was no significant increase in estimated yield between the good and good + poor treatments (Table 2).

Discussion

This study demonstrates the strong influence that weather conditions have on pollinator activity during the bloom period of an early spring-blooming crop and the implications of this for pollination and yield of blueberry. Many previous studies have examined differences in bee foraging behavior under different weather conditions in other plant systems (Bergman et al. 1996, Vicens and Bosch 2000, Peat and Goulson 2005) and have compared bumble bees to honey bees

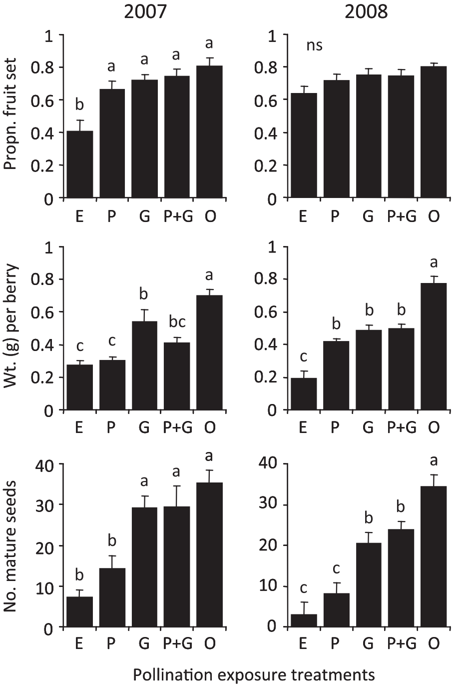

Fig. 3. Effect of flower exposure under different weather conditions on fruit set, berry weight, and number of mature seeds in highbush blueberry Bluecrop over 2 yr at the Trevor Nichols Research Center, Fennville, MI. E, enclosed control; P, exposed during poor weather; G, exposed during good weather; P+G, exposed when P and G were exposed; and O, open control (exposed for the duration of bloom). Bars within a graph with the same letter are not significantly different (Tukey's HSD test). ns, no significant difference among treatments.

Table 2. Estimated yield (kg/ha ± SE) calculated from berry weight, berries harvested per cluster, and estimated number of clusters per ha of highbush blueberry[a] Bluecrop when flowers were exposed to pollinators under different weather conditions

Treatment	2007	2008
Open control	12,953 ± 1,168a	14,400 ± 1,717a
Good + poor	6,722 ± 844bc	8,282 ± 1,297b
Good	8,521 ± 993b	6,816 ± 1,270bc
Poor	4,225 ± 626cd	4,957 ± 845bc
Enclosed control	2,240 ± 342d	1,892 ± 410c
	$F_{4,94} = 22.94$; $P < 0.0001$	$F_{4,91} = 14.09$; $P < 0.0001$

Values within a column with different letters are significantly different (Tukey's HSD test).

[a] Based on the assumption of 1,250 bushes per ha and 1,774 clusters per bush.

in terms of pollination effectiveness (Thomson and Goodell 2001, Stanghellini et al. 2002, Adler and Irwin 2006). A few studies have investigated the link between these changes in behavior or differences in effectiveness with the productivity of a particular crop (Calzoni and Speranza 1996, Dag and Kammer 2001). Given what is known about honey bee and bumble bee foraging behavior under different weather conditions, for early spring-blooming crops such as blueberry, it has been suggested that increasing the abundance of bees that forage under cooler weather conditions than honey bees may provide an advantage to growers aiming to maximize crop pollination.

In this study, bumble bees were the main flower visitor during poor weather, which suggests that most of the pollination occurring during inclement weather was due to bumble bees. On a per bee basis, bumble bees have been shown to be highly effective pollinators compared with honey bees in a number of horticultural crops [e.g., in raspberry, Willmer et al. (1994); apples, Thomson and Goodell (2001); cucumbers and watermelon, Stanghellini et al. (2002); and cranberry, Cane and Schiffhauer (2003)]. Bumble bees visit more flowers per minute in both lowbush, *Vaccinium angustifolium* Ait. (Javorek et al. 2002), and highbush blueberry (J.K.T., unpublished data), and have been shown to deposit more pollen per visit than honey bees (Javorek et al. 2002). Therefore, on a per-bee basis, bumble bees have consistently higher pollination potential than honey bees for a number of crops.

Comparisons among the flower exposure treatments in this study provide insight into the amount of pollination achieved, and the relative contribution of different pollinators during different weather conditions. Compared with the enclosed control treatment, exposure of flowers during poor weather conditions resulted in significant increases in fruit set during 2007 and weight per berry in 2008. These increases were always lower than was observed in the good weather treatments. Despite a doubling in the estimated yield in *poor* compared with *enclosed* clusters, this difference was not significant in either year indicating that these differences were relatively small or highly variable among bushes. This finding suggests either that the bees present during poor weather were not providing sufficient pollen deposition for adequate pollination, that there were too few pollinators active during that time or that weather conditions did not support pollen germination, pollen tube growth, or ovule fertilization given sufficient pollen deposition (Stephenson et al. 1992).

In both years of this study, flowers exposed during good weather conditions produced berries that were significantly larger and with more seeds than the berries from the enclosed control. This resulted in a fourfold increase in estimated yield in 2007 and a threefold increase in 2008, although the latter year was not significantly different from the enclosed control. The open control clusters were exposed for the full 2–3 wk of bloom which consisted of 282 h of potential pollinator contact in 2007 and 249 h of potential pollinator contact during 2008 (73 and 54% of which were considered hours of good weather in 2007 and 2008, respectively), whereas the good weather clusters were exposed for only 20–30 h during peak bloom. Despite the restricted exposure time, approximately half of the potential yield was set during this period. Blueberry flowers within each cluster open sequentially over the course of bloom and flower viability declines with age (Brevis et al. 2006), so it is unlikely that all the flowers in each cluster were receptive during the time when the bags were removed.

'Bluecrop' blueberries used in this study are representative of most highbush blueberry cultivars in that it is self-fertile and has a relatively high degree of parthenocarpy (Eck 1988); however, self-pollination is improbable due to floral morphology. The rate of pollen tube growth is temperature-dependent and can take from 1 to 4 d to reach an ovule depending on temperatures during the pollination period, with warmer temperatures favoring more rapid growth (Eck 1988). Some cultivars differ in the amount of time needed for pollen tube growth, with more rapid growth associated with a higher percentage of fruit set (Eck 1988). Highbush blueberry flowers can remain receptive to pollination up to 8 d after anthesis (Moore et al. 1972); however, pollen germination and successful fertilization are optimal during the first 3 d after anthesis (Merrill 1936). These plant-based limits on pollination suggest that blueberry fields should be stocked with sufficient bees to ensure rapid pollen transfer to a high proportion of stigmas when weather conditions are suitable.

Whether considering fruit set, berry weight, mature seeds, or estimated yield, we found no significant difference between clusters exposed during good weather and those exposed during good + poor weather in either year. This similarity, despite bumble bees actively foraging during poor weather, suggests that cool temperatures may inhibit the plant physiology sufficiently to suppress fertilization. Alternatively, bumble bees may not have been present in sufficient numbers to provide measurable benefit. Separating the contributions of different species of bees to crop pollination is possible using methods such as those employed by Winfree et al. (2008) that measure pollen deposition and fruit size when flowers are visited by a single bee. Adaptation of that technique to flowers that have pollen deposited during different weather conditions, or controlled experiments using manual pollen deposition during different weather conditions, would allow the relative roles of bee visitation (amount of pollen) and suitability of conditions for fertilization (weather) to be examined. Regardless of their lower per bee efficiency in pollinating blueberry, during good weather, honey bees may be able to compensate for their relatively lower pollination efficiency with their much higher abundance at the rates that are currently used in stocking commercial blueberry fields. Further elucidation of the interactions between weather, pollinators, and crop physiology will help fruit farmers make informed decisions regarding the appropriate pollinator investment strategy to ensure pollination under variable spring weather conditions.

Acknowledgments

We thank John Wise and the staff at the Trevor Nichols Research Complex for assistance with plot maintenance; Courtney Hendon, Jack Langdon, and Scott Prajzner for technical assistance; Koppert Biological Inc. for supplying the bumble bee colonies; and two anonymous reviewers for helping to improve an earlier version of this manuscript. We gratefully acknowledge funding for this research by Michigan State University Project GREEEN and by MBG Marketing.

References Cited

Adler, L. S., and R. E. Irwin. 2006. Comparison of pollen transfer dynamics by multiple floral visitors: experiments with pollen and fluorescent dye. Ann. Bot. 97: 141–150.

Bergman, P., U. Molau, and B. Holmgren. 1996. Micrometeorological impacts on insect activity and plant reproductive success in an Alpine environment, Swedish Lapland. Arctic Alpine Res. 28: 196–202.

Brevis, P. A., D. S. NeSmith, and H. Y. Wetzstein. 2006. Flower age affects fruit set and stigmatic receptivity in rabbiteye blueberry. HortScience 41: 1537–1540.

Brewer, J. W., and R. C. Dobson. 1969. Seed count and berry size in relation to pollinator level and harvest date for the highbush blueberry, *Vaccinium corymbosum.* J. Econ. Entomol. 62: 1353–1356.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. *In* C. E. Jones and R. J. Little (eds.), Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

Cane, J. H., and D. Schiffhauer. 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). Am. J. Bot. 90: 1425–1432.

Calzoni, G. L., and A. Speranza. 1996. Pear and plum pollination: honey bees, bumble bees, or both? Acta Hortic. 423: 83–90.

Dag, A., and Y. Kammer. 2001. Comparison between the effectiveness of honey bee (*Apis mellifera*) and bumble bee (*Bombus terrestris*) as pollinators of greenhouse sweet pepper (*Capsicum annuum*). Am. Bee J. 141: 447–448.

Delaplane, K. S. and D. F. Mayer. 2000. Crop pollination by bees. CABI Publishing, New York.

Dogterom, M. H., M. L. Winston, and A. Mukai. 2000. Effect of pollen load size and source (self, outcross) on seed and fruit production in highbush blueberry cv. Bluecrop (*Vaccinium corymbosum:* Ericaceae). Am. J. Bot. 87: 1584–1591.

Eck, P. 1988. Blueberry science. New Rutgers University Press, Brunswick, NJ.

Free, J. B. 1993. Insect pollination of crops. Academic, London, England.

Heinrich, B. 2004. Bumblebee economics. Harvard University Press, Cambridge, MA.

Isaacs, R., and A. K. Kirk. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. J. Appl. Ecol. (in press).

Javorek, S. K., K. E. MacKenzie, and S. P. Vander Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). Ann. Entomol. Soc. Am. 95: 345–351.

MacGregor, S. E. 1976. Insect pollination of cultivated crop plants. Agriculture Handbook No. 46. United States Department of Agriculture, Agricultural Research Service, Washington, DC.

Martin, E. C. 1966. Honey bee pollination of highbush blueberry. Am. Bee J. 106: 366–367.

Marucci, P. E., and H. J. Moulter. 1977. Blueberry pollination in New Jersey. Acta Hortic. 61: 175–186.

Merrill, T. A. 1936. Pollination of highbush blueberry. Tech. Bull. Mich. (St. Coll.) Agric. Exp. Stn. 151.

Moore, J. N., B. D. Reynolds, and G. R. Brown. 1972. Effects of seed number, size, and development on fruit size of cultivated blueberries. HortScience 7: 268–269.

Peat, J., and D. Goulson. 2005. Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris.* Behav. Ecol. Sociobiol. 58: 152–156.

Ratti, C. M., H. A. Higo, T. L. Griswold, and M. L. Winston. 2008. Bumble bees influence berry size in commercial *Vaccinium* spp. cultivation in British Columbia. Can. Entomol. 140: 348–363.

Stanghellini, M. S., J. T. Ambrose, and J. R. Schultheis. 2002. Diurnal activity, floral visitation and pollen deposition by honey bees and bumble bees on field-grown cucumber and watermelon. J. Apicult. Res. 41: 27–34.

Stephenson, A. G., T.-C. Lau, M. Quesada, and J. A. Winsor. 1992. Factors that affect pollen performance, pp. 119–134. *In* R. Wyatt [ed.], Ecology and evolution of plant reproduction. Chapman & Hall, New York.

Stubbs, C. S., and F. A. Drummond. 2001. Bombus impatiens (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. J. Econ. Entomol. 94: 609–616.

Thomson, J. D., and K. Goodell. 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. J. Appl. Ecol. 38: 1032–1044.

Tuell, J. K., J. S. Ascher, and R. Isaacs. 2009. Wild bees (Hymenoptera: Apoidea: Apiformes) of the Michigan highbush blueberry agroecosystem. Ann. Entomol. Soc. Am. 102: 275–287.

Vicens, N., and J. Bosch. 2000. Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae). Environ. Entomol. 29: 413–420.

Willmer, P. G., A.A.M. Bataw, and J. P. Hughes. 1994. The superiority of bumblebees to honey bees as pollinators: insect visits to raspberry flowers. Ecol. Entomol. 19: 271–284.

Winfree, R., N. M. Williams, H. Gaines, J. Ascher, and C. Kremen. 2008. Wild pollinators provide majority of crop visitation across land use gradients in New Jersey and Pennsylvania. J. Appl. Ecol. 45: 793–802.

Winston, M. L. 1987. The biology of the honey bee. Harvard University Press, Cambridge, MA.

Winston, M. L., and L. H. Graf. 1982. Native bee pollinators of berry crops in the Fraser Valley of British Columbia. J. Entomol. Soc. Br. Columbia 79: 14–19.

Received 13 November 2009; accepted 2 April 2010.