Journal of the American Pomological Society 70(3): 124-137 2016

Fruit Set Improvement of Highbush Blueberry *(Vaccinium corymbosum)* West of the Cascade Range in the Pacific Northwest: A Review

MATTHEW ARRINGTON[1] AND WASKO DEVETTER[2]

Additional index words: Flower morphology, pollination, calcium, boron, nutrient supplementation

Abstract

Highbush blueberry is an economically important crop across North America and has become important worldwide. Under certain climatic conditions experienced in various geographical regions, fruit set in blueberry remains relatively poor and contributes to reduced yields. The mechanisms contributing to fruit set are complex. Poor fruit set may be associated with improper or incomplete pollination, inadequate nutrient availability, disease pressure, or poor climatic conditions experienced during critical stages of flowering and fruit set. Improving fruit set in blueberry necessitates the evaluation of floral morphology and the impact of morphology on pollinator efficiency. Pollination requirements as they relate to floral morphology among specific cultivars of blueberry and pollen saturation, as well as the assessment of nutrient applications and their impact on reproductive processes pivotal for fruit set and development, are also in need of further investigation. The objective of this report is to provide a review of the literature addressing pollination and fruit set of highbush blueberry. The development of reproductive buds and flowers are impacted by nutrient availability and associated metabolic compounds and processes. Calcium and boron may be of specific importance for reproductive developmental processes and the requirements, roles, and potential application of these nutrients will be discussed. Variation exists in floral morphology across blueberry cultivars. Additional consideration is given to this variation and how it may impact the efficiency of pollination by primary commercial pollinators. Additionally, the efficacy of pollination may be influenced by pollinator species, the interaction between species of pollinator and cultivar of blueberry, and the environmental conditions during bloom time. These issues are important to understand, especially when considering the development of solutions for the improvement of fruit set for this economically important crop.

The production of highbush blueberries (*Vaccinium corymbosum*) has increased over the past ten years. Approximately 680 thousand metric tons (MT) of blueberries were produced worldwide in 2014 from 100,303 hectares of land (Brazelton, 2015). Cultivated production areas in the United States nearly doubled between 2004 (17,980 hectares) and 2014 (34,054 hectares) [United States Department of Agriculture (USDA), 2005 and 2015]. As a high-value and economically important crop, production efficiency is paramount. Regional climatic conditions impact the management of highbush blueberry and present a number of unique production issues. Pollination and subsequent fruit set remain among the most important challenges for ensuring sustained yields in various regions, including the Pacific Northwest (PNW), a major production region. Pollination of highbush blueberry is complicated by several factors, including: 1) a relatively short duration of pollen viability (5-12 days); 2) the limited effectiveness of traditional commercial pollinators; and 3) environmental conditions at bloom that are not conducive to honey bee (*Apis mellifera*) foraging (Kevan, 1990; Torchio, 1990b). Here, the contributions of flower development, pollination, and fruit development towards highbush blueberry productivity will be reviewed and suggestions will be made regarding future re-

---

[1] Graduate Research Assistant, E-mail: matthew.arrington@wsu.edu

[2] Assistant Professor and corresponding author, E-mail: lisa.devetter@wsu.edu
Department of Horticulture, Washington State University Northwestern Research and Extension Center, Mount Vernon, WA 98273

search directions to improve highbush blueberry yields and cropping efficiency.

Bud and flower development. Floral buds of highbush blueberry contain 5 to 12 flowers, with a wide variation in number and morphology between cultivars and little within (Pritts et al., 1992). Blueberries have both reproductive (flower) and vegetative (leaf) buds, which develop on one-year-old or older wood. Vegetative buds, which typically break from January to April, depending on accumulated growing degree days, region, and germplasm (e.g., northern versus southern highbush), only result in shoot and leaf growth. Flower buds, which are larger and rounder than vegetative buds, begin their formation in late-summer to early fall, and continue to develop until temperatures are excessively cold (approximately 7°C) (Kovaleski et al., 2015; Strik, 2015). Floral bud counts have been used to estimate crop yields (Salvo et al., 2012). Within flower buds are flower primordia, which can result in flower clusters that have the potential to become fruit. The development and occurrence of floral and vegetative buds is controlled in part by auxin and plant carbohydrate status (Darnell, 1991; Maust et al., 2000). Soluble carbohydrates regulate auxin synthesis; therefore, insufficient carbohydrate levels in some cultivars of blueberry may lead to decreased reproductive development, including floral bud development (Maust et al., 2000; Sairanen et al., 2012).

Additionally, photoperiod (day length) is an integral part of bud break. Plants exposed to chilling treatments without also experiencing short days were shown to not initiate bud break following chilling (Bañados and Strik, 2006).Prior to bud break, dormant buds are tightly closed and protected by bud scales. Typically a range from 200 to 300 chilling hours for southern highbush cultivars and over 800 chilling hours for northern highbush cultivars are needed to break endodormancy and approximately 4-8 weeks of short days are required to satisfy the photoperiod requirements (Bañados and Strik, 2006; Strik et al., 2014). Once requirements for flowering have been met, buds swell and break. These phenological stages are referred to as "bud swell" and "bud break", respectively. Bud swell can be discerned when the outer bud scales begin to separate as the flower buds enlarge and swell. Early green tip (referencing leaf buds) comes next and tends to develop in late winter or early spring. This stage is characterized by emerging vegetative tissues consisting of tightly rolled leaves. Bud break (referencing floral buds) often coincides with green tip and can be described as the opening of flower buds and increased visibility of individual flowers. Following bud break, plants progress into the late green tip and tight cluster stages, wherein leaves begin to unfold, but flowers remain closed and tightly packed together, respectively. Next, blueberry plants enter into a phase of shoot expansion in which multiple leaves emerge and begin to enlarge. The early and late pink bud stages represent a period of flower expansion and separation within the inflorescence, as well as the continued development of the corolla tubes. The corollas also transition in coloration from pink to white during this stage. The early bloom stage occurs when some corolla tubes are expanded and fully opened, but the majority of flowers remain closed. Early bloom eventually gives way to full bloom. During full bloom, a majority of the flowers are fully opened. This stage can last for 5-12 days depending on cultivar and climatic conditions (Pritts et al., 1992).

Flower morphology. Flowers in blueberry are characterized by their bell-shaped corollas, with stamens and anthers inside and a stigma sometimes protruding past the flower aperture (Eck and Mainland, 1971) (Figure 1). Blueberry flowers have elongated corolla tubes and poricidal anthers, which tends to make pollination by honey bees difficult (Ritzinger and Lyrene, 1999). Variation in flower size and morphology between cultivars has been shown to impact insect foraging activity and, as a result, fruit set (Courcelles et al., 2013). Corolla length and aperture diameter appear to be some of the most

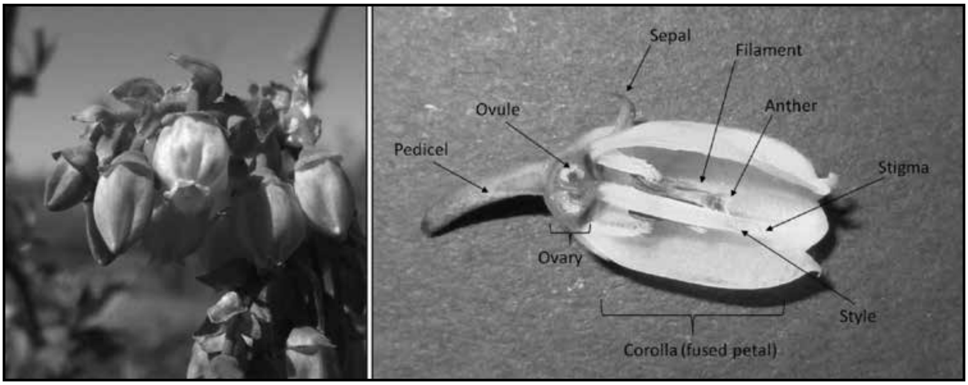

Fig. 1: (a) Flower of *Vaccinium corymbosum* 'Draper' (b) *V. corymbosum* 'Bluecrop' longitudinal cross-section with morphological features labeled.

important floral traits for pollen and nectar accessibility to honey bees, which impacts pollination and fertilization. As shown by Courcelles et al. (2013), there is a clear relationship between floral morphology and honey bee visitation rates in 'Duke', 'Bluecrop', 'Liberty', and 'Draper' blueberry. Both "legitimate visits" (through the flower entrance and thus, the pollen-bearing anthers) and "nectar robbing" (bypassing the entrance of the flower to harvest nectar at the base of the corolla) by honey bees visiting 'Bluecrop', 'Liberty', and to some extent, 'Draper' flowers, are common. 'Duke' flowers have a large aperture and flexible corolla, which allows honey bees to force their heads into flowers and access pollen. Flowers from 'Duke' are visited more often by honey bees relative to 'Draper' and 'Bluecrop'. Relative to 'Duke', shorter corolla lengths with smaller throat diameter does not facilitate efficient penetration of the flower by the head of honey bees to reach nectar and pollen rewards.

Outcrossing. The introduction of unrelated genetic material to the breeding cycle of a species or cultivar is known as outcrossing. Self-incompatible plants ensure genetic diversity by rejecting their own pollen and accepting unrelated pollen within the same species. In blueberry, variability exists between the effectiveness of fertilization with self- and outcrossed- pollen between cultivars. Cultivars of cultivated highbush blueberry are to a large extent self-fertile. However, it is well established that fertilization and yields are significantly increased when flowers are cross pollinated (Ehlenfeldt, 2001; Krebs and Hancock, 1990; Vander Kloet, 1984; Vander Kloet and Lyrene, 1987; Wood, 1968). Yields are also generally increased through cross pollination with the aid of insect pollinators (Ehlenfeldt, 2001; Krebs and Hancock, 1990). Generally, fewer tetrads of outcrossed pollen are required to reach pollen-load saturation than with self-pollination (Parrie and Lang, 1992). However, pollen tubes from self-pollinated plants grow at the same rate as outcrossed pollen once germination occurs (Krebs and Hancock, 1988; Vander Kloet and Lyrene, 1987). Only a fraction of ovules develop into seeds, with over 100 ovules being common to highbush blueberry fruit and fewer than 50 seeds forming (Pritts et al., 1992). Seed number is positively correlated to fruit size (until saturation occurs) and seed abortion is dependent on the level of self-fertility (Pritts et al., 1992; Vestrheim et al., 1996).

Pollination in highbush blueberry. In blueberry production, commercially managed honey bees, specifically the Italian honey bee (*Apis mellifera* 'ligustica'; commonly referred to as "honey bee") are primarily responsible for pollination. Wet and cool spring weather limits honey bee activity and subsequently can negatively affect pollination and fruit set. The Northeastern region of the United States, including Michigan, is climatically similar to the PNW in average spring low and high temperatures [Baker et al., 1994; National Oceanic and Atmospheric Administration (NOAA), 2015]. However, highbush blueberry is native to the Northeastern United States and a variety of alternative insect pollinators have strong populations in the region (Garibaldi et al., 2013; Winfree et al., 2008). The co-evolution of some bee species with *Vaccinium* spp. may make them ideal blueberry pollinators relative to commercial honey bees (Tuell et al., 2009). The primary pollinators of wild highbush blueberry are bumblebees (*Bombus* spp.), mining bees (*Andrena* spp.*)*, sweat bees (*Halictus* spp.)*,* orchard/mason bees *(Osmia* spp.), leafcutter bees (*Megachile* spp.), and European sweat bees (*Lasioglossum* spp.)*,* many of which exhibit sonication (Buchmann, 1985; Torchio, 1990b).

Honey bees are indigenous to Europe, with a number of subspecies inhabiting all parts of Europe and Africa (Jensen et al., 2005; Whitfield et al., 2006). Honey bees were introduced to North America from Europe in the early 1600's and have become vital to crop production. Pollination in many crops, like blueberry, is achieved through obtaining saturating populations of honey bees through the provision of commercially rented hives (Paini, 2004). In contrast to honey bees, many of the above species (including bumblebees) remain active and forage at lower temperatures (below 13°C), which can be advantageous in areas that are climacterically characterized as having cool and/or wet springs where honey bees are less active (Delaplane et al., 2000).

It is common for commercial plantings of blueberry to be stocked with 2 to 6 honey bee hives per hectare in the PNW. Honey bee stocking rates are influenced by the strength of the colony at bloom and the level of attractiveness of a specific cultivar's flowers to honey bees (Marucci and Moulter, 1976; Sagili and Burgett, 2011; Wood, 1961). Honey bees introduced to plantings during early and late pink phenological stages commonly forage elsewhere and are slow to return to blueberries (Jay, 1986; Kevan et al., 1990). Consequently it is recommended to place honey bee hives between 5% to 25% bloom in blueberry and cranberry *(Vaccinium macrocarpon*), another related species (Delaplane et al., 2000; Moeller, 1973). Pollination by honey bees is carried out by nectar and pollen foragers. Foraging honey bees do not sonicate (otherwise known as buzz pollinate, which is the vibration of flight muscles causing dehiscence of poricidal anthers) and must consequently rub against anthers to obtain pollen. Several native and alternative pollinating species, including bumble bees, are able to sonicate and consequently can collect more pollen per flower visit than honey bees (Garibaldi et al., 2013). Honey bees also have an average tongue length of approximately 6.5 mm. This is short compared to some non-*Apis* bee species, such as bumble bees, that have tongues that are approximately 8.5 mm long (Balfour et al., 2013). The short tongue of honey bees can make it difficult to reach nectar sources in flowers with long corolla tubes that are present in some blueberry cultivars. Bumblebees enter through the opening of the flower and brush against stigmas and anthers, occasionally robbing nectar, but with less frequency than honey bees (Courcelles et al., 2013; Stubbs and Drummond, 1996). Significantly higher crop yields have been realized in plots where honey bees and bumblebees have been used together for pollination, making bumblebees an important resource for pollination and fruit set enhancement (Garibaldi et al., 2013).

Apiculture is the practice of maintaining honey bee colonies for their products and encompasses hive maintenance and promoting bee health. Nutrition can be promoted by increasing the diversity and availability of surrounding forage material (Toth and Robinson, 2005). Often hives are under significant stress during pollination, having been stored and moved by semi-trucks across hundreds of kilometers. In transit, honey bees must rely on feeding trays with solutions of sucrose and nutrients for nourishment, which may be nutritionally lacking (Crailsheim, 1990; Standifer, 2003). Additionally, it has been reported that as high as 50% of queen honey bees are replaced within 6 months, with temperature fluctuations in shipment being linked to low sperm viability in queens and, as a result, the decreased ability of queens to lay fertilized eggs and maintain colony strength, leading to colony decline (Pettis et al., 2016). In evaluating hive health, the percent of filled or capped brood cells per frame (or uniform capping pattern) is indicative of overall hive health, and honey bees generally forage more with large brood populations to support (Eckert et al., 1994; Fewell and Winston, 1992; Free, 1967).

Foraging activity of honey bees can be increased when environmental conditions are ideal and by using brood pheromones to influence the hive activity (Pankiw et al., 1998). Brood pheromones are naturally produced by uncapped brood and increases honey bee foraging. There are two main types of brood pheromones: brood ester pheromone (BEP) and E-β-ocimene. Brood ester pheromones primarily regulate which bees can lay eggs through suppression of worker bee ovary development and egg laying, while E-β -ocimene influences the nurse-forage ratio, as well as the type and number of foragers. Another bee pheromone, queen mandibular pheromone (QMP), is produced by the queen and fed to attendants. Queen mandibular pheromone can be used to slow hive growth and deter reproductive swarming in order to increase hive strength and foraging activity (Pankiw et al., 1994; Winston et al., 1991). Both brood and QM pheromones are periodically used in commercial production of horticultural crops in order to increase honey bee visitations and resultant crop yields, but research on their potential benefits is lacking in blueberry.

While *Apis mellifera* 'ligustica' may be the most common commercial honey bee subspecies, others are also used for pollination in specific regions (Bailey and Ball, 2013). The Carniolan honey bee (*A. mellifera* 'carnica') is a subspecies of *A. mellifera* and maintains a higher level of activity early and late in the day (before 8am and after 4pm) and in cool and wet conditions as compared to 'ligustica' (Biasiolo and Comparini, 1990; Moritz and Hillesheim, 1985). Carniolan honey bees are native to Austria and Croatia, and are presently not widely utilized in North America. Carniolan bees have more foragers entering and leaving the hive in conditions of precipitation and cool temperatures than 'ligustica' [>18°C] (Alqarni, 1995). High levels of foragers entering and leaving hives is indicative of increased activity. The European black bee (*A. mellifera* 'mellifera') is also less sensitive to cool, wet conditions and has been known to overwinter well in small populations in northern United Kingdom (Corbet et al., 1993). The European black bee has a larger body than either the Italian or Carniolan honey bees, which may present problems with small, tubular blueberry flowers (Daly et al., 1995). European black bees may also be more susceptible to tracheal mites, which nearly destroyed 'mellifera' populations in the early 1900's (Baily and Ball, 2013). Regardless of general pollination efficiency, poor weather including cold temperatures, high winds, and steady rain can deter even the most effective pollinator species. The short bloom window of blueberry imposes an additional challenge, regardless of the pollinator chosen. Under these circumstances and to maximize pollination, there is an industry-wide preference for honey bee availability and field placement of hives in the early bloom stage (5% to 25% bloom), when only some flowers are fully open (Delaplane et al., 2000).

Adverse weather not only limits honey bee activity, but can also limit the rate of plant reproductive processes, ultimately reducing fertilization and subsequent yields (Hepler and Yarborough, 1991; MacKenzie, 1997; Seely, 1994). Alternative pollinator species better adapted to foraging during the environmental conditions encountered during blueberry bloom time, as well as the morphology of blueberry flowers, may improve pollination in highbush blueberry (Bosch and Kemp, 2003; Courcelles et al., 2013; Heinrich, 1975; Seeley, 1994). Understanding the contributions of honey bees in blueberry, irrespective of the potential limitations, would benefit blueberry growers experiencing chronic pollination deficits and subsequent reduced yields. Mason and bumblebee species may be especially adapted to blueberry pollination, with higher levels of activity in cool and wet conditions and specialized physical traits (i.e. longer tongue, smaller body size, sonicating flight muscles) for pollen collection and transfer among the small, tubular flowers of blueberry (Balfour et al., 2013; Buchman, 1985; Desjardins and Oliveira, 2006; Sampson and Cane, 2000; Stubbs et al., 1994; Torchio, 1990a; Whidden, 1996).

Although native species of insect pollinators may be especially adapted for blueberry pollination, population dynamics and species habitat are also important considerations from a management perspective. Monoculture field situations that are intensively managed with frequent field maintenance can deter populations of native pollinators (MacKenzie and Winston, 1984). However, planting strips of wildflowers or greenbelts between fields can increase the attractiveness of field sites to pollinator habitation, as well as increase the diversity and abundance of pollinators (Blaauw and Isaacs, 2014; Kremen et al., 2002). Establishment of nesting boxes or hive systems for attracting and maintaining mason and bumblebee species has increased pollination and, as a result, fruit set in orchard crops (Bosch et al., 2000; Knight et al., 2005). In addition to habitat availability, the frequency of field cultivation practices decreases the permanent population of native bees in the area (Carré et al., 2009; Carvell et al., 2011). While investigations of native pollinator population decline are ongoing, causal factors continue to be confounding. Widespread use of broad spectrum insecticides is a danger to bees and other beneficial insects; however, the resilience of some species suggests we need continued research of additional factors beyond pesticides for causes of population decline (Gels et al., 2002; Goulson et al., 2008). Findings to date suggest that the successful utilization of native species as pollinators in blueberry production will likely have to be combined with habitat management practices that promote abundance and activity, such as reduced pesticide applications during critical periods of pollinator activity and reduced tillage. These management practices are complicated by the threat of spotted wing drosophila (SWD; *Drosophila suzukii*). In an effort to minimize the habitat for this insect pest, wooded areas are frequently reduced and pesticide applications utilized (Lee et al., 2011).

Fertilization and berry development. From early bloom through full bloom, pollination and fertilization in highbush blueberry can occur in as few as 5 to12 days (Dogterom et al., 2000). Fertilization of ovules and fruit development depends on successful pollination and fertilization. Reproductive tissues (i.e., pollen, ovules, and developing embryos) are sensitive to nutrient levels in the flower and stem tissue (May and Killingbeck, 1992). Pollen and ovary tissues are also sensitive to temperature and humidity. Warm and dry conditions can increase the speed of metabolic systems in plants (~20°C), thereby shortening the effective pollination period (De Vries and Dubois, 1987; Hedhly et al., 2004). In contrast, cool and wet conditions speed the decay of flower tissues and increase the potential for fungal and bacterial infections (Daykin and Milholland, 1990; Ngugi et al., 2002; Ngugi and Scherm, 2004; Ngugi and Scherm, 2006; Verma et al., 2006). Nutrients involved in pollen tube elongation, membrane integrity, and other reproductive processes critical for berry development, such as boron or calcium, could potentially increase fruit set and decrease the number of berries lost to abscission under conditions that are otherwise limiting. Pollen viability is positively correlated in blueberry with seed counts and fruit size until a saturation threshold is reached (Vander Kloet, 1984).

Fertilized seeds contribute to fruit development and ultimate berry size in blueberry, although this is somewhat influenced by cultivar (Dogterom et al., 2000; Lang and Danka, 1991; Payne et al., 1989). Approximately 30 days following bloom, new fruit go through a period of rapid cell division (Cano-Medrano and Darnell, 1997). After initial growth by cell division, fruit enlargement occurs almost exclusively as the result of cell enlargement. In highbush blueberry, fruit size is positively related to seed number. Larger fruit generally have a greater number of cells, however, marketable size has been achieved with as few as 10-20 seeds per fruit (Coombe, 1976; Vorsa et al., 1991). The primary growth phase, which dictates ultimate fruit size, occurs during the initial 30 days immediately following bloom (Strik et al., 1993). Increased fruit size and seed number is reported to be due to the release of hormones from fertilized seeds, which stimulate fruit enlargement (i.e., auxins) (Pritts et al., 1992). Improvement of fruit size should target the periods of early cell division, as this is a critical stage that determines berry size. Provision of adequate moisture and mineral nutrients during early cell division are two strategies to ensure that this critical period goes unrestricted.

Following fertilization, fruits begin to enlarge, and competition for carbohydrates can manifest into fruit drop if carbohydrate resources are limiting (Racskó et al., 2007). The abscission of plant parts, including leaves and immature or ripe fruit, can occur naturally at multiple points throughout the season. However, under certain conditions, abscission of leaves and developing fruit can occur prematurely. Premature abscission of leaves and fruit often results from pest or pathogen pressures, nutrient deficiencies, and/or water stress (Arteca, 1996; Darnell and Birkhold, 1996; Hildebrand et al., 2001; McNicol and Williamson, 1989). In 'Draper' blueberry, plants can experience pre-mature fruit drop in western Washington and British Columbia. This phenomenon is commonly referred to as "Draper drop" and can result in severe crop losses. Similar fruit drop symptoms preceded by transient red coloration in young leaves and flowers is attributed to Fruit Drop Virus in blueberry (Martin et al., 2006). The cause of this premature fruit drop in 'Draper' is not known. Further discussion of plant nutrition in relation to fruit development is addressed in the section, "Nutrient Application".

Abscission may also result as a consequence of limited plant carbohydrates, with more sink material than source material, as occurs and described in pear (*Pyrus communis*) and apple (*Malus domestica*) (Byers et al., 1990; Dennis, 2000; McArtney et al., 2004; Wertheim, 2000). Developing fruit are strong carbohydrate sinks, leading to the diversion of soluble sugars from carbohydrate producing and storage organs to fruit. In apple and pear, fruit are thinned to increase the size of remaining fruit and to manage the overall carbohydrate source:sink ratio (Wertheim, 2000). Solar radiation and temperature can also influence photosynthesis and the production of carbohydrates. Consistent high light, above the light compensation point, drives carbohydrate production. Conversely, consistently low light conditions or prolonged high temperatures (>35°C) can reduce net photosynthesis and drive a carbohydrate deficit (Hancock et al., 1992). Adequate plant spacing between rows may also increase light interception, increasing overall photosynthates (Bryla and Strik, 2004).

Nutrient application. Nutrient management in blueberry production is crucial for successful and productive plantings. When various chemical elements are inadequate, the general health, yield, and quality of the crop may be reduced so long as other factors are not limiting. Severe nutrient deficiency can lead to discolored leaves, wilted flowers, reduced yields, decreased cane initiation and growth, and plant death. Calcium and boron have been used as supplemental fertilizers in blueberry production and have the potential to positively influence fruit set and yield.

Calcium. Calcium is an essential macronutrient in blueberry production (Chen et al., 1998). The roles that calcium plays in plants are many and include structural (calcium bound to pectin cell walls), defense, and communication (between cells and tissues) (Dixon et al., 1994; Evans et al., 2001; Jarvis, 1984; Sanders et al., 1999). Calcium is particularly important for the function of calcium ion transporters and their subsequent role in environmental and biotic responses (Hepler and Wayne, 1985). Calcium is frequently applied as a soil amendment in the form of agricultural and/or dolomitic limestone or, when pH must remain stable, as calcium sulfate (gypsum) (Hart et al., 2006). Hanson and Berkheimer (2004) have shown that integration of soil-applied calcium into leaves and fruit is inconsistent and ineffective in blueberry. This response is similar to other fleshy fruits, including apple (*Malus domestica*) and tomato (*Solanum lycopersicum*) (Dong et al., 2005; Shear and Faust, 1970). Foliar applications of calcium chloride have been used to a smaller degree in blueberry. However, due to salt sensitivity, chlorine-containing nutrients are generally avoided in fertilizer programs (Korcak, 1988).

Nutrient levels vary across blueberry cultivars and the time of year, but levels remain most stable in late July or early August (Strik and Vance, 2015). Despite stability of macronutrients, high variability can occur in micronutrients. There is often a disparity between calcium content in leaves and in fruit, with higher levels of calcium being found in transpiring tissues, such as leaves (Strik and Vance, 2015; Wiersum, 1966). In addition, calcium movement and distribution in blueberry appears to vary greatly by cultivar (Strik and Vance, 2015). Plants which are not self-fertile and require cross-pollination with compatible genotypes have been found to produce pollen with lower levels of calcium relative to plants that do not require cross-pollination (Brewbaker and Kwack, 1963). Low calcium concentrations in pollen has been correlated with a reduced rate of pollen germination, with some dependence of germination on calcium levels found within the stigma (Bednarska, 1991; Brewbaker and Kwack, 1963; Ge et al., 2009; Taylor and Hepler, 1997). Post-harvest calcium chloride dips have also increased firmness in blueberries, a valuable trait in fresh market production; however, fruit was reported to taste salty and, as a result, fresh market blueberries are generally not dipped (Hanson et al., 1993). However, no significant increase in berry firmness has been realized when berries are treated with foliar applications of calcium chloride during the production season (Hanson, 1995). Mobility of calcium to fruit in blueberry is limited because fruit have low transpiration rates relative to the leaves, thereby limiting the movement of dissolved calcium in the xylem to fruit (Angeletti et al., 2010).

Boron. Boron is a micronutrient that is often deficient in blueberry production, particularly in western Washington and Oregon. Boron is important for pollen formation and health, with pollen germination, tube length, and speed of pollen tube growth all influenced by boron availability in reproductive tissues (Thompson and Batjer, 1950; Visser, 1955; Wang et al., 2003). Because of this, many commercial growers in western Washington and Oregon provide boron through foliar nutrient applications in order to improve pollen health and subsequent fruit set; however, research validating their use is lacking. Boron deficiency is common among soil types with coarse texture (Goldberg, 1997). Absorption and uptake of boron as undissociated boric acid (tetrahydroxyborate) occurs at the roots. Boron deficiency can result in reduced pollen viability, tube elongation, and lower germination rates of pollen in almond (*Prunus dulcis*) (Nyomora et al., 1997). Pollen tube growth rate and overall length are indicative of viability and general health (Huang and Johnson, 1996; Knox and Friederich, 1974; Sahar and Spiegel-Roy, 1984). Evaluation of pollen germination and tube formation in the presence of given nutrients would allow for a more direct evaluation of reproductive responses to nutrients like boron in the environment and provide additional support for their commercial use. Even when leaf tissue samples indicate sufficient concentrations of boron, deficiencies can persist in meristematic and floral tissues (Shorrocks, 1997). However, there is a fine line between sufficiency and toxicity of boron in plants. Typically, boron is not applied in excess of 500 ppm in blueberry due to increased occurrences of phytotoxiciy. Culture media prepared with boron increases pollen germination rates *in vitro,* as well (Sotomayor et al., 2001). Significant differences between *in vitro* pollen germination of 'Rubel' and 'Jersey' blueberries were strongly correlated to fruit set, with higher germination positively correlated with increased fruit set (Brewer and Dobson, 1969). Boron deficiency can retard seed formation and reduce viability (Marschner, 1995; Marschner et al., 1996). While boron is readily absorbed and mobile within the xylem of plants, concentrating applications to the dynamic growth phase occurring during floral development, pollen germination, fertilization, and early berry development may increase absorption to target tissues (Angeletti et al., 2010; Brown and Hu, 1996; Lord and Russell, 2002). This intense period of development is metabolically demanding and plant nutrient levels at this stage may have far-reaching consequences on future fruit set, berry size, and fruit composition at harvest across different cultivars.

Conclusion

Pollination and fruit set are complex processes in blueberry production, being influenced by bud and flower development, pollinator activity, pollen compatibility, floral morphology, fertilization, and flower and fruit nutrient status. A systems-based approach is required to increase pollination and fruit set in blueberry, particularly in primary production regions west of the Cascades that experience chronically low fruit set. There is a positive relationship between productive cultivars with high fruit set and large, open flowers. Therefore, the link between floral morphology and cultivar attractiveness to pollinators should be investigated further, which may influence regional cultivar recommendations and pollination practices. Currently, the stocking rates for honey bee hives to achieve saturating conditions for pollination is derived from largely non-region-specific stocking density recommendations and may be unrealistic considering continually increased demand for honey bees. Optimization of honey bee stocking recommendations and understanding the role that alternative pollinator species can contribute to improving the overall success of pollination is important for difficult-to-pollinate crops, like blueberry. The potential benefits of supplementing additional boron and calcium are promising and are under investigation. Overall, further research and development of pollination and fruit set enhancement tools in highbush blueberry have great potential to close the regional production gaps in the PNW, which presently exist for this economically important crop.

Literature cited

Alqarni, A. S. 1995. Morphometrical and biological studies of the native honeybee race *Apis mellifera* L.; the carniolan *A. m. carnica* 'Pollmann' and their F1 hybrid. King Saud University, Riyadh, Saudi Arabia. Doctoral dissertation, MSc Thesis.

Angeletti, P., H. Castagnasso, E. Miceli, L. Terminiello, A. Concellón, A. Chaves, and A. Vicente. 2010. Effect of preharvest calcium applications on postharvest quality, softening and cell wall degradation of two blueberry (*Vaccinium corymbosum*) varieties. Postharvest Biol. Tech. 58(2): 98-103.

Arteca, R. N. 1996. Plant growth substances: principles and applications. Chapman & Hall, London, UK. 165-172.

Bailey, L. and B. V. Ball. 2013. Honey bee pathology (second edition). Academic Press/Elsevier, San Diego, CA. 1-5.

Baker, C.B., J.K. Eischeid, T.R. Karl, and H.F. Diaz. 1994. The quality control of long-term climatological data using objective data analysis. Preprints of AMS Ninth Conference on Applied Climatology, Dallas, TX.

Balfour, N. J., M. Garbuzov, and F. L. Ratnieks. 2013. Longer tongues and swifter handling: why do more bumble bees (*Bombus* spp.) than honey bees (*Apis mellifera*) forage on lavender (*Lavandula* spp.)? Ecol. Entomol. 38(4): 323-329.

Bañados, M. P. and B. Strik. 2006. Manipulation of the annual growth cycle of blueberry using photoperiod. In VIII International Symposium on Vaccinium Culture, Acta Hort. 715: 65-72.

Bednarska, E. 1991. Calcium uptake from the stigma by germinating pollen in *Primula officinalis* L. and *Ruscus aculeatus* L. Sex. Plant Reprod. 4(1): 36-38.

Biasiolo, A. and A. Comparini. 1990. Esterase-6 locus, a new enzyme polymorphism in *Apis mellifera*. Apidologie 21(2): 123-126.

Blaauw, B. R. and R. Isaacs. 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. 51(4): 890-898.

Bosch, J., W.P. Kemp, and S. S. Peterson. 2000. Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. Environ. Entomol. 29(5): 874-883.

Bosch, J. and W. P. Kemp. 2003. Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). Environ. Entomol. 32(4): 711-716.

Brazelton, C. 2015. World blueberry statistics and global market analysis. U.S. Highbush Blueberry Council, Folsom, CA.

Brewbaker, J. L. and Kwack, B. H. 1963. The essential role of calcium ion in pollen germination and pollen tube growth. Am. J. Bot. 50(9): 859-865.

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* 1. *J.* Econ. Entomol. 62(6): 1353-1356.

Brown, P. H. and H. Hu. 1996. Phloem mobility of boron is species dependent: evidence for phloem mobility in sorbitol-rich species. Ann. Bot. 77(5): 497-506.

Bryla, D. and B. C. Strik. 2004. Variation in plant and soil water relations among irrigated blueberry cultivars planted at two distinct in-row spacings. In VIII International Symposium on Vaccinium Culture. 715: 295-300.

Buchmann, S. L. 1985. Bees use vibration to aid pollen collection from non-poricidal flowers. J. Kans. Entomol. Soc. 58(3): 517-525.

Byers, R. E., J.A. Barden, R. F. Polomski, R. W. Young, and D. H. Carbaugh. 1990. Apple thinning by photosynthetic inhibition. J. Am. Soc. Hortic. Sci. 115(1): 14-19.

Cano-Medrano, R. and L. Darnell. 1997. Cell number and cell size in parthenocarpic vs. pollinated blueberry (*Vaccinium ashei*) fruits. Ann. Bot. 80(4): 419-425.

Carré, G., P. Roche, R. Chifflet, N. Morison, R. Bommarco, J. Harrison-Cripps, and J. Settele. 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133(1): 40-47.

Carvell, C., J. L. Osborne, A. F. G. Bourke, S. N. Freeman, R. F. Pywell, and M. S. Heard. 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecol. Appl. 21(5): 1760-1771.

Chen, Y., J. M. Smagula, W. Litten, and S. Dunham. 1998. Effect of boron and calcium foliar sprays on pollen germination and development, fruit set, seed development, and berry yield and quality in lowbush blueberry (*Vaccinium angustifolium* Ait.). J. Am. Soc. Hortic. Sci. 123(4): 524-531.

Coombe, B. G. 1976. The development of fleshy fruits. Annu. Rev. Plant Physiol. 27(1): 207-228.

Corbet, S. A., M. Fussell, R. Ake, A. Fraser, C. Gunson, A. Savage, and K. Smith. 1993. Temperature and the pollinating activity of social bees. Ecol. Entomol. 18(1): 17-30.

Courcelles, D. M. M., L. Button, and E. Elle. 2013. Bee visit rates vary with floral morphology among highbush blueberry cultivars (*Vaccinium corymbosum* L.). J. Appl. Entomol. 137(9): 693-701.

Crailsheim, K. 1990. The protein balance of the honey bee worker. Apidologie 21(5): 417-429.

Daly, H. V., R. G. Danka, K. Hoelmer, T. E. Rinderer, and S. M. Buco. 1995. Honey bee morphometrics: linearity of variables with respect to body size and classification tested with European worker bees reared by varying ratios of nurse bees. J. Apic. Res. 34(3): 129-145.

Darnell, R. L. 1991. Photoperiod, carbon partitioning, and reproductive development in rabbiteye blueberry. J. Am. Soc. Hortic. Sci. 116(5): 856-860.

Darnell, R. L. and K. B. Birkhold. 1996. Carbohydrate contribution to fruit development in two phenologically distinct rabbiteye blueberry cultivars. J. Am. Soc. Hortic. Sci. 121(6): 1132-1136.

Daykin, M. E. and R. D. Milholland. 1990. Histopathology of Blueberry Twig Blight Caused by *Phomopsis vaccinii*. Phytopathology 80: 736-740.

De Vries, D. P. and L. A. Dubois. 1987. The effect of temperature on fruit set, seed set and seed germination in 'Sonia'×'Hadley' hybrid Tea-rose crosses. Euphytica 36(1): 117-120.

Delaplane, K. S., D. R. Mayer, and D. F. Mayer. 2000. Crop pollination by bees. Cabi, Boston, MA.

Dennis, F. J. 2000. The history of fruit thinning. Plant Growth Regul. 31(1-2): 1-16.

Desjardins, È. C. and D. De Oliveira. 2006. Commercial bumble bee *Bombus impatiens* (Hymenoptera: Apidae) as a pollinator in lowbush blueberry (Ericale: Ericaceae) fields. J. Econ. Entomol. 99(2): 443-449.

Dixon, R. A., M. J. Harrison, and C. J. Lamb. 1994. Early events in the activation of plant defense responses. Annu. Rev. Phytopathol. 32(1): 479-501.

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(11): 1584-1591.

Dong, C. X., J. M. Zhou, X. H. Fan, H. Y. Wang, Z. Q. Duan, and C. Tang. 2005. Application methods of calcium supplements affect nutrient levels and calcium forms in mature tomato fruits. J. Plant Nutr. 27(8): 1443-1455.

Eck, P. and C. M. Mainland. 1971. Highbush blueberry fruit set in relation to flower morphology. HortScience 8(2): 494-495.

Eckert, C. D., M. L. Winston, and R. C. Ydenberg. 1994. The relationship between population size, amount of brood, and individual foraging behavior in the honey bee, *Apis mellifera* L. Oecologia 97(2): 248-255.

Ehlenfeldt, M. K. 2001. Self-and cross-fertility in recently released highbush blueberry cultivars. HortScience 36(1): 133-135.

Evans, N. H., M. R. McAinsh, and A. M. Hetherington. 2001. Calcium oscillations in higher plants. Curr. Opin. Plant Biol. 4(5): 415-420.

Fewell, J. H. and M. L. Winston. 1992. Colony state and regulation of pollen foraging in the honey bee, *Apis mellifera* L. Behav. Ecol. Sociobiol. 30(6): 387-393.

Free, J. B. 1967. Factors determining the collection of pollen by honeybee foragers. Anim. Behav. 15(1): 134-144.

Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, and A. M. Klein. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339(6127): 1608-1611.

Ge, L. L., C. T. Xie, H. Q. Tian, and S. D. Russell. 2009. Distribution of calcium in the stigma and style of tobacco during pollen germination and tube elongation. Sex. Plant Reprod. 22(2): 87-96.

Gels, J. A., D. W. Held, and D. A. Potter. 2002. Hazards of insecticides to the bumble bees *Bombus impatiens* (Hymenoptera: Apidae) foraging on flowering white clover in turf. J. Econ. Entomol. 95(4): 722-728.

Goldberg, S. 1997. Reactions of boron with soils. Plant and Soil 193:35-48.

Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. 53: 191-208.

Hancock, J. F., K. Haghighi, S. L. Krebs, J. A. Flore, and A. D. Draper. 1992. Photosynthetic heat stability in highbush blueberries and the possibility of genetic improvement. HortScience 27(10): 1111-1112.

Hanson, E. J., J. L. Beggs, and R. M. Beaudry. 1993. Applying calcium chloride postharvest to improve highbush blueberry firmness. HortScience 28(10): 1033-1034.

Hanson, E. J. 1995. Preharvest calcium sprays do not improve highbush blueberry (Vaccinium corymbosum L.) quality. HortScience 30(5): 977-978.

Hanson, E. J. and S. F. Berkheimer. 2004. Effect of soil calcium applications on blueberry yield and quality. Small Fruits Rev. 3(1-2): 133-139.

Hart, J. M., B. Strik, L. White, and W. Yang. 2006. Nutrient management for blueberries in Oregon. Oregon State University Extension Service. EM 8918.

Hedhly, A., J. I. Hormaza, and M. Herrero. 2004. Effect of temperature on pollen tube kinetics and dynamics in sweet cherry, *Prunus avium* (Rosaceae). Am. J. Bot. 91(4): 558-564.

Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. Evolution 29(2): 325-334.

Hepler, P. K. and R. O. Wayne. 1985. Calcium and plant development. Annu. Rev. Plant Physiol. 36(1): 397-439.

Hepler, P. R. and D. E. Yarborough. 1991. Natural variability in yield of lowbush blueberries. HortScience 26(3): 245-246.

Hildebrand, P. D., K. B. McRae, and X. Lu. 2001. Factors affecting flower infection and disease severity of lowbush blueberry by *Botrytis cinerea*. Can. J. Plant Pathol. 23(4): 364-370.

Huang, Y. and C.E. Johnson. 1996. A convenient and reliable method to evaluate blueberry pollen viability. HortScience 31(7): 1235-1235.

Jarvis, M. C. 1984. Structure and properties of pectin gels in plant cell walls. Plant Cell Environ. 7(3): 153-164.

Jay, S. C. 1986. Spatial management of honeybees on crops. Bee World 67(3), 98-113.

Jensen, A. B., K. A. Palmer, J. J. Boomsma, and B. V. Pedersen. 2005. Varying degrees of *Apis mellifera* *ligustica* introgression in protected populations of the black honeybee, *Apis mellifera* 'mellifera', in northwest Europe. Mol. Ecol. 14(1): 93-106.

Kevan, P. G. 1990. Pollination: keystone process in sustainable global productivity. In VI International Symposium on Pollination 288: 103-110.

Kevan, P. G., E. Clark, and V. G. Thomas. 1990. Insect pollinators and sustainable agriculture. Am. J. Alternative Agr. 5(01): 13-22.

Knight, M. E., A. P. Martin, S. Bishop, J. L. Osborne, R. J. Hale, R. A. Sanderson, and D. Goulson. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Mol. Ecol. 14(6): 1811-1820.

Knox, R. B. and E. Friederich. 1974. Tetrad pollen grain development and sterility in Leschenaultia formosa (Goodeniaceae). New Phytol. 73(1): 251-258.

Korcak, R. F. 1988. Nutrition of blueberry and other calcifuges. Hortic. Rev. 10: 183-227.

Kovaleski, A. P., J. G. Williamson, J. W. Olmstead, and R. L. Darnell. 2015. Inflorescence bud initiation, development, and bloom in two southern highbush blueberry cultivars. J. Am. Soc. Hortic. Sci. 140(1): 38-44.

Krebs, S. L. and J. F. Hancock. 1988. The consequences of inbreeding on fertility in *Vaccinium corymbosum* L. J. Amer. Soc. for Hort. Sci. 113(6): 914-918.

Krebs, S. L. and J. H. Hancock. 1990. Early-acting inbreeding depression and reproductive success in the highbush blueberry, *Vaccinium corymbosum* L. *Theor.* Appl. Genet. 79(6): 825-832.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. U.S.A. 99(26): 16812-16816.

Lang, G. A. and R. G. Danka. 1991. Honey-bee-mediated cross-versus self-pollination of 'Sharpblue' blueberry increases fruit size and hastens ripening. J. Am. Soc. Hortic. Sci. 116(5): 770-773.

Lee, J. C., D. J. Bruck, H. Curry, D. Edwards, D. R. Haviland, R. A. Van Steenwyk, and B. M. Yorgey. 2011. The susceptibility of small fruits and cherries to the spotted‐wing drosophila, Drosophila suzukii. Pest Manag. Sci. 67(11): 1358-1367.

Lord, E. M. and S. D. Russell. 2002. The mechanisms of pollination and fertilization in plants. Annu. Rev. Cell Dev. Biol. 18(1): 81-105.

MacKenzie, K. E. and M. L. Winston. 1984. Diversity and abundance of native bee pollinators on berry crops and natural vegetation in the lower Fraser Valley, British Columbia. Can. Entomol. 116(07): 965-974.

MacKenzie, K. E. 1997. Pollination requirements of three highbush blueberry (*Vaccinium corymbosum* L.) cultivars. J. Am. Soc. Hortic. Sci. 122(6): 891-896.

Marschner, H. 1995. Functions of mineral nutrients: macronutrients. Mineral nutrition of higher plants. 2: 379-396.

Marschner, H., E. A. Kirkby, and I. Cakmak. 1996. Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. J. Exp. Bot. 47(Special Issue): 1255-1263.

Martin, R. R., I. E. Tzanetakis, M. Sweeney, and L. Wegener. 2006. A virus associated with blueberry fruit drop disease. Acta Hortic. 715: 497.

Marucci, P. E. and H. J. Moulter. 1976. Blueberry pollination in New Jersey. In Symposium on Vaccinium Culture in Europe. 61: 175-186.

Maust, B. E., J. G. Williamson, and R. L. Darnell. 2000. Carbohydrate reserve concentrations and flower bud density effects on vegetative and reproductive development in southern highbush blueberry. J. Am. Soc. Hortic. Sci. 125(4): 413-419.

May, J. D. and K. T. Killingbeck. 1992. Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. Ecology 73(5): 1868-1878.

McArtney, S., M. White, I. Latter, and J. Campbell. 2004. Individual and combined effects of shading and thinning chemicals on abscission and dry-matter accumulation of 'Royal Gala' apple fruit. J. Hortic. Sci. Biotech 79(3): 441-448.

McNicol, R. J. and B. Williamson. 1989. Systemic infection of black currant flowers by *Botrytis cinerea* and its possible involvement in premature abscission of fruits. Ann. Appl. Biol. 114(2): 243-254.

Moeller, F. E. 1973. Timing of placement of colonies of honey bees for pollination of cranberries. J. Econ. Entomol. 66(2): 370-372.

Moritz, R. F. and E. Hillesheim. 1985. Inheritance of dominance in honeybees (*Apis mellifera* capensis Esch.). Behav. Ecol. Sociobiol. 17(1): 87-89.

Ngugi, H. K. and H. Scherm. 2004. Pollen mimicry during infection of blueberry flowers by conidia of *Monilinia vaccinii-corymbosi*. Physiol. Mol. Plant Pathol. 64(3): 113-123.

Ngugi, H. K. and H. Scherm. 2006. Biology of flower-infecting fungi. Annu. Rev. Phytopathol. 44: 261-282.

NOAA's National Weather Service. (n.d.). Retrieved June 9, 2015, from http://ptwc.weather.gov/?region=1andid=pacific.TSU-PAC.2014.11.15.0304

Nyomora, A. M., P. H. Brown, and M. Freeman. 1997. Fall foliar-applied boron increases tissue boron concentration and nut set of almond. J. Am. Soc. Hortic. Sci. 122(3): 405-410.

Paini, D. R. 2004. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: a review. Austral Ecol. 29(4): 399-407.

Pankiw, T., M. L. Winston, and K. N. Slessor. 1994. Variation in worker response to honey bee (*Apis mellifera* L.) queen mandibular pheromone (Hymenoptera: Apidae). J. Insect Behav. 7(1): 1-15.

Pankiw, T., R. E. Page Jr, and M. K. Fondrk. 1998. Brood pheromone stimulates pollen foraging in honey bees (*Apis mellifera*). Behav. Ecol. Sociobiol. 44(3): 193-198.

Parrie, E. J. and G. A. Lang. 1992. Self-and cross-pollination affect stigmatic pollen saturation in blueberry. HortScience 27(10): 1105-1107.

Payne, J. A., J. H. Cane, A. A. Amis, and P. M. Lyrene. 1989. Fruit size, seed size, seed viability and pollination of rabbiteye blueberries (Vaccinium ashei Reade). Acta Hortic. 241(3): 38-43.

Pettis, J. S., N. Rice, K. Joselow, and V. Chaimanee. 2016. Colony failure linked to low sperm viability in honey bee (Apis mellifera) queens and an exploration of potential causative factors. PloS one 11(2): 1-10.

Pritts, M. P., J. F. Hancock, B. C. Strik, M. Eames-Sheavly, and D. Celentano. 1992. Highbush blueberry production guide. Northeast Regional Agricultural Engineering Service, Ithaca, NY.

Racskó, J., G. B. Leite, J. L. Petri, S. Zhongfu, Y. Wang, Z. Szabó, and J. Nyéki. 2007. Fruit drop: The role of inner agents and environmental factors in the drop of flowers and fruits. Int J Hortic Sci. 13(3): 13-23.

Ritzinger, R. and P. M. Lyrene. 1999. Flower morphology in blueberry species and hybrids. HortScience 34(1): 130-131.

Sagili, R.R. and D.M. Burgett. 2011. Evaluating honey bee colonies for pollination: A guide for commercial growers and beekeepers. Pacific Northwest Extension publication. PNW 623.

Sahar, N. and P. Spiegel-Roy. 1984. In vitro germination of avocado pollen. HortScience 19(6): 886-888.

Sairanen, I., O. Novák, A. Pěnčík, Y. Ikeda, B. Jones, G. Sandberg, and K. Ljung. 2012. Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in Arabidopsis. Plant Cell 24(12): 4907-4916.

Salvo, S., C. Muñoz, J. Ávila, J. Bustos, M. Ramirez-Valdivia, C. Silva, and G. Vivallo. 2012. An estimate of potential blueberry yield using regression models that relate the number of fruits to the number of flower buds and to climatic variables. Sci. Hortic. 133: 56-63.

Sampson, B. J. and J. H. Cane. 2000. Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. J. Econ. Entomol. 93(6): 1726-1731.

Sanders, D., C. Brownlee, and J. F. Harper. 1999. Communicating with calcium. Plant Cell 11(4): 691-706.

Seeley, T. D. 1994. Honey bee foragers as sensory units of their colonies. Behav. Ecol. Sociobiol. 34(1): 51-62.

Shear, C. B. and M. Faust. 1970. Calcium transport in apple trees. Plant Physiol. 45(6): 670-674.

Shorrocks, V. M. 1997. The occurrence and correction of boron deficiency. Plant Soil 193(1-2): 121-148.

Sotomayor, C., H. Silva, and J. Castro. 2001. Effectiveness of boron and zinc foliar sprays on fruit setting of two almond cultivars. In III International Symposium on Pistachios and Almonds, 591: 437-440.

Standifer, L. N. 1980. Honey bee nutrition and supplemental feeding. Beekeeping in the United States Agricultural Handbook 335: 39-45.

Strik, B., C. Brun, M. Ahmedullah, A. Antonelli, L. Askham, D. Barney, and D. Havens. 1993. Highbush blueberry production. Pacific Northwest Extension Publication. PNW 215.

Strik, B.C., C.E. Finn, and P.P. Moore. 2014. Blueberry cultivars for the Pacific Northwest. Pacific Northwest Extension Publication. PNW 656.

Strik, B. 2015. Blueberry plant physiology – Why it's important to understand the plant to manage it well. Proc. Oregon State Univ. Blueberry School: 57-61.

Strik, B. C. and A. J. Vance. 2015. Seasonal variation in leaf nutrient concentration of northern highbush blueberry cultivars grown in conventional and organic production systems. HortScience 50(10): 1453-1466.

Stubbs, C. S., F. A. Drummond, and E. A. Osgood. 1994. *Osmia ribifloris* biedermannii and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. J. Kans. Entomol. Soc. 67(2): 173-185.

Stubbs, C. S. and F. A. Drummond. 1996. Blueberry and cranberry (*Vaccinium* spp.) pollination: a comparison of managed and native bee foraging behavior. In VII International Symposium on Pollination. 437: 341-344.

Taylor, L. P. and P. K. Hepler. 1997. Pollen germination and tube growth. Annu. Rev. Plant. *Biol.* 48(1): 461-491.

Thompson, A. H. and L. P. Batjer. 1950. The effect of boron in the germinating medium on pollen germination and pollen tube growth for several deciduous tree fruits. P. Am. Soc. Hortic. Sci. 56: 227-30.

Toth, A. L. and G. E. Robinson. 2005. Worker nutrition and division of labor in honeybees. Anim. Behav. 69(2): 427-435.

Torchio, P. F. 1990a. Bees as crop pollinators and the role of solitary species in changing environments. In VI International Symposium on Pollination 288: 49-61.

Torchio, P. F. 1990b. Diversification of pollination strategies for US crops. Environ. Entomol. 19(6): 1649-1656.

Tuell, J. K., J. S. Ascher, and R. Isaacs. 2009. Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. Ann. Entomol. Soc. Am. 102(2): 275-287.

United States Department of Agriculture, 2005. Noncitrus fruits and nuts 2005 summary. 14 Jan. 2016. http://usda.mannlib.cornell.edu/usda/nass/NoncFruiNu//2000s/2005/NoncFruiNu-07-06-2005.pdf>.

United States Department of Agriculture, 2014. Noncitrus fruits and nuts 2014 summary. 14 Jan. 2016. <http://usda.mannlib.cornell.edu/usda/nass/NoncFruiNu//2010s/2015/ NoncFruiNu-07-17-2015.pdf>.

Vander Kloet, S. P. 1984. Effects of Pollen Donors on Seed Production, Seed Weight, Germination and Seedling Vigor in *Vaccinium corymbosum* L. Am. Midl. Nat. 112(2): 392-396.

Vander Kloet, S. V. and P. M. Lyrene. 1987. Self-incompatibility in diploid, tetraploid, and hexaploid *Vaccinium corymbosum*. Can. J. Bot. 65(4): 660-665.

Verma, N., L. MacDonald, and Z. K. Punja. 2006. Inoculum prevalence, host infection and biological control of *Colletotrichum acutatum*: causal agent of blueberry anthracnose in British Columbia. Plant Pathol. 55(3): 442-450.

Vestrheim, S., K. Haffner, and K. Grønnerød. 1996. Highbush blueberry production and research in Norway. In VI International Symposium on Vaccinium Culture 446: 177-180.

Visser, T. 1955. Germination and storage of pollen. Landbouwhogeschool, Wageningen. PhD dissertation.

Vorsa, N. and J. R. Ballington. 1991. Fertility of triploid highbush blueberry. J. Am. Soc. Hortic. Sci. 116(2): 336-341.

Wang, Q., L. Lu, X. Wu, Y. Li, and J. Lin. 2003. Boron influences pollen germination and pollen tube growth in *Picea meyeri*. Tree Physiol. 23(5): 345-351.

Wertheim, S. J. 2000. Developments in the chemical thinning of apple and pear. Plant Growth Regul. 31(1-2): 85-100.

Whidden, T. L. 1996. The fidelity of commercially reared colonies of *Bombus impatiens* Cresson (Hymenoptera: Apidae) to lowbush blueberry in southern New Brunswick. Can. Entomol. 128(05): 957-958.

Whitfield, C. W., S. K. Behura, S. H. Berlocher, A. G. Clark, J. S. Johnston, W. S. Sheppard, and N. D. Tsutsui. 2006. Thrice out of Africa: ancient and recent expansions of the honey bee, *Apis mellifera*. Science 314(5799): 642-645.

Wiersum, L. K. 1966. Calcium content of fruits and storage tissues in relation to the mode of water supply. Acta. Bot. Neerl. 15(2): 406-418.

Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. J. Appl. Ecol. 45(3): 793-802.

Winston, M. L., H.A. Higo, S. J. Colley, T. Pankiw, and K. N. Slessor. 1991. The role of queen mandibular pheromone and colony congestion in honey bee (*Apis mellifera* L.) reproductive swarming (Hymenoptera: Apidae). J. Insect Behav. 4(5): 649-660.

Wood, G. W. 1961. The influence of honeybee pollination on fruit set of the lowbush blueberry. Can. J. Plant Sci. 41(2): 332-335.

Wood, G. W. 1968. Self-fertility in the lowbush blueberry. Can. J. Plant Sci. 48(4): 431-433.