VARYING STRATEGIES OF MANAGED POLLINATOR INVESTMENT TO OPTIMIZE HIGHBUSH BLUEBERRY (VACCINIUM CORYMBOSUM L.) CROP POLLINATION AND YIELD

By

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ABSTRACT

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Production of most pollination-dependent crops, including highbush blueberry (Vaccinium corymbosum), relies mainly on managed hives of the European honey bee (Apis mellifera L.). In highbush blueberry, bumble bees (Bombus spp.), which are the only commercially-available alternative to honey bees, are more efficient pollinators than honey bees, as lower numbers are necessary to achieve full pollination of the crop. The goal of this research was to develop a model of blueberry pollination to test hypotheses about how to best utilize these two pollinators for blueberry pollination. I first analyzed temperature-dependent growth and development of flowers for each of five common blueberry cultivars. Greenhouse and field experiments compared blueberry flower viability at different ages after flower opening, and declining fruit set was found with increasing floral age after one day. Finally, bee activity was observed on blueberry flowers in multiple farms across three growing seasons that included variable weather conditions. Using these data, a deterministic model of blueberry pollination, BLUEPOLL, was developed to predict annual yield from one acre of highbush blueberry (Vaccinium coymbosum L.) under typical spring weather conditions. This model relies upon inputs of highbush blueberry cultivar, weather conditions, and managed pollinator inputs to calculate pollination during the bloom period and subsequent blueberry yield, based on the experimentally-derived parameter estimates.

The BLUEPOLL model was used to examine effects of different pollinator stocking levels and combinations on yield and to determine profit-maximizing pollinator input strategies. For the 'Bluecrop' cultivar, the profit-maximizing stocking level of honey bees was determined to be 4.5 hives per acre compared to 2.5 bumble bee colonies per acre for fields stocked only with bumble bees. When examining combinations of the two pollinators, under average weather conditions the least-cost input combination when seeking to achieve 80 percent of full crop yield was 0.25 honey bee hives per acre in combination with 1.25 bumble bee colonies per acre. Assuming that rented honey bee hives cost \$50 and purchased bumble bee colonies cost \$65, the least-cost combination of honey bees and bumble bees would cost a grower \$93.75 per acre. This cost rises to \$225 or \$162.50 when considering the profit-maximizing input level of only stocking honey bees or bumble bees, respectively. Under less suitable weather conditions, the cost per acre increased for all combinations of managed honey bees and bumble bees, indicating that growers should invest more in managed pollination services in years when anticipating poor weather in order to ensure consistent crop yields.

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CHAPTER 1

Pollination of highbush blueberry and optimizing strategies for investing in managed bees

Pollination in Commercial Agriculture

Pollination is the process of pollen transfer and subsequent sexual reproduction in plants; it is an essential component for production of most fruits and vegetable crops (Free, 1993; Delaplane and Mayer, 2000). Eighty-seven percent of all flowering plants (Ollerton et al., 2011) and over seventy percent of plant species grown for food (Klein et al., 2007) benefit from animal and insect-mediated pollination, and production of bee-pollinated crops is increasing across the world (Aizen et al., 2008). In most fruit and vegetable production, managed honey bees are brought to crop fields during bloom to maintain high populations of pollinators and ensure maximum pollination of the crop. Honey bees (Apis mellifera L.) are not native to North America and it is estimated that they were introduced into the United States around 1620 by European settlers (Buchmann and Nabhan, 1996). Honey bees are generalist foragers and as such, are versatile and efficient at pollinating a wide range of agricultural crops. Since the introduction of the Langstroth hive in 1851, honey bees have also become easily managed and transported from field to field (Morse and Calderone, 2000). When used to pollinate commercial agriculture crops, they can enhance crop yield and quality and shorten fruit development time, reducing the time required to complete harvest (McGregor, 1976; Free, 1993; Delaplane and Mayer, 2000).

It has recently been estimated that global food crop pollination is worth over \$200 billion annually (Gallai et al., 2008). Pollination services provided to crops in the United

States have been valued at \$14.6 billion for honey bees (Morse and Calderone, 2000) and \$3.1 billion for wild bees (Losey and Vaughan, 2006). Although these pollination valuation methods may be need improvement (Winfree et al., 2011), they highlight the dependence of specialty crop agriculture on honey bees and the important contribution that native bees provide to food production.

Given its tremendous importance to agriculture and thus to all of human society, there is significant global concern over the long-term sustainability of pollination by bees. This uncertainty is a result of many factors including the recent loss of honey bee colonies due to Colony Collapse Disorder (CCD) (Ellis et al., 2010; Ratnieks and Carreck, 2010) and declining populations of wild bees (Osborne et al., 1991; Biesmeijer et al., 2006; Kluser and Peduzzi, 2007, Daz et al., 2010; Potts et al., 2010; Cameron et al., 2011). The number of managed honey bee colonies is estimated to have dropped 59 percent in North America alone between 1947 and 2005 (National Research Council, 2007). Another severe drop of 35.8 percent was recorded from 2007 to 2008 (vanEngelsdorp, 2008). Bumble bee populations have also declined both in numbers and geographic distribution within the United States in recent years (Cameron et al., 2011). Despite evidence that many native North American bee species are not in a state of decline (Colla et al., 2012), the marked declines of managed honey bees has brought increased attention to human dependence on pollinators as essential components of our food systems. Overall, our global food supply will not be crippled from pollinator decline, however, losses of pollinators could bring about other consequences such as decreased nutritional value of available foods and losses of important cultural food sources (Klein et al., 2007; Eilers et al., 2011). A wide variety of fruits and vegetables are highly vulnerable to declines in pollinator abundance and the hypothetical loss of all pollinators

would make it impossible to economically meet the global consumption demands for fruits, nuts and vegetables at a time when demand for these healthy foods, and their production are increasing (Aizen et al., 2008; Gallai et al., 2008; Aizen and Harder, 2009). Research into the complex system of crop pollination and production is therefore necessary to optimize our increasingly scarce resources and improve the sustainability of global crop production.

Highbush Blueberry

Blueberries are the fruit of a flowering plant belonging to the genus *Vaccinium* which is native to North America. Early American settlers discovered the wild berries that were already well known to Native Americans, but it wasn't until the early 20th century that blueberry plants began to be cultivated (Eck and Childers, 1966; Gough, 1994). Today, there are three commonly cultivated types of blueberry: lowbush blueberry (*Vaccinium angustifolium* Aiton and *V. myrtilloides* Michaux), highbush blueberry (*V. australe* Small and *V. corymbosum* L.), and rabbiteye blueberry (*Vaccinium virgatum* Ait. syn. *V. ashei* Reade). Highbush blueberry is produced commercially in 36 U.S. states and 6 Canadian provinces, with the state of Michigan as the largest producer of blueberry in the world (McGregor, 1976; Hanson and Hancock, 1990; Moore, 1993).

In 2011, the state of Michigan produced 72,000,000 lbs of blueberry (USDA, 2012). The most popular cultivars were 'Aurora', 'Bluecrop', 'Croatan', 'Draper', 'Duke', 'Elliott', 'Jersey' and 'Liberty' (Retamales and Hancock, 2012). Most growers of blueberry plant multiple cultivars in order to achieve an extended range of berry ripening, harvesting, and period of sale. Typical highbush blueberry bloom in Michigan usually occurs in late May, however bloom may begin earlier or later each year depending on winter weather conditions

as development is determined by the level of temperature accumulation above a limiting base temperature. Bloom is a crucial time for ensuring high crop yield for the season as blueberries can set 100 percent fruit if sufficient pollination services are available (Pritts and Hancock, 1992). Some of the biggest challenges for growers seeking maximum pollination include acquiring enough managed pollinators for pollination before petal fall and having suitable weather conditions during the period of bloom, as they determine both the speed of bloom as well as pollinator activity. In a study of highbush blueberry pollination under different weather conditions, Tuell and Isaacs (2010) demonstrated that blueberry clusters that had been exposed for pollination only during good weather had a higher percent fruit set, more mature seeds and larger berries than those enclosed in pollinator exclusion mesh. Further investigation into the effects of weather on blueberry flower development, fruit set, and pollinator activity can elucidate the influence of weather conditions during bloom on pollination and subsequent crop yield. These relationships can also lay the foundation for being able to predict crop yield based on the weather conditions during bloom.

The flowers of blueberry and other *Vaccinium* species such as cranberry, *Vaccinium macrocarpon*, have poricidal anthers that must be shaken for pollen to be released and subsequently transferred. For optimal pollen release, bees must grasp the flower while vibrating their wing muscles, a behavior often referred to as buzz-pollination (Buchmann, 1983). For blueberry flowers, this buzz-pollination requirement means that the type of bee visitor is predictive of the likelihood of pollen transfer, with greater pollen deposition and release when bumble bees visit flowers than when honey bees or some small native bees visit (Javorek et al., 2002). Cross pollination is achieved through bee vectors and ensures high quality fruit, increased levels of fruit set and faster ripening times in some cultivars (Eck and

Childers, 1966; Vander Kloet, 1984; Dogterom et al., 2000). Cultivars of highbush blueberry also differ in their ability to set fruit without pollination as well as their receptivity to self-pollination (Krebs and Hancock, 1990; 1991; Retamales and Hancock, 2012). These factors contribute to the importance of insect-mediated cross pollination for satisfactory levels of fruit set and crop yield. However, most popular cultivars of blueberry are self-compatible, setting fruit and producing large berries without out-cross pollen, so most Michigan blueberry fields are planted as single cultivars to facilitate management, foregoing the potential benefit of cross-pollination. One unique attribute of highbush blueberry, is that of parthenocarpy, where flowers will set fruit to a limited extent without any pollination (Coville, 1910; Eck, 1988; Gough, 1994; MacKenzie, 1997; Dogterom et al., 2000). Although there remain questions surrounding the extent of parthenocarpy in highbush blueberry (J. Hancock, pers. comm.), this trait allows for crop yield during poor weather conditions when adequate pollination may not occur. However, berries produced through parthenocarpy or sub-optimal pollination are often small, of poor quality, and ripen slowly.

To achieve the highest possible levels of production, blueberry farmers are dependent on managed insect pollination for their crop production (Delaplane and Mayer, 2000; Isaacs and Kirk, 2010). Traditionally, rented honey bee hives are brought into blueberry fields at about five percent bloom to perform the majority of these pollination services (Pritts and Hancock, 1992). Some highbush blueberry farmers also use managed bumble bees in addition to honey bees for pollination (A.K. Kirk, personal observation). Decisions concerning the number of pollinators to stock per acre are very economically important. Too few bees will leave a grower without enough pollination services, resulting in smaller, lower quality berries and less overall crop yield. On the other hand, the renting of honey bee hives

or purchase of bumble bee colonies is an input cost that growers need to manage so they are not spending more than is necessary. Current recommendations for honey bee stocking densities in highbush blueberry fields date from the early 1990's and are included in Table 1. This highlights the variability among cultivars in their need for honey bees.

Table 1.1. Recommended honey bee stocking densities for some cultivars of highbush

 blueberry (Pritts and Hancock, 1992).

Cultivar	Honey bee hives (number / acre)
Rubel, Rancocas	0.5
Weymouth, Bluetta, Pemberton, Darrow	1.0
Bluecrop	1.5
Elliott, Coville, Berkeley, Stanley	2.0
Jersey, Earliblue	2.5

Although honey bees are recommended widely for the pollination of fruit crops, including blueberries, they are not always the most effective pollinators available (McGregor, 1976; Pritts and Hancock, 1992; Free, 1993; Delaplane and Mayer, 2000). Honey bees are relatively inefficient at buzz-pollination, which is required by some flowering plants, including *Vaccinium* species, for pollen release (Buchmann and Hurley, 1978). Additionally, honey bees become inactive in typical cool, spring weather that can occur when many perennial fruit crops are in bloom, and as a result they may not be active when flowers are open. Honey bees also exhibit strong preference for some blueberry cultivars (Pritts, 1996), making it difficult to pollinate other nearby cultivars that may not be as attractive. Despite these drawbacks, high numbers of honey bee colonies may be able to compensate for pollination inefficiencies, and growers have been known to stock fields with many times the recommended hive density as a form of 'pollination insurance' (A.K. Kirk, personal observation).

Bombus spp. bumble bees, such as *Bombus impatiens* which is the dominant native species in Michigan are, on the other hand, capable of buzz-pollination. They are more efficient pollinators of blueberry than honey bees (Javorek et al., 2002) and they remain active during cool weather (Heinrich, 1979; Tuell and Isaacs, 2010). Given the expected relative performance of honey bees and bumble bees, a smaller number of bumble bees may provide adequate pollen transfer and mitigate potential yield declines during periods of honey bee inactivity. Studies in lowbush blueberry (V. angustifolium) have demonstrated that pollination by bumble bees results in equal or better pollination than honey bees, with higher fruit set, berry weight, and seeds per berry (Stubbs and Drummond, 2001). That research suggested that one bumble bee can pollinate as many lowbush blueberry flowers as 10-20 honey bees in the same period of time. As bumble bees are one of the few commerciallyavailable alternative pollinators to honey bees, it is important to understand the implications of augmenting honey bee pollination services with these insects. Also, as bumble bees differ in morphology and ecology from honey bees, there is potentially great value in taking advantage of their pollination services under different environmental conditions. A pollination strategy that relies on multiple managed bee sources rather than only honey bees

in crops such as blueberry may serve as insurance against insufficient pollination services under sub-optimal conditions for pollination.

Pollinator Decline

Worldwide, concern has arisen in recent years surrounding the declines of both managed and wild insect pollinator populations (Cane and Tepedino, 2001; Daz et al., 2010; Ellis et al., 2010; Potts et al., 2010). For managed pollinators, the decline of honey bees as a result of CCD has received much attention (Oldroyd, 2007; vanEngelsdorp et al., 2009; Johnson, 2010; Ratnieks and Carreck, 2010). Managed honey bees are also highly susceptible to diseases and pests such as varroa mite (*Varroa destructor*), tracheal mite (*Acarapis woodie*), Nosema infections (*Nosema ceranae*), and American foulbrood (*Paenibacillus larvae*) (Morse and Flottum, 1998). These challenges to healthy honey bee populations are managed by beekeepers, but it is increasingly challenging to maintain healthy colonies (Genersch, 2010). Honey bees are the most economically valuable managed pollinators worldwide, and if their populations continue to decline as the production of pollinator-dependent crops increases, it is possible that we may encounter a pollination crisis in which the pollination needs of many food crops cannot be met (Aizen et al., 2008; Aizen and Harder, 2009).

Wild pollinator populations are also being threatened by habitat fragmentation (Rundlöf et al., 2008), habitat loss (Dobson et al., 2006), and increased pesticide use (Kevan, 1975; Roy et al., 2003), all of which can be associated with agricultural intensification (Kremen et al., 2002; Winfree, 2010). With valuable ecosystem services at risk from the decline of wild pollinators, there are calls from around the world for increased research and conservation efforts as well as restoration of native pollinator habitats (Allen-Wardell et al.,

1998; Ricketts et al., 2008; Kennedy et al., 2013). Another concern surrounding the loss of native pollinators is that with continuing losses, we will become more limited in the ability to develop alternatives to managed honey bees for pollination in commercial agriculture.

In light of much concern surrounding the long-term availability of pollination services from managed and wild bees, it is important to explore how best to optimize the use of managed bees in times of potential stress on honey bee availability. Without increased attention to the decline in pollinator availability, we may run the risk of limiting the potential growth of global crop yields in pollinator dependent crops (Aizen et al., 2008). Research concerning the potential implications of pollinator decline can help to maintain successful yields of the pollination-dependent crops that currently comprise 35 percent of human food (Klein et al., 2007; Ricketts et al., 2008).

Alternative Pollinators

Although honey bees are the primary source of commercial crop pollination, native bee pollinators are worthy of investigation either to augment or replace managed honey bees (Torchio, 1990; Batra, 1995; Mader et al., 2010). Researchers are encouraging the diversification of pollination practices in order to increase productivity and to avoid overreliance on honey bees (Klein et al., 2007). In blueberry production in Michigan, native bees provide as much as 10 percent of pollination services and are the dominant pollinators in many small blueberry fields (Isaacs and Kirk, 2010). The contribution of native bees is variable across different systems - a recent study in New Jersey and Pennsylvania watermelon crops has shown that native bees can provide sufficient pollination without the addition of managed honey bee colonies (Winfree et al., 2007). Additional research in Pak

Choi (*Brassica rapa*) supported these results, indicating that native bees provided consistently effective pollination services in two of the four years of their study (Radar et al., 2009). In large agricultural fields that are crop monocultures it may be necessary to inundate the fields with managed honey bees to achieve sufficient pollination services and to compensate for low efficiency and sensitivity to poor weather (Martin, 1966). Some growers are already doing this (A.K. Kirk, personal observation), but such a practice may become less financially and practically feasible in the event that we encounter more severe declines in honey bee populations, and rental prices rise. The intensification of agriculture has created a need for alternative managed pollinators to decrease farmers' reliance on honey bees.

Despite this need for alternative managed pollinators, there are fewer than 10 bee species other than the honey bee that have been developed as managed pollinators for agricultural production (Cane, 1997; Pitts-Singer and Cane, 2011). The alfalfa leafcutter bee (*Megachile rotundata*) was accidentally introduced into the eastern United States in the early 20th century where it quickly spread and was discovered to be an abundant pollinator of alfalfa. It was found to be easily manageable, at low cost, and it is now widely purchased for pollination services in the Northwest Region of the United States (Torchio, 1991). The alfalfa leafcutter bee was also found to be comparable in its pollination capability of lowbush blueberry to other native *Bombus* and *Andrena* species (MacKenzie et al., 1997) and is now used for lowbush blueberry pollination in western Canada and the United States (MacKenzie, 2009). Assorted species of mason bees including *Osmia lignaria*, *O. ribifloris*, *O. cornifrons*, and *O. cornuta* have also been developed as managed pollinators in a variety of cropping systems (Torchio, 1990; Cane, 1997). *Osmia lignaria* has been used widely in tree fruit pollination (Bosch and Kemp, 2002; MacKenzie, 2009) and while it has potential for

highbush blueberry pollination, it is currently more expensive than traditional, managed honey bees (Dogterom pers. comm. cited by MacKenzie, 2009). *Osmia ribifloris* and *O. cornifrons* have also been deemed suitable pollinators of blueberry but have yet to be established as managed pollinators in this crop system (Torchio, 1990; Stubbs et al., 1994; West and McCutcheon, 2009). Even with these advancements in the availability of alternative, managed pollinators, each have existing drawbacks. Mason bees (*Osmia* spp.) are susceptible to parasitism and mites, plus the overwintering survival may be negatively affected by low winter temperatures, so active management is essential. The alfalfa leafcutter bee is typically active in the summer season and its use in spring-blooming blueberry fields has lead to concerns of disrupting their reproductive cycles and increased winter mortality (Sheffield, 2008).

Managed colonies of bumble bees have recently become available commercially through companies such as Koppert Inc., Biobest, BioBee, etc., and these are now commonly used as managed pollinators in greenhouse tomato production (Banda and Paxton, 1991; Morandin et al., 2001), as well as in open field settings (Free, 1993; Delaplane and Mayer, 2000). Bumble bees have many advantages over honey bees when it comes to pollination services. One of the most significant differences is that bumble bees are able to control their body temperature through thermoregulation (Heinrich, 1975). This allows them to be capable of flight at cooler temperatures in the morning and evening when honey bees have long ceased foraging (Plowright and Laverty, 1984; Corbet et al., 1993; Willmer et al., 1994). Bumble bees are also capable of flying longer distances for foraging than are honey bees (Greenleaf et al., 2007). In highbush blueberry agriculture, bumble bees have been shown to be better pollinators than honey bees with lower numbers necessary to achieve full

pollination of the crop (Ratti et al., 2008). They deposit more pollen per visit than honey bees (Javorek et al., 2002), have a higher floral constancy for blueberry than honey bees (Stubbs and Drummond, 1997), and have been shown to be capable of visiting 135,000 flowers per hour in Oregon blueberry (Stephen et al., 2009). Based on these factors, different studies have estimated that one bumble bee is as efficient at pollinating blueberry as four (Javorek et al., 2002) to 10-20 (Stubbs and Drummond, 2001) honey bees. At least one study has concluded that it may be more effective to use a combination of honey bees and bumble bees to pollinate fields of highbush blueberry, because of the range of environmental conditions under which pollen could be transferred (Stubbs and Drummond, 2001).

Systems Modeling

One goal of this research is to use honey bees and bumble bees in the blueberry system as a model for testing hypotheses about how to optimally combine different pollinators for sustainable crop pollination, thereby helping to ensure a reliable food supply for future generations. This research brings a systems approach to understanding the complex interactions between crop, weather, and insect pollinators to identify optimal pollination strategies. The results of these experiments will allow for application of managed pollination strategies over different agricultural settings and optimization of the pollination services provided by honey bees and bumble bees in highbush blueberry. Actual manipulation and experimentation with these variables is challenging as it would be all but impossible to control the activity of pollinator populations or weather components. Thus, one of the most important aspects of this research is the inclusion of a comprehensive modeling component.

model will allow for the testing of explicit assumptions concerning pollinator, weather, and crop relationships.

Systems modeling is a mathematical method of characterizing the components and relationships of an integrated whole. This manner of illustrating system relationships was pioneered in the field of environmental science as described in The Limits to Growth by Meadows and Meadows (1972), which illustrates the entire human population on earth as a system. An important characteristic of a system is that the behavior of the whole can not be perceived by looking at an individual component. Systems modeling therefore has found great application in the field of ecology where observing an individual relationship is often not enough to gain understanding of the behavior of the biological whole. Given the challenges described above, this approach can provide valuable insights to pollination systems and has been used to investigate alfalfa pollination (Strickler, 1996; Strickler, 1997; Breazeale et al., 2008), apple pollination (DeGrandi-Hoffman et al., 1996). However, each pollination system is unique and must be examined separately to best understand the underlying component dynamics.

For the system of highbush blueberry pollination, it is important to consider not only the plant and pollinator system components, but also the weather parameters that drive them. Highbush blueberry yield is the product of both parthenocarpy and pollination, therefore a systems model of highbush blueberry must include both of these elements. Pollinator activity is highly dependent upon weather conditions such as air temperature, solar radiation, and wind speed, so these parameters should be included to demonstrate these relationships. Another basic component essential to blueberry yield is the number of flowers available to develop into blueberries. Therefore, the relationship of blueberry flower opening with respect

to accumulating temperature should also be included. Finally, after a flower opens it is not available for pollination indefinitely. There is a limited amount of time a flower will be viable for pollination and this is an important restriction on crop yield to include in a model of highbush blueberry pollination.

Agricultural Economics

One of the most basic decision making tools of agricultural economics is that of the profitmaximizing input level (Kay et al., 1994). There are many inputs to agricultural systems, including water for crops, feed for animals, or even managed pollination services for better crop yield. The profit-maximizing input level for a farm manager is that level of input at which it is no longer profitable to add more of that input. In other words, it is the input level where spending more money on an additional level of input is more expensive than the corresponding increase in output (product) value. This economic concept is especially relevant when considering managed pollination services as an agricultural input. Farmers should be stocking their pollination-dependent crops with only enough pollinators to justify the return in crop yield however, in highbush blueberry it is not known what this level of managed pollinators is or whether it changes under variable weather conditions or different crop cultivars.

When considering a combination of two or more substitutable inputs for agricultural production, a farm manager can use the least-cost input combination as a decision making tool (Kay et al., 1994). In order to determine the least-cost input combination for a given output level, a farm manager must first examine the input substitution ratio, or the amount of input to be replaced in relation to the amount of input added. In the case of managed

pollination, this input substitution ratio would be equivalent to the amount of honey bee hives to be replaced in relation to the amount of alternative pollinators, managed bumble bees for example, to be added. Next, the farm manager must compare this input substitution ratio to the inverse input price ratio (the price of input being added in relation to the price of input being replaced). The point at which these two ratios are equal will constitute the least-cost input combination. In the case of managed pollination and farmers who seek alternatives to honey bees as their only source of pollination services, this decision making tool can be quite useful to avoid overspending on pollinators.

Objectives

The goal of this research is to develop and validate a deterministic model of blueberry pollination to test pollination strategies and to identify those that provide optimal pollination and economic efficiency under variable environmental conditions. This research brings a systems approach to understanding the complex interactions between crop, weather, and insect pollinators to identify optimal pollination strategies. Due to the complexity of these interactions, experimental manipulations would have been insufficient to capture the range of possible pollinator, weather, and crop combinations so a modeling component was included in this research. The first objective was to determine mathematical relationships that describe bee activity and blueberry flowering as a function of weather conditions. These relationships were then used to project blueberry bloom phenology, the abundance and activity of pollinators during bloom, and the resulting fruit set and yield of the blueberry crop. The second objective was to develop and validate a model of blueberry pollination that integrated the plant, insect, and weather components of the system. It was expected that varying

combinations of honey bees and bumble bees would provide different and predictable levels of fruit set and blueberry crop yield. The third objective was to use the model to compare alternative pollination strategies under variable environmental conditions.

CHAPTER 2

Predicting Flower Phenology and Viability of Highbush Blueberry

INTRODUCTION

A wide variety of variables, both genetic and environmental in origin, are known to influence plant growth and development. In agricultural systems, light intensity, air quality, soil nutrients, moisture, air and soil temperature are particularly important environmental factors (Pessarakli, 2002). Monitoring environmental conditions can be crucial for farmers wishing to implement management practices at specific stages of crop development. For example, the phenological development of pollination-dependent agricultural crops is important to farmers seeking to maximize yield. Many farmers depend upon rented honey bee hives for pollination (Delaplane and Mayer, 2000; James and Pitts-Singer, 2008). It is important for these managed pollinators to be introduced into agricultural crops only after flowering has begun to ensure pollination of the crop of interest, as opposed to alternative foraging resources such as wildflowers (Free, 1993). The ability to predict timing of crop flowering can improve placement of managed bee colonies near fields at the optimal time for pollination and also aid in maximizing crop yield.

Accurate prediction of biological events is fundamental to planting at an appropriate time, protecting crops from pests and inclement weather conditions, ensuring sufficient pollination and planning the eventual harvest of crops (Bailey, 1947; Wielgolaski, 1999). The ability to predict important components of flower development, such as flower opening and viability after anthesis would be useful for growers of crops dependent upon insect-mediated pollination. If a crop requires cross-pollination, as is the case for many fruit crops

(McGregor, 1976), it is also important to know the phenology of each participant cultivar to ensure that reproductively compatible varieties within the same area are in bloom at the same time. Finally, knowledge of the period of time during which flowers remain viable for pollination enables sufficient bee colonies to be purchased or rented in order to achieve the concentration of bees required for full crop pollination and yield potential.

For a large majority of fruit crop species, temperature and consequent heat accumulation are the most influential environmental factors that control development (Rathcke and Lacey, 1985; Schaffer and Anderson, 1994) and these are commonly monitored by farmers in early spring. One method of measuring heat accumulation incorporates both time and temperature into a unit called a growing degree-day (GDD), described in detail by Baskerville and Emin (1969). Because GDD are calculated using a species-specific value for the critical lower threshold temperature below which plant development does not occur (base temperature), these heat units are universally functional and therefore allow bloom phenology to be predicted in many regions, across a range of environments. The prediction of crop bloom based on GDD has been used in the past to predict bloom in almond [Prunus dultis (Mill) D.A. Webb] (DeGrandi-Hoffman et al., 1996; Rattigan and Hill, 1986), apple [Malus x sylvestris (L.) Mill. Var. domestica (Borkh.) Mansf.] (Anstey, 1966; DeGrandi-Hoffman et al., 1987), tomato [Lycopersicon esculentum Mill.] (Zalom and Wilson, 1999), apricot [Prunus armeniaca L.], cherry [Prunus avium L.], peach [Prunus persica (L.) Batsch], pear [Pyrus communis L.] (Anstey, 1966) and sunflower [Helianthus anuus L.] (Goyne et al., 1977) but this has not been accomplished for highbush blueberry [Vaccinium corymbosum (L.)].

Similarly, few studies have focused on the duration of flower viability in modern blueberry cultivars. An early study of 'Rubel' suggested that viability is greatest 1 to 2 d after flower opening (Merrill, 1936), however, this cultivar has been planted less frequently in recent years. In 1964, Moore documented that 'Bluecrop' flowers were receptive to pollen up to 5 d after flower opening under greenhouse conditions while fruit set and seed number both decreased if the flower was pollinated more than 4 d after opening. Moore (1964) also investigated flower viability under field conditions for 'Coville' and 'Blueray'. His results indicate significant differences in flower viability for these cultivars, with flowers of 'Blueray' receptive to pollination for a longer period of time than those of 'Coville'. Rabbiteye blueberry (*Vaccinium virgatum* Ait. syn. *V. ashei* Reade) flowers are viable up to 5 d after anthesis (Brevis and NeSmith, 2006).

Additional data for highbush blueberry phenology and flower viability can be incorporated into mathematical models that predict bloom dependent upon accumulated GDD. Such decision-support tools would provide highbush blueberry growers with a means to predict the dynamics of flower opening and flower viability using forecasted weather conditions. It would also allow for pollination strategies and management practices to be adapted depending on the projected length of blueberry bloom.

This study characterized and compared the bloom phenology of five common cultivars of highbush blueberry with respect to temperature accumulation. This was accomplished by first measuring bloom phenology as a function of temperature so that a lower threshold base temperature could be determined. Base temperatures were then used to calculate accumulated GDD and relate that temperature accumulation to the bloom phenology of bushes grown under greenhouse and field conditions. In addition, flower

viability was examined in each of the five cultivars under greenhouse and field conditions in order to determine the relationship between flower age and viability within and among cultivars.

MATERIALS AND METHODS

Highbush Blueberry Plants

Five commonly planted cultivars of northern highbush blueberry, *V. corymbosum*, were chosen to represent a range of early to late harvest periods. The cultivars used for all experiments were 'Duke', 'Bluecrop', 'Jersey', 'Elliott' and 'Liberty'. Base temperature, phenology and flower viability experiments were conducted in growth chambers in 2010-2011, under greenhouse conditions in 2009 and 2011 and in Michigan highbush blueberry fields in 2009-2011, respectively. Bushes used for growth chamber and greenhouse experiments were purchased from a local nursery in mid-winter of each year. All plants were ca. 2 years old, in 3.8 L pots, and remained in cold storage (1 to 2 °C) until removed for experimentation. In growth chamber experiments, plants were maintained at a 16:8 light to dark photoperiod. Mature bushes used for field experiments were selected within commercial fields that received similar levels of maintenance and were all located in the main blueberry production region of southwest Michigan, in Ottawa, Allegan, Van Buren and Berrien counties.

Base Temperature of Five Highbush Blueberry Cultivars

Five sets of five plants, one from each cultivar, were removed from cold storage and one set was placed in each of five growth chambers set at constant temperatures of either 13, 17, 20,

23 or 26 °C. Temperatures were chosen to span the range typically encountered during the period of blueberry bloom in the main regions where this crop is grown. The position of bushes was randomized in each chamber and light levels were recorded once a week using a field scout quantum meter (Spectrum Technologies, Inc., Plainfield, IL, USA) to ensure consistency. Plants were allowed to progress from dormancy through flower bloom. Newly-opened flowers were counted every 1 to 2 d and marked with permanent marker in order to avoid duplicate counts. Each progression through bloom constituted one replicate, and three to five replicates were conducted for each cultivar/temperature pairing. Only three replicates were completed for the lowest temperature (13 °C), as the bloom period was significantly extended.

Development rate was calculated as the inverse of the time elapsed between the start of bloom and 50% total bloom. Results were then plotted as temperature vs. development rate for each of five replicates. A one-way analysis of covariance (ANCOVA) compared the relationship of temperature and development rate for complete replicates (those including at least four temperature/development rate pairings) among the cultivars (PROC GLM; SAS Institute Inc. 2003, Cary, NC, USA), using the development rate as the independent variable. The dependent variable was the temperature and the covariate was the experimental replicate. For each of the five cultivars, base temperature was calculated as the x-intercept of the best fit regression line.

Highbush Blueberry Bloom Phenology under Greenhouse Conditions

Ten potted highbush blueberry plants of each of the five cultivars were maintained at greenhouse temperatures of 15 ± 5 °C. Temperature data were recorded using two HOBO[®]

pendant temperature loggers (Onset Corporation, Bourne, MA, USA) suspended at plant height in the greenhouse. To account for differences in base temperature among cultivars, air temperature data and individual cultivar base temperatures determined in the experiment described above were used to calculate accumulated GDD values. Accumulated GDD was measured from the time plants were removed from cold storage and placed in the greenhouse. Numbers of newly opened flowers were counted daily on each bush and marked with permanent marker to avoid duplicate counts.

Highbush Blueberry Bloom Phenology under Field Conditions

In order to observe highbush blueberry bloom under field conditions, three separate blueberry plantings in southwest Michigan were sampled during the 2009 and 2010 field seasons. Sites were chosen based on the availability of the five cultivars of interest being planted in close proximity. In 2009, the three sites sampled were located at the Southwest Michigan Research and Extension Center in Benton Harbor, the Michigan Blueberry Growers Association (MBG) headquarters in Grand Junction, and the Trevor Nichols Research Complex in Fennville. In 2010, the three sites sampled were located at the MBG headquarters in Grand Junction, Cornerstone Ag. in Lacota, and DeGrandchamp Farms in South Haven. Each site was equipped with a HOBO[®] Weather Station (Onset Corporation, Bourne, MA, USA) that monitored on-site temperature conditions 1.5 m above ground level.

To determine the progression of flower bloom as a function of temperature, bushes from each of the five cultivars were monitored for flower opening throughout the period of bloom while simultaneously collecting air temperature data at the three individual sites. At each site, 12 flower clusters in each of three plots per cultivar were flagged and monitored for flower opening (a total of 36 clusters per cultivar). For each plot, four flower clusters were flagged near the apical tip of a shoot, another four were flagged along the middle of a shoot, and the final four were flagged near the base of a shoot. Newly opened flowers from selected clusters were counted two to three times a week and marked with permanent marker to keep track of which flowers had opened recently. Flagged flower clusters were observed throughout the entire period of bloom. Again, individual cultivar base temperatures determined previously were used to calculate accumulated GDD values, beginning on 1 Jan. of each year.

For all bloom phenology experiments, the relationship between percent total bloom and accumulated GDD for each cultivar was first analyzed using linear regression. No significant linear relationships were identified for either the original or transformed data taken from the greenhouse or field. The data were then plotted as percent total bloom vs. accumulated GDD for each cultivar in order to distinguish possible non-linear relationships. Gaussian, gamma and logistic nonlinear regression analyses were performed and parameters were compared among these non-linear curve types (PROC NLIN; SAS Institute Inc. 2003, Cary, NC, USA). While variations of each of these regressions fit the majority of phenology curves, only the logistic function was able to describe the relationships between percent total bloom and accumulated GDD for each of the 15 individual curves. The PROC NLIN function was used to fit the following general logistic function to each curve:

$$\% totalbloom = \left[\frac{a + 4b * \exp\left(-\left(\frac{GDD - p}{v}\right)\right)}{\left(1 + \exp\left(-\left(\frac{GDD - p}{v}\right)\right)\right)^2}\right]$$

In this equation, parameter a is a measure of both the amplitude and variance of each logistic curve while parameter b describes the amplitude of the curve. Most importantly, the parameter p represents an estimate of the number of accumulated GDD where peak percent total bloom occurs and the parameter v is an estimated value representative of the variance of each logistic bloom phenology curve. Parameters a, b, p, and v were then compared among cultivars for each experimental setting using the estimated 95% confidence intervals provided by the PROC NLIN procedure to determine significant differences among the phenology curves of the cultivars. Only when the 95% confidence intervals had no overlap between cultivars were those cultivars determined to differ significantly for that particular bloom phenology characteristic.

Highbush Blueberry Flower Viability under Greenhouse Conditions

To examine the relationship between flower age when pollinated and the resulting fruit set for individual flowers, ten bushes of each of the five cultivars were maintained at greenhouse temperatures of 15 ± 5 °C. To begin, all open flowers were removed from each bush. Each day, newly opened flowers for each cultivar were counted and assigned into groups of five. Groups of newly opened flowers were bagged with pollinator-exclusion mesh which remained in place throughout the experiment, being removed only for hand pollination. Each group of five flowers constituted one replicate, and flowers were individually labeled using a hang tag with the replicate number (1-10), treatment (number of days to be allowed until pollination), date of opening and date of pollination for ease of identification. For each of the ten replicates per cultivar, one healthy flower was hand pollinated at each of 0, 1, 2, 3 and 5 d after flower opening. Hand pollination was achieved by removing the corolla from the flower to be pollinated and depositing pollen from the same cultivar on the stigma of the flower with a small paintbrush. The pollen used for this hand pollination was collected by using a tuning fork to sonicate flowers and release pollen from additional potted bushes of the each of the cultivars (Buchmann and Hurley, 1978). After pollination, flowers were monitored until berries ripened or the receptacle dried out to record presence or absence of fruit set.

Highbush Blueberry Flower Viability under Field Conditions

Flower viability was examined under field conditions in the summer of 2011 for each of the five cultivars. Beginning before the start of flower bloom, one cane on each of ten bushes per cultivar was bagged with pollinator-exclusion mesh and then monitored daily for flower opening. The pollinator-exclusion mesh remained on each cane throughout the experiment and was only removed for counting and hand pollination of flowers. Newly opened flowers were counted daily and assigned into ten replicate groups of six flowers. Each group of six flowers constituted one replicate and flowers were individually labeled with a hang tag that described the replicate number (1-10), treatment (number of days allowed before pollination), date of opening and date pollinated. For each of the ten replicates per cultivar, one healthy flower was hand pollinated at each of 0, 1, 2, 3, 4 and 5 d after flower opening. Hand pollination was achieved in the same manner as the greenhouse flower viability experiments using pollen collected from bushes of the same cultivar, in the same field. After pollination, flowers remained under pollinator-exclusion mesh and were monitored until berries ripened or the receptacle dried out to record presence or absence of fruit, and percent fruit set was calculated for each cultivar x day combination.
For all flower viability experiments, percent fruit set values were compared using a two way analysis of variance (ANOVA), with cultivar and pollination treatment (time allowed between flower opening and hand pollination) as the main factors (PROC GLM; SAS Institute Inc. 2003, Cary, NC, USA). Comparisons of pollination treatments were performed using Tukey's mean separation test at P = 0.05.

RESULTS

Base Temperature of Highbush Blueberry Cultivars

There were no significant differences among complete replicates within cultivars in the predicted base temperatures ('Bluecrop' $F_{2,14} = 0.23$, P = 0.80; 'Duke' $F_{2,12} = 4.06$, P = 0.07; 'Elliott' $F_{2,9} = 0.90$, P = 0.47; 'Jersey' $F_{2,14} = 1.81$, P = 0.22; 'Liberty' $F_{2,8} = 0.23$, P = 0.63), so simple linear regression of all data points was performed for each cultivar. There were significant positive correlations between temperature and development rate for each cultivar (P < 0.0001), with r² values ranging from 0.623 for 'Jersey' to 0.806 for 'Elliott'. Base temperatures calculated as the x-intercept of the best fit regression lines for the five cultivars ranged from 7.14 °C for 'Duke' to 7.96 °C for 'Liberty' (Table 2.1). These base temperature values were used to calculate cultivar specific accumulated GDD for subsequent analyses.

Cultivar	Base temperature (^o C)	r^2	Regression equation
Duke	7.14	0.77	y = 0.0028x - 0.019
Bluecrop	7.42	0.75	y = 0.0031x - 0.023
Elliott	7.52	0.81	y = 0.0027x - 0.020
Jersey	7.93	0.62	y = 0.0031x - 0.025
Liberty	7.96	0.76	y = 0.0028x - 0.022

Table 2.1. Simple linear regression equations and calculated base temperatures for five highbush blueberry cultivars where x represents temperature ($^{\circ}C$) and y represents

Highbush Blueberry Bloom Phenology

development rate.

Bloom phenology curves were calculated with respect to accumulated GDD for each of the five cultivars using the previously determined base temperatures. In the greenhouse phenology experiments, the peak of bloom varied significantly among cultivars. Bushes of 'Duke' exhibited the earliest peak percent bloom (*p*), followed by 'Bluecrop', and then 'Liberty', 'Elliott' and 'Jersey' which were not significantly different from one another (Table 2.2). Differences in peak percent bloom among cultivars were less apparent under field conditions in 2009 and 2010, but the order of peak percent bloom by cultivar was noticeably different from that observed under greenhouse conditions. Under field conditions, 'Liberty' exhibited the earliest peak percent bloom, followed by 'Bluecrop', 'Duke', 'Jersey' and 'Elliott'. Parameter values for phenology curve variance (*v*) were consistent among most

cultivars in both field seasons with the exception of 'Jersey' which exhibited high inter- and intra-year variability. Parameters a and b were highly consistent, with slight differences among cultivars appearing only for parameter b under greenhouse conditions.

In general, highbush blueberry bloom occurred at much lower levels of accumulated GDD under field conditions when compared to bloom phenology observed under greenhouse conditions. Analysis of all cultivars revealed that peak percent bloom occurred at 291 accumulated GDD under field conditions compared with 420 accumulated GDD under greenhouse conditions. Bloom phenology for each cultivar was consistent for the parameters p and v between the 2009 and 2010 field seasons and showed few differences for parameters a and b (Table 2.2).

Table 2.2. Parameter estimates and 95% confidence intervals for the best fit logistic

 phenology curves for five highbush blueberry cultivars measured under greenhouse and field

 conditions. For each experiment, values within the same column are not significantly

 different from one another if followed by the same letter.

	Logistic curve parameter						
- Cultivar	p ^z	\mathbf{v}^{y}	\mathbf{a}^{X}	b ^w			
Greenhouse							
Duke	386 ± 7 a	28 ± 5 a	0.009 ± 0.010 a	0.130 ± 0.016 bc			
Bluecrop	409 ± 21 a	$56\pm19\ b$	0.005 ± 0.018 a	0.079 ± 0.013 ab			
Liberty	$444 \pm 15 \text{ b}$	$49\pm12\ b$	$0.002 \pm 0.015 \ a$	$0.074\pm0.009\ ab$			
Elliott	$447\pm9~b$	60 ± 8 b	$-0.002 \pm 0.007 \ a$	$0.067 \pm 0.004 \ a$			
Jersey	$465\pm30\ b$	44 ± 26 ab	0.008 ± 0.041 a	$0.103\pm0.025~b$			
Field 2009							
Duke	309 ± 81 a	41 ± 78 b	-0.020 ± 0.363 a	0.176 ± 0.101 a			
Bluecrop	275 ± 24 a	$21\pm16 b$	0.083 ± 0.048 a	$0.181 \pm 0.080 \ a$			
Liberty	$240\pm103~\mathrm{a}$	-31 ± 33 a	-0.313 ± 2.157 a	0.251 ± 0.331 a			
Elliott	313 ± 14 a	$22\pm9 \qquad b$	0.031 ± 0.063 a	$0.280 \pm 0.094 \; a$			
Jersey	$292\pm17~a$	17 ± 10 b	0.044 ± 0.093 a	0.327 ± 0.161 a			
Field 2010							
Duke	280 ± 16 a	19 ± 12 b	0.029 ± 0.069 a	0.205 ± 0.096 a			
Bluecrop	$273\pm19\ a$	$25\pm14 b$	0.024 ± 0.065 a	$0.175 \pm 0.059 \ a$			
Liberty	263 ± 62 a	-45 ± 36 a	-0.131 ± 0.453 a	$0.170 \pm 0.080 \ a$			
Elliott	$349\pm36~a$	$39\pm20 b$	0.009 ± 0.119 a	$0.196 \pm 0.072 \ a$			
Jersey	$319\pm27~a$	32 ± 19 b	0.001 ± 0.112 a	$0.223 \pm 0.088 \ a$			

^zEstimate of the number of accumulated GDD at which peak percent total bloom occurs.

^y Estimate of logistic curve variance.

^x Measure of logistic curve amplitude and variance.

^w Measure of logistic curve amplitude.

Highbush Blueberry Flower Viability

Under greenhouse conditions, fruit set for newly opened flowers was $80.0 \pm 8.9\%$ for all cultivars, declining to $16.2 \pm 8.2\%$ 5 d later. There was significant variation in fruit set among the different times allowed between flower opening to pollen deposition (F_{4,211} = 17.92, *P* < 0.0001), with pollination 5 d after flower opening resulting in significantly lower fruit set than the other four treatments (Fig. 2.1A). Under field conditions, fruit set was not found to differ among pollination treatments (F_{5,220} = 1.31, *P* = 0.26) (Fig. 2.1B).



Figure 2.1. Average fruit set of highbush blueberry when hand pollinated 0 to 5 d after flower opening, under greenhouse (A) and field (B) conditions. Error bars represent standard error. Hand pollination was not performed at 4 d after opening under greenhouse conditions.

'Jersey' had the highest fruit set under greenhouse conditions (69.3 \pm 17.1%), while 'Bluecrop' had the lowest average fruit set of 51.3 \pm 13.7%. Fruit set did not differ significantly among cultivars (F_{4,211} = 1.73, *P* = 0.19) (Fig. 2.2A). Under field conditions, fruit set varied significantly among the five cultivars (F_{4,220} = 13.34, *P* < 0.0001) and ranged from 37.8 \pm 11.1% for 'Liberty' to 93.3 \pm 2.3% for 'Bluecrop' (Fig. 2.2B). A significant interaction between cultivar and duration until pollen deposition was found in both the greenhouse experiment (F_{16,211} = 1.80, *P* = 0.03) and field experiment (F_{20,220} = 1.94, *P* = 0.01).



Figure 2.2. Average fruit set for all treatments of five highbush blueberry cultivars under greenhouse (A) and field (B) conditions. Error bars represent standard error.

DISCUSSION

This study provides quantification of the bloom and flower ageing phenology in highbush blueberry cultivars, revealing significant inter-cultivar differences that will support prediction of pollination in this crop. The relative values of bloom parameters determined here will also help managers plan their plantings of cultivars that require cross pollination by compatible cultivars. The results of this research show that for the five cultivars of highbush blueberry studied, base development temperatures fall between 7 and 8 $^{\circ}$ C. These values reveal little variation in the base temperatures of five common highbush blueberry cultivars and suggest that it may be appropriate to assign the same range of base temperatures to all cultivars of highbush blueberry. Previous values used for the base temperature of highbush blueberry include 3 °C (Gough, 1994), 4.4 °C (Gough, 1983), 7.2 °C (Darrow, 1942; Eck and Childers, 1966) and 10 °C (Bryla et al., 2009). A study seeking to determine heat-unit models for predicting harvest of 13 highbush blueberry cultivars found that base temperatures of -7 °C, 2 °C, 4 °C or 7 °C could be used, depending on the cultivar (Carlson and Hancock, 1991). My base temperature values determined here are relevant only for bloom prediction and should not be considered base temperatures for full season development of highbush blueberry.

This study has also determined the relative bloom phenology, based on GDD accumulation, of five highbush blueberry cultivars. It is commonly accepted that the highbush blueberry cultivars used in this study fall into a sequence of 'Duke', 'Bluecrop', 'Jersey', 'Liberty' and 'Elliott' when ordered according to the relative timings of berry harvest (Hancock et al., 2001; Hancock, 2004) There are no previously published data,

however, on the comparative sequence of flower bloom in these cultivars; it has even been suggested that cultivar has no effect on the relative timing of blueberry bloom phenology (Eck, 1988). My results suggest that highbush blueberry bloom phenology significantly differs according to cultivar and that it is predictable based on air temperature.

Bloom sequence under greenhouse conditions, as measured by accumulated GDD at peak percent bloom, was found to follow a similar pattern as berry harvest: 'Duke', 'Bluecrop', 'Liberty', 'Elliott', and 'Jersey'. Because there was no significant difference in accumulated GDD at peak percent bloom for 'Liberty', 'Elliott' and 'Jersey', these findings support the previously assumed order of highbush blueberry cultivar phenology and justify grower planting choices that are based on strategies of staggering the bloom periods of multiple cultivars in individual or adjacent fields. Such a strategy can help spread the demand for bees to pollinate fields at one time, and enable more efficient pollination. Evidence for Highbush blueberry exhibits a degree of parthenocarpy (Coville, 1910; Eck, 1988; Gough, 1994; MacKenzie, 1997; Dogterom et al., 2000) but the extent of parthenocarpy varies according to cultivar. There is also a benefit of cross-pollination socombining overlapping compatible cultivars can also help ensure cross-pollination that may provide increased berry size (Meader and Darrow, 1947; McGregor, 1976; Vander Kloet, 1984; Luby et al., 1991; MacKenzie, 1997).

For all cultivars, peak percent bloom occurred at significantly lower accumulated GDD under field conditions than in the greenhouse environment. These differences could be attributed to horticultural differences between potted blueberry plants and those under field conditions, receiving regular fertilization, tilling, etc. Bushes grown in the greenhouse also experienced different light quality (spectral wavelength distributions) than the natural

sunlight received by field plants, another factor which may have contributed to the differences observed in bloom phenology (Smith, 1982). Also, the differences in age between potted bushes used for greenhouse experiments and the mature bushes under field settings could account for the differences in bloom phenology. While many growers observe no difference in the blooming characteristics of young versus mature blueberry plants (M. DeGrandchamp, personal communication), plant development over time is sometimes nonlinear and can change with age (Wang, 1960). Similarly, plant development with respect to environmental variables is also often a nonlinear relationship (Evans, 1972).

Possibly the most influential factor contributing to the differences observed in greenhouse and field phenology is the amount of chilling hours experienced. NeSmith and Bridges (1992) examined the relationship between accumulated chilling hours and rabbiteye blueberry bloom phenology and found an increased rate of bloom development with increased chilling hours. Assuming a similar relationship between chilling hours and development for highbush blueberry, this difference would account for the observed shift in bloom for greenhouse plants where bloom was delayed by approximately 100 GDD. Although both field and greenhouse bushes in this experiment received the minimum recommended amount of chilling hours, 600-1000 chilling hours (Pritts and Hancock, 1992), the bushes pulled out of cold storage and grown in the greenhouse received a lower number of chilling hours than those assessed in the field. The effect of this on bloom phenology means that greenhouse data provide relative, but not absolute, values for bloom timing in the cultivars tested.

We found that highbush blueberry flowers are most viable for fruit set when pollinated up to 4 d after flower opening. Greenhouse and field experiments yielded contrasting results, but

this is to be expected as environmental and management conditions are different between the two. Field conditions involve variable air and soil temperatures, soil moisture and nutrients, pruning, fertilization, and other factors known to be important components of highbush blueberry development and fruit set (Hall et al., 1963; Goulart et al., 1997; Strik and Buller, 2003; Holzapfel et al., 2004) while greenhouse experimentation allows for consistent levels of many of these variables. The interaction between cultivar and duration until pollen deposition found in both greenhouse and field experiments can be considered to be the result of multiple blueberry cultivars responding differently to increasing intervals of time before pollination. Even taking into account these differences, greenhouse and field results indicate that the reduction in fruit set is most significant when increasing the amount of time elapsed between flower opening to pollination to 5 d. In fact, at 5 d after anthesis many floral stigmas either appeared unsuitable for pollination or had fallen off entirely. Previous studies on highbush blueberry flower viability have found flowers to remain viable up to 5 (Merrill, 1936) or 8 d after anthesis although fruit set, berry weight and seed number were found to decrease after 4 d (Moore, 1964). Interestingly, under greenhouse and field conditions blueberry flowers appeared to show slightly increased viability when pollinated 1 to 2 d after opening rather than when pollinated on the day of opening. These results support those of Merrill (1936) who suggested that the optimum time of pollination is 24 to 48 h after flower opening.

Finally, the cultivar of highbush blueberry appeared to have no effect on flower viability in the greenhouse but was a significant variable affecting flower viability under field conditions. This difference appears to have been driven in part by the low fruit set values of the field planted 'Liberty' that led to a significant variation among cultivars. These results

may be explained to some extent by winter injury to young bushes. 'Liberty' was introduced into commercial highbush blueberry production relatively recently and its performance in the field has been variable in Michigan to date. Had these bushes been closer in maturity to those of the other more established cultivars, differences in fruit set values may have been less apparent.

These results are important for the growers of highbush blueberry as they can use this knowledge of blueberry phenology to better schedule management practices relative to the timing of bloom and the placement of managed honey bee hives in the field between 5% and 25% bloom (Howell et al., 1972, Pritts and Hancock, 1992). When combined with other pollination guidelines, such as observing four to eight honey bees per bush for optimum pollination (Pritts and Hancock, 1992) growers may be able to make more knowledgeable managed pollination decisions. It is important to further explore this optimization of managed pollination efforts as a response to potential pollinator declines that may threaten the productivity of pollination-dependent crops (Aizen et al., 2008).

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CHAPTER 3

Pollinator Activity During Highbush Blueberry Bloom in Michigan

INTRODUCTION

The European honey bee (*Apis mellifera*) has been used extensively for pollination services to commercial agriculture worldwide since the early 1900's (Todd and McGregor, 1960). Today, 35 percent of our global food production depends on animal pollination (Klein et al., 2007) with a large majority of those pollination services provided by managed honey bees (Delaplane and Mayer, 2000; NRC, 2007). Recent estimates have placed a global value of \$14.8 billion on honey bee pollination services (Morse and Calderone, 2000). In the commercial blueberry industry, the need for managed honey bee pollination was recognized as early as the 1960's (Filmer and Marucci, 1963). Marucci (1966) found honey bees to be suitable for blueberry pollination with flooding of the blueberry fields with bees to be the most effective pollination strategy. However, there are drawbacks to this use as honey bees are generalist foragers and do not always forage on the intended crop (Jay, 1986; Westerkamp, 1991), possibly making it impractical, or uneconomical, to purchase an overabundance of honey bees. Also, there is currently much concern over the decline of managed honey bees (NRC, 2007; Johnson, 2010; VanEnglesdorpet al., 2010; Oldroyd, 2007), and because of this it may prove increasingly difficult to attain the numbers of honey bees necessary to flood large, commercial agricultural fields during bloom to ensure full pollination. Indeed, it has been determined that rate of increase of managed honey bee hives is not currently sufficient to keep pace with the corresponding increase in acreage of pollination-dependent crops (Aizen and Harder, 2009).

With approximately 17,000 other bee species in existence (Michener, 2000), it is also important to explore new options for alternative managed pollinators to supplement or even replace managed honey bees in some agricultural systems. Crops such as highbush blueberry (Vaccinium corymbosum L.) that are native to North America may be better pollinated by bees that are native to the same region, rather than the foreign European honey bee, as these plants and pollinators have coevolved over centuries. These native bees represent a relatively underutilized pollinating resource. In Michigan, up to 10 percent of overall highbush blueberry pollination can be attributed to native bees, with much higher proportions in less intensively managed fields (Isaacs and Kirk, 2010). These bees enhance or complement the pollination of honey bees (Chagnon et al., 1993; Greenleaf and Kremen, 2006; Brittain et al., 2013). Managed bumble bees (*Bombus* spp.) are a recently developed alternative to honey bees, first used for pollination in tomato greenhouse production (Velthuis and van Doorn, 2006). They have been shown to be superior to honey bees as pollinators in open fields of pumpkin (Artz and Nault, 2011), raspberry (Willmer et al., 1994), cranberry (MacKenzie, 1994), watermelon, cucumber (Stanghellini et al. 1998; 2002) and blueberry (Stubbs and Drummond, 2001; Javorek et al., 2002; Ratti et al., 2008).

Another advantage of using managed bumble bees for crop pollination is that they are capable of thermoregulation whereas honey bees require a high thoracic temperature to initiate flight (Heinrich, 1979). Differences in bee energetics such as this have lead many researchers to investigate the influences of different weather conditions on pollinator foraging activity. The majority of this foraging activity research has focused on honey bee activity, however results are often variable. For instance, the lower temperature threshold of honey bee activity has been determined to be 7 $^{\circ}$ C (Heinrich, 1979), 9 $^{\circ}$ C (Burrill and Dietz,

1981), 8.7-11.2 °C (Corbet et al., 1993), and 12-15 °C (Vicens and Bosch, 2000). Most studies agree that solar radiation, temperature, relative humidity, and wind speed are the most influential weather factors on bee activity (Szabo, 1980; Burril and Dietz, 1981; DeGrandi-Hoffman, 1987; Corbet et al., 1993; Vicens and Bosch, 2000). As the optimal production of pollination-dependent crops depends on a thorough understanding of pollinator activity and efficiency, we must further investigate the foraging of both native and managed bees in order to better understand how to optimize use of these bees for crop pollination. The purpose of this study was to observe honey bees (*Apis mellifera*) and bumble bees (*Bombus impatiens*) during foraging at highbush blueberry flowers and subsequently determine whether flower visitation rate is affected by environmental conditions such as air temperature, wind speed, solar radiation, and relative humidity, as well as the percent total bloom.

MATERIALS AND METHODS

To determine the relationships between pollinators and individual weather parameters, pollinator observations were made approximately three times a week throughout the period of blueberry bloom at each of three study sites in Michigan during 2009, 2010 and 2011. Observations were conducted to gather data on as wide of a range of environmental conditions as possible, and during early, mid, and late bloom. In 2009, the three sites sampled were located at the Trevor Nichols Research Center in Fennville, the Southwest Michigan Research and Extension Center in Benton Harbor, and DeGrandchamp Farms in South Haven. In 2010 and 2011, the three sites sampled included two fields from DeGrandchamp Farms in South Haven, and one Cornerstone Ag. field in Lacota. Each site was equipped with a HOBO[®] Weather Station (Onset Corporation, Bourne, MA, USA) that monitored on-site weather conditions 1.5 m above ground level and was stocked with commercial honey bee hives and/or bumble bee colonies. Observations were made on Bluecrop and Jersey cultivars and sites were rotated so that they were visited at different times during the day (morning, afternoon, evening) across the period of bloom. Six, five minute samples were recorded in each cultivar per observation. For each five minute sample, the numbers of pollinating honey bees, bumble bee queens and bumble bee workers making legitimate pollination visits to blueberry flowers were counted. During each sample, observers counted pollinators while walking along rows and observing approximately 10 bushes. Observations were made across a variety of weather conditions in order to adequately observe pollinator response to varying weather parameters.

Pollinator frequency data were averaged for each observation, then transformed to proportion values based on the total number of managed pollinators that were stocked in the field at the time of observation. The following equation was used to calculate proportion of stocked honey bees foraging on one acre of blueberry:

In this equation, *PropHB* is the calculated proportion of stocked honey bees estimated to be foraging on one acre of blueberry, *#HB* is the number of honey bees observed foraging on blueberry in a five minute observation, and *#Hives* is the number of stocked honey bee hives per acre. The other values included in the above equation serve to expand a five minute pollinator observation of approximately ten blueberry bushes to an hourly predicted number of pollinators on one acre of blueberry. It was assumed that one managed honey bee hive contained an average of 20,000 honey bee foragers (Stanghellini et al., 1998; Pfeiffer and Crailsheim, 1999; Downs and Ratnieks, 2000; Pankiw, 2004).

In a similar manner, the equation below was used to calculate proportion of stocked bumble bees foraging on one acre of blueberry:

In this second equation, *PropBB* is the calculated proportion of stocked bumble bees estimated to be foraging on one acre of blueberry, *#BB* is the number of honey bees observed foraging on blueberry in a five minute observation, and *#Colonies* is the number of stocked bumble bee colonies per acre. The other values included in the above equation serve to extrapolate a five minute pollinator observation of approximately ten blueberry bushes to an hourly predicted number of pollinators on one acre of blueberry. It was assumed that one managed bumble bee colony contained an average of 150 bumble bee foragers (Kim Skyrm, Koppert Biological Systems, personal communication).

Variable selection analyses were performed to relate *PropHB* and *PropBB* to the weather variables of air temperature (°C), wind speed (m/s), percent relative humidity, solar flux density (kJ/m²), wind speed and percent total bloom by backwards step elimination (PROC REG, SAS 9.2, SAS Institute, Cary, NC) with a significance level of 0.15 required for variables remaining in the model. Because this method of variable selection removed weather parameters known to be influential on bee activity (air temperature, solar radiation, and percent relative humidity), partial least squares regression was performed as a less restrictive means of variable selection (PROC PLS). The partial least squares regression resulted in the same models as backwards step elimination, therefore multiple linear regression was conducted for both *PropHB* as well as *PropBB* with respect to each of the recorded weather variables (PROC GLM). The multiple linear regression analysis was

significant for *PropBB* but not for *PropHB*, so polynomial multiple regression was performed for each weather variable with respect to *PropHB* and *PropBB*. Equations of best fit were determined for each individual relationship between pollinator proportion and weather parameter.

RESULTS

Observations of honey bee activity were performed under weather conditions ranging from 10.7 °C to 33.9 °C air temperature, 106.6 to 3406.6 kJ/m² solar flux density, 0 to 4.3 m/s wind speed, and 1 to 97.6 percent relative humidity (Figure 3.1). Also, honey bee observations were recorded from 6.7 to 96.6 percent of total highbush blueberry bloom. Calculated proportions of stocked honey bees ranged from 0 to 1.67, indicating some possible immigration of honey bees from surrounding farms. Bumble bee observations were fewer blueberry fields stocked with commercial bumble bees. Sampling for bumble bees occurred under conditions ranging from 14.9 °C to 30.5 °C air temperature, 725.2 to 3268.8 kJ/m² solar flux density, 0 to 4 m/s wind speed, and 53.1 to 90.6 percent relative humidity (Figure 3.2). These bumble bee observations also occurred over a range of 9.4 to 66.5 percent of total highbush blueberry bloom. Calculated proportions of stocked bumble bees ranged from 0 to 8.41, suggesting that some fields had a large amount of native bumble bees that are indistinguishable from the managed colonies placed in the fields by growers.



Figure 3.1 A, B, C. Average proportion of stocked noney bees observed pointaining highbush blueberry flowers in relation to the parameters of air temperature (C), solar flux density (kJ/m^2) , and wind speed (m/s). Each datum represents the average of six, five minute observational samples in a commercial highbush blueberry field stocked with honey bees. Equations of best fit were determined by multiple polynomial regression and are summarized in Table 3.1.

Figure 3.1 (cont'd)



Figure 3.1 D, E. Average proportion of stocked honey bees observed pollinating highbush blueberry flowers in relation to the parameters of relative humidity and percent total bloom. Each datum represents the average of six, five minute observational samples in a commercial highbush blueberry field stocked with honey bees. Equations of best fit were determined by multiple polynomial regression and are summarized in Table 3.1.



Figure 3.2 A, B, C. Average proportion of stocked bumble bees observed pollinating highbush blueberry flowers in relation to the parameters of air temperature (C), solar flux density (kJ/m²), wind speed (m/s). Each datum represents the average of six, five minute observational samples in a commercial highbush blueberry field stocked with bumble bees. Equations of best fit were determined by multiple polynomial regression and are summarized in Table 3.2.

Figure 3.2 (cont'd)



Figure 3.2 D, E. Average proportion of stocked bumble bees observed pollinating highbush blueberry flowers in relation to the parameters of relative humidity and percent total bloom. Each datum represents the average of six, five minute observational samples in a commercial highbush blueberry field stocked with bumble bees. Equations of best fit were determined by multiple polynomial regression and are summarized in Table 3.2.

Equations relating the proportion of stocked honey bees foraging on blueberry flowers to individual weather parameters were fit using multiple polynomial regression to determine what power equation best fit the foraging data to individual parameters. Regression relationships were significant in only two of the five relationships investigated (Table 3.1). The proportion of honey bees foraging was found to be related to percent relative humidity, and solar flux density by different quadratic equations, however air temperature, wind speed and percent total bloom were best related to proportion of honey bees foraging by linear relationships. Equations of best fit for weather parameters with respect to honey bee foraging are listed in Table 3.1.

Table 3.1. Summary of best fit regression equations for proportion of foraging honey bees versus air temperature ($^{\circ}$ C), solar flux density (kJ/m²), wind speed (m/s), relative humidity, and percent total bloom.

Coefficients						
Parameter	Intercept	Parameter	Parameter ²	R^2	d.f.	P-value
Air Temperature	0.14	0.0062		0.009	1,88	0.36
Solar Flux Density	-0.0088	0.00035	-8.4E-8	0.057	2,87	0.08
Wind Speed	0.16	0.061		0.034	1,88	0.08
Relative Humidity	0.15	0.013	-0.00016	0.160	2,87	0.0005
Percent Total Bloom	0.064	0.0051		0.077	1,77	0.01

Multiple polynomial regression was also used to determine relationships between all weather parameters and proportion of stocked bumble bees foraging on blueberry. For these analyses, no regressions were found to be significant. For bumble bees, all weather parameters were best explained by linear regression with the proportion of bees stocked foraging on blueberry (Table 3.2).

Table 3.2. Summary of best fit regression equations for proportion of foraging honey bees versus air temperature ($^{\circ}$ C), solar flux density (kJ/m²), wind speed (m/s), relative humidity, and percent total bloom.

Coefficients						
Parameter	Intercept	Parameter	Parameter ²	R ²	d.f.	P-value
Air Temperature	0.35	0.053		0.023	1,16	0.55
Solar Flux Density	2.3	-0.00037		0.023	1,16	0.55
Wind Speed	2.1	-0.38		0.059	1,16	0.33
Relative Humidity	0.37	0.016		0.011	1,16	0.68
Percent Total Bloom	0.57	0.025		0.024	1,15	0.55

DISCUSSION

The variable selections conducted on weather parameters air temperature, solar flux density, wind speed, and relative humidity and on percent total bloom with respect to the proportion of foraging pollinators indicated that percent total bloom and wind speed were the most influential parameters on pollinator foraging. While previous research has supported the conclusion that these two parameters influence pollinator foraging, it has also indicated that the other parameters investigated (air temperature, solar flux density and relative humidity) are influential on the foraging activity of pollinators (Kevan and Baker, 1983; Vicens and Bosch, 2000), suggesting that these parameters are expected to be influential on pollinator foraging in highbush blueberry. It is possible that additional pollinator observations would have elucidated these relationships, especially in blueberry fields stocked with bumble bees as there were only a total of 18 of the observations included in this study. Few blueberry growers consistently stock their fields with managed bumble bees, however, and future researchers may find it necessary to provide these managed bees in a more controlled design in which bumble bees are added to crop fields at high densities to allow more thorough sampling of these bees foraging in blueberry.

Some calculated proportions of stocked honey bees and bumble bees were greater than one, indicating an observation of more foraging pollinators in one acre of blueberry than were stocked. These results are to be expected as it is unrealistic to expect mobile pollinators to remain in the acre their hives or colonies were initially stocked. It is also possible that native pollinators contributed to these proportions greater than one. Although there are very few natural populations of honey bees remaining in Michigan, natural colonies of bumble

bees are quite common and were not taken into account when calculating these proportion values.

The proportion of stocked honey bees foraging on highbush blueberry was significantly and positively linearly correlated with percent total bloom and not significantly correlated with air temperature and wind speed. The positive relationship with percent total bloom can be explained by a positive response by honey bee foragers to an increasing area of floral resources. It has been documented that once honey bees discover a rewarding floral resource, they then recruit other honey bee workers to collect the same resource (Frisch, 1968). As the floral resource declines in quality or quantity, it follows that pollinators will be less likely to return and will switch attention to foraging in more rewarding areas. The positive linear relationship between honey bee activity and air temperature coincides with the fact that honey bees require a high thoracic temperature to maintain flight (Heinrich, 1979), and therefore are less capable of foraging at lower temperatures. It also supports the results of Burrill and Dietz (1981), Corbet et al. (1993), and Vicens and Bosch (2000) who observed a positive linear relationship between honey bee activity and air temperature. Wind speed was also related to honey bee activity through a positive linear relationship. This result however, contradicts the results of previous research which indicated that increasing wind speed has a negative effect on honey bee activity (Vicens and Bosch, 2000). However, this may reflect a poorly understood correlation between weather variables.

The proportion of stocked bumble bees foraging on highbush blueberry was found to exhibit non-significant, linear relationships with all parameters. In relation to air temperature, bumble bee activity increased with warmer temperatures. As bumble bees are known to forage down to temperatures of 0 $^{\circ}$ C (Heinrich, 1979) and activity observations for the

current study were made from a range of 15 $^{\circ}$ C to 31 $^{\circ}$ C, a weak positive correlation appears to be a logical representation of this relationship. Bumble bee activity was negatively related to solar flux density and wind speed. While the negative, linear relationship with wind speed corroborates the results of previous research, a consistently negative, linear relationship with increasing solar radiation is surprising. As was the case with honey bee activity, the positive relationship with percent total bloom can be attributed to a pollinator response to increasing floral resources. A linear relationship between bumble bee activity and relative humidity may simply be the result of a low number of observations, obscuring a more complex relationship.

The predictors of pollinator foraging activity are many and complex. For example, factors beyond those included in this study that are known to influence bee activity include atmospheric pressure (Lundie, 1925), floral heat rewards (Rands and Whitney, 2008), demand for food and availability of resources (Dogterom and Winston, 1999; Dornhaus and Chittka, 2004; Pelletier and McNeil, 2004), floral volatiles (Rodriguez-Saona et al., 2011), nectar secretion (Stout and Goulson, 2002), sugar content of nectar (Waller, 1977) among others. Yet another potential factor involved in bee activity is the proposed competition between honey bees and bumble bees. This interaction has been shown to lead to decreased bumble bee size (Goulson and Sparrow, 2009), health and foraging (Thomson, 2004), and positional and temporal displacement of bumble bees (Walther-Hellwig et al., 2006). This suggests that further, more detailed investigation of managed pollinator activity is necessary to elucidate relationships between bee activity and microclimatic conditions.

Although the results of this research do not offer clear explanations for the relationships between weather parameters and the foraging activity of honey bees and bumble bees on highbush blueberry, additional research into these relationships could greatly

benefit the field of pollination biology. If combined with other knowledge such as flight distance, we could make great progress toward predicting foraging under agricultural conditions where pollination is crucial for quality yield in many cropping systems. With increased attention on the benefits of pollinator diversity (Hoehn et al., 2008) and interest in the development of alternative managed pollinators (Pitts-Singer, 2008), it is increasingly important that we understand the behavior of these managed insects within their intended agricultural environments. It is only with this knowledge that we can move towards a more efficient and sustainable approach to the managed pollination of key agricultural systems.

CHAPTER 4

BLUEPOLL Model Development and Validation

INTRODUCTION

Pollination-dependent commercial agriculture has long relied on the rental of managed European honey bee, *Apis mellifera* L., hives to satisfy crop pollination needs (Free 1993, Delaplane and Mayer 2000). In recent years however, there has been much concern over the decline of both feral and managed honey bees (Kraus and Page, 1995; Jaffée et al., 2010; Ratnieks and Carreck, 2010) and the long-term sustainability of managed crop pollination (Aizen and Harder, 2009). These declines have brought increased attention to the global dependence of agriculture on honey bees and have lead researchers and farmers to seek options for alternative pollinators either as a replacement or supplement for managed honey bee hives. Pollination-dependent crops currently comprise 35 percent of human food (Ricketts et al., 2008) and have a wide variety of potential insect pollinators that vary in their foraging behavior and efficiency (Javorek, 2002; NRC, 2007; Radar et al., 2009; 2012). These pollinators can also interact with one another in ways that have the potential to increase their individual pollination efficiency (DeGrandi-Hoffman, 2000; Greenleaf and Kremen, 2006; Brittain et al., 2013), and therefore, having a diverse community of managed pollinators in a crop system may serve as insurance for the stability of crop yield (Klein et al., 2007; Hoehn et al., 2008; Rogers, 2012). If managed efficiently, alternative managed pollinators may support commercial agriculture and promote more reliable production of pollination-dependent crops.

In highbush blueberry (Vaccinum corymbosum L.), honey bees are currently the most

commonly used managed pollinators, with colonies of bumble bees, *Bombus* spp., also being used by some farmers interested in diversifying their sources of pollination. These two pollinator groups have contrasting ways of interacting with flowers and thus have different pollination efficiencies (Westerkamp, 1991; Thomson and Goodell, 2001; Javorek et al., 2002). Many flowering plant species, including highbush blueberries, have anthers that must be shaken for pollen to be released. For optimal pollen release, bees must grasp the flower while vibrating their wing muscles, a behavior often referred to as buzz-pollination (Buchmann, 1983). Bumble bees engage in buzz-pollination while honey bees do not. Bumble bees are also able to carry more pollen on their bodies and remain active during cool weather, making them more effective pollinators of blueberry than honey bees (Javorek et al., 2002). Thus, it may be that a smaller number of bumble bees would be needed to provide the same pollination service as honey bees in some crops.

Given their ability to fly at low temperatures (Heinrich, 1979), bumble bees may provide pollen transfer and mitigate potential crop yield limitation caused by periods of honey bee inactivity when conditions are cool in the spring. Native bees, such as bumble bees, are the dominant pollinators in many small blueberry fields, and provide as much as 10 percent of pollination services for the entire Michigan blueberry industry (Isaacs and Kirk, 2010). Studies in lowbush blueberry (*Vaccinium angustifolium* L.) have demonstrated that pollination by bumble bees resulted in equal or better pollination than honey bees, with higher fruit set, berry weight, and seeds per berry (Stubbs and Drummond, 2001). Furthermore, the results of that research with *Bombus impatiens* L. suggest that one bumble bee can pollinate as many lowbush blueberry flowers as 10-20 honey bees in the same period of time.

While most blueberry farmers rent honey bee hives for pollination annually, current recommendations for stocking levels of honey bee hives per acre lack the support of thorough comparisons of different stocking densities. Rather, these recommendations are based on experience. Farm managers commonly make pollinator stocking decisions based solely on what was done in previously successful years or by following rule of thumb guidelines passed down by the previous generation. Due to the large scale and complexity of conducting experimental manipulations of crop pollination, it is very challenging to explore the range of possible pollinator, weather, and crop combinations. Therefore, to investigate stocking of blueberry fields by managed pollinators, I approached this study by developing a mathematical model of the highbush blueberry pollination system, based largely on observational data of pollinator activity and blueberry phenology with respect to weather conditions.

When logistical, temporal, or financial difficulties are encountered in large scale ecological experimentation, mathematical models can be used instead to indirectly investigate the structure and function of these systems. In agricultural systems, it is often unreasonable to consider experimentation at a scale of hundreds of acres, especially when factors such as insects, which are mobile organisms and difficult to contain, are involved. Instead, mathematical modeling can allow an investigator to explore the importance of specific factors and relationships of interest in the system. Modeling can reveal the most influential factors of an ecological system, identify gaps in the scientific knowledge, and expose investigator assumptions of system behavior that may or may not be accurate. When ecological models are combined with economic data, resulting valuation methods can be useful in conservation, management and policy decisions (Costanza et al., 1993; Turner et al.,

2000; Nelson et al., 2009). Modeling is therefore becoming increasingly common in conservation, ecological, and entomological research (Jorgensen and Bendoricchio, 2001).

Within pollination research, modeling has been used to predict optimal bumble bee foraging behaviors (Best and Bierzychudek, 1982), pollinator abundance across different agricultural landscapes (Lonsdorf et al., 2009), and the effect of cropping systems and climate on cross-pollination in maize (Angevin et al., 2008). Pollination modeling has also been used to extensively examine and optimize alfalfa pollination and seed yields (Strickler, 1996; Strickler, 1997; Breazeale et al., 2008), apple pollination and fruit set (DeGrandi-Hoffman et al., 1987), and almond pollination and nut set (DeGrandi-Hoffman et al., 1996). Models such as these not only expand scientific knowledge concerning the pollination of agricultural crops, they can also be used to support farm management decisions, if combined with economic values of input cost and yield value (Swinton and Black, 2000).

The goal of this research was to develop and validate a model of highbush blueberry pollination, BLUEPOLL, in order to further investigate variable managed pollinator stocking strategies under different weather conditions.

MATERIALS AND METHODS

Model Development

Researchers who wish to use modeling to examine their system of interest often use software such as R and MATLAB where users must write their own mathematical code; however, more user-friendly simulation software is becoming widespread. One such program is STELLA by iSee Systems, Inc. (Lebanon, NH) which allows for simplified building, testing and publication of mathematical models. Although users of STELLA may be more limited in their ability to customize models than with open-ended programming, the ease of use allows users with limited modeling experience to avoid many of the complications of coding and debugging. STELLA users build a visual model of their system using stocks (state variables), flows (variable interactions), and converters (additional parameters) and then enter values or mathematical relationships for each component. The overall model code is then automatically compiled by the STELLA program. Users also have the ability to then share the complete system code (prepared by the STELLA program) with others as well as prepare a userfriendly interface for more simplified presentation or online publication of the model (Costanza and Ruth, 1998; Bice, 2006). For these reasons, I chose to use the STELLA modeling program to develop a model of blueberry pollination, named the BLUEPOLL model.

To model highbush blueberry pollination, it was first necessary to define the problem of interest, set boundaries to the system, and decide upon the specific purposes of the proposed model. For this research, I sought to investigate three areas of interest: 1) the effect of different weather conditions on pollinator activity and flower phenology in highbush blueberry; 2) the profit-maximizing level of managed pollinator input for honey bees and bumble bees; 3) the least-cost input combination of honey bees and bumble bees. To allow for practical, in-field experimentation concerning the pollination system, a boundary was placed to model one acre of blueberry.

In modeling, it is unrealistic to include all system components and interactions. Therefore, in the BLUEPOLL model farm management decisions such as fertilization, pruning, harvesting technique, etc. and additional factors such as wild pollinators, hive/colony strength, pollinator cultivar preferences, plant responses to temperature, etc.

were intentionally omitted or assumed to be constant in order to focus on specific hypotheses regarding managed pollinator stocking density, weather variables and their effects on blueberry yield. Also, the BLUEPOLL model was developed as a deterministic model and does not include stochastic relationships.

The BLUEPOLL model, summarized in Figure 4.1, was developed using a combination of experimental data (Kirk and Isaacs, 2012; Chapters 2 and 3) and information from the honey bee, bumble bee, and highbush blueberry pollination literature. The model is constructed to simulate one acre of highbush blueberry and is designed to run on an hourly time step for a time period characteristic of the length of blueberry bloom for all cultivars (Bluecrop, Jersey, Duke, Elliott, and Liberty); either 30, 20, or 15 days depending on the selected weather conditions (cool, average, or warm weather, respectively). The four major components of the system included in the model are honey bees, bumble bees, highbush blueberry plants and ambient weather.



Figure 4.1. BLUEPOLL model structure including honey bees (orange), bumble bees (black), weather (blue) and highbush blueberry plant components (green). For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation. The text of this figure is not meant to be readable but is for visual reference only.
The honey bee components of the system are represented in the model by the color orange (Figure 4.1). These managed pollinators can be rented or purchased, and users of the model are able to manipulate these inputs (*HB Hives Rented*) to simulate variable stocking strategies. For the BLUEPOLL model, it is assumed that each rented honey bee hive contains 20,000 bees (*HB per Hive*). This number was chosen as a conservative estimate of honey bee workers per hive in early spring (Stanghellini et al., 1998; Pfeiffer and Crailsheim, 1999; Downs and Ratnieks, 2000; Pankiw, 2004). The numbers of honey bees foraging on blueberry are represented by the stock *HB on Bberry*. The input flow of this stock is calculated from the number of hives purchased (*HB Hives Rented*), the number of honey bees per hive (*HB per Hive*), and an equation that relates bee activity to air temperature, wind speed, solar radiation and available highbush blueberry flower density (Table 4.1). This calculation is based on empirical data of honey bee activity on highbush blueberry found in Chapter 3 (A.K. Kirk, unpublished data). The output flow of this stock allows for all bees to return to their hives at the end of each day.

Table 4.1. Mathematical relationships relating honey bee activity (proportion of stocked honey bees per acre) to individual variables of air temperature ($^{\circ}$ C), solar radiation (kJ/m²), wind speed (m/s), and proportion of bloom ((total open flowers)/(total potential flowers)).

Parameter	Lower limit	Upper limit	Regression equation
Air temperature	12 ^a	35 ^b	$y = -0.0013x^2 + 0.0626x - 0.4016$
Solar radiation	10	3407	$y = -8E - 8x^2 + 0.0004x - 0.0088$
Wind speed	0	6 ^c	$y = -0.0278x^2 + 0.1609x - 0.1016$
Proportion of bloom	0	1	y =0.0051x + 0.064

^{a,b} Average temperature thresholds (Vicens and Bosch, 2000; Heinrich, 1979).

^c Honey bees fly at about 6 m/s (Williams and Sims, 1977).

The bumble bee components of this system (represented in black) are very similar to the honey bee components and also based on empirical data of bumble bee activity on highbush blueberry (A.K. Kirk, unpublished data). Instead of hives, bumble bees are purchased in colony units (*BB Units Purchased*) which are assumed to have 150 bumble bee workers per unit (*BB per Unit*) (Kim Skyrm, Koppert Biological Systems, personal communication). Note that there are four bumble bee colonies in a QuadTM, the unit that is typically purchased for use in commercial blueberry production. With the exception of different relationships allowing for differences between honey bee and bumble bee foraging

behaviors, the input and output flows of the bumble bee component reflect those of the honey bee component, described above. The input flow is representative of how many bumble bees are stocked into the one acre planting (*BB Units Purchased * BB per Unit*), regulated by an equation similar to that with honey bees that relates bee activity to weather conditions and available blueberry flower density (Table 4.2).

Table 4.2. Mathematical relationships relating bumble bee activity (proportion of stocked bumble bees per acre) to individual variables of air temperature ($^{\circ}$ C), solar radiation (kJ/m²), wind speed (m/s), and proportion of bloom ((total open flowers)/(total potential flowers)).

Parameter	Lower limit	Upper limit	Regression equation
Air temperature	8 ^a	35 ^b	$y = -0.0194x^2 + 0.9304x - 8.905$
Solar radiation	10	3269	$y = -6E - 7x^2 + 0.00196x - 0.27$
Wind speed	0	5.5 ^c	y = -0.38x + 2.1
Proportion of bloom	0	1	y = 0.0248x + 0.5698

^{a,b} Average temperature thresholds (Heinrich, 1979; Corbet et al., 1993).

^c Estimate from Chapter 3 data.

The values of *HB on Bberry* and *BB on Bberry* are combined into the converter *Combined Pollinator Activity*, which includes a mathematical equation to calculate how many blueberry flowers are pollinated per hourly time step based on values for honey bee and bumble bee flower visits per hour as well as their pollination efficiencies (Javorek et al., 2002). Also included in the *Combined Pollinator Activity* converter is an equation to estimatethe time spent by bees flying to and from the hive or colony based on average flight speed, distance from hive to crop, and number of trips per day (Table 4.3). The *Combined Pollinator Activity* is then partitioned across the six different floral ages, relative to the proportion of flowers of a certain age with respect to the total flowers open (e.g., *Combined_Pollinator_Activity*(Flowers_Day_0/Total_Open_Flowers))*. This is to ensure that the pollinators are not all acting on *Flowers Day 0*. Rather, the available pollination services are divided into six groups of different sizes, all working on the total number of flowers open each hour to determine the number of pollinated blueberry flowers per time step.

Table 4.3. Parameter values used to calculate the time spent daily by bees flying to and from the hive or colony.

	Average flight speed	Average foraging trip	Average trips	
	(m /s)	distance (km)	per day	
Honey bees	6.15	1.5	10	
Bumble bees	4.16	1.5	20	

The BLUEPOLL model was developed to include cool, average or warm (in regards to suitability for pollination) weather conditions and will run on the user-selected set of weather parameters. To develop cool, average, and warm weather datasets for inclusion in the model, historical weather data from a period during spring time when blueberries are in bloom in South Haven, Michigan were examined from 2001. Single weeks of weather data were then chosen to represent cool, average, or warm conditions (Table 4.4). These weeks of hourly weather data were then replicated to cover the necessary time period for each weather dataset for the period of full bloom. This was found to be 30, 20, or 15 days for cool, average, and warm weather, respectively, based on bloom being completed more rapidly during warmer conditions.

Table 4.4. Range and average values for each weather parameter used in the cool, average and warm sets of weather conditions.

Air temperature (°C)		Wind speed (m/s)		Solar Radiation (kJ/m ²)	
Average	Range	Average	Range	Average	Range
14.3	6.6 – 22.2	1.2	0.2 – 3.9	553	0-3100
17.4	4.1 - 30.1	1.7	0.2 – 4.3	736	0-3100
21.0	13.1 – 32.2	1.1	0.2 - 3.0	769	0 - 3097
	Air tempo Average 14.3 17.4 21.0	Air temperature (°C) Average Range 14.3 6.6 - 22.2 17.4 4.1 - 30.1 21.0 13.1 - 32.2	Air temperature (°C) Wind space Average Range Average 14.3 6.6 - 22.2 1.2 17.4 4.1 - 30.1 1.7 21.0 13.1 - 32.2 1.1	Air temperature (°C) Wind speed (m/s) Average Range Average Range 14.3 6.6 - 22.2 1.2 0.2 - 3.9 17.4 4.1 - 30.1 1.7 0.2 - 4.3 21.0 13.1 - 32.2 1.1 0.2 - 3.0	Air temperature (°C) Wind speed (m/s) Solar Radia Average Range Average Range Average 14.3 6.6 - 22.2 1.2 0.2 - 3.9 553 17.4 4.1 - 30.1 1.7 0.2 - 4.3 736 21.0 13.1 - 32.2 1.1 0.2 - 3.0 769

In the model, individual weather parameters are represented by converters that contain hourly data points of the three most important weather parameters for bee activity (Air Temp, Solar Radiation, Wind Speed) for the entire period of bloom. These weather parameters were selected through examination of both experimental data (Chapter 3) and from the literature on the effects of weather on bee activity (Heinrich, 1979; Szabo, 1980; Burrill and Dietz, 1981; DeGrandi-Hoffman, 1987; Corbet et al., 1993; Vicens and Bosch, 2000). The final weather component of the BLUEPOLL model is that of accumulating growing degree days (Accumulating GDD). Growing degree-days (Baskerville and Emin, 1969) are a measure of temperature accumulation above a specific base temperature and are used to characterize a wide variety of biological processes (Pruess, 1983; Griffin and Honeycutt, 2000; Marra et al., 2002). Accumulated GDD determines the flower opening behavior of the plant component of this model. Base temperatures and equations for flower opening were derived from field experimental data (Kirk and Isaacs, 2012; Chapter 2). Finally, the starting value of Accumulating GDD is regulated by GDD Start, and the converters Time Converter and GDDStartValue, as the period of highbush blueberry bloom does not begin at 0 GDD each year. For example, when running the model with average weather conditions for the Bluecrop cultivar, the starting value of AccumulatingGDD is defined by *GDDStartValue*. The hour at which growing degree-days begin to accumulate is regulated by the *TimeConverter*, as it is different for each of the three weather conditions. Finally, GDDStart pulses the value of GDDStartValue once, at the hour specified by the *TimeConverter*. This allows for the value of *AccumulatingGDD* to start at a value other than zero, at a specific time step, without having the value of AccumulatingGDD added to each time step.

To simulate highbush blueberry flower opening and fruit development (represented by the color green). To begin, the total number of potential flowers within the one acre system is calculated from the number of blueberry bushes per acre, determined by the *Row* Spacing and Bush Spacing input parameters (9 feet by 4 feet is considered standard), and the average number of flowers per bush (Flowers per bush) (Table 4.5). Flowers open as a function of Accumulating GDD over the growing season (Flower opening per GDD). These relationships have been characterized by data collected from blueberry bloom (Kirk and Isaacs, 2012; Chapter 2; Table 4.6). As flowers age from *Flowers Day 0* (day of first opening) to Flowers Day 5 (five days after opening), they are less likely to set fruit if pollinated (Kirk and Isaacs, 2012; Chapter 2). These relationships are included in the Pollinated 0-5 flows. My earlier research has demonstrated that highbush blueberry flowers are highly unlikely to be healthy enough for successful pollination and fruit set more than five days after opening and exhibit declining flower viability up until that point (Kirk and Isaacs, 2012; Chapter 2). If pollinated on the day of first opening, a highbush blueberry flower has approximately 80 percent chance of fruit set. If pollinated five days after flower opening, this chance of fruit set decreases to about 20 percent (Kirk and Isaacs, 2012; Chapter 2). If a flower is not pollinated, it will age (Age 1-5) and eventually Wilt. These wilted flowers accumulate in the Unpollinated Flowers stock. The potential for fruit set in flowers that are not visited by bees (Coville, 1910; Eck, 1988; Kirk and Isaacs, 2012; Chapter 2) (Unpollinated Flowers) is included in the Yield converter, along with the average weight of berries from unpollinated flowers (Table 4.5). These are converted to blueberry yield in pounds. This model uses pounds as the unit of yield since this is most commonly used in the blueberry industry. If flowers are pollinated, they move from the *Pollinated Flowers* stock

through the *Pollinated Berries* flow which, similar to the *Unpollinated Berries* flow, takes into account the known rate of fruit set for pollinated flowers (Kirk and Isaacs, 2012; Chapter 2), the average weight (in grams) of the future pollinated fruit (A.K. Kirk, unpublished data), and a conversion factor to change the weight of blueberry yield from grams to pounds. From this *Yield* converter, a number is calculated as the *Harvest* flow to result in the *Blueberry Yield* (in pounds) from one acre of highbush blueberry.

Cultivar	Flowers	Flowers Average pollinated Average unpollin		Base Temperature
	per bush	berry weight (g)	berry weight (g)	(°C)
Bluecrop	3628	1.55	0.496	7.42
Jersey	5556	1.21	0.496	7.93
Duke	2944	1.61	0.496	7.14
Elliott	2540	1.24	0.496	7.52
Liberty	2540	1.55	0.496	7.96

Table 4.5. Cultivar specific values for model parameters.

Table 4.6. Parameter estimates and 95% confidence intervals for the best fit logistic phenology curves for five highbush blueberry cultivars (refer to Chapter 2 for phenology equation and parameter descriptions).

	Logistic curve parameter					
Cultivar	р	V	a	b		
Bluecrop	277.3	24.0643	0.0326	0.1786		
Jersey	301.3	27.383	0.0351	0.2187		
Duke	287.5	29.8351	0.0478	0.1697		
Elliott	320.7	25.4193	0.0478	0.2108		
Liberty	266.9	27.5326	0.0263	0.1653		

A final component of the BLUEPOLL model takes into account the highbush blueberry cultivar of interest. Experimental data were collected and are included from five cultivars (Jersey, Bluecrop, Duke, Elliott and Liberty) (Kirk and Isaacs, 2012; A.K. Kirk, unpublished data; Chapter 2), all commonly planted in Michigan. The chosen cultivar input will alter the following variables in the model: the number of flowers per bush, base temperature, GDD start value, the size of pollinated and unpollinated berries (Table 4.5), and the relationship between accumulating GDD and flower opening (Table 4.6). Complete model code can be found in Appendix A.

Model Operation

The BLUEPOLL model is interactive in that users are able to select values for individual input parameters such as blueberry planting measurements, cultivar, level of managed pollinators and the expected weather conditions for the period of bloom. Standard highbush blueberry planting measurements are considered to be 9 feet (*Row Spacing*) by 4 feet (*Bush Spacing*), however this may vary by grower. Next, a cultivar is chosen from Jersey, Bluecrop, Duke, Elliott or Liberty. Users can choose from a range of 0-10 honey bee hives per acre as well as 0-10 bumble bee colonies per acre. Finally, to run the BLUEPOLL model the user must choose the expected weather conditions for the period of blueberry bloom. Weather is a highly influential variable in the pollination of crops as it can influence honey bee and bumble bee flight activity as well as the speed of which GDD accumulate. *Accumulating GDD* will determine flower opening as well as the length of time that blueberry flowers remain viable for pollination. Therefore, examining the highbush blueberry pollination system under an array of weather conditions allows testing of predictions related to optimal crop pollination strategies.

BLUEPOLL Validation and Sensitivity Analysis

After development, the BLUEPOLL model was validated and subjected to a sensitivity analysis to determine the most influential variables within this ecological system. Although it is generally agreed upon that validation is necessary, there is no one accepted validation test that can be used for all models (Mayer and Butler, 1993). Therefore, it is important for a modeler to explicitly state the purpose of the model, the performance criteria, and the model context (Rykiel, 1996) before deciding on a unique strategy for validation. Validation can be subjective or objective but as is the case with most analyses, the more selective the criteria, the stronger the argument for model validation (Kirchner et al., 1996). Along with the validation process, subjecting a model to a sensitivity analysis will also provide useful information about system behavior and the magnitude of influence of individual input parameters.

The purposes of the BLUEPOLL model are to investigate honey bees, bumble bees, and the combination of the two as managed pollinators in the highbush blueberry agricultural system and to aid farm managers in making economically-informed decisions on managed pollinator stocking strategies. Because the BLUEPOLL model is the first attempt at modeling highbush blueberry pollination, the chosen validation criteria were straightforward.

Stakeholder Focus Group. First, the BLUEPOLL model was presented to a group of stakeholders of highbush blueberry agriculture including growers, a horticultural crop consultant, and an extension educator in order to receive opinions on its structure, function, and use.

Parameter Boundary Testing. Next, the BLUEPOLL model was tested at input parameter boundaries to ensure consistent and rational results. When examining weather extremes, pollinator stocking was set to the recommended two honey bee hives per acre (zero bumble bee colonies). Conversely, when pollinator input extremes were examined, average weather conditions were chosen.

Observed Yield vs. Predicted Yield. Finally, the model was run using a sequence of historical weather data from the period of blueberry bloom and model yield results were compared to actual blueberry yield recorded by farmers. This validation method of plotting observed vs. predicted data is simple and commonly used as a first validation assessment (Mayer and Butler, 1993). Weather data for the model-predicted yield were used from the same historical period of yield and were recorded in Fennville, Michigan, a location centered in the area of highest blueberry production in Michigan.

Sensitivity Analysis. The BLUEPOLL model was then subjected to a sensitivity analysis to determine the influence of input parameters on model output values. The model was deemed sensitive to an input parameter if changing that parameter's typical value by 10 percent led to a change in output greater than 10 percent (Jackson et al., 2000).

RESULTS

Stakeholder Focus Group. Response from the blueberry stakeholder focus group (as part of the model validation) was positive and participants were eager for the BLUEPOLL model to be completed and publicly accessible. I found that growers of highbush blueberry are generally concerned with their crop yields from previous years, the predicted weather for the current season of blueberry bloom, and having enough bees to pollinate high densities of blueberry flowers. Decisions pertaining to the stocking rate of managed honey bees are generally made based on what has always been done, or follow the recommended rate of two hives per acre. Growers usually purchase the same amount of managed honey bees each year, but may shift the distribution of hives depending on which fields appear to be healthiest or

have the best history of high crop yield. Some growers currently stock managed bumble bees in their blueberry fields during bloom, but others did not feel that investment to be worthwhile. The most important factors when considering decisions of how many managed bees to purchase were the cost of pollinators, whether or not there were neighboring farms stocked with bees, and the projected price of the crop. Once complete, extension educators believe BLUEPOLL will be helpful in future training sessions with blueberry growers.

Parameter Boundary Testing. Under average weather conditions but without any managed pollinators present, one acre of Bluecrop was predicted to yield 1,986 lbs of blueberry, highlighting the parthenogenetic capacity of this crop and cultivar. At extremely high levels of both honey bees (20 hives per acre) and bumble bees (20 colonies per acre), one acre of Bluecrop was predicted to yield the maximum of 10,612 lbs of blueberry. When examining the effect of extreme weather conditions on predicted blueberry yield, a consistently high temperature of 40 °C throughout bloom yielded 1,669 lbs of blueberry per acre and a consistently low temperature of 8 °C yielded 1,849 lbs per acre. Zero solar flux density led to 1,986 lbs of blueberry per acre while a consistent solar flux density of 3,500 kJ/m² resulted in a yield of 10,336 lbs per acre. Finally, no wind during bloom resulted in a blueberry yield of 4,570 lbs per acre while a consistent wind of 10 m/s throughout bloom resulted in 1,986 lbs per acre.

Observed Yield vs. Predicted Yield. When plotting observed highbush blueberry yield values against BLUEPOLL predicted yield values for one commercial blueberry field in 2008-2011

(Figure 4.2), a positive linear trend was apparent. However, this relationship was not statistically significant ($r^2 = 0.38$, d.f. = 2, P = 0.38). The BLUEPOLL model consistently underpredicted crop yield values.



Figure 4.2. Validation of observed highbush blueberry yield versus BLUEPOLL model predicted blueberry yield for one commercial blueberry field from 2008-2011. The dotted line indicates perfect correlation between observed and predicted yield.

Sensitivity Analysis. Based on the sensitivity analysis, where the average weather conditions were altered to warm weather conditions, the BLUEPOLL model was determined to be sensitive only to changing weather conditions. All other parameter inputs (honey bee hives per acre, bumble bee colonies per acre, blueberry planting row spacing, blueberry planting bush spacing) were not found to significantly influence the output yield values of the BLUEPOLL model in terms of the sensitivity analysis (where an input is considered significant if a 10 percent change in its typical value will produce greater than a 10 percent change in the output).

DISCUSSION

Stakeholder Focus Group. The initial development of the BLUEPOLL model of highbush blueberry pollination has been met with approval and support from both extension experts and blueberry growers from the area of highest blueberry production in Southwest Michigan. As in other regions of blueberry production (Retamales and Hancock, 2012), I encountered great interest in the use of commercial bumble bees for alternative or supplemental pollination services. Blueberry growers are very concerned about achieving high rates of pollination, and are eager to receive managed pollinator stocking recommendations supported by current scientific research. As a result of stakeholder response, this research will be tailored to achieving high rates of pollination under expected future weather conditions, while at the same time avoiding the unnecessary expense of overspending on managed pollinator inputs. *Parameter Boundary Testing.* Results of the validation through parameter boundary testing of the BLUEPOLL model were satisfactory to continue with further experimentation of this system. Because highbush blueberry is capable of parthenocarpic fruit set, a crop yield of 1,986 lbs without any managed pollinator input, under zero solar flux density, or under consistently high wind speeds of 10 m/s is considered realistic. The average yield per acre of blueberry in Michigan was 4,420 lbs in 2012 (USDA, 2013); however, highly successful growers are known to receive up to as much as 12,000 lbs of blueberry per acre (A.K. Kirk, personal observation). This high value of blueberry yield per acre is similar to the maximum output of the BLUEPOLL model when pollinator inputs are set at extremely high levels of 50 units per acre (10,612 lbs) or solar flux density is set to consistently high levels of 3,500 kJ/m² (10,336 lbs), but this high level of production can also be achieved with more realistic levels of pollinator stocking through horticultural practices such as pruning and nutrition that increase the number of flowers per bush and through irrigation that increases the average berry weight.

At consistently high temperatures of 40 $^{\circ}$ C, the BLUEPOLL model output of 1,669 lbs per acre can be better understood when considering that blueberry flower development is dependent upon accumulating growing degree-days. With constant temperatures of 40 $^{\circ}$ C, blueberry flower development may proceed so quickly that pollinators are not able to pollinate flowers before they wilt and in the BLUEPOLL model, honey bees and bumble bees do not forage at this high of an air temperature. Conversely, at consistently low temperatures of 8 $^{\circ}$ C, we would expect the predicted crop yield to be very low, as blueberry plant development does not occur below 7-8 $^{\circ}$ C (Kirk and Isaacs, 2012; Chapter 2). The yield of 1,849 lbs at a constant 8 $^{\circ}$ C was slightly less than the 1,986 lbs yielded without any managed pollinator input.

Observed Yield vs. Predicted Yield. Validation of the BLUEPOLL model by comparing actual blueberry yield per acre values to the values predicted by BLUEPOLL proved difficult to achieve. The real-world information necessary for this analysis would include annual grower records of blueberry cultivar, acreage, bush and row spacing, managed pollinator stocking rate and corresponding crop yield, as well as detailed hourly weather data for the area of interest during the period of blueberry bloom for corresponding years. I was not able to find many blueberry growers who kept such detailed records, and obtained the necessary information from only one grower, for only four years. The resulting relationship between observed values of blueberry crop yield per acre versus BLUEPOLL predicted crop yield was positive, but not significant. The BLUEPOLL model predicted values consistently under predict observed crop yield. While this indicates inaccuracy on the part of BLUEPOLL predictions, it also means that managed pollinator stocking recommendations based on BLUEPOLL simulations will consistently predict below the optimal pollinator input level and therefore growers will not be in danger of overspending through overstocking because of this model imprecision. Further validation of the BLUEPOLL model with detailed real-world input and output values of the parameters mentioned above is needed from farms that maintained detailed pollination and yield data.

Sensitivity Analysis. The results of the sensitivity analysis indicated that the BLUEPOLL model was not highly sensitive to managed pollinator inputs or blueberry bush or row

spacing. These sensitivity results come from examining the change in crop yield when altering the typical input values of managed pollinator inputs (two honey bee hives, zero bumble bee colonies), row spacing (nine feet), or bush spacing (four feet) by 10 percent increments. The sensitivity of model parameters is unique in that results may change depending on the input starting value. For example, the BLUEPOLL model will become less sensitive to increasing levels of managed pollinator inputs because this relationship follows the law of diminishing returns (as more and more managed pollinator inputs are added, lower increases in crop yield are observed). Further investigation into the sensitivity of the BLUEPOLL model will better elucidate the relationship between crop yield output and these input parameters, revealing to what extent the model is sensitive to these parameters at variable levels of input.

The BLUEPOLL model is a first attempt at capturing and demonstrating the most essential components of the system of highbush blueberry pollination and as such, there remains room for improvement upon model components and relationships. Factors such as the age of the highbush blueberry planting and weather effects on plant reproduction would be valuable additions to the model in order to further elucidate the relationships involved in blueberry yield each season. Furthermore, the incorporation of stochasticity into the model would provide users with a range of predicted blueberry crop yield instead of one fixed number. This adjustment would also allow for examination of the effect of blueberry grower risk preferences upon their decision making and how this may change under variable circumstances. In the future, the BLUEPOLL model can be altered to include newly available managed pollinators and used to address issues of honey bee loss or even the

effects of climate change on managed pollination. The results of this research will ensure that farmers are not spending unnecessarily on managed pollination services and will lead to the development of sustainable strategies for crop pollination. Ecological modeling is an iterative process, so while the BLUEPOLL model may not be a final answer to decisions of managed pollination, it is an important first step towards a more thorough understanding of the pollination of highbush blueberry.

CHAPTER 5

Optimizing the Use of Managed Honey Bees and Bumble Bees for Highbush Blueberry using the BLUEPOLL Model

INTRODUCTION

Highbush blueberry (*Vaccinium corymbosum* L.) is an Ericaceous crop native to North America, grown primarily in the countries of Australia, France, Germany, Italy, New Zealand, Poland, Chile and the USA. In the United States, the main areas of production include the Pacific Northwest, New Jersey, and Michigan (Retamales and Hancock, 2012), with Michigan accounting for approximately 26 percent of the total blueberry production in the United States in 2012 (USDA, 2013). This can be equated to a crop yield valued at about \$123 million annually, and as such, blueberry is considered one of the major fruit crops grown in Michigan. With increasing interest and demand from consumers for blueberries, driven in part by the health benefits of blueberry antioxidants (Malin et al., 2011; Seeram, 2012), growers of this crop are constantly seeking methods to optimize management decisions and increase crop yield and profit.

One area of commercial blueberry management in need of improvement surrounds the crucial decisions regarding managed pollination. Evidence from exclusion and selective pollen deposition studies indicate that *V. corymbosum* has some level of fruit set without pollination (pathenocarpy) (Coville, 1910; Eck, 1988; Gough, 1994; MacKenzie, 1997; Dogterom et al., 2000). However, berries that develop through fertilization have better fruit set and more seeds, are larger, and ripen faster than those that develop through parthenocarpy

(Dogterom et al., 2000). Therefore, adequate pollination of blueberry flowers is essential for achieving high blueberry crop yield and quality (MacKenzie, 2009).

As is the case with most pollination-dependent commercial agriculture, managed honey bee hives are commonly rented each spring to provide pollination during highbush blueberry bloom (McGregor, 1976). Although convenient because they are polylectic and their hives are mobile, honey bees may be inefficient pollinators or may not forage on the intended crop (Jay, 1986; Westerkamp, 1991). They also are easily deterred from foraging by inclement weather conditions (Heinrich, 1979; Free, 1993) and incapable of the buzzpollination required to most efficiently release pollen from blueberry flowers (Buchmann, 1983). In light of these shortcomings of honey bees, some blueberry growers have turned to alternative managed pollinators. Currently, the most commonly used alternative is managed bumble bees, which must be purchased as packaged colonies annually through companies such as Biobest or Koppert Biological Systems. These companies sell Bombus impatiens Cresson bumble bees, a species that is native to eastern North America and well-adapted to the buzz pollination required by highbush blueberry flowers. They are also capable of flying under poor weather conditions (Heinrich, 1979), giving them the potential to be successful pollinators in the early spring when blueberries are in bloom. Growers of highbush blueberry are quite attentive to the variable spring weather conditions as they are influential on the foraging activity of managed pollinators (Heinrich, 1979; Burrill and Dietz, 1981; Corbet et al., 1993; Vicens and Bosch, 2000) as well as floral development and speed of blueberry bloom (Kirk and Isaacs, 2012; Chapter 2).

Although both managed honey bees and bumble bees can be found stocked in highbush blueberry fields during bloom, there has been little research into optimal stocking

levels of each. It is recommended that bumble bees are stocked at a rate of two quads (eight colonies) per acre if they are the only managed pollinator used (Retamales and Hancock, 2012). On the other hand, honey bees exhibit cultivar preferences (Brewer and Dobson, 1969; Pritts, 1996) and there are variable levels of dependence on pollen deposition for fruit set and yield, so stocking recommendations range from 0.5 to six hives per acre, depending on the attractiveness of the cultivar of interest (Table 5.1; Pritts and Hancock, 1992; Retamales and Hancock, 2012).

Table 5.1. Recommended honey bee stocking densities for some cultivars of highbush blueberry (Pritts and Hancock, 1992). Cultivars included in this study are in bold.

Cultivar	Honey bee hives (number / acre)
Rubel, Rancocas	0.5
Weymouth, Bluetta, Pemberton, Darrow	1.0
Bluecrop	1.5
Elliott, Coville, Berkeley, Stanley	2.0
Jersey, Earliblue	2.5

It is unclear whether these pollinator stocking recommendations aim for 100 percent pollination of the blueberry flowers or whether they are seeking a stocking strategy to maximize profit, an important point to distinguish when making pollination management decisions. For example, a grower who is seeking 100 percent pollination of his/her blueberry field may need to spend much more on managed pollinator inputs than one who aims for 80 percent pollination (the recommended level for a full blueberry crop) because of diminishing crop yield returns. In other words, to increase pollination from 70 to 80 percent would require less of an increase in pollinator input than an increase of 90 to 100 percent pollination. However, it may still be cost-effective to attempt pollination of the remaining 10 percent if this returns greater value of crop production than the cost of the additional bee hives. Further research into the profitability of managed pollination decisions will allow growers a better understanding of, and more control over, their investments in pollination services.

To better understand the effects of variable weather, pollinator stocking strategies, and prices of both pollinators and blueberries on the yield and economic returns in this system, the BLUEPOLL model of highbush blueberry pollination was developed (Chapter 4). This model can be run for any of five common cultivars of highbush blueberry including Bluecrop, Jersey, Duke, Elliott or Liberty with managed pollinator inputs of honey bees, bumble bees, or a combination of the two. BLUEPOLL was also developed to be run under cool, average, or warm weather conditions. The crop yield outputs from running the BLUEPOLL model can be used in combination with basic economic principles to aid in farm management decision-making related to managed pollination. For instance, the profitmaximizing input level of managed pollinators can be determined by comparing the marginal input cost (MIC, cost of purchasing an additional unit of input, i.e. additional bees) with the marginal value product (MVP, extra income from blueberry yield received from that additional unit of input) (Kay et al., 1994). When the MVP is less than or equal to the MIC,

it is no longer economically worthwhile to purchase additional units of that input. As applied to the blueberry system, when the value of the additional yield realized by increasing the level of pollinator investment at field is worth the same or less than the cost of the additional pollinators, growers should no longer invest in additional bees.

A similar decision-making method is that of the least-cost input combination when considering two substitutable inputs (such as honey bees and bumble bees). For this decision, the input substitution ratio (amount of input replaced/amount of input added) must be compared to the input price ratio (price of input being added/price of input being replaced). The least-cost input combination is then determined by selecting the combination where the marginal rate of input substitution is equal to the input price ratio (Kay et al., 1994). Because honey bees and bumble bees have variable pollinating efficiencies under different weather conditions, the marginal rate of input substitution for these two managed pollinators will be different depending on the expected weather forecast for the period of blueberry bloom. Therefore, this relationship will change depending on the predicted weather during blueberry bloom, as well as the decision-maker's desired output level (blueberry crop yield). Understandably, blueberry growers will generally need to stock their fields with a higher level of managed pollinators if seeking to achieve 100 percent crop yield rather than 80 percent crop yield.

Although previous validation of the BLUEPOLL model indicated that resulting blueberry crop yield predictions are consistently lower than real-world crop yield values (Chapter 4), experimentation with this model is still valuable to reveal characteristics of the system relationships within the blueberry pollination system. The goal of this research was to examine the use of managed honey bees and bumble bees for pollination services to one acre

of highbush blueberry under a variety of weather conditions through the use of the previously developed BLUEPOLL model of highbush blueberry pollination.

MATERIALS AND METHODS

Varying stocking strategies of managed honey bees and bumble bees were tested under three different weather situations by using the previously developed BLUEPOLL model of highbush blueberry pollination (Chapter 4). Weather data were chosen from the typical period of blueberry bloom in 2001, from a weather station in South Haven, Michigan. The cool weather conditions were characterized by low air temperature and solar radiation, while the warm weather conditions were characterized by consistently high temperatures and solar radiation. A detailed discussion of weather selection is included in Chapter 4. The level of yield predicted by the model was determined for each level of stocking by increasing the level of honey bees and bumble bees in 0.25 hive or colony increments until yield reached 100 percent. This was done for each of the three weather conditions described previously: cool, average, and warm.

The profit-maximizing input level of managed honey bees was determined by increasing the stocking density of hives by increments of 0.25 hives per acre to determine the input level where the marginal value product is equal to or greater than the marginal input cost. The same decision method was used to determine the profit-maximizing input level of managed bumble bees, again using increments of 0.25 colonies per acre. For both honey bees and bumble bees, the profit-maximizing input level was determined for a range of managed pollinator prices. The prices used for renting honey bee hives ranged from \$40 per hive to

\$100 per hive, while the prices used for purchasing bumble bee colonies ranged from \$50 per colony to \$80 per colony.

The profit-maximizing input level was also determined for stocking either honey bees or bumble bees in each of five common highbush blueberry cultivars: Bluecrop, Jersey, Duke, Elliott and Liberty, using the cultivar-specific parameters developed in Chapter 2. The effects of different weather conditions during bloom on the profit-maximizing input level were also compared for both honey bees and bumble bees for the Bluecrop cultivar.

The BLUEPOLL model was then used to determine the least-cost input combination for stocking one acre of highbush blueberry with both managed honey bees and managed bumble bees. Fruit set of 80 percent of the available flowers in a blueberry field is considered to yield a full blueberry crop, however highbush blueberry is capable of 100 percent fruit set with adequate pollination (Pritts and Hancock, 1992). For this reason, the least-cost input combination of managed honey bees and bumble bees was determined and compared for output levels of 80 percent and 100 percent potential blueberry yield for one acre.

Finally, the effects of different weather conditions during bloom on the least-cost input combination of both honey bees and bumble bees were examined by running the model under cool, average and warm weather conditions.

RESULTS

The minimum predicted crop yield of highbush blueberry for the five cultivars with zero pollinator input ranged from 1,173 lbs per acre for Liberty to 3,402 lbs per acre for Jersey. The maximum predicted crop yield of highbush blueberry for the five cultivars ranged from

6,703 lbs per acre for Liberty to 15,158 lbs per acre for Jersey. To achieve this maximum predicted crop yield, stocking levels of managed honey bee hives ranged from three hives per acre for Liberty to eight hives per acre for Jersey. Maximum predicted crop yield required a range of 1.25 bumble bee colonies per acre for Liberty to 4.00 bumble bee colonies per acre for Jersey. When seeking maximum predicted yield under the three different weather conditions, the stocking levels required of honey bees ranged from three hives per acre to ten hives per acre. For bumble bees, the required stocking levels under different weather conditions to achieve maximum predicted crop yield ranged from 1.25 colonies per acre to 7.25 colonies per acre.

Variable weather conditions had a minimal effect on the production function of Bluecrop blueberry yield when only stocking managed honey bee hives (Figure 5.1). Interestingly, cool and warm weather conditions both reduced the rate of predicted yield increase with respect to honey bee stocking level, as compared to that seen under average conditions.



Figure 5.1. Highbush blueberry yield (cv. Bluecrop) per acre predicted by the BLUEPOLL model when stocking increasing levels of managed honey bee hives, under three different weather conditions.



Figure 5.2. Highbush blueberry yield (cv. Bluecrop) per acre predicted by the BLUEPOLL model when stocking increasing levels of managed bumble bee colonies under three different weather conditions (four colonies = one quad).

The profit-maximizing input level of honey bees ranged from 2.75 hives per acre to 7.5 hives per acre depending on the cultivar of interest, while the profit-maximizing input level of bumble bees ranged from 1.25 colonies per acre to 4 colonies per acre (Table 5.2).

Table 5.2. Profit-maximizing input level of honey bees and bumble bees for one acre highbush blueberry under average predicted weather conditions. Prices reflect the current ranges for honey bee hives and bumble bee colonies.

	Honey Bee Hives		Bumble Bee Colonies	
Cultivar	\$40 per hive	\$100 per hive	\$50 per colony	\$80 per colony
Bluecrop	4.50	4.25	2.50	2.25
Jersey	7.50	7.25	4.00	4.00
Duke	3.25	3.25	1.75	1.75
Elliott	3.25	3.25	2.00	2.00
Liberty	2.75	2.75	1.25	1.25

Increasing the price of rented honey bees from \$40 per hive to \$100 per hive only changed the profit-maximizing input level by one quarter of a honey bee hive per acre for Bluecrop and Jersey, while the profit-maximizing input level remained the same for Duke, Elliott, and Liberty. This relationship between price change of honey bees and change in the profitmaximizing input level in Bluecrop can be observed in Table 5.3. Given the high degree of pollinator investment needed before it becomes unprofitable to add more colonies, it is instructive to explore how much the bees would need to cost before they would have a large impact on the predicted stocking density. In order to reduce the profit-maximizing input level of honey bees from 4.5 hives per acre to 3.5 hives per acre in Bluecrop, the cost of honey bee hives would have to rise from \$40 per hive to \$526 per hive (when using increments of one honey bee hive per acre) or \$1,632 per hive (when using increments of one quarter honey bee hive per acre).

Increasing the price of purchased bumble bees from \$50 per colony to \$80 per colony only changed the profit-maximizing input level by one quarter of a bumble bee colony per acre for Bluecrop, while remaining the same for all other cultivars.

Input	Blueberry	Total Value	Marginal Value	Marginal Input Cost	
Level	Yield (lbs)	Product (\$)	Product (MVP) (\$)	(MIC) (\$)	
Hives		Crop volvo	Crop value increase	Price of honey bee inpu	
per acre		Crop value	per added 0.25 hive (\$40 or \$100 pe		00 per hive)
1.00	5455	10910	1400	10	25
1.25	6204	12408	1498	10	25
1.50	6909	13818	1410	10	23
1.75	7573	15146	1328	10	25
2.00	8178	16356	1210	10	25
2.25	8688	17376	1020	10	25
2.50	9143	18286	910	10	25
2.75	9540	19080	794	10	25
3.00	9871	19742	662	10	25
3.25	10144	20288	546	10	25
3.50	10348	20696	408	10	25
3.75	10484	20968	272	10	25
4.00	10562	21124	156	10	25
4.25	10601	21202	78	10	25
4.50	10/11	21222	20	10	25
4.50	10611	21222	2	10	25
4.75	10612	21224			

Table 5.3. Selection of the profit-maximizing input level of honey bees for Bluecrophighbush blueberry production (blueberry priced at \$2 per lb) when honey bee rental costs\$40 per hive (thin box) vs. \$100 per hive (thick box).

The profit-maximizing input level was sensitive to weather conditions during bloom with only honey bee investment to maximize profit ranging from 5.5 hives per acre under cool weather conditions to 6.25 hives per acre under warm weather conditions. The production function of Bluecrop blueberry yield when only stocking managed bumble bees was observably different under the three weather conditions (Figure 5.2). Blueberry crop yield reached 100 percent at the lowest level input of managed bumble bees under warm weather conditions, while requiring the highest level input of managed bumble bees ranged from 2.25 colonies per acre under warm weather conditions to 4.00 colonies per acre under cool weather conditions (Table 5.4).

The cost per acre of stocking only one type of managed pollinator at the profitmaximizing input level ranged from \$146.25 to \$312.50, with the input cost of bumble bees always less than that of honey bees (Table 5.4). The profit-maximizing input level for honey bee hives was lowest under average weather conditions while the profit-maximizing input level of bumble bee colonies decreased from cool to average weather, and again from average to warm weather conditions. **Table 5.4.** Input level of bee units per acre and cost comparison for the profit-maximizing input level of one acre highbush blueberries, c.v. Bluecrop, under cool, average, or warm weather conditions when using only managed honey bees or managed bumble bees. Honey bee hives are assumed to cost \$50 while bumble bee colonies cost \$65.

	Honey	y Bees	Bumble Bees		
Weather	Input Level	Input Cost	Input Level	Input Cost	
Cool	5.25	\$262.5	4.00	\$260.00	
Average	4.50	\$225.0	2.50	\$162.50	
Warm	6.25	\$312.5	2.25	\$146.25	

The least-cost input combination of honey bees and bumble bees was different depending on the weather conditions and desired level of crop yield (Table 5.5). A combination of managed honey bees and bumble bees was only the most profitable choice when seeking 80 percent crop yield under average weather conditions. Otherwise, stocking with only honey bees or bumble bees was the most profitable managed pollinator stocking decision. These combinations ranged from zero honey bee hives per acre and 4.75 bumble bee colonies per acre under cool weather conditions when seeking 100 percent crop yield to 2.75 honey bee hives per acre and zero bumble bee colonies per acre under cool weather conditions of managed pollinator under three different weather conditions and two different goal crop yields ranged in cost from \$81.25 to \$308.75 (Table 5.5).

Table 5.5. Least-cost input combination of honey bees and bumble bees for one acre of highbush blueberries, c.v. Bluecrop, under three different weather conditions and goals of 80 and 100 percent crop yield. Honey bee hives are assumed to cost \$50 while bumble bee colonies cost \$65.

	80% Yield			100% Yield		
Weather	Honey Bee	Bumble Bee	Total	Honey Bee	Bumble Bee	Total
	Hives	Colonies	Cost	Hives	Colonies	Cost
Cool	2.75	0.00	\$137.5	0	4.75	\$308.75
Average	0.25	1.25	\$93.75	0	2.50	\$162.50
Warm	0.00	1.25	\$81.25	0	2.25	\$146.25

DISCUSSION

This study provides a thorough view of the relationship between managed pollinator stocking density, weather, and blueberry crop yield based on the outputs of a deterministic model of blueberry pollination. The range of predicted crop yield values from the BLUEPOLL model closely resembled those typically received from blueberry plantings in southwest Michigan (USDA, 2013), with a minimum yield of about 1,000 lbs per acre and maximum yield of about 15,000 lbs per acre. The production functions representing increasing crop yields as a result of increasing pollinator inputs were expected as it is well known that pollination increases berry size and crop yield (Meader and Darrow, 1947; McGregor, 1976; Vander Kloet, 1984; Luby et al., 1991, MacKenzie, 1997), and these outputs were developed based on measurements of blueberry pollination components (Chapter 2). These production

functions also clearly show diminishing crop yield returns when incrementally increasing the input level of managed pollinators while holding levels of all other inputs constant. The law of diminishing marginal returns is a well known economic concept relating to the production process where at some point, adding more of an input will, at some point, lead to lower marginal returns (Kay et al. 1994).

The optimal levels of managed pollinator stocking predicted by the BLUEPOLL model based on the profit-maximizing input level are considerably different than those provided by Pritts and Hancock (1992), but more in line with those of Retamales and Hancock (2012). The BLUEPOLL model predictions for the profit-maximizing input level of only managed honey bees ranged from 2.75 to 7.5 hives per acre, all of which are higher than the previously recommended 0.5 to 2.5 hives per acre (Table 5.5). It is important to take into account the age of the blueberry planting in question when considering the recommended managed pollinator stocking levels, particularly for Jersey. For most plantings of Jersey blueberry in Michigan and certainly for those that experimental data were taken from during the development of BLUEPOLL, the bushes are much older and larger than those in plantings of other common cultivars (A.K. Kirk, personal observation). Larger and well maintained bushes of any cultivar, or even more recently developed cultivars that have a higher density of flowers, will require higher numbers of managed pollinators to visit the flowers before they wilt.

While few formal recommendations exist for stocking managed bumble bees in blueberry, the profit-maximizing input levels predicted by BLUEPOLL range from 1.25 to 4 colonies per acre under all cultivar and weather combinations. Desjardins and de Oliveira (2006) recommended 688 bumble bees (*B. impatiens*) per hectare for the optimal pollination
of lowbush blueberry. When this number is translated to managed bumble bee colonies of 150 workers, it would be equivalent to approximately 1.86 bumble bee colonies per acre. This is consistent with the range of BLUEPOLL recommendations for bumble bees, although in the lower end of that range. Differences between the highbush and lowbush blueberry systems (MacKenzie, 2009) may account for BLUEPOLL recommended stocking levels of bumble bees ranging up to four colonies per acre.

An unexpected result of this research was that when examining the profit-maximizing input level of honey bees and bumble bees at each end of their respective price ranges (\$50-\$100 for honey bees, \$60-\$80 for bumble bees), the recommended stocking levels were quite similar and often equal. While often the case when only using managed honey bees, this was even more apparent when only using bumble bees. When comparing the marginal input cost (MIC) at an increase of 0.25 hives or colonies per acre, the resulting marginal value product (MVP) is almost always of greater value than the corresponding input cost, highlighting the benefit of pollination to growers of high value crops such as blueberry. Only when the highbush blueberry production function approaches 100 percent maximum yield do the MVPs become close to the \$12.5-\$25 MICs (the cost of one quarter of a honey bee hive or bumble bee colony). Often, there is only one increment of pollinator input where the MVP is less than the MIC before blueberry yield is 100 percent. This relationship generally held true whether blueberry value was \$1 per lb or \$2.50 per lb, again because MVPs are so high. This insensitivity of pollination benefit to the price of blueberries suggests that growers should not be concerned about the expected cost of the crop when making pollinator investment decisions.

The profit-maximizing input level of honey bees was similarly insensitive to the price of managed honey bee hives. In order to achieve a more significant reduction in the profitmaximizing input level of honey bees (when blueberries were valued at \$2 per lb), it was necessary to raise the price of honey bee hives to \$596-\$1,632, depending on the increment of increased honey bee hives per acre examined. These results suggest that blueberry growers should also not be highly concerned about the cost of managed honey bees when making pollinator investment decisions as the price of managed honey bee hives in Michigan is currently around \$50 per hive (A.K. Kirk, personal observation).

Different weather conditions had contrasting effects on the profit-maximizing input level for stocking only honey bees and for stocking only bumble bees. The profit-maximizing input level of bumble bee colonies increased with declining suitability of weather conditions, as would be expected if foraging activity were negatively affected by cool weather conditions. This was not the case, however, with only stocking managed honey bees where the profit-maximizing input level was greatest under average weather conditions, then declined with either cool or warm weather conditions. These results could be attributed to lower honey bee activity under cool weather conditions which has been previously demonstrated in highbush blueberry (Tuell and Isaacs, 2010). Under warm weather conditions, low honey bee efficiency in pollinating blueberry flowers could negatively affect fruit set and crop yield as blueberry bloom proceeds as a much faster rate than when the weather is cooler. This results in the flowers opening in greater numbers than the stocked bees can visit in the time available before they age and wilt. Under either situation, more honey bees would need to be stocked to account for low activity or efficiency.

A managed pollinator stocking strategy comprised of both honey bees and bumble bees was the most profitable only when aiming for 80 percent crop yield under average weather conditions. Stocking only managed honey bees was the most profitable choice with a goal of 80 percent crop yield under cool weather conditions. Stocking only managed bumble bees was the most profitable under all other tested situations of crop yield goals and weather conditions. From these results, it appears that the higher pollination efficiency of bumble bees is more important under warm weather conditions while the higher numbers of honey bees is more important for pollination under cool weather conditions when foraging activity may be decreased. This finding does not agree with previous assumptions of higher bumble bee foraging activity under cool weather conditions, indicating that differences in flight activity as a function of weather conditions between honey bees and bumble bees may not be as influential as commonly thought, and supporting the conclusions of Tuell and Isaacs (2010). For all combinations of managed honey bees and bumble bees, the cost of managed pollinator inputs per acre increased under cool weather conditions, again indicating that growers should invest more in managed pollination services in years when anticipating cool weather in order to ensure consistent crop yields. Uncertainty surrounding the future weather conditions during blueberry bloom is cited by some growers as the reason that they stock pollinators at higher densities than typical (A. Kirk, personal observation), in order to avoid crop yield loss due to lack of pollination. These behaviors are consistent with the predictions of the BLUEPOLL model, suggesting that this will be a useful tool for blueberry growers wishing to examine the potential consequences of poor weather conditions on the productivity of their fields.

A final point of interest for blueberry growers wishing to combine honey bees and bumble bees as managed pollinator inputs is related to the targeted output level of crop yield. For this research, least-cost input pollinator combinations were determined under cool, average, and warm weather conditions for goals of 80 and 100 percent potential crop yield. In reality, a goal of 100 percent crop yield is often impractical because of the relationship of diminishing returns, where returns on investment of input costs decline at incrementally higher levels of output. It is generally the case for farm managers that an output level less than 100 percent will be the most profitable goal when making decisions regarding input level.

The results of the BLUEPOLL model provide a strong argument for further experimentation with using managed bumble bees for pollination services in highbush blueberry, and investigation of the predicted best combined strategies. As previous validation of the BLUEPOLL model revealed that it consistently under-predicts highbush blueberry crop yield (Chapter 4), there is little danger of a blueberry grower overspending on managed pollinator inputs by following the above recommendations. Growers should understand that these recommendations are conservative estimates. In addition, another consideration supporting the use of managed bumble bees is the prospect of managed honey bee prices rising upwards of \$200 per hive as was the case during almond bloom in California in February of 2013 (Wines, 2013).

CHAPTER 6

Future directions in modeling crop pollination

Highbush blueberry (Vaccinium corymbosum L.) is one of the leading fruit crops produced in Michigan (USDA, 2013) and as such, growers of this commodity are constantly looking for ways to improve upon production. One of the most important inputs to production of highbush blueberry is managed pollinators, as their foraging activity and subsequent pollination of blueberry flowers is well known to increase fruit set and quality (Marucci, 1966; Vander Kloet, 1984; Dogterom et al., 2000). Larger blueberries can be sold fresh and at prices sometimes twice those received for berries sold for frozen processing (USDA, 2013). Although blueberry growers are aware of the benefits of managed pollination through the renting of honey bee (Apis mellifera L.) hives, recommendations for the stocking level of honey bee hives per acre are out of date and are based on rules of thumb rather than comparative experimental research. Therefore, the goal of my research was to investigate the pollination of highbush blueberry by managed honey bees, and also to examine pollination of highbush blueberry by an alternative, commercially available managed pollinator, bumble bees (Bombus impatiens Cresson). I also sought to examine the effect of variable weather conditions on the foraging and pollination activity of these two pollinators, as well as the resulting crop yield.

To examine highbush blueberry pollination, it was first necessary to gain a better understanding of the floral phenology underlying pollination. Base temperatures and bloom phenology curves were characterized for five cultivars of highbush blueberry common to Michigan growers: Bluecrop, Jersey, Duke, Elliott and Liberty. The results of the base

temperature experiments established a range of base temperatures of approximately 7-8 $^{\circ}$ C and clarified a bloom sequence for the five cultivars of Liberty, Bluecrop, Duke, Jersey and then Elliott, according to increasing accumulated growing degree-days (Chapter 2). These results should be useful to growers wishing to plant blueberry cultivars of overlapping bloom in close proximity, or for determining which fields are in need of managed pollinators earliest in the season. In the future, base temperatures and bloom phenology of newly developed cultivars can be compared to the five characterized by this study.

Flower viability was also examined for the five cultivars as well as for up to five days after flower opening, to determine the effect of flower age on viability for fruit set after pollination. These results demonstrate decreasing flower viability with increasing floral age, and therefore a need for rapid pollination of flowers, ideally within five days of flower opening. My research has focused primarily on the pollinator side of this interaction, but future research should investigate the effect of temperature on pollen tube growth and subsequent fertilization to better predict the probability of fruit set under different weather conditions. Additionally, understanding how flower viability varies with degree days, rather than days, would allow opportunities to better predict pollination as a function of weather conditions.

The foraging activity of all managed pollinators must also be better understood, especially when considering the development of new alternative managed pollinators. The results of my research supported the conclusions of previous studies that wind speed and percent total bloom are influential factors on pollinator foraging activity (Szabo, 1980; DeGrandi-Hoffman, 1987; Vicens and Bosch, 2000; Chapter 3). However, a more detailed investigation is needed to better examine other influential weather factors such as air

temperature, solar flux density, relative humidity, and others to more firmly characterize their effects on pollinator foraging activity. These studies should also include other managed pollinators, such as the alfalfa leafcutter bee and species of managed mason bees (*Osmia* spp.), as well as further investigation into the variable pollination efficiencies of each managed pollinator. Knowledge such as this for each available managed pollinator will allow for more informed decisions by growers of pollination-dependent crops.

The BLUEPOLL model was developed as a means to experiment by simulation with variable stocking levels of two managed pollinators of highbush blueberry under three different weather conditions. This model has been met with enthusiasm by growers and extension experts in highbush blueberry (Chapter 4), however, it can be improved upon in the future in a number of ways. First, simple factors such as age of blueberry bushes and management practices such as pruning should be incorporated into the model for better predictions of total blueberry flowers available per hectare. Crop yield is directly related to the number of flowers available for pollination and fruit set, so increased accuracy of these values for multiple cultivars is crucial.

Another important addition to the BLUEPOLL model would be the incorporation of stochasticity into each relationship. This would allow for output values to be represented as a range of potential crop yields, rather than one predicted value for each input combination. This alteration to the BLUEPOLL model would open up the decision making process of the stocking of managed pollinators to include consideration of the risk preferences of blueberry growers (Hardaker et al., 1997). A decision tree could be constructed to illustrate both the choices available (managed pollinator input) as well as the uncertainty involved in the decision (future weather conditions and/or range of predicted crop yield). With such

information readily available, blueberry growers can make more informed decisions based on their risk preferences.

Finally, further validation of the BLUEPOLL model would be useful to ensure that its crop yield predictions and resulting managed pollinator stocking recommendations are accurate representations of real-world occurrences. During the initial development of BLUEPOLL, it was found to be challenging to acquire the necessary data from blueberry growers to thoroughly validate model predictions by comparison to actual, historical crop yield. One way to avoid this problem in the future would be to design field studies specifically to collect the data needed for validation. These experiments would involve replications of highbush blueberry fields stocked with different combinations of managed honey bee hives and bumble bee colonies, and monitoring on-site weather conditions as well as crop yield. If repeated over multiple growing seasons, these studies would provide variable spring weather conditions that could be used along with recorded managed pollinator stocking densities and planting measurements as inputs to the BLUEPOLL model. Then, predicted crop yield could be judged against actual recorded crop yield for these years as a more rigorous observed vs. predicted crop yield comparison.

Beyond improvements in the structure and components of the BLUEPOLL model, it is important to make this decision-making tool available to the general public. I plan to publish the BLUEPOLL model online as a feature of the Michigan State University Blueberries website (www.blueberries.msu.edu), so that blueberry growers and extension educators across the country will have access to the information and results of my research. This website will include background information on the status of highbush blueberry pollination, specific highbush blueberry research results, and an overview of the development

of the BLUEPOLL model. Information regarding the interpretation of BLUEPOLL output values and subsequent decision-making will also be included.

The BLUEPOLL model can also serve as an example for the development of other models of crop pollination to aid in improving the efficiency of pollinator-dependent crop production. Regardless of whether or not we are facing a pollinator crisis with the potential collapse of managed honey bees, I believe that it is in everyone's best interest to focus on the wise and efficient use of our natural resources. Since the BLUEPOLL model of highbush blueberry pollination incorporates real-world weather conditions, it also has the potential to be adapted to explore questions related to global climate change predictions, especially the implications of earlier spring warming (Wolfe et al., 2005). This, in turn, could be combined with predicted blueberry and managed pollinator prices to examine the potential conditions of highbush blueberry pollination in a world with earlier and warmer springs, scarce managed honey bees, and greater demand for highly nutritious, antioxidant rich crops such as blueberry. APPENDICES

APPENDIX A

BLUEPOLL Model Code

 $Accumulating_GDD(t) = Accumulating_GDD(t - dt) + (Hourly_GDD_Converter +$

GDD_Start) * dt

INIT Accumulating_GDD = 0

INFLOWS:

Hourly_GDD__Converter = (MAX(0,(((Air_Temp-

Blueberry_Base_Temperature)+(PrevTemp-Blueberry_Base_Temperature))/2)/24))

GDD_Start = GDDStartValue*Time__Converter

Accumulating_GDD_2(t) = Accumulating_GDD_2(t - dt) + (Hourly_GDD_Converter_2 + $(Hourly_GDD_Converter_2 + (Hourly_GDD_Converter_2))$

Noname_5) * dt

INIT Accumulating_GDD_2 = 0

INFLOWS:

Hourly_GDD__Converter_2 = MAX(0,(((Air_Temp_2-

Blueberry_Base_Temperature_2)+(PrevTemp_2-Blueberry_Base_Temperature_2))/2)/24)

Noname_5 = GDDStart_2*Time_Converter_2

 $Accumulating_GDD_3(t) = Accumulating_GDD_3(t - dt) + (Hourly_GDD_Converter_3 + (Hourly_GDD_2(t) - dt) + (Hourly_GD_2(t) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) + (Hourly_2(t) - dt) + (Hourly_2(t) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) + (Hourly_2(t) - dt) +$

Noname_4) * dt

INIT Accumulating_GDD_3 = 0

INFLOWS:

Hourly_GDD__Converter_3 = (MAX(0,(((Air_Temp_3-

Blueberry_Base_Temperature_3)+(PrevTemp_3-

Blueberry_Base_Temperature_3))/2)/24))

Noname_4 = GDDStart_3*Time_Converter_3

 $Average_Blueberry_Yield(t) = Average_Blueberry_Yield(t - dt) + (Harvest) * dt$

INIT Average_Blueberry_Yield = 0

INFLOWS:

Harvest = PULSE(Yield, 24, 24)

 $BB_on_Bberry(t) = BB_on_Bberry(t - dt) + (Active_BB - BB_Daily_Return) * dt$

INIT BB_on_Bberry = 0

INFLOWS:

Active_BB = (BB_per_Unit*BB_Units_Purchased/4)*

(IF(Air_Temp<8)THEN(0)ELSE(IF(Air_Temp<35)THEN(-

0.0194*(Air_Temp^2)+0.9304*(Air_Temp)-8.905)ELSE (0)))*

(IF(Solar_Radiation<10)THEN(0)ELSE(-

0.0000006*(Solar_Radiation^2)+0.00196*(Solar_Radiation)+0.27))*

(IF(Wind_Speed<5.5)THEN(-0.38*(Wind_Speed)+2.1)ELSE(0))*

(0.0248*((Total_Open_Flowers/Total_Potential_Flowers)*100)+0.5698)

OUTFLOWS:

BB_Daily_Return = PULSE(BB_on_Bberry, 24, 24)

 $BB_on_Bberry_2(t) = BB_on_Bberry_2(t - dt) + (Active_BB_2 - BB_Daily_Return_2) * dt$

INIT BB_on_Bberry_2 = 0

INFLOWS:

Active_BB_2 = (BB_per_Unit*BB_Units_Purchased/4)*

```
(IF(Air_Temp_2<8)THEN(0)ELSE(IF(Air_Temp_2<35)THEN(-
```

0.0194*(Air_Temp_2^2)+0.9304*(Air_Temp_2)-8.905)ELSE (0)))*

(IF(Solar_Radiation_2<45)THEN(0)ELSE(-

```
0.0000006*(Solar_Radiation_2^2)+0.00196*(Solar_Radiation_2)+0.27))*
```

(IF(Wind_Speed_2<4)THEN(-0.38*(Wind_Speed_2)+2.1)ELSE(0))*

(0.0248*((Total_Open_Flowers_2/Total_Potential_Flowers_2)*100)+0.5698)

OUTFLOWS:

BB_Daily_Return_2 = PULSE(BB_on_Bberry_2,24,24)

 $BB_on_Bberry_3(t) = BB_on_Bberry_3(t - dt) + (Active_BB_3 - BB_Daily_Return_3) * dt$

INIT BB_on_Bberry_3 = 0

INFLOWS:

Active_BB_3 = (BB_per_Unit*BB_Units_Purchased/4)*

(IF(Air_Temp_3<8)THEN(0)ELSE(IF(Air_Temp_3<35)THEN(-

0.0194*(Air_Temp_3^2)+0.9304*(Air_Temp_3)-8.905)ELSE (0)))*

(IF(Solar_Radiation_3<45)THEN(0)ELSE(-

0.0000006*(Solar_Radiation_3^2)+0.00196*(Solar_Radiation_3)+0.27))*

(IF(Wind_Speed_3<4)THEN(-0.38*(Wind_Speed_3)+2.1)ELSE(0))*

(0.0248*((Total_Open_Flowers_3/Total_Potential_Flowers_3)*100)+0.5698)

OUTFLOWS:

BB_Daily_Return_3 = PULSE(BB_on_Bberry_3,24,24)

 $Flowers_Day_0(t) = Flowers_Day_0(t - dt) + (Flower_Opening_per_GDD - Pollinated_0$

- Age_1) * dt

INIT Flowers_Day_0 = 0

INFLOWS:

```
Flower_Opening__per_GDD = ((ABS(
```

(IF(Bluecrop=1)THEN((Total_Potential_Flowers)*((0.0326+(4*0.1786)*exp(-

((Accumulating_GDD-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD-

277.3)/24.0643)))^2)))ELSE

(IF(Jersey=1)THEN((Total_Potential__Flowers)*((0.0351+(4*0.2187)*exp(-

((Accumulating_GDD-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD-

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers)*((0.0478+(4*0.2108)*exp(-

((Accumulating_GDD-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD-

320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential_Flowers)*((0.0263+(4*0.1653)*exp(-

((Accumulating_GDD-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD-

266.9)/27.5326)))^2)))ELSE(0)))))-

(DELAY((

(IF(Bluecrop=1)THEN((Total_Potential_Flowers)*((0.0326+(4*0.1786)*exp(-

((Accumulating_GDD-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD-

277.3)/24.0643)))^2)))ELSE

```
(IF(Jersey=1)THEN((Total_Potential__Flowers)*((0.0351+(4*0.2187)*exp(-
```

```
((Accumulating_GDD-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD-
```

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers)*((0.0478+(4*0.2108)*exp(-

((Accumulating_GDD-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD-

320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential__Flowers)*((0.0263+(4*0.1653)*exp(-

((Accumulating_GDD-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD-

266.9)/27.5326)))^2)))ELSE(0)))))),1,0))))

OUTFLOWS:

Pollinated_0 =

```
PULSE((Combined_Pollinator_Activity*(Flowers_Day_0/Total_Open_Flowers)*0.744
```

7),24,24)

Age_1 = PULSE((Flowers_Day_0-Pollinated_0),24,24)

 $Flowers_Day_1(t) = Flowers_Day_1(t - dt) + (Age_1 - Pollinated_1 - Age_2) * dt$

INIT Flowers_Day_1 = 0

INFLOWS:

Age_1 = PULSE((Flowers_Day_0-Pollinated_0),24,24)

OUTFLOWS:

 $Pollinated_1 =$

PULSE((Combined_Pollinator_Activity*(Flowers_Day_1/Total_Open_Flowers)*.7496

),24,24)

Age_2 = PULSE((Flowers_Day_1-Pollinated_1),24,24)

 $Flowers_Day_10(t) = Flowers_Day_10(t - dt) + (Age_9 - Pollinated_10 - Age_10) * dt$

INIT Flowers_Day_10 = 0

INFLOWS:

Age_9 = PULSE((Flowers_Day_9-Pollinated_9),24,24)

OUTFLOWS:

 $Pollinated_{10} =$

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_10/Total_Open_Flowers_2)*

.3837),24,24)

 $Age_{10} = PULSE((Flowers_Day_{10}-Pollinated_{10}), 24, 24)$

 $Flowers_Day_11(t) = Flowers_Day_11(t - dt) + (Age_10 - Pollinated_11 - Wilt_2) * dt$

INIT Flowers_Day_11 = 0

INFLOWS:

Age_10 = PULSE((Flowers_Day_10-Pollinated_10),24,24)

OUTFLOWS:

Pollinated_11 = 1

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_11/Total_Open_Flowers_2)*

.1672),24,24)

Wilt_2 = PULSE((Flowers_Day_11-Pollinated_11),24,24)

 $Flowers_Day_12(t) = Flowers_Day_12(t - dt) + (Flower_Opening_per_GDD_3 - GDD_3 - GDD_3)$

```
Pollinated_12 - Age_11) * dt
```

INIT Flowers_Day_12 = 0

INFLOWS:

Flower_Opening__per_GDD_3 = (ABS(

(IF(Bluecrop=1)THEN((Total_Potential__Flowers_3)*((0.0326+(4*0.1786)*exp(-

((Accumulating_GDD_3-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD_3-

277.3)/24.0643)))^2)))ELSE

(IF(Jersey=1)THEN((Total_Potential__Flowers_3)*((0.0351+(4*0.2187)*exp(-

((Accumulating_GDD_3-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD_3-

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers_3)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD_3-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD_3-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers_3)*((0.0478+(4*0.2108)*exp(-

((Accumulating_GDD_3-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD_3-

320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential__Flowers_3)*((0.0263+(4*0.1653)*exp(-

((Accumulating_GDD_3-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD_3-

266.9)/27.5326)))^2)))ELSE(0)))))-

(DELAY((

```
(IF(Bluecrop=1)THEN((Total_Potential_Flowers_3)*((0.0326+(4*0.1786)*exp(-
```

((Accumulating_GDD_3-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD_3-

277.3)/24.0643)))^2)))ELSE

(IF(Jersey=1)THEN((Total_Potential__Flowers_3)*((0.0351+(4*0.2187)*exp(-

((Accumulating_GDD_3-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD_3-

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers_3)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD_3-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD_3-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers_3)*((0.0478+(4*0.2108)*exp(-

((Accumulating_GDD_3-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD_3-

320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential__Flowers_3)*((0.0263+(4*0.1653)*exp(-

((Accumulating_GDD_3-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD_3-

266.9)/27.5326)))^2)))ELSE(0)))))),1,0))))

OUTFLOWS:

Pollinated_12 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_12/Total_Open_Flowers_3)*

0.7447),24,24)

Age_11 = PULSE((Flowers_Day_12-Pollinated_12),24,24)

 $Flowers_Day_13(t) = Flowers_Day_13(t - dt) + (Age_{11} - Pollinated_{13} - Age_{12}) * dt$

INIT Flowers_Day_13 = 0

Age_11 = PULSE((Flowers_Day_12-Pollinated_12),24,24)

OUTFLOWS:

Pollinated_13 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_13/Total_Open_Flowers_3)*

.7496),24,24)

Age_12 = PULSE((Flowers_Day_13-Pollinated_13),24,24)

Flowers_Day_14(t) = Flowers_Day_14(t - dt) + $(Age_12 - Pollinated_14 - Age_13) * dt$

INIT Flowers_Day_14 = 0

INFLOWS:

 $Age_{12} = PULSE((Flowers_Day_{13}-Pollinated_{13}), 24, 24)$

OUTFLOWS:

Pollinated_14 =

```
PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_14/Total_Open_Flowers_3)*
```

.6975),24,24)

Age_13 = PULSE((Flowers_Day_14-Pollinated_14),24,24)

 $Flowers_Day_15(t) = Flowers_Day_15(t - dt) + (Age_13 - Pollinated_15 - Age_14) * dt$

INIT Flowers_Day_15 = 0

INFLOWS:

 $Age_{13} = PULSE((Flowers_Day_{14}-Pollinated_{14}), 24, 24)$

OUTFLOWS:

Pollinated_15 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_15/Total_Open_Flowers_3)* .5884),24,24) Age_14 = PULSE((Flowers_Day_15-Pollinated_15),24,24)

 $Flowers_Day_16(t) = Flowers_Day_16(t - dt) + (Age_14 - Pollinated_16 - Age_15) * dt$

INIT Flowers_Day_16 = 0

INFLOWS:

Age_14 = PULSE((Flowers_Day_15-Pollinated_15),24,24)

OUTFLOWS:

Pollinated_16 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_16/Total_Open_Flowers_3)*

.3837),24,24)

Age_15 = PULSE((Flowers_Day_16-Pollinated_16),24,24)

 $Flowers_Day_17(t) = Flowers_Day_17(t - dt) + (Age_15 - Pollinated_17 - Wilt_3) * dt$

INIT Flowers_Day_17 = 0

INFLOWS:

 $Age_{15} = PULSE((Flowers_Day_{16}-Pollinated_{16}), 24, 24)$

OUTFLOWS:

Pollinated_17 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_17/Total_Open_Flowers_3)*

.1672),24,24)

Wilt_3 = PULSE((Flowers_Day_17-Pollinated_17),24,24)

 $Flowers_Day_2(t) = Flowers_Day_2(t - dt) + (Age_2 - Pollinated_2 - Age_3) * dt$

INIT Flowers_Day_2 = 0

INFLOWS:

 $Age_2 = PULSE((Flowers_Day_1-Pollinated_1), 24, 24)$

OUTFLOWS:

Pollinated_2 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_2/Total_Open_Flowers)*.6975

),24,24)

Age_3 = PULSE((Flowers_Day_2-Pollinated_2),24,24)

 $Flowers_Day_3(t) = Flowers_Day_3(t - dt) + (Age_3 - Pollinated_3 - Age_4) * dt$

INIT Flowers_Day_3 = 0

INFLOWS:

Age_3 = PULSE((Flowers_Day_2-Pollinated_2),24,24)

OUTFLOWS:

Pollinated_3 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_3/Total_Open_Flowers)*.5884

),24,24)

Age_4 = PULSE((Flowers_Day_3-Pollinated_3),24,24)

 $Flowers_Day_4(t) = Flowers_Day_4(t - dt) + (Age_4 - Pollinated_4 - Age_5) * dt$

INIT Flowers_Day_4 = 0

INFLOWS:

Age_4 = PULSE((Flowers_Day_3-Pollinated_3),24,24)

OUTFLOWS:

Pollinated_4 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_4/Total_Open_Flowers)*.3837

),24,24)

 $Age_5 = PULSE((Flowers_Day_4-Pollinated_4), 24, 24)$

 $Flowers_Day_5(t) = Flowers_Day_5(t - dt) + (Age_5 - Pollinated_5 - Wilt) * dt$

INIT Flowers_Day_5 = 0

INFLOWS:

 $Age_5 = PULSE((Flowers_Day_4-Pollinated_4), 24, 24)$

OUTFLOWS:

Pollinated_5 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_5/Total_Open_Flowers)*.1672

),24,24)

Wilt = PULSE((Flowers_Day_5-Pollinated_5),24,24)

 $Flowers_Day_6(t) = Flowers_Day_6(t - dt) + (Flower_Opening_per_GDD_2 + Flower_Opening_per_GDD_2 + Flower_Opening_per_GD]2 + Flower_Opening]2 + Flower_Opening]2 + Flower$

Noname_6 - Pollinated_6 - Age_6) * dt

INIT Flowers_Day_6 = 0

INFLOWS:

Flower_Opening__per_GDD_2 = (ABS(

(IF(Bluecrop=1)THEN((Total_Potential__Flowers_2)*((0.0326+(4*0.1786)*exp(-

((Accumulating_GDD_2-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD_2-

277.3)/24.0643)))^2)))ELSE

(IF(Jersey=1)THEN((Total_Potential__Flowers_2)*((0.0351+(4*0.2187)*exp(-

((Accumulating_GDD_2-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD_2-

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers_2)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD_2-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD_2-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers_2)*((0.0478+(4*0.2108)*exp(-((Accumulating_GDD_2-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD_2-320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential__Flowers_2)*((0.0263+(4*0.1653)*exp(-((Accumulating_GDD_2-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD_2-266.9)/27.5326)))^2)))ELSE(0)))))-

(DELAY((

(IF(Bluecrop=1)THEN((Total_Potential__Flowers_2)*((0.0326+(4*0.1786)*exp(-

((Accumulating_GDD_2-277.3)/24.0643)))/(1+(exp(-((Accumulating_GDD_2-

277.3)/24.0643)))^2)))ELSE

(IF(Jersey=1)THEN((Total_Potential__Flowers_2)*((0.0351+(4*0.2187)*exp(-

((Accumulating_GDD_2-301.3)/27.383)))/(1+(exp(-((Accumulating_GDD_2-

301.3)/27.383)))^2)))ELSE

(IF(Duke=1)THEN((Total_Potential__Flowers_2)*((0.0203+(4*0.1697)*exp(-

((Accumulating_GDD_2-287.5)/29.8351)))/(1+(exp(-((Accumulating_GDD_2-

287.5)/29.8351)))^2)))ELSE

(IF(Elliott=1)THEN((Total_Potential__Flowers_2)*((0.0478+(4*0.2108)*exp(-

((Accumulating_GDD_2-320.7)/25.4193)))/(1+(exp(-((Accumulating_GDD_2-

320.7)/25.4193)))^2)))ELSE

(IF(Liberty=1)THEN((Total_Potential__Flowers_2)*((0.0263+(4*0.1653)*exp(-

((Accumulating_GDD_2-266.9)/27.5326)))/(1+(exp(-((Accumulating_GDD_2-

266.9)/27.5326)))^2)))ELSE(0)))))),1,0))))

Noname_6 = GRAPH(TIME)

(0.00, 0.00), (1.00, 0.00), (2.00, -1.7e+005), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.(0.00), (7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00), (10.0,(0.00), (14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00), (10.0,0.00), (21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00), (28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (42.1, 0.00), (43.1, 0.00), (44.1, 0.00), (45.1, 0.00), (46.1, 0.00), (47.1, 0.00), (48.1, 0.00), (49.1, 0.00), (50.1, 0.00), (51.1, 0.00), (52.1, 0.00), (53.1, 0.00), (54.1, 0.00), (55.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (63.1, 0.00), (64.1, 0.00), (65.1, 0.00), (66.1, 0.00), (67.1, 0.00), (68.1, 0.00), (69.1, 0.00), (70.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (74.1, 0.00), (75.1, 0.00), (76.1, 0.00), (77.1, 0.00), (78.1, 0.00), (79.1, 0.00), (80.1, 0.00), (81.1, 0.00), (82.1, 0.00), (83.1, 0.00), (84.1, 0.00), (85.1, 0.00), (86.1, 0.00), (87.1, 0.00), (88.1, 0.00), (89.1, 0.00), (90.1, 0.00), (91.1, 0.00), (92.1, 0.00), (93.1, 0.00), (94.1, 0.00), (95.1, 0.00), (96.1, 0.00), (97.1, (0.00), (98.1, 0.00), (99.1, 0.00), (100, 0.00), (101, 0.00), (102, 0.00), (103, 0.00), (104,(105, 0.00), (106, 0.00), (107, 0.00), (108, 0.00), (109, 0.00), (110, 0.00), (111, 0.00), (112, 0.00), (11(0.00), (113, 0.00), (114, 0.00), (115, 0.00), (116, 0.00), (117, 0.00), (118, 0.00), (119, 0.(120, 0.00), (121, 0.00), (122, 0.00), (123, 0.00), (124, 0.00), (125, 0.00), (126, 0.00), (127, 0.00))(0.00), (128, 0.00), (129, 0.00), (130, 0.00), (131, 0.00), (132, 0.00), (133, 0.00), (134, 0.(135, 0.00), (136, 0.00), (137, 0.00), (138, 0.00), (139, 0.00), (140, 0.00), (141, 0.00), (142, 0.00), (141, 0.00), (142, 0.00), (141, 0.00), (142, 0.00), (141, 0.00), (142, 0.00), (141, 0.00), (142, 0.00), (141, 0.00), (142, 0.00), (14(0.00), (143, 0.00), (144, 0.00), (145, 0.00), (146, 0.00), (147, 0.00), (148, 0.00), (149, 0.(150, 0.00), (151, 0.00), (152, 0.00), (153, 0.00), (154, 0.00), (155, 0.00), (156, 0.00), (157, 0.00), (150, 0.00), (15

(0.00), (158, 0.00), (159, 0.00), (160, 0.00), (161, 0.00), (162, 0.00), (163, 0.00), (164, 0.(165, 0.00), (166, 0.00), (167, 0.00), (168, 0.00), (169, 0.00), (170, 0.00), (171, 0.00), (172, 0.00), (171, 0.00), (172, 0.00), (171, 0.00), (172, 0.00), (171, 0.00), (172, 0.00), (171, 0.00), (172, 0.00), (171, 0.00), (172, 0.00), (17(0.00), (173, 0.00), (174, 0.00), (175, 0.00), (176, 0.00), (177, 0.00), (178, 0.00), (179, 0.(180, 0.00), (181, 0.00), (182, 0.00), (183, 0.00), (184, 0.00), (185, 0.00), (186, 0.00), (187, 0.00), (180.00), (188, 0.00), (189, 0.00), (190, 0.00), (191, 0.00), (192, 0.00), (193, 0.00), (194, 0.00), (195, 0.00), (196, 0.00), (197, 0.00), (198, 0.00), (199, 0.00), (200, 0.00), (201, 0.00), (202, 0.00)), (201, 0.00), (202, 0.00))0.00), (203, 0.00), (204, 0.00), (205, 0.00), (206, 0.00), (207, 0.00), (208, 0.00), (209, 0.00), (210, 0.00), (211, 0.00), (212, 0.00), (213, 0.00), (214, 0.00), (215, 0.00), (216, 0.00), (217, 0.00))0.00), (218, 0.00), (219, 0.00), (220, 0.00), (221, 0.00), (222, 0.00), (223, 0.00), (224, 0.00), (225, 0.00), (226, 0.00), (227, 0.00), (228, 0.00), (229, 0.00), (230, 0.00), (231, 0.00), (232, 0.00))0.00), (233, 0.00), (234, 0.00), (235, 0.00), (236, 0.00), (237, 0.00), (238, 0.00), (239, 0.00), (240, 0.00), (241, 0.00), (242, 0.00), (243, 0.00), (244, 0.00), (245, 0.00), (246, 0.00), (247, 0.00), (247, 0.00), (247, 0.00), (247, 0.00), (248, 0.00), (240.00), (248, 0.00), (249, 0.00), (250, 0.00), (251, 0.00), (252, 0.00), (253, 0.00), (254, 0.00), (255, 0.00), (256, 0.00), (257, 0.00), (258, 0.00), (259, 0.00), (260, 0.00), (261, 0.00), (262, 0.00))0.00), (263, 0.00), (264, 0.00), (265, 0.00), (266, 0.00), (267, 0.00), (268, 0.00), (269, 0.00), (270, 0.00), (271, 0.00), (272, 0.00), (273, 0.00), (274, 0.00), (275, 0.00), (276, 0.00), (277, 0.00))0.00), (278, 0.00), (279, 0.00), (280, 0.00), (281, 0.00), (282, 0.00), (283, 0.00), (284, 0.00), (285, 0.00), (286, 0.00), (287, 0.00), (288, 0.00), (289, 0.00), (290, 0.00), (291, 0.00), (292, 0.00))0.00), (293, 0.00), (294, 0.00), (295, 0.00), (296, 0.00), (297, 0.00), (298, 0.00), (299, 0.00), (300, 0.00), (301, 0.00), (302, 0.00), (303, 0.00), (304, 0.00), (305, 0.00), (306, 0.00), (307, 0.00), (30(0.00), (308, 0.00), (309, 0.00), (310, 0.00), (311, 0.00), (312, 0.00), (313, 0.00), (314, 0.(315, 0.00), (316, 0.00), (317, 0.00), (318, 0.00), (319, 0.00), (320, 0.00), (321, 0.00), (322, 0.00), (322, 0.00))(0.00), (323, 0.00), (324, 0.00), (325, 0.00), (326, 0.00), (327, 0.00), (328, 0.00), (329, 0.

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0.00), (504, 0.00), (505, 0.00), (506, 0.00), (507, 0.00), (508, 0.00), (509, 0.00), (510, 0.00), (511, 0.00), (512, 0.00), (513, 0.00), (514, 0.00), (515, 0.00), (516, 0.00), (517, 0.00), (518, 0.00), (510.00), (519, 0.00), (520, 0.00), (521, 0.00), (522, 0.00), (523, 0.00), (524, 0.00), (525, 0.00), (526, 0.00), (527, 0.00), (528, 0.00), (529, 0.00), (530, 0.00), (531, 0.00), (532, 0.00), (533, 0.00), (532, 0.00), (533, 0.00), (532, 0.00), (533, 0.00), (530.00), (534, 0.00), (535, 0.00), (536, 0.00), (537, 0.00), (538, 0.00), (539, 0.00), (540, 0.00), (541, 0.00), (542, 0.00), (543, 0.00), (544, 0.00), (545, 0.00), (546, 0.00), (547, 0.00), (548, 0.00), (547, 0.00), (548, 0.00), (540.00), (549, 0.00), (550, 0.00), (551, 0.00), (552, 0.00), (553, 0.00), (554, 0.00), (555, 0.00), (556, 0.00), (557, 0.00), (558, 0.00), (559, 0.00), (560, 0.00), (561, 0.00), (562, 0.00), (563, 0.00), (562, 0.00), (563, 0.00), (553, 0.00), (553, 0.00), (553, 0.00), (553, 0.00), (560.00), (564, 0.00), (565, 0.00), (566, 0.00), (567, 0.00), (568, 0.00), (569, 0.00), (570, 0.00), (571, 0.00), (572, 0.00), (573, 0.00), (574, 0.00), (575, 0.00), (576, 0.00), (577, 0.00), (578, 0.00), (579, 0.00), (579, 0.00), (578, 0.00), (579, 0.00), (570.00), (579, 0.00), (580, 0.00), (581, 0.00), (582, 0.00), (583, 0.00), (584, 0.00), (585, 0.00), (586, 0.00), (587, 0.00), (588, 0.00), (589, 0.00), (590, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (591, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (592, 0.00), (593, 0.00), (590.00), (594, 0.00), (595, 0.00), (596, 0.00), (597, 0.00), (598, 0.00), (599, 0.00), (600, 0.00), (601, 0.00), (602, 0.00), (603, 0.00), (604, 0.00), (605, 0.00), (606, 0.00), (607, 0.00), (608, 0.00), (607, 0.00), (608, 0.00), (600.00), (609, 0.00), (610, 0.00), (611, 0.00), (612, 0.00), (613, 0.00), (614, 0.00), (615, 0.00), (616, 0.00), (617, 0.00), (618, 0.00), (619, 0.00), (620, 0.00), (621, 0.00), (622, 0.00), (623, 0.00), (619, 0.00), (620, 0.00), (621, 0.00), (622, 0.00), (623, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (619, 0.00), (621, 0.00), (622, 0.00), (623, 0.00), (619, 0.00), (610.00), (624, 0.00), (625, 0.00), (626, 0.00), (627, 0.00), (628, 0.00), (629, 0.00), (630, 0.00), (631, 0.00), (632, 0.00), (633, 0.00), (634, 0.00), (635, 0.00), (636, 0.00), (637, 0.00), (638, 0.00), (639, 0.00), (63(0.00), (639, 0.00), (640, 0.00), (641, 0.00), (642, 0.00), (643, 0.00), (644, 0.00), (645, 0.(646, 0.00), (647, 0.00), (648, 0.00), (649, 0.00), (650, 0.00), (651, 0.00), (652, 0.00), (653, (0.00), (654, 0.00), (655, 0.00), (656, 0.00), (657, 0.00), (658, 0.00), (659, 0.00), (660, 0.(661, 0.00), (662, 0.00), (663, 0.00), (664, 0.00), (665, 0.00), (666, 0.00), (667, 0.00), (668, 0.00), (669, 0.00), (66(0.00), (669, 0.00), (670, 0.00), (671, 0.00), (672, 0.00), (673, 0.00), (674, 0.00), (675, 0.

(676, 0.00), (677, 0.00), (678, 0.00), (679, 0.00), (680, 0.00), (681, 0.00), (682, 0.00), (683, 0.00), (684, 0.00), (685, 0.00), (686, 0.00), (687, 0.00), (688, 0.00), (689, 0.00), (690, 0.00), (691, 0.00), (692, 0.00), (693, 0.00), (694, 0.00), (695, 0.00), (696, 0.00), (697, 0.00), (698, 0.00), (699, 0.00), (700, 0.00), (701, 0.00), (702, 0.00), (703, 0.00), (704, 0.00), (705, 0.00), (706, 0.00), (707, 0.00), (708, 0.00), (709, 0.00), (710, 0.00), (711, 0.00), (712, 0.00), (713, 0.00))

OUTFLOWS:

 $Pollinated_6 =$

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_6/Total_Open_Flowers_2)*0

.7447),24,24)

Age_6 = PULSE((Flowers_Day_6-Pollinated_6),24,24)

 $Flowers_Day_7(t) = Flowers_Day_7(t - dt) + (Age_6 - Pollinated_7 - Age_7) * dt$

INIT Flowers_Day_7 = 0

INFLOWS:

 $Age_6 = PULSE((Flowers_Day_6-Pollinated_6), 24, 24)$

OUTFLOWS:

Pollinated_7 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_7/Total_Open_Flowers_2)*.

7496),24,24)

Age_7 = PULSE((Flowers_Day_7-Pollinated_7),24,24)

 $Flowers_Day_8(t) = Flowers_Day_8(t - dt) + (Age_7 - Pollinated_8 - Age_8) * dt$

INIT Flowers_Day_8 = 0

Age_7 = PULSE((Flowers_Day_7-Pollinated_7),24,24)

OUTFLOWS:

Pollinated_8 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_8/Total_Open_Flowers_2)*.

6975),24,24)

Age_8 = PULSE((Flowers_Day_8-Pollinated_8),24,24)

 $Flowers_Day_9(t) = Flowers_Day_9(t - dt) + (Age_8 - Pollinated_9 - Age_9) * dt$

INIT Flowers_Day_9 = 0

INFLOWS:

 $Age_8 = PULSE((Flowers_Day_8-Pollinated_8), 24, 24)$

OUTFLOWS:

Pollinated_9 =

```
PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_9/Total_Open_Flowers_2)*.
```

5884),24,24)

Age_9 = PULSE((Flowers_Day_9-Pollinated_9),24,24)

 $HB_on_Bberry(t) = HB_on_Bberry(t - dt) + (Active_HB - HB_Daily_Return) * dt$

INIT HB_on_Bberry = 0

INFLOWS:

Active_HB = (HB_per_Hive*HB_Hives_Rented*4)*

(IF(Air_Temp<12)THEN(0)ELSE(IF(Air_Temp<35)THEN(-

0.0013*(Air_Temp^2)+0.0626*(Air_Temp)-0.4016)ELSE(0)))*

(IF(Solar_Radiation<10)THEN(0)ELSE(-

 $.00000008*(Solar_Radiation^2) + 0.0004*(Solar_Radiation) - 0.0088))*$

(IF(Wind_Speed<6)THEN(-

0.0278*(Wind_Speed^2)+0.1609*(Wind_Speed)+0.1016)ELSE(0))*

(0.0051*((Total_Open_Flowers/Total_Potential_Flowers)*100)+0.064)

OUTFLOWS:

HB_Daily_Return = PULSE(HB_on_Bberry, 24, 24)

 $HB_on_Bberry_2(t) = HB_on_Bberry_2(t - dt) + (Active_HB_2 - HB_Daily_Return_2) * dt$

INIT HB_on_Bberry_2 = 0

INFLOWS:

Active_HB_2 = (HB_per_Hive*HB_Hives__Rented*4)*

(IF(Air_Temp_2<12)THEN(0)ELSE(IF(Air_Temp_2<35)THEN(-

0.0013*(Air_Temp_2^2)+0.0626*(Air_Temp_2)-0.4016)ELSE(0)))*

(IF(Solar_Radiation_2<10)THEN(0)ELSE(-

.00000008*(Solar_Radiation_2^2)+0.0004*(Solar_Radiation_2)-0.0088))*

(IF(Wind_Speed_2<6)THEN(-

0.0278*(Wind_Speed_2^2)+0.1609*(Wind_Speed_2)+0.1016)ELSE(0))*

(0.0051*((Total_Open__Flowers_2/Total_Potential__Flowers_2)*100)+0.064)

OUTFLOWS:

HB_Daily_Return_2 = PULSE(HB_on_Bberry_2,24,24)

 $HB_on_Bberry_3(t) = HB_on_Bberry_3(t - dt) + (Active_HB_3 - HB_Daily_Return_3) * dt$

INIT HB_on_Bberry_3 = 0

INFLOWS:

Active_HB_3 = (HB_per_Hive*HB_Hives__Rented*4)*

(IF(Air_Temp_3<12)THEN(0)ELSE(IF(Air_Temp_3<35)THEN(-

0.0013*(Air_Temp_3^2)+0.0626*(Air_Temp_3)-0.4016)ELSE(0)))*

(IF(Solar_Radiation_3<10)THEN(0)ELSE(-

 $.00000008*(Solar_Radiation_3^2)+0.0004*(Solar_Radiation_3)-0.0088))*$

(IF(Wind_Speed_3<6)THEN(-

0.0278*(Wind_Speed_3^2)+0.1609*(Wind_Speed_3)+0.1016)ELSE(0))*

(0.0051*((Total_Open__Flowers_3/Total_Potential__Flowers_3)*100)+0.064)

OUTFLOWS:

HB_Daily_Return_3 = PULSE(HB_on_Bberry_3,24,24)

 $Pollinated_Flowers(t) = Pollinated_Flowers(t - dt) + (Pollinated_3 + Pollinated_4 + Pollinated_4)$

Pollinated_5 + Pollinated_0 + Pollinated_1 + Pollinated_2 - Pollinated_Berries) * dt

INIT Pollinated_Flowers = 0

INFLOWS:

Pollinated_3 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_3/Total_Open_Flowers)*.5884

),24,24)

Pollinated_4 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_4/Total_Open_Flowers)*.3837),24,24)

Pollinated_5 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_5/Total_Open_Flowers)*.1672

),24,24)

 $Pollinated_0 =$

PULSE((Combined_Pollinator_Activity*(Flowers_Day_0/Total_Open_Flowers)*0.744

7),24,24)

 $Pollinated_1 =$

PULSE((Combined_Pollinator_Activity*(Flowers_Day_1/Total_Open_Flowers)*.7496

),24,24)

Pollinated_2 =

PULSE((Combined_Pollinator_Activity*(Flowers_Day_2/Total_Open_Flowers)*.6975

),24,24)

OUTFLOWS:

Pollinated__Berries = PULSE(Pollinated_Flowers, 24, 24)

 $Pollinated_Flowers_2(t) = Pollinated_Flowers_2(t - dt) + (Pollinated_9 + Pollinated_10 + Pollinated_10)$

Pollinated_11 + Pollinated_6 + Pollinated_7 + Pollinated_8 - Pollinated_Berries_2) * dt

INIT Pollinated_Flowers_2 = 0

INFLOWS:

Pollinated_9 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_9/Total_Open_Flowers_2)*. 5884),24,24)

 $Pollinated_{10} =$

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_10/Total_Open_Flowers_2)* .3837),24,24)

Pollinated_11 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_11/Total_Open_Flowers_2)*

.1672),24,24)

Pollinated_6 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_6/Total_Open_Flowers_2)*0

.7447),24,24)

Pollinated_7 =

PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_7/Total_Open_Flowers_2)*.

7496),24,24)

 $Pollinated_8 =$

```
PULSE((Combined_Pollinator_Activity_2*(Flowers_Day_8/Total_Open_Flowers_2)*.
```

6975),24,24)

OUTFLOWS:

Pollinated__Berries_2 = PULSE(Pollinated_Flowers_2,24,24)

 $Pollinated_Flowers_3(t) = Pollinated_Flowers_3(t - dt) + (Pollinated_15 + Pollinated_16 + Pollinated_16) + (Pollinated_16) + (Pollinated$

 $Pollinated_17 + Pollinated_12 + Pollinated_13 + Pollinated_14 - Pollinated_Berries_3) * dt$

INIT Pollinated_Flowers_3 = 0

Pollinated_15 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_15/Total_Open_Flowers_3)* .5884),24,24)

Pollinated_16 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_16/Total_Open_Flowers_3)*

.3837),24,24)

 $Pollinated_17 =$

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_17/Total_Open_Flowers_3)*

.1672),24,24)

Pollinated_12 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_12/Total_Open_Flowers_3)*

0.7447),24,24)

Pollinated_13 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_13/Total_Open_Flowers_3)*

.7496),24,24)

Pollinated_14 =

PULSE((Combined_Pollinator_Activity_3*(Flowers_Day_14/Total_Open_Flowers_3)*

.6975),24,24)

OUTFLOWS:

Pollinated__Berries_3 = PULSE(Pollinated_Flowers_3,24,24)

Poor_Blueberry_Yield(t) = Poor_Blueberry_Yield(t - dt) + (Harvest_2) * dt

INIT Poor_Blueberry_Yield = 0

Harvest_2 = PULSE(Yield_2,24,24)

Superior_Blueberry_Yield(t) = Superior_Blueberry_Yield(t - dt) + (Harvest_3) * dt

INIT Superior_Blueberry_Yield = 0

INFLOWS:

Harvest_3 = PULSE(Yield_3,24,24)

 $Unpollinated_Flowers(t) = Unpollinated_Flowers(t - dt) + (Wilt - Unpollinated_Berries)$

* dt

INIT Unpollinated___Flowers = 0

INFLOWS:

Wilt = PULSE((Flowers_Day_5-Pollinated_5),24,24)

OUTFLOWS:

Unpollinated__Berries = PULSE(Unpollinated__Flowers,24,24)

Unpollinated__Flowers_2(t) = Unpollinated__Flowers_2(t - dt) + (Wilt_2 -

Unpollinated__Berries_2) * dt

INIT Unpollinated___Flowers_2 = 0

INFLOWS:

Wilt_2 = PULSE((Flowers_Day_11-Pollinated_11),24,24)

OUTFLOWS:

Unpollinated__Berries_2 = PULSE(Unpollinated__Flowers_2,24,24)

Unpollinated__Flowers_3(t) = Unpollinated__Flowers_3(t - dt) + (Wilt_3 -

Unpollinated_Berries_3) * dt

INIT Unpollinated__Flowers_3 = 0

Wilt_3 = PULSE((Flowers_Day_17-Pollinated_17),24,24)

OUTFLOWS:

Unpollinated__Berries_3 = PULSE(Unpollinated__Flowers_3,24,24)

Air_Temp = GRAPH(TIME)

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Blueberry__Base_Temperature =

IF(Bluecrop=1)THEN(7.42)ELSE(IF(Jersey=1)THEN(7.93)ELSE(IF(Duke=1)THEN(7.14)E LSE(IF(Elliott=1)THEN(7.52)ELSE(IF(Liberty=1)THEN(7.96)ELSE(1)))))

Blueberry_Base_Temperature_2 =

IF(Bluecrop=1)THEN(7.42)ELSE(IF(Jersey=1)THEN(7.93)ELSE(IF(Duke=1)THEN(7.14)E

LSE(IF(Elliott=1)THEN(7.52)ELSE(IF(Liberty=1)THEN(7.96)ELSE(1)))))

Blueberry_Base_Temperature_3 =

IF(Bluecrop=1)THEN(7.42)ELSE(IF(Jersey=1)THEN(7.93)ELSE(IF(Duke=1)THEN(7.14)E

LSE(IF(Elliott=1)THEN(7.52)ELSE(IF(Liberty=1)THEN(7.96)ELSE(1)))))

Bluecrop = 0

 $Bush_spacing = 4$

Combined_Pollinator_Activity = (((HB_on_Bberry*28.5))+(BB_on_Bberry*135.55))

Combined_Pollinator_Activity_2 =

(((HB_on_Bberry_2*28.5))+(BB_on_Bberry_2*135.55))

Combined_Pollinator_Activity_3 =

((((HB_on_Bberry_3*28.5))+(BB_on_Bberry_3*135.55))

Duke = 0

Elliott = 0

Flowers__per_bush =

IF(Bluecrop=1)THEN(3628)ELSE(IF(Jersey=1)THEN(5556)ELSE(IF(Duke=1)THEN(2944

)ELSE(IF(Elliott=1)THEN(2540)ELSE(IF(Liberty=1)THEN(2540)ELSE(0)))))

Flowers__per_bush_2 =

IF(Bluecrop=1)THEN(3628)ELSE(IF(Jersey=1)THEN(5556)ELSE(IF(Duke=1)THEN(2944

)ELSE(IF(Elliott=1)THEN(2540)ELSE(IF(Liberty=1)THEN(2540)ELSE(0)))))

```
Flowers_per_bush_3 =
```

```
IF(Bluecrop=1)THEN(3628)ELSE(IF(Jersey=1)THEN(5556)ELSE(IF(Duke=1)THEN(2944
```

```
)ELSE(IF(Elliott=1)THEN(2540)ELSE(IF(Liberty=1)THEN(2540)ELSE(0)))))
```

GDDStartValue =

```
IF(Bluecrop=1)THEN(207)ELSE(IF(Jersey=1)THEN(223)ELSE(IF(Duke=1)THEN(199)EL
```

```
SE(IF(Elliott=1)THEN(253)ELSE(IF(Liberty=1)THEN(189)ELSE(1)))))
```

 $GDDStart_2 =$

```
IF(Bluecrop=1)THEN(207)ELSE(IF(Jersey=1)THEN(225)ELSE(IF(Duke=1)THEN(198)EL
```

```
SE(IF(Elliott=1)THEN(253)ELSE(IF(Liberty=1)THEN(190)ELSE(1)))))
```

 $GDDStart_3 =$

```
IF(Bluecrop=1)THEN(207)ELSE(IF(Jersey=1)THEN(223)ELSE(IF(Duke=1)THEN(199)EL
```

```
SE(IF(Elliott=1)THEN(253)ELSE(IF(Liberty=1)THEN(189)ELSE(1)))))
```

 $HB_Hives_Rented = 7$

 $HB_per_Hive = 20000$

Jersey = 0

Liberty = 0

```
PrevTemp = GRAPH(TIME)
```

(0.00, 0.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.00),(7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00),(14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00),(21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00),(28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00),(35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00),

(42.1, 0.00), (43.1, 0.00), (44.1, 0.00), (45.1, 0.00), (46.1, 0.00), (47.1, 0.00), (48.1, 0.00),(49.1, 0.00), (50.1, 0.00), (51.1, 0.00), (52.1, 0.00), (53.1, 0.00), (54.1, 0.00), (55.1, 0.00),(56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00),(63.1, 0.00), (64.1, 0.00), (65.1, 0.00), (66.1, 0.00), (67.1, 0.00), (68.1, 0.00), (69.1, 0.00),(70.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (74.1, 0.00), (75.1, 0.00), (76.1, 0.00),(77.1, 0.00), (78.1, 0.00), (79.1, 0.00), (80.1, 0.00), (81.1, 0.00), (82.1, 0.00), (83.1, 0.00),(84.1, 0.00), (85.1, 0.00), (86.1, 0.00), (87.1, 0.00), (88.1, 0.00), (89.1, 0.00), (90.1, 0.00),(91.1, 0.00), (92.1, 0.00), (93.1, 0.00), (94.1, 0.00), (95.1, 0.00), (96.1, 0.00), (97.1, 0.00),(98.1, 0.00), (99.1, 0.00), (100, 0.00), (101, 0.00), (102, 0.00), (103, 0.00), (104, 0.00), (105, (0.00), (106, 0.00), (107, 0.00), (108, 0.00), (109, 0.00), (110, 0.00), (111, 0.00), (112, 0.00), (100, 0.00), (110, 0.(113, 0.00), (114, 0.00), (115, 0.00), (116, 0.00), (117, 0.00), (118, 0.00), (119, 0.00), (120, 0.00))(0.00), (121, 0.00), (122, 0.00), (123, 0.00), (124, 0.00), (125, 0.00), (126, 0.00), (127, 0.00), (127, 0.00), (127, 0.00), (128, 00(128, 0.00), (129, 0.00), (130, 0.00), (131, 0.00), (132, 0.00), (133, 0.00), (134, 0.00), (135, 0.00), (136, 0.00), (137, 0.00), (137, 0.00), (138, 0.00), (13(0.00), (136, 0.00), (137, 0.00), (138, 0.00), (139, 0.00), (140, 0.00), (141, 0.00), (142, 0.00), (142, 0.00), (142, 0.00), (141, 0.00), (142, 0.(143, 0.00), (144, 0.00), (145, 0.00), (146, 0.00), (147, 0.00), (148, 0.00), (149, 0.00), (150, 0.00), (15(0.00), (151, 0.00), (152, 0.00), (153, 0.00), (154, 0.00), (155, 0.00), (156, 0.00), (157, 0.(158, 0.00), (159, 0.00), (160, 0.00), (161, 0.00), (162, 0.00), (163, 0.00), (164, 0.00), (165, 0.00), (160, 0.00), (161, 0.00), (160.00), (166, 0.00), (167, 0.00), (168, 0.00), (169, 0.00), (170, 0.00), (171, 0.00), (172, 0.00), (173, 0.00), (174, 0.00), (175, 0.00), (176, 0.00), (177, 0.00), (178, 0.00), (179, 0.00), (180, 0.00))0.00), (181, 0.00), (182, 0.00), (183, 0.00), (184, 0.00), (185, 0.00), (186, 0.00), (187, 0.00), (188, 0.00), (189, 0.00), (190, 0.00), (191, 0.00), (192, 0.00), (193, 0.00), (194, 0.00), (195, 0.00), (196, 0.00), (197, 0.00), (197, 0.00), (198, 0.00), (190.00), (196, 0.00), (197, 0.00), (198, 0.00), (199, 0.00), (200, 0.00), (201, 0.00), (202, 0.00), (203, 0.00), (204, 0.00), (205, 0.00), (206, 0.00), (207, 0.00), (208, 0.00), (209, 0.00), (210, 0.00))

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Solar_Radiation = GRAPH(TIME)

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Solar_Radiation_2 = GRAPH(TIME)

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Time__Converter = GRAPH(TIME)

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(0.00, 1.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.00), (7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00), (14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00), (21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00), (28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (50.1, 0.00), (44.1, 0.00), (45.1, 0.00), (46.1, 0.00), (47.1, 0.00), (48.1, 0.00), (49.1, 0.00), (50.1, 0.00), (51.1, 0.00), (52.1, 0.00), (53.1, 0.00), (54.1, 0.00), (55.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (70.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (71.1, 0.00), (72.1, 0.00), (81.1, 0.00), (82.1, 0.00), (83.1, 0.00), (84.1, 0.00), (85.1, 0.00), (87.1, 0.00), (88.1, 0.00), (89.1, 0.00), (90.1, 0.00), (91.1, 0.00),

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(0.00, 0.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.00), (7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00), (14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00), (21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00), (28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (42.1, 0.00), (43.1, 0.00), (44.1, 0.00), (45.1, 0.00), (46.1, 0.00), (47.1, 0.00), (48.1, 0.00), (49.1, 0.00), (50.1, 0.00), (51.1, 0.00), (52.1, 0.00), (53.1, 0.00), (54.1, 0.00), (55.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (50.1, 0.00), (62.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00), (58.1, 0.00), (59.1, 0.00), (60.1, 0.00), (61.1, 0.00), (62.1, 0.00), (56.1, 0.00), (57.1, 0.00),

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(233, 0.00), (234, 0.00), (235, 0.00), (236, 0.00), (237, 0.00), (238, 0.00), (239, 0.00), (240, 0.00))0.00), (241, 0.00), (242, 0.00), (243, 0.00), (244, 0.00), (245, 0.00), (246, 0.00), (247, 0.00), (248, 0.00), (249, 0.00), (250, 0.00), (251, 0.00), (252, 0.00), (253, 0.00), (254, 0.00), (255, 0.00), (256, 0.00), (257, 0.00), (258, 0.00), (250.00), (256, 0.00), (257, 0.00), (258, 0.00), (259, 0.00), (260, 0.00), (261, 0.00), (262, 0.00), (263, 0.00), (264, 0.00), (265, 0.00), (266, 0.00), (267, 0.00), (268, 0.00), (269, 0.00), (270, 0.00))0.00), (271, 0.00), (272, 0.00), (273, 0.00), (274, 0.00), (275, 0.00), (276, 0.00), (277, 0.00), (278, 0.00), (279, 0.00), (280, 0.00), (281, 0.00), (282, 0.00), (283, 0.00), (284, 0.00), (285, 0.00), (280, 0.00), (281, 0.00), (280.00), (286, 0.00), (287, 0.00), (288, 0.00), (289, 0.00), (290, 0.00), (291, 0.00), (292, 0.00), (293, 0.00), (294, 0.00), (295, 0.00), (296, 0.00), (297, 0.00), (298, 0.00), (299, 0.00), (300, 0.00), (20(0.00), (301, 0.00), (302, 0.00), (303, 0.00), (304, 0.00), (305, 0.00), (306, 0.00), (307, 0.00), (307, 0.00), (307, 0.00), (307, 0.00), (307, 0.00), (307, 0.00), (308, 0.(308, 0.00), (309, 0.00), (310, 0.00), (311, 0.00), (312, 0.00), (313, 0.00), (314, 0.00), (315, 0.00), (316, 0.00), (317, 0.00), (31(0.00), (316, 0.00), (317, 0.00), (318, 0.00), (319, 0.00), (320, 0.00), (321, 0.00), (322, 0.00), (322, 0.00), (322, 0.00), (320, 0.00), (321, 0.00), (322, 0.00), (320, 0.(323, 0.00), (324, 0.00), (325, 0.00), (326, 0.00), (327, 0.00), (328, 0.00), (329, 0.00), (330, 0.00), (32(0.00), (331, 0.00), (332, 0.00), (333, 0.00), (334, 0.00), (335, 0.00), (336, 0.00), (337, 0.(338, 0.00), (339, 0.00), (340, 0.00), (341, 0.00), (342, 0.00), (343, 0.00), (344, 0.00), (345, 0.00), (346, 0.00), (340.00), (346, 0.00), (347, 0.00), (348, 0.00), (349, 0.00), (350, 0.00), (351, 1.00), (352, 0.00), (353, 0.00), (354, 0.00), (355, 0.00), (357, 0.00), (358, 0.00), (359, 0.00), (360, 0.00), (361, 0.00), (360, 0.00), (361, 0.00), (360, 0.00), (360, 0.00), (361, 0.00), (360, 0.00), (36(0.00), (362, 0.00), (363, 0.00), (364, 0.00), (365, 0.00), (366, 0.00), (367, 0.00), (368, 0.(369, 0.00), (370, 0.00), (371, 0.00), (372, 0.00), (373, 0.00), (374, 0.00), (375, 0.00), (376, 0.00), (370.00), (377, 0.00), (378, 0.00), (379, 0.00), (380, 0.00), (381, 0.00), (382, 0.00), (383, 0.00), (384, 0.00), (385, 0.00), (386, 0.00), (387, 0.00), (388, 0.00), (389, 0.00), (390, 0.00), (391, 0.00), (390.00), (392, 0.00), (393, 0.00), (394, 0.00), (395, 0.00), (396, 0.00), (397, 0.00), (398, 0.00), (399, 0.00), (400, 0.00), (401, 0.00), (402, 0.00), (403, 0.00), (404, 0.00), (405, 0.00), (406, 0.00), (40

0.00), (407, 0.00), (408, 0.00), (409, 0.00), (410, 0.00), (411, 0.00), (412, 0.00), (413, 0.00), (414, 0.00), (415, 0.00), (416, 0.00), (417, 0.00), (418, 0.00), (419, 0.00), (420, 0.00), (421, 0.00), (42(0.00), (422, 0.00), (423, 0.00), (424, 0.00), (425, 0.00), (426, 0.00), (427, 0.00), (428, 0.(429, 0.00), (430, 0.00), (431, 0.00), (432, 0.00), (433, 0.00), (434, 0.00), (435, 0.00), (436, 0.00), (437, 0.00), (438, 0.00), (439, 0.00), (440, 0.00), (441, 0.00), (442, 0.00), (443, 0.00), (444, 0.00), (445, 0.00), (446, 0.00), (447, 0.00), (448, 0.00), (449, 0.00), (450, 0.00), (451, (0.00), (452, 0.00), (453, 0.00), (454, 0.00), (455, 0.00), (456, 0.00), (457, 0.00), (458, 0.(459, 0.00), (460, 0.00), (461, 0.00), (462, 0.00), (463, 0.00), (464, 0.00), (465, 0.00), (466, 0.00), (467, 0.00), (468, 0.00), (469, 0.00), (470, 0.00), (471, 0.00), (472, 0.00), (473, 0.00), (474, 0.00), (475, 0.00), (476, 0.00), (477, 0.00), (478, 0.00), (479, 0.00), (480, 0.00), (481, 0.00), (482, 0.00), (483, 0.00), (484, 0.00), (485, 0.00), (486, 0.00), (487, 0.00), (488, 0.00), (489, 0.00), (490, 0.00), (491, 0.00), (492, 0.00), (493, 0.00), (494, 0.00), (495, 0.00), (496, 0.00), (497, 0.00), (498, 0.00), (499, 0.00), (500, 0.00), (501, 0.00), (502, 0.00), (503, 0.00), (504, 0.00), (505, 0.00), (506, 0.00), (507, 0.00), (508, 0.00), (509, 0.00), (510, 0.00), (511, 0.00), (511, 0.00), (511, 0.00), (511, 0.00), (510.00), (512, 0.00), (513, 0.00), (514, 0.00), (515, 0.00), (516, 0.00), (517, 0.00), (518, 0.00), (519, 0.00), (520, 0.00), (521, 0.00), (522, 0.00), (523, 0.00), (524, 0.00), (525, 0.00), (526, 0.00), (520.00), (527, 0.00), (528, 0.00), (529, 0.00), (530, 0.00), (531, 0.00), (532, 0.00), (533, 0.00), (534, 0.00), (535, 0.00), (536, 0.00), (537, 0.00), (538, 0.00), (539, 0.00), (540, 0.00), (541, 0.00), (541, 0.00), (540, 0.00), (541, 0.00), (540, 0.00), (540, 0.00), (540, 0.00), (541, 0.00), (540, 0.00), (54(0.00), (542, 0.00), (543, 0.00), (544, 0.00), (545, 0.00), (546, 0.00), (547, 0.00), (548, 0.(549, 0.00), (550, 0.00), (551, 0.00), (552, 0.00), (553, 0.00), (554, 0.00), (555, 0.00), (556, 0.00), (55(0.00), (557, 0.00), (558, 0.00), (559, 0.00), (560, 0.00), (561, 0.00), (562, 0.00), (563, 0.(564, 0.00), (565, 0.00), (566, 0.00), (567, 0.00), (568, 0.00), (569, 0.00), (570, 0.00), (571, 0.00), (571, 0.00), (570, 0.00), (571, 0.00), (570, 0.00), (570, 0.00), (571, 0.00), (570, 0.00), (57(0.00), (572, 0.00), (573, 0.00), (574, 0.00), (575, 0.00), (576, 0.00), (577, 0.00), (578, 0.

(579, 0.00), (580, 0.00), (581, 0.00), (582, 0.00), (583, 0.00), (584, 0.00), (585, 0.00), (586, 0.00), (580.00), (587, 0.00), (588, 0.00), (589, 0.00), (590, 0.00), (591, 0.00), (592, 0.00), (593, 0.00), (594, 0.00), (595, 0.00), (596, 0.00), (597, 0.00), (598, 0.00), (599, 0.00), (600, 0.00), (601, 0.00), (600.00), (602, 0.00), (603, 0.00), (604, 0.00), (605, 0.00), (606, 0.00), (607, 0.00), (608, 0.00), (609, 0.00), (610, 0.00), (611, 0.00), (612, 0.00), (613, 0.00), (614, 0.00), (615, 0.00), (616, 0.00), (610.00), (617, 0.00), (618, 0.00), (619, 0.00), (620, 0.00), (621, 0.00), (622, 0.00), (623, 0.00), (624, 0.00), (625, 0.00), (626, 0.00), (627, 0.00), (628, 0.00), (629, 0.00), (630, 0.00), (631, 0.00), (630.00), (632, 0.00), (633, 0.00), (634, 0.00), (635, 0.00), (636, 0.00), (637, 0.00), (638, 0.00), (639, 0.00), (640, 0.00), (641, 0.00), (642, 0.00), (643, 0.00), (644, 0.00), (645, 0.00), (646, 0.00), (647, 0.00), (648, 0.00), (649, 0.00), (650, 0.00), (651, 0.00), (652, 0.00), (653, 0.00), (654, 0.00), (655, 0.00), (656, 0.00), (657, 0.00), (658, 0.00), (659, 0.00), (660, 0.00), (661, 0.00), (660, 0.00), (661, 0.00), (660, 0.00), (660, 0.00), (661, 0.00), (660.00), (662, 0.00), (663, 0.00), (664, 0.00), (665, 0.00), (666, 0.00), (667, 0.00), (668, 0.00), (669, 0.00), (670, 0.00), (671, 0.00), (672, 0.00), (673, 0.00), (674, 0.00), (675, 0.00), (676, (0.00), (677, 0.00), (678, 0.00), (679, 0.00), (680, 0.00), (681, 0.00), (682, 0.00), (683, 0.(684, 0.00), (685, 0.00), (686, 0.00), (687, 0.00), (688, 0.00), (689, 0.00), (690, 0.00), (691, 0.00), (692, 0.00), (693, 0.00), (694, 0.00), (695, 0.00), (696, 0.00), (697, 0.00), (698, 0.00), (699, 0.00), (700, 0.00), (701, 0.00), (702, 0.00), (703, 0.00), (704, 0.00), (705, 0.00), (706, 0.00), (707, 0.00), (708, 0.00), (709, 0.00), (710, 0.00), (711, 0.00), (712, 0.00), (713, 0.00) Total Open Flowers =

1+Flowers_Day_0+Flowers_Day_1+Flowers_Day_2+Flowers_Day_3+Flowers_Day_ 4+Flowers_Day_5 Total_Open__Flowers_2 =

1+Flowers_Day_6+Flowers_Day_7+Flowers_Day_8+Flowers_Day_9+Flowers_Day_

10+Flowers_Day_11

Total_Open__Flowers_3 =

1+Flowers_Day_12+Flowers_Day_13+Flowers_Day_14+Flowers_Day_15+Flowers_

Day_16+Flowers_Day_17

Total_Potential__Flowers = (Flowers__per_bush*((43560/(Bush_spacing*Row_spacing))))

Total_Potential__Flowers_2 =

(Flowers_per_bush_2*((43560/(Bush_spacing*Row_spacing))))

Total_Potential__Flowers_3 =

(Flowers_per_bush_3*((43560/(Bush_spacing*Row_spacing))))

Wind_Speed = GRAPH(TIME)

(0.00, 0.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.00), (7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00), (14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00), (21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00), (28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (42.1, 0.00), (43.1, 0.00), (44.1, 0.00), (45.1, 0.00), (46.1, 0.00), (47.1, 0.00), (48.1, 0.00), (49.1, 0.00), (50.1, 0.00), (51.1, 0.00), (52.1, 0.00), (53.1, 0.00), (54.1, 0.00), (55.1, 0.00), (56.1, 0.00), (57.1, 0.00), (55.1, 0.00), (66.1, 0.00), (67.1, 0.00), (68.1, 0.00), (69.1, 0.00), (70.1, 0.00), (71.1, 0.00), (72.1, 0.00), (73.1, 0.00), (74.1, 0.00), (75.1, 0.00), (76.1, 0.00), (70.1, 0.00), (72.1, 0.00), (73.1, 0.00), (74.1, 0.00), (75.1, 0.00), (76.1, 0.00), (76.1, 0.00), (75.1, 0.00),

(77.1, 0.00), (78.1, 0.00), (79.1, 0.00), (80.1, 0.00), (81.1, 0.00), (82.1, 0.00), (83.1, 0.00),(84.1, 0.00), (85.1, 0.00), (86.1, 0.00), (87.1, 0.00), (88.1, 0.00), (89.1, 0.00), (90.1, 0.00),(91.1, 0.00), (92.1, 0.00), (93.1, 0.00), (94.1, 0.00), (95.1, 0.00), (96.1, 0.00), (97.1, 0.00),(98.1, 0.00), (99.1, 0.00), (100, 0.00), (101, 0.00), (102, 0.00), (103, 0.00), (104, 0.00), (105, (0.00), (106, 0.00), (107, 0.00), (108, 0.00), (109, 0.00), (110, 0.00), (111, 0.00), (112, 0.00), (100, 0.(113, 0.00), (114, 0.00), (115, 0.00), (116, 0.00), (117, 0.00), (118, 0.00), (119, 0.00), (120, 0.00))(0.00), (121, 0.00), (122, 0.00), (123, 0.00), (124, 0.00), (125, 0.00), (126, 0.00), (127, 0.00), (127, 0.00), (127, 0.00), (128, 00(128, 0.00), (129, 0.00), (130, 0.00), (131, 0.00), (132, 0.00), (133, 0.00), (134, 0.00), (135, 0.00), (136, 0.00), (137, 0.00), (137, 0.00), (138, 0.00), (130.00), (136, 0.00), (137, 0.00), (138, 0.00), (139, 0.00), (140, 0.00), (141, 0.00), (142, 0.00), (143, 0.00), (144, 0.00), (145, 0.00), (146, 0.00), (147, 0.00), (148, 0.00), (149, 0.00), (150, 0.00), (15(0.00), (151, 0.00), (152, 0.00), (153, 0.00), (154, 0.00), (155, 0.00), (156, 0.00), (157, 0.00), (157, 0.00), (157, 0.00), (150, 0.(158, 0.00), (159, 0.00), (160, 0.00), (161, 0.00), (162, 0.00), (163, 0.00), (164, 0.00), (165, 0.00), (160, 0.00), (161, 0.00), (160.00), (166, 0.00), (167, 0.00), (168, 0.00), (169, 0.00), (170, 0.00), (171, 0.00), (172, 0.00), (173, 0.00), (174, 0.00), (175, 0.00), (176, 0.00), (177, 0.00), (178, 0.00), (179, 0.00), (180, 0.00))0.00), (181, 0.00), (182, 0.00), (183, 0.00), (184, 0.00), (185, 0.00), (186, 0.00), (187, 0.00), (188, 0.00), (189, 0.00), (190, 0.00), (191, 0.00), (192, 0.00), (193, 0.00), (194, 0.00), (195, 0.00), (196, 0.00), (197, 0.00), (197, 0.00), (198, 0.00), (190.00), (196, 0.00), (197, 0.00), (198, 0.00), (199, 0.00), (200, 0.00), (201, 0.00), (202, 0.00), (203, 0.00), (204, 0.00), (205, 0.00), (206, 0.00), (207, 0.00), (208, 0.00), (209, 0.00), (210, 0.00))(0.00), (211, 0.00), (212, 0.00), (213, 0.00), (214, 0.00), (215, 0.00), (216, 0.00), (217, 0.(218, 0.00), (219, 0.00), (220, 0.00), (221, 0.00), (222, 0.00), (223, 0.00), (224, 0.00), (225, 0.00))0.00), (226, 0.00), (227, 0.00), (228, 0.2), (229, 0.2), (230, 0.2), (231, 0.2), (232, 0.2), (233, 0.2), (234, 0.2), (235, 0.2), (236, 0.5), (237, 1.70), (238, 1.40), (239, 1.40), (240, 0.7), (241, 0.3), (242, 0.2), (243, 0.6), (244, 0.6), (245, 0.2), (246, 0.2), (247, 0.2), (248, 0.2), (249, 0.2),

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0.2), (609, 0.2), (610, 0.2), (611, 0.3), (612, 0.5), (613, 0.4), (614, 0.4), (615, 0.4), (616, 0.6), (617, 0.5), (618, 0.7), (619, 1.70), (620, 1.60), (621, 1.90), (622, 2.80), (623, 3.70), (624, 4.30), (625, 3.70), (626, 3.90), (627, 3.80), (628, 3.60), (629, 3.80), (630, 3.10), (631, 3.20), (632, 2.00), (633, 3.30), (634, 4.30), (635, 3.80), (636, 3.40), (637, 3.80), (638, 3.70), (639, 3.60), (640, 3.70), (641, 3.80), (642, 3.30), (643, 3.20), (644, 3.70), (645, 3.20), (646, 3.70), (647, 3.70), (648, 3.10), (649, 2.90), (650, 3.10), (651, 2.20), (652, 2.30), (653, 1.90), (654, 1.90), (655, 1.30), (656, 1.80), (657, 1.80), (658, 2.40), (659, 3.70), (660, 4.10), (661, 3.70), (662, 3.40), (663, 3.20), (664, 3.10), (665, 2.90), (666, 3.00), (667, 3.00), (668, 3.00), (669, 3.10), (670, 3.10), (671, 2.20), (672, 1.10), (673, 1.40), (674, 2.00), (675, 2.70), (676, 2.70), (677, 2.90), (678, 2.40), (679, 2.70), (680, 2.00), (681, 1.50), (682, 2.20), (683, 0.9), (684, 0.4), (685, 0.7), (686, 1.40), (687, 1.90), (688, 2.50), (689, 2.20), (690, 1.90), (691, 1.80), (692, 1.70), (693, 2.00), (694, 2.00), (695, 2.40), (696, 2.10), (697, 2.10), (698, 1.70), (699, 1.60), (700, 1.70), (701, 1.90), (702, 1.40), (703, 0.5), (704, 0.2), (705, 0.2), (706, 0.2), (707, 1.10), (708, 2.00), (709, 0.4), (710, 0.7), (711, 0.4), (712, 0.4), (713, 0.2)

Wind_Speed_2 = GRAPH(TIME)

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Wind_Speed_3 = GRAPH(TIME)

(0.00, 0.00), (1.00, 0.00), (2.00, 0.00), (3.00, 0.00), (4.01, 0.00), (5.01, 0.00), (6.01, 0.00), (7.01, 0.00), (8.01, 0.00), (9.01, 0.00), (10.0, 0.00), (11.0, 0.00), (12.0, 0.00), (13.0, 0.00), (14.0, 0.00), (15.0, 0.00), (16.0, 0.00), (17.0, 0.00), (18.0, 0.00), (19.0, 0.00), (20.0, 0.00), (21.0, 0.00), (22.0, 0.00), (23.0, 0.00), (24.0, 0.00), (25.0, 0.00), (26.0, 0.00), (27.0, 0.00), (28.0, 0.00), (29.0, 0.00), (30.0, 0.00), (31.0, 0.00), (32.0, 0.00), (33.0, 0.00), (34.0, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (30.1, 0.00), (41.1, 0.00), (35.0, 0.00), (36.1, 0.00), (37.1, 0.00), (38.1, 0.00), (39.1, 0.00), (39.1, 0.00), (40.1, 0.00), (41.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00), (40.1, 0.00),

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1.20), (387, 0.9), (388, 1.30), (389, 1.60), (390, 1.60), (391, 1.30), (392, 1.40), (393, 1.50), (394, 1.30), (395, 0.3), (396, 0.2), (397, 0.3), (398, 0.7), (399, 0.7), (400, 0.6), (401, 0.9),(402, 0.7), (403, 0.4), (404, 0.9), (405, 0.8), (406, 0.7), (407, 1.10), (408, 1.80), (409, 2.00),(410, 1.90), (411, 1.80), (412, 1.40), (413, 1.60), (414, 0.8), (415, 0.7), (416, 0.9), (417, 0.7), (418, 0.2), (419, 0.2), (420, 0.2), (421, 0.2), (422, 0.2), (423, 0.2), (424, 0.2), (425, 0.2), (4260.3), (427, 0.5), (428, 0.5), (429, 1.20), (430, 1.20), (431, 1.30), (432, 1.60), (433, 1.80), (434, 1.10), (435, 0.3), (436, 0.7), (437, 1.40), (438, 1.20), (439, 1.20), (440, 0.8), (441, 0.7),(442, 0.4), (443, 0.2), (444, 0.2), (445, 0.2), (446, 0.2), (447, 0.2), (448, 0.2), (449, 0.2), (4500.3), (451, 0.2), (452, 0.2), (453, 0.4), (454, 0.9), (455, 1.00), (456, 1.50), (457, 2.10), (458, 1.60), (459, 1.20), (460, 1.70), (461, 1.90), (462, 1.10), (463, 0.8), (464, 0.7), (465, 0.2), (466, 0.2), (467, 0.2), (468, 0.2), (469, 1.90), (470, 2.30), (471, 2.00), (472, 2.10), (473, (474, 2.40), (475, 1.00), (476, 0.8), (477, 1.00), (478, 1.70), (479, 1.30), (480, 1.40), (480(481, 1.90), (482, 1.40), (483, 1.10), (484, 2.20), (485, 2.30), (486, 2.30), (487, 2.00), (488, (0.7), (489, 2.30), (490, 3.00), (491, 1.40), (492, 1.30), (493, 1.10), (494, 1.70), (495, 0.3), (49(496, 0.2), (497, 0.7), (498, 1.10), (499, 1.10), (500, 0.5), (501, 0.3), (502, 1.00), (503, 1.50), (504, 2.30), (505, 2.00), (506, 2.00), (507, 0.9), (508, 1.40), (509, 1.80), (510, 2.80), (511, 2.80), (511, 2.80), (511, 2.80), (511, 2.80), (511, 2.80), (512, 2.80), (512, 2.80), (513, 2.80), (513, 2.80), (513, 2.80), (513, 2.80), (5142.30), (512, 2.00), (513, 2.10), (514, 2.20), (515, 1.90), (516, 1.90), (517, 2.20), (518, 1.20), (519, 2.40), (520, 2.40), (521, 1.20), (522, 1.30), (523, 0.7), (524, 0.3), (525, 0.3), (526, 0.5),(527, 0.6), (528, 1.00), (529, 1.10), (530, 1.50), (531, 2.10), (532, 2.10), (533, 1.40), (534(535, 1.50), (536, 1.00), (537, 0.8), (538, 0.3), (539, 0.2), (540, 0.2), (541, 0.2), (542, 0.2), (541, 0.2), (542, 0.2), (541, 0.2), (542, 0.2), (541, 0.2), (542, 0.2), (541, 0.2), (542, 0.2), (542, 0.2), (542, 0.2), (543, 0.2), (544, 0.2), (50.2), (543, 0.2), (544, 0.2), (545, 0.2), (546, 0.2), (547, 0.2), (548, 0.2), (549, 0.2), (550, 0.3), (551, 0.5), (552, 0.6), (553, 0.8), (554, 1.20), (555, 0.9), (556, 1.30), (557, 1.60), (558, 1.60),(559, 1.30), (560, 1.40), (561, 1.50), (562, 1.30), (563, 0.3), (564, 0.2), (565, 0.3), (566, 0.7),

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Yield =

(Unpollinated__Flowers*0.616*0.496*0.00220462262)+(Pollinated_Flowers*((IF(Bluecrop =1)THEN(1.55)ELSE(IF(Jersey=1)THEN(1.21)ELSE(IF(Duke=1)THEN(1.61)ELSE(IF(Elli ott=1)THEN(1.24)ELSE(IF(Liberty=1)THEN(1.55)ELSE(0))))))*(0.00220462262))

 $Yield_2 =$

 $(Unpollinated_Flowers_2*0.616*0.496*0.00220462262) + (Pollinated_Flowers_2*((IF(Blue crop=1)THEN(1.55)ELSE(IF(Jersey=1)THEN(1.21)ELSE(IF(Duke=1)THEN(1.61)ELSE(IF(Elliott=1)THEN(1.24)ELSE(IF(Liberty=1)THEN(1.55)ELSE(0))))))) \\ (0.00220462262))$

 $Yield_3 =$

 $(Unpollinated_Flowers_3*0.616*0.496*0.00220462262) + (Pollinated_Flowers_3*((IF(Blue crop=1)THEN(1.55)ELSE(IF(Jersey=1)THEN(1.21)ELSE(IF(Duke=1)THEN(1.61)ELSE(IF(Elliott=1)THEN(1.24)ELSE(IF(Liberty=1)THEN(1.55)ELSE(0))))))) \\ (0.00220462262))$

APPENDIX B

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: _____2013-03_____

Varying strategies of managed pollinator investment to optimize highbush blueberry (*Vaccinium corymbosum* L.) pollination and yield

by Anna K. Kirk

Museum(s) where deposited:

Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

T.LL D 1	377 1	•
Table B.I.	voucher	specimens.

Family	Genus-Species	Life Stage	Quantity	Preservation
Apidae	Apis mellifera	adult	10	pinned
Apidae	Bombus impatiens	adult	10	pinned

LITERATURE CITED

LITERATURE CITED

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