CONSIDERING A ROLE FOR NATIVE PLANT CULTIVARS IN ECOLOGICAL LANDSCAPING: AN EXPERIMENT EVALUATING INSECT PREFERENCES AND NECTAR FORAGE VALUES OF *PHLOX* SPECIES VS. ITS CULTIVARS

by

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ABSTRACT

In the face of rapidly declining pollinator populations and a growing awareness of biological diversity lost through habitat destruction, many citizens are opting to transform their home landscapes into native plant havens to support wildlife. When gardeners visit nurseries to purchase native plants, however, they often encounter numerous cultivars, which may or may not provide equivalent ecological benefits to insects and other wildlife. To address this issue, in 2015 research was conducted in the Mt. Cuba Center Trial Garden in Hockessin, Delaware, USA that compared insect attraction, nectar quality and floral characteristics between U.S. Eastern *Phlox* species and associated cultivars. In total, 6 straight species, 2 subspecies and 15 cultivars were sampled to evaluate the factors having the greatest influence on insect visitation.

The results from this experiment suggest that certain *Phlox* cultivars, especially those selected from the wild, are more attractive to insects than their straight species counterparts. For the majority of *Phlox* cultivars, however, insect attraction and nectar quality did not differ significantly in comparison to their associated straight species. In the case of *Phlox paniculata* and its cultivars, the narrowness of a flower's corolla, in particular, has a strong influence on insect attraction. These results lend support to the

notion that specific cultivars can serve an important role in ecological landscaping by providing vital habitat to insects and other wildlife.

This study was among the first to test attraction between multiple cultivars and straight species for a specific genus. With myriad untested plants, there are significant opportunities for advancement of this type of research moving forward. Ultimately, additional experiments are recommended to better assess the individual characteristics governing insect preference in native plant cultivars.

Chapter 1

INTRODUCTION

With increasing public awareness of pollinator declines and burgeoning interest in sustainable and ecological gardening, the time is ripe for widespread adoption and sales growth of native plants. Choosing native plants at a nursery can prove challenging, however, as cultivars of native plants have become increasingly ubiquitous in the marketplace. Since native cultivars are often sold directly alongside straight species plants, it is important to evaluate whether the ecological benefits they provide to insects are enhanced, diminished or similar in comparison to straight species. Indeed, testing the effects that ecological gardening and landscaping have on bolstering invertebrate populations will better inform nursery owners, plant breeders and the gardening public about the species and cultivars with the greatest potential for supporting wildlife in their home regions. With this in mind, in 2015 I established a comparative experiment at the Mt. Cuba Center in Hockessin, Delaware to evaluate insect attraction and measure nectar quality in *Phlox* cultivars versus straight species. Since few trials have been conducted in the United States (and globally) to assess ecological differences between these two plant groups, each study adds considerable value in helping regional gardeners to better understand the impact of their planting choices.

Challenges of Habitat Loss and Species Extinction in the Contemporary Era

Today, human society faces unparalleled species declines and rates of extinction, which threaten biodiversity across the planet (Pimm & Raven 2000; Barnosky et al. 2011). The rate of species loss is so pronounced that anthropologists increasingly refer to our current era as the Anthropocene, whereby human activities have an effect on the Earth's environment similar to that transpiring on a geologic time scale (Ehlers 2006; Lewis & Maslin 2015). Widespread losses of biological diversity across multiple taxonomic orders have led some researchers to claim that we have entered a 6th major extinction period, where the rate and magnitude of species extinctions is significantly higher (estimated at 1000x) than the background extinction rate (Ceballos et al. 2015; De Vos et al. 2015). In particular, habitat destruction, deforestation, industrial agriculture, urbanization and global climate change, are altering planetary environmental systems, with serious repercussions for species declines in impacted ecosystems across the planet (Rockström et al. 2009). As our global population continues to increase, more land will inevitably be developed, leading to further habitat losses in ecosystems across the planet (Holdren & Erlich 1974). Furthermore, as Earth's climate changes, plant and wildlife species will face exacerbating stressors that threaten their future survival, which will have cascading effects on trophic food webs, ultimately affecting community ecology on both widespread and local levels (Petchey et al. 1999; Walther et al. 2002; Hoegh-Guldberg & Bruno 2010). At its current trajectory, anthropogenic climate change is expected to result in biodiversity losses of 20-30% for species across the planet (Barker et al. 2007).

In the United States, explosive population growth throughout the 20th and 21st centuries has fuelled the conversion of natural landscapes towards agricultural, industrial, commercial and residential uses, resulting in losses in ecosystem services (Lawler et al. 2014). In 2014, the National Resource Conservation Service classified 112 million acres of land in the U.S. as urban use, while the National Agricultural Statistics Service recognizes 406 million acres as cropland (Nickerson et al. 2015). The conversion of these vast acreages of habitat has significant effects on native plant and wildlife species, resulting in alterations to community assemblages (McKinney 2002). As our awareness grows about the loss of biodiversity across the globe, many ecologists are striving to educate the public about the need for increased conservation measures including planting native plants, controlling the spread of invasive species, instituting protections for sensitive and ecologically-important landscapes, practicing adaptive land stewardship, and launching effective ecological restoration projects (Kessler et al., 1992; Wilson et al., 2007; Bullock et al., 2011).

While industrial and agricultural development frequently result in drastic, long-lasting land disturbance, strategic residential development can incorporate native vegetation at a property's margins, providing small but important pockets of refugia for urban wildlife species (Lerman & Warren 2011; Ikin et al. 2013; Soga et al. 2014). Additionally, landscaping with an appropriate mix of plant species can increase habitat for wildlife species displaced by human development by providing areas of shelter, food and other resources (Rudd et al. 2002; Burghardt et al. 2009). Unfortunately, landscaping in residential areas frequently does not reflect the natural plant community that existed in an area prior to development, but instead is associated with the replacement of native flora by exotic species (McKinney 2006). Furthermore, some of these species have the potential to become invasive in the landscape, which can intensify stressors on native ecosystems (Gavier-Pizarro et al. 2010). While exotic plants are often selected for their aesthetic qualities, widespread availability and affordability, an increasing awareness of their deleterious ecological effects is leading some homeowners to re-evaluate their landscaping choices on a broader level (Ecological Landscaping Alliance, *personal communication*, 9 March 2016).

One measure to promote habitat recovery is through the application of native plants in residential landscapes (Tallamy 2009). While gardening with native plants is gaining popularity (Castorani, S. & Pilker, T., *personal communication*, 15 February 2016), options are often limited in the marketplace (Hooper et al. 2008; Crewe 2013). Frequently, what are available from retail nurseries are cultivars of native plants, which may or may not provide equivalent benefits to wildlife as their straight species counterparts. Significantly, very few studies have attempted to measure ecological differences between native plant cultivars and straight species, and herein lies the principal basis for this experiment.

Introduction to Pollination and Contemporary Challenges

Since plants are non-motile, they rely on vectors to transfer genetic material. Abiotic factors like wind and water are estimated to be involved in 20% of angiosperm pollinations, while biotic agents are responsible for the remaining 80% (Ackerman 2000). The pollination process in angiosperms begins with pollen grains being produced by stamens, male reproductive organs in flowering plants. Pollination describes the actual process through which pollen gets transferred from the anther to the stigma in plants, by way of wind, water or a wildlife agent. When pollen lands on a plant stigma, the pollen travels down the style via a pollen tube, eventually penetrating the ovule and delivering sperm cells to form an embryo. The result of fertilization and subsequent reproduction via seeds is the emergence of a new generation of plants exhibiting characteristics from both parents.

Insect pollinators are an integral component of global biodiversity, uniting two biological kingdoms through entomophily, a fundamental ecological process resulting in plant reproduction. Pollination by insects is a globally significant ecosystem service, providing immense economic and environmental benefits to humans. In 2005, the global economic value of insect pollination was estimated at over $173 billion USD (Gallai et al. 2009). In the United States alone, insects are estimated to produce economic benefits totalling $57 billion USD per year through pollination, pest control, wildlife nutrition and nutrient recycling (Losey & Vaughan 2006). Insect pollinators which commonly include bees, beetles, butterflies, moths, ants, flies, and wasps, play a significant role in the daily lives of humans by enabling the process of pollination and reproduction in 75% of the world's leading food crops, which results in increased fruit yield and seed set (Klein et al. 2007).

Many of Earth's landscapes are naturally rich with pollinators. Across the world's tropical and temperate zones, 87.5% of the world's 352,000 flowering plants have evolved to attract pollinators and rely on them for reproduction (Ollerton et al. 2011). Hundreds of thousands of pollinators are thought to exist on the planet with the overwhelming majority (~99%) in class *Insecta* (Nabhan & Buchmann 1997). With approximately 1,000,000 described insect species and an estimated 6-10 million total extant species, the coevolution of plants with their insect counterparts represents a major advantage in ensuring a high degree of reproductive success (Chapman 2009).

Alarmingly, the last few decades have witnessed sharp declines in populations of pollinators globally. Many factors have likely contributed to these declines including: habitat degradation, increased insecticide usage, and widespread prevalence of diseases and pests (Cane & Tepedino 2001). Though pollination is considered a key ecosystem service, it is frequently cited as having an uncertain future in both agricultural and ecological systems (Kearns et al. 1998). As one example, recent media coverage has informed the public about the growing problem of "Colony Collapse Disorder", a phenomenon in which European honeybees (*Apis mellifera*) experience mass die-offs or simply disappear from their hives without a detectable trace (vanEngelsdorp et al. 2009). While managed honeybee hives provide significant pollination benefits for fruit and vegetable farmers worldwide, by many contemporary estimates they account for only 39-57% of total pollination events, with wild pollinators contributing the rest (Allsopp et al. 2008). Additionally, European honeybees are thought to be poor substitutes for pollinating many North American native plant species in comparison to their wild counterparts (Garibaldi et al. 2013). Several deleterious agricultural practices have been implicated in causing pollinator deaths (Kluser & Peduzzi 2007), but in spite of this, policy actions at the governmental level to support pollinators have been insufficient in stemming continued losses (Byrne & Fitzpatrick 2009). The decline of both wild and domesticated pollinators is a serious cause for alarm, and future research and efforts aimed at preserving habitat and reversing this trend are important to ensure continued pollination services for mankind and the natural world.

Plant-Insect Relationships (Coevolution and Mutualism)

In 1964, Dr. Peter Raven and Dr. Paul Erlich published a seminal article introducing the notion of coevolution. In their paper they explained how butterflies alter their metabolism to overcome plant defenses, resulting in an evolutionary response in both groups, which drives specialization and speciation (Erlich & Raven 1964). This hypothesis was ground-breaking in that it established a primary mechanism driving evolutionary change (selective pressure) across biological kingdoms, resulting in two or more species that can become dependent on each other for their success and/or survival. An example of this may include insect pollination, where insect groups induce a plant's flowers to undergo morphological changes, leading, in turn, to adaptive radiation of insect mouth parts. Additionally, plants may adapt the chemical constituents of their nectar to attract individual species (specialization) or a broad array of species (generalization), to ensure successful pollination. Included within the former is the relationship between yucca moths (primarily *Tegeticula* spp. and *Parategeticula* spp.) and various Yucca species, which are reliant on each other for reproduction and continued survival (Pellmyr 1999).

Coevolution and, indeed, mutualisms (cooperative interactions among species) are key concepts for anyone practicing ecological gardening and landscaping since they reveal evidence that planting natives imparts greater ecological benefits to native wildlife than exotic species. In most cases, native plant species evolved in tandem with native insects to provide them with: nectar and pollen as floral rewards, habitat as their preferred host species, and with other resources essential to their continued existence (Memmott & Waser 2002; Burghardt et al. 2009; Issacs et al. 2009;). In fact, many ecologists now believe that virtually every insect species on earth is involved in one or more coevolutionary interactions (Bronstein et al. 2006).

The early evolution of flowering plants developed through coevolution with insect pollinators (Ren 1998). As time has proceeded, evolutionary changes and speciation in plants and pollinators is likely more a reflection of diffuse multispecies interactions, where selection pressures imposed by one species may be opposed, constrained or modified by selection imposed by another species (Fenster et al. 2004). In the case of pollination, an example exists in *Collinsia heterophylla*, which has evolved specialized attraction characteristics for a functional group of long-tongued bees, while still being capable of pollination by 14 different animal species (Armbruster et al. 2002). Although *Phlox* are not reliant on a single invertebrate species for pollination, the majority of Eastern U.S. species are adapted for pollination by diurnal Lepidopterans, indicating a strong mutualistic relationship (Grant & Grant 1965). With regard to *Phlox*, their ability to attract pollinators and serve as a nectar source through much of the summer qualify them as good options for gardeners interested in supporting wildlife in the home landscape.

Introduction to Nectar

As a primary variable in my study, a definition and overview of nectar is warranted. In brief, nectar is a sugary liquid produced by glands in flowers as a means of attracting pollinating agents to plants, thus improving reproduction (Wykes 1952a). The principal component of nectar is sugar, in the form of the disaccharide sucrose and its component monosaccharides, fructose and glucose (Nicholson & Thornburg 2007). For years, researchers have known that sucrose-dominant nectars are closely associated with long-tubed flowers, while fructose and glucose-dominant nectars typify more "open" flowers with exposed nectars (Percival 1961). In addition to sugar, nectar contains a plethora of minor constituents including proteins, amino acids, lipids, antioxidants, alkaloids, ions, phenolics, vitamins, organic acids, and other compounds (Baker & Baker 1983). While relatively few studies have attempted to determine the biological significance of the gamut of minor nectar constituents, investigations have uncovered strong pollinator relationships with sugar and amino acid concentrations in flowers (Baker & Baker 1990; Mevi-Schütz & Erhardt 2005; Nepi 2014). For instance, flowers where sucrose is the dominant sugar tend to attract a wide range of Hymenopterans, Lepidopterans, and hummingbirds as their principal pollinators (Wykes 1952a; Percival 1961). On the other hand, flowers with dominant glucose and/or fructose tend to be preferred by passerine-birds, bats, Dipterans and Coleopterans (Baker & Baker 1990; Petanidou 2005; Nicholson 2007). With regard to amino acids, both proteinogenic and non-proteinogenic based amino acids have been shown to attract and provide fitness benefits to various pollinator functional groups (Mevi-Schütz & Erhardt 2005; Nepi 2014).

Nectar is thought to have originated before the late-Jurassic Period as inferred by the evolution of specialized nectar-sucking mouthparts in Dipterans (Ren 1998). Contemporary examples of pollination in basal angiosperms provide further evidence that the earliest pollinators likely included flies, moths (Gnetales) and beetles (Cycadales) (Thien et el. 2000). Prior to the emergence of nectar, plants likely generated excess pollen as a primary reward for visiting insects (Bronstein et al. 2006). The development of nectar in flowering plants to entice biotic pollination represented a major evolutionary advance in Kingdom Plantae, which biologists have theorized helps explain the vast diversification of angiosperms (Bronstein et al. 2006). In particular, plant evolution appears to have developed around suites of floral traits aimed at attracting specialized functional groups of pollinators, resulting in the concept of pollination syndromes (Grant & Grant 1965; Fenster et al. 2004; Bronstein et al. 2006). While pollination syndromes can be useful as a metric for arranging plants by pollinator functional group (Fenster et al. 2004), current prevailing theories suggest that plants are mostly primed towards attracting generalist species rather than specialists (Armbruster et al. 1999; Ollerton et al. 2009;

Gómez et al. 2014). Although the phlox family (Polemoniaceae) initially provided one of the most influential arguments for adaptation to specialized pollinators (Grant & Grant 1965), the genus *Phlox* represents a blend of the two concepts, where pollination is accomplished primarily through attraction of a range of Lepidopterans, with a few exceptions for Western U.S. species that appear to be pollinated solely by long-tongued Hymenoptera (Tepedino 1979; Strakosh & Ferguson 2005).

For the majority of *Phlox* in this study, a range of both endothermic (internal heat generating) and ectothermic (dependent on external heat) pollinators are attracted to nectar, indicating that phlox is able to meet the energetic needs of a broad range of Lepidopterans. For instance, hovering hummingbird clearwing moths (*Hemaris thysbe*) as endothermic pollinators, theoretically require a higher nectar concentration than ectothermic butterflies, yet both successfully pollinate a majority of Eastern U.S. *Phlox* species (Corbet 2006). Again, through their ability to attract a broad range of native Lepidoptera, *Phlox* present a compelling selection for gardeners seeking to support native wildlife in their home yards and landscapes.

Introduction to Phlox

Phlox L. (family Polemoniaceae) is a genus of 67 total species (66 native to North America and one native to Siberia), with a geographic range encompassing Alaska to New England, including southern Canada, and Florida to California, including northern Mexico (Wherry 1955). *Phlox* are native to a wide array of habitat types including:

deserts, prairies, marshlands, forests, meadows, tundra and sub-alpine zones (Locklear 2011). They exhibit a wide variety of growth habits, from mat-forming montane species, to tall (over 1 metre) herbaceous types encountered in prairies and woodlands. In general, *Phlox* in the Western U.S. inhabit xeric ecosystems including: deserts, sagebrush steppe, open pine forests, rocky slopes, volcanic fields, serpentine outcrops, canyons, thickets and cliff sides (Wherry 1955). *Phlox* in the Eastern U.S. are common in habitats including moist woods and meadows, and tend to encompass larger, more erect growing forms than the U.S. West (Wherry 1955).

Phlox flowers are showy and attractively coloured, and have been consistently popular ornamental plants since colonial times (Locklear 2011). Their use is especially entrenched in rock gardens and perennial borders worldwide. *Phlox* were among the first plant genera traded to Europe by American nurserymen, with *Phlox glaberrima* listed as being grown in 1726 in the Society of Apothecaries' Physic Garden in London's Chelsea District, the first published account of its cultivation in Europe (Locklear 2011). Over the years, many *Phlox* species (most notably *P. paniculata*, *P. divaricata* and *P. subulata*) have been selected and hybridized to develop bolder, longer-lasting blooms, new colour combinations and a range of other traits. In the contemporary era, plant breeders in Japan and Holland have led the production of new phlox cultivars (Google Patents 2016). As Locklear (2011) states, "The Dutch have been the most serious breeders of summer phlox in recent years, aiming at unnatural flower sizes and colorations and for very short plants that can be used at the front of the border or in containers." Phlox series emanating from the Netherlands include: Flame® and Volcano® (aka Bar series from breeder Gosen B.H.

Bartels), Candy Store® (breeder Hubertus Joseph Tonies), Junior™ (breeder Mart Vester), and multiple introductions from Jan Verschoor (Google Patents 2016).

Although Carl Linnaeus named the genus *Phlox* (Greek meaning "flame") in reference to a description of *Phlox glaberrima* from *Hortus Elthamensis,* typical *Phlox* flowers run in the blue and red spectra, and most commonly include shades of white, pink and lavender (Locklear 2011). These colours combined with their fragrant nature and salverform flower shapes lend themselves to pollination by various Lepidoptera species including a variety of moths and butterflies (Grant & Grant 1965). The fact that they tend to be long-lived plants with a protracted blooming period has resulted in them being recognized as a top pollinator plant by Federal agencies, gardening advocacy organizations, and businesses across the United States, including the United States Department of Agriculture (USDA)- Natural Resources Conservation Service (NRCS), the Pollinator Partnership, American Beauties Native Plants and others. (United States Department of Agriculture 2016b; Pollinator Partnership 2016; American Beauties 2016). Most varieties of *Phlox* have been shown to produce consistent nectar throughout their flowering season, attracting a wide diversity of insect pollinators and non-pollinating species including: butterflies, moths, flies and bees (Strakosh & Ferguson 2005). In addition, the leaves of *Phlox* are documented to provide an important source of food for Lepidoptera larvae including: Tiger moths (*Grammia* spp.), Owlet moths (Noctuidae), and *Schinia indiana*, the phlox moth, which is an endangered species in the upper Midwest that feeds exclusively on prairie phlox, *Phlox pilosa* (Swengel & Swengel 1999; Singer & Stireman 2001; Wagner 2011).

The majority of *Phlox* are self-incompatible and, therefore, rely on insect pollination for successful reproduction (Levin 1978; Hendrix 2000; Wiggam & Ferguson 2005). In a study by Shelly Wiggam and Carolyn Ferguson (2005), 11 different species of pollinators were noted over a 2-year sampling season on *Phlox divaricata*. While most visitors were evaluated to be effective pollinators, the lack of visitation frequency for many of the insects led them to conclude that the frequently occurring snowberry clearwing moth (*Hemaris diffinis*) is far and away the most important pollinator compared to all other insects for *Phlox divaricata* reproduction.

In 1955, Edgar Wherry produced the first comprehensive reference monograph devoted to the systematics of the genus *Phlox*, placing its 67 species into 3 sections (Protophlox, α-Phlox, Microphlox) and 17 subsections based primarily on floral and seed characteristics (Wherry 1955). More recently, phylogenetic analysis work carried out by Dr. Carolyn Ferguson and her team at Kansas State University has led to additional conclusions about the evolutionary relationships among *Phlox* species (Figure 1.1), but notably, significant incongruence still exists among published *Phlox* phylogenies (*personal communication* with Dr. Ferguson). Current and ongoing phylogenetic sampling is important to help shed light on the relationships among *Phlox*, which can assist plant breeders in their efforts to produce new selections and hybrids for garden landscapes.

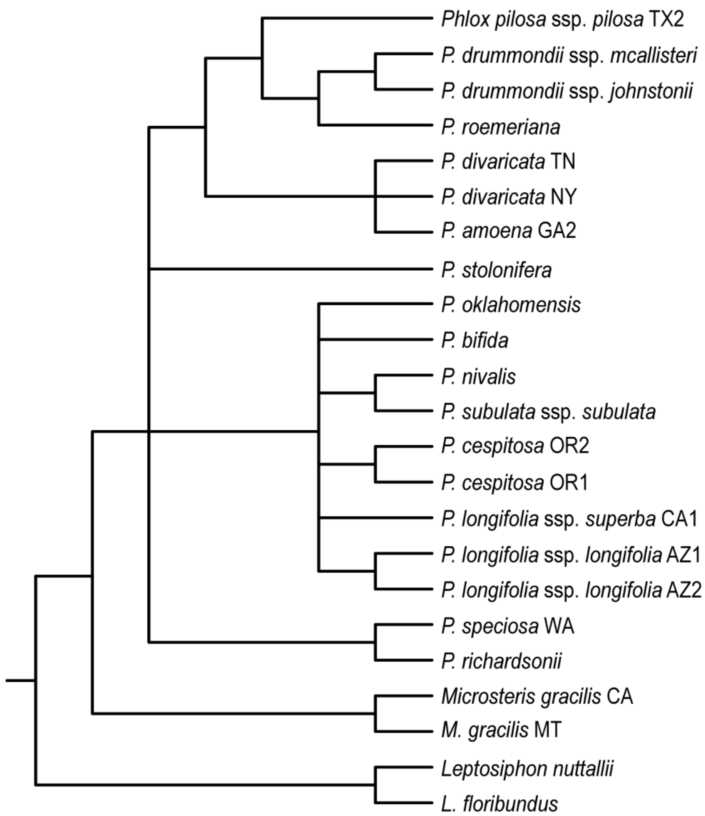


Figure 1.1 Phylogenetic tree of Eastern North American Phlox species (and close relatives) produced by Dr. Carolyn Ferguson at Kansas State University. The Polemoniaceae species in this pruned phylogenetic tree show completely resolved relationships entirely in common between Internal Transcribed Spacer (ITS) and Chloroplast DNA (cpDNA) sequencing outcomes (unpublished data 2015 from Ferguson Lab, cited with permission - http://www.k-state.edu/fergusonlab/phlox.html).

Background of *Phlox* Trial at Mt. Cuba Center

In October 2014, I met with Mr. George Coombs, Mt. Cuba Center's Research Horticulturist, to discuss plant trials and ecological experiments being conducted in their trial garden through the Mt. Cuba Center Ecological Fellowship (University of Delaware

2016). At this meeting we determined an opportunity for research focused on *Phlox*, to investigate differences in nectar quality and insect attraction between cultivars and straight species.

The Mt. Cuba Center (henceforth referred to as MCC) is a public garden located in the rolling hills of northern Delaware with over 50 acres of display gardens and over 500 acres of natural lands. As a public garden, MCC's mission is to "inspire an appreciation for the beauty and value of native plants and a commitment to protect the habitats that sustain them" (Mt. Cuba Center 2016a). Through this vision, living plant collections at MCC are focused on taxa native to the Eastern temperate forests of the United States, with a particular emphasis on Appalachian Piedmont species (Mt. Cuba Center 2016b). For public outreach, MCC conducts research, teaches courses and hosts workshops designed to inspire environmental stewardship (Mt. Cuba Center 2016a). Since 1988, MCC has also worked with nursery owners to introduce over a dozen native cultivars with exceptional ornamental attributes to the marketplace, including widely popular selections Golden Fleece autumn goldenrod (*Solidago sphacelata* 'Golden Fleece') and Purple Dome New England Aster (*Symphyotrichum novae-anglicum* 'Purple Dome') among others (Mt. Cuba Center 2010).

In support of research, MCC conducts plant trials to evaluate and promote native species and their related cultivars for their horticultural merits to gardeners in the Mid-Atlantic region. Plant trials at MCC began in 2002, and in July 2012 a formal trial garden was unveiled, affirming their commitment to provide quality research information to the greater public garden community. Plant trials at MCC encompass select groupings of native plants and associated cultivars, which are evaluated in 3-year trials for their ornamental characteristics and garden performance including pest and disease resistance, frost tolerance (USDA Plant Hardiness Zone 7a), and other measures (United States Department of Agriculture 2016a). The MCC Trial Garden includes a 5,000 square foot shade structure that was installed in 2014, which allows for testing shade-adapted species such as *Phlox stolonifera* and *Phlox divaricata*. To date, plant trials completed at MCC have included *Aster*, *Echinacea*, *Heuchera*, *Coreopsis* and *Baptisia*, with *Monarda* (to be completed in 2016) and *Phlox* (running through 2017) still under trial.

The *Phlox* trial at MCC encompasses over 140 species and cultivars, and as such, is the largest trial ever to be conducted on an individual genus in their history. In the *Phlox* trial, the majority of varieties planted are *Phlox paniculata* cultivars, which reflects their dominance in the nursery marketplace. By and large, *Phlox* cultivars have been developed from 3 species: P. *drummondii*, *P. paniculata*, and *P. subulata*; nevertheless, additional species have been introduced into the horticulture trade in recent years and are gaining popularity (Zale 2014). To further this effort, researchers at the Ohio State University Ornamental Plant Germplasm Center have focused on obtaining comprehensive germplasm materials for *Phlox* of the Eastern United States, with a goal of facilitating their commercial development in the nursery sector and enhancing the study of their ecological, phylogenetic and medicinal attributes (Zale 2014).

Relationship of Invertebrates to *Phlox*

A major focus of this research is predicated on identifying the range of pollinators that are attracted to *Phlox* in the U.S. Mid-Atlantic region, in order to assess species richness for wild types versus their cultivar counterparts. While a book was written that specifically addressed pollinators of *Phlox* (Grant & Grant 1965), their surveys were carried out on wild types exclusively and made no attempt to sample cultivars in the garden. In general, the morphometry of flowers in the genus *Phlox* lend themselves to pollination by various lepidopteran species, however, the work of Karen and Verne Grant documented a number of other invertebrates utilizing phlox including: bumblebees (*Bombus* sp.), mason bees (*Osmia* sp.), leafcutter bees (*Megachilidae* sp.), beeflies (*Bombylius* sp.), hoverflies (*Syrphus* sp.), and *Conops* flies. In addition, a 2-year study by Dr. Carolyn Ferguson and Shelly Wiggam (2005) of Kansas State University which measured individual pollinator effectiveness through isolating pollination events by species, found that 4 pollinators were strongly correlated with successful seed set. These species included a dipteran beefly (*Bombylius* sp.), along with Lepidopterans: snowberry clearwing moth (*Hemaris diffinis*), Bilobed looper (*Megalographa biloba*), and Eastern tiger swallowtail (*Papilio glaucus*). The researchers were clear, however, in pointing out that variation in climatic conditions such as high winds, fluctuating temperatures and precipitation can all have an effect on the suite of pollinators that visit *Phlox* in any given year. Furthermore, the suite of pollinators may shift from region to region across the native range of a *Phlox* species, particularly if plants occur in an array of habitat types.

Anecdotal evidence from Dr. Peter Zale suggests that most insect visitors to natural *Phlox* populations are active early in the day, shortly after sunrise (*personal communication*, February 20, 2015). This applied to many of the species Dr. Zale encountered in the wild, which included 19 of the 22 species present in the Eastern United States. With *Phlox* flowers open throughout the day, butterflies and diurnal moths are the primary species of interest in the *Phlox* pollination system.

Project Overview

In this experiment, I set out to measure insect attraction and nectar sugar concentration of various *Phlox* species and cultivars, to determine which varieties provide habitat benefits for native pollinators and other insects. Ideally, these results will be used to make recommendations to landscapers and gardeners seeking appropriate *Phlox* types to maximize habitat value in the U.S. Mid-Atlantic region.

Research objectives include:

- Identify all insect visitors to the species level and compare their attraction to *Phlox* cultivars and straight species in the experiment.
- Measure nectar volume and sugar concentration in *Phlox* flowers, and correlate these values with insect visitation abundance and species richness.

- Measure the floral traits (including corolla length and width) of *Phlox* species and cultivars, and correlate with insect visitation abundance and species richness.

I hypothesize that *Phlox* straight species will attract greater insect abundance and species richness than cultivars. I theorize that this will result primarily from straight species producing more sugar-rich nectar, with a more complete nutritional profile than cultivars.

Chapter 2

LITERATURE REVIEW

This chapter reviews many of the known experiments that have been conducted to evaluate insect attraction and nectar benefits for North American native plant cultivars vs. straight species. With few specific experiments implemented, a review of research comparing ecological values of native plants with exotic species will also be described. Additionally, an overview of various measuring protocols used in nectaring studies will be described to elucidate the methods used in my experiment. Ultimately, this synopsis of research is aimed at justifying the primary research question of this thesis – are native plant cultivars as effective as straight species in attracting and supplying nectar resources to insects?

Benefits and Challenges of Planning Pollinator-Friendly Gardens

There is growing interest in landscaping with native plants, as gardeners address problems associated with losses of biological diversity brought about through habitat destruction. In particular, documented pollinator declines in recent years have inspired increasing citizen advocacy, resulting in the passage of legislation designed to protect pollinators and their habitats (Kluser & Peduzzi 2007; Byrne & Fitzpatrick 2009; Obama

2014). For gardeners wanting to integrate native plants into their home landscape, a trip to their local garden centre often yields an impressive array of native cultivars, with fewer options for native straight species plants. The breadth of native cultivars developed in the past few decades are frequently a result of nursery owners seeking distinctive products to distinguish themselves from their competitors. In many cases, these cultivars are marketed and sold alongside native plants, which gives the consumer the impression that they are interchangeable with straight species at providing habitat for native wildlife.

Since native cultivars can possess flowers that differ from straight species in colour, shape, size, abundance and bloom period, as well as nectar and pollen load and quality, they may not be comparable at attracting nectaring insects and furnishing them with ecological benefits. On the other hand, the increased blooming period and diverse floral characteristics of cultivars could serve to enhance insect visitation or even complement the rewards provided by straight species. With little research having investigated this topic, however, some leading conservation advocacy groups have taken a prohibitive stance on native cultivars, suggesting that they be considered inferior to straight species pending additional research to determine their habitat suitability for native wildlife (Wild Ones 2013). Herein lies the rationale for conducting an experiment of this nature, to determine if native cultivars attract and support an equal, greater, or lesser amount of nectaring insects than their native straight species counterparts.

Table 2.1 Benefits and Challenges associated with using Native Straight Species Plants and Cultivars. Adapted from White, A. (2016).

Benefits - Natives	Challenges - Natives	Benefits - Cultivars	Challenges - Cultivars
Provide ecological benefits to wildlife	Sometimes require large spaces in the garden to achieve maturity	Smaller forms can be tidier in gardens	May be inaccessible to pollinators and other wildlife
Safeguard plant conservation through maintaining genetic diversity	May spread aggressively and take over other plants in garden	New colour forms provide increased options for landscape design	Novelty means untested performance in the garden
Typically require fewer inputs than exotic plants	Fewer options for designing into landscape than cultivars	May entice gardeners to plant more ecologically	May be sterile leading to limited garden dispersal
Observing wildlife interactions may result in public's deeper commitment to environmental stewardship	Often difficulty sourcing plants from local ecotypes	Future market growth means more ornamental attributes available yearly	Less genetically diverse and potential for hybridization with native straight species

The impetus to increase pollinator habitat across the U.S. is being driven in part by Federal initiatives including the Pollinator Health Task Force, which has charged agencies with "planting pollinator-friendly vegetation and increasing flower diversity in plantings, limiting mowing practices, and avoiding the use of pesticides in sensitive pollinator habitats" (Obama 2014). In addition, the National Pollinator Garden Network was formed by a coalition of non-profit and garden industry leaders, with a goal of registering one million pollinator-friendly public and private gardens (National Pollinator Garden Network 2015). These initiatives have created strong incentives for landscapers to take advantage of the growing popularity of native plants by integrating them into their clients' gardens. Undoubtedly, these efforts to plant pollinator-friendly landscapes will result in the installation of thousands of acres of native cultivars, thereby creating a large-scale trial with uncertain ecological outcomes. This research, along with the following described experiments, provides a foundation for future work evaluating and comparing native cultivars with their straight species counterparts. With thousands of native cultivars presently on the market, the possibilities for future research are vast.

Ecological Studies Comparing Native Cultivars vs. Straight Species

At present, few experiments have published results comparing native cultivars vs. straight species for their ecological benefits. Research reveals only 6 projects in the United States, two of which are ongoing and four of which have been completed. All six projects are located in the Eastern United States. Of the 6 projects, only 2 (including this one) explored attraction and nectar characteristics for multiple species within a specific genus. The other 4 projects focused their comparisons on a single species and cultivar, selecting an array of genera.

While all 6 projects compared insect attraction between native straight species and their cultivars, 4 of the projects were focused on pollinator visitation to flowering perennials, while the other two evaluated leaf preferences as food for Hemipterans and caterpillars, respectively.

Evaluation of Pollinator Preferences for Native Flowering Perennial Species vs. Cultivars

The first known experiment that was initiated on this subject was a research project at the University of Vermont (UVM) carried out by Dr. Annie White, who analyzed 14 pairs of Eastern U.S. native flowering perennials. These pairs included a straight species and a commonly available cultivar. Ms. White began her experiment in 2011, under the guidance of UVM Extension professor Dr. Leonard Perry, and her preliminary data show that only one cultivar (*Veronicastrum virginicum* 'Lavendelturm') had enhanced attraction for insect pollinator groups (native bees, European honey bees) over its straight species analogue (White 2016). For 4 of the 14 comparisons, no measurable insect preference was noted (*Ascelpias tuberosa* 'Hello Yellow', *Monarda fistulosa* 'Claire Grace', *Penstemon digitalis* 'Husker Red', *Rudbeckia fulgida* 'Goldstrum'). The 9 remaining comparisons yielded results showing that straight species attract greater pollinator activity than their cultivar counterparts (*Achillea millefolium* 'Strawberry Seduction', *Agastache foeniculum* 'Golden Jubilee', *Baptisia australis* 'Twilite Prairieblues', *Echinacea purpurea* 'Pink Double Delight', *Echinacea purpurea* 'Sunrise Big Sky', *Echinacea purpurea* 'White Swan', *Helenium autumnale* 'Moerheim Beauty', *Symphyotrichum novae-angliae* 'Alma Poetschke', *Tradescantia ohiensis* 'Red Grape'). At the time of this writing, Ms. White has 3 research projects in preparation for publication (White 2016).

The first completed project that compared insect attraction between native flowering perennials and cultivars was the Bees, Bugs & Blooms Trial conducted through

Penn State University (PSU) Extension. This project began on August 29th, 2011 when Penn State Master Gardeners planted 4500 plugs on a 1/3-acre plot at PSU's Southeast Agricultural Research and Extension Center in Manheim, PA (Penn State University Department of Entomology 2016). From 2012-2015, two teams of staff and Master Gardeners monitored plants weekly for insect visitation, while also noting their horticultural performance in the garden. The PSU study compared 14 sets of flowering perennials, with 1-2 cultivars and a straight species analogue. After 3 years of data collection, the researchers concluded that "about 50% of the time, the species was better than the cultivar" (Penn State University Department of Entomology 2016). Interestingly, there were 2 instances in which one cultivar was more attractive than the straight species, while a second cultivar was less attractive than the same straight species (*Coreopsis verticillata* 'Zagreb' > *Coreopsis verticillata* > *Coreopsis verticillata* 'Moonbeam': *Symphyotrichum oblongifolium* 'October Skies' > *Symphyotrichum oblongifolium* > *Symphyotrichum oblongifolium* 'Raydons Favorite'). In one comparison, the cultivar and straight species each attracted 81 pollinators over the 3-year period (*Physostegia virginiana* vs. *Physostegia virginiana* 'Vivid'). In two cases, the straight species attracted far more pollinators than the cultivar (341 for *Symphyotrichum novae-angliae* vs. 66 for *Symphyotrichum novae-angliae* 'Purple Dome': 478 for *Monarda fistulosa* vs. 106 *Monarda fistulosa* 'Claire Grace'). Contrast this with a couple of cases where the cultivar outperformed the species (357 for *Coreopsis verticillata* 'Zagreb' vs. 180 for *Coreopsis verticillata*: 381 for *Symphyotrichum oblongifolium* 'October Skies' vs. 102 for *Symphyotrichum oblongifolium*). In their overall analysis of the project, these researchers concluded, “it appears that it is not possible to generalize that the cultivar is better than or poorer than the species.”

The final known study that is investigating insect attraction to native flowering perennials species vs. cultivars is being carried out by Owen Cass, M.S. student in Entomology and Wildlife Ecology at the University of Delaware. In 2016, Mr. Cass is entering into his third year of monitoring ecological trials at Mt. Cuba Center, and he will be examining insect attraction and nectar characteristics for the genus *Monarda* for a second consecutive year. In 2014, he examined various species and cultivars of *Coreopsis*. He has yet to publish the results of his experiments (Cass, *personal communication*).

Evaluation of Hemipteran Preferences for Leaves of Native Species vs. Cultivars

At present, a single study was completed which investigated hemipteran leaf preferences between native species and cultivars. The premise of this experiment is that cultivars are often selected for pest resistance, which could potentially limit their availability as food for leaf-sucking hemipterans and other invertebrate species.

This experiment was initiated in 2013 by University of Georgia Master of Science student Joseph Poythress III, under the direction of Dr. James M. Affolter (Poythress III 2015). Mr. Poythress’s experiment was established at the Mimsie Lanier Center for Native Plant Studies at the State Botanical Garden of Georgia in Athens. Five plant pairs were chosen with one commonly available cultivar and one straight species. Four of the pairs were Eastern U.S. native perennials (*Amsonia tabernaemontana* vs. *Amsonia* 'Blue Ice'; *Coreopsis grandiflora* vs. *Coreopsis* x 'Tequila Sunrise'; *Monarda fistulosa* vs. *Monarda fistulosa* 'Claire Grace'; *Oenothera fruticosa* vs. *Oenothera fruticosa* x 'Cold Crick') and the final pair was an Eastern U.S. native grass species (*Schizachyrium scoparium* vs. *Schizachyrium scoparium* 'Prairie Blues'). The target invertebrates for Mr. Poythress's study were true bugs (Order: Hemiptera) and insects were vacuumed, killed and sorted to species. His results showed that in the case of *Coreopsis grandiflora*, the straight species attracted far greater abundance and diversity of insects than the hybrid cultivar 'Tequila Sunrise', while for *Oenothera fruticosa*, the purported hybrid cultivar x 'Cold Crick' attracted a greater abundance, though no significant difference in terms of species richness (Poythress III 2015).

According to Mr. Poythress, his results suggest "that the ecological value of a plant species does not depend on whether the plant material is a selection (cultivar) or wild-propagated, but rather on the particular cultivar that is chosen." An important caveat with this study is that three of the selected cultivars are of known or suspected hybrid origin (known: *Coreopsis* x 'Tequila Sunrise'; suspected: *Oenothera fruticosa* 'Cold Crick' and *Amsonia* 'Blue Ice'). While this research helps to expand our knowledge of insect attraction to native plant cultivars in the southeastern U.S., it may be more helpful to compare cultivars with the species from which they are directly derived.

Evaluation of Caterpillar Preferences for Leaves of Native Species vs. Cultivars

The final known experiment investigating attraction to native species vs. cultivars is presently being carried out by Emily Baisden, M.S. candidate in Entomology and Wildlife Ecology at the University of Delaware. With a strong relationship between Lepidoptera and woody plants described through the evolution of plant defenses (Ehrlich & Raven 1964), her research is attempting to compare preferences for native woody plants and cultivars with altered leaf chemistry, stemming from their selection for pest-resistance. Ms. Baisden's research is focused on six traits that commonly drive cultivar selection: leaf color, plant habit, leaf variegation, disease resistance, fall color and enhanced fruiting. In 2016, she is entering into her third year of experimental monitoring and she has yet to publish results from her study (Baisden, *personal communication*).

Comparing Ecological Value of Native vs. Exotic Plants

Over the past few decades, a number of experiments have demonstrated the beneficial relationship that native plants have in supporting wildlife species. One of the more prominent recent studies to emerge comes via research by University of Delaware professor Dr. Doug Tallamy, who thoroughly surveyed academic literature to determine the number of lepidopteran larvae (caterpillars) supported by various ornamental and native host plants (Tallamy & Shropshire 2009). Of the top 20 most productive genera, all but one (*Pyrus*- 19th most productive) were plants native to the U.S. Mid-Atlantic region. For native Lepidoptera, native (particularly woody) plants supported fifteen times greater species richness than introduced ornamentals. Furthermore, the importance of planting natives to support caterpillars is apparent when considering terrestrial food webs, since they provide a vital source of nourishment for a wide variety of avian species, and are particularly vital to warblers and neotropical migrants (Tallamy & Shropshire 2009).

In another study, Burghardt et al. (2008) compared 6 pairs of landscaped properties in Southeastern Pennsylvania, with one site-pair conventionally planted in Eurasian grasses, Asian shrubs and introduced understory trees, and the other landscaped largely with native plants across vegetative strata. The researchers found that lepidopteran abundance was 4 times greater on native sites than on conventional sites, with 3 times the level of species richness. For breeding birds, diversity and abundance were greater on native properties for both insectivorous species and birds of conservation concern, a designation bestowed by the Cornell Lab of Ornithology to denote steadily declining avian migrating species (Rich et al. 2004).

While a number of studies have shown that native plants provide enhanced ecological benefits for birds and certain invertebrate orders (French et al. 2005; Burghardt et al. 2008), not all research has demonstrated clear advantages of natives over exotics for insect pollinators. For instance, The Biodiversity in Urban Gardens (BUGS) study out of Sheffield, England documented that "abundance and diversity of invertebrate species captured in gardens was rarely related to native plant species richness, indicating that 'wildlife-friendly' gardens need not be dominated by native planting" (Goddard et al.

2009). One plausible explanation is that gardens in urban locations (especially in the UK) tend to be planted with artificially dense amounts of vegetation that can be greater than would occur in unmanaged semi-natural areas (Goddard et al. 2009). Under this scenario, abundant floral rewards would ensure ample access to the resources necessary to successfully complete the life cycle of generalist pollinators in the UK and elsewhere.

Furthermore, a study by Matteson and Langellotto (2011) failed to observe an improvement in beneficial invertebrate richness (pollinators and predators) in gardens supplemented with small amounts of native plants, suggesting no improvement over gardens planted primarily in exotic plant species. On the contrary, these researchers actually recommend more substantial additions of native plants in order to have a greater measurable impact on beneficial insect richness. Indeed, conventional urban development fundamentally transforms the native vegetative composition of its immediate and surrounding areas in myriad ways through levelling forests, draining wetlands, paving meadows and erecting buildings across the landscape. These losses of large swaths of native plants undoubtedly alter the composition of native invertebrate communities, resulting in less species richness with dramatic, perhaps, irrevocable changes in native food webs. For these reasons, advocacy for planting native plants may have reduced ecological value for wildlife species in the urban heart of a city, whereas promoting native plantings outside of the urban sphere may provide significant ecological gains for wildlife denizens in suburban and rural areas.

Measuring Protocols used in Plant Evaluation Studies

As previously mentioned, relatively few studies have compared insect attraction for cultivars vs. straight species; therefore a brief survey of methods is in order to rationalize the approach used in this experiment. The following study provided guidance in determining a protocol for measuring insect visits in my experiment.

In 1999, Livio Comba and his colleagues carried out an experiment at the University of Cambridge Botanic Garden that compared insect visits among straight species and horticulturally-modified cultivars. This experiment was one of the first to compare these two plant groups, and was conducted over two summers in 1995 and 1996. In their study, the researchers made three sweeps of their trial plots in quick succession every 60-120 minutes, in an effort to obtain mean insect count values for each plant variety. As the study was located in an urban setting with a small range of invertebrate visitors, researchers were able to sight identify insects to species level or at least to colour group for bumblebees (Prŷs-Jones & Corbet 1991). An advantage of their methodology was that it employed a non-destructive insect sampling protocol, thereby adhering to ethical guidelines, without killing or harming invertebrates in order to conduct the experiment.

For *Phlox*, which are pollinated principally by Lepidopterans, my experiment did not require the capturing of insects for the purposes of identification using microscopy since they are relatively easy to identify with the unaided eye. Furthermore, visitors to phlox were staggered throughout the day, ensuring that monitoring was able to detect individual visits to each variety. Contrast this with studies on plants visited by numerous Hymenoptera, where estimation techniques are typically utilized to obtain an approximate visitor count. Such is the case for the research of my University of Delaware colleague Owen Cass, who has developed his own unique system for sorting through recorded samples to determine the richness and abundance of insects nectaring on *Monarda* and *Coreopsis* species and cultivars (Cass, *personal communication*).

Guidelines for Measuring Nectar

Extraction of nectar from flowers to measure volume and sugar content has been performed in experiments for decades (Kenoyer 1916; Corbet et al 1979; McKenna & Thomson 1988; Corbet 2003). Testing nectar is useful in that it provides a metric to gauge macronutritional benefits for visiting insects and can help to explain pollinator attraction to specific plant species (Perret et al 2001). When testing nectar, different approaches can be taken depending on experimental design and available resources. Many nectar surveys in the past have focused on standing crop measurements, which are taken from exposed flowers freely visited by insects. For researchers concerned with isolating nectar characteristics, placing bags on flowers to prevent invertebrate access can be an appropriate way to measure such values as: nectar recharge rate, flower nectar load and pollination efficacy (access granted to a single pollinator or pollinator group then restricted afterwards). A seminal text for researchers interested in establishing pollination studies is Techniques for Pollination Biologists by Carol Ann Kearns and David Inouye

(1993). The researchers highlight numerous considerations for designing experiments including abiotic and biotic factors, distance effects between plants, suitable plant patch size, ideas for tracking foraging behaviour, and other issues.

With regard to nectar, Kearns and Inouye document multiple methods for extraction starting with commonly used microcapillary tubes. Microcapillary tubes are inexpensive, readily available and have been used for a century to extract small amounts of nectar from flowers (Kenoyer 1916). Other advantages of microcapillary tubes include the speed of extraction and the ability to easily measure nectar volume by spanning the column length and dividing by total tube length. Particularly in experiments where flowers are harvested (destructive sampling) and single nectar measurements are obtained (non-repeat sampling), microcapillary tubes are great for field observations since they do not require the use of laboratory equipment and chemicals to capture volume and other data. Where repeated sampling of a flower is desired, however, microcapillary tubes can damage floral nectaries, and other techniques may be better suited under this scenario.

For capturing sugar content in the field, Kearns and Inouye touch on the ease of using a hand-held light refractometer, which measures the refractive index of the liquid in a sample. Hand-held refractometers most commonly display their measurements in degrees brix, which is a scale indicating sugar content in an aqueous solution- g solute/100g solution (Bolten et al 1979). The first proposed use of a refractometer is attributed to Park (1932) who suggested this method as an alternative to microchemical methods that had been used previously.

Modern day studies which measured nectar and provided inspiration for the techniques used in my study include the work of Livio Comba et al. (1999) who recorded standing crop nectar values for 10 species of British natives and naturalized plants in determining suitable resources for pollinators. In their study, the researchers used Microcaps® glass microcapillary tubes to extract nectar and a Bellingham + Stanley low-volume pocket refractometer to measure sugar content in nectar samples. The efficacy of these tools led me to employ them in my experiment as well.

Guidelines for Measuring Floral Parts

Floral parts can be an important metric when considering pollinator access, as well as exclusion, which can lead to nectar robbing. For instance, the depth of the corolla may designate which species are able to extract nectar through the front opening of a flower and which ones cannot, with the latter sometimes resorting to nectar robbing. Nectar robbing describes a process where invertebrates and other species pierce or chew their way through the back end of a corolla in order to access nectar, thereby bypassing a plant's reproductive parts and preventing pollination from occurring (Inouye 1983). In general, *Phlox* flowers are salverform, with a long slender tube containing copious nectar and usually possessing an appealing scent to entice insect visitors (Grant & Grant 1965). These traits along with their diurnally open flowers make them well suited for pollination by day-flying moths (phalaenophily) and butterflies (psychophily) (Grant & Grant 1965; Levin & Kerster 1968). As flowers are too deep for most Hymenoptera, nectar robbing is common, with various types of bees making an incision in the back end of the flowers. Floral parts were measured in conjunction with monitoring, to assess the ease and difficulty invertebrates had in accessing nectar for the various *Phlox* types in this experiment. The following guidelines on measuring floral parts proved useful in designing this experiment.

Kearns and Inouye (1999) state that the length of the corolla may prove to be the most significant floral dimension with regard to resource partitioning by flower visitors. Other measurements that may also be a factor include corolla width, petal size and distance of anthers to stigma. Even among individual plants, morphometric measurements can vary significantly, for both cultivars and straight species. For this reason, enough flowers should be sampled to obtain mean values with low standard deviation to be statistically relevant.

Of particular note are the differences in the widths of *Phlox* corollas in the experiment between cultivars and straight species. While many *Phlox* straight species tend to have uniformly medium-sized flower corollas, cultivars include flowers with both wider and narrower corolla widths. In natural plant populations, evolution towards specificity in pollination systems is implicated in playing a central role in the diversification of angiosperms (Muchhala 2007). Even though phlox varieties differed significantly in their corolla opening diameters, these values are still narrow enough to indicate pollination by Lepidopterans. This specialization, which is a strong characteristic of *Phlox* within its family Polemoniaceae, is critical to its effective pollination, and future cultivar breeding that results in larger and wider flower corollas may begin to alter the fundamental relationship between *Phlox* and Lepidoptera over the long term (Campbell et al 1997; Muchhala 2007).

Chapter 3

MATERIALS AND METHODS

Experiment Setting

This experiment was conducted from April through September 2015 in the Mt. Cuba Center (MCC) Trial Garden in Hockessin, Delaware. Physiographically, MCC is located in the Piedmont rolling hills region of northern Delaware and is characterized as having a medium-high level of forest coverage in the Eastern oak-hickory forest type class (United State Department of Agriculture- Forest Service 1993). Vegetation surrounding the MCC Trial Garden includes Eastern deciduous trees and woodland understory species. Primary canopy species include: black cherry (*Prunus serotina*), tulip poplar (*Liriodendron tulipifera*), black walnut (*Juglans nigra*), American beech (*Fagus grandifolia*), hickories (*Carya* spp.), and various oaks (*Quercus* spp.). Woodland understory species are well represented at MCC and include Plant Collections Network Nationally Accredited holdings of *Hexastylis* and *Trillium* (American Public Gardens Association 2016). With over 500 acres of natural lands and 50 acres of display gardens, MCC contains many native plant species which function as host plants for the invertebrates observed in my experiment (Appendix B).

<u>*Phlox* Trial Overview</u>

Over 135 *Phlox* species and cultivars were procured for the Mt. Cuba Center plant trial, which involves a 3-year evaluation to determine ideal garden types for the Mid-Atlantic region based on horticultural performance. The *Phlox* trial at MCC is the largest plant trial being conducted in their history, and includes 8 straight species and over 125 cultivars. From this extensive list, I selected 6 straight species, 2 subspecies and 15 cultivars for my experiment testing insect attraction and nectar quality. Cultivars included primarily selectively bred variants, as well as a few wild-derived cultivars as designated in Table 3.1.

Table 3.1 *Phlox* varieties examined in my experiment (W= Wild-selected cultivars, G= Garden/Nursery derived cultivars). * Indicates varieties with an image in Appendix A.

Straight species and subspecies	**Associated Cultivar(s)**
*Phlox stolonifera**	*P. stolonifera* 'Blue Ridge'* (G)
*Phlox divaricata**	*P. divaricata* 'Charleston Pink'* (G)
Phlox carolina, carolina ssp. *carolina, carolina* ssp. *alta*	*P. carolina* 'Bill Baker'* (G), 'Gypsy Love' (G), 'Kim' (W)*, 'Lil' Cahaba'* (W)
Phlox glaberrima (*triflora*) ssp. *triflora*	*P. glaberima* ssp. *triflora* 'Triple Play'* (G), 'Morris Berd' (G), 'Forever Pink'* ('Bill Baker' x *glaberrima* ssp. *triflora*) (G)
*Phlox amplifolia**	No associated cultivars on market
*Phlox paniculata**	*P. paniculata* 'Volcano Red'* (G), 'Lavelle'* (G), 'Jeana' (W)*, 'Delta Snow'* (G), 'Robert Poore'* (G), 'Dick Weaver'* (G)

With regard to the planting layout for trials at MCC, each variety is installed in a row with 5 individuals to obtain a more accurate assessment of its horticultural performance. For the *Phlox* trial, Mr. George Coombs, MCC's Research Horticulturist, primarily selected Eastern U.S. species, with an emphasis on those having native provenance in the Mid-Atlantic region. From this list, commonly available nursery cultivars with parentage of one or more of the selected native types were chosen, with a research aim of having multiple cultivars representing each straight species. Note, however, that not all *Phlox* species in the MCC trial have known associated cultivars (i.e. *Phlox amplifolia*, *Phlox buckleyi*, *Phlox latifolia*) (Dr. Peter Zale, *personal communication*).

Plants were ordered and transplanted into the MCC Trial Garden from June through August 2014. Two distinct sections exist in the trial area: one exposed to full sun (Figure 3.1) and the other sheltered from direct sun by a large shade structure (Figure 3.2).

Figure 3.1 Mt. Cuba Center Trial Garden on 08/04/15. Photo courtesy of Longwood Graduate Program.

Figure 3.2 Mt. Cuba Center Trial Garden shade structure sign.

Varieties of *Phlox stolonifera* and *P. divaricata* were planted under the shade structure while *P. carolina*, *P. amplifolia*, *P. glaberrima* ssp. *triflora* and *P. paniculata* were planted in the section exposed to full sun and all ambient weather conditions. All plants in the MCC trial are mulched with shredded bark to reduce moisture loss and manage weed pressure. Irrigation is available, but in general, plants do not receive supplemental water, except in cases of extreme drought, so as to obtain more accurate results regarding plant performance through less than ideal environmental conditions.

The 6 straight species and 2 subspecies selected for my experiment represent 4 of the 6 designated subsections of *Phlox* found in the Eastern United States (Wherry 1955). The 15 cultivars chosen for my experiment were selected for inclusion based on traits including: widespread availability in the nursery trade, early/profuse flowering, and documented disease resistance in past plant trials (Hawke 2011). *Phlox* used in this experiment were purchased from 20 nurseries across the Eastern United States and Nebraska (Table 3.2).

Table 3.2 *Phlox* varieties sampled in my experiment along with their nursery source.

***Phlox* variety**	**Nursery source**
Phlox amplifolia	Ohio State Ornamental Plant Germplasm Center, Columbus, OH
Phlox carolina	The Primrose Path, Scottdale, PA
Phlox carolina ssp. *alta*	The Primrose Path, Scottdale, PA
Phlox carolina ssp. *carolina*	The Primrose Path, Scottdale, PA
Phlox carolina 'Bill Baker'	Groff's Nursery, Pitman, NJ
Phlox carolina var. *angusta* 'Gypsy Love'	Gateway Garden Center, Hockessin, DE
Phlox carolina 'Kim'	Lazy S'S Farm, Barboursville, VA
Phlox carolina 'Lil Cahaba'	Plant Delights Nursery, Raleigh, NC
Phlox divaricata	Bluebird Nursery, Clarkson, NE
Phlox divaricata 'Charleston Pink'	Plant Delights Nursery, Raleigh, NC
Phlox glaberrima ssp. *triflora*	The Primrose Path, Scottdale, PA
Phlox glaberrima 'Morris Berd'	Mt. Cuba Center, Hockessin, DE
Phlox glaberrima ssp. *triflora* 'Triple Play' (USPP21329 P2)	North Creek Nurseries, Landenberg, PA

Phlox 'Forever Pink' (USPP24918) (*glaberrima* ssp. *triflora* x 'Bill Baker')	Bluebird Nursery, Clarkson, NE
Phlox paniculata	Nearly Native Nursery, Fayetteville, GA
Phlox paniculata 'Delta Snow'	Perennial Pleasures, East Hardwick, VT
Phlox paniculata 'Dick Weaver'	Plant Delights Nursery, Raleigh, NC
Phlox paniculata 'Jeana'	Groff's Nursery, Pitman, NJ
Phlox paniculata 'Lavelle'	Lazy S'S Farm, Barboursville, VA
Phlox paniculata 'Red Caribbean' (USPP20823)	Overdevest Nurseries, Bridgeton, NJ
Phlox paniculata 'Robert Poore'	North Creek Nurseries, Landenberg, PA
Phlox paniculata 'Barthirtysix' Volcano Red (USPP16721)	Prides Corner, Lebanon, CT
Phlox stolonifera	Gateway Garden Center, Hockessin, DE
Phlox stolonifera 'Blue Ridge'	North Creek Nurseries, Landenberg, PA

<u>Nectar Sampling Protocol</u>

In this experiment, nectar sampling occurred from April 30th through August 26th, 2015. In order to better compare cultivars with their analogue straight species, a procedure was established to sample each variety shortly after the other, to reduce abiotic effects on nectar volume and sucrose concentration. During each sampling period, an average of 5.26 nectar readings were taken for each variety. I performed all sampling without assistance to reduce sampling differences.

The nectar collecting and sugar measuring protocols observed were described in *Techniques for Pollination Biologists* (Kearns and Inouye 1993) as well as Comba et al. (1999). Nectar samples were obtained using 5 µl Microcaps®, disposable microcapillary tubes manufactured by the Drummond Scientific Company (Broomall, PA; www.drummonsci.com). Individual flowers were selectively harvested from each plant in the trial row, so that one flower was sampled from the first plant, another flower from the second plant, and so on for each of the 5 plants in a row. After 5 samples were measured, sampling would start again (time permitting) with the first plant in the row, thus repeating for a total of two sweeps.

Figure 3.3 Cross section of *Phlox carolina* 'Gypsy Love' flower. Nectar is located at the base of the corolla tube in the white portion above.

Figure 3.4 Procedure for extracting nectar using a microcapillary tube to probe the back end of a flower. Photo courtesy of Jennifer James.

Each flower was probed through the back end of the corolla tube for approximately 5 seconds to provide enough time for all of a flower's nectar to enter the microcapillary tube (Figure 3.4). Probing the back end of a *Phlox* flower reduces the chance of nectar contamination by pollen (Figure 3.3), which typically results when sampling through the corolla entrance. Since probing flowers with a glass capillary tube may destroy or damage floral nectaries, harvesting individual flowers (destructive sampling technique) allows for a fixed reading of nectar, even as it excludes the possibility of repeated sampling. All nectar in this experiment was measured from an exposed standing crop, which is a measure of resource availability at a single point in time (Possingham 1989). No attempts were made to determine the recharge rate of nectar by installing bags on *Phlox* flowers, though this technique may be desirable to future researchers investigating the influence on nectar on insect attraction.

I used iGaging® EZ Cal fractional digital calipers (San Clemente, CA; www.igaging.com) to measure nectar volume to the closest hundredth of a millimetre by spanning the nectar column and dividing by the total microcapillary tube length. The nectar in the column was then ejected onto the reading surface of a Bellingham & Stanley Eclipse hand-held refractometer (Basingstoke, Hants, UK; www.bellinghamandstanley.com) to obtain a sugar concentration percentage relative to water volume (Figure 3.5). The nectar sugar content per flower was calculated from the following equation, as described by Bolten et al. (1979): $s = dv\ C/100$, where v is the volume (μl), and d is the density of a sucrose solution at a concentration (%) (g solute per 100 g solution) as read on the refractometer.

Figure 3.5 The author observing sugar concentration using a handheld refractometer. Photo courtesy of Jennifer James

The Bellingham & Stanley Eclipse low volume brix refracotometer is specifically manufactured for low volume measurements (its technical specifications state less than 1 microlitre), and with its extremely close-set prisms was actually capable of measuring sucrose concentration readings as low as .04 µl in this experiment.

After each nectar reading, the surface of the refractometer was swabbed with extra low-lint Kimwipes® (Roswell, GA; www.kcprofessional.com) Delicate Task Wipers to remove sugar residue for subsequent measurements. All measurements were recorded in a notebook and later transferred into a Microsoft Excel® (Redmond, WA; www.microsoft.com) spreadsheet for statistical analysis.

For all sampling periods, weather and environmental data were logged to investigate any patterns between nectar volume and sugar concentration with abiotic conditions. Recorded weather data included temperature, relative humidity, wind speed and solar radiation. All weather data were obtained from the Delaware Environmental Observing System station (ID marker DMTC) located on Mt. Cuba Center's property in Hockessin, DE (Delaware Environmental Observing System- http://www.deos.udel.edu/). Delaware Environmental Observing System stations provide updates on weather conditions every 5 minutes continuously throughout the year.

Floral Measuring Protocol

To obtain more information about *Phlox* flowers and how their morphology relates to invertebrate attraction, I measured each harvested flower's parts to the closest hundredth of a millimetre including: width of corolla opening and overall length of corolla tube (Figure 3.6). iGaging® EZ Cal fractional digital calipers were used to record these parts and all values were added into a notebook for later transfer into an Excel® spreadsheet.

Figure 3.6 Preparing to measure the corolla width on a *Phlox paniculata* ‘Dick Weaver’ flower.

Insect Monitoring Protocol

Insect monitoring and recording was carried out from June 7th- August 28th, 2015. In order to be recorded, each visit required either of the following: an insect to insert its proboscis or tongue into the front of the corolla tube and then extract it completely, or an insect exhibiting robbing behaviour by inserting its proboscis or tongue directly into the nectar end of the corolla tube. A sweep of the phlox in trial was conducted every 60 minutes on each day that monitoring occurred, and each sweep lasted between 5-10 minutes to accurately log all visitors. Additionally, photos and video recordings of insects were taken using a Canon® G12 camera (Tokyo, Japan; www.canon.com) for later use in data interpretation and presentations. Under this experimental protocol, a nectaring event constituted an individual insect visiting either a single flower or multiple flowers in a patch before moving on to another *Phlox* variety.

For the vast majority of insect visitors to *Phlox* in the trial, identification was possible through unaided eye observation and photographic records, precluding the need for capture. A few specimens with lookalike species, however, were aspirated and asphyxiated for voucher submission to the University of Delaware's Entomological Reference Collection for species-level identification. This identification was carried out by Dr. Charles Bartlett, Associate Professor of Entomology and Wildlife Ecology, and Director of the University of Delaware's Insect Reference Collection.

Statistical Analysis

All nectar measurements and insect visits were logged in a Microsoft Excel® spreadsheet and later transferred into JMP®, a statistical software program developed by the SAS® Institute, Inc. of Cary, North Carolina (www.jmp.com). To determine significant differences in insect attraction between a straight species and its associated cultivars, a non-parametric test was run using Steel's method, with the straight species serving as the control treatment. Additionally, a non-parametric Wilcoxon signed-rank test was run to compare insect visitation among cultivars, to assess whether their population mean ranks differed. To determine which floral characteristics exerted the strongest influence on insect attraction within a phlox group, a correlation table was generated through JMP®, allowing each measured variable to be compared with one another to assess their relationships. JMP® was also used to ascertain and analyze the logarithmic function of insect visits per sampling period, since peak insect visitation during summer resulted in outlier data. Finally, JMP® was used to create a regression analysis to investigate the relationship between a dependent variable (insects/sampling interval) and several independent measured variables in the experiment.

Chapter 4

RESULTS

During the 2015 field season of insect monitoring and nectar sampling in the Mt. Cuba Center Trial Garden, I found that certain *Phlox* cultivars, particularly those selected from the wild, attracted an abundance and diversity of invertebrates compared with their straight species counterparts when growing in a side-by-side setting. One reason for this is likely due to variations in flower morphology, allowing for more efficient access to floral rewards in certain cases. Conversely, cultivars that are selectively bred for traits such as novel flower colour or larger flowers did not necessarily result in an abundance or richness of insects in the trial, indicating that the cultivar choice is an important consideration for gardeners wanting to supplement their native landscapes to support pollinators. These results contradict my hypothesis that cultivars underperform ecologically in the garden in comparison to their straight species counterparts.

Comparing Insect Attraction, Nectar Characteristics and Floral Part Measurements among *Phlox* groups

In this experiment, insect visitation, floral part measurements and nectar comparisons were made between cultivars and straight species of *Phlox* including: *Phlox* *paniculata*, *P. carolina*, *P. glaberrima* ssp. *triflora*, *P. divaricata*, and *P. stolonifera*. The following sections highlight in detail the measured comparisons between cultivars and species for specific phlox groups.

Phlox paniculata group- Descriptive Statistics

Within the *Phlox paniculata* group, the cultivar 'Jeana' was the clear insect favourite, attracting 14 times the abundance of the straight species with over twice the diversity (Table 4.1). An important point to note is that in the trial, straight species *Phlox paniculata* did not begin blooming until July 19th, which was 2.5 weeks after all of the other cultivars had initiated their bloom cycle. Since the species and cultivars did not bloom over the same total duration, the amount of insects per sampling interval was calculated, and from this measure, 'Jeana' was over 7x more attractive than the straight species and nearly 2.5x more visited than the second attractive cultivar in the trial 'Dick Weaver'.

Table 4.1 Comparing *Phlox paniculata* and its cultivars for insect attraction, nectar characteristics, and floral measurements. Mean values listed for nectar volume, sugar concentration, corolla length, corolla width and flower quantity on main inflorescence. Total values provided for insect sampling intervals, insect visits, and species richness.

Insect sampling intervals	*Phlox* type	Total insect visits	Insect visits/ sampling interval	Species richness	Nectar volume (µl)	Sugar concentration (%)	Corolla length (mm)	Corolla width (mm)	Flower quantity on main inflorescence
43	'Jeana'	187	4.35	12	0.52	11.73%	15.4	1.56	184
35	'Dick Weaver'	62	1.77	11*	0.31	17.79%	22.78	2.44	77
32	'Delta Snow'	52	1.63	8	0.41	14.92%	25.38	2.29	103

37	'Lavelle'	45	1.22	8	0.67	11.21%	14.96	2.38	117
31	'Robert Poore'	28	.90	7*	0.28	17.91%	25.71	2.38	108
22	*Phlox paniculata*	13	.59	6*	0.38	14.62%	22.91	2.47	74
33	'Volcano Red'	9	.27	3	1.85	8.16%	17.59	3.43	96

***indicates hummingbird visitation (+1 value included)**

The second most visited variety in the trial was *Phlox paniculata* 'Dick Weaver'. This variety attracted twice the diversity of insects than the straight species and over 4 times the abundance (Table 4.1). Based on the insects observed per sampling period, 'Dick Weaver' was exactly 3x more attractive than the straight species. In terms of nectar, 'Dick Weaver' had the second highest sugar concentration in the trial and the second lowest volume. Furthermore, this variety began blooming over a week before the straight species, thus it appears to be a good candidate for extending the nectaring season in an ecological landscape.

The third most visited *Phlox* in the trial was *P. paniculata* 'Delta Snow', which attracted 4 times as many insects as the straight species (Table 4.1). Notably, 'Delta Snow' was the most preferred phlox by nectar robbing Hymenoptera, which represented half of the species richness and 11/13 of total insect visitation (44 out of 52 visits). In the trial, nectar robbing was first noted on 07/13/15, when all four hymenopteran visitors were observed: Eastern carpenter bees (*Xylocopa virginica*), European honeybees (*Apis mellifera*), a species of halictid bee (*Lasioglossum* sp.) and a native bumblebee species (*Bombus* sp.). *P. paniculata* 'Delta Snow' began flowering over two weeks earlier than the straight species in the trial, showcasing its applicability as a nectar plant for insects, especially Hymenopterans.

Another variety that attracted more insects than the straight species in the trial was *P. paniculata* ‘Lavelle’, which attracted over 3x the insect abundance (Table 4.1). *Phlox paniculata* ‘Lavelle’ had the shortest corolla length among phlox in the *paniculata* group, and exhibited good attraction for nectaring insects with 6 different species observed. These attributes, taken along with the fact that ‘Lavelle’ began blooming in early July (two and a half weeks before the straight species) lend support to its use in ecological landscapes to support native pollinators and other wildlife.

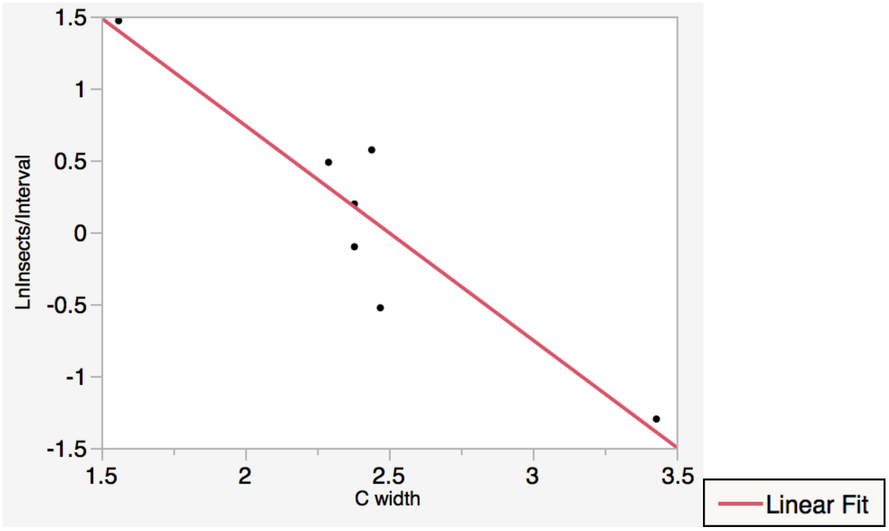
<u>*Phlox paniculata* group- Multivariate Correlation and Regression</u>

To determine which variables had the strongest influence on insect attraction to phlox in the *P. paniculata* group, a correlation table was generated, allowing each variable to be compared with other variables to assess their relationships (Table 4.2). Again, with an unequal amount of sampling intervals, the number of insects per sample was estimated and analyzed to provide a more balanced measure of comparison. Furthermore, the logarithmic function was taken for the insects per interval value to minimize the effect of outliers, since the quantity of insects nectaring on *P. paniculata* ‘Jeana’ was disproportionately high when compared with other types.

Table 4.2 Correlation table assessing the relationship between specified measured variables for the *Phlox paniculata* group. Correlation coefficient values are listed. Values range from -1 to 1. Blue values are positive, indicating variables are directly correlated. Red values are negative, indicating variables are inversely correlated. Stronger colour shade indicates stronger correlation. To showcase the effects of nectar characteristics and floral measurements on overall insect attraction (Ln Insects/Interval) to *P. paniculata* varieties, applicable correlation values are highlighted below.

	Ln Insects/ Interval	**Nectar volume**	**Sugar concentration**	**Corolla length**	**Corolla width**	**Flower quantity on main inflorescence**
Ln Insects/ Interval	-	-0.6374	0.3047	-0.1262	-0.9240	0.6502
Nectar volume	-0.6374	-	-0.8313	-0.4873	0.7452	-0.0255
Sugar concentration	0.3047	-0.8313	-	0.7996	-0.3404	-0.3398
Corolla length	-0.1262	-0.4873	0.7996	-	0.0658	-0.5707
Corolla width	-0.9240	0.7452	-0.3404	0.0658	-	-0.6600
Flower quantity on main inflorescence	0.6502	-0.0255	-0.3398	-0.5707	-0.6600	-

In interpreting the correlation table we find that the strongest relationship governing insect visitation to *Phlox paniculata* and its cultivars is the narrowness of the flower corolla (-0.924). This is well illustrated through the positive attraction of insects to 'Jeana' with its narrow flowers and the dearth of visitors to the wider corolla cultivar 'Volcano Red'. To a lesser extent than corolla width, the quantity of flowers on the main inflorescence is also highly correlated to insects observed per sampling interval (0.6502). Nectar volume is negatively correlated (-0.6374). Sugar concentration of nectar was not well correlated to visitation per sampling (0.3047), while corolla length had the weakest potential relationship to visitation (-0.1262).



Linear Fit: Ln (Insects/Interval) = 3.7257903 - 1.4917253*C width

Summary of Fit

R Square	0.8538
R Square Adjusted	0.8245
Root Mean Square Error	0.3687
Mean of Response	0.1137
Observations (or Sum Weights)	7

Figure 4.1 Bivariate relationship between Ln (Insects/Interval) and flower corolla width for each cultivar and straight species in the *Phlox paniculata* group. Cultivar 'Jeana' is represented by the point located in the upper left. Cultivar 'Volcano Red' by the point in the lower right. Other phlox varieties are clustered in the middle of the graph.

The effect of flower corolla width on insect visitation is especially evident in the bivariate relationship for *P. paniculata* cultivars and the straight species (Figure 4.1). The bivariate relationship between corolla width and the logarithmic function of insects/interval demonstrates that the cultivars 'Delta Snow', 'Lavelle', 'Dick Weaver' and 'Robert Poore' are clustered roughly around the line of regression, while 'Jeana' and 'Volcano

Red' are quite disparate. With an R^2 value of 0.8538, a very strong relationship between corolla width and insect visitation is present. However, with only N=7 present in the *Phlox paniculata* trial, the addition of more phlox taxa would better assess the strength of this connection.

Phlox paniculata group- Non-Parametric Tests of Significance

Insects attracted to *Phlox paniculata* and its cultivars included an array of Lepidoptera and Hymenoptera (Table 4.3), with the cultivar 'Jeana' displaying the greatest attraction in the trial (Table 4.1). Recall that Hymenopterans occur as nectar robbers on Eastern North American *Phlox* species, as their mouthparts are insufficiently long to obtain nectar through the front end of the corolla tube.

Table 4.3 Insect species observed nectaring on *Phlox paniculata* group.

Insects	Quantity
Eastern tiger swallowtail (*Papilio glaucus*)	147
Eastern carpenter bee (*Xylocopa virginica*)	84
Hummingbird clearwing (*Hemaris thysbe*)	44
European honey bee (*Apis mellifera*)	29
Peck's skipper (*Polites peckius*)	16
Silver spotted-skipper (*Epagyreus clarus*)	14

Halictid bee (*Lasioglossum* sp.)	13
Monarch (*Danaus plexippus*)	6
Bumblebee (*Bombus* sp.)	6
Great spangled fritillary (*Speyeria cybele*)	4
Red admiral (*Vanessa atalanta*)	4
Black swallowtail (*Papilio polyxenes*)	2
Others	5
Total insects	**374**

As varieties did not flower concurrently across their bloom period, resident insect populations were likely disparate with regard to their assemblages at sampling points throughout the season. Furthermore, few to no insects were observed during many of the insect sampling intervals, while a profusion of insects was observed on preferred cultivars during the peak of the visitation season, resulting in data which were non-normalized with regard to distribution. To account for this, non-parametric tests of significance were used to analyze data, and two separate statistical analyses were utilized to compare cultivars and straight species for insect attraction. The first method, a non-parametric comparison between each pair of *Phlox* using Wilcoxon's signed rank test (Table 4.4), was used to determine probability values (p-values) that the monitored insect data in the experiment for each phlox type differed significantly from each other (Wilcoxon 1945).

Table 4.4 Nonparametric comparisons for each *Phlox paniculata* pair using Wilcoxon's signed rank test. Colour p-values (< 0.05) express significant differences in insect attraction between *Phlox* varieties in each pair. Orange values represent lower p-values (strongly significantly different), while red values are closer to < 0.05.

q*	Alpha
1.95996	0.05

Level	- Level	Score Mean Difference	Standard Error Difference	Z	p-Value
Volcano Red	Robert Poore	-10.6979	3.973004	-2.69266	0.0071*
Robert Poore	*paniculata*	4.4685	3.897125	1.14661	0.2515
Volcano Red	*paniculata*	-4.4697	3.442041	-1.29856	0.1941
Robert Poore	Lavelle	-2.5493	4.528991	-0.56288	0.5735
paniculata	Lavelle	-7.0670	4.269630	-1.65517	0.0979
Volcano Red	Lavelle	-13.9025	4.286911	-3.24302	0.0012*
Lavelle	Jeana	-14.6072	5.076098	-2.87764	0.0040*
Robert Poore	Jeana	-15.9880	4.923392	-3.24735	0.0012*
paniculata	Jeana	-18.2770	4.800892	-3.80699	0.0001*
Volcano Red	Jeana	-26.0564	4.838779	-5.38491	<.0001*
Jeana	Dick Weaver	11.2465	5.042451	2.23037	0.0257*
Lavelle	Dick Weaver	-2.8077	4.706349	-0.59658	0.5508
Robert Poore	Dick Weaver	-4.9272	4.484965	-1.09860	0.2719
paniculata	Dick Weaver	-8.5130	4.207310	-2.02338	0.0430*
Volcano Red	Dick Weaver	-15.0719	4.260234	-3.53780	0.0004*
Jeana	Delta Snow	12.4001	4.967831	2.49607	0.0126*
Dick Weaver	Delta Snow	1.7647	4.525108	0.38999	0.6965
Lavelle	Delta Snow	-0.7867	4.567341	-0.17225	0.8632
Robert Poore	Delta Snow	-2.7626	4.311486	-0.64075	0.5217
paniculata	Delta Snow	-5.9446	3.952244	-1.50411	0.1326
Volcano Red	Delta Snow	-11.4181	3.999211	-2.85508	0.0043*

A few noteworthy results emerge from the data table above, the first being that only the cultivars 'Jeana' and 'Dick Weaver' indicate significant differences in insect visitation from *P. paniculata* and other cultivars (based on alpha 0.05 significance level). In particular, the difference in insect visitation between *Phlox paniculata* and *P. paniculata* 'Jeana' indicates significantly more visits to the latter ($p < 0.001$), while 'Dick Weaver' also hosted significantly more visits than the straight species ($p = 0.043$). Interestingly, the third and fourth most attractive phlox in terms of insect abundance in the trial, *P. paniculata* 'Delta Snow' and 'Lavelle', did not exhibit significant insect attraction differences (p = 0.1326 and p = 0.0979, respectively) in relation to the straight species.

The second point is that the cultivar *P. paniculata* 'Volcano Red' had very few visitors compared with all other cultivars, save for the straight species of *P. paniculata*. Even though it experienced fewer overall insect visitors with less richness than the straight species, this difference was not significantly different (p = 0.1941).

In addition to the Wilcoxon Method, a nonparametric comparison using Steel's method (Table 4.5) was run to determine insect attraction differences for the *P. paniculata* group (Steel 1959). This test analyzes each variety in relation to a control group, which is the straight species *Phlox paniculata* in this instance.

Table 4.5 Nonparametric Comparisons with Control Group using Steel's Method. Control Group = *P. paniculata*. P-value (< 0.05) in orange indicates a significant difference in insect attraction between *Phlox* varieties in each pair.

q*	Alpha
2.52597	0.05

Level	Control level	Score Mean Difference	Standard Error Difference	Z score	p-Value
Robert Poore	paniculata	4.4685	3.897125	1.14661	0.6670
Volcano Red	paniculata	-4.4697	3.442041	-1.29856	0.5546
Delta Snow	paniculata	-5.9446	3.952244	-1.50411	0.4134
Lavelle	paniculata	-7.0670	4.269630	-1.65517	0.3237
Dick Weaver	paniculata	-8.5130	4.207310	-2.02338	0.1616
Jeana	paniculata	-18.2770	4.800892	-3.80699	0.0008*

Under this statistical test, only *Phlox paniculata* 'Jeana' (Z = -3.80699; p = 0.0008) demonstrated clear preference in insect attraction over the straight species. For most other cultivar types there were either too few samplings taken during the field season or the straight species was not significantly different from these cultivars in attracting and supporting nectaring invertebrates.

Phlox carolina group- Descriptive Statistics

In this experiment, insect visitation to the *Phlox carolina* group was far below that observed for the *Phlox paniculata* group; nevertheless, a few wild-selected cultivars and one subspecies attracted more insects than the straight species in the trial (Table 4.6). An important consideration, however, is that *Phlox carolina* did not begin blooming until July 20th, which was over 6 weeks after the cultivar *P. carolina* 'Kim' started to bloom, and exactly 5 weeks after all other types in the group began blooming. Due to this, the sampling intervals were not equal; therefore, the number of insects/sampling interval was estimated to provide a better measure for comparing attraction among types. It is also worth noting that the quantities of flowers on the main inflorescences for all types in the Phlox carolina group were not especially different; therefore, these were not interpreted as a factor influencing insect attraction.

Table 4.6 Comparing *Phlox carolina* and its cultivars for insect attraction, nectar characteristics, and floral measurements. Mean values listed for nectar volume, sugar content, corolla length and corolla width. Total values provided for insect sampling intervals, insect visits, and species richness.

Insect sampling intervals	*Phlox* type	Total insect visits	Insect visits/ sampling interval	Species richness	Nectar volume (µl)	Sugar concentration (%)	Corolla length (mm)	Corolla width (mm)
14	*Phlox carolina*	5	0.36	4	0.41	19.75%	23.01	2.03
17	*carolina ssp. alta*	11	0.65	7	1.12	19.2%	24.40	2.31
15	*carolina ssp. carolina*	3	0.20	2	1.01	19.92%	20.94	1.71
16	'Kim'	9	0.56	5	1.41	17.42%	26.12	1.93
19	'Lil Cahaba'	10	0.53	5	0.87	14.54%	22.73	1.85
9	'Gypsy Love'	3	0.33	2	0.83	19.77%	27.05	2.35

Within the *Phlox carolina* group, the subspecies *alta* had the most insect visits, and attracted 3 more nectaring species than the straight species. Although total visitation for all types in this group was small relative to the *P. paniculata* group, the varieties fall into two distinct levels of attraction. *Phlox carolina* ssp. alta, and the cultivars 'Lil Cahaba' and 'Kim' had at least one insect visitor for every 2 monitoring periods, while the cultivar 'Gypsy Love', subspecies *carolina* and straight species had fewer observed visitors per sampling period. Both 'Kim' and 'Lil Cahaba' are wild-selected cultivars, emanating from Alabama, while 'Gypsy Love' was discovered as a spontaneous garden seedling, suggesting that certain cultivars chosen from wild populations may have enhanced attraction over their straight species parents. Through this experiment, these types show great promise for application in ecological landscaping, and gardeners may want to consider using them to extend the nectaring season to complement native straight species plantings.

Phlox carolina group- Multivariate Correlation

With few total insects visiting *Phlox carolina* and its cultivars, determining the variables exerting strong influence on insect attraction is difficult. Nevertheless, a correlation table was generated, to test the relationship between nectar, floral characteristics and insect visitation (Table 4.7).

Table 4.7 Correlation table assessing the relationship between specified measured variables for the *Phlox carolina* group. Correlation coefficient values are listed. Values range from -1 to 1. Blue values are positive, indicating variables are directly correlated. Red values are negative, indicating variables are inversely correlated. Stronger colour shade indicates stronger correlation. To showcase the effects of nectar characteristics and floral measurements on overall insect attraction (Ln Insects/Interval) to *P. paniculata* varieties, applicable correlation values are highlighted below.

	Insects/ interval	**Nectar volume**	**Sugar concentration**	**Corolla length**	**Corolla width**
Insects/Interval	-	0.4460	-0.5135	0.3655	0.3350
Nectar Volume	0.4460	-	-0.2280	0.2982	-0.0978
Sugar Concentration	-0.5135	-0.2280	-	0.0550	0.3579
Corolla Length	0.3655	0.2982	0.0550	-	0.7175
Corolla Width	0.3350	-0.0978	0.3579	0.7175	-

In contrast with plants in the *P. paniculata* group, flower corolla width was not a significant factor in explaining insect attraction, and instead was weakly correlated with visitation (0.3350). In fact, no measured variables were strongly correlated with insect visitation in the *Phlox carolina* trial, and nectar concentration was the only measure with an *r*-value below -0.05 (-0.05135), indicating perhaps paradoxically, a closer association between visitation and weaker sugar concentration than with any other measured variable.

Ultimately, the results on insect visitation for the *Phlox carolina* group suggest that more trialing may be needed to accurately assess which floral characteristics have the greatest impact in attracting invertebrates. In addition, isolating plants from more attractive species and genera may yield more robust results, allowing for a better interpretation of the variables that draw insects to nectar on *Phlox carolina* and its cultivars.

Phlox glaberrima ssp. *triflora* group- Descriptive Statistics

With very few insects observed nectaring on plants in the *Phlox glaberrima* ssp. *triflora* group, an interpretation of the floral traits having the greatest influence on attraction is impractical. Like plants in the *P. carolina* group, *P. glaberrima* ssp. *triflora* and its cultivars struggled to get established in the Mt. Cuba Center Trial Garden in the year following their transplantation to the garden, and other concurrent blooming species and genera likely drew insects away from nectaring on plants in this phlox group. The number of flowers for each type in this group was inconsequential in this comparative trial, since visitation was so paltry and plants had relatively few flowers to sustain nectaring invertebrates. What the limited collected data show is that the cultivar 'Triple

Play' and the patented hybrid 'Forever Pink' attracted insects at a slightly higher rate than the straight species, though this should certainly be examined in subsequent years to determine if this pattern holds true (Table 4.8). Similarly to *Phlox carolina* and *Phlox paniculata*, the straight species *Phlox glaberrima* ssp. *triflora* exhibited delayed blooming vis-à-vis its associated cultivars, with plants coming into bloom on 06/06/15, 10 days after 'Triple Play', 'Forever Pink', and 'Morris Berd' had started blooming.

Table 4.8 Comparing *Phlox glaberrima* ssp. *triflora* and its cultivars for insect attraction, nectar characteristics, and floral measurements. Mean values listed for nectar volume, sugar content, corolla length and corolla width. Total values provided for insect sampling intervals, insect visits, and species richness.

Insect sampling intervals	*Phlox* type	Total insect visits	Insect visits/ sampling interval	Species richness	Nectar volume (μl)	Sugar concentration (%)	Corolla length (mm)	Corolla width (mm)
5	*Phlox glaberrima* ssp. *triflora*	1	0.20	1	0.88	13.67%	19.05	2.54
5	Forever Pink	2	0.40	2	1.01	15.45%	22.24	2.02
2	Triple Play	1	0.5	1	1.01	21.12%	19.67	-
1	Morris Berd	0	0	0	0.99	21.95%	23.26	-

The floral factors having the greatest bearing on insect attraction could not be determined due to the lack of insects visiting *Phlox glaberrima* ssp. *triflora* and its cultivars. Sampling in future years is recommended to better grasp the factors affecting visitation in comparative trials of *Phlox glaberrima* ssp. *triflora* and its cultivars.

Other *Phlox* groups in trial

In addition to evaluating the floral characteristics influencing attraction for *Phlox paniculata*, *P. carolina* and *P. glaberrima* ssp. *triflora*, nectar was sampled for the early flowering species *Phlox divaricata* and *Phlox stolonifera* (Tables 4.9 and 4.10), and each was compared with a popular cultivar. As *Phlox divaricata* and *Phlox stolonifera* were planted under a shade structure with screens on 3 sides, insect accessibility into the growing area was impeded, and no insects were noted throughout the course of their blooming period. Floral part measurements were therefore not taken, since they could not be assessed for their influence on insect visitation. Nevertheless, nectar measurements are reported to compare types in this trial, and future research could investigate insect attraction differences for both of these species and their associated cultivars, in gardens with direct exposure to nectaring insects.

Table 4.9 Comparing *Phlox divaricata* and its cultivar for nectar volume and sugar concentration. Mean values listed for nectar volume and sugar concentration

***Phlox* type**	**Nectar volume (μl)**	**Sugar concentration (%)**
P. divaricata	0.351	52.30%
'Charleston Pink'	0.342	40.61%

Table 4.10 Comparing *Phlox stolonifera* and its cultivar for nectar volume and sugar concentration. Mean values listed for nectar volume and sugar concentration

***Phlox* type**	**Nectar volume (μl)**	**Sugar concentration (%)**
P. stolonifera	2.93	23.84%
'Blue Ridge'	2.70	19.47%

Finally, *Phlox amplifolia* was sampled for nectar volume, sugar concentration and insect visitation although it has no commercially available cultivars (Table 4.11). The rationale for measuring and reporting data on *Phlox amplifolia* in this trial is to assess its usefulness in ecological designs and to potentially recommend its development by plant breeders. While insect visits to *P. amplifolia* were sparse, it had one of the longest flowering periods in the trial, with its first flowers emerging on 06/01/15 and continuing to bloom until 07/30/15. Additional trialing of *Phlox amplifolia* is recommended to obtain more data on its suitability in attracting nearing insects in an ecological landscape.

Table 4.11 Nectar characteristics and insect visitation data for *Phlox amplifolia*. Mean values listed for nectar volume and sugar concentration. Total values provided for insect visits and species richness.

***Phlox* type**	**Nectar volume (μl)**	**Sugar concentration (%)**	**Total insect visits**	**Species richness**
amplifolia	0.58	20.25%	3	3

Overall Insect Monitoring and Nectar Sampling Results

In total, insect monitoring and recording occurred on 33 sampling days, from June 7th- August 28th, 2015. Prior to June 7th, no insects appeared in the trial, although nectar sampling commenced on April 30th. On June 7th, a single syrphid fly (*Eupeodes americanus*) was noted, and then no other insects were observed again until June 29th. Although the original experimental protocol planned for even sampling throughout the course of the day, only one insect was observed visiting prior to 8 a.m. (*Eupeodes americanus*) and very few were noted after 9 p.m. Therefore, with a majority of visitors to phlox in the trial occurring diurnally in mid-morning and afternoon, insect sampling was shifted primarily to these times in order to capture the greatest amount of visitation (Figure 4.2).

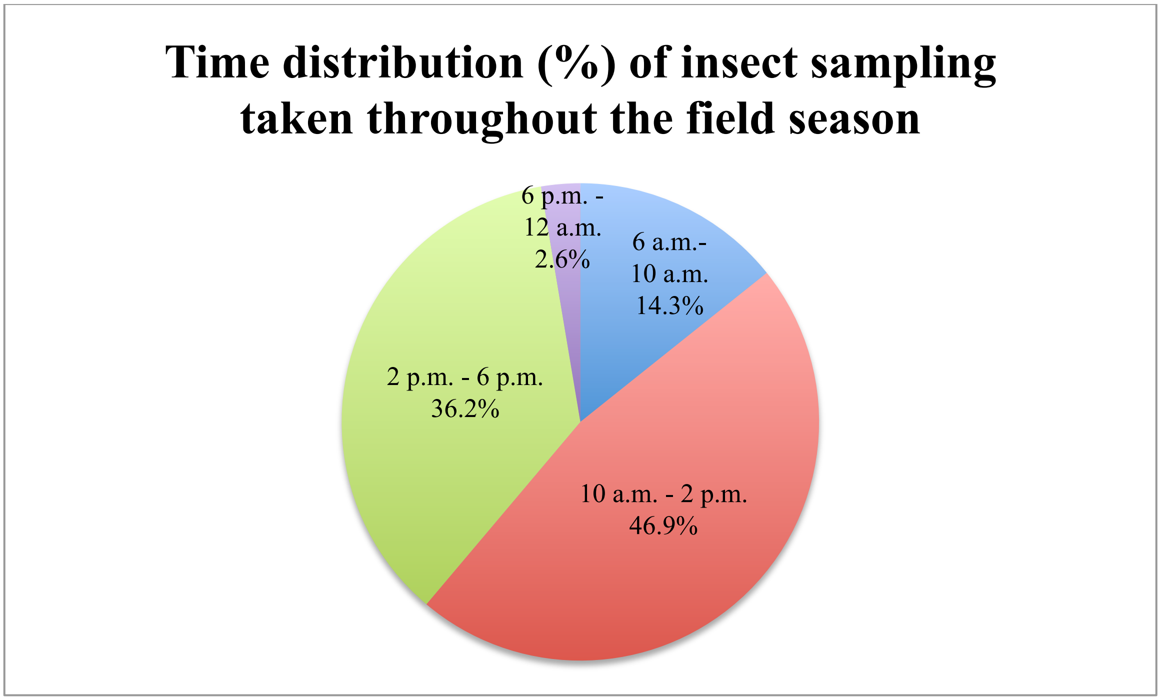


Figure 4.2 Time distribution (U.S. Eastern Daylight Time) of insect sampling across all days in the 2015 field season.

A total of 714 insects were observed throughout the course of the experiment. Lepidoptera was the primary insect order observed nectaring in the trial, with 459 individuals counted over the course of the trial. Hymenoptera was ranked second, with 243 robbing insects counted. Syrphid flies in the order Diptera comprised the remainder of individual insects (12) observed during the trial season (Table 4.12).

Table 4.12 Insect species observed nectaring on all *Phlox* types in trial.
* marks those with images in Appendix A

Insects	**Quantity**
Eastern tiger swallowtail* (*Papilio glaucus*)	230
Eastern carpenter bee* (*Xylocopa virginica*)	172
Hummingbird clearwing* (*Hemaris thysbe*)	130
European honey bee* (*Apis mellifera*)	45
Peck's skipper* (*Polites peckius*)	21
Silver spotted-skipper* (*Epagyreus clarus*)	18
Halictid bee* (*Lasioglossum* sp.)	18
Monarch* (*Danaus plexippus*)	14
Syrphid fly (*Eupeodes americanus*)	12
Great spangled fritillary* (Speyeria cybele)	12
Red admiral (*Vanessa atalanta*)	9
Bumblebee* (*Bombus* sp.)	8
Black swallowtail* (*Papilio polyxenes*)	2
Others	31
Total Insects	**722**

Nectar sampling occurred over a 119-day span from April 30th - August 26th, 2015. Samples were gathered from as early as 6 a.m. to as late as 11:20 p.m. (Eastern Daylight Time), with the greatest percentage of samples collected from 2 to 6 p.m.

(Figure 4.3). A total of 1,019 nectar samples were obtained on 33 days, with an average sampling occurring every 3.6 days over the 119-day duration of the experiment.

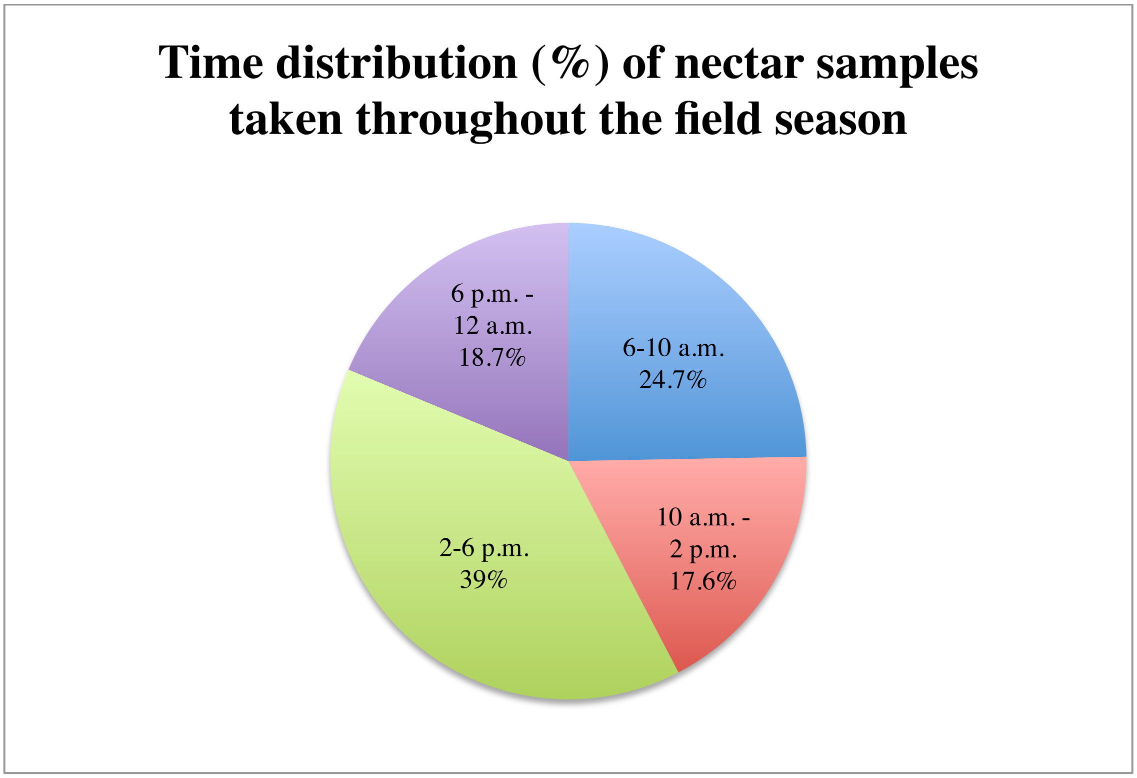


Figure 4.3 Time distribution (U.S. Eastern Daylight Time) of nectar sampling across all days in the 2015 field season.

Nectar sampling was more evenly distributed temporally than insect monitoring in the experiment in order to assess how abiotic conditions altered its characteristics throughout the course of the day. The fewest samples were collected between 10 a.m. and 2 p.m. due in part to extra time spent monitoring and recording insect visits.

Chapter 5

DISCUSSION AND RECOMMENDATIONS

Phlox Comparative Trial Assessment

Though this experiment was conducted entirely within the course of a single field season, results emerged which begin to shed light on the variables having the strongest bearing on insect preference to native cultivars of *Phlox*. Ultimately, additional research should prove useful in helping to accurately assess the characteristics of plants that promote visitation, which could help guide breeding programs aimed at developing cultivars to enhance ecological gardens. As native plants continue to swell in popularity, it is increasingly important to establish comparative trials to test the ecological differences between straight species and cultivars, in order to recommend plants that provide superior habitat benefits for pollinators and other wildlife.

Phlox paniculata group

In comparison to *Phlox paniculata*, the wild-derived cultivar 'Jeana' was strongly preferred by nectaring invertebrates in this experiment. Insect preference for *P.*

paniculata 'Jeana' is primarily attributable to the ease with which invertebrates are able to access nectar, through its comparative abundance of flowers and the narrowness and shallowness of its corolla tubes from opening to nectary. While *Phlox paniculata* 'Jeana' did not have the shallowest corolla tube in the paniculata complex, it possessed the narrowest flowers, allowing Lepidopterans to quickly probe flowers and thoroughly access nectar (Grant 1949). *Phlox paniculata* 'Jeana' was also the tallest plant in the trial, and other studies have demonstrated a positive correlation between invertebrate feeding and ovipositing on plants of greater stature (Firempong & Zalucki 1990; Pöyry et al. 2006). The inflorescences of *Phlox paniculata* 'Jeana' are comprised of many more flowers than *P. paniculata* and the other cultivars in trial (Table 4.1), thereby physically providing more space for insects to nectar simultaneously. While the abundance of flowers and accessibility to nectar demonstrate a clear advantage of 'Jeana' over the straight species and other cultivars in the trial (Table 4.2), it is important to recognize that the phlox trial at Mt. Cuba Center was in its first full year in the ground in 2015, and in the next two years of trialing, plants will likely continue to fill out and have additional flowers on their inflorescences, thus providing more abundant habitat for nectaring insects.

Additionally, whereas *Phlox paniculata* had a mean nectar volume and sugar concentration similar to many of the cultivars, 'Volcano Red' had the largest mean nectar volume and the lowest mean sugar concentration in the trial. This characteristic is likely due to its wider corollas allowing infiltration of rainwater, which results in nectar dilution and presumably affects insect visitation. The phenomenon of flowers being inundated with rainwater, thus diluting nectar and restricting visitation, was observed in a study on *Gentiana straminea* which demonstrated that non-pollinated flowers close in response to drops in temperature rather than changes in humidity (He et al 2005). As summer rainstorms are common weather occurrences in northern Delaware and other temperate regions throughout the Eastern United States, flowers that are shaped in a way that promote inundation would be expected to dilute more quickly, particularly during humid environmental conditions not accompanied by a decrease in temperature. Interestingly, *Phlox paniculata* 'Volcano Red' was derived in Holland using selective breeding techniques, and the shape of their flowers with their characteristically wide corolla openings and short corolla lengths almost certainly had an impact in limiting insect visitation. With this in mind, plant breeders in the future may wish to consider the shape of flowers in their protocol as a primary criterion for evaluating taxa designed for ecological applications.

Although this experiment was designed to monitor and record insect visitation, there were a few instances where ruby-throated hummingbirds (*Archilochus colubris*) were observed nectaring on *Phlox paniculata*, *P. paniculata* 'Dick Weaver' and *P. paniculata* 'Robert Poore'. These three Phlox types had the second, third and fourth widest corollas in the trial and past research by Campbell et al (1991) demonstrated that wider corolla tubes significantly increased hummingbird visitation frequency, suggesting consistent phenotypic selection for wider corollas through pollination via hummingbirds (*P. paniculata* 'Volcano Red' notwithstanding). In the case of *P. paniculata* 'Jeana' and *P. paniculata* 'Delta Snow', their narrower corollas may not provide the requisite room for hummingbirds to successfully access nectar with their tongues. While *Phlox* are often marketed as hummingbird plants, the paucity of total visits in the experiment combined with their frequent visitation to *Monarda* species and cultivars in Mt. Cuba Center's Trial Garden, leads me to reason that they generally prefer other plants from which to obtain nectar. In any case, future phlox research in other parts of the country may yield different results, and a designed experiment may answer this question with greater accuracy.

While these results provide a statistical basis indicating insect preference of *P. paniculata* 'Jeana' due to its abundant flowers and narrow corollas, it is important to recognize that these physical characteristics may not explain insect preference in comparative trials of other plant species.

Phlox carolina group

Analysis of insect preferences for phlox types within the *Phlox carolina* group is difficult to ascertain, since the number of visitors in the first year of trial were so dispersed and few. While there are myriad possible reasons to explain the lack of visitation throughout the season, two plausible ideas involve competition with the *Phlox paniculata* group, *Monarda* spp. and other plants blooming both inside and outside of the trial. Additionally, the slow growth of plants recovering from transplantation into the trial garden from the preceding autumn seemed to have a negative effect on insect visitation to all varieties in the *Phlox carolina* group. Indeed, the number of flowers for all types in the *P. carolina* group was substantially fewer than types in the *P. paniculata* group, further rendering difficult an analysis on the relationship between floral abundance and insect visitation for these phlox types. Realistically, more trialing is needed on plants in the *Phlox carolina* group to test the variables having the strongest influence in attracting insect visitors, and future researchers should consider isolating plants to buffer against competition for more preferable plant species.

Considerations for Setting up Future Experiments

With few studies conducted that have evaluated attraction and nectar differences between straight species and cultivars, the results of this experiment begin to shed light on the floral preferences and ecological benefits imparted to invertebrate species in the native plant garden. Since this experiment was carried out in a single field season, however, the results only capture a snapshot of the full picture of the relationship between *Phlox* cultivars and insects, and sampling in subsequent years is recommended to obtain more accurate results. Additionally, while this experiment successfully demonstrated that some cultivars have enhanced invertebrate visitation to ecological gardens in northern Delaware and the Mid-Atlantic region, additional studies are recommended for other areas of the country, involving phlox species occurring naturally in those areas. Future experiments in this arena should also be expanded to include additional species and cultivars in trial, and extended across a complete growing season, in order to capture how nectar and insect visitation change from day to day. The strength of this approach will provide more meaningful results for gardeners in specific locales interested in knowing the full array of plant combinations (cultivars and straight species) within a genus that will support the native pollinators of their region.

As each plant variety can reasonably be expected to perform differently from year to year in a garden, the ecological benefits they provide to wildlife will likely vary in subsequent years as well. Repeated and robust data collection will therefore yield an increasingly accurate understanding of attraction and ecological benefits provided to invertebrates via native cultivars and straight species. While nectar was a key measurement in attempting to explain attraction in this experiment, there are a number of other characteristics that could be studied which may provide additional explanations for attraction. The following sections may prove useful to researchers in determining what metrics to measure in the future to uncover ecological value in their own studies.

Abiotic Factors

Before establishing a research plot, consider that a wide variety of abiotic variables can affect insect visitation and pollination. In studies on *Viola*, Beattie (1976) found that daily sunlight duration, the slope of the study habitat, and the number of days of sunshine preceding sampling all affected insect plant pollination. Additionally, a study on honey bee and native bee pollination of apple cultivars in a Canadian orchard found that environmental factors such as temperature and humidity had more of an effect on honey bee pollination, while factors such as cultivar type and slope direction were responsible for differences in pollination by native bees (Boyle-Makowski & Philogène 1985).

The trial garden at Mt. Cuba Center is sited on a mostly flat parcel of land that receives ample morning and mid-day sunlight. The west end of the garden in flanked by a forest of Eastern native trees, which in summer begin casting shade on plants in the trial starting in early afternoon, resulting in the garden being fully shaded by late afternoon. As such, plants on the eastern end of the garden received fewer sunlight hours than varieties located on the western end. Undoubtedly, this affected both horticultural and ecological performance, and in an ideal design, all plants would be subjected to equal amounts of sunlight and other abiotic elements. While the shading effect is unfortunate, the slope and other conditions of the trial garden grant equal exposure to wind and rainfall. In the future, experiments focusing on evaluating ecological performance of cultivars and straight species in trial gardens should be sited in ways that mitigate abiotic impacts.

Ultimately however, even after designing an experiment in such a way that ensures abiotic factors are experienced evenly, daily weather fluctuations and yearly climatic trends are expected to influence the suite of pollinators present in a trial. Past research has indicated that daily variations in an insect visitor pool are a regular feature in temperate ecosystems (McCall & Primack 1992). Expanding this across seasons, yearly variation in temperature and climatic conditions will certainly have an influence on patterns of visitation, as certain insect populations are activated by favourable circumstances and hindered by ones injurious to their existence (Gross & Werner 1983).

In the long-term, the effects of climate change will likely shift invertebrate communities which nectar on native plant species from specialist pollinators towards more adaptable generalist species, which have evolved features allowing them to overcome barriers that would otherwise inhibit access to floral rewards (Memmott et al. 2007; Hegland et al. 2008). A final consideration for establishing comparative plant trials is the soil profile of the garden, and steps should be taken to amend research plots evenly so that all plants have similar access to nutrients, water, soil biological activity and other characteristics. Room for growth in the field comparing native cultivars for their ecological functions is rich, and ecological plant trials should be established in regions throughout the world to adequately test whether these plants stack up to straight species in providing habitat benefits to wildlife. Furthermore, additional research will elucidate which abiotic factors ultimately have the greatest impact on an experiment's results.

Biotic factors

Abiotic conditions can be mitigated, but they are fundamentally uncontrollable. On the other hand, researchers can manage biotic factors to a certain degree by controlling nearby vegetation and directing insect visitation through the use of netting, cages, etc. In the case of Mt. Cuba Center, native vegetation around the Trial Garden contains many of the host plants for the insects observed in my experiment (Appendix B). This quality allows for more accurate results around the full suite of visiting insects to *Phlox* in the Delaware Piedmont region. By comparison, phlox trials conducted at Ohio

State University's Ornamental Plant Germplasm Center received very few insect visitors, which is speculated to be attributed to its urban location and a conspicuous lack of surrounding native flora to support invertebrates (*personal communication* with Dr. Peter Zale). Indeed, urbanization frequently results in biotic homogenization, with a few species (particularly "invasives") succeeding at the expense of most others- so called "winners" vs. "losers" (McKinney & Lockwood 1999). The recognition that urbanization has several deleterious impacts on native flora and fauna should be acknowledged by future researchers conducting comparative trials in urban areas, since their results will likely be influenced by the plant and invertebrate communities surrounding their experimental area.

Another vegetative element to consider when establishing comparative ecological plant trials is how nearby plants affect attraction through competition. For the 2015 field season, the Mt. Cuba Trial Garden had concurrent trial evaluations for *Monarda*, *Baptisia* and a small sampling of *Lilium* and *Clematis*. *Monarda*, in particular, was highly attractive to Hymenoptera, and also attracted sufficient numbers of Lepidoptera to potentially influence visitation results for *Phlox*. My University of Delaware colleague Owen Cass evaluated *Monarda* for nectar quality and insect attraction in 2015 and is in preparation for another monitoring field season in 2016. Though he has yet to publish results of his data, Mr. Cass frequently observed hundreds of nectaring invertebrates on *Monarda* at times when the *Phlox* patch was relatively void of visitors. While it is difficult to predict how these two plant genera affect each other without follow-up research, future investigations may seek to compare how different combinations of plant species planted side-by-side influence overall visitation to both plant types.

Based on the analysis of Levin & Anderson (1970) interspecific competition for floral resources had a strong effect on plant reproductive success measured through the relative frequency of pollinator visits. In their equation they showed that the minority species for visitation was at a reproductive handicap due to experiencing a larger percentage of heterospecific pollinator visitors. In turn, this might lead to a positive feedback loop, whereby each successive generation experiences fewer successful pollinations, leading to a greatly reduced crop and eventually localized extirpation or functional extinction. While this scenario represents an extreme example of direct competition not likely to transpire in the short run in a trial setting, steps should be taken to ensure that plantings directly adjacent to the flora in study are not competing to attract similar suites of pollinators. Certainly in the case of *Phlox* vs. *Monarda*, phlox is the so-called minority species attracting significantly fewer visitors with lower species richness, therefore the results of this trial should reasonably be expected to differ in trial gardens where directly competing plant species have been removed or are not naturally present.

Other Experimental Considerations

Besides abiotic and biotic factors, there are additional research questions to consider when designing comparative ecological trials. An obvious place to start is thinking about the number of samples that will be needed to achieve desired statistical accuracy. The field season for flowering perennial species is relatively short and inclement weather and other abiotic limitations can thwart monitoring plans. Particularly on stormy days in the garden, pollinator visits can be nonexistent, and flowers may be physically knocked off or become saturated with rainwater, which can dilute nectar and impact visitation on ensuing days. With these considerations in mind, an ideal monitoring protocol should include a contingency strategy, allowing researchers to be flexible in their approach to monitoring. Simply selecting set days for monitoring may not provide enough "fair weather" days to produce accurate representative statistics. Furthermore, sampling both nectar and recording insect visitation is tedious and time-consuming, and resources, human and otherwise, should be mustered to ensure that an adequate number of samples will be gathered to obtain a meaningful analysis. For a discussion on determining a suitable amount of samples, consult Kearns and Inouye (1993) who present a few equations in their chapter on Experimental Considerations to help researchers achieve a desired level of statistical accuracy.

Additional suggestions on planning future studies may include determining if a repeat or destructive sampling methodology will be used. The former will be employed for instance, when trying to assess nectar production throughout a flower's lifetime. Researchers will want to be aware that sampling nectar may stimulate increased nectar production later, provided that nectaries are not damaged (Gill 1988). Of course, nectaries which receive damage through the sampling procedure should be identified, and these measurements should be excluded in an overall analysis of total flower nectar production. Additionally, nectar production varies from year to year in plants due to a variety of factors including soil moisture and relative humidity (Real & Rathcke 1991). For this reason, and the aforementioned yearly cycling of invertebrate species, experiments should be conducted over a few field seasons, as resources permit, to achieve the most accurate results possible.

Additional Methods for Measuring Nectar

In this experiment, all nectar was sampled from a standing crop, which are plants having completely exposed flowers accessible to pollinators at all times. Measuring the standing crop of nectar is easier and less time-consuming than setting up exclusionary devices to prevent pollinator access in order to obtain a more complete picture of nectar volume. Of course, in measuring standing crop only, results are subject to a variety of biotic pressures such as partial or complete depletion by recently visiting nectaring insects and seasonal invertebrate population booms/crashes that result in altered incidence of nectaring occurrences. Increased resources notwithstanding, bagging flowers and excluding pollinators from visiting some inflorescences is a preferable method for accurately arriving at a nectar recharge rate, which is a valuable measure documenting the potential ecological benefits imparted to insects via nectar. Furthermore, this technique ensures that the full nectar potential throughout the life of a flower is being considered, rather than destructive methods where each flower is harvested individually for subsequent probing, which yields more random nectar values. By obtaining nectar recharge rates for the various cultivars and species of *Phlox* and other plants, a more complete comparative picture results, which can help illuminate the utmost varieties providing consistent ecological benefits over the course of the season.

In addition, the presence of nectar can be quite patchy throughout the day, therefore, obtaining more samples will result in improved accuracy in interpreting nectar resource availability. An example illustrating this concept are so-called “lucky hits”, which are flowers sampled late in the day (crepuscular p.m.) containing up to twice the amount of nectar as those sampled earlier in the day. These nectar-rich flowers are postulated to encourage pollinators to carry on nectaring late into evening (Southwick 1982). If sampling occurs unevenly throughout the day and across a field season, greater or fewer lucky hits may skew interpretation of the nectar volume average attributed to a specific plant type. Furthermore, Gill (1988) postulates that removal of nectar early in the day, when production rates are highest, may have a greater net impact on production than removal later in the day. He observed this case while studying hummingbird-pollinated *Heliconia* flowers, where nectar production peaked subsequent to hummingbird visitation in the morning, versus a reduced nectar recharge rate noted later in the day concurrent with reduced hummingbird visitation.

Finally, while using microcapillary tubes is a convenient and inexpensive method for sampling nectar, other methods may ensure greater accuracy, which could be more desirable for researchers with increased resources wanting more precise measurements. These materials and techniques include: syringes, centrifugation, paper wicks and rinsing flowers, and Kearns and Inouye (1993) describe the issues with these methods in their book *Techniques for Pollination Biologists*.

Additional Methods for Monitoring Insects

This experiment was originally designed to utilize a GoPro HERO3 camera fixed on a cluster of inflorescences to record nectar visits. The infrequency of insect visits however, failed to capture useful data, with long periods *sans* activity. In order to supplement observations, approximately every hour at the top of the hour during the field season, I walked the trial garden and recorded all nectaring insects in a notebook. From an ethical standpoint, my preference was to utilize non-destructive techniques, and in the case of *Phlox*, I found the above methods to be sufficient for noting and identifying all visiting insects in the trial. For plant species with far greater attraction to invertebrates, however, destructive sampling may be necessary to ensure proper documentation and classification of all species visiting the plants in trial. Common insect capture and killing materials for pollinators include: aerial sweep nets, vacuum aspirators and asphyxiation jars. Ultimately, having a reference collection of nectaring invertebrates for native plant species in a localized region is valuable information, and researchers who desire to translate their work to general audiences should strive to educate the public about the native invertebrates they can expect to see when planting certain varieties in the garden.

Areas for Future Research

While projects evaluating the ecological benefits of native plant cultivars in comparison with straight species are novel and important, all of the projects thus far have made insect attraction their primary focus. In spite of this, there are additional avenues for research that could be useful in ascribing ecological value to plants in these kinds of trials. For instance, knowing the nutritional composition of nectar and pollen, and how these aspects contribute to the health of invertebrates could be used to make recommendations about the ideal varieties to plant to promote insect well being. As an example, nutritional information including the amino acid profile, vitamin and mineral content, and the ratio of phenolics, volatiles, alkaloids and other compounds could all be gathered and individually studied to more fully grasp the arrangement that provides suitable nutrition for various types of invertebrates. In particular, the presence and ratio of amino acids in nectar could provide useful insight into insect attraction, and how different compositions attract specific invertebrate species across taxonomic groups.

Insect Attraction to Amino Acids in Nectar

While my experiment analyzed insect attraction solely using nectar volume and sugar concentration, the role that amino acids have in attracting insects, is an area that should be explored in greater depth in the future. Past studies have shown that butterflies, in particular, are attracted to flowers containing nectar with a high diversity and abundance of amino acids (Baker & Baker 1973; Alm et al. 1990). In a study testing butterfly and honey bee attraction to amino acid-rich nectar vs. nectar not containing amino acids, researchers found that female cabbage white butterflies and honey bees were both overwhelmingly attracted to artificial flowers containing nectar with amino acids mimicking those found in *Lantana camara*, a common landscaping shrub in the southern U.S. Interestingly, male cabbage white butterflies did not discriminate between the two nectars, which indicates the importance of amino acids to female butterflies' reproductive success through egg laying. Indeed, a pioneering study in 2015 by Jovanne Mevi-Schütz and Andreas Erhardt documented that map butterflies (*Araschnia levana*) provisioned with amino acid-rich nectar laid more eggs than those supplemented with nectar not containing amino acids (Mevi-Shütz & Erhardt 2005). Since amino acids comprise such a small total composition of nectar, decades ago it had been assumed that their contribution to pollinator attraction was low, and that in the case of Lepidopterans, larvae obtained all necessary amino acids feeding on foliage in their early life stages (Baker & Baker 1973). However, the first comprehensive study to test for amino acids in nectar was carried out in (1973) by Herbert George Baker and Irene Baker, which showed that "occurrence of significant concentrations of amino-acids in nectar is the rule" (pg. 544). Their results showed that just 0.3 ml of nectar from "butterfly flowers" (pollination system) contained about 840 nanomoles of amino acids, which is a quantity equivalent to what would be obtained by Hymenopterans from a day's harvest of pollen (Baker & Baker 1973; Gilbert 1972). From their survey of 266 species of flowering plants, and with chromatographic analysis of 44 nectar types, Baker and Baker discovered that a wide range of different amino acids were present, "with all essential amino-acids available from the nectar of one species or another." However, within their nectar subset, *Dianthus barbatus* (Sweet William) contained at least 12 different amino acids, the greatest diversity identified in their experiment. Long been considered a favourite butterfly gardening plant, Sweet William seems to present evidence that evolution of specialized pollination systems, particularly for Lepidopterans has driven development of increasing amino acid rich nectars. To further illustrate this point, the researchers confirmed that even "primitive plants" (*Drimys winteri*, *Liriodendron tulipifera*, various Palmae) contained some amino acids in their nectar, albeit in smaller concentrations than species typically noted for butterfly gardening.

Since *Phlox* is touted as being a great genus for butterfly gardening, future research into attraction should survey the amino acid composition of straight species vs. cultivars. In my cursory analysis of this topic, the cultivar *Phlox carolina* 'Bill Baker' contained a greater array of amino acids than both *Phlox carolina* and *Phlox paniculata*. The following High Performance Liquid Chromatography procedure was carried out by Papa Nii Asare-Okai, Co-Director of the University of Delaware's Mass Spectrometry Laboratory (Figure 5.1).

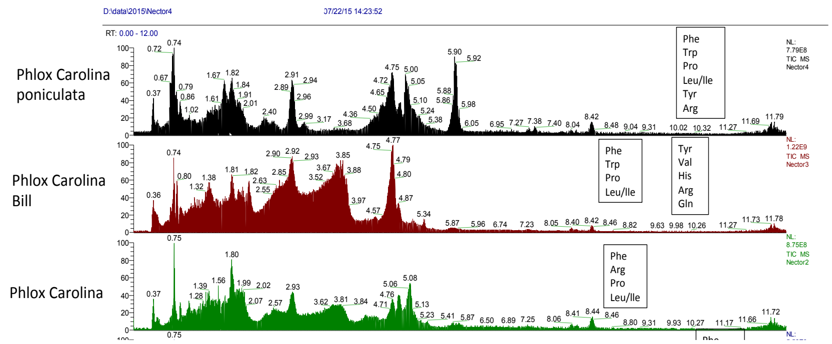


Figure 5.1 Representative chromatogram featuring High Performance Liquid Chromatography (HPLC) analysis, indicating presence of amino acids in three nectar samples (Phlox Carolina poniculata [sic.] paniculata, Phlox Carolina Bill [sic.] 'Bill Baker', and Phlox Carolina). Each spike indicates presence of a distinct amino acid. To make a quantitative assessment of amino acids, a sample of each individual amino acid is injected and its peak height or peak area is measured. In many cases, there is a linear relationship between the height or area and the amount of sample. Big spikes are the main substances in the sample, while smaller spikes indicate trace substances. The amino acids listed in boxes on the chart were detected as present in each sample. Run time in this HPLC analysis was 12 minutes.

As indicated in the chromatogram above, the cultivar *Phlox carolina* 'Bill Baker' contained 9 amino acids (Phenylanine, Tryptophan, Proline, Leucine/Isoleucine, Tyrosine, Valine, Histidine, Arginine, Glutamine) while straight species *P. carolina* and *P. paniculata* contained only 4 and 6 types respectively. For researchers with access to the requisite resources, future investigation into the role that essential amino acids play in attracting insects to phlox and other species is recommended. Researchers may ultimately discover that nectar preference is a product of invertebrates being attracted to specific amino acid compositions that ensure they meet their nutritional and energetic needs.

Insect Attraction to Non-Proteinogenic Amino Acids and Secondary Compounds in Nectar

While a few studies have been carried out to investigate the role essential amino acids have in providing nutrition for pollinating species, the role that non-proteinogenic amino acids have in attracting insects is an emerging science with very little attempted research. Non-proteinogenic amino acids (aka “unnatural” amino acids) are not found in the genetic code of organisms, and unlike essential amino acids, they are not biosynthesized by organisms (Ambrogelly et al. 2007). There are well over 200 non-protein amino acids found in various plant species (about 700 have presently been identified in other sources); however, it is difficult to generalize about their distribution in plants, since some are restricted to a limited range of species, while others occur broadly through specific plant families (Fowden 1981; Lamberth 2010). In the past, research has determined that some non-protein amino acids may serve, along with alkaloids, as defense compounds discouraging predation (Rhodes 2009). In contrast, a recent survey of academic literature on the subject of non-protein amino acids indicates that they may positively affect foraging behaviour in insects in myriad ways including: directly benefitting the nervous system, contributing in regulating feeding rates and helping to increase the activity of flight muscles (Nepi 2014). Although no studies have attempted to determine if non-protein amino acids are present in phlox specifically, increasing sophistication of analytical equipment and techniques have shown that non-protein amino acids are much more ubiquitous in floral nectar than previously thought (Nepi 2014). For the few studies that have been attempted, results indicate that non-protein amino acids are more common in plants that attract Hymenoptera as their principal pollinators (Petanidou et al. 2006; Heil 2011; Nepi et al. 2012). With that said, future researchers may wish to investigate the role that non-protein amino acids have in steering attraction for lepidopteran pollinated plants.

Insect Attraction to Sugars in Nectar

Beyond the role that amino acids have in attraction, future research on comparative nectar trials should attempt a complete laboratory analysis of sugars present in *Phlox* and other species to determine a ratio of composition and how this affects attraction for visiting invertebrate groups. In addition to the 3 major sugars found in nectar (sucrose, glucose, fructose), minor sugars have been identified which could provide a compelling interpretation for the constituent elements attracting invertebrates to nectar on flowers. For instance, disaccharide and trisaccharide sugars previously identified in nectar such as maltose, melibiose, raffinose and other oligosaccharide sugars could play a part in attracting certain pollinator groups to visit and nectar on various cultivar types and species (Wykes 1952b). In fact, the adaptive significance of floral nectars is widely accepted by researchers to be correlated to their ability to attract pollinators (Simpson & Neff 1983). Through evolution, this may be expected to result in certain insect guilds being attracted to particular plant species and/or families that provide them with the right ratio of sugars and other nutritional elements necessary to ensure their survival.

While a survey of various *Phlox* species for nectar sugars is not available, an extensive study on *Ipomopsis longiflora*, a long corolla-tubed member of the phlox family Polemoniaceae, revealed a pattern of variation clearly related to geographic distribution of *in situ* populations (Freeman et al. 1985). In particular, sucrose concentrations between two distinct subspecies ranged from 73.2% to 91.9%, which interestingly was not believed to result from pollinator differences, since both subspecies are visited principally by the *Hyles lineata* hawkmoth. Rather, the discrepancy in sucrose concentration may be a result of other factors such as abiotic conditions, which subject each subspecies population of *Ipomopsis* to uneven temperature, rainfall, wind and humidity regimes. Since we know through the work of Grant and Grant (1965) that *Phlox* are pollinated principally by Lepidoptera, and that this order of insects ranges across much of North America in a wide array of ecosystems, it is plausible that phlox will exhibit an intriguing range of sugars across taxa, which may yield insight into the concentration of sugars linked to habitat type and aligned with the various lepidopteran pollinators present in their native range. From this data, researchers may be able to analyze and compare sugars for *Phlox* species and cultivars to determine if sugar concentration and composition in cultivars is more closely linked to parentage or if growing conditions have more of a bearing.

Other Avenues for Research

Along with the proposed research topics I previously suggested, there are myriad other avenues to approach investigating comparative trials on the ecological differences between cultivars and straight species of *Phlox*. For instance, some *Phlox* species serve as host plants for invertebrates (*Microsteris (Phlox) gracilis- Grammia genuera* [Singer & Stireman 2001], *Phlox pilosa- Schinia indiana* [Swengel & Swengel 1999]) and a field trial could be set up to determine if cultivars derived from these parent species are also capable of supporting caterpillars and other immature invertebrates. However, since ornamental plants are often selected for qualities that make them resistant to herbivory by invertebrates, one might not expect many cultivars to be able to support populations of caterpillars and other insects. If certain cultivars show promise, these may be subject to additional research and or breeding to develop marketable cultivars that can be both aesthetically pleasing and ecologically beneficial for native wildlife species.

Another avenue that should certainly be probed is identifying the specific morphological traits that make cultivars more or less attractive to invertebrates. For instance, in my experiment the abundant small flowers of *Phlox paniculata* 'Jeana' and the large stature of the plants seemingly made them more attractive to nectaring insects. Additionally, *Phlox paniculata* 'Jeana' had the narrowest corolla opening and the second shortest corolla tube of any *Phlox paniculata* derived cultivar in the trial. While all of these attributes almost certainly bear an influence on its superior attraction vis-à-vis other cultivars and the straight species, additional work could set-up an experiment testing each component individually, in order to ascertain which characteristics have the greatest influence on invertebrate attraction. Joseph Poythress (2015) in interpreting his results on differences between cultivars and species asks, “which characteristics of a cultivar might be used to predict how well it fills an ecological role in the landscape?” Indeed, this type of research may be so-called “low-hanging fruit” since these characteristics are relatively easy to measure and may yield significant differences with regard to attraction. With so few overall studies having looked into the unique qualities that distinguish attraction between cultivars and species, morphometric flower measurements are arguably an excellent place to begin all future investigations into this field. Furthermore, with thousands upon thousands of potential plants to test in regions across the planet, studying morphological characteristics that relate to accessibility of both nectar and pollen will likely result in distinct patterns of visitation by invertebrates which may provide a solid framework from which to discuss this topic moving forward.

Finally, a developing research area with great promise for comparing straight species and cultivars is focused on floral scent chemistry and how it affects insect attraction. In particular, the work of Dr. Cassie Majetic and others (2015) on a wild population of *Phlox divaricata* showed that median flower scent emissions peaked in mid-morning and in evening, consistent with peak visitation by diurnal moths in a northeastern Kansas prairie population. Interestingly, two separate groups of scent compounds were implicated in influencing this attraction, with linalool and associated lilac aldehyde/alcohol compounds contributing a larger proportion to scent from 1000-1200h and aromatic compounds exerting a greater influence from 1930-2130h. In an additional study by Majetic and her team (2014), they identified significant variation in floral scent among species of *Phlox*, between colour morphs within species, and among cultivars. Of particular interest is their assessment that demonstrated significant differences between the volatile characteristics of wild-originated *Phlox drummondii* and horticulturally-derived cultivars. While cultivar colour morphs exhibited rampant variation in scent, wild types did not, indicating that cultivars developed through selective breeding techniques likely represent the bulk of variability in scent for cultivar types. As pollinator-mediated natural selection is considered to be a primary driver in scent divergence, it follows that straight species and wild-type cultivars will be more closely aligned with the pollinators that evolved to visit them. Ultimately, there are many factors influencing visitation to *Phlox* and other native plant species, nevertheless, as our knowledge grows about the effects that individual floral characteristics have in attracting pollinators, we may better predict the suite of traits that effectively draw them in and impart ecological benefits to insects and other wildlife.

Recommendations for Future Experimentation and Projects

Recommendation 1: Before establishing a comparative trial for cultivars vs. straight species, consider the metrics that will be most useful in interpreting your results.

While this is perhaps an obvious step in the process, investing forethought into the protocol for an experiment including sampling techniques, sampling frequency, and other practical measures will guide the eventual forum most appropriate for translating your results. Again, think about what information will be most relevant to your intended audience. If planning to publish this study in a peer-reviewed journal, more energy should be expended into designing a rigorous measuring and monitoring protocol. If this experiment is intended as an informal study that will catalogue the range of invertebrates attracted to cultivars and native species for your region, then perhaps a simple pairwise survey will suffice. Ultimately, there are many possible measures for attraction including, sugar concentration, amino acid composition, flower morphological access, etc. Before proceeding, ensure that your experiment is set-up to obtain the most useful results possible for your target audience(s).

Prior to establishing any experiment, consult literature describing how many samples are necessary to achieve a desired level of accuracy (Eckblad 1991). While taking a few samples is relatively easy, following a systematic sampling protocol will require resources of time and energy, which may come at the expense of pulling staff from other research areas. For reference, consult Techniques for Pollination Biologists by Kearns and Inouye (1993) which is chalk full of helpful information for researchers investigating pollinators.

Recommendation 2: Establish more comparative trials with greater diversity of plant species and cultivars, for greater duration of time, in regions throughout the world.

As of 2016, only 5 studies are known to have been conducted in the U.S., which have investigated insect attraction for cultivars of native plants vs. straight species. Since native cultivars are increasingly popular and available in the domestic nursery marketplace, additional trials should be established in regions throughout the U.S. and elsewhere to assess these plant types for their ecological characteristics. Furthermore, declines of pollinators are occurring across many regions, and results for different native plant species may be different from state to state, county to county and yard to yard, illustrating then need for additional and ongoing testing.

Of the 5 studies that have been conducted, only 2 have analyzed nectar and none have specifically reported on any significance with regard to floral part measurements or other floral physical traits. Additional documentation on a range of floral characteristics will contribute in important ways to advancing research in this field. For instance, while nectar is fairly straightforward to collect and analyze using field techniques, analysis of pollen could yield quite interesting results, pertaining to differences in the two plant groups. Unfortunately, pollen sampling requires laboratory equipment, and the extra resources involved may entail securing research assistants to carry out collection and interpretation.

Testing pollen and other floral physiognomies will contribute meaningful data to this field, but additionally, studies should transpire over multiple years in order to document patterns that are present from year to year or across climatic regions. Yearly cyclic variation is common and climate change is further expected to exacerbate challenges to specific pollinator and plant groups as both struggle to confront issues such as chronic drought, flooding, sporadic weather episodes and other extreme weather events.

Perhaps a way to build capacity for these kinds of experiments is through the citizen science movement, which seeks to enlist volunteers on scientific monitoring projects in order to collect data and foment support for science with an environmental bent. Relying on citizen scientists is not without challenges (Dickinson et al. 2010), but if executed adeptly, it will significantly increase our knowledge of the inherent differences between cultivars and straight species. An example of this in action is the Bees, Bugs & Blooms Trial, which was conducted by Penn State University Extension. This project partnered entomologist extension agents with volunteers to collect observational data on pollinators visiting and nectaring on native plant species in the trial. Through their collective efforts, they were able to report mixed results for plant preference, with certain cultivars exhibiting enhanced attraction and others experiencing diminished visitation (PSU Department of Entomology 2016). Since tens of thousands of potential cultivars and species are available for testing, with results varying from region to region, each additional experiment adds immense value to our understanding of this field of research.

Recommendation 3: Proceed with caution when considering planting native cultivars in landscapes adjacent to vulnerable *in situ* straight species populations.

Native cultivars may certainly have a place in an ecological landscape, but to reduce the threat of genetic crossing with natural populations, this place should be located apart from vulnerable *in situ* straight species populations. Since cultivars can differ significantly from straight species in colour, shape, size, scent and other ways, they may interrupt signals between native pollinators and native plants, resulting in diminished visitation and, thus reproduction, in wild plant populations (Arias & Rieseberg 1994; Stewart et al. 2003; Whelan et al. 2006). Additionally, cultivars of hybrid origin in *Phlox* and a few other species can be sterile and/or exhibit reproduction limitations, which make them unsuited for use in environmental restoration projects (Levin 1975; Zale *personal communication*).

A caveat should be levelled against cultivars that are developed through intensive breeding and selection. In this case, manipulation over multiple generations to yield a plant with desirable ornamental characteristics, may result in a plant far removed from its parent species in an ecological sense. For those cultivars which were originally selected from wild populations, the threat of genetic admixture with regular straight species may be reduced vis-à-vis bred types, since crossing would likely result in plants that are less divergent genetically and perhaps phenotypically from the "normal" species. Furthermore, where aberrant populations of native plants exist *in situ* (said to be the case of *Phlox paniculata* 'Jeana', which is reported to have been found growing along the Harpeth River in Tennessee), that are faced with extirpation via destruction of habitat, deliberate crossing and propagation could prove useful in preserving genetic lines. While this is certainly the exception rather than the rule, researchers and land managers should evaluate reintroduction strategies for cultivars on a case-by-case basis, while ensuring the gardening public is aware of potential threats resulting from introgression with natural populations.

Recommendation 4: Consider complementing straight species in the home landscape with native cultivars to extend the nectaring season.

In the case of *Phlox* flowers, the different species and cultivars in the trial opened across a wide range of days from spring through fall, so it is advisable to plant multiple types to provide a continuous supply of nectar and floral rewards. Based on the enhanced attraction of cultivars in this experiment and the comparable nectar benefits they provided native wildlife, home gardeners and landscapers may want to consider planting cultivars to complement a landscape design palette of native plants. In recognizing the benefits they impart to wildlife in a home garden setting, the use of native cultivars becomes a positive stance, rather than a negative or neutral one, since they can be seen supplementing the ecological garden rather than detracting from it. Fundamentally, ongoing habitat destruction and the decline of species worldwide means that gardeners and land stewards should endeavour to inspire the public to plant biodiverse gardens with a mixture of trees, shrubs, perennials and grasses to support ecological food webs rather than maintaining lawns of non-native turf grass which are devoid of wildlife (Burghardt et al. 2009). While a few public gardens and conservation organizations have recently taken stances against the use of native cultivars for the perceived threats they pose to native plant populations (Wild Ones 2013; Knoxville Botanical Garden and Arboretum 2015), the scope of wholesale biodiversity losses warrants us to seek alternatives to conventional landscaping, including the replacement of monocultures with native plants and cultivars. This is not to say that concerns about cultivars interbreeding with locally-adapted straight species should not be considered (see Recommendation 3), but for home gardeners who increasingly maintain landscapes removed from ecologically intact natural habitats, encouraging the planting of native plants (including cultivars) over exotics presents an opportunity to support extant wildlife populations that have adapted to life among humans in the face of severe landscape alteration. Ultimately, advocates for the environment should embrace concepts that employ simple, direct messaging to the public to inspire stewardship. Doing so reduces the risk of losing their attention, as often happens through technical debates on the merits and challenges of straight species vs. native cultivars. Rather, passionate, exclusively native-planting home gardeners should consider investing their energies into contacting nurseries and requesting that they stock more native straight species, in order to give consumers greater options when shopping for environmentally-friendly plants.

When deciding to add cultivars to your design seek out types that were selected from the wild, since these plants were demonstrated in this trial to exhibit superior attraction. For *Phlox*, even selectively bred cultivars, and those that emerged as spontaneous seedlings in the garden, were demonstrated to attract and provide ecological benefits for native wildlife. Indeed, more research is needed to fully evaluate all of the new cultivars on the market, but for the cultivars sampled in this trial, many showed that they were equal or better at attracting adult invertebrates than their straight species analogues. Reasons for why cultivars may attract enhanced visitation centre on the ease of access to nectar and floral rewards granted to wildlife species through the reduction in size of flower parts, greater abundance of blooms, stature of plants, and other qualities. Cultivars sourced from wild populations will typically possess floral characteristics that enhance insect attraction, rather than preventing nectaring and pollination. By contrast, selectively bred cultivars of native plants sometimes include radically divergent forms, including double-flowered varieties that can completely block access to floral rewards, thus rendering them ecologically inferior to both straight species and wild cultivars. Perhaps in the future, researchers should design trials to differentiate between wild-derived cultivars and bred varieties with dramatically different morphological characteristics, in order to streamline testing the potential pool of native species and cultivars. If indeed, patterns are observed whereby cultivars with significant structural and anatomical modifications from their parent species consistently show weak attraction, then we may better inform nursery owners and encourage them to consider dropping these options from their catalogues. They may also choose to go a step further by distinguishing their native cultivar offerings between those that potentially support pollinators and those that serve an ornamental function exclusively.

Finally, for wild selected cultivars endemic to a particular region, nursery growers may want to develop marketing materials that describe their ecological merits, to foment interest and instil a sense of civic pride around plants. As an example, the cultivar *Phlox paniculata* 'Jeana', which attracted the greatest abundance and diversity of invertebrates in the trial, was originally sourced by plantswoman Jeana Prewitt along the Harpeth River in Nashville, Tennessee (Missouri Botanical Garden 2015). *Phlox paniculata* 'Jeana' is an excellent candidate to begin this marketing approach, which capitalizes on budding interest in ecological horticulture and local goods, and can help to generate robust sales for garden centres in the future.

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Appendix A

PHLOX AND INSECT IMAGES

Figure A1. *Phlox divaricata* on 05/05/15. Note how the anthers and stigma are recessed in the flower (contrasted with the other *Phlox* species in study). This characteristic is less common in the genus *Phlox* and taxonomists place them within the Protophlox Section (Wherry 1955).

Figure A2. *Phlox divaricata* ‘Charleston Pink’ on 05/05/15. ‘Charleston Pink’ was discovered in the garden of Charleston, Illinois plant enthusiast Dr. Wesley Whiteside.

Figure A3. *Phlox stolonifera* blooming on 05/05/15. *Phlox stolonifera* and its cultivar 'Blue Ridge' were the first blooming phlox in the Mt. Cuba Trial, sending forth their first flowers on April 30th. Both types are low-growing, mat-forming varieties that are good additions to the woodland garden or as a shady groundcover.

Figure A4. *Phlox stolonifera* 'Blue Ridge' on 05/05/15. Contrast with colour of straight species.

Figure A5. *Phlox carolina* 'Bill Baker' on 05/26/15. In the Mt. Cuba Center trial, *Phlox* 'Bill Baker' was the longest-bloomer in the trial, initially opening on May 26th and continuing with sporadic flowering until July 30th, a period of over 2 months. In spite of its long flowering duration, however, 'Bill Baker' attracted a single nectaring insect in the trial.

Figure A6. *Phlox* x 'Forever Pink' on 06/01/15. Introduced in 2009 by Dr. James Ault, Director of Ornamental Plant Research for the Chicago Botanic Garden, and Chair and Manager of the Chicagoland Grows® Plant Introduction Program. This variety is described as a "compact, carefree, and long-blooming" phlox with repeat blooming characteristics. In the trial it bloomed for over 2 months.

Figure A7. Syrphid or hover fly (*Eupeodes americanus)* on *Phlox glaberrima* 'Triple Play' 06/07/15. This was the first observed pollinator in the trial, and it was noted over 3 weeks before the next nectaring insects were observed! In my study, hover flies were the first insects spotted in the morning, and among the last seen in evening. They are active at lower temperatures than both Hymenopterans and Lepidopterans

Figure A8. *Phlox amplifolia* on 06/15/15. This species was collected in the wild by Dr. Peter Zale and sent to Mt. Cuba Center for their phlox trial. *Phlox amplifolia* was an exceptionally long bloomer and remained free of disease throughout the field season. Though a few cultivars are sold claiming *P. amplifolia* parentage, Dr. Zale challenges this claim based on dissimilarity of flowers and other distinguishing features.

Figure A9. *Phlox carolina* 'Lil Cahaba' on 06/17/15. This cultivar was collected by Jan Midgley from a population growing along the Little Cahaba River in Bibb Co., Alabama. Its flowers were among the most brilliant in the trial, with intense magenta hues that lasted from June 15th through August 14th.

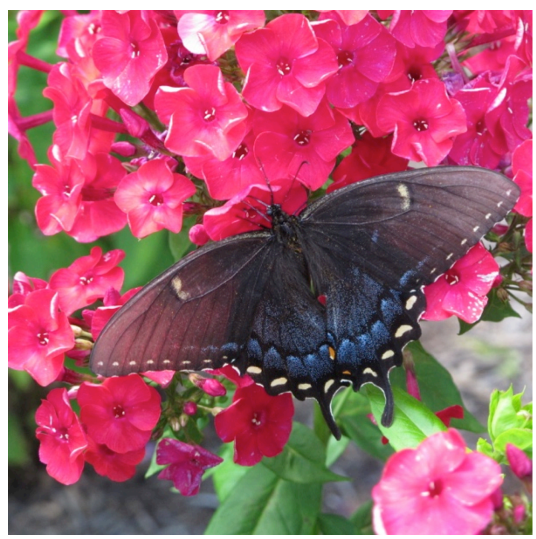

Figure A10. Female tiger swallowtail, dark morph (*Papilio glaucus*) nectaring on *Phlox paniculata* 'Volcano Red' on 06/29/15.

Figure A11. Syrphid fly (*Eupeodes americanus)* on *Phlox carolina* 'Kim' on 07/03/15. Like the variety 'Lil Cahaba', 'Kim' was wild selected by Jan Midgley from a wild population found growing in Alabama.

Figure A12. Hummingbird clearwing moth (Hemaris thysbe) pollinating *Phlox paniculata* 'Robert Poore' on 07/10/15. Sphinx moths (family Sphingidae) are the primary pollinators of numerous phlox species throughout North America (Grant & Grant 1965).

Figure A13. European honey bee (*Apis mellifera*) robbing nectar of *Phlox paniculata* 'Delta Snow' on 07/13/15. 'Delta Snow' was the preferred cultivar for robbing by various Hymenopterans in the trial.

Figure A14. Bumblebee (*Bombus* sp.) robbing nectar on *Phlox paniculata* 'Delta Snow' on 07/13/15.

Figure A15. Silver-spotted skipper (*Epargyreus clarus*) nectaring on *Phlox paniculata* 'Lavelle' on 07/13/15. 'Lavelle' was the third most attractive *Phlox paniculata* type in the trial.

Figure A16. Male Tiger Swallowtail (*Papilio glaucus*) nectaring on *Phlox paniculata* 'Jeana' on 07/13/15. 'Jeana' was far and away the most attractive *Phlox paniculata* cultivar in the trial.

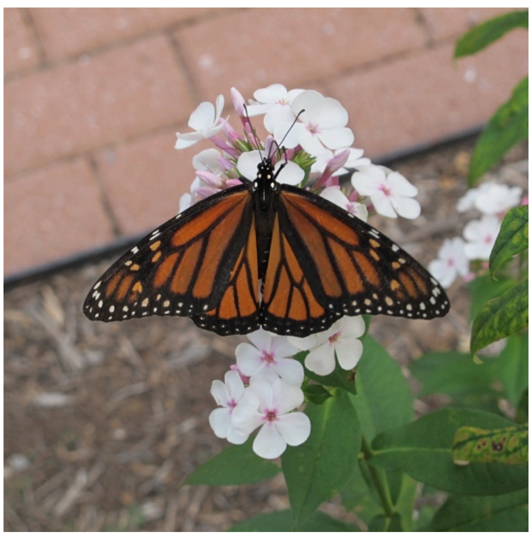

Figure A17. Monarch butterfly (*Danaus plexippus*) nectaring on *Phlox paniculata* 'Lavelle' on 07/13/15.

Figure A18. *Phlox paniculata* 'Jeana' on 07/16/15. Photo taken from eye level displaying 'Jeana's' tall stature (tallest variety in the trial).

Figure A19. *Phlox paniculata* 'Jeana' on 07/16/15. Note the small but abundant flowers on this variety which distinguish it from most other types. These characteristics made it the most attractive phlox in the trial to nectaring insects.

Figure A20. *Phlox paniculata* on 07/19/15. First day with open flowers in the trial.

Figure A21. *Phlox paniculata* 'Lavelle' on 07/19/15. 'Lavelle' was discovered growing in the garden of plantswoman Jeana Prewitt. Its parentage is thought to include *P. paniculata* 'Jeana'.

Figure A22. *Hemaris thysbe* nectaring on *Phlox paniculata* 'Jeana' on 07/20/15. Note how far from the flower this moth is in order to nectar due to the shallowness of the corolla. 'Jeana's' more abundant and easier to access flowers made it the most attractive cultivar in the trial.

Figure A23. Peck's skipper (*Polites peckius*) nectaring on *Phlox paniculata* 'Jeana' on 07/20/15.

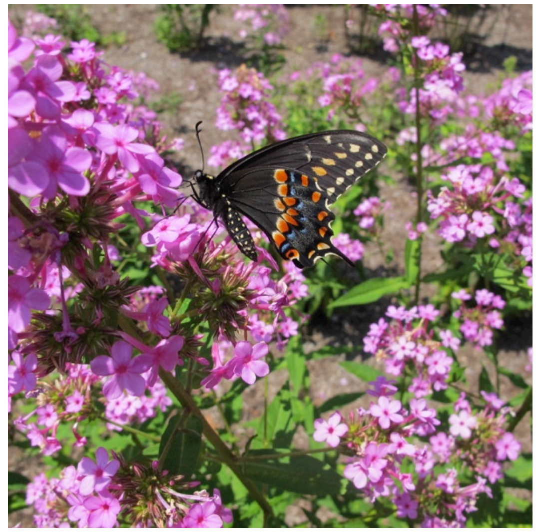

Figure A24. Black swallowtail (*Papilio polyxenes*) nectaring on *Phlox paniculata* 'Jeana' on 07/20/15.

Figure A25. Eastern carpenter bee (*Xylocopa virginica*) robbing nectar on *P. paniculata* 'Jeana' on 07/20/15.

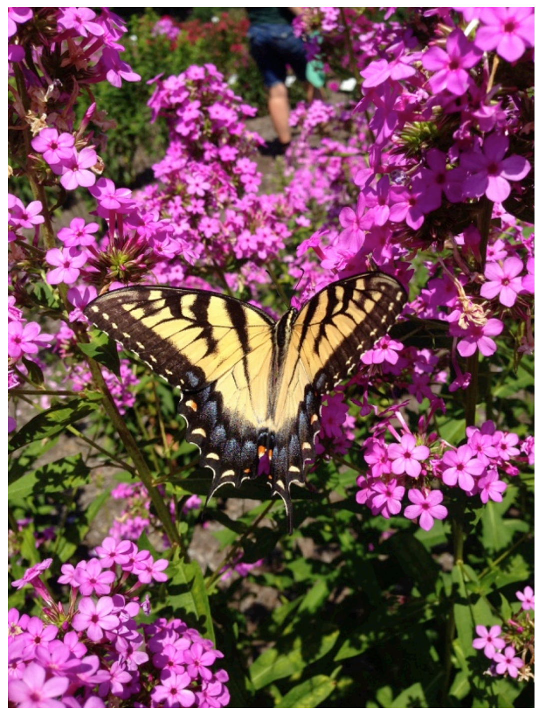

Figure A26. Female tiger swallowtail (*Papilio glaucus*) nectaring on *P. paniculata* 'Jeana' on 07/22/15.

Figure A27. *Phlox paniculata* 'Dick Weaver' on 07/22/15. 'Dick Weaver' was the second most attractive paniculata cultivar in the trial.

Figure A28. Sweat bee (family Halictidae) robbing nectar on *P. paniculata* 'Dick Weaver' on 07/24/15.

Figure A29. Female Eastern carpenter bee (*Xylocopa virginca*) preparing to rob nectar on *P. paniculata* 'Robert Poore' on 07/27/15.

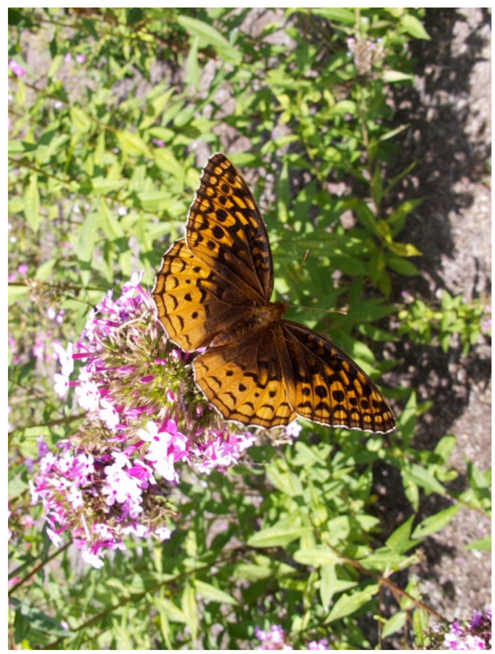

Figure A30. Great spangled fritillary (*Speyeria cybele*) nectaring on *P. paniculata* 'Jeana' on 08/28/15.

Appendix B

HOST PLANTS FOR LEPIDOPTERA IN TRIAL

Crambus agitatellus- Double-banded grass-veneer moth
Host plants: Grasses and low plants (Beadle & Leckie 2012)

Danaus plexippus- Eastern monarch butterfly
Host plants: Various *Asclepias* spp. (Soukarov 2014).

Epagyreus clarus- Silver-spotted skipper
Host plants: Various herbs, vines, shrubs and trees in the Fabaceae family (Hall 2011).

Hemaris thysbe- Hummingbird clearwing moth
Host plants: Honeysuckle (*Lonicera* spp.), snowberry (*Symphoricarpos* spp,), hawthorns (*Crataegus* spp.), cherries and plums (*Prunus* spp.), and European cranberry bush (*Viburnum opulus*) (Butterflies and Moths of North America 2016a).

Papilio glaucus- Eastern tiger swallowtail
Host plants: Commonly feed on plants of the Magnoliaceae and Rosaceae, including: Black cherry (*Prunus serotina*) and mountain ash (*Sorbus* spp.), and Tulip tree (*Liriodendrum tulipifera*) and sweet bay (*Magnolia virginiana*), the latter used almost exclusively in Florida. Additional host plants include: basswood (*Tilia* spp.) and ash (*Fraxinus* spp.). (Hall & Butler 2011) (Butterflies and Moths of North America 2016b)

Papilio polyxenes- Black swallowtail
Host plants: Various wild, adventive and cultivated species within the Apiaceae family. (Hall 2014)

Speyeria cybele- Great spangled fritillary
Host plants: Various violet family species (*Violaceae* spp.) (Butterflies and Moths of North America 2016c)

Vanessa atalanta- Red admiral
Host plants: Various nettle family species (*Urticaceae* spp.) (Hall & Butler 2009)