INFLUENCE OF FLOWER STRIPS ON INSECT POLLINATOR RECRUITMENT AND CROP YIELD IN DAY-NEUTRAL STRAWBERRY PRODUCTION

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DEDICATION

I would like to dedicate this work to my granddad, Harold Swanson, whose endless curiosity as a scientist and philosopher, and whose compassionate spirit as a father and friend, has always inspired me to stay curious, be generous, work hard, and laugh joyfully at your own jokes.

ABSTRACT/SUMMARY

Around 35% of our food comes from pollinator-dependent crops, especially many fruit crops. In light of emerging threats to the honey bee industry, recent research has highlighted the importance of wild insect pollination services in agroecosystems. Pollinator "farmscaping" practices, which provide habitat and floral resources for wild insect pollinators on farms over space and time, are being investigated for horticultural crops. However, there is relatively little research directly linking pollinator farmscaping practices to crop yields, especially considering the wide variation in pollination requirements between crop species. Strawberries (*Fragaria x ananassa*), though self-fertile, appear to produce higher quality fruit when flowers are more thoroughly fertilized by pollinating insects. Ensuring effective pollination services for strawberry crops may be even more beneficial in day-neutral cultivars, which flower and fruit continuously throughout the growing season, as opposed to the short-day (June-bearing) cultivars commonly grown in the US Midwest. While some research has shown increased pollinator abundance in strawberry fields adjacent to annual wildflower strips, there is less research on direct benefits to strawberry production, particularly for day-neutral strawberries. In addition, most flower strip research focuses on diverse wildflower strips, despite evidence that bees may benefit more from flower plantings with clumps of single species rather than heterogeneous mixtures. This research investigates the potential of planting an attractive annual flower strip as a "magnet species" to recruit wild pollinators and enhance pollination services, and therefore yield, in an organic day-neutral strawberry production system over two growing seasons. Flowering borage (*Borago officinalis*) strips were established on one end of three experimental fields of day-neutral strawberries. Strawberry yield and pollinator presence were hypothesized to decrease with distance from the flower strip. Though distance from the flower strip did not have a statistically significant impact on production parameters and pollinator presence, average strawberry yield and berry number was lowest in plots furthest from the flower strip in both years. Individual berry weights of the ‘Evie-2’ cultivar decline with distance from the flower strip, perhaps due to high pollination requirements. Strawberry floral visitor abundance declines steadily with distance from the flower strip in 2017, but this pattern is not clearly observed in 2018. The borage flower strip was highly attractive to insects, though primarily honey bees (*Apis mellifera)* and bumble bees (*Bombus spp.)*. Primary strawberry flower visitors were hoverflies (Syrphidae), root maggot flies (Anthomyiidae) and native bees (Halictidae, Megachilidae, etc.), suggesting day-neutral strawberry pollination may rely more on Diptera taxa and small bees rather than larger pollinators like honey bees or bumble bees. More research is necessary to examine the potential of borage as a “magnet species” to facilitate day-neutral strawberry crop pollination. This project presents further evidence on the potential of pollinator farmscaping practices, such as annual flower strips, to recruit wild insect pollinators and improve pollination services for the benefit of small fruit crops.

TABLE OF CONTENTS

Acknowledgements i

Dedication ii

Abstract/Summary iii

Table of Contents v

List of Tables vii

List of Figures ix

Chapter 1 – Literature Review: Flower strips as an agroecological farmscaping tool to recruit wild pollinators and support strawberry pollination and production 1

Reimagining Modern Agriculture 2

Agroecological Farm Management 3

Farmscaping and Ecosystem Services 3

Importance of Pollination Services 4

Farmscaping to Support Crop Pollinators 5

Strawberries 8

Strawberry Production 8

Strawberry Cultivars 9

Importance of Pollination in Strawberries 9

Supporting Pollinators in the Strawberry Agroecosystem 10

Farmscaping for Pollinators in Day-neutral Strawberry Systems 10

Borage Strips for Pollinators 11

Measuring Pollination Success in Day-neutral Strawberries 12

Hypothesis 13

Objective 1 14

Research Question 1 14

Objective 2 14

Research Question 2 14

Chapter 2–The influence of a magnet species flower strip (*Borago officinalis*) on pollinator recruitment and production of day-neutral strawberry cultivars in Minnesota 15

Introduction 16

Materials and Methods 18

Study Site 18

Field Preparation and Pest Management 18

Experimental Design 19

Floral Visitor Surveys 21

Insect Identification 22

Strawberry Yield 22

Statistical Analysis 23

Results & Discussion 24

Strawberry Floral Visitors 24

Borage "Magnet Species" Potential and Plant-pollinator Dynamics 26

Strawberry Yield across Day-neutral Cultivars 28

Conclusions 30

Tables and Figures 35

Literature Cited 52

List of Tables

Table 1. Primary floral visitor defined within taxonomic order, described by category (in bold) and within insect family. Insect families are separated between specimens found on borage flowers vs. those found on strawberry flowers. Insect families found on both flowers are included in both columns. Dotted line indicates that the family specific to that row was not found on flowers within the column. "Other" includes insect taxa (i.e. Order: Coleoptera) with unlikely or minor pollination influence. 36

Table 2. Total counts of insect families collected on borage (*Borago officinalis*) flowers and strawberry flowers with increasing distance ranges from borage flower strip (I, II, III, IV) during 2017 and 2018. Insect order is in brackets within family column. Blank cells indicate absence of family in all categories for that year. "Other" includes other insect taxa with unlikely or minor pollination influence. 37

Table 3: Average abundance (mean ± s.e.) of primary floral visitors collected on borage (*Borago officinalis*) flowers and strawberry flowers with increasing distance ranges from borage flower strip during 2017 and 2018, across three experimental fields. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. 38

Table 4. Results of Chi square test used on fitted glmer model to determine how well variables predicted floral visitor count data in 2017 and 2018. In order to determine significance of factors, models of increasing complexity were compared with each other to isolate which factor contributed most to data variability. Date was the most significant factor for predicting strawberry floral visitor count data in both years. . 39

Table 5. Harvest data for 2017 & 2018 compared among day-neutral cultivars as well as distances from flower strip. Average yield and berry number were calculated per plant by the end of the growing season. Berry weights are averaged from 10 harvests at the peak of the season. 40

Table 6. ANOVA of linear mixed effects model with effect of distance and cultivar on total strawberry yield (g) in 2017 and 2018, with experimental block as a random effect. 41

Table 7. ANOVA of linear mixed effects model with effect of distance and cultivar on total berry count 2017 and 2018, with experimental block as a random effect. 41

Table 8. ANOVA of linear mixed effects model with effect of distance, cultivar, and harvest date on average individual berry weight in 2017 and 2018, with experimental block as a random effect. 42

LIST OF FIGURES

Figure 1. Experimental design 2017 and 2018. Plots are arranged in a randomized block design, with 4 single rows of day-neutral strawberries. Day-neutral strawberry cultivars 'Albion' (pink), 'Portola' (green), 'Evie-2' (yellow), and 'Seascape' (blue) are blocked by distance range. Each distance range (I, II, III, IV) is 7.6m long, with increasing distance from the flowering borage strip at 0m. The purple diamond section represents the flowering borage (*Borago officinalis*) strip (2.1m x 7.3m). .. 43

Figure 2. Number of total floral visitors by main insect categories for borage (*Borago officinalis*) and distance ranges within strawberry rows, averaged across three fields. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. 44

Figure 3. Average number of strawberry floral visitors among categories (Honeybee, Native bee, Other flies, Root maggot flies, Syrphids) compared across days from planting in 2017 (a) and 2018 (b), averaged across three fields. 45

Figure 4. Relative abundance of primary floral visitor categories (bumble bee, honey bee, native bee, syrphids, root maggot flies, other flies, tarnished plant bug, other insect taxa) found on borage flowers in flower strips during 2017(a) and 2018(b) growing seasons. 46

Figure 5. Relative abundance of primary floral visitor categories (bumble bee, honey bee, native bee, syrphids, root maggot flies, other flies, tarnished plant bug, other insect taxa) found on strawberry flowers during 2017(a) and 2018(b) growing seasons. 47

Figure 6. Borage (*Borago officinalis*) and day-neutral strawberry cultivar flowering phenology in 2017 (a) and 2018 (b) plotted days from planting. Average percent flowering indicates percentage of season total flowers counted open on that day. Day-neutral cultivar flowers are represented in solid colors, borage flowers are represented by dashed black line. 48

Figure 7. Total yield (average cumulative weight ± s.e) per plant displayed by cultivar and distance range in 2017 and 2018. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates. 49

Figure 8. Total berry number (average cumulative berry count ± s.e) per plant displayed by cultivar and distance range in 2017 and 2018. Each distance range (I, II, III, IV)

is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates. 50

Figure 9. Average individual berry weight (average ± s.e.) across 10 harvests in the middle of the season compared across distance ranges in 2017 and 2018. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates. 51

Chapter 1 – Literature Review: Flower strips as an agroecological farmscaping tool to recruit wild pollinators and support strawberry pollination and production

Reimagining Modern Agriculture

Conventional production agriculture is based on a model of intensification, designed to take limited natural resources and produce the highest yields possible (Matson et al., 1997). Given that its efficient functioning requires simplicity, linear supply-chains, and homogeneity, conventional agriculture focuses on supplying crops with the primary nutrients through chemical fertilizers, supporting a limited number of commodity crops, and farming large-scale monocultures where yields are maximized per unit area with ever increasing precision (Stewart et al., 2005). This way of producing food is leading to multiple environmental issues, including soil erosion, nutrient leaching, loss of biodiversity, and landscape homogenization. These symptoms of agricultural intensification damage the foundations of ecological functioning and ecosystem services that ultimately support crop production (Grab et al., 2018; Landis, 2017)

Without reimagining agriculture to support healthy, resilient agroecosystems, we cannot sustain, let alone increase, food production in any durable way for a growing planet. We need to reimagine an agricultural system based on ecological intensification, rather than economic intensification. This vision would mean redesigning agricultural landscapes to support ecological diversity and ultimately, life-sustaining processes, enjoying an abundance and diversity of food as a result (Kovács-Hostyánszki et al., 2017). It is a model that can help to alleviate environmental issues by building soil, recycling nutrients, increasing biodiversity, and increasing landscape heterogeneity with multiple ecosystem services. Skeptics claim that the ecological intensification of agriculture cannot feed the world, but a growing body of research is showing that not only can this system be as productive as conventional agriculture (Pywell et al., 2015), it is also designed to be resilient and adaptable to change in a future likely characterized by climate instability (Landis, 2017).

AGROECOLOGICAL FARM MANAGEMENT

Farmscaping and Ecosystem Services

Agroecological farm management is based on the understanding of agricultural landscapes as types of ecosystems (Jackson and Jackson, 2002). With an understanding of the ecological functions of these agroecosystems, farmers can optimize management in ways that meet production needs while ultimately maintaining and supporting the essential services provided by a diverse system. These functions of ecosystems that benefit human agriculture are referred to as "ecosystem services." Ecosystem services include provisioning services like food and fiber production and the regulating services that impact crop production like pest management, weed control, and pollination (Smukler, S.M., 2012). However, the focus of modern agriculture on maximizing yield through agricultural intensification has led to simplified agroecosystems and management practices that ultimately diminish the ability of natural systems to provide these services over space and time (Zhang et al., 2007). Techniques like mono-cropping and the use of synthetic fertilizers may make sense for short-term production goals, but there is increasing interest in ecological intensification and other efforts to diversify farming systems and maintain critical ecosystem services for the long-term (Landis, 2017).

Farmscaping is a term used to describe the practice of increasing and enhancing desirable ecosystem services on farms by creatively managing plant life in an agroecosystem (Smukler et al., 2010; Philips et al., 2014). Common farmscaping techniques for pest management include practices that protect crops from pests, like intercropping and companion planting, as well as practices that enhance pest natural enemy populations, such as insectary plantings, beetle banks, and hedgerows. Farmscaping techniques for insect pollination services include flower strips, reduced mowing, and maintaining natural areas. These techniques are focused on providing resources and habitat for beneficial arthropods, including pest natural enemies and pollinators, as a way of supporting the important arthropod-mediated ecosystem services of pest control and crop pollination (Isaacs et al., 2009; Philips et al., 2014).

Importance of Pollination Services

Of the many ecosystem services important to agriculture, crop pollination by insects has received attention in recent years because of emerging risks to bee populations and the critical, but undervalued, service of pollination to humanity (Spivak et al., 2011). Globally, about 35% of our food comes from pollinator-dependent crops (Klein et al., 2007), and at least 75% of all crop species benefit from animal pollination for fruit development and yield (Bartomeus et al., 2014). These proportions may rise as crop production shifts towards pollinator-dependent crops, such as fruit and vegetables, to meet global nutrition needs (KC et al., 2018). While honey bees often receive attention for their role in crop pollination services, there is growing evidence of the economic value and critical pollination service of wild pollinator populations (Winfree et al., 2011; Garibaldi et al., 2014). In fact, our food supply is becoming more dependent on pollination services over time, especially in the least-developed parts of the world, where populations depend more heavily on pollinator-dependent crops (Aizen et al., 2009). However, honey bees and wild bees are facing threats to their populations that some fear may constitute a "pollination crisis", including habitat fragmentation, wide-spread broad-spectrum pesticide use, and reduced floral resources over space and time (Goulson et al., 2015). Implementing farmscaping practices to support pollinator populations in our agroecosystems is critical in order to help ensure the continuation of this vital ecosystem service (Zhang et al., 2007).

Farmscaping to Support Crop Pollinators

Given large areas of homogenous agricultural landscapes, efforts to support pollinator populations in agroecosystems have focused on providing habitat and floral resources for bees over space and time (Kremen et al., 2004). There are many farmscaping techniques designed to support pollinator-dependent crop production and address the pollination crisis by maintaining or increasing landscape-level plant biodiversity, which has been shown to enhance insect pollinator communities (Carvalheiro et al.; Nicholls and Altieri, 2013). It is important to note that farmscaping efforts to increase plant biodiversity can be managed over time (crop rotations, cover crops, etc.) or in space (polycultures, intercropping, flower strips, etc.). This review will focus primarily on efforts to increase plant diversity in space because of the potential for high floral diversity to recruit pollinator populations from the landscape and facilitate targeted crop pollination. Before examining specific research efforts to attract wild pollinators and facilitate pollination, it is important to address some basic questions of farmscaping efforts to support crop pollination.

First, farmscapes exist within a landscape context. How do characteristics of the surrounding landscape influence wild pollinator populations? Several studies have shown that having more natural/semi-natural areas, and thus more plant diversity, on the farm increases pollinator populations (Ricketts et al., 2008; Garibaldi et al., 2014; Connelly et al., 2015). Efforts to enhance wild pollinator populations on crops by adding floral resources will be most successful if there are nearby natural areas that can be a source for wild bees (Ricketts and Lonsdorf, 2013). Second, if the goal of increasing plant diversity is to improve pollination services, will farmscaping efforts facilitate pollination of the crop species or will it increase floral competition amongst limited pollinators? While this is highly context dependent, there is evidence that attracting pollinators to an area with a “magnet species” can facilitate pollination in the crop species (Johnson et al., 2003; Feltham et al., 2015) and that plant diversity at finer spatial scales (more flowers in a smaller space) also improves crop pollination (Hegland, 2014). Third, what plant species should be part of farmscaping efforts to enhance wild pollinator populations? Native plants are often considered to be ideal in supporting native pollinators (Isaacs et al., 2009). However, diversity of floral form and function and intentional provisioning of resources may be more important than nativeness alone (Garbuzov and Ratnieks, 2014; Stouffer et al., 2014; Salisbury et al., 2015). Thus, when considering farmscaping techniques to enhance pollination services in agroecosystems, it is important to understand the larger landscape context, design plantings to help ensure facilitation rather than competition, and choose plant species by desired characteristics rather than simply origin.

While there has been significant interest in wild pollinator conservation, there has been relatively few studies linking pollinator supporting techniques with pollination success, especially in terms of crop yield and quality (Garibaldi et al., 2014). Wildflower plantings adjacent to blueberry fields were found to both increase wild pollinator abundance in the field during crop bloom and also enhance pollination and blueberry yield (Blaauw and Isaacs, 2014a). Likewise, small patches of native wild flowers helped to facilitate pollination on large mango farms, as long as some natural habitat was preserved and pesticides were used carefully (Carvalheiro et al., 2012). In smallholder almond orchards, simultaneously flowering groundcover helped support wild bees and facilitated almond pollination (Norfolk et al., 2016). Even non-native flowering vegetation can help facilitate pollination in pollinator-dependent crops. Pereira et al., 2015 found that intercropping bell pepper with flowering basil increased local abundance and richness of bees and improved fruit and seed production.

In 2015, Feltham et al. looked to see if planting wildflower strips adjacent to strawberry crops in Scotland would increase pollinator visits. While they found that the abundance of pollinator visits in strawberry rows increased significantly with wildflower plantings, they inferred an increase in yield based on the work of Blaauw & Isaacs, 2014. In 2018, wildflower borders helped to increase yields in strawberries (var. 'Jewel') by supporting pollination services when surrounded by intermediate natural habitat (Grab et al., 2018).

STRAWBERRIES

Strawberry Production

Soft fruit production is increasing worldwide (Ellis et al., 2017), with strawberry production area in the US increasing by almost 26% between 2000 and 2014 (FAOSTAT, accessed May 2018). Most of the production in the US is concentrated in California and Florida, though there is increasing demand for local and organic produce nationwide. In the Upper Midwest, the majority of production occurs during a short window between

June and July (Petran et al., 2016). If quality organic strawberries could be grown throughout the growing season in the Midwest, this would be an opportunity to meet local demand.

Strawberry Cultivars

Strawberry production in the Upper Midwest occurs during the early summer because most growers manage perennial, June-bearing strawberries, a genetic phenotype that is photoperiodic and initiates flowers with shortening day-lengths. Day-neutral phenotypes are non-photoperiodic and will flower and fruit continuously when temperatures are optimal for plant growth. Recent research efforts at the University of Minnesota have focused on optimizing a system for organic, day-neutral strawberry production in the Upper Midwest (Petran et al., 2016). However, the pollination requirements of day-neutral strawberries in the Midwest are unknown.

Importance of Pollination in Strawberries

While strawberries can self-pollinate, fruit quality and yield are often improved by insect pollination (Ariza et al., 2012; Bartomeus et al., 2014; Klatt et al., 2014b). The benefit of insect pollination for strawberries is due to the mechanism by which strawberry fruits develop. Although strawberries are self-fertile, wind and self-pollination alone are unlikely to fertilize every pistil of the strawberry carpel; insects can help to allocate pollen more homogeneously (Ariza et al., 2011). When an ovule is fertilized, it stimulates growth of the receptacle through release of the growth hormone auxin.

Achenes, the true “nut” fruit of the strawberry, will develop from fertilized ovules. Areas of the receptacle where ovules were not fertilized will not develop into achenes and can lead to small or misshapen berries (Nye and Anderson, 1974). In this way, insect pollination can help enhance strawberry fruit production by improving ovule fertilization, thus increasing berry size. A diversity of floral visitors is also important for strawberries, with one pivotal study showing that honey bees and wild bees provide complementary pollination services by foraging on different areas of the flower (Chagnon et al., 1993).

SUPPORTING POLLINATORS IN THE STRAWBERRY AGROECOSYSTEM

Farmscaping for Pollinators in Day-neutral Strawberry Systems

In order to compete with weeds and prevent disease, most strawberry production occurs on raised beds with plastic or straw mulch. In addition, some farmers use polytunnels or plastic low-tunnels to help improve production. These systems are designed to control weedy vegetation, so establishing additional pollinator resources in strawberry production systems is uncommon. Feltham et al. (2015) predicted that the presence of wildflower strips at the entrances of long polytunnel strawberry rows would enhance pollinator visits to the strawberry crop over the course of the season. They concluded that sowing wildflower strips adjacent to the strawberry rows increased pollinator visits to the strawberries and that this could be a strategy for reducing reliance on commercial pollinators, thus building a more resilient production system. However, as was acknowledged by Feltham et al., it is not always clear which species in the wildflower mix will be most attractive to local pollinator populations. In fact, there is some work that suggests bees may benefit from flower plantings with clumps of single species rather than homogeneous mixtures (Fowler et al., 2016). Day-neutral strawberry production may benefit from crop pollination facilitated by farmscaping techniques that support pollinator populations, like single-species annual flower strips. This would also provide an opportunity for growers to establish flowering plants that support pollinators while also growing an additional crop or cut-flower for market.

In order to design an integrated pollinator management strategy for day-neutral strawberries, there are important elements to consider. With a flower strip, it is important to consider size, location, composition, and time of flowering. Ideally, the flower strip would not host crop pests, would not increase weed seedbanks, and would not compete with the primary crop. On an economic level, growers would want something that is cheap and quick to establish, and ideally has some market value or secondary use.

Borage Strips for Pollinators

Borage (Boraginaceae: *Borago officinalis*), an herb with blue, star-shaped flowers, appears to fit these basic criteria for a flower strip in day-neutral strawberries. It is grown primarily in Europe and the Mediterranean basin and is a specialty oil crop in some regions (El-Shafei and Gotoh, 2010; Thom et al., 2016). Borage is attractive to bees

(Garbuzov and Ratnieks, 2014) and has long been considered by strawberry growers and gardeners as a companion plant, (Bradley, 2009; Riotte, 1998) though there is as yet no academic research examining this companion plant relationship. As a pollinator resource, blue flowers are considered to be highly attractive to honey bees and bumble bees and are often recommended for pollinator plantings (Briscoe and Chittka, 2001; Raine and Chittka, 2007). Borage blooms eight weeks after planting and produces flowers all season long, similar to day-neutral strawberries (Figure 6). Additionally, borage has a rapid growth rate, and its leaves are large, basal, and covered in small spiny hairs, making them competitive with weeds and resistant to most pest insects. Borage has been found to be an unsuitable host for most mite species and was determined to be an unlikely “hotbed” for spider mites, which is a significant pest in strawberry plasticulture systems (El-Shafei and Gotoh, 2010). In addition, volatiles from borage may attract beneficial natural enemies, such as parasitoid wasps (Fujinuma et al., 2010). By integrating borage into the day-neutral production system in a flower strip, it may be possible to facilitate strawberry pollination while avoiding undesirable side-effects.

Measuring Pollination Success in Day-neutral Strawberries

Showing an increase in pollinator abundance and richness is a good indicator that pollination services are enhanced by floral resources, but it is important to be able to show that this translates to pollination success, especially with regards to crop production. Klatt et al. 2013, who found that June-bearing strawberry fruit quality, shelf life, and commercial value were improved by bee pollination, measured pollination success by counting the number of fertilized achenes per berry. Compared with wind and self-pollination, bee pollination increased the number of fertilized achenes by about 26% and 62% respectively, and improved fruit shape and weight, providing further evidence for the positive relationship between achene number and berry weight (Strik and Proctor, 1988). Even amongst different strawberry cultivars, there may be differences in floral morphology and pollen quality that influence pollination success (Connor, 1975; Zebrowska, 1998; Carew, James. G., 2003). Given the continual flowering habit of day-neutral strawberry phenotypes, their pollination requirements may be greater over time than June-bearing varieties, especially considering differences in flower development and morphology (Petran et al., 2016). To our knowledge, there is no research examining the influence of insect floral visitors on day-neutral strawberry pollination and production. The objective of this research is to determine the influence of a planted annual borage (*Borago officinalis)* flower strip on recruitment of day-neutral strawberry floral visitors and facilitated crop yield from improved pollination services.

Hypothesis

An annual borage flower strip will be attractive to wild pollinators and serve as a "magnet species" for day-neutral strawberries by increasing floral visitors, thereby improving fruit set and strawberry crop yield.

Objective 1

Determine how day-neutral strawberry floral visitors relate to an annual borage (*Borago officinalis)* flower strip and evaluate the "magnet species" potential of borage for day-neutral strawberry production.

Research Question 1

Do day-neutral strawberry floral visitors change as a function of distance from a flowering borage strip?

Objective 2

Determine if day-neutral strawberry production is influenced by proximity to an annual borage (*Borago officinalis*) flower strip across four day-neutral cultivars.

Research Question 2

Does day-neutral strawberry production change as a function of distance from a flowering borage strip?

CHAPTER 2–THE INFLUENCE OF A MAGNET SPECIES FLOWER STRIP (*BORAGO OFFICINALIS*) ON POLLINATOR RECRUITMENT AND PRODUCTION OF DAY-NEUTRAL STRAWBERRY CULTIVARS IN MINNESOTA

INTRODUCTION

The value of wild insect pollinators for agroecosystems is now well recognized (Garibaldi et al., 2014), but questions have arisen regarding how to design agricultural landscapes to maintain, and even enhance, this vital ecosystem service. There is increasing evidence suggesting that maintaining natural areas and planting wildflower patches enhances the abundance of native and wild pollinators in agricultural settings (Blaauw and Isaacs, 2014b; Williams et al., 2015), such as in strawberry production (Feltham et al., 2015; Grab et al., 2018). Although commercial strawberries (*Fragaria x ananassa*) are self-fertile, recent research has demonstrated the significant impact of insect pollinators on improving strawberry yield, quality, and shelf-life (Klatt et al., 2014a; Abrol et al., 2017). This is because optimal strawberry fruit set depends on the successful distribution of pollen to the hundreds of pistils per flower, which are more efficiently pollinated by a diverse compliment of insect floral visitors (Chagnon et al., 1993). However, no research has examined the potential of flower strips to enhance berry production in day-neutral strawberries, which may have higher pollination requirements due to their continual flowering growth habit. Additionally, day-neutral strawberry cultivars may respond differently due to differences in floral development and morphologies (Petran, 2016). In the Midwest, day-neutral strawberries are grown as annuals due to the lack of winter hardiness. Much of the pollinator habitat intended to improve crop yield in agroecosystems are designed to be perennial (Blaauw and Isaacs, 2014a; Kremen and M'Gonigle, 2015), though this may not always be practical for growers. Alternatively, annual flower strips are being considered for integration in crop settings to help recruit local pollinators and facilitate crop pollination over shorter time periods, rather than as permanently established habitat (Pereira et al., 2015; Ganser et al., 2018; Hodgkiss et al., 2019). While there is a growing body of research on the importance of wild pollinators in agroecosystems, there is less research on the strategic use of specific species in flower strips that serve as "magnet species" to recruit wild pollinators at smaller spatial scales, with the intention of creating a spillover effect from a highly attractive floral resource to a pollinator-dependent crop (Johnson et al., 2003; Hegland, 2014; Feltham et al., 2015). Borage (*Borago officinalis*) has long been considered a pollinator companion plant for strawberry (Riotte, 1998) due to its highly attractive blue flowers and strawberry pollination requirements, but there is, to our knowledge, no research examining the dynamics of this relationship. This chapter presents research on the impact of planting an annual flower strip, using borage (*Borago officinalis*) as a magnet species, on a) strawberry pollinator recruitment and b) day-neutral strawberry fruit production in Minnesota over two seasons.

MATERIALS AND METHODS

Study Site

Our experiment was established at the West Central Research and Outreach Center (WCROC) in Morris, MN in the spring of 2017, and repeated in 2018. WCROC is located at 45°35'36.8"N, 95°52'42.6"W in Stevens County, MN, USDA hardiness zone 4a. WCROC is at the edge of the western prairie and hosts applied research programs, including organic dairy and swine production in addition to horticultural research trials.

Field Preparation and Pest Management

In 2017, soil was prepped with 272 kg of elemental sulfur/acre for pH correction. In the previous year, one of the field plots was planted with day-neutral strawberries, while the other two were tillage radish or had been left fallow in perennials.

Pyrethrin (Pyganic® 5.0, MGK, Minneapolis, MN), was sprayed every two weeks throughout the season to control for tarnished plant bug (*Lygus lineolaris*) at a rate of 14.8mL/22.7L of water. Spinosad (Conserve®, DOW AgroSciences LLC, Indianapolis, IN) and mineral oil (PureSpray™ GREEN, Suncor Energy Inc., Mississauga, Ontario) were used during the peak of the season to aid in tarnished plant bug control. An OMRI approved organic herbicide of acetic and citric acid (AllDown®, KPT LLC Summerset Products, Chaska, MN) was sprayed twice between strawberry rows to control weeds in 2018. Spraying took place primarily in the early evening, once temperature and wind speed had dropped, to avoid drift and to mitigate any impact on local pollinator communities. All products were applied per label recommended rates.

Experimental Design

Once soils were suitable for tractor activity in the spring, three day-neutral strawberry fields were installed in fenced deer enclosures, on May 12th in 2017, and May 15th in 2018. Fields were separated by at least 200m. This distance represents a design balance, given experimental goals of ensuring site independence while maintaining equivalent pollinator communities and landscape contexts.

The fields were prepared with a tractor by rotovating the soil, forming raised-beds (2121-D bed shaper), and laying plastic mulch and drip tape irrigation (model 2133 mulch layer) with tractor attachments from Buckeye Tractor Company (Columbus Grove, OH). Bare-root seedlings (Nourse Farms, MA) were planted into white-on-black plastic mulch (1.2m wide, 1mm thick) at 0.3m intervals in single rows. Plants were irrigated for two hours after establishment and then as needed throughout the season. Winter rye (Agassiz Seed & Supply) was seeded as a ground cover between raised beds using a Gandy Drop Spreader and raked by hand to improve seed to soil contact.

Each of the three experimental fields contained four, 30.5m long raised-bed rows of day-neutral strawberries, with 12.7cm row centers. Four day-neutral strawberry (*Fragaria x* *ananassa*) cultivars ('Albion', 'Portola', 'Evie-2', 'Seascape') were planted in a random complete block design across four distance ranges (0-7.6m, 7.6-15.2m, 15.2-22.9m, 22.9-30.5m), hereafter named I, II, III, and IV respectively, with a borage flower strip at 0m. The experimental unit is defined as the 7.6m long subplots within each 30.5m row, for a total of 16 subplots per field (Figure 1). Each subplot had 25 plants of a single cultivar.

A 2.1x7.6m flower patch of borage (*Borago officinalis*) was sown in a dense strip (1g/m^2) perpendicular to the strawberry rows in each field the day after strawberry planting (Figure 1). Strawberry yield and floral visitor population parameters were measured by subplot as a function of distance from the flower strip. Borage seeds (Nature's Crops International) were sown in 7.6m rows perpendicular to the raised beds, with 15cm separation between rows using a Jang single row push seeder (Beets 18105: tray # 1002-22). A 30cm pathway was left unseeded in the middle of the strip for access. The strip was lightly raked to promote seed to soil contact and was hand weeded for the first several weeks in order to ensure borage establishment in both years. The flower strips were not irrigated or fertilized during the growing season. Borage flowers emerged after 8 weeks of growth and flowering density was measured every two weeks during the growing season by counting borage flowers in 1x1m quadrats, averaging among three random tosses within the strip and then averaged across fields.

Floral Visitor Surveys

In 2017 and 2018, insects found on all open strawberry flowers (floral visitors) were counted, collected, and identified to family to determine potential pollinators. Samples were collected every two weeks between 10am and 4pm using a Skil Insect Vacuum (Bioquip) in all three fields within the four distance ranges (I, II, III, and IV) across cultivars, using a separate collection canister for each distance range. Insects observed on open strawberry flowers were collected while walking in a serpentine pattern alongside each experimental unit within a distance range, for four complete passes at a pace of ~0.3m/sec. (~5min per distance range). Open strawberry flowers were also counted and recorded per subplot. Floral visitors were sampled in the borage flower strip, collecting for 5 min in each of the three fields. The insect vacuum was moved in a zig-zag pattern in the flower strip to collect floral visitors from open borage flowers. The field, order of plot visitation, and starting direction were selected randomly for each date of collection, in order to minimize collection bias. Insect samples were placed on ice immediately after collection for transport and were terminated in a freezer. Samples from each distance range and borage strip plots in all three fields (15 collections/date) were placed in petri dishes, labeled, and stored in the freezer for later processing and identification.

Insect Identification

Insect samples were pinned and labeled with location, collection date, collector information, and a unique identification code. Samples were originally organized by date and distance range in collection boxes. They were then reorganized phylogenetically after being identified at least to the level of family. Insect identification was completed with the aid of the Discover Life and BugGuide.net websites, as well as taxonomist John Luhman from the University of Minnesota Insect Collection (UMSP). This insect collection is stored in the Organic and Sustainable Horticulture lab at the University of Minnesota. A representative sample of specimens will be submitted to the UMSP for cataloging.

Insect families were further categorized as bumble bee, honey bee, native bee, syrphid fly, root maggot flies, other flies, and other taxa of insects, in order to group primary floral visitors for comparison (Table 1).

Strawberry Yield

Strawberry inflorescences were removed until July 1 in both years, to encourage vegetative growth and root establishment after planting. In 2017, harvest began 31 July and ended 03 October, and in 2018, harvest began 03 August and ended 26 September. Ripe fruit from each field plot was harvested twice a week. After each harvest, all berries picked within a subplot were counted and weighed (g) using a digital scale to determine yield. Average individual berry weight was calculated by dividing total yield by total number of berries for each subplot. In addition to cultivar, strawberry production parameters were measured as a function of distance from a flower strip (I, II, III, IV).

Statistical Analysis

Statistical analysis was completed in R (version 3.5.3). To analyze floral visitor count data, we fitted a generalized linear mixed model and tested the significance of predictors by sequentially dropping them from a full model that included date, distance range, and date by distance as fixed effects. We then used a likelihood ratio test (chi square statistic) to test the models. The models were fitted assuming a Poisson distribution, given that we were analyzing count data and assumed non-normality. The models were tested for homogeneity. We used the lmer and glmer functions in the lme4 package to fit the models (Bates 2015). The response variables of total yield (cumulative berry weight) and total berry number were analyzed using a linear mixed effects model (lmer). We designated distance range and cultivar as fixed effects, with field as a random effect. The models were tested for homogeneity and normality. Mean separations were determined using the lsmeans function as part of the emmeans package (Lenth 2019).

RESULTS & DISCUSSION

Strawberry Floral Visitors

Although total insect floral visitor counts were highest in the borage flower strip and tended to decline in 2017 with increasing distance, this pattern was not clearly observed in 2018 (Table 2), and there were no significant differences in mean abundance of strawberry floral visitors compared by category between distance ranges (I, II, III, IV) in either 2017 ($p=0.18$) or 2018 ($p=0.29$) (Table 3). Counts of floral visitors by category were combined over collection dates to obtain a total count of floral visitors at the end of each year (Table 2). Yearly data were averaged across the three experimental field sites and compared across distance ranges (Table 3). Collection date was significant ($p<0.001$) and there was no interaction between distance and date (Table 4).

The borage strip was highly attractive to honey bees and bumble bees, as well as syrphid flies and other Diptera taxa. Strawberry floral visitors were primarily syrphid flies, root maggot flies, other Diptera taxa, and native bees (Figure 2). In 2017, there was a peak in abundance of syrphid flies and root maggot flies in the middle of the season (Figure 3a), whereas in 2018 there were primarily syrphid flies found on strawberry flowers (Figure 3b). Native bees and other flies were found in roughly the same abundance across distance ranges in both years (Table 3).

While there are no statistical differences in abundance of strawberry floral visitors as distance from the borage strip increased, there are some patterns worth investigating. In this experiment, primary strawberry floral visitors were non-bee pollinators like syrphid flies, root maggot flies, and other Diptera (fly) taxa. Syrphid flies are the primary strawberry floral visitor and there is a decline in abundance with distance from the borage strip (Figure 2) in 2017. This pattern of decline in Syrphid flies appears to be in agreement with other research showing that syrphid fly abundance is enhanced up to 50m from a number of different floral resources in agricultural settings (Kohler et al., 2008).

Root maggot flies (Anthomyiidae), though considered pestiferous as larvae in field crops, feed on nectar and pollen as adults and may be acting as pollinators in this system. There were also many other adult flies from different families found on strawberry flowers (Table 1) indicating that non-syrphid Diptera may be important and underestimated strawberry pollinators (Orford et al., 2015). The prevalence of Diptera taxa on strawberry flowers, though heretofore undocumented in day-neutral strawberries, is consistent with early research on strawberry pollinators (Nye and Anderson, 1974).

There were honey bee hives located at WCROC within foraging range of these experimental fields. The borage strip was notably a magnet for larger bees like honey bees and bumble bees (Figure 2 and Figure 4). Native bee families were found primarily on strawberry flowers, with very few honey bees as strawberry floral visitors (Table 3), indicating that strawberries may rely more on native bee pollinators rather than managed honey bees in this system.

Future research should investigate the pollination potential of Diptera families found in abundance on day-neutral strawberry (Table 1) flowers, especially syrphids (hover flies), anthomyiids (root maggot flies) (Figure 2), as well as some of the larger flies such as those found in the families Muscidae and Calliphoridae.

Borage "Magnet Species" Potential and Plant-pollinator Dynamics

The borage flowers attracted and hosted a wide range of insects, with the flower strip primarily hosting honey bees and bumble bees (Figure 4). Bumble bees were never found on strawberry flowers and honey bees were found infrequently. Similarly, flies (Diptera) and native bees were the primary visitors on strawberry flowers (Figure 5), and these taxa were not found with the same diversity and abundance in the borage strip (Table 1). This may be due to inherent discrepancies in insect collection between the strawberry flowers and borage flowers. An insect vacuum was used to collect floral visitors found on open strawberry blooms, which are solitary and upward facing, and also to collect floral visitors in the flower strip, where borage flowers are dense and downward facing. Thus, collection on strawberry blooms was more direct and complete compared to on borage flowers, even though collection times were standardized per unit area. Assuming the diversity of floral visitors captured were representative, the borage patch appears to more strongly recruit larger pollinators like honey bees and bumble bees, whereas the primary strawberry floral visitors in this experiment tend to be smaller insects such as syrphid flies, anthomyiid flies, and native bees.

The floral phenology, or seasonal pattern of flowering, is an important element in evaluating the effectiveness of a “magnet species” flower strip. In ideal circumstances, the flower strip could help to attract more pollinating insects during key portions of the season by flowering prolifically when crop flowers are less abundant, and vice versus during peak crop flowering. Borage flowering peaked at the beginning of the season when strawberry flowers were less abundant, and steadily declined over the season with some self-seeding and new flowers around 97 days from planting (Figure 6).

Though there appears to be some indications of pollinator spillover from the borage strip to the strawberry rows, it is important to consider the possibility of borage flowers serving as a “trap” and increasing competition for pollinators rather than facilitating pollinator spillover to the crop species. Recent research has found that wildflower strips enhance strawberry pollination at small scales (Ganser et al., 2018), and others have indicated that increasing floral resources at small scales can have facilitative effects for crop pollinators, whereas competition may increase when floral resources increase at a coarser scale (Hegland, 2014). The small size and high floral density of the borage strips in this project are consistent with these recommended conditions. Further research should compare pollinator communities between fields with a borage strip and control fields without in order to more fully answer questions of pollinator competition vs facilitation.

Strawberry Yield across Day-neutral Cultivars

Strawberry cultivar and distance from flower strip are the main effect factors considered for their influence on strawberry yield in this experiment. Distance is defined by 4 distance ranges (I, II, III, IV, of 7.6m each) from a flowering borage strip at 0m. These two factors, cultivar and distance, were tested for their influence on strawberry production parameters, including total yield per plant, total berry number per plant, and average individual berry weight.

Total yield and total berry number vary significantly ($p<0.05$) by cultivar in both years. ‘Evie-2’ produced the highest yields, followed by ‘Portola’ and ‘Seascape’, with ‘Albion’ producing the lowest total yield by the end of both harvest seasons. ‘Evie-2’ also produced the highest total berry numbers, followed by ‘Seascape’, then ‘Portola’, and ‘Albion’ with the lowest berry numbers (Table 5). The 2018 growing season had a lower overall total yield across all cultivars, but has a higher total berry number. This is supported by results of individual berry weight, which are higher in 2017 than in 2018, indicating plant resources were allocated to a greater number of berries rather than to berry weight. ‘Albion’ and ‘Portola’ characteristically produce the least number of berries, in part, because they produce the largest berries (Table 5).

Strawberry production parameters were also measured as a function of four distance ranges (I, II, III, IV) from a planted borage (*Borago officinalis)* flower strip. Yield was marginally significant (p=0.09) and total berry number varied significantly (p=0.02) between distance ranges in 2017 (Table 6, Table 7), with both parameters decreasing over all four distance ranges from the flower strip (Table 5), particularly in ‘Evie-2’ and ‘Albion’ cultivars (Figure 7a). There were no significant differences in total berry number or total yield with increasing distance from the flower strip in 2018 (Figure 7b & Figure 8b).

Because fruit set (number of fertilized achenes) correlates directly to berry weight (Chagnon et al., 1993; Carew, 2003), improved pollination success may, in part, be measured by examining average individual berry weights. Results for individual berry weights were averaged across 10 harvest dates during the middle of the season in both years. The subset of data corresponds to the peak of the growing season in order to get a more representative sample; given that some cultivars produce very little at the beginning and end of the season, average values are skewed. Average individual berry weights did not differ significantly between distance ranges in either year across cultivars (Table 5). However, compared with the other cultivars, ‘Evie-2’ individual berry weights decrease consistently with distance from the flower strip in both years (Figure 9). Given that 'Evie-2' produces the highest number of berries, it may have a greater need for pollinators throughout the season, especially during peak berry production weeks. Of all four day-neutral cultivars, it may be responding to small changes in pollinator numbers between distance ranges (Figure 2).

Overall, proximity to the flower strip did not appear to significantly influence strawberry yield, berry number, or individual berry size. There was a trend for harvest parameters to decrease with distance from the flower strip, especially for the day-neutral cultivar 'Evie-2', that warrants further investigation. The four distance ranges are coarse and an evaluation on a more continuous, longer gradient might allow for more nuanced analysis. Rows of 31m may not have been a long enough distance to observe any harvest differences from magnet species pollinator spillover. Further research on day-neutral production benefits from pollinator "magnet-species" annual flower strips are advised to either establish control plots or measure harvest parameters over larger distance ranges from the flower strip.

CONCLUSIONS

As an annual flower strip, borage appears to attract an abundant and diverse insect population, primarily larger pollinators like honey bees and bumble bees, but smaller insects found on strawberry flowers such as native bees, syrphid flies, and other Diptera taxa, as well. Overall abundance of strawberry floral visitors tends to decrease with distance from the flower strip, though not statistically significant. These small differences in abundance may, however, be biologically significant, especially given the continual production of day-neutral strawberry flowers throughout the growing season. Diptera taxa, such as syrphid flies (Syrphidae), root maggot flies (Anthomyiidae) and some larger fly families (i.e. Muscidae, Calliphoridae) may be important and previously unrecognized pollinators in day-neutral strawberries.

Day-neutral cultivars had an effect on strawberry yield, berry number, and individual berry weight, as was to be expected from previous research on day-neutral cultivars at the University of Minnesota (Petran et al., 2016). ‘Albion’, while producing the lowest overall yields, produced the highest individual berry weight in 2017. ‘Portola’ produced the second highest overall yield in 2017 and 2018, and produced the highest individual berry weight in 2018. ‘Evie-2’, while outproducing all other cultivars in yield over both years, had relatively lower individual berry weights. ‘Seascape’ performed adequately in all years, with the second lowest yields, second highest berry number, and lowest individual berry weights.

Yield, berry number, and individual berry weight all trend downwards in 2017, and trend downwards to the center of the field in 2018, with the farthest distance range (IV) having the lowest strawberry yield and number in both years. This is especially the case for the average individual berry weight of the day-neutral cultivar 'Evie-2', which may be the most responsive to small increases in floral visitors due to the cultivar's high production rate. These effects may be more apparent over longer distances or in more pollinator-limited environments.

Total syrphid fly abundance increased with proximity to the flower strip, which may be significant for strawberry flower pollination over a full growing season. Given that primary strawberry floral visitors were Diptera taxa and small native bees, borage (*Borago officinalis*) may not be the ideal "magnet species" for recruiting strawberry pollinators, because of its draw for larger bee taxa. In fact, the borage flower strip may have competed with the strawberry flowers for larger pollinators like honey bees and bumble bees, leading to the prevalence of smaller pollinator taxa found on strawberry flowers. In gardening literature, borage is often described as a companion plant for strawberry production, presumably because of the herb's insect attractive flowers and the importance of insect pollination for strawberry production. Although we found borage to be highly attractive to wild insects, this research exemplifies the complexity of farmscaping with "magnet species" to facilitate crop pollination. Planting an annual flower that attracts the specialist crop pollinators for a particular region is the goal, rather than simply planting a flower species known to be attractive to pollinating insects in general. More research is required on the borage-strawberry relationship to better understand pollinator behavior and pollination dynamics, especially for day-neutral strawberry cultivars.

If annual flower strips are to be integrated into production systems to support and recruit wild pollinators for pollinator-dependent crops, this research suggests several strategies for success. First, the selected flower species should be attractive to the full diversity of crop floral visitors, including Hymenoptera (bees) and Diptera (flies) taxa, so that all potential pollinators are represented. Second, flower strips should be planted parallel with strawberry rows to ensure adequate dispersal of recruited wild pollinators to the target crop. Third, flower strips should be managed with floral phenology in mind, so that flower strip resources decline when crop flowers are at peak production in order to reduce competition for insect pollinators.

The use of annual flower strips to recruit wild pollinators is a new agroecological farmscaping strategy that has potential for supporting pollinator-dependent crops. Day-neutral strawberries are a crop worthy of further investigation because of their pollination requirements and high productivity throughout the growing season. Annual flower strips may be a good strategy in the Midwest, where annual day-neutral strawberry production systems are necessary, but more research is required to identify ideal species with the potential to facilitate strawberry pollination. Diptera taxa should be considered important potential pollinators for day-neutral strawberries and flower strip species should be chosen that ensure representation from these pollinators.

TABLES AND FIGURES

Table 1. Primary floral visitor defined within taxonomic order, described by category (in bold) and within insect family. Insect families are separated between specimens found on borage flowers vs. those found on strawberry flowers. Insect families found on both flowers are included in both columns. Dotted line indicates that the family specific to that row was not found on flowers within the column. "Other" includes insect taxa (i.e. Order: Coleoptera) with unlikely or minor pollination influence.

Order	**Category**	**Family: Borage**	**Family: Strawberry**
Hymenoptera	**bumble bee**	Apidae: Bombus	…
	honey bee	Apidae: Apis	Apidae: Apis
	native bees	Apidae	Apidae
		…	Andrenidae
		…	Colletidae
		Halictidae	Halictidae
		Megachilidae	Megachilidae
Diptera	**syrphids**	Syrphidae	Syrphidae
	root maggot flies	Anthomyiidae	Anthomyiidae
	other flies	Calliphoridae	Calliphoridae
		Chloropidae	Chloropidae
		…	Conopidae
		Culicidae	Culicidae
		Dolichopodidae	Dolichopodidae
		Drosophilidae	Drosophilidae
		…	Empididae
		…	Ephydridae
		…	Faniidae
		Muscidae	Muscidae
		…	Piophilidae
		Sarcophagidae	Sarcophagidae
		…	Scathophagidae
		…	Sepsidae
		…	Sphaeroceridae
		Tachinidae	Tachinidae
		Ulidiidae	Ulidiidae
Hemiptera	**tarnished plant bug**	Miridae	Miridae
Coleoptera	**others†**	Curculionidae	Curculionidae
		spp	spp
Neuroptera		spp	…
Hymenoptera		Formicidae	Formicidae
		…	Vespidae
Hemiptera		spp	spp
Lepidoptera		spp	spp

Table 2. Total counts of insect families collected on borage (*Borago officinalis*) flowers and strawberry flowers with increasing distance ranges from borage flower strip (I, II, III, IV) during 2017 and 2018. Insect order is in brackets within family column. Blank cells indicate absence of family in all categories for that year. "Other" includes other insect taxa with unlikely or minor pollination influence.

	2017					2018				
FAMILY	**Borage**	**I**	**II**	**III**	**IV**	**Borage**	**I**	**II**	**III**	**IV**
[Hymenoptera]										
Andrenidae	0	1	0	0	0	0	1	0	0	0
Apidae	429	17	7	13	7	210	4	3	4	0
Colletidae	0	0	1	3	3	0	0	1	0	0
Halictidae	12	20	19	20	12	6	5	12	10	10
Megachilidae	0	1	0	1	1	1	0	0	0	0
[Diptera]										
Anthomyiidae	62	91	74	89	97	13	9	4	6	9
Calliphoridae	5	2	1	1	2	7	5	1	2	1
Chloropidae	6	3	3	2	1	0	1	0	0	0
Conopidae	0	0	0	1	0	0	0	1	0	1
Culicidae	18	0	0	0	1					
Dolichopodidae	4	1	1	0	0					
Drosophilidae	6	4	0	0	0	0	0	0	1	1
Empidae	0	0	0	2	0	0	0	1	0	0
Ephydridae	0	1	0	0	0					
Fanniidae	0	0	0	0	1					
Muscidae	9	10	5	4	7	7	0	1	0	1
Piophilidae	0	0	1	0	0					
Sarcophagidae	3	3	0	1	2	1	1	1	1	1
Scathophagidae	0	1	0	0	0					
Sepcidae	0	6	3	1	4	1	1	1	1	2
Sphaeroceridae	0	0	0	3	1					
Syrphidae	82	126	106	74	69	243	216	204	173	223
Tachinidae	2	0	0	0	0	0	0	1	0	0
Ulidiidae	3	2	7	3	2	12	5	1	3	1
[Hemiptera]										
Miridae	39	18	16	13	11	47	30	29	18	24
[Other]										
(other)	32	27	12	9	12	40	17	17	17	17
TOTALS	712	334	256	240	233	588	295	278	236	291
GRAND TOTAL	**1775**					**1688**				

Table 3: Average abundance (mean ± s.e.) of primary floral visitors collected on borage (*Borago officinalis*) flowers and strawberry flowers with increasing distance ranges from borage flower strip during 2017 and 2018, across three experimental fields. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m.

2017

	Borage	*I*	*II*	*III*	*IV*
Bumble bee	45 ±10.7	0	0	0	0
Honey bee	97 ±13.6	5 ±0.7	2 ±1.9	4 ±1.9	2 ±1.9
Native bee	4 ±0.6	7 ±2.8	7 ±0.9	8 ±1.7	5 ±0.7
Syrphids	27 ±6.3	42 ±7.1	35 ±5.2	25 ±5.6	23 ±4.5
Root maggot flies	21 ±5.4	30 ±13.8	25 ±13.3	30 ±12.0	32 ±11.6
Other flies	19 ±5.7	11 ±1.2	7 ±2.0	5 ±2.1	6 ±2.8
Tarnished Plant Bug	13 ±2.5	6 ±0.6	5 ±1.2	4 ±0.7	4 ±1.3

2018

	Borage	*I*	*II*	*III*	*IV*
Bumble bee	3 ±0.7	0	0	0	0
Honey bee	59 ±5.0	1 ±1.3	1 ±0.6	1 ±0.7	0
Native bee	5 ±1.5	3 ±0.9	5 ±1.5	4 ±0.7	4 ±1.5
Syrphids	81 ±12.1	72 ±10.3	68 ±3.8	58 ±5.7	74 ±13.1
Root maggot flies	4 ±1.2	3 ±0.6	1 ±0.3	2 ±0.6	3 ±0.6
Other flies	9 ±2.6	4 ±0.9	3 ±0.7	3 ±1.2	3 ±0.9
Tarnished Plant Bug	16 ±3.3	10 ±4.2	10 ±1.3	10 ±1.7	8 ±0.0

Table 4. Results of Chi square test used on fitted glmer model to determine how well variables predicted floral visitor count data in 2017 and 2018. In order to determine significance of factors, models of increasing complexity were compared with each other to isolate which factor contributed most to data variability. Date was the most significant factor for predicting strawberry floral visitor count data in both years.

Strawberry Floral Visitor Counts in 2017

Variables in Model	Chisq	DF	p-value
Distance	4.8328	3	0.1845
Distance, Date	281.9321	6	<2e-16
Distance, Date, Distance: Date	16.0309	18	0.5904

Strawberry Floral Visitor Counts in 2018

Variables in Model	Chisq	DF	p-value
Distance	3.7437	3	0.2905
Distance, Date	328.7352	5	<2e-16
Distance, Date, Distance: Date	13.7755	13	0.3898

Table 5. Harvest data for 2017 & 2018 compared among day-neutral cultivars as well as distances from flower strip. Average yield and berry number were calculated per plant by the end of the growing season. Berry weights are averaged from 10 harvests at the peak of the season.

Year	2017			2018		
	Yield	Berry Number	Berry weight	Yield	Berry Number	Berry weight
	g/plant	*#/plant*	*grams*	*g/plant*	*#/plant*	*grams*
Cultivar						
Albion	211 c†	16 d	13.5 a	251 b	25 c	10.3 b
Evie-2	516 a	47 a	10.6 b	439 a	47 a	9.3 b
Portola	357 b	26 c	13.2 a	340 b	31 bc	11.3 a
Seascape	334 b	33 b	8.8 c	260 b	37 b	6.8 c
Distance from flower strip§						
I	389	33 a	11.6	329	35	9.4
II	378	31 ab	11.5	326	35	9.3
III	342	29 ab	11.7	333	36	9.4
IV	310	27 b	11.3	308	33	9.6

† Letters indicate significant differences ($p \leq 0.05$) between cultivars and distance measurements according to a LSM test of a linear mixed effects model. Numbers within columns without letters are not significantly different at $p \leq 0.05$.
§ Each distance range (I, II, III, IV) is 7.6m long, with increasing distance from the flowering borage strip (0m), such that I=0-7.6m, II=7.6-15.2m, III=15.2-22.9m, IV=22.9-30.5m.

Table 6. ANOVA of linear mixed effects model with effect of distance and cultivar on total strawberry yield (g) in 2017 and 2018, with experimental block as a random effect.

Yield 2017

Variables in Model	DF	F-value	p-value
(Intercept)	1	250.126	< 0.0001
Distance	3	2.376	0.0897
Cultivar	3	28.650	< 0.0001
Distance:Cultivar	9	0.936	0.5090

Yield 2018

Variables in Model	DF	F-value	p-value
(Intercept)	1	471.967	< 0.0001
Distance	3	0.224	0.8789
Cultivar	3	13.838	< 0.0001
Distance:Cultivar	9	0.315	0.9637

Table 7. ANOVA of linear mixed effects model with effect of distance and cultivar on total berry count 2017 and 2018, with experimental block as a random effect.

Total Berry Number 2017

Variables in Model	DF	F-value	p-value
(Intercept)	1	10278.997	< 0.0001
Distance	3	3.781	0.0206
Cultivar	3	48.141	< 0.0001
Distance:Cultivar	9	1.249	0.3040

Total Berry Number 2018

Variables in Model	DF	F-value	p-value
(Intercept)	1	214.585	< 0.0001
Distance	3	0.295	0.8288
Cultivar	3	15.882	< 0.0001
Distance:Cultivar	9	0.375	0.9377

Table 8. ANOVA of linear mixed effects model with effect of distance, cultivar, and harvest date on average individual berry weight in 2017 and 2018, with experimental block as a random effect.

Individual Berry Weight 2017

Variables in Model	DF	F-value	p-value
(Intercept)	1	1671.525	< 0.0001
Distance	3	0.422	0.7374
Cultivar	3	111.979	< 0.0001
Harvest	10	8.861	< 0.0001
Distance:Cultivar	9	2.727	0.0044
Distance:Harvest	30	0.675	0.9038
Cultivar:Harvest	30	2.204	0.0004
Distance:Cultivar:Harvest	90	0.450	0.9999

Individual Berry Weight 2018

Variables in Model	DF	F-value	p-value
(Intercept)	1	291.917	< 0.0001
Distance	3	1.932	0.1234
Cultivar	3	17.373	< 0.0001
Harvest	15	2.006	0.0134
Distance:Cultivar	9	0.645	0.7585
Distance:Harvest	45	0.827	0.7822
Cultivar:Harvest	45	1.636	0.0070
Distance:Cultivar:Harvest	135	0.885	0.8024

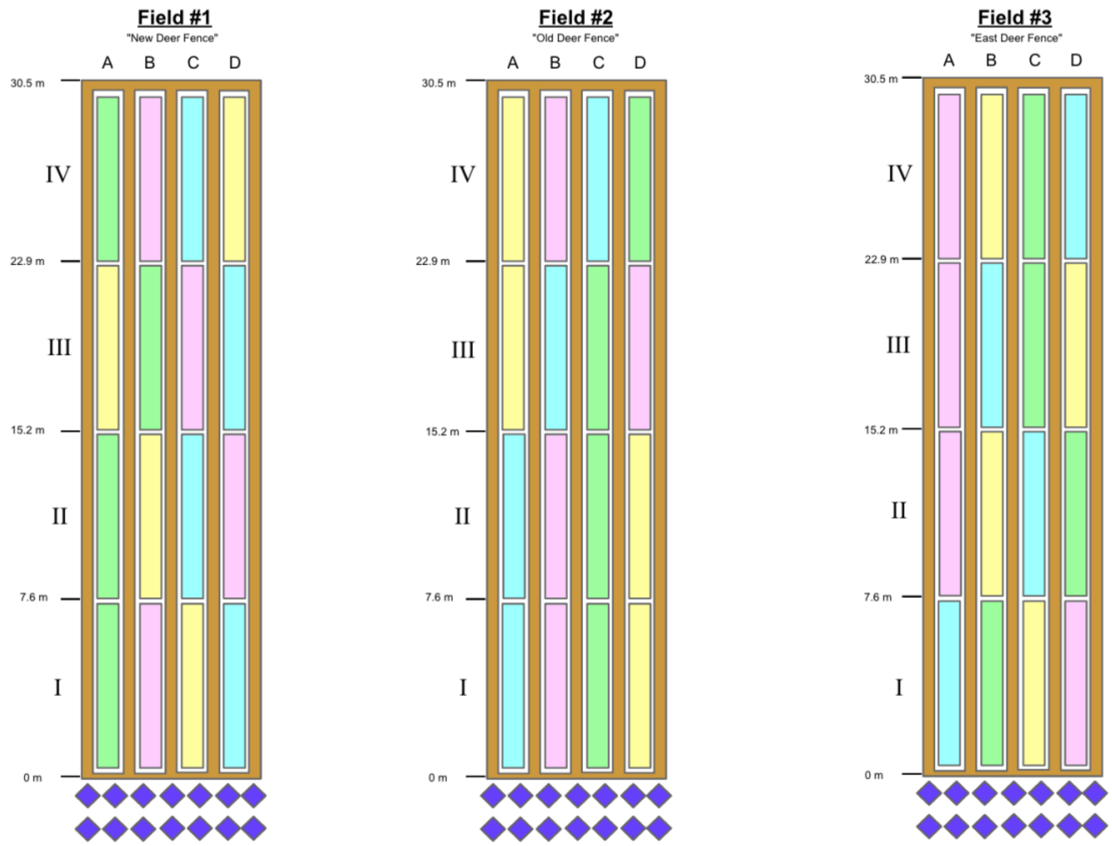
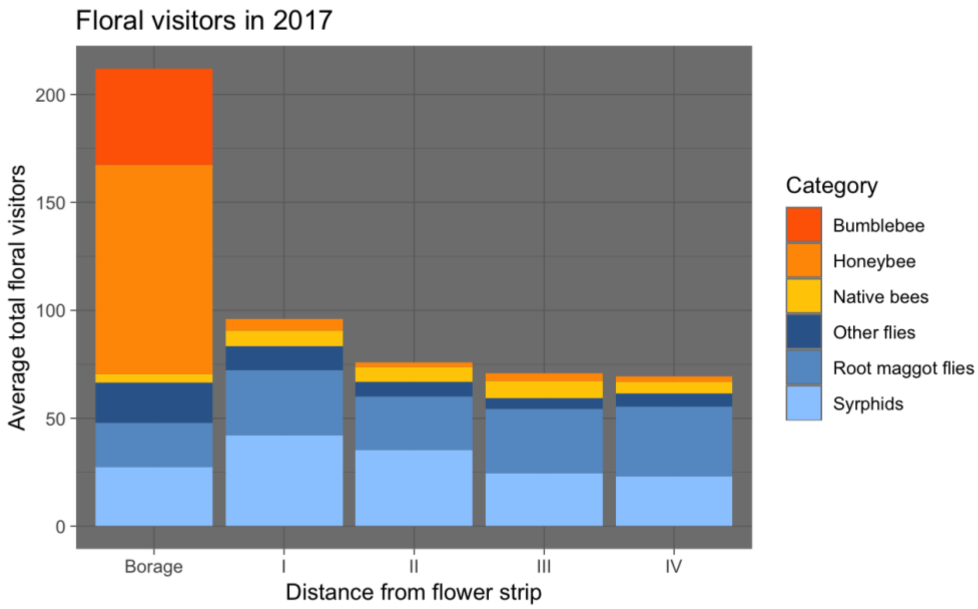
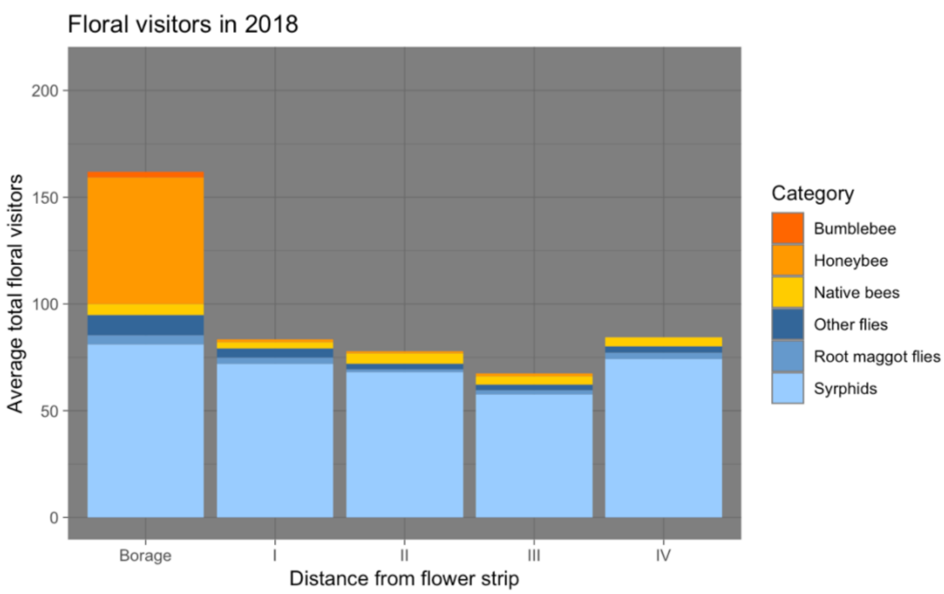


Figure 1. Experimental design 2017 and 2018. Plots are arranged in a randomized block design, with 4 single rows of day-neutral strawberries. Day-neutral strawberry cultivars 'Albion' (pink), 'Portola' (green), 'Evie-2' (yellow), and 'Seascape' (blue) are blocked by distance range. Each distance range (I, II, III, IV) is 7.6m long, with increasing distance from the flowering borage strip at 0m. The purple diamond section represents the flowering borage (*Borago officinalis*) strip (2.1m x 7.3m).

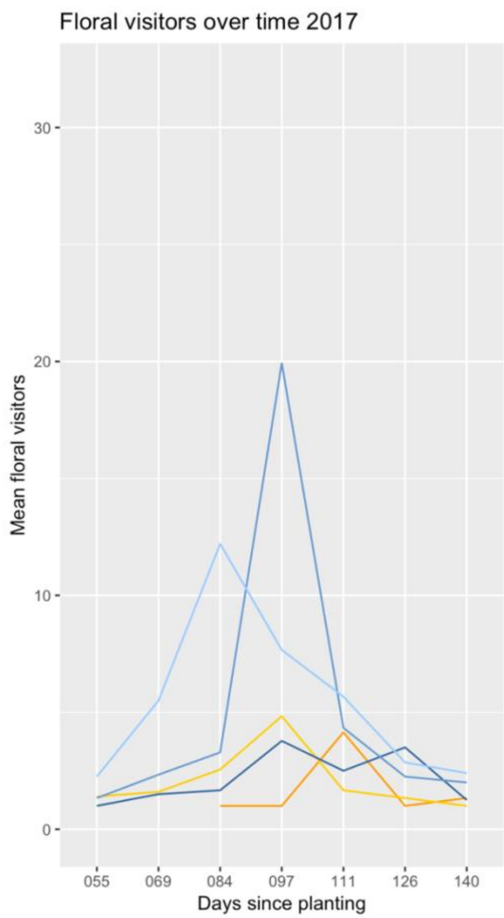


(a)

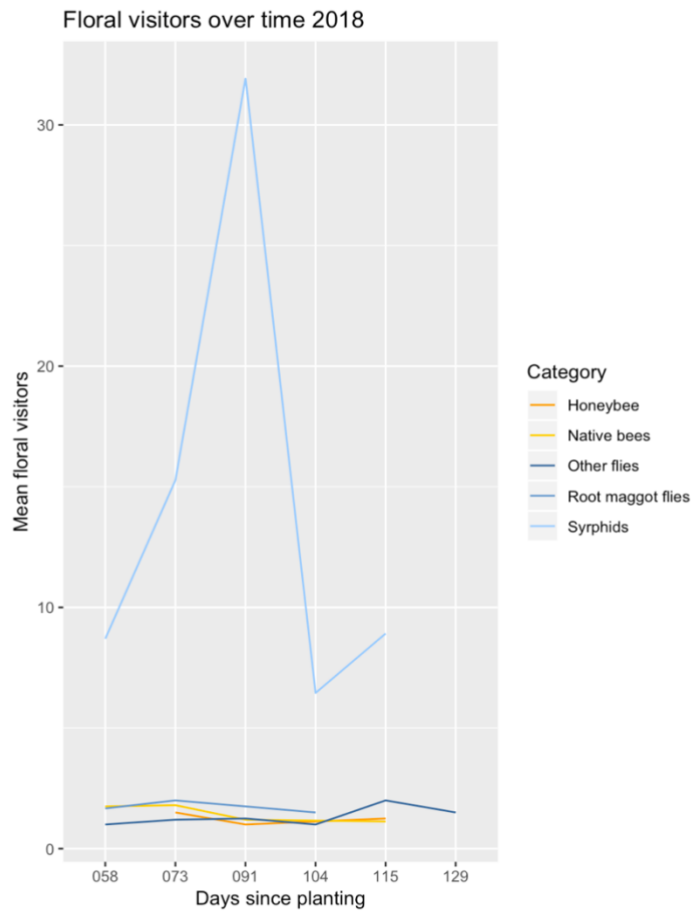


(b)

Figure 2. Number of total floral visitors by main insect categories for borage (*Borago officinalis*) and distance ranges within strawberry rows, averaged across three fields. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m.

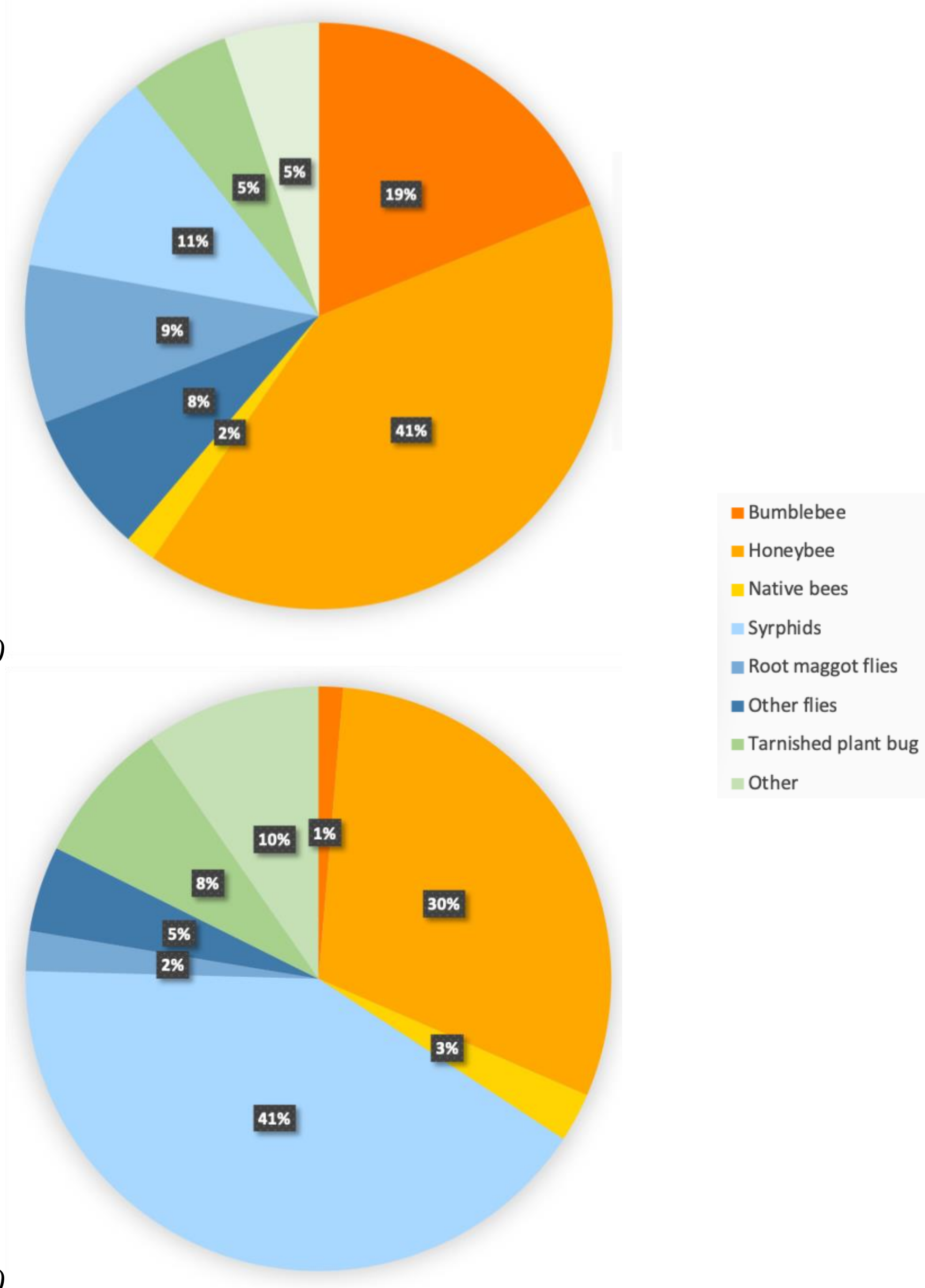


(a)



(b)

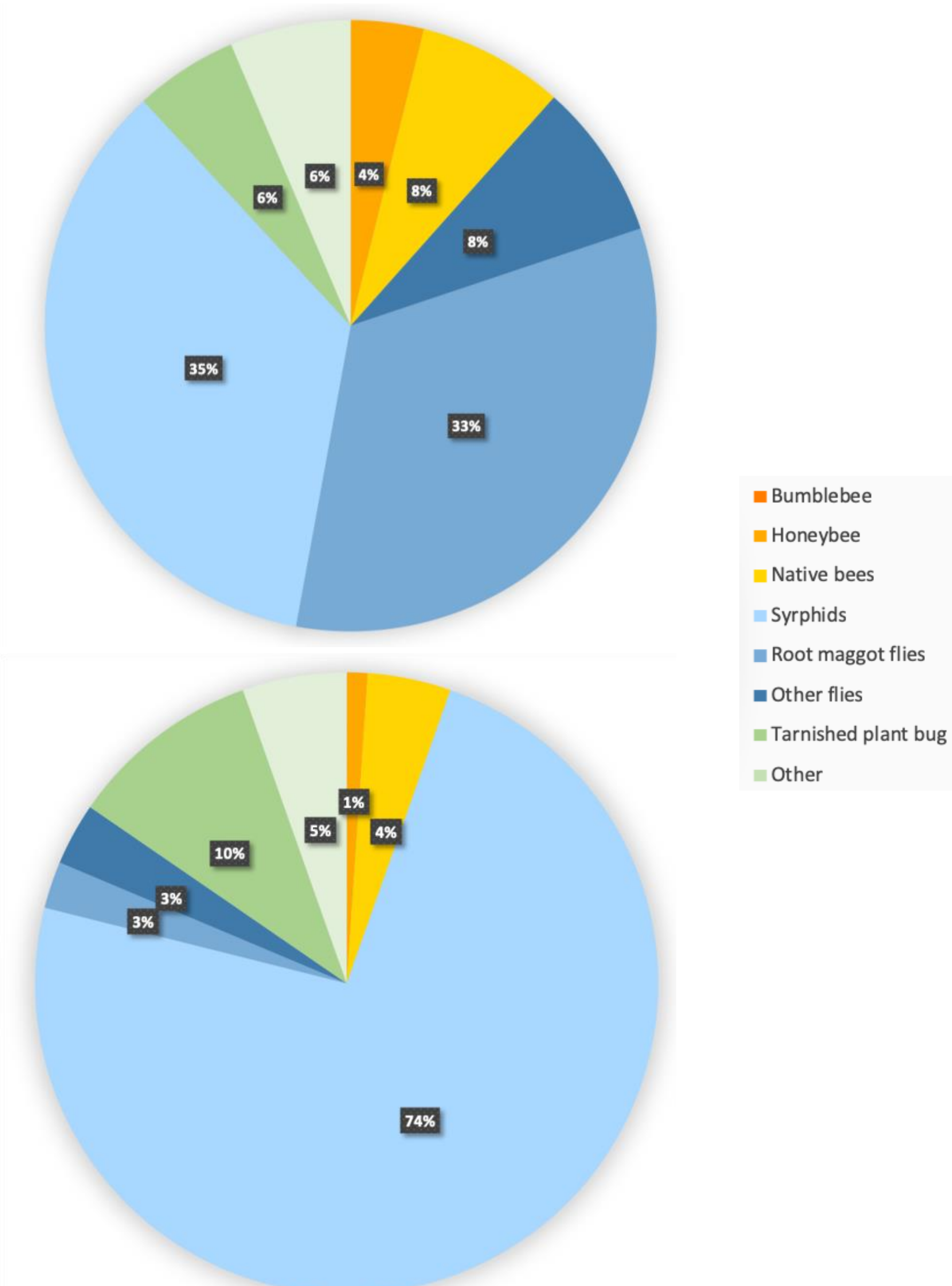
Figure 3. Average number of strawberry floral visitors among insect categories (honey bee, native bee, other flies, root maggot flies, syrphids) compared across days from planting in 2017 (a) and 2018 (b), averaged across three fields.



(a)

(b)

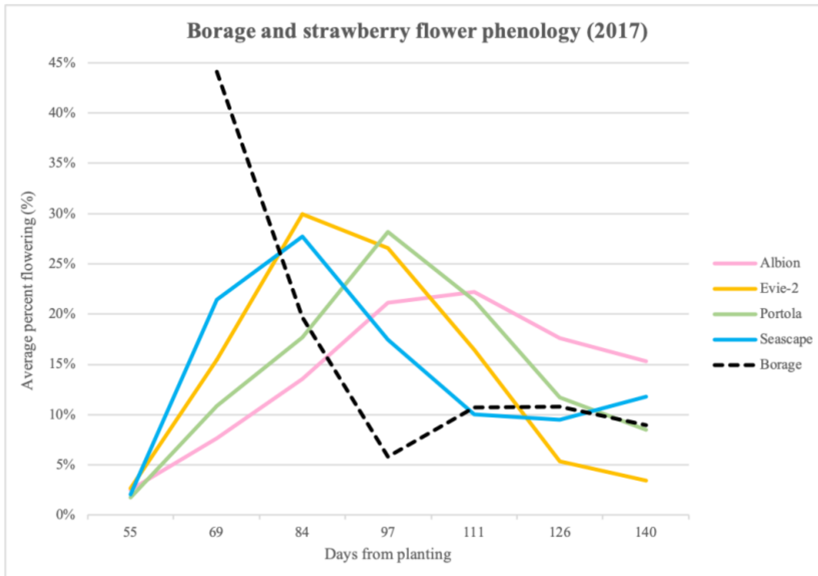
Figure 4. Relative abundance of primary floral visitor categories (bumble bee, honey bee, native bee, syrphids, root maggot flies, other flies, tarnished plant bug, other insect taxa) found on borage flowers in flower strips during 2017(a) and 2018(b) growing seasons.



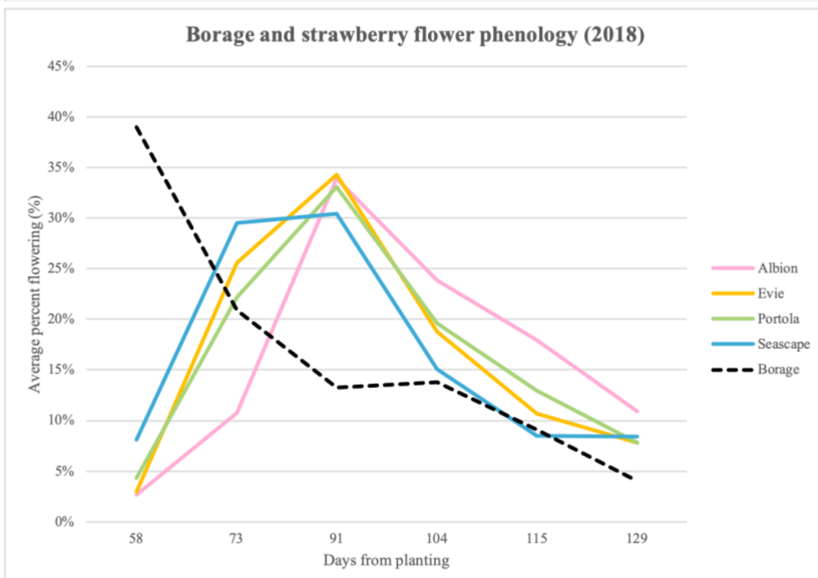
(a)

(b)

Figure 5. Relative abundance of primary floral visitor categories (bumble bee, honey bee, native bee, syrphids, root maggot flies, other flies, tarnished plant bug, other insect taxa) found on strawberry flowers during 2017(a) and 2018(b) growing seasons.

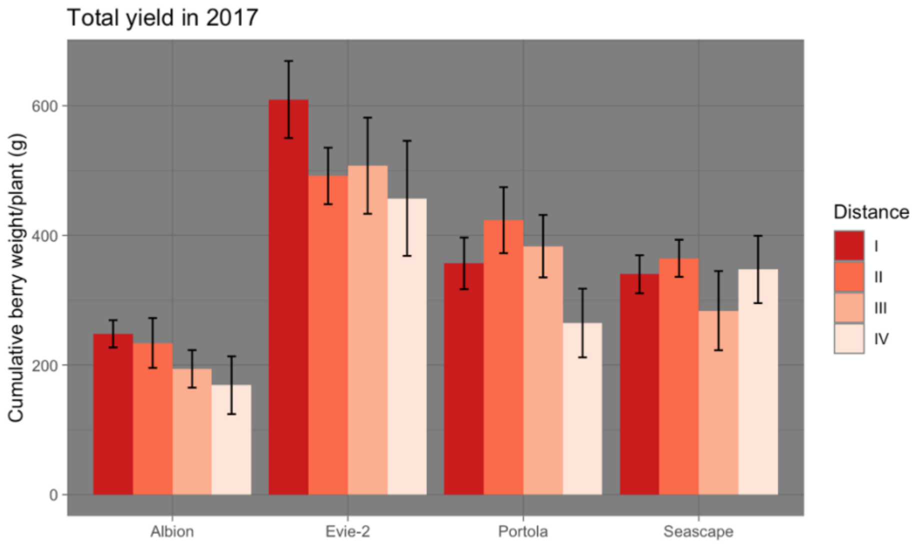


(a)

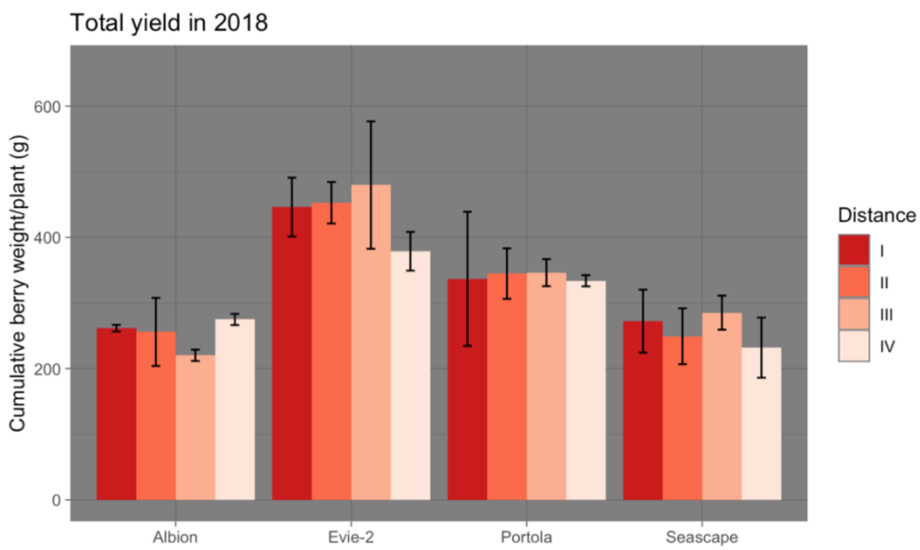


(b)

Figure 6. Borage (*Borago officinalis*) and day-neutral strawberry cultivar flowering phenology in 2017 (a) and 2018 (b) plotted days from planting. Average percent flowering indicates percentage of season total flowers counted open on that day. Day-neutral cultivar flowers are represented in solid colors, borage flowers are represented by dashed black line.

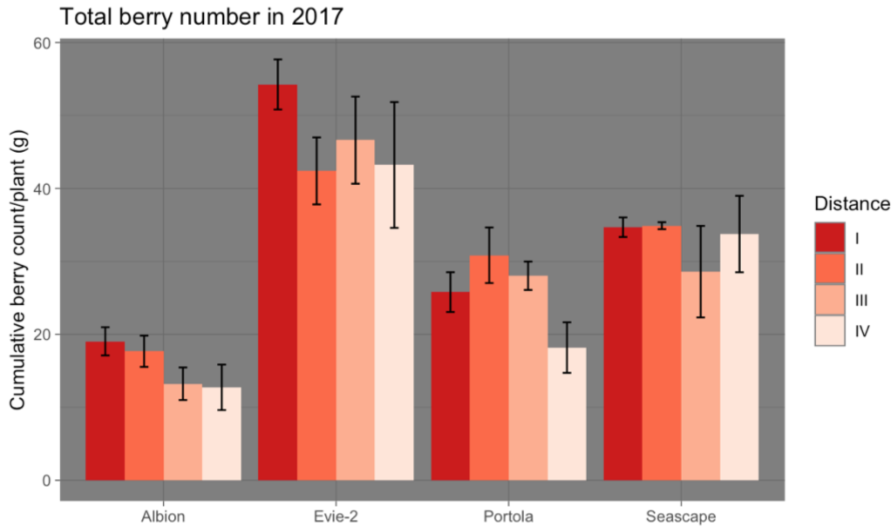


(a)

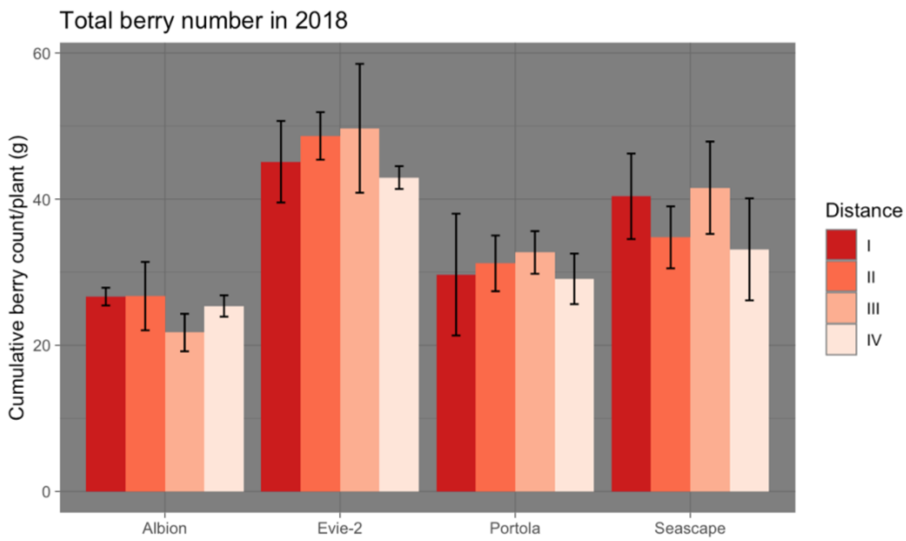


(b)

Figure 7. Total yield (average cumulative weight ± s.e) per plant displayed by cultivar and distance range in 2017 and 2018. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates.

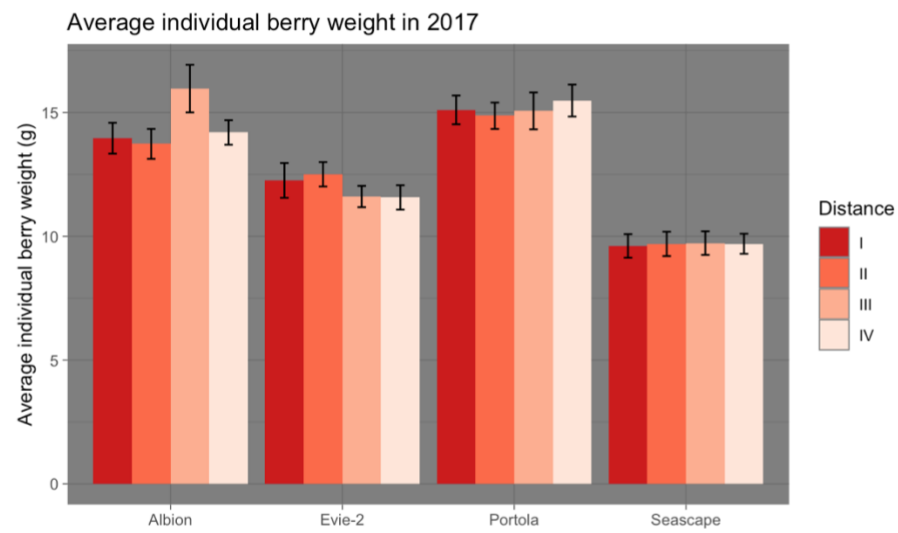


(a)

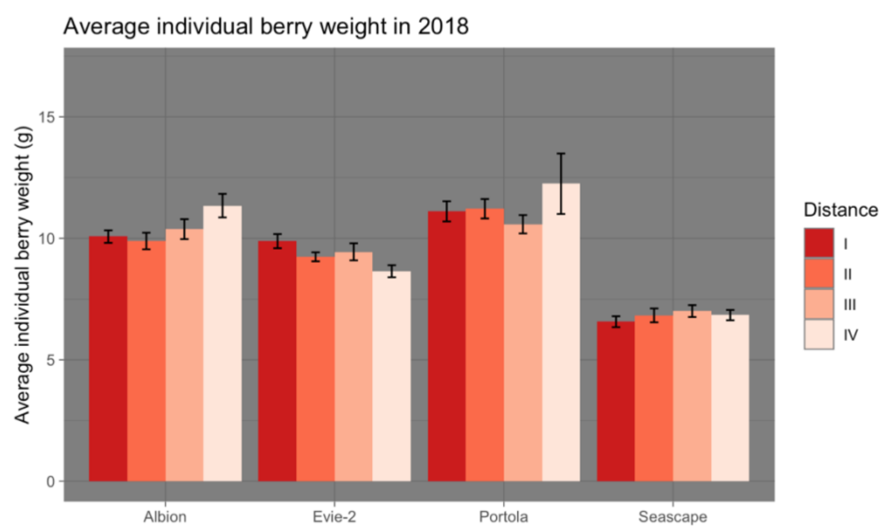


(b)

Figure 8. Total berry number (average cumulative berry count ± s.e) per plant displayed by cultivar and distance range in 2017 and 2018. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates.



(a)



(b)

Figure 9. Average individual berry weight (average ± s.e.) across 10 harvests in the middle of the season compared across distance ranges in 2017 and 2018. Each distance range (I, II, III, IV) is 7.5m long, with increasing distance from the flowering borage strip at 0m. Values are averaged across three field replicates.

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