ABSTRACT

MCCLURE, TRAVIS JAMES. Optimizing Biological Control of Aphids with Banker Plant Systems. (Under the direction of Steven D. Frank).

The following studies were conducted to establish protocols and teach growers how to best implement and improve the efficacy of banker plant systems. Aphids are serious greenhouse pests due to their short generation time, parthenogenetic reproduction, and ability to develop pesticide resistance. Green peach aphid (*Myzus persicae* Sulzer) (Hemiptera: Aphididae) is particularly devastating because of its broad host range. It can be difficult to control using insecticides or augmentative releases, as such; banker plants systems are a common alternative.

Banker plant systems for biological control of *M. persicae* consist of grain plants infested with *R. padi* which are alternative hosts for the parasitoid *Aphidius colemani*. Thus *A. colemani* can reproduce on the banker plant when *M. persicae* are populations are low or absent. This system can increase pest suppression; however, like other biological control tools, the efficacy of banker plant systems is inconsistent. One of the main reasons for this is a lack of research and standards for optimal implementation.

Several different grain species have been used in this aphid banker plant system. In each of our studies we monitored how these different species affected the efficacy of the system. In addition to observing the individual species our studies also determined if there were additive benefits of planting interspecific mixture bankers, similar to those observed in open agricultural systems.

In Chapter 1, we set out to establish the initial knowledge required to create such standards. All banker plants regardless of species or treatment were effective, actively

producing parasitoids, for roughly four weeks. Mixture banker plants were slightly taller, and covered more area than plants grown as monocultures. Rye produces the largest plant area while barley produces stockier plants with more basal area which *R. padi* preferentially feed on, making these the most ideal for growers. Regardless whether banker plants are grown as monoculture or mixtures, *A. colemani* will disperse at least 9.1m from a banker plant and pest suppression is similar at 3, 6.1, and 9.1m from the banker plant. A demonstration project suggested banker plants sustain parasitoids, and growers do not need more than one banker plant every 37.2m^2.

Chapter 2 focuses on the effects of mixtures in the context of the banker plant system. At the species level we found rye banker plants produced the most *R. padi* and *A. colemani*, and oat produced the fewest, but there were no differences in the number of *R. padi* or *A. colemani* between monoculture and mixture banker plants. Mixture banker plants produce a higher frequency of female parasitoids, but the parasitoids produced off crops associated with mixtures banker plants were smaller than those associated with monoculture banker plants. Ultimately, pest suppression by *A. colemani* was not different between monoculture and mixture treatments. The lack of differences between monoculture and mixture banker plants suggests growers can simply plant whatever is easiest.

Optimizing Biological Control of Aphids with Banker Plant Systems

by
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DEDICATION

To my family and friends who have supported and encouraged me to continual pursue my passions and goals.

BIOGRAPHY

Travis McClure earned a B. S. degree in Entomology from Michigan State University in May, 2012. Prior to graduation he worked as a research technician for several entomology and plant pathology laboratories at Michigan State University. While working in these laborites Travis got a lot of experience working as a component of research team, as well as analyzing a wide range of plants for insect and nematode damage. In August, 2012 Travis started a Masters program in Entomology at North Carolina State University under adviser Steve Frank.

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CHAPTER 1: Building a better banker plant: Analyzing logistical factors to improve banker plant efficacy

Introduction

Aphids are among the most important pests of ornamental and vegetable greenhouse crops. Aphids are significant pests because they have short generation times and reproduce parthenogentically which allow for rapid population growth and increases the likelihood of insecticide resistance (Goh et al., 2001). Aphids cause direct feeding damage, affect plant aesthetics, transmit viruses, and their honeydew can lead to sooty mold (Agrios, 1988). *Myzus persicae* Sulzer (Hemiptera: Aphididae) and *Aphis gossypii* Glover (Hemiptera: Aphididae) are particularly important because they have broad host ranges which include many vegetable and ornamental crop species (Heathcote, 1962; Ebert & Cartwright, 1997; Slosser et al., 1989).

Biological control of *A. gossypii* and *M. persicae* can be achieved by releasing the commercially produced parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) (Rabasse & van Steenis, 1999). *Aphidius colemani* are solitary, polyphagous, koinobiont, endoparasitoids of many economically important pest aphids (Starý, 1975). Pest suppression by *A. colemani* can be similar to insecticides such as imidacloprid (Vásquez et al., 2006). However, augmentative biological control can be unpredictable (Collier & Van Steenwyk, 2004) and control by *A. colemani* can be more expensive than insecticides (Vásquez et al., 2006).

The efficacy of *A. colemani* can be improved by using a banker plant system (Prado & Frank, 2014). The goal of a banker plant system is to support a reproducing natural enemy population within a crop to provide pest suppression for an extended period (Frank, 2010; Huang et al., 2011). Banker plants are typically non-crop plants grown within a greenhouse that provide natural enemies with alternative food, such as pollen, or alternative hosts for parasitoids (Frank, 2010; Prado & Frank, 2013; Wong & Frank, 2013). The most common banker plant system sustains *A. colemani* populations on the aphid *Rhopalosiphum padi* L. (Hemiptera: Aphididae), which only feed on monocots and thus are not pests of many greenhouse crops (Frank, 2010).

This system can increase parasitism of *A. gossypii* and *M. persicae*, which *A. colemani* prefer to *R. padi* (Bilu et al., 2006; Prado & Frank, 2014), but efficacy has been inconsistent (Jacobson & Croft, 1998; Van Driesche et al., 2008). One potential source of inconsistency is that several different grain species have been used as banker plants (Frank, 2010). Another potential source of inconsistency is lack of knowledge about *A. colemani* dispersal from a banker plant. *Aphidius colemani* has been shown to locate and oviposit on aphids at least 16m from a release point (Langhof et al., 2005), and are more effective at suppressing pests 0.5m from a release point than 2.9m from the release point (van Steenis, 1995). To our knowledge, no such studies have been conducted with banker plants. A third potential source of inconsistency is the size and density of which banker plants are deployed. For example, Kim & Kim, 2004 used 500 seedling banker plants at a density of 1/90m^2 and Nagasaka et al., 2010 used 100 seedling banker plants at densities of 1/166 m^2 and 1/250 m^2.

Grower interest in banker plant systems is increasing but adoption is hindered by concerns about reliability and the logistics of implementation. We compared (1) growth characteristics and the effective duration of banker plants, (2) *A. colemani* dispersal and the most effective distance for pest suppression for the four most commonly used banker plant species alone and in interspecific mixtures, (3) we also tested the role of banker plant density within a complete IPM release program. In open agricultural systems plant diversity has been demonstrated to increase insect natural enemy abundance, fitness, and efficacy by providing alternative hosts and food resources (Altieri, 1999; Landis et al., 2000; Tahvanainen & Root, 1972). Comparing these species as both monocultures and mixtures will help determine the best banker plant species and if mixing species is beneficial.

Methods

2.1 Study Organisms

We used Black Pearl pepper plants (*Capsicum anuum* L. ‘Black Pearl’) infested with the pest aphid *M. persicae* as sentinel plants in sections 2.3 and 2.4. We propagated Black pearl pepper plants from cuttings. We cut source plants roughy 5 cm below the bud. Then we dipped cut tips into “Rhizopon AA Dry Powder Rooting Hormone #1” (Active ingredient: 0.1% 3-Indolebuteric acid) (Earth City, MO*)* and potted them into a sifted Fafard 2P mix (Agawam, MA). We planted cuttings in 48 cell trays (56cm by 25.5cm tray), and left them to root for 6 weeks before we transplanted each into separate 15.2cm-diameter pots containing Fafard 2P soil mix and 8.86g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer (Marysville, OH) per pot. We used plants once they had reached 20cm tall for section 2.3, and plants were between 30 and 40cm for section 2.4.

We maintained aphid colonies in the laboratory from field collected aphids. Our *M. persicae* were reared on Black Pearl pepper plants. Our *R. padi* colonies were reared in cages containing monoculture and mixture pots of the same grain species and cultivars used in experiments within the same cage (Table 1). We originally purchased *A. colemani*, from Koppert Biological (Howell, MI); and then maintained them in colony in cages on *R. padi*, as is done by Koppert Biological. Our R. *padi* were reared on monoculture and mixture pots of the same grain species and cultivars used in experiments. We kept all colonies in separate 60 x 60 x 60 cm BugDorm cages (BugDorm Store; Taipei, Taiwan) for two years in a greenhouse receiving ambient light with temperatures ranging from approximately 18.5° C to 34.5° C depending season.

2.2 Banker plant growth characteristics

To understand how plant species and mixtures affect banker plant growth and longevity we conducted a greenhouse experiment with the four most common aphid banker plant species barley, oat, rye, and wheat (Frank, 2010). Barley, oat, rye, and wheat were all tested as monocultures. Within each species we used 3 different cultivars so the effect of species was not determined by a single cultivar. The species and cultivars used were barley, *Hordeum vulgare* L.('Price', 'Thoroughbred', and 'Nomni'), oat, *Avena sativa* L.('Cat Grass', 'Brooks', and 'Rodgers'), rye, *Secale cereale* L. ('Matt time', 'Wrens Abrozzi', and 'AGS 104'), and winter wheat, *Triticum aestivum* L. ('Roane', USG 3209/Jaypee', and 'Neuse') (Table 1). We planted three replicate pots of each cultivar of each plant species. This provides 36 pots of the monoculture treatment to compare the overall effects of growing banker plants in monocultures compared to mixtures. It also provided 9 pots of each species within the monoculture treatment to determine if the species differed in their growth characteristics or the effective banker plant duration. The mixture treatment was made up of 12 unique four species mixes, containing one cultivar from each of the four species, used in the monoculture treatment (n = 3 each), planted in equal proportions (6 seeds each) for a total of 36 mixture pots. We planted all treatments with 24 seeds unsystematically arranged in 15.2 cm-diameter pots with Fafard 2P soil mix (Agawam, MA) and 8.86g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer (Marysville, OH).

We unsystematically placed the pots onto two 2.4 x 1.2 m greenhouse bench sections arranged in 5 rows with 14 or 15 pots per row. Pots were staggered with 15cm diagonally between each. Starting twelve days after planting, we measured four plant growth characters for each pot twice a week for twelve weeks. We counted the number of plants that had germinated in each pot, and numbers decreased once plants began to die. If a pot had no live plants we did not include the pot in the other measures. We measured the height from the top of the soil to the tip of the tallest plant in a given pot. We measured the straightened length of three random leaves per pot from leaf-tip to the node. We calculated the area of plant material in each pot by measuring the widest expanse of plant material from a pot as viewed from above and the width perpendicular to this measurement, adding them together and dividing by four to get the average radius, then squared this number and multiplied the product by π. (Fig. 1). Eighteen days after planting we added 30 *R. padi* of mixed instars to each pot. While parasitoids were not released in this experiment, our pots were uncaged and exposed to resident parasitoids. To determine the effective duration of a banker plant, we recorded the percentage of banker plants per treatment with more than 10 aphids, the minimum number of aphids at which a banker plant still has the potential to produce parasitoids. The ten aphid threshold was used as a minimum effective density, because although *A. colemani* perform well at low aphid densities, some aphidaphagous species will not feed on a plant if aphid density is less than 10 (van Steenis & El-Khawass, 1995; El Titi, 1972). Effective duration measurements were collected for six weeks following aphid introduction.

To determine how banker plant treatment (monoculture or mixture) and day affected each of the four plant growth characters and effective banker plant duration, we used 2-way repeated measures ANOVA, banker plant treatment and day were fixed independent variables while the four plant growth characters and effective duration were dependent variables, date was the repeated measure with the subject of replicate nested within treatment (1-36), which was also included as a random factor. Two-way repeated measures ANOVA were run for the fixed independent variables of banker plant species (barley, oat, rye, and wheat) and day evaluating their effects on the dependent variables, the four plant growth characters and the effective banker plant duration, date was the repeated measure. While replicate nested within treatment was the subject as well as a random factor. These tests were also carried out at the cultivar level but there were no significant differences. In each analyses Data for all characters other than number of live plants per plot were log(x+1) transformed to meet the assumptions of normality. We performed these statistical analyses in SAS (version 9.2), using the MIXED procedure.

2.3 Distance effects on banker plant efficacy

We conducted a greenhouse experiment to determine how far *A. colemani* would disperse from a banker plant and measured pest aphid suppression at various distances over three time blocks. Each time block used different cultivars of the monoculture ad different mixture combinations. At the end of the third block each of the three cultivars for each of four species and all 12 mixture combinations were represented (Table 1).

We used the same monoculture and mixture treatments from the previous experiment to create banker plants. Fourteen days after planting we placed two monoculture and two mixture banker plants into two 60 x 60 x 60cm 'Bugdorm' cages (4 plants each, 8 plants total), and infested each pot with 30 *R. padi* of mixed in stars. Twenty-four hours later we released 8 female parasitoids into each cage. Twelve days later we standardized each banker plant by removing mummies so that each contained the same number of mummies as the plant with the lowest number of mummies in a given time block. We placed four monocultures, one variety of each of the four species selected via a random number generator, and four mixture pots at the end of separate 9.5 m greenhouse benches in 13.72 x 19.51m greenhouse bays. Bays were filled with seasonal flowers the density and species of which varied by time block and greenhouse bay. No parasitoids were released into the bays except those emerging from our banker plants. Typically we placed one replicate in each greenhouse bay but on two occasions we placed two replicates 12 m apart within the same greenhouse bay. We infested sentinel plants with 25 *M. persicae* each and placed these plants 3m (near), 6.1m (medium), and 9.1m (far) from the banker plant. Sentinel plants were exposed for four days (Monday – Thursday) after which each was stored in a separate 61 x 61 x 61cm cage built using PVC pipe and organza, for one week. We counted and removed newly formed mummies from sentinel plants daily.

We used two-way ANOVA to determine how the independent variables distance, banker plant treatment, and their interaction affected the dependent variable, the number of

A. colemani mummies of oviposited at each distance. Time, and replication nested within time were included as random variables. These data were not normal, so we log(x+1) transformed them before analysis. We performed these statistical analyses in SAS (version 9.2) using the MIXED procedure.

2.4 Banker plants as a component of a demonstration project

To determine how banker plant density affects pest suppression within an IPM program we partnered with local grower Ralph “Screech” Sweger, of Screech Owl Greenhouses (Pittsboro, NC). Screech Owl Greenhouses allowed us to conduct research in five active greenhouses of various crops and sizes: “start” house (contained lettuce, tomato, herb, and eggplant seedlings) 74.3 m^2, cucumber house 74.3 m^2, lettuce house 111.5 m^2, pepper house 148.6 m^2, and tomato house 185.8 m^2.

We used barley, *H. vulgare* ‘Price’ as our banker plants. We unsystematically planted seeds into 15.2cm-diameter pots with Fafard 2P soil mix and 8.86g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer. Plants were grown in 61 x 61 x 61cm organza cages, nine pots per cage. One week after planting, we infested banker plants with 30 *R. padi* of mixed instars per pot and released 10 adult parasitoids in each cage. Fourteen days later we counted the number of aphids and mummies in each pot. We used four houses at a time to test the effects of banker plants at three different densities: low (1 banker plant / 37.2m^2, banker plants roughly 8m apart), medium (2 banker plants / 37.2m^2, banker plants roughly 4.5m apart), high (4 banker plant / 37.2m^2, banker plants roughly 3.1m apart) and an augmentative release which did not receive any banker plants. We did not include a no treatment control because this would not have been practical for our grower, and is not commonly practiced. We standardized the banker plants so the average number of aphids and mummies per pot was the same, by adding or removing when necessary, for each banker plant density during a given time block. We placed banker plants in greenhouses for four weeks. Augmentative release houses received a proportional number of adult *A. colemani* as there were total of mummies at the start of the low density banker plant treatment during a given time block. Releases of 85, 100, and 140 parasitoids were performed at the same time banker plants were deployed.

Since each greenhouse contained different crops and pests we used black pearl pepper plants infested with *M. persicae* as sentinel plants to assess parasitism rate on a standard plant and pest in each house. Sentinel plants were between 30cm and 40cm tall and infested with 30 *M. persicae* one day prior to being placed in the greenhouse. Once per week, we placed 2 sentinel plants / 37.2m^2 (spaced evenly between banker plants; in the low density this meant roughly 4m from banker plants, medium density 2.25m, and high density 1.6m) in each greenhouse. We collected each sentinel plant after 24 hours, and placed them into cages with the other sentinel plants from the same greenhouse, as we were only interested in per house totals. Sentinel plants were checked for mummies seven and ten days after they were placed into the cages. We counted the number of aphids (of various species) (Hemiptera: Aphididae), mummies *Aphidius spp.* or *Aphelinus spp.* (Hymenoptera*:* Braconidae / Aphelinidae), minute pirate bugs (*Orius spp:* Hemiptera: Anthocoridae), and ladybird beetles (*Coccinelids*: Coleoptera: Coccinellidae) in one 18.6m^2 section of each greenhouse once a week. This experiment was repeated three times.

Separate Spearman's correlations were used to determine how the number of mummies on sentinel plants was associated with time after banker plant implementation for each banker plant density and the augmentative release (12 data points). To test the overall effect of banker plants relative to augmentative releases on the association between the number of mummies on sentinel plants and time, we combined the data from each of the banker plant density treatments (36 data points), and compared them to our augmentative release treatments. Averages and standard deviations were calculated for aphid and natural enemy counts. We performed these statistical analyses in SAS (version 9.2).

Results

3.1 Banker plant growth characteristics

There was not a significant main effect of banker plant treatment (monoculture vs. mixture) on the number of plants surviving within a pot ($F_{1, 70} = 0.90$, $p = 0.346$). There was a significant effect of day since plants died over time, but not of the banker plant treatment by day interaction (day: $F_{24, 1680} = 30.35$, $p < 0.001$, and treatment*day: $F_{24, 1680} = 0.65$, $p = 0.902$) (Fig. 2A). There was a significant main effect of banker plant treatment, day, and their interaction on banker plant height (treatment: $F_{1, 70} = 5.12$, $p = 0.027$, day: $F_{24, 1662} = 52.17$, $p < 0.001$, and treatment*day: $F_{24, 1662} = 1.64$, $p = 0.026$) wherein mixture pots had taller plants in the last half of the experiment. (Fig.2B). There was not a significant main effect of banker plant treatment on average leaf length ($F_{1, 70} = 1.45$, $p = 0.233$). There was a significant effect of day since plants grew over time, but not of the banker plant treatment by day interaction on average leaf length (day: $F_{24, 1662} = 122.35$, $p < 0.001$, and treatment*day: $F_{24, 1662} = 0.99$, $p = 0.474$) (Fig.2C). There was significant main effect of banker plant treatment and day on banker plant area wherein mixtures had a greater area but all plants increased in area over time ($F_{1, 70} = 8.90$, $p = 0.004$; $F_{24, 1662} = 54.18$, $p < 0.001$). The interaction was not significant ($F_{24, 1662} = 0.80$, $p = 0.736$) (Fig. 2D).

Banker plant species, day, and their interaction on each of the four plant growth characters (species: $F_{3, 32} = 4.29$, $p = 0.012$; day: $F_{24, 768} = 16.72$, $p < 0.001$; and species*day: $F_{72, 768} = 1.71$, $p < 0.001$) (Fig. 3A). Barley had significantly more live plants than oat and rye, and wheat had significantly more live plants than rye (barley-oat: $t_{32} = 2.02$, $p = 0.051$; barley-rye: $t_{32} = 3.33$, $p < 0.001$; and wheat-rye: $t_{32} = 2.58$, $p = 0.015$) (Fig. 3B). There were significant effects of species, day, and their interaction on the height of the tallest plant (species: $F_{3, 32} = 17.71$, $p < 0.001$; day: $F_{24, 751} = 24.82$, $p < 0.001$; and species*day: $F_{72, 751} = 10.23$, $p < 0.001$) (Fig. 3C). Oat and rye were significantly taller than wheat and barley by the end of the experiment (oat-barley: $t_{32} = 5.50$ $P <0.001$; rye-barley: $t_{32} = 5.11$, $p < 0.001$; oat-wheat: $t_{32} = 5.17$, $p < 0.001$; and rye-wheat: $t_{32} = 4.78$, $p < 0.001$) (Fig. 3D). There were significant main effects of average leaf length, day, and their interaction (species: $F_{3, 32} = 10.74$, $p < 0.001$; day: $F_{24, 751} = 55.40$, $p < 0.001$; and species*day: $F_{72, 751} = 3.82$, $p < 0.001$) (Fig. 3E). Oat and rye were significantly larger from barley, and oat was significantly larger from wheat by the end of the experiment (oat-barley: $t_{32} = 5.33$ $P <0.001$; rye-barley: $t_{32} = 3.53$, $p < 0.001$; and oat-wheat: $t_{32} = 3.73$, $p < 0.001$) (Fig. 3F). There were a significant main effects of banker plant area, day, and their interaction (species: $F_{3, 32} = 4.89$, $p < 0.001$; day: $F_{24, 751} = 28.49$, $p < 0.001$; and species*day: $F_{72, 751} = 3.32$, $p < 0.001$) (Fig. 3G). Rye had the largest area and was significantly greater than each of the other three species by the end of the experiment (rye-barley: $t_{32} = 2.39$, p = 0.023; rye-oat: $t_{32} = 2.79$, p = 0.009; and rye-wheat: $t_{32} = 3.66$, p < 0.001) (Fig. 3H).

Between banker plant treatments both day and treatment had significant effects on the effective duration of banker plants (treatment: $F_{1, 70} = 6.80$, p = 0.011; day: $F_{13, 910} = 216.25$, p < 0.001), but the interaction between day and treatment was not significant ($F_{13, 910} = 1.09$, p = 0.365) (Fig. 4A). Between banker plant species day had a significant effect on the effective duration of banker plants ($F_{13, 416} = 97.23$, p < 0.001), but species and the interaction between day and species did not ($F_{3, 32} = 1.65$, p = 0.198; $F_{39, 416} = 0.92$, p = 0.608) (Fig. 4B).

3.2 Distance effects on banker plant function

There were not significant main effect for banker plant treatment, distance, or their interaction on the number of mummies oviposited on a given plant ($F_{1, 55} = 1.74$, p = 0.193; $F_{2, 55} = 2.49$, p = 0.092; $F_{2, 55} = 2.72$, p = 0.075) (Fig. 4).

3.3 Banker plants as a component of a demonstration project

The correlation between time and mummies on sentinel plants for the augmentative release (no banker plant treatment) houses was negative (N = 12, p = 0.027, r = -0.633) indicating as time increases the number of mummies on sentinel plants decreases. In contrast, there were no significant correlations for any of the three banker plant densities (low banker plant density N = 12, p = 0.736, r = 0.109, medium banker plant density N = 12, p = 0.815, r = 0.076, and high banker plant density N = 12, p = 0.233, r = 0.372) indicating as time passed the number of mummies produced on sentinel plants was similar. When data from all banker plant houses were combined the relationship between time and mummies was also not significant (N = 36, p = 0.285, r = 0.183) indicating as time passed the number of mummies produced on sentinel plants was similar.

On average (mean ± SEM) there were 5852.1 ± 2834.9 aphids, 299.5 ± 155.5 *Aphidius spp.*, 75.4 ± 41.8 *Aphelinus spp.*, 11.8 ± 5.1 *Orius spp.*, and 74.3 ± 36.9 *Coccinelids* in 18.6m^2 of greenhouse space on any given collection day.

Discussion

Diverse plant mixtures should reduce aphid population growth and increase plant growth (Cardinale et al., 2007; Fargione et al., 2007; Tahvanainen & Root, 1972; Tilman et al., 2001; van Ruijven & Berendse, 2005). These potential benefits did not occur in our banker plants. Mixture and monoculture banker plants grew to similar sizes and almost all banker plants remained effective sources of parasitoids – contained more than 10 aphids - for four weeks. After four weeks the percentage of plants which remain effective rapidly drops, such that after 4.5 weeks roughly 50% of all banker plants remain effective. The number drops to roughly 30% after five weeks, and after 5.5 weeks essentially no banker plants remain effective. To our knowledge this is the first time effective banker plant duration, has been tested. The effective duration can be used to help alert growers when to replace banker plants, recommendations for which are currently highly variable in the literature (Huang et al., 2011). A common replacement recommendation for *Aphidius* banker plant systems is every 10-12 weeks (Koppert 2009), but most growers will likely never want to be without effective banker plants and should replace them every four weeks. If growers wanted to follow our protocols, and in order to constantly have effective banker plants they would need to plant new banker plants roughly every 10 days. This allows the banker plants to grow prior to replacing the banker plants which are no longer effective. Potentially this length could be longer based on the number of pest aphids; our study was conducted with only banker plants. Apparent competition predicts parasitism on the banker plants would be reduced as a proportion of oviposition would be taking place on pest aphids (Prado and Frank, 2014) and allowing longer aphid production, and less need to replace banker plants.

A grower's primary goal is to produce the most and highest quality crops. Grower's prefer banker plants to be easy to cultivate, long-lasting, and to not compete with their crop plants for light, space or nutrients (Parolin et al., 2012). Several different banker plant species have been used in this aphid banker plant system (Frank, 2010). Jandricic et al., 2014 *in press* found that the four plant species we tested each had different effects on aphid and parasitoid life history characters such as sex-ratio and hind-tibiae length. However, due to the competing nature of several life history characters they were unable to determine a best banker plant species. Our open bench study suggests banker plants remain effective sources of parasitoids for the same duration, regardless of species. Barley banker plants took up less space since they had shorter leaves, and height than oat and rye, and had a smaller area than rye. Barley pots also contained more plants than oat and rye pots. *Rhopalosiphum padi* often prefer to feed on the basal area of plants (personal observation) or other concealed locations (Ni et al., 2000), meaning barley, with their higher number of plants per pot and shorter stockier nature, may make particularly favorable hosts for *R. padi*. Higher numbers of *R. padi* could ultimately lead to more parasitoid production, and in turn more complete pest suppression (Collier & Van Steenwyk, 2004; Crowder, 2007). *Rhopalosiphum padi* and other aphids will feed on all parts of a plant (Miles, 1987). As such, rye banker plants, which provide the most plant area, are also a good option for growers if they have or are willing to allow more space for their banker plants.

In both our distance and our density experiments the distances we tested were shorter than the known dispersal distance of 16m for augmentative releases of *A. colemani* (Langhof et al., 2005). We hypothesized that *A. colemani* dispersal distances would be less from baker plants than augmentative release as they would not need to leave banker plants to sustain their population. However, other studies have shown *A. colemani* prefer *M. persicae* to *R. padi*, and thus we would expect some dispersal from this less preferred host (Bilu et al., 2006; Ode et al., 2005; Prado & Frank, 2014). Studies have shown some insects can detect olfactory cues at distances of at least 100m (Evans & Allen-williams, 1993), and olfaction to host plants drives parasitoid long distance navigation (Godfray, 1994). Once on a plant *A. colemani* rely on visual stimuli to locate prey (Mackauer & Michaud, 1996). In our demonstration project, we observed *Aphidius* ovipositing on all sentinel plants when banker plants were roughly 8m apart, the spacing of our low density treatment (1/37m^2). We did not see differences in the number of mummies oviposited on sentinel plants between any of our tested densities. Banker plants can be deployed at densities at least as low as 1/37.2m^2. In our distance study we observed *A. colemani* dispersing 9.1m from their less preferred host, *R. padi*, to their more preferred host, *M. persicae.* Theoretically, using a combination of olfactory and visual cues, *A. colemani* should be able to provide equal pest suppression over an entire area when banker plants are placed a minimum of 18.2m apart, roughly a density of 1/84.6m^2. Neither our study nor Langhof et al., 2005 had plants at a distance too great for *A. colemani* to locate and oviposit on, as such, the maximum potential of *A. colemani* dispersal from a release point and a banker plant are still unknown. Future work should test even further distances.

There are no standards for how large, or at what density banker plants should be implemented (Frank, 2010; Huang et al., 2011; Kim & Kim, 2004; Nagasaka et al., 2010). During our demonstration project we tested banker plants composed of 24 seedlings. When more grain seeds are planted in small pots, the plants become root bound (personal observation). Twenty-four seedlings is fewer than is commonly planted for banker plant systems (100 to 500), to compensate for this smaller size we placed pots at densities ranging from $1/37.2m^2$ to $4/37.2m^2$ which were higher than other published densities ($1/90m^2$ to $1/250m^2$) (Kim & Kim, 2004; Nagasaka et al., 2010). A primary objective of a banker plant system is to sustain natural enemies within a greenhouse for an extended time (Frank, 2010). Papers have shown banker plants to increase pest suppression compared to augmentative releases (Pickett et al., 2004; Prado & Frank, 2014; Xiao et al., 2011) but none have shown banker plants sustaining parasitoids better than augmentative releases. We observed a significant negative correlation between time since the single augmentative release and the number of mummies collected on sentinel plants. As time since the release passed, the parasitoids in these greenhouses were either dying or dispersing out of the greenhouse. There were no correlations between time since implementation of banker plants and the numbers of mummies collected on sentinel plants for any of our banker plant densities. Banker plants sustained parasitoids within the greenhouse for the entire four week period. Despite being just one aspect of our local grower's IPM program the presence of our banker plants allowed parasitism to remain consistent over a four week period. This finding coincides with the four week effective duration of our open bench study.

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APPENDICES

Monoculture		
Barley	Price	3
	Throughbred	1
	Nomini	2
Oat	Cat grass	1
	Brooks	2
	Rodgers	3
Rye	Matt time	1
	Wrens Abrozzi	2
	AGS 104	3
Wheat	Roane	3
	USG 3209	2
	Neuse	1

Mixture				
Barley	Oat	Rye	Wheat	
Price	Cat grass	Wrens Abrozzi	Roane	3
Nomini	Cat grass	Matt time	USG 3209	1
Nomini	Cat grass	Wrens Abrozzi	Neuse	2
Throughbred	Rodgers	Matt time	USG 3209	1
Price	Brooks	Wrens Abrozzi	Neuse	3
Price	Rodgers	AGS 104	Roane	2
Nomini	Brooks	AGS 104	USG 3209	1
Throughbred	Cat grass	Wrens Abrozzi	Neuse	3
Throughbred	Rodgers	Matt time	Roane	2
Throughbred	Brooks	AGS 104	Neuse	3
Nomini	Cat grass	Wrens Abrozzi	Roane	2
Throughbred	Brooks	AGS 104	USG 3209	1

Table 1. Species and cultivars composition of the monoculture and mixture banker plant treatments. The numbers on the right indicate which cultivars and mixtures were used in which time blocks during distance trials (section 2.3 and 3.2).

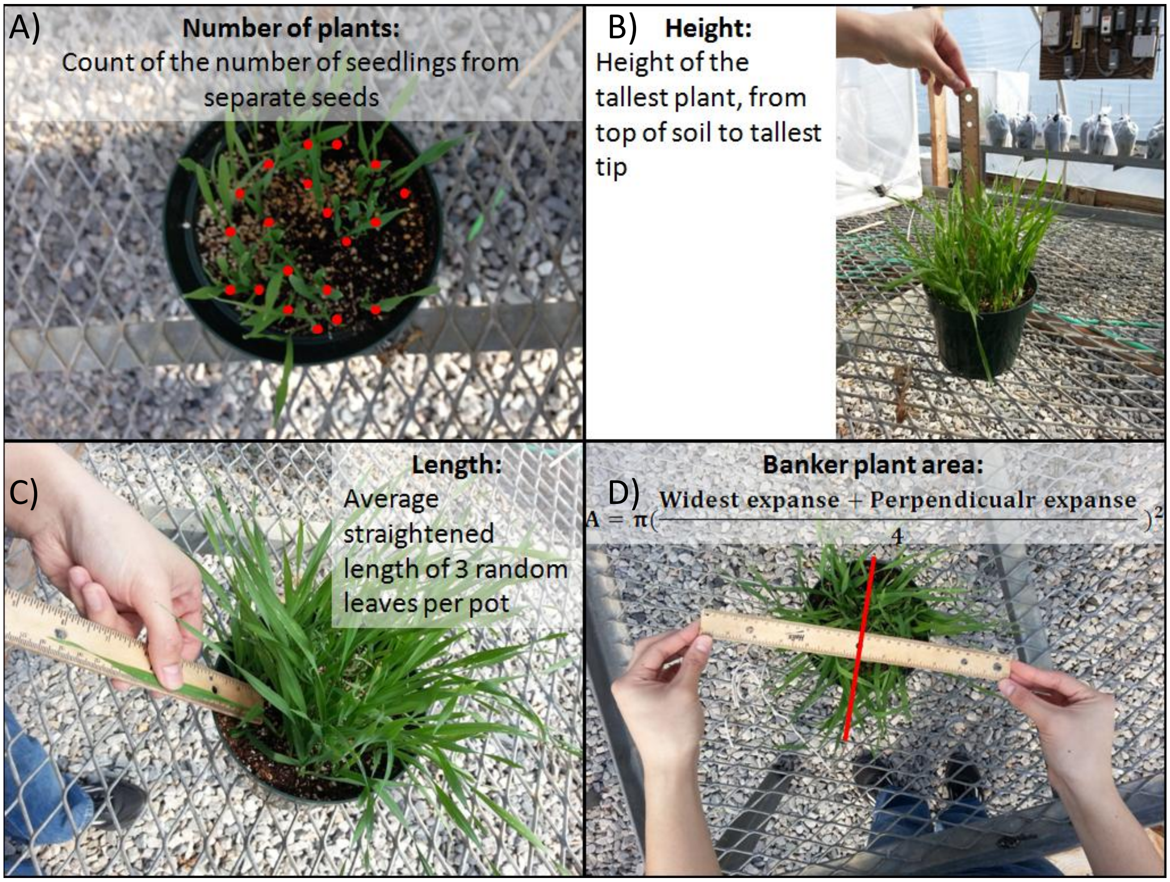

Figure 1. A visual depiction of how plant growth characters were measured. A) Number of plants were pot, the number of seedlings sporting from different seeds were counted. B) Height measured from the top of the soil to the tallest plant tip. C) Average leaf length was calculated by straightening 3 random leaves per pot and measure their length from leaf-tip to node. D) Banker plant area was calculated by adding the width of the widest overhanging expanse to the width of the perpendicular expanse to create the averaging overhanging radius, this value was then multiplying by π.

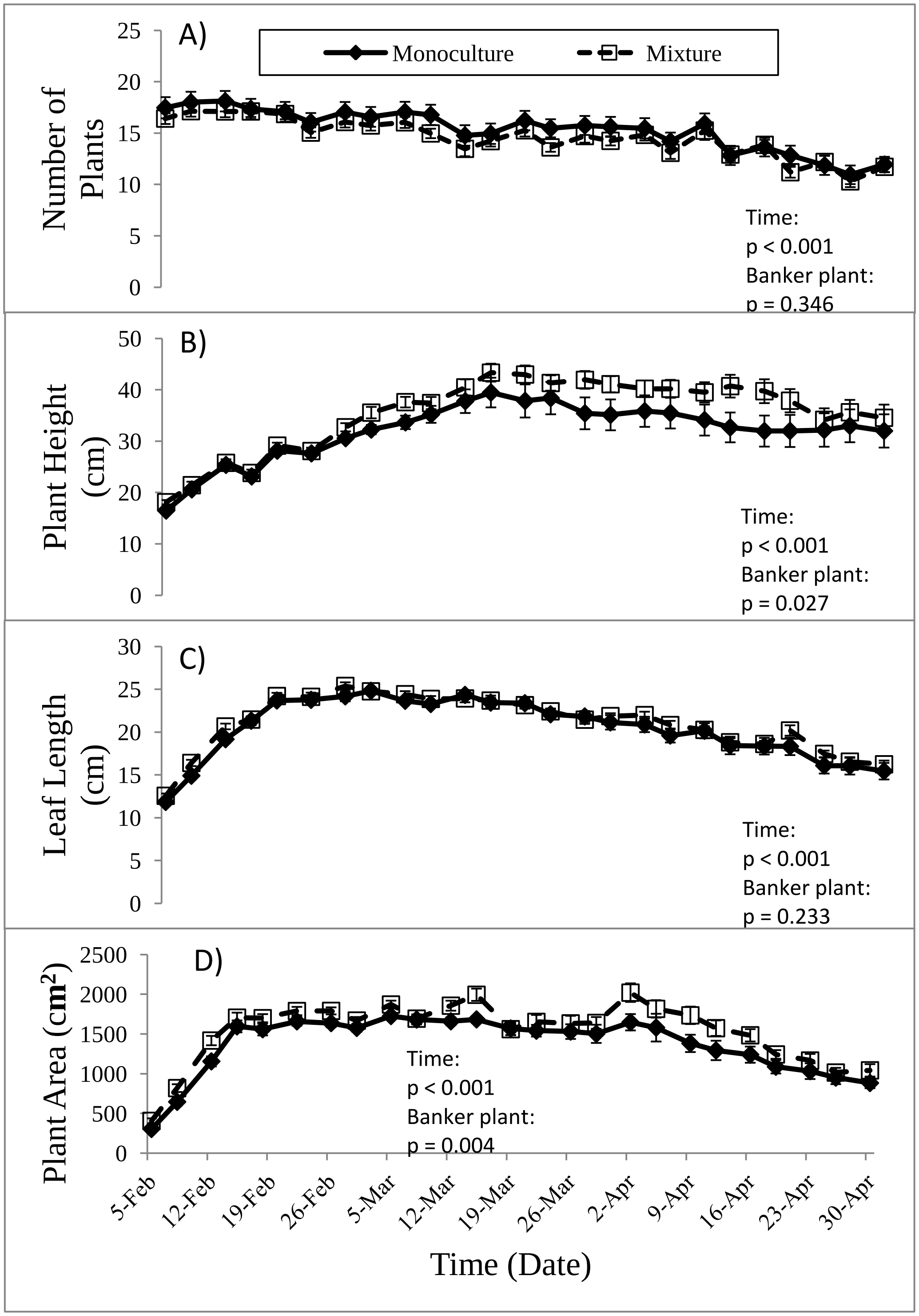

Figure 2. A) Mean (±SEM) number of plants surviving within a pot for monoculture and mixture grain pots for each collection day. B) Mean (±SEM) height of the tallest plant per pot. C) Mean (±SEM) length of the leaves per pot. D) Mean (±SEM) pot area.

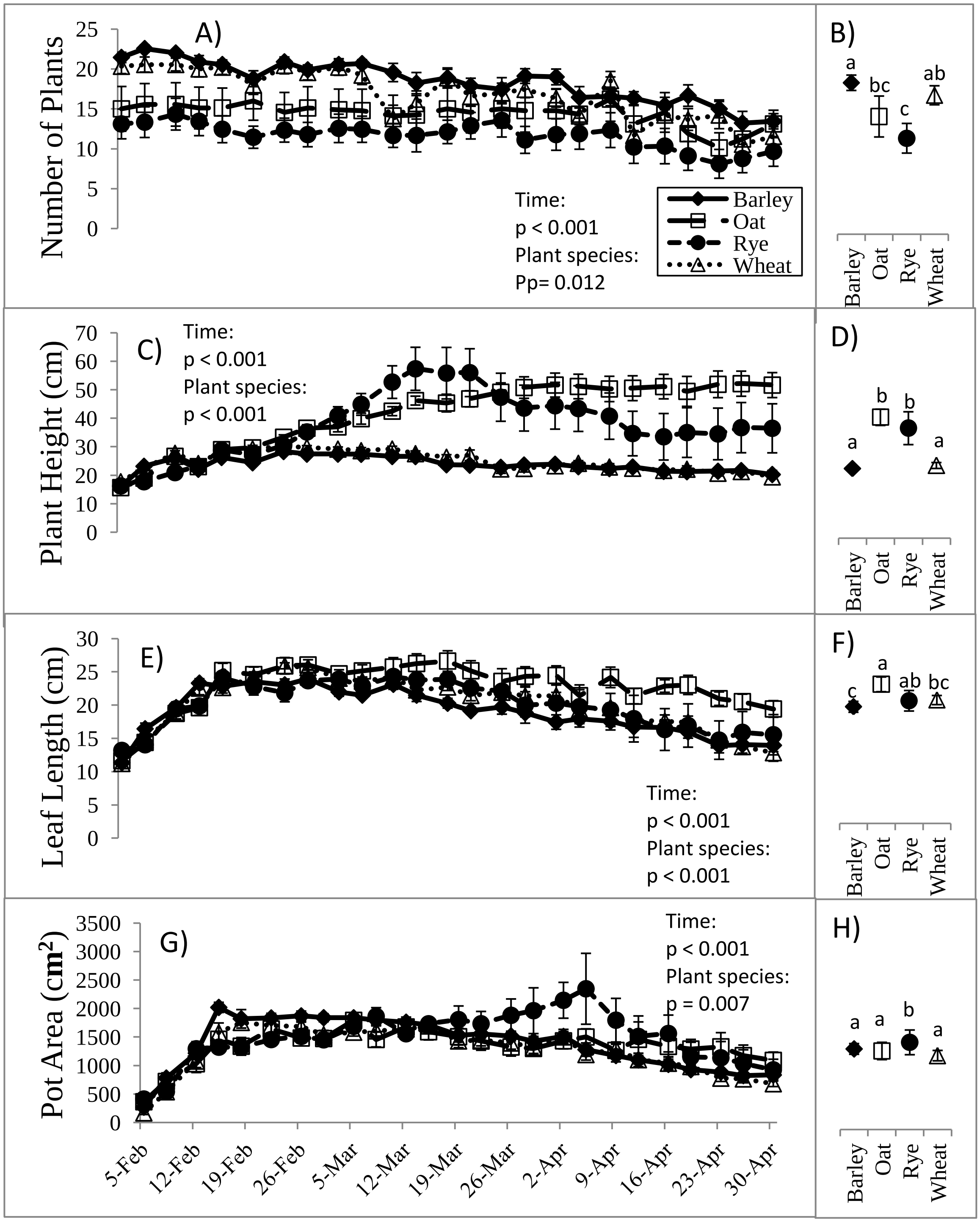

Figure 3. A) Mean (±SEM) number of plants surviving per pot for each plant species: barley, oat, rye, and wheat. B) Main effects for species on number of plants surviving. C) Mean (±SEM) height of the tallest plant per pot. D) Main effects for species on height of the tallest plant per pot. E) Mean (±SEM) length of the leaves per pot. F) Main effects for species on

average leaf length G) Mean (±SEM) plant area. H) Main effects for species on plant area. Main effects with different letters are significantly different ($p < 0.05$).

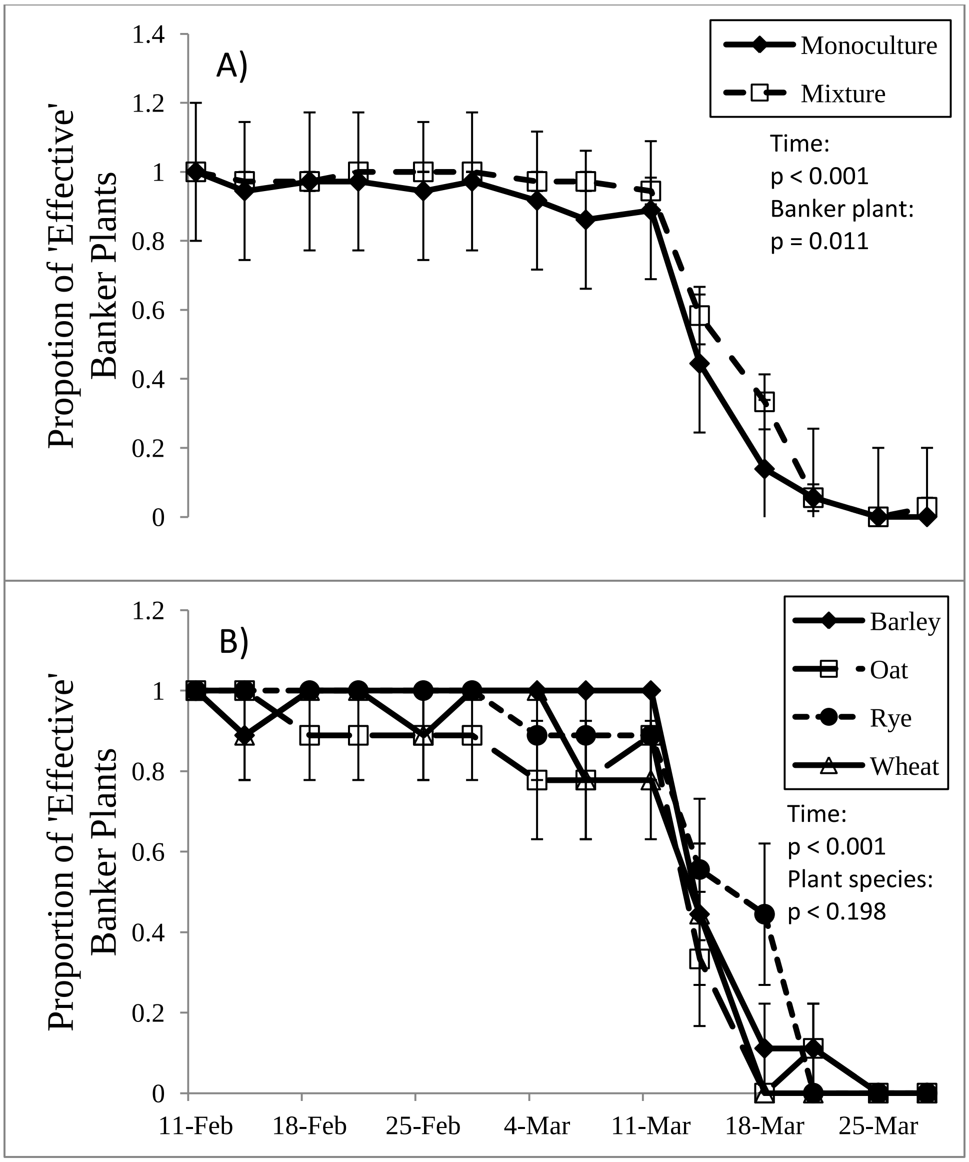

Figure 4. A) Mean (±SEM) proportion of pots which contained an efficient number of aphids, to function as a banker plant, for both monoculture and mixture treatments until plants no longer supported an efficient number of aphids March 21st (5.5 weeks). B) Mean (±SEM) proportion of pots which contained an efficient number of aphids, to function as a banker plant, each of the four monoculture species are shown until plants no longer supported an efficient number of aphids March 21st (5.5 weeks).

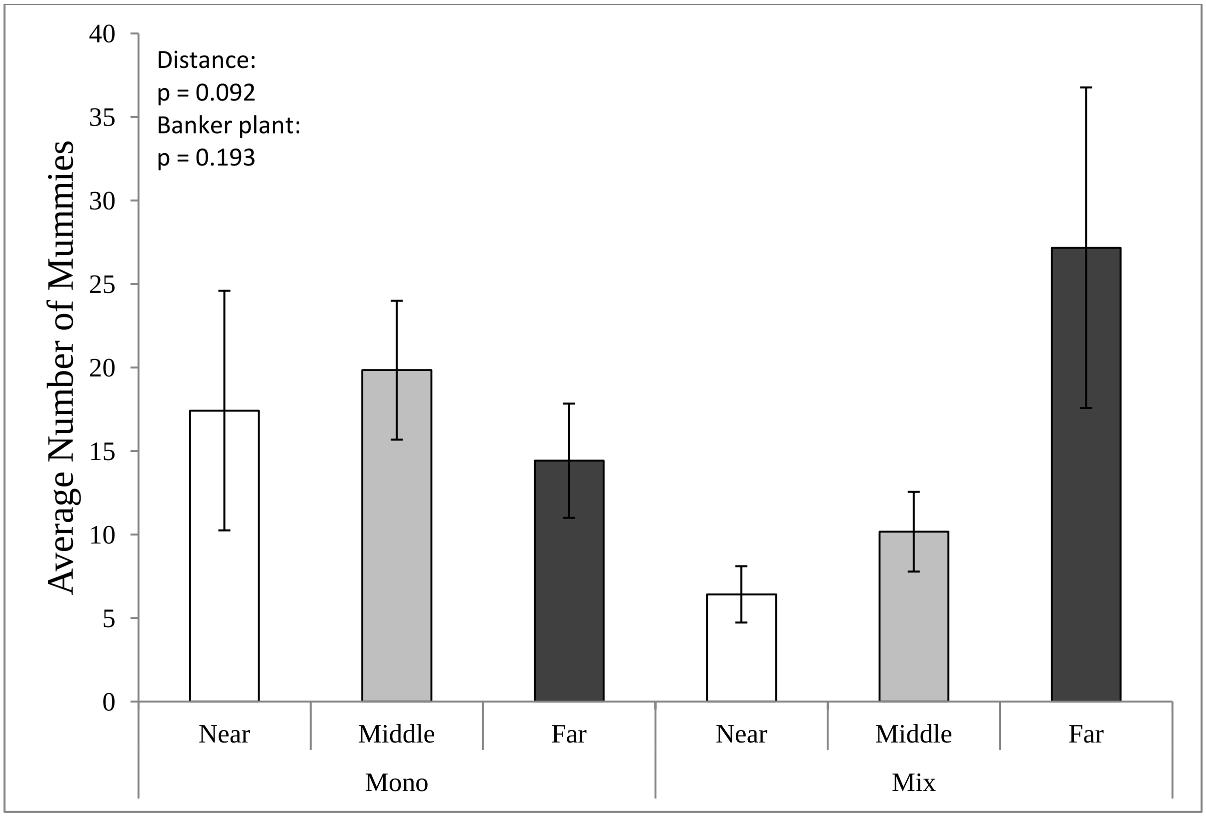

Figure 5. The average number of mummies on each of the three crop plants (±SEM) by distance (top x-axis label) in the presence of both banker plant treatments (bottom x-axis label). Numbers of mummies are displayed as raw numbers for analyses data were log(x+1) transformed.

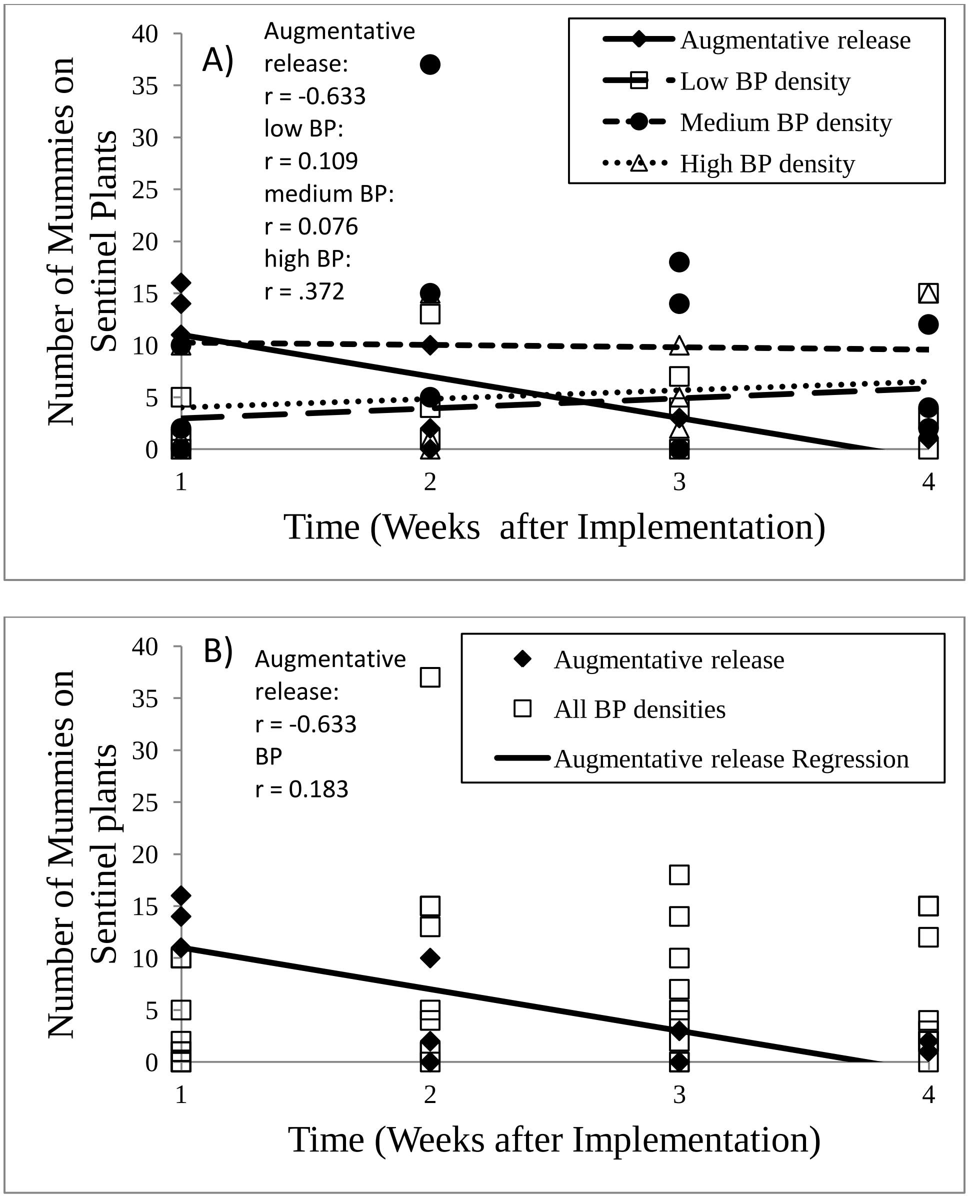

Figure 6. A) Correlation between the number of mummies on sentinel plants and time after initial implementation (in weeks), for each of the three banker plant densities and the augmentative release houses. Different banker plant densities are represented by different symbols. Augmentative release was significant p = 0.027, but none of the banker plant densities were significant at a level of p = 0.05, but trend lines are included for clarity. B) Correlation between the number of mummies on sentinel plants and time after initial implementation (in weeks) for all banker plant treatments pooled together and the augmentative release houses.

CHAPTER 2: Plant diversity effects on parasitoid preference and pest suppression

Introduction

Increasing plant diversity can be an effective conservation biological control strategy in many cropping systems. Plant diversity can increase insect natural enemy abundance, fitness, and efficacy by providing alternative hosts and food resources (Altieri, 1999; Landis et al., 2000; Tahvanainen & Root, 1972). Natural enemies are scarcer in greenhouses than outdoor cropping systems because greenhouse construction excludes them. In addition, greenhouses often contain a monoculture or a low crop diversity which may not provide sufficient resources for natural enemies. Banker plant systems are a conservation biological control strategy for greenhouses which increase plant diversity and provide resources for natural enemies (Frank, 2010; Huang et al., 2011). The goal of a banker plant system is to support a reproducing natural enemy population within a crop to provide pest suppression for an extended period (Frank, 2010).

Banker plants are typically non-crop plants grown within a greenhouse that provide natural enemies with alternative food, such as pollen, or alternative hosts for parasitoids (Frank, 2010; Prado & Frank, 2013; Wong & Frank, 2013). The most common banker plant system consists of grain 'banker' plants infested with *Rhopalosiphum padi* L. (Hemiptera: Aphididae). Since *R. padi* only feed on monocots, they are not pests of most greenhouse crops. *Rhopalosiphum padi* are hosts for the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) commonly used to suppress important greenhouse pests *Aphis gossypii* Glover and *Myzus persicae* Sulzer (Hemiptera: Aphididae). By reproducing on *R.*

padi, A. colemani can maintain a population within a greenhouse even when pest abundance is low. Studies on this system have shown that where banker plants are used parasitism is increased and pest aphid populations are decreased compared to greenhouses without banker plants (Goh et al., 2001).

Plants can affect parasitoid fitness by influencing the fitness of their insect hosts (Barbosa et al., 1982). Plant species or varieties that are poor quality for herbivores due to allelochemicals or low nutritional quality can reduce parasitoid fitness (Campbell & Duffey, 1979; Smith, 1957; Tanga et al., 2013). For example, aphid resistant soybean varieties have been shown to reduce parasitoid development (Ghising et al., 2012). At least eight different grain species have been used as banker plants to maintain *R. padi* (Frank, 2010). The effects of these species on parasitoid fitness are not known but a recent study found that A. colemani populations reared on aphids fed on barley, oats, rye, or wheat expressed a different suite of life history characteristics including size, and sex ratio (Jandricic et al., *in press*). Theory predicts diverse natural enemy communities or phenotypes should increase pest suppression (Cardinale et al., 2007; Snyder et al., 2006). Since *A. colemani* life history characters vary among the grain species which their natal hosts fed on, an interspecific mixture that produces a variety of phenotypes may increase pest suppression by *A. colemani* in greenhouses.

In aphid banker plant systems, using an interspecific grain mixture could have several advantages or disadvantages compared to monoculture banker plants. For example, plant species mixtures can reduce aphid population growth due to associational resistance (Tahvanainen & Root, 1972). This could be advantageous if reducing *R. padi* abundance on banker plants increased the banker plant lifespan, and thus reduced replacement frequency. In addition, *A. colemani* are attracted to denser aphid populations (Jarošík & Lapchin, 2001). Reducing the number of aphids present on banker plants may encourage *A. colemani* to oviposit on the potentially denser pest aphids. On the other hand, if grain mixtures reduce aphid abundance on banker plants, this could reduce the number of hosts available for *A. colemani* and thus reduce parasitoid abundance. Plant diversity can also change plant volatile and visual cues which increase attractiveness to parasitoids (Khan et al., 1997; Mackauer & Michaud, 1996; Shoffner & Tooker, 2013). In our aphid banker plant system this could be an advantage if it helps retain *A. colemani* within the greenhouse when pest abundance is low. However, increased banker plant attractiveness could be a disadvantage if *A. colemani* preferentially oviposit on the banker plants rather than on the crop, reducing pest suppression. Alternatively, since *A. colemani* reared on different grain species have different attributes, such as size, they could increase pest suppression by targeting different aphid instars or sizes (Finke & Snyder, 2008). However, research on the closely related *A. ervi* suggests larger parasitoids are able to overcome aphid defensive behaviors and parasitize aphids of all instars and sizes (Henry et al., 2009). Further, Lin and Ives (2003), suggest *A. colemani* prefer larger aphids which also reproduce the most. Diverse *A. colemani* phenotypes could be a disadvantage because not every individual is unable target all aphid life stages, particularly the largest and most economically important.

Our objective was to determine if interspecific mixture banker plants increase parasitoid fitness and pest suppression compared to monoculture banker plants in the aphid banker plant system. We used greenhouse experiments to determine if mixture banker plants (1) affect *R. padi* and *A. colemani* production; (2) increase *A. colemani* preference for *R. padi* on banker plants compared to *M. persicae* on the crop; and (3) increase *A. colemani* pest suppression and fitness. Based on these results we will determine if growers should be advised to use mixture banker plants over the traditional monoculture banker plants.

Methods

2.1 Study System

For all experiments, we used Black Pearl pepper plants (*Capsicum anuum* L. ‘Black Pearl’) infested with the pest aphid *M. persicae* as crop plants. We propagated black pearl pepper plants from cuttings. We cut source plants roughly 5 cm below the bud. Then we dipped cut tips into “Rhizopon AA Dry Powder Rooting Hormone #1” (Active ingredient: 0.1% 3-Indolebuteric acid) (Earth City, MO*)* and potted them into a sifted Fafard 2P mix (Agawam, MA). We planted cuttings in 48 cell trays (56cm by 25.5cm tray), and allowed them to root for 6 weeks before we transplanted each into separate 15.2cm-diameter pots containing Fafard 2P soil mix and 8.86g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer (Marysville, OH) per pot. We only used plants between 25cm and 40cm tall.

We maintained aphid colonies in the laboratory from field collected aphids. Our *M. persicae* were reared on Black Pearl pepper plants. Our *R. padi* colonies were reared in cages containing monoculture and mixture pots of the same grain species and cultivars used in experiments (Table 1). We originally purchased *Aphidius colemani*, from Koppert Biological (Howell, MI); and then maintained them in colony in cages with *R. padi* on the same monoculture and mixture grain plants as we used in experiments. We kept all colonies in separate 60 x 60 x 60 cm BugDorm cages (BugDorm Store; Taipei, Taiwan) for two years in a greenhouse receiving ambient light with temperatures ranging from approximately 18.5° C to 34.5° C depending season.

2.2 Effect of interspecific grain mixtures on aphid and parasitoid population growth

We conducted a greenhouse experiment to determine how grain monocultures and mixtures affect *R. padi* abundance and the total number of *Aphidius* mummies produced during a four week interval. The monoculture treatment consisted of 4 grain species. Within each species we used 3 different cultivars so the effect of species was not determined by a single cultivar. The species and cultivars used were barley, *Hordeum vulgare* L. (‘Price’, ‘Thoroughbred’, and ‘Nomni’), oat, *Avena sativa* L. (‘Cat Grass’, ‘Brooks’, and ‘Rodgers’), rye, *Secale cereal* L. (‘Matt time’, ‘Wrens Abrozzi’, and ‘AGS 104’), and winter wheat, *Triticum aestivum* L. (‘Roane’, USG 3209/Jaypee’, and ‘Neuse’) (Table 1). We planted three replicate pots of each cultivar of each plant species. This provides 36 pots of the monoculture treatment to compare the overall effects of growing banker plants in monocultures compared to mixtures. It also provided 9 pots of each species within the monoculture treatment. The mixture treatment was made up of 12 unique four species mixes, containing one cultivar from each of the four species, used in the monoculture treatment (n = 3 each), planted in equal proportions (6 seeds each) for a total of 36 pots. We planted all treatments with 24 seeds unsystematically arranged in 15.2 cm-diameter pots with Fafard 2P soil mix (Agawam, MA) and 8.86g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer (Marysville, OH).

We unsystematically placed the pots onto two 2.4 x 1.2 m greenhouse bench sections arranged in 5 rows with 14 or 15 pots per row. Pots were staggered with 15cm diagonally between each. Eighteen days after planting we added 30 *R. padi* aphids of mixed instars to each pot. We did not release any parasitoids for this experiment but our plants were uncaged and exposed to local parasitoids. We counted aphids and parasitoids (mummies) in each pot twice per week for four weeks. Aphid and mummy counts were cumulative and represent the total number of aphids and mummies produced by a banker plant. Mummy counts were continued for one more session (3 days later) to include the most recent aphids converted to mummies.

We used two-way repeated measures ANOVA to determine the independent variables, banker plant treatment (monoculture and mixture), days after introduction of *R. padi*, and their interaction affected dependent variables of cumulative *R. padi* and mummy abundance during the four week effective banker plant duration. Days after introduction of R. padi were the repeated measure. The subject was pot nested within treatment (1-36), which was also included as a random variable. Within the monoculture treatment we used two-way repeated measures ANOVA to determine how the independent variables banker plant species (barley, oat, rye, and wheat), days after introduction of *R. padi* and their interaction affected the dependent variables cumulative *R. padi* and mummy abundance. Days after introduction of *R. padi* were the repeated measure. The subject was pot nested within species (1-9), which was also included as a random variable. We further analyzed significant ANOVA results with pair wise comparisons using Tukey's HSD. Data were not normally distributed so we log(x+1) transformed the number of aphids and mummies before analysis. We performed these statistical analyses in SAS (version 9.2) using the MIXED procedure.

2.3 Mixture banker plant effects on A. colemani host preference

To determine if mixture banker plants cause a change in *A. colemani* host preference between *R. padi* and *M. persicae* we performed a two x two factorial choice assay. We crossed two *A. colemani* rearing habitats, *M. persicae* on pepper and *R. padi* on grain, with two banker plant treatments, monoculture or mixture. We conducted this experiment in 48, 61 x 61 x 61cm cages, built using PVC pipe and organza, each of which contained one crop plant and one banker plant. Each cage was assigned to one of the four treatment combinations, resulting in 12 possible replicates of treatment combination. We infested crop plants and banker plants with 30 *M. persicae* and *R. padi* respectively. Two days later we released one female parasitoid into each cage. Three hours after releasing the parasitoids we collected them from their cages using an aspirator. In cages where we could not find the parasitoid we hung a yellow sticky trap for 24 hours to collect the parasitoid. If no parasitoid was recovered from a cage after 24 hours it was not included in the analysis. One week after the release and collection of the parasitoids we inspected the crop and banker plants and recorded the number of mummies on each. If no parasitism occurred cages were not included in the analysis. This experiment was repeated twice, resulting in 24 possible replicates for each of the four treatment combinations.

We used 2-way ANOVA to determine how the independent variables natal habitat (*M. persicae* on pepper and *R. padi* on grain), banker plant treatment (monoculture and mixture), and the interaction affected the dependent variable of where and how often *A. colemani* oviposited. Time block, location in the greenhouse, and collection method (aspirator 3-hour or sticky card 24-hour) were included as random variables. Data for number of mummies were not normal, so we square root transformed them before analysis. We performed these statistical analyses in SAS (version 9.2) the MIXED procedure.

2.4 Effects of banker plant mixtures on Aphidius colemani pest suppression and fitness

To compare the overall efficacy of monoculture and mixture banker plants in a cage experiment we used two treatments monoculture and mixture banker plants as in section 2.3 and one "industry control" of one augmentative release of *A. colemani* with no banker plant but otherwise treated the same as the monoculture and mixture treatments. We used 61 x 61 x 61cm organza cages each containing one black pearl pepper crop plant and one of the banker plant treatments. For this experiment we had 12 monoculture (3 cultivar of each of the four species) and12 mixture cages (each of the 12 mixture combinations), and 12 augmentative cages for 36 cages total. On 5 October 2012 we planted banker plants contaminated with *R. padi* of various sizes and instars. To standardize these grains, we trimmed each to a height of 10cm and aphids were removed until roughly 30 remained on 8 November 2012. One day prior to the start of the experiment we placed 30 *M. persicae* on the crop plants. Parasitoids were released into cages via petri dishes placed in the center of each cage. Parasitoids were used directly from Koppert Biological, the first four cages of each treatment received ten adults, and the remaining eight cages of each treatment received 20 mummies at the start of the experiment, 9 November 2012. We added parasitoids to cages sequentially; monoculture 1, mixture 1, augmentative 1, monoculture 2, mixture 2, augmentative 2, etc.

Ten, twenty, and twenty-seven days after releasing parasitoids, we counted the number of aphids and mummies on each plant (19 November 2012, 29 November 2012, and 6 December 2012). The final count was made seven days after the previous count instead of ten days because health of several banker plants was declining. We used the number of *M. persicae* on the crop plant as a measure of pest suppression. *Rhopalosiphum padi*, mummies on banker plants, and mummies on the crop were also recorded in order to determine how monoculture or mixture banker plants affected the density dependent response by *A. colemani*. We could not readily distinguish between eclosed and non-eclosed mummies or remove eclosed mummies without disturbing the plants and aphids. Therefore we counted the total number of mummies on each sampling date and estimated new mummies by subtracting mummies from the previous count.

After completion of the last count, we collected mummies (when present) from each banker plant and each crop plant separately. Mummies were kept in petri dishes for 10 days until adults' eclosed, almost twice the average eclosion time of 5-6 days (Kalule and Wright, 2005). We determined the sex of each parasitoid and measured hind tibia length as a proxy of adult parasitoid size (Nicol & Mackauer 1999).

We used a two-way ANOVA to determine how the independent variables of banker plant treatment (monoculture and mixture), days after parasitoid release, and their interaction affected the dependent variable of the number of *M. persicae*. These data were not normal so we square root transformed them for analysis. Whether cages received adults or mummies on the initial release was included as a random factor, after there was not a significant effect when the model included it as a fixed effect. To determine if the percentage *M. persicae* in a cage was related to the percentage of mummies on the crop within a cage, we used separate Spearman's correlation for monoculture and mixture banker plant treatments on each of the three data collection days, control cages were not included in correlation analyses because 100% of the in cage aphids and mummies were *M. persicae*.

For each banker plant treatment we combined and summed the frequency of females wasps from each plant and used a Chi squared test to calculate the differences between the cage totals. We analyzed size for emerging parasitoids collected off of banker plants and crop plants, but since the controls did not have banker plants we could not compare the size of females collected on banker plants to the size of females on crop plants. We used separate ANOVA to analyze the effect of banker plant treatment on size of parasitoids emerging banker plants and crop plants. We performed these statistical analyses in SAS (version 9.2) using the MIXED procedure, CORR procedure, the FREQ procedure, and again the MIXED procedures respectively.

Results

3.1 Interspecific grain effects on aphid and parasitoid population growth

There was not a significant main effect of banker plant treatment on *R. padi* or mummy production during (*R.padi*: $F_{1, 70} = 0.66$, $p = 0.420$ and mummy: $F_{1, 70} = 0.17$, $p = 0.684$ respectively) (Fig. 1). There was a significant effect of day in both cases (*R.padi*: $F_{7, 490} = 1356.46$, $p < 0.001$ and mummy: $F_{7, 490} = 1800.06$, $p < 0.001$), as cumulative *R. padi* and cumulative mummy productions increased over time. There was not a significant interaction between plant mixture and day on either *R. padi* or mummy production (*R.padi*: $F_{7, 490} = 0.16$, $p = 0.992$ and mummy: $F_{7, 490} = 0.90$, $p = 0.503$).

Within monoculture plat species significantly affected *R. padi* production ($F_{3, 32} = 4.47$, $p = 0.010$). Rye produced significantly more *R. padi* than any of the other species (rye-barley: $t_{32} = 2.47$, $p = 0.019$; rye-oat: $t_{32} = 3.45$, $p = 0.002$; and rye-wheat: $t_{32} = 2.68$, $p = 0.012$) (Fig. 2). There was also a significant effect of plant species on mummy production ($F_{3, 32} = 5.81$, $p = 0.003$). Rye produced significantly more total mummies than barley or oat. Wheat also produced significantly more total mummies than oat (rye-barley: $t_{32} = 2.84$ $p = 0.008$; rye-oat: $t_{32} = 3.93$, $p < 0.001$; wheat-oat: $t_{32} = 2.47$ $p = 0.019$) (Fig. 2). There was a significant effect of day for both *R. padi* and mummy production (*R.padi*: $F_{7, 224} = 549.92$, $p < 0.001$, mummy: $F_{7, 224} = 853.54$, $p < 0.001$) as *R. padi* and mummy production increased over time. There was no significant effect of the banker plant by day interaction for either *R. padi* or mummy production (*R.padi*: $F_{21, 224} = 1.53$, $p = 0.070$ and mummy: $F_{21, 224} = 1.08$, $p = 0.372$).

3.2 Mixture banker plant effects on Aphidius colemani host preference

There was no significant effect of rearing habitat, banker plant treatment, or their interaction on the percent of parasitism of *M. persicae* on the crop ($F_{1, 54} = 2.95$, $p = 0.092$; $F_{1, 54} = 1.59$, $p = 0.213$, and $F_{1, 54} = 0.00$, $p = 0.953$ respectively) (Fig. 3). There was also, no significant effect of rearing habitat, banker plant treatment, or their interaction on the number of mummies on the crop ($F_{1, 54} = 2.46$, $p = 0.123$, $F_{1, 54} = 2.08$, $p = 0.155$, and $F_{1, 54} = 0.00$, $p = 0.952$) (Fig. 3).

3.3 Effects of banker plant mixtures on Aphidius colemani pest suppression and fitness

There was not a significant effect of banker plant treatment on *M. persicae* abundance during the 27 days of the experiment ($F_{2, 92} = 2.48$, $p = 0.089$) (Fig. 4). There was a significant effect of day, as *M. persicae* abundance increased and decreased over time, but there was not a significant interaction of banker plant treatment and day (day: $F_{2, 92} = 14.40$, p

< 0.001 and treatment*day: $F_{4, 92} = 1.06$, $p = 0.381$). The percentage *M. persicae* in a cage was positively correlated with the percentage of mummies on the crop in a cage. This correlation was stronger in the monoculture banker plant treatment than mixture banker plant treatment for each day (10: monoculture N = 11, p = 0.020, r = 0.684, mixture N = 11, p = 0.153, r = 0.462; 20: monoculture N = 11, p = 0.009, r = 0.740, mixture N = 11, p = 0.044, r = 0.614; 27: monoculture N = 11, p = 0.005, r = 0.774; mixture, N = 11, p = 0.013, r = 0.716 Fig. 5). There was a stronger correlation between percentage of *M. persicae* in a cage and the percentage mummies in a cage on the crop, for the monoculture treatment compared to the mixture treatment.

For the per cage totals (both plants in each cage) we found a significant effect of treatment on frequency of females. The mixture treatment had the highest female frequency followed by monoculture, and then the control (overall $\chi^2 = 44.34$, $p < 0.001$, monoculture vs. control $\chi^2 = 27.85$, $p < 0.001$, mixture vs. control $\chi^2 = 43.18$, $p < 0.001$, and monoculture vs. mixture $\chi^2 = 4.04$, $p = 0.044$) (Fig. 6).

There was a significant main effect of banker plant treatment on female parasitoid size and on parasitoids collected on crop plants ($F_{2, 181} = 30.70$, $p < 0.001$). Parasitoids collected from crop plants were significantly larger in monoculture cages than either other treatment, and parasitoids from crop plants in mixture cages were the smallest of all three treatments (mixture-control: $t_{181} = -4.83$, $p < 0.001$, mixture-monoculture: $t_{181} = -7.70$, $p < 0.001$, and monoculture-control: $t_{181} = -2.37$, $p = 0.019$). There was no significant main effect of banker plant treatment on female parasitoids size, of parasitoids collected off banker plants ($F_{1, 116} = 0.28$, $p = 0.595$).

Discussion

We predicted associational resistance would reduce the number of *R. padi* produced on banker plants in mixtures compared to grown in monoculture (Tahvanainen & Root, 1972) and that mixtures would be more attractive to *A. colemani.* In the open bench experiment we did not find differences in numbers of aphids or cumulative mummies between monoculture and mixture treatments, but there were differences in *R. padi* and mummy production between species in our monoculture treatment. Rye produced the most *R. padi* and mummies while oat produced the fewest *R. padi* and mummies. Our results were similar to Jandricic et al. *in press*, in that in both studies oat had one of the smallest aphid and mummy populations. The total number of parasitoids released is a major factor in determining the success of augmentative releases (Collier & Van Steenwyk, 2004; Crowder, 2007). As such, optimal banker plant species should produce as many parasitoids as possible over their effective duration, and our studies suggest that rye banker plants may be preferable to the other species we tested.

For each banker plant species in the open bench experiment there was a positive correlation between *R. padi* and mummy production, which was expected as *A. colemani* oviposit based on host density (Jarosik & Lapchin, 2001). We also observed *A. colemani* displaying a density dependent response in our pest suppression study, where the percentage of mummies on the crop in a cage increased as the percentage of *M. persicae* in a cage increased. Correlations in banker plant mixtures were not as strong as the monoculture treatment, which suggests something was drawing parasitoids in the mixture treatment away from the *M. persicae*. One potential explanation for this could be more or different volatiles given off by the mixture banker plants (Khan et al., 1997). However, in our preference experiment the number of aphids on banker plants and crop plants was equal (30). In this case *A. colemani* showed no preference for any of our four treatment combinations. This result is surprising since *A. colemani* often exhibits a preference for their natal host (Bilu et al., 2006; Douloumpaka & Van Emden, 2003; Messing & Rabasse, 1995; Storeck et al., 2000) and findings which suggest *A. colemani* prefer *M. persicae* to *R. padi*, regardless of natal host (Bilu et al., 2006; Ode et al., 2005; Prado & Frank, 2014).

In our 27 day pest suppression experiment, there were no differences in pest suppression between monoculture banker plants, mixture banker plants, or augmentative release. The similarities in pest suppression between monoculture and mixture banker plants are better understood when considering all three experiments together. In our open bench study, we observed similar numbers of aphids and mummies produced on monoculture and mixture grain plants. For our preference study, we observed *A. colemani* displaying no preference for either natal host or banker plant treatment. Considering these results, pest suppression between the monoculture and mixture banker plants should be similar. From our caged study monoculture and mixture banker plant cages produced parasitoids with competing life history characters. Although mixture banker plants produced a higher female frequency, females off pepper plants from monoculture cages were larger. Larger parasitoids generally have increased fitness and egg loads (Sampaio et al., 2008; Visser, 1994). Thus lower female frequency but larger female size in monoculture cages could result in a similar oviposition compared to the higher female frequency and smaller female size in mixture cages. We believe our augmentative cages were able to perform just as well as the banker plant cages due to cage effects. Since aphid numbers on the crop plants remained high and *A. colemani* were unable to disperse from the plant the augmentative cages were able to sustain *A. colemani* populations and suppressed pests without the aid of a banker plant. In open greenhouse experiments, banker plants have proven more effective than augmentative releases (Pickett et al., 2004; Prado & Frank, 2014; Xiao et al., 2011).

Using interspecific mixture banker plants would require growers to acquire a number of different grain seeds. Female frequency is increased but it does not overcome the smaller female size of parasitoids off crop plants or females being drawn more to the banker plants to affect the outcome of pest suppression. Mixture banker plants are neither a benefit nor a detriment to the aphid banker plant system. However, compared to a single augmentative release banker plants offer some potential advantages to parasitoid efficacy such as increased female frequency and the potential to sustain natural enemies for longer periods. These qualities support the use of banker plants as a helpful tool for growers.

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APPENDICES

Monoculture		Mixture			
		Barley	**Oat**	**Rye**	**Wheat**
Barley	Price	Price	Cat grass	Wrens Abrozzi	Roane
	Throughbred	Nomini	Cat grass	Matt time	USG 3209
	Nomini	Nomini	Cat grass	Wrens Abrozzi	Neuse
Oat	Cat grass	Throughbred	Rodgers	Matt time	USG 3209
	Brooks	Price	Brooks	Wrens Abrozzi	Neuse
	Rodgers	Price	Rodgers	AGS 104	Roane
Rye	Matt time	Nomini	Brooks	AGS 104	USG 3209
	Wrens Abrozzi	Throughbred	Cat grass	Wrens Abrozzi	Neuse
	AGS 104	Throughbred	Rodgers	Matt time	Roane
Wheat	Roane	Throughbred	Brooks	AGS 104	Neuse
	USG 3209	Nomini	Cat grass	Wrens Abrozzi	Roane
	Neuse	Throughbred	Brooks	AGS 104	USG 3209

Table 1. Species and cultivars composition for the monoculture and mixture banker plant treatments.

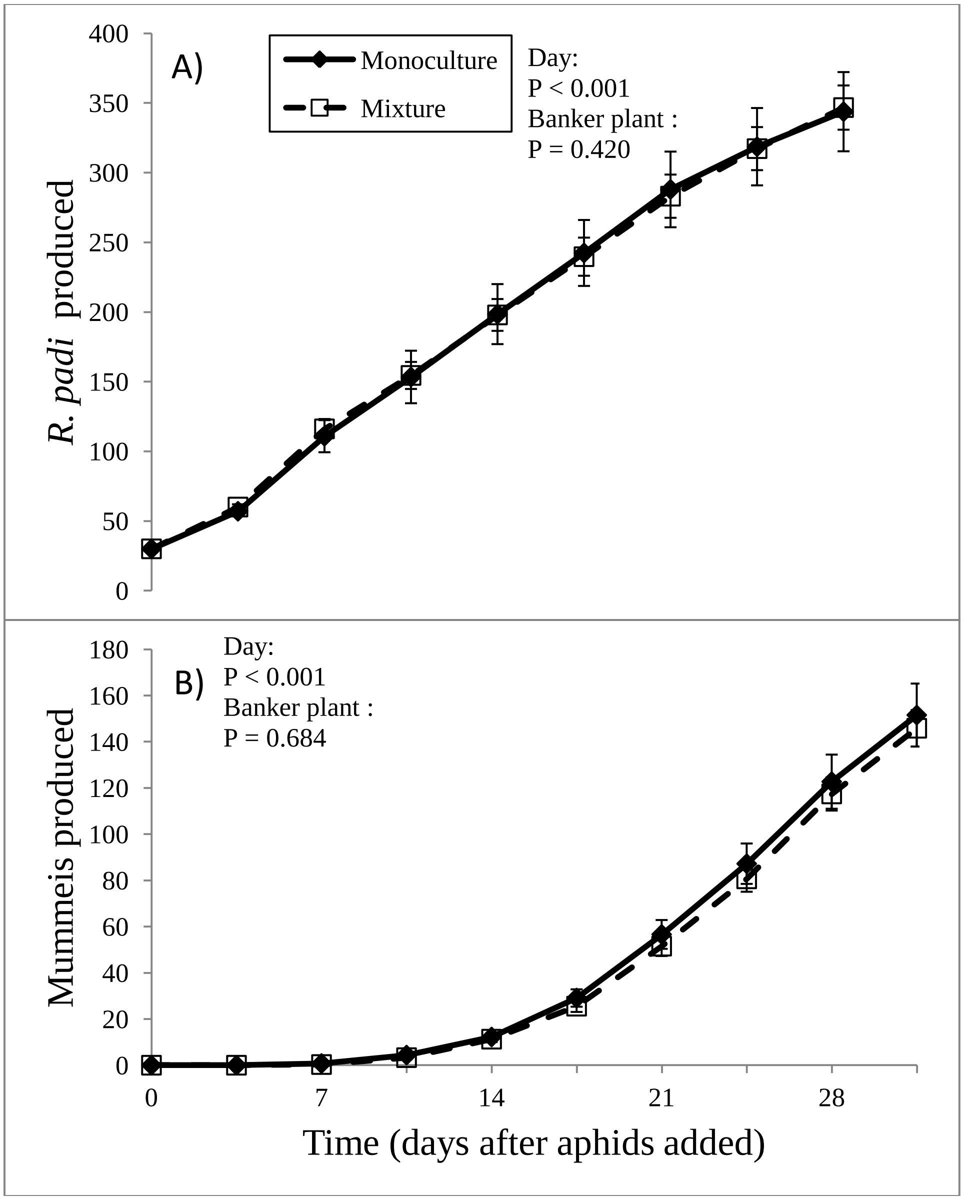

Figure 1. A) Mean (±SEM) number of *R. padi* produced for both monoculture and mixture grain pots for each data collection day. B) Mean (±SEM) number of mummies produced for both monoculture and mixture grain pots for each data collection day.

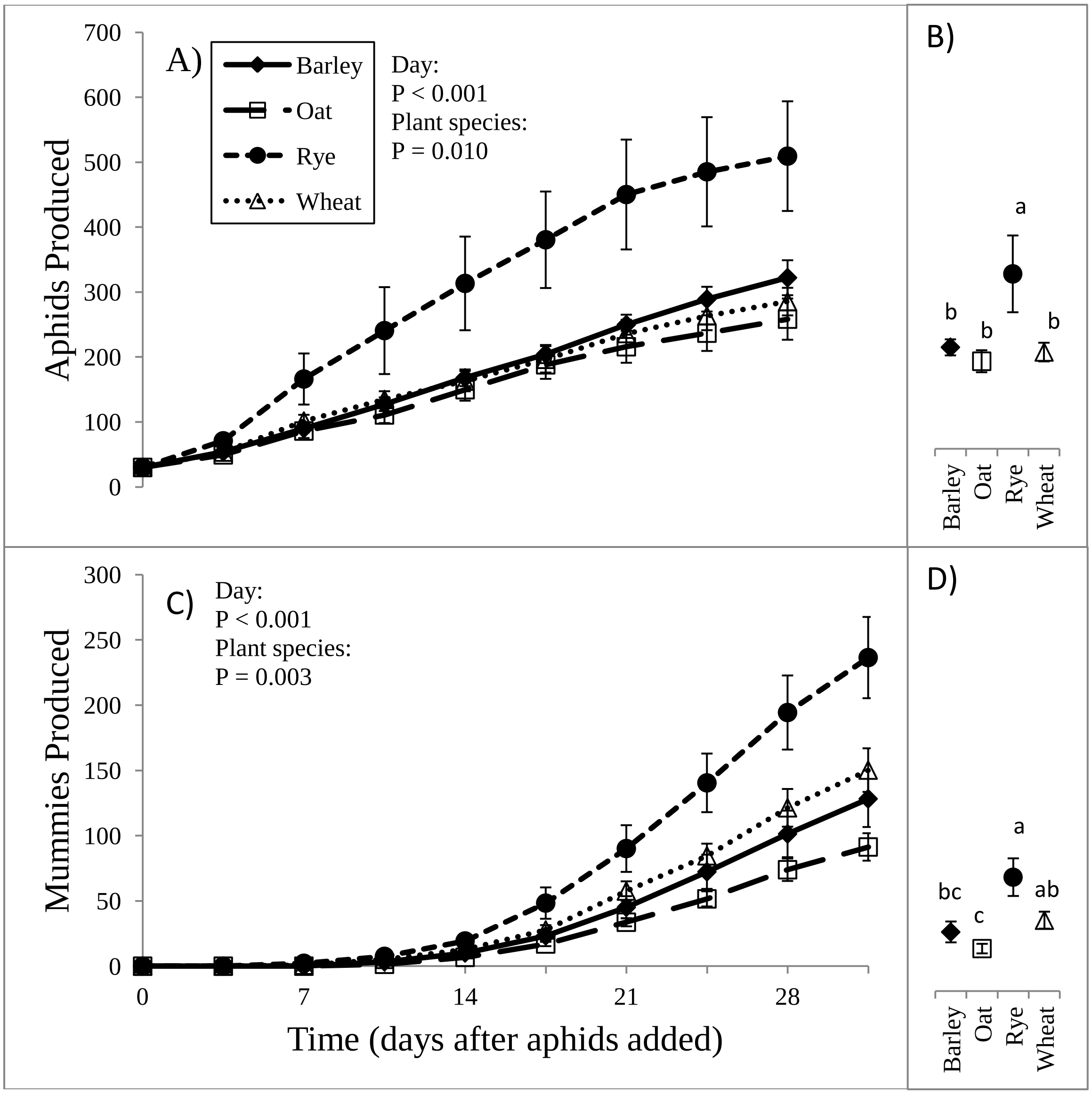

Figure 2. A) Mean (±SEM) total number of *R. padi* produced for each species: barley, oat, rye, and wheat pots for each data collection day. B) Main effects of plant species on *R. padi* using the same symbols as A. C) Mean (±SEM) total number of mummies produced for each species, using the same labels as A. D) Main effects of plant species on mummy production using the same symbols as A. Main effects with different letters are significantly different ($p < 0.05$).

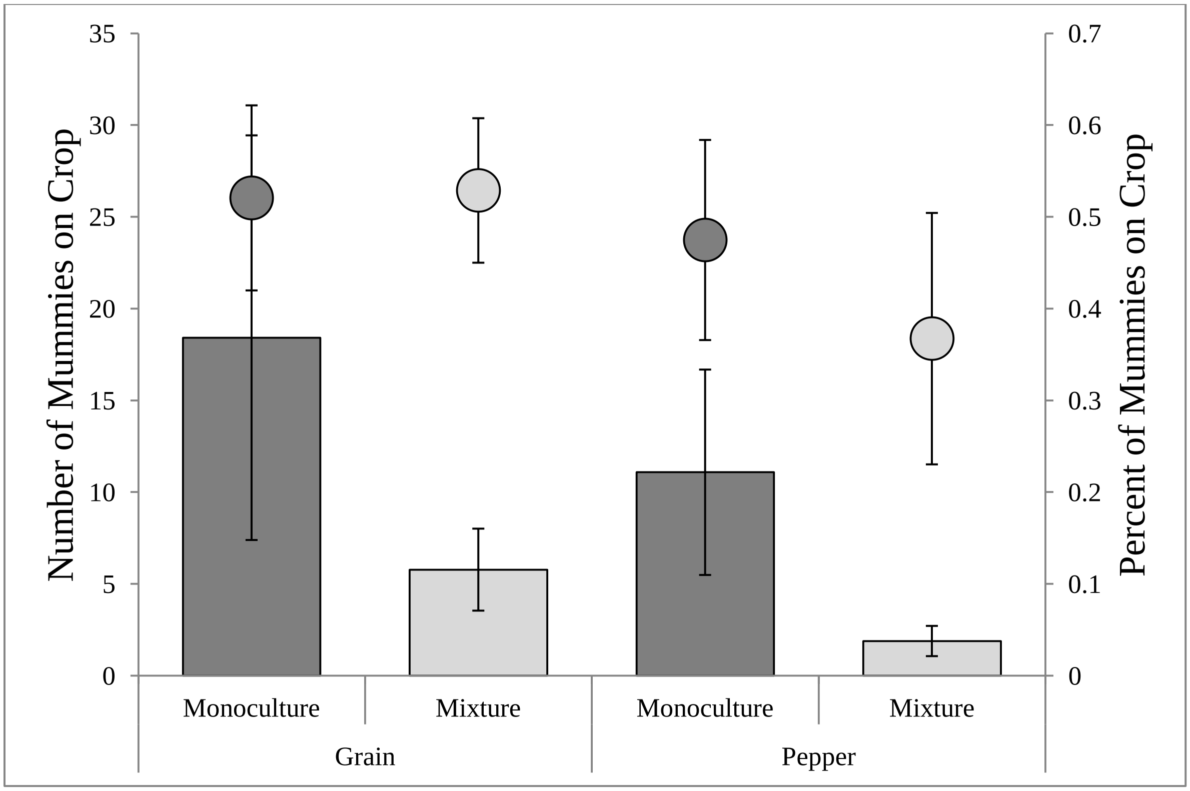

Figure 3. Mean (±SEM) percent of parasitism occurring on the crop (right axis, circles) and mean (±SEM) number of mummies on the crop (left axis, bars) from both natal habitats (bottom x-axis label) and both treatments (top x-axis label). There were no significant differences in the number of mummies or percent of mummies occurring on the crop plant.

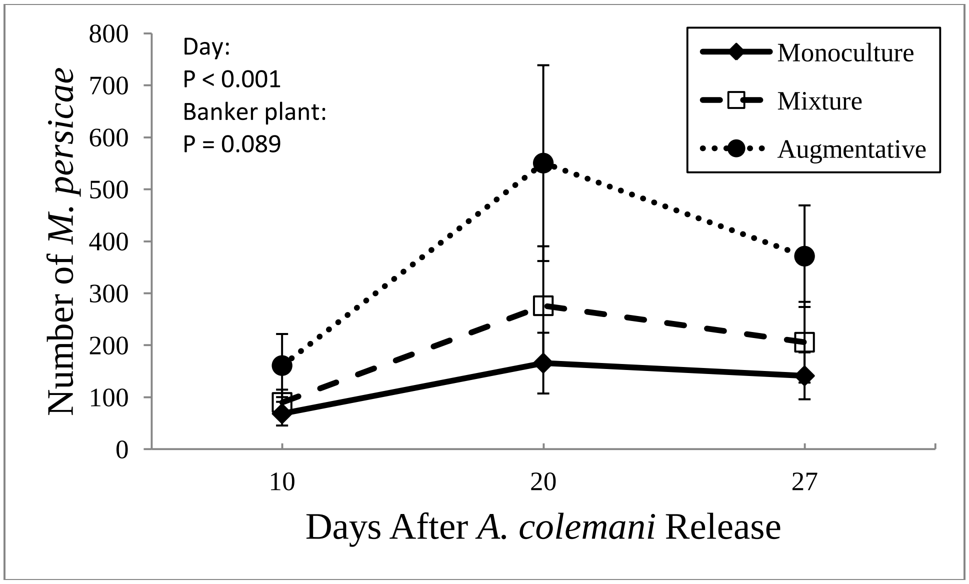

Figure 4. Mean (±SEM) number of pest aphids (*M. persicae*) on crop plants for each of the three treatments monoculture, mixture, and augmentative per collection day.

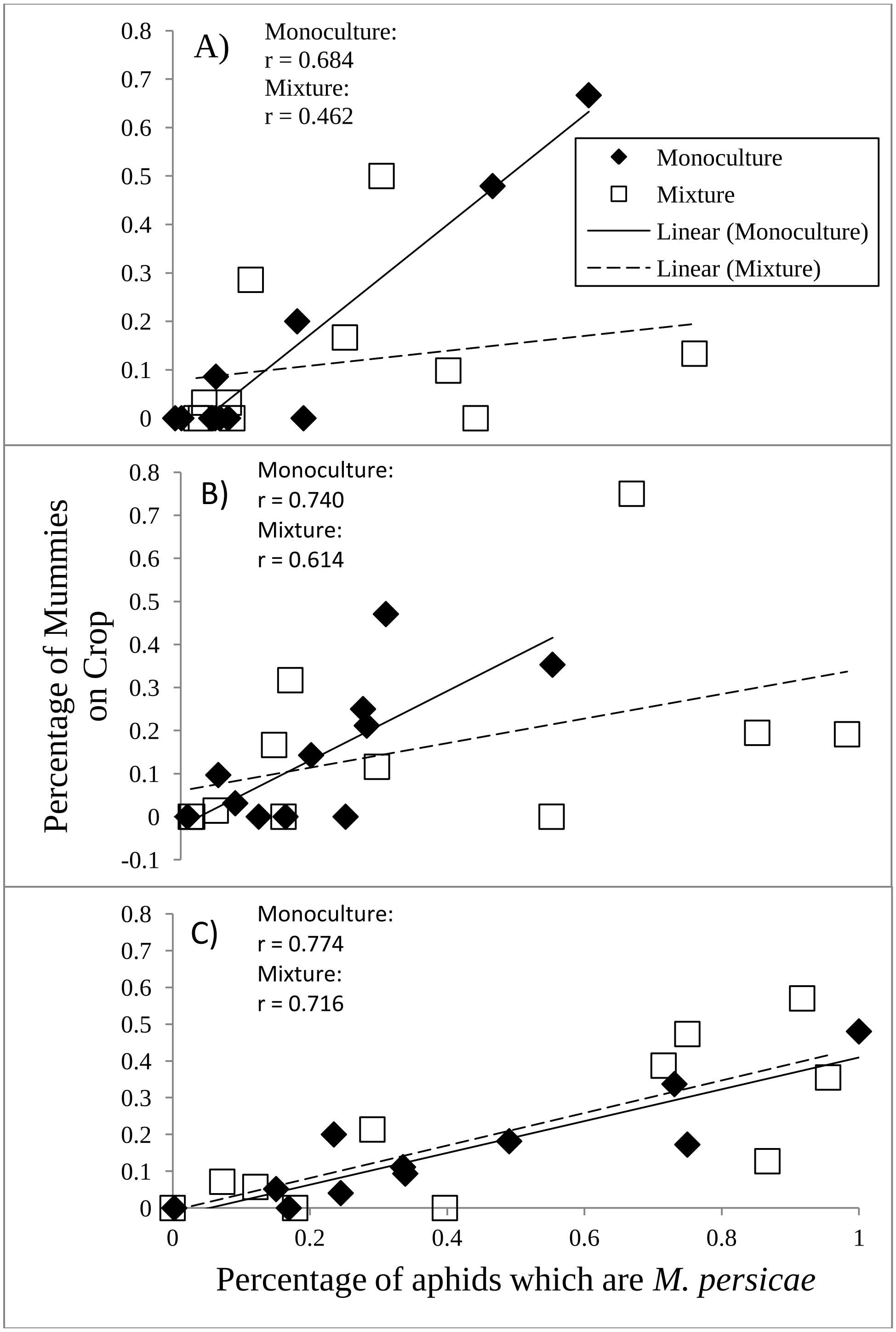

Figure 5. A) Correlation between percentage of *M. persicae* in a cage and percentage of in mummies on the crop plant in a cage 10 days after parasitoid release for both monoculture and mixture treatments. B) 20 days. C) 27 days.

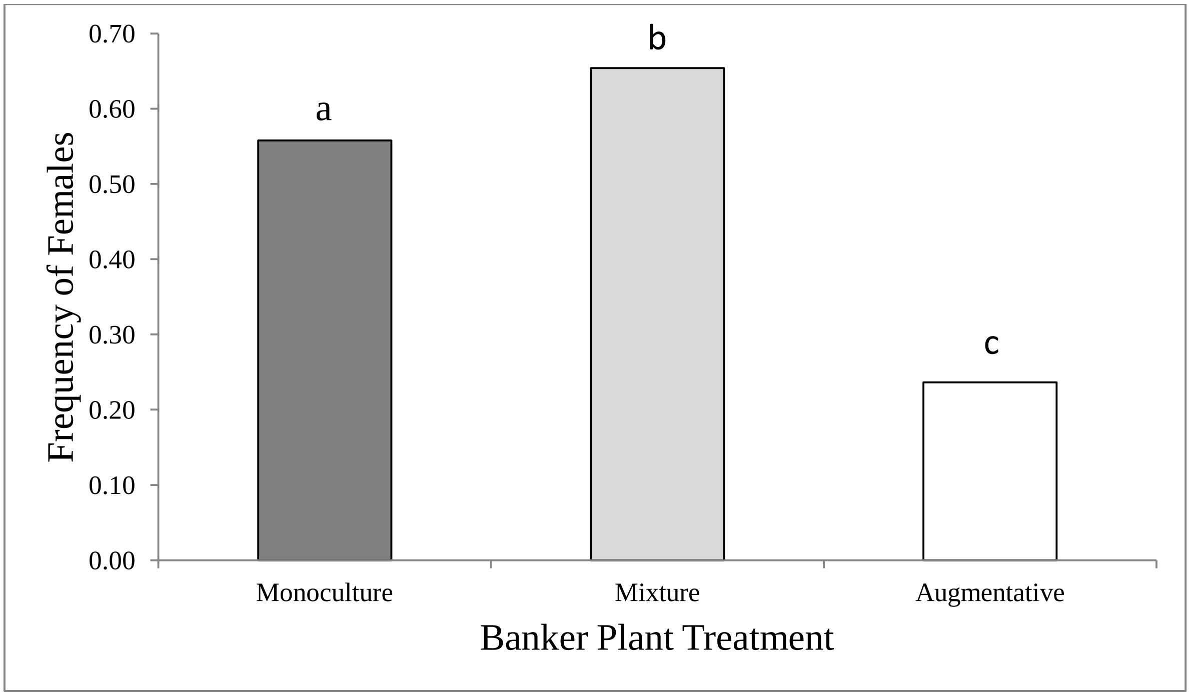

Figure 6. Mean frequency of *A. colemani* emerging from cages of each of the three banker plant treatments, monoculture (dark), mixture (light), control (no color). Includes parasitoids emerged from banker and crop plants for the monoculture and mixture treatments (no banker plant was present in augmentative). Bars with different letters are significantly different at the p = 0.05 level.

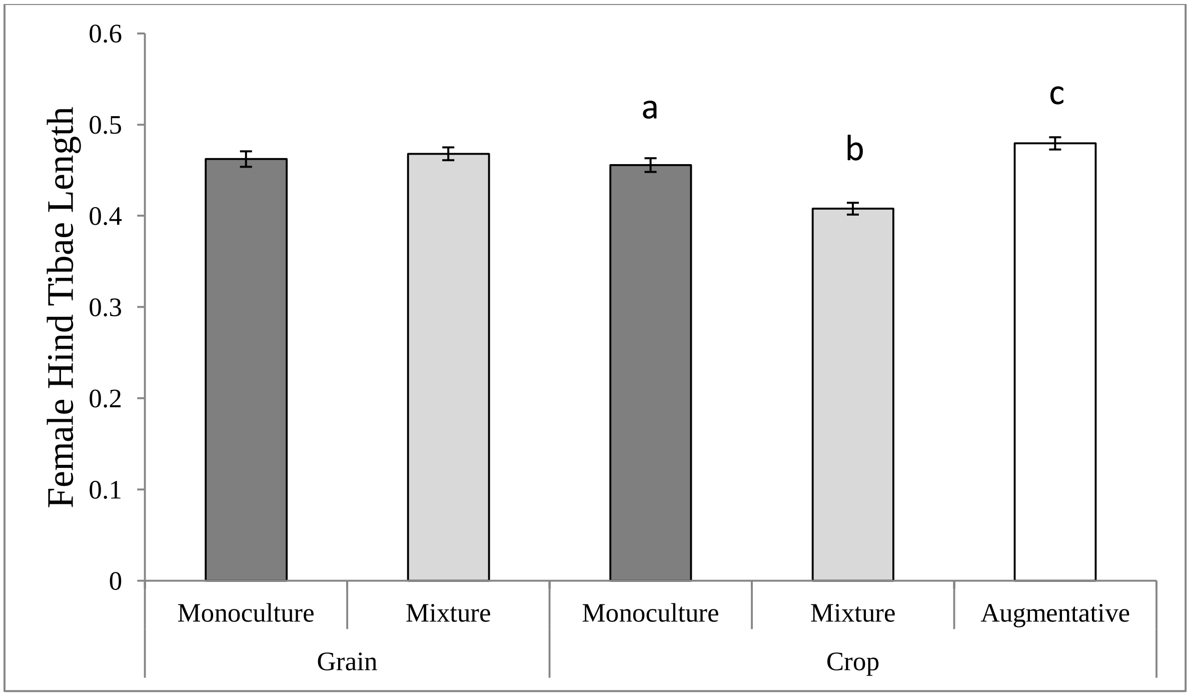

Figure 7. Mean (±SEM) size of female *A. colemani* hind tibae collected from each plant (bottom x-axis label) for each treatment (top x-axis label). Monoculture treatments are represented by the dark bars, mixture the light bars, and augmentative the empty bars. There was no significant difference in female size of parasitoids collected off grain (banker) plants. For females collected off crop plants means with different letters are significantly different at the $p = 0.05$ level. Comparisons between grain and crop plant or combined per cage totals were not possible because augmentative cages did not contain grain (banker) plants.