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Turfgrass Cultivar Diversity Provides Associational Resistance in the Absence of Pest Resistant Cultivars

Ethan M. Doherty,[1,4] Robert L. Meagher,[2] and Adam G. Dale[3]

[1]Entomology and Nematology Department, University of Florida, Gainesville, FL 32611, [2]USDA-ARS CMAVE, Gainesville, FL 32608, [3]Entomology and Nematology Department University of Florida Gainesville, FL 32611, and [4]Corresponding author, e-mail: edoherty13@ufl.edu

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Abstract

Turfgrasses are ubiquitous in urban landscapes and can provide numerous ecosystem services. However, most warm season turfgrasses are produced, planted, and maintained as cultivar monocultures, which may predispose them to herbivore attack and reduce the services lawns provide. Though rarely done, host plant resistance can be used as a strategy to reduce herbivory and preserve beneficial services. Increasing turfgrass cultivar diversity may provide similar or greater benefits through associational resistance, whereas conserving desirable maintenance and aesthetic traits. However, no studies have examined this in warm season turfgrasses. To address this, we evaluated host plant resistance to fall armyworm (*Spodoptera frugiperda* [J.E. Smith] [Lepidoptera: Noctuidae]) in commercially available cultivars of St. Augustinegrass (*Stenotaphrum secundatum* [(Walt.) Kuntz] [Lepidoptera: Noctuidae]) and then investigated if the resistance or susceptibility of *St. secundatum* cultivars carried over in mixed cultivar plantings. Through a no-choice experiment and a limited-choice experiment, we detected no host plant resistance in monocultures of *St. secundatum* cultivars. However, we did find that as cultivar diversity increased, female *Sp. frugiperda* larval weight and herbivory decreased. Additionally, choice tests indicated that larvae prefer less diverse stands of *St. secundatum* cultivars. Interestingly, our results suggest that in the absence of host plant resistance, warm season turfgrass cultivar diversity may reduce herbivore pest fitness and damage. These results demonstrate that warm season turfgrass cultivar diversity may be a viable integrated pest management tool that warrants further investigation.

Key words: cultivar, diversity, *Spodoptera*, *Stenotaphrum*, resistance

Turfgrasses occupy over three times the surface area of any other irrigated crop in the continental United States (Milesi et al. 2005). Moreover, these plants provide human health, economical, and ecological benefits by creating recreational space, improving aesthetics, increasing property values, reducing soil erosion, and dissipating heat (Beard and Green 1994, Beard 2000). Unfortunately, turfgrasses are frequently damaged by herbivorous insects, which reduce plant benefits and introduce environmental risks. For example, pest-damaged lawns do not reduce surface runoff or filter nutrients as efficiently as healthy, actively growing turfgrass, and, therefore, require supplemental maintenance to provide these services (Mugaas et al. 1997, Telenko et al. 2015, Shaddox et al. 2016). Moreover, professional turf managers frequently make calendar-based, cover-spray applications of pesticides to preventively control pests (Potter 2005, Held and Potter 2012). Such indiscriminate use of pesticides is not sustainable and can harm beneficial insects, cause pesticide resistance, and trigger secondary pest outbreaks (Reinert 1974, Terry et al. 1993, Muchovej and Rechcigl 1994, Potter 2005, Peck and Olmstead 2010).

Cultural pest control tactics like pest resistant plants or promoting plant health and defense through proper plant selection are critical components of integrated pest management (IPM) (Quisenberry 1990, Reinert et al. 2004a). When used properly, they can reduce pests, pesticide use, and associated risks (Raupp et al. 1985). For example, Reinert et al. (2004b) found that several cultivars of *Poa pratensis* L. (Poales: Poaceae) were highly resistant to fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), causing over 89% mortality when fed upon. Unfortunately, few insect-resistant warm season turfgrasses are commercially available for residential landscapes in tropical or subtropical climates (Rangasamy et al. 2009a,b). Not only are there few pest-resistant species or cultivars, but urban lawn communities are often dominated by one or a few species (Wheeler et al. 2017), which may predispose them to pest attack and reduce their economic and environmental value.

An alternative tactic to pest-resistant plants is increasing plant diversity to increase a plant community's resilience or resistance

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to pests (Elton 1958, Pimentel 1961, Root 1973, Santamour 2002, Barbosa et al. 2009). Plant diversity can directly affect herbivorous arthropods through diet mixing or by creating associational resistance (Andow 1991, Raupp et al. 2010). Tahvanainen and Root (1972) first described associational resistance as a reduction in a host plant's vulnerability to herbivores due to its proximity to a neighboring plant of a different species. Neighboring plants may obscure the focal plant visually (Rausher 1981), chemically (Schoonhoven et al. 1981), or by other mechanisms (Holmes and Barrett 1997). Root (1973) proposed the resource concentration hypothesis which postulates that more diverse plantings will incur less herbivory than monocultures because herbivores, especially dietary specialists, are less able to find, colonize, and increase to damaging levels in mixed stands containing host and nonhost plants (Tahvanainen and Root 1972, Root 1973). In contrast, diverse plantings may also generate associational susceptibility, where a neighboring plant makes a host more apparent to pests, or facilitates the pest's consumption of a host (White and Whitham 2000, Barbosa et al. 2009). Associational susceptibility may be driven by an increase in diet diversity (Hägele and Rowell-Rahier 1999), if a more diverse plant diet provides nutrients that preferred hosts do not provide in isolation. For example, Kotowska et al. (2010) found that herbivore biomass and survival rate increased with the genotypic diversity of its plant diet.

Warm season turfgrasses dominate urban and residential landscapes in warmer climates like the southern United States due to their heat- and drought-tolerant photosynthetic framework (Brilman 2005). Genotypes of these plant species are selectively bred for qualities like pest resistance, aesthetic quality, and tolerance to environmental stressors (Brilman 2005, Fraser et al. 2012). To conserve these traits, and in the absence of viable seeds, most warm season turfgrasses are produced through vegetative propagation and planted as sod or plugs (Casler and Duncan 2003). Thus, most warm season lawns are composed of genotypic monocultures of cultivated varieties. It is well supported that mixing some cool season turfgrass species or cultivars increases a lawn's tolerance to traffic (Newell et al. 1996) and disease (Dunn et al. 2002). Additionally, Simmons et al. (2011) found that mixing seven warm season grass species increased leaf density and resistance to weed invasion. Despite this, warm season turfgrass species are never intentionally planted as mixtures because planting different species together is likely less marketable and more difficult to produce and maintain.

Fortunately, evidence from agricultural and natural systems suggests that intraspecific diversity can provide pest management and agronomic benefits similar to interspecific diversity (Riihimäki et al. 2005, Tooker and Frank 2012, Grettenberger and Tooker 2016). For instance, Grettenberger and Tooker (2016) found that increasing intraspecific diversity in wheat (*Triticum aestivum* L. [Poaceae: Poales]) reduced aphid [*Rhopalosiphum padi* (L.) (Aphididae: Hemiptera)] body size and reproduction. Moreover, mixing cultivars of the same species is more likely to meet turfgrass consumer and industry standards because species-specific cultural requirements create significant logistic challenges to produce and maintain interspecific mixtures (Tooker and Frank 2012).

To increase the sustainability of urban landscape plant maintenance, we must develop new cultural IPM tactics that reduce reliance on management inputs and promote ecosystem services provided by plants. To date, no studies have documented the relative susceptibility of cultivars of the most common residential warm season lawn species, *Stenotaphrum secundatum* (Walt.) Kuntz, to an important herbivore pest, the fall armyworm (*Sp. frugiperda*). Here, we investigated the effects of common commercially produced *St. secundatum* cultivars on *Sp. frugiperda* life history traits and herbivory. We hypothesized that life history traits would be differentially affected by *St. secundatum* cultivars provided in monoculture. Using the same *St. secundatum* cultivars, we investigated if creating mixtures of two or four cultivars is a viable approach to reducing *Sp. frugiperda* fitness and plant damage. We hypothesized that under no-choice conditions, *Sp. frugiperda* fitness would increase with *St. secundatum* cultivar diversity through diet mixing. In contrast, we predicted that when reared on mixed plantings of *St. secundatum* cultivars, *Sp. frugiperda* fitness would decrease via associational resistance. Finally, based on the resource concentration hypothesis, we predicted that *Sp. frugiperda* host choice would be biased towards monocultures over more diverse plantings.

Materials and Methods

Study Organisms

Warm season turfgrasses in the United States are primarily composed of 10 species within seven genera (Trenholm and Unruh 2005, Haydu et al. 2006). A single species, *St. secundatum*, makes up 70% of lawns (Casler and Duncan 2003) and over 50% of commercial sod produced in Florida, the largest turfgrass industry in the United States (Hodges and Stevens 2010). Importantly, over 80% of *St. secundatum* grown in Florida is a single cultivar, 'Floratam', suggesting that over 170 km^2 of Florida lawns are highly genetically similar (Satterthwaite et al. 2009). We used *St. secundatum* as our host plant species because our results may inform immediate IPM strategies with high economic and environmental impact.

Fall armyworm is a common herbivorous pest of graminaceous plants, including *St. secundatum,* and is a frequently used model organism for ecological research (Erb et al. 2011, Unbehend et al. 2013, Jakka et al. 2014). For this study, we used *Sp. frugiperda* (rice strain) reared at the United States Department of Agriculture, Agricultural Research Service (Gainesville, FL) on a soybean-based 'multiple species diet' (Southland Products, Lake Village, AR) in rearing trays (Frontier Agricultural Science, Newark, DE; model RT32W) at 25°C under a photoperiod of 16:8 (L:D) h. Upon egg hatch, first-instar neonates were moved into growth chambers (Percival Scientific, Perry, IA) maintained at 27°C, 70% RH, and a photoperiod of 14:10 (L:D) h at the University of Florida (Gainesville, FL).

Experimental Design

The most commonly produced and planted *St. secundatum* cultivars in Florida are 'Captiva', 'Classic', 'Floratam', 'Bitterblue', 'Seville', and 'Palmetto'. In 2016, we obtained sod (ca. 40 m^2) of each cultivar from a single certified Florida sod producer (JB Farms, Lake Placid, FL) and planted each as standalone 40 m^2 plots at the University of Florida Plant Science Research and Education Unit (Citra, FL). These plots were used as source material for potted plants (15-cm diameter) kept in a greenhouse for experiments. Potting media was one-part potting soil (SunGro Profession Growing Mix, Fafard 3 and 3B Mixes, Agawam, MA) and one-part pure sand. Plants were watered as needed and fertilized once every 2 wk (Miracle-Gro Water Soluble All Purpose Plant Food, 24-8-16 %N-P-K).

Using the six *St. secundatum* cultivars listed above, we created three treatment groups for *Sp. frugiperda*, referred to henceforth as M1, M2, and M4 (Table 1). The M1 treatment consisted of three replicates of each cultivar planted or provided in monoculture (n = 18). The M2 treatment consisted of all unique combinations of two cultivars from the pool of six, which resulted in 15 unique combinations (n = 15). The M4 treatment consisted of all unique combinations of four cultivars from the pool of six cultivars, which again resulted in 15 unique combinations (n = 15).

Table 1. All M1, M2, and M4 treatment cultivar combinations

M1	M2	M4
'Bitterblue' 1	'Bitterblue'-'Captiva'	'Bitterblue'-'Captiva'-'Classic'-'Floratam'
'Bitterblue' 2	'Bitterblue'-'Seville'	'Bitterblue'-'Captiva'-'Classic'-'Seville'
'Bitterblue' 3	'Bitterblue'-'Floratam'	'Bitterblue'-'Captiva'-'Floratam'-'Seville'
'Captiva' 1	'Bitterblue'-'Classic'	'Bitterblue'-'Classic'-'Floratam'-'Palmetto'
'Captiva' 2	'Bitterblue'-'Palmetto'	'Bitterblue'-'Classic'-'Palmetto'-'Seville'
'Captiva' 3	'Captiva'-'Palmetto'	'Bitterblue'-'Captiva'-'Classic'-'Palmetto'
'Classic' 1	'Captiva'-'Floratam'	'Bitterblue'-'Floratam'-'Palmetto'-'Seville'
'Classic' 2	'Captiva'-'Seville'	'Bitterblue'-'Captiva'-'Palmetto'-'Seville'
'Classic' 3	'Captiva'-'Classic'	'Bitterblue'-'Classic'-'Floratam'-'Seville'
'Floratam' 1	'Classic'-'Seville'	'Bitterblue'-'Captiva'-'Floratam'-'Palmetto'
'Floratam' 2	'Classic'-'Palmetto'	'Captiva'-'Classic'-'Palmetto'-'Seville'
'Floratam' 3	'Classic'-'Floratam'	'Captiva'-'Classic'-'Floratam'-'Palmetto'
'Palmetto' 1	'Floratam'-'Palmetto'	'Captiva'-'Classic'-'Floratam'-'Seville'
'Palmetto' 2	'Floratam'-'Seville'	'Captiva'-'Floratam'-'Palmetto'-'Seville'
'Palmetto' 3	'Palmetto'-'Seville'	'Classic'-'Floratam'-'Palmetto'-'Seville'
'Seville' 1		
'Seville' 2		
'Seville' 3		

The M1 treatment is composed of St. Augustinegrass cultivar monocultures; the M2 treatment is composed of mixtures of two St. Augustinegrass cultivars; the M4 treatment is composed of mixtures of four St. Augustinegrass cultivars.

We used the M1 treatment to evaluate the relative susceptibility of each *St. secundatum* cultivar to *Sp. frugiperda*. Afterward, the effects of *St. secundatum* cultivar diversity were evaluated based on the diversity treatment, rather than the cultivar composition of each treatment replicate.

No-Choice Experiment

To determine if cultivar diet mixing affects *Sp. frugiperda* fitness, we performed a no-choice experiment in growth chambers (Percival Scientific, Perry, IA) maintained at 27°C, 70% RH, and a photoperiod of 14:10 (L:D) h. First, we assigned treatments to individual 4 × 4 × 1-cm cells in rearing trays (Frontier Agricultural Science, Newark, DE) and placed one randomly selected first-instar *Sp. frugiperda* larva into each cell. We assigned one larva to each treatment replicate described above, resulting in 18 M1, 15 M2, and 15 M4 individuals. Next, we provided caterpillars with grass clippings of their respective treatment. Clippings came from *St. secundatum* monocultures planted in pots and maintained in a greenhouse as described above. Clippings in each cell were replaced every 2 d with fresh plant material. For the M1 treatment, larvae were randomly assigned one of the six cultivars and given clippings of that cultivar every 2 d. Caterpillars in the M2 and M4 treatments received clippings of one cultivar at a time in a randomized order, such that each caterpillar in the M2 treatment fed on two different cultivars every 4 d and each caterpillar in the M4 treatment fed on four different cultivars over an 8-d period. Caterpillars were always given more clippings than they could consume within the 2 d. To control for the physical disruption of changing plant material, caterpillars in the monoculture treatment also had their diet replenished every 2 d, but with the same cultivar that was replaced. This experiment was repeated four times, totaling 72 M1, 60 M2, and 60 M4 *Sp. frugiperda* individuals.

To determine the effects of cultivars and cultivar diet mixing on *Sp. frugiperda* fitness, we recorded larval body weight, days to pupation, pupal weight, days to eclosion, and sex. We measured larval body weight (mg) after 9 d of feeding, as it can be an important indicator of fecundity and survival (Berger et al. 2008). Development rate is also important as it can affect the timing and application of pest control efforts, the duration of feeding and associated damage, as well as the rate at which populations can increase. Therefore, we recorded development time from first-instar larva to pupa and to adult for each individual. We also measured sex ratio and survival rate for all treatments since these factors can affect population composition and growth rates.

Limited-Choice Experiment

To conduct a more realistic evaluation of the effects of *St. secundatum* cultivars and cultivar diversity on *Sp. frugiperda* fitness, we designed a greenhouse experiment where we planted each diversity treatment in pots (15-cm diameter) using rooted cuttings of each cultivar equally represented per planting. Cuttings were washed and free of soil before planting, and roots were ~7 cm in length. The M1 treatment was created by potting eight cuttings from the same cultivar at once. To create the M2 treatment, we potted four cuttings from two cultivars simultaneously, and the M4 treatments were created by simultaneously potting using two cuttings from four cultivars together. As with their source pots, soil was composed of one-part potting mix (SunGro Profession Growing Mix Fafard 3B, Agawam, MA) and one-part sand. Plants were watered as needed and fertilized once every 2 wk (Miracle-Gro Water Soluble All Purpose Plant Food, Marysville, OH, 24-8-16 %N-P-K). These plantings mirrored the M1, M2, and M4 treatments used in the no-choice experiment (Fig. 1A).

Plants were trimmed weekly to an ~7.5 cm height to mimic a mowed lawn. As cultivars grow over and under one another within the pots, the location of cultivars within the pots was not tracked. After 3–6 wk of growth, two second-instar larvae were placed into each pot and enclosed within a microcosm. Two larvae were used per microcosm to improve the quality of data obtained, while keeping caterpillar density low so that cannibalism would be unlikely to occur. Microcosms were made of a cylindrical 32 oz supermarket container (10-cm height, 14-cm top diameter; Genpak, Charlotte, NC) with mesh (Casa Collection Organza Fabric, Joann, Hudson, OH) hot-glued in place of the closed end. These containers were adhered to the rim of each pot with Parafilm (Pechiney, Chicago, IL). Microcosms were placed into a 60 × 60 × 60-cm PCV pipe cage covered with mesh (Casa Collection Organza Fabric) and kept within a greenhouse (min: 21°C, max: 43°C).

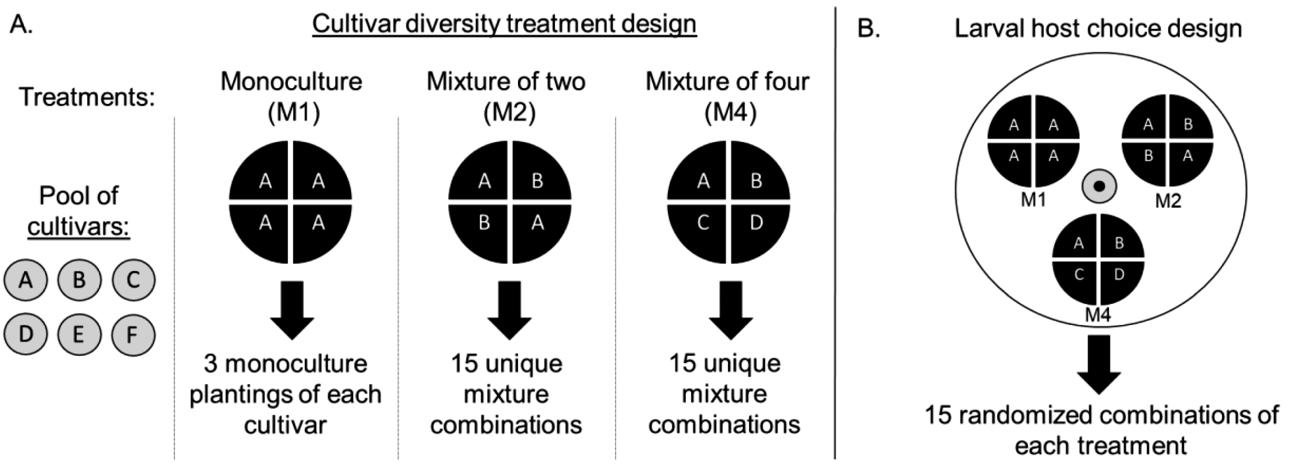

Fig. 1. An illustration of how rooted sprigs from St. Augustinegrass cultivars were organized to create the M1, M2, and M4 treatment pots for the limited-choice and host choice experiments (A). An example of how M1, M2, and M4 pots were organized within buckets for the larval host choice experiment (B).

As in the no-choice experiment, we measured multiple life history traits to determine whether there was an effect of cultivar diversity on insect fitness. Eleven to twelve days after hatching, we measured larval weight by placing individual larvae in weigh boats on a scale. We recorded the number of days to eclosion, sex, and survival for each individual. We also recorded visual estimates of percent herbivory in 10% intervals based on larval chewing damage per pot for each planting 11–12 d after egg hatch as in the planted monoculture experiment described above. Percent herbivory estimated the volume of grass of eaten compared with the amount of grass that would have been present otherwise.

We repeated this experiment four times, resulting in 72 M1, 60 M2, and 60 M4 replicates. A fifth experimental replicate was started, but not completed due to seasonal photoperiod changes drastically delaying eclosion, although larval weight and herbivory were similar to the previous four replicates. Thus, sex ratio, survival rate, and development rate were not recorded for that replicate, only larval weight and percent herbivory at 11–12 d after larval introduction.

Spodoptera frugiperda Host Choice

In addition to effects of *St. secundatum* cultivar diversity on *Sp. frugiperda* fitness, cultivar diversity may also affect insect host choice. To test this, we planted rooted cuttings of each cultivar in 9.5-cm diameter pots as in the previously described limited-choice experiment. This included 15 M1 pots with no single cultivar represented more than three times, and one pot of each unique cultivar combination for M2 (n = 15) and M4 (n = 15) treatments, totaling 45 pots.

To evaluate larval host choice, we randomly selected one pot of each treatment without replacement and placed them into a bucket (30-cm diameter) filled with pure sand, such that the top rim of each pot was flush with the sand and 24 cm below the lip of the bucket (Fig. 1B). Combinations of pots and orientations within the buckets were randomized. Pots were placed at the edges of the bucket equidistant from each other, resulting in 2.5 cm from the center of the bucket to each pot, and 5 cm from pot to pot. We repeated this process until all pots were used across 15 buckets, each containing one pot of each cultivar diversity treatment. Next, we placed 10 third-instar larvae onto the sand in the center of each bucket equidistant from the pots. We then recorded the number of larvae within each planting 10 min, 24 h, 48 h, and 72 h after introduction.

To determine if *St. secundatum* diversity treatment affected *Sp. frugiperda* adult oviposition choice, we used the same treatment arrangement as in the larval host choice, however, instead of buckets, each set of three pots (15 cm diameter) were placed 33 cm apart in a 60 × 60 × 60-cm PCV pipe cage covered with white mesh (Casa Collection Organza Fabric) and kept within a greenhouse (min: 21°C, max: 43°C). We placed 10 recently eclosed adults (5 males, 5 females) into the center of each mesh cage. The number of moths were chosen for parity with similar experiments (Meagher et al. 2004, 2011). After 72 h, we recorded the number of egg masses on each treatment, weighed each mass, and calculated total egg mass weight per pot. This experiment and the larval host choice experiment were each repeated three times.

Statistical Analyses

To determine the effects of *St. secundatum* cultivars in monoculture on *Sp. frugiperda*, we conducted analyses of variance (ANOVA) comparing life history trait measures between cultivars in the M1 treatment for the no-choice and limited-choice experiments (JMP Pro 13.1, SAS institute). For all analyses of the effects of cultivar diversity, we treated each cultivar in monoculture and each unique cultivar combination of two and four as single treatments, M1, M2, and M4, respectively. We used ANOVA to determine the effect of cultivar diversity on each measure of fitness during the no-choice and limited-choice experiments. Experimental replicate was used as a random covariate in all analyses. We used logistic regression and χ^2 to test for effects of cultivar diversity on sex ratios. To detect effects of *St. secundatum* diversity level, time, and their interaction during the host choice experiments, we conducted repeated-measures ANOVA on the number of larvae present per treatment at each time interval. Paired t-tests were performed for post-hoc pairwise means comparisons of host choice for each diversity treatment at each time point. We also used ANOVA to determine the effect of diversity treatment on oviposition measures (egg mass quantity, average egg mass weight, and total egg mass weight). When ANOVA identified a significant main effect, we used Tukey's HSD post-hoc tests for pairwise means comparisons to detect differences between treatment means. Alpha was set at 0.05 for all analyses. All data are presented as means ± SEM.

Results

Relative Susceptibility of *St. secundatum* Cultivars

Utilizing data from the monoculture treatment (M1), we separated the effects of each cultivar (n = 12). In the no-choice experiment, we found no effect of cultivar on larval weight, time to eclosion, or survival rate (Table 2). However, we did find an effect on time to pupation ($F_{5,58}$ = 5.7, $P < 0.01$; Table 2). Specifically, larvae feeding on 'Bitterblue' took significantly longer to pupate than those feeding on 'Captiva', 'Floratam', 'Palmetto', or 'Seville'. We detected no cultivar effects on any life history traits in the M1 treatment of the limited-choice test (Table 2). Average percent herbivory ranged from 50 to 58% with a mean of 52 ± 2 and was no different between cultivars.

No-Choice Experiment

In the no-choice experiment, 9-d larval weight ranged from 106 to 576 mg with a mean of 320 ± 6 mg and pupal weight ranged from 116 to 247 mg with a mean of 189 ± 2 mg. We found that when provided with a known diet of *St. secundatum* clippings, increasing cultivar diversity significantly reduced larval body weight (Table 3, Fig. 2A). More specifically, larval weight was over 10% greater in the M1 treatment (341 ± 10 mg) compared with the M2 (309 ± 11 mg) and M4 (304 ± 10 mg) treatments. However, this difference was only significant between the M1 and M4 treatments. Although only nearly significant, this trend held true for pupal weight (Table 3, Fig. 2B).

Sex ratios were also nearly significantly affected by cultivar diversity, suggesting an increasing female bias as cultivar diversity increased. The M1 treatment had a relatively balanced sex ratio (*n* = 60, 0.55 ± 0.06 m/f), whereas the M2 (*n* = 46, 0.38 ± 0.07 m/f) and M4 treatments (*n* = 50, 0.35 ± 0.07 m/f) were female biased. The population percentage of females steadily increased with cultivar diversity (M1: 39%; M2: 48%; M4: 53%), whereas the percentage of surviving males dropped sharply between monoculture and mixed cultivar treatments (M1: 45%; M2: 28%; M4: 28%).

When separated by sex, the trend of reduced larval weight with increasing cultivar diversity persisted for females only (Table 4). Average female larval weight in the M1 (*n* = 28, 339 ± 17 mg) group was significantly higher than both the M2 (*n*= 29, 282 ± 11 mg) and M4 groups (*n* = 32, 297 ± 14 mg). Male larvae were about 10% larger than females on average (345 ± 11 mg) but were no different between diversity treatments. Male pupae (*n*= 67, 194 ± 2) were also larger than female pupae (*n* = 89, 186 ± 2 mg; $F_{1,149}$=10.6, $P < 0.01$), but neither were affected by cultivar diversity.

On average, larvae took 13.9 ± 0.1 d to develop from a first-instar larva to a pupa and 22.3 ± 0.1 d to an adult. Cultivar diversity had no effect on development rate to pupation (Table 3, Fig. 2C) but did affect development to an adult. Larvae in the M2 treatment developed most rapidly (*n* = 46, 21.9 ± 0.2 d), whereas larvae developing on the M1 group took the longest (*n* = 60, 22.6 ± 0.19 d) (Fig. 2D). When separated by sex, there was no difference in days to pupation or eclosion. Males took the same amount of time to pupate (13.9 ± 0.1 d, 13.7 ± 0.1 d) as females, but nearly 2 d longer to eclose (23.2 ± 0.1 d) than females (21.6 ± 0.1 d).

Limited-Choice Experiment

In the limited-choice experiment, 11–12 d larval weight ranged from 14 to 607 mg, with a mean of 314 ± 11 mg. Although different from the no-choice experiment, larval weight was also affected by treatment such that M2 larvae (*n* = 51, 353 ± 17 mg) were significantly larger than those from the M4 treatment (*n* = 61, 298 ± 18 mg) (Fig. 3A). Development rate was also affected by diversity level. Larvae feeding on the M4 treatment (24.9 ± 0.4 d) took significantly longer to eclose than those feeding on M2 (24.0 ± 0.3 d), although this difference was <1 d. We saw no effect of *St. secundatum* diversity on *Sp. frugiperda* survival rate (Table 3).

Unlike the no-choice experiment, sex ratios became less female biased as cultivar diversity increased (Fig. 3D). Those reared on monocultures were most female-biased (*n* = 61, 0.40 ± 0.1 m/f), whereas the M4 group had the most balanced sex ratio (*n* = 52, mean = 0.50 ± 0.06 m/f) and the M2 group fell between (*n* = 50, mean = 0.40 ± 0.06 m/f).

Finally, percent herbivory in the limited-choice experiment ranged from 10 to 90% with a mean of 47.0 ± 1.4%. Most importantly, increasing cultivar diversity significantly reduced herbivory (Table 3; Fig. 4). On average, M1 plantings had 12% more herbivory than M4 plantings and 5% more than M2 plantings.

Table 2. Effects of *St. secundatum* cultivar monocultures on *Sp. frugiperda* life history traits in no-choice (larvae individually fed clippings) and limited-choice (larvae provided rooted grasses in pots) experiments.

St. secundatum cultivar	Larval weight (mg)	Days to pupation	Days to eclosion	Survival rate
No-choice				
'Classic'	339 ± 23	14.2 ± 0.3ab	22.5 ± 0.5	92 ± 8
'Bitterblue'	386 ± 28	14.9 ± 0.3a	23.1 ± 0.5	67 ± 14
'Captiva'	319 ± 28	13.6 ± 0.3b	22.8 ± 0.4	92 ± 8
'Floratam'	320 ± 19	13.6 ± 0.2b	22.1 ± 0.4	83 ± 11
'Palmetto'	349 ± 33	13.8 ± 0.3b	22.5 ± 0.5	83 ± 11
'Seville'	333 ± 22	13.6 ± 0.3b	22.6 ± 0.5	83 ± 11
	n = 72, *F* = 1.0, df = 5, *P* = 0.44	*n* = 67, *F* = 5.7, df = 5, *P* < 0.01	*n* = 61, *F* = 0.8, df = 5, *P* = 0.55	*n* = 72, *F* = 0.3, df = 5, *P* = 0.89
Limited-choice				
'Classic'	299 ± 38	NA	23.8 ± 0.7	67 ± 7
'Bitterblue'	290 ± 48	NA	25.3 ± 0.9	50 ± 9
'Captiva'	358 ± 56	NA	24.5 ± 0.7	58 ± 10
'Floratam'	245 ± 43	NA	24.6 ± 1.1	42 ± 10
'Palmetto'	354 ± 51	NA	25.4 ± 1.1	46 ± 7
'Seville'	255 ± 42	NA	24.6 ± 0.8	67 ± 9
	n = 62, *F* = 2.0, df = 5, *P* = 0.09		*n* = 61, *F* = 1.6, df = 5, *P* = 0.18	*n* = 72, *F* = 1.5, df = 5, *P* = 0.21

Means and SEs are listed for each measured variable. Means and SEs followed by different letters are significantly different ($P < 0.05$) using Tukey's HSD means comparison. NA indicates no data were collected for that item.

Table 3. One-way ANOVA results for the effects of *St. secundatum* cultivar diversity (one, two, or four cultivars) on *Sp. frugiperda* life history traits in no-choice (larvae individually fed clippings) and limited-choice experiments (larvae provided rooted grasses in pots)

Parameter	*N*	df	DFDen	*F* Ratio	*P*-value
No-choice					
Larval weight	191	2	185	4.2	0.02*
Pupal weight	178	2	172	2.5	0.09
Days to pupation	178	2	172	0.9	0.42
Days to eclosion	158	2	152	3.7	0.03*
Survival	192	2	186	0.5	0.62
Sex ratio	158	2	NA	(χ2) 5.2	0.07
Limited-choice					
Larval weight	170	2	167	3.6	0.03*
Days to eclosion	163	2	157	3.9	0.02*
Percent survival	192	2	186	1.8	0.17
Sex ratio	163	4	NA	(χ^2) 14.0	0.01*
Percent herbivory	240	2	233	13.3	<.01*

Asterisks (*) indicate statistically significant results. NA indicates no data were collected for that item.

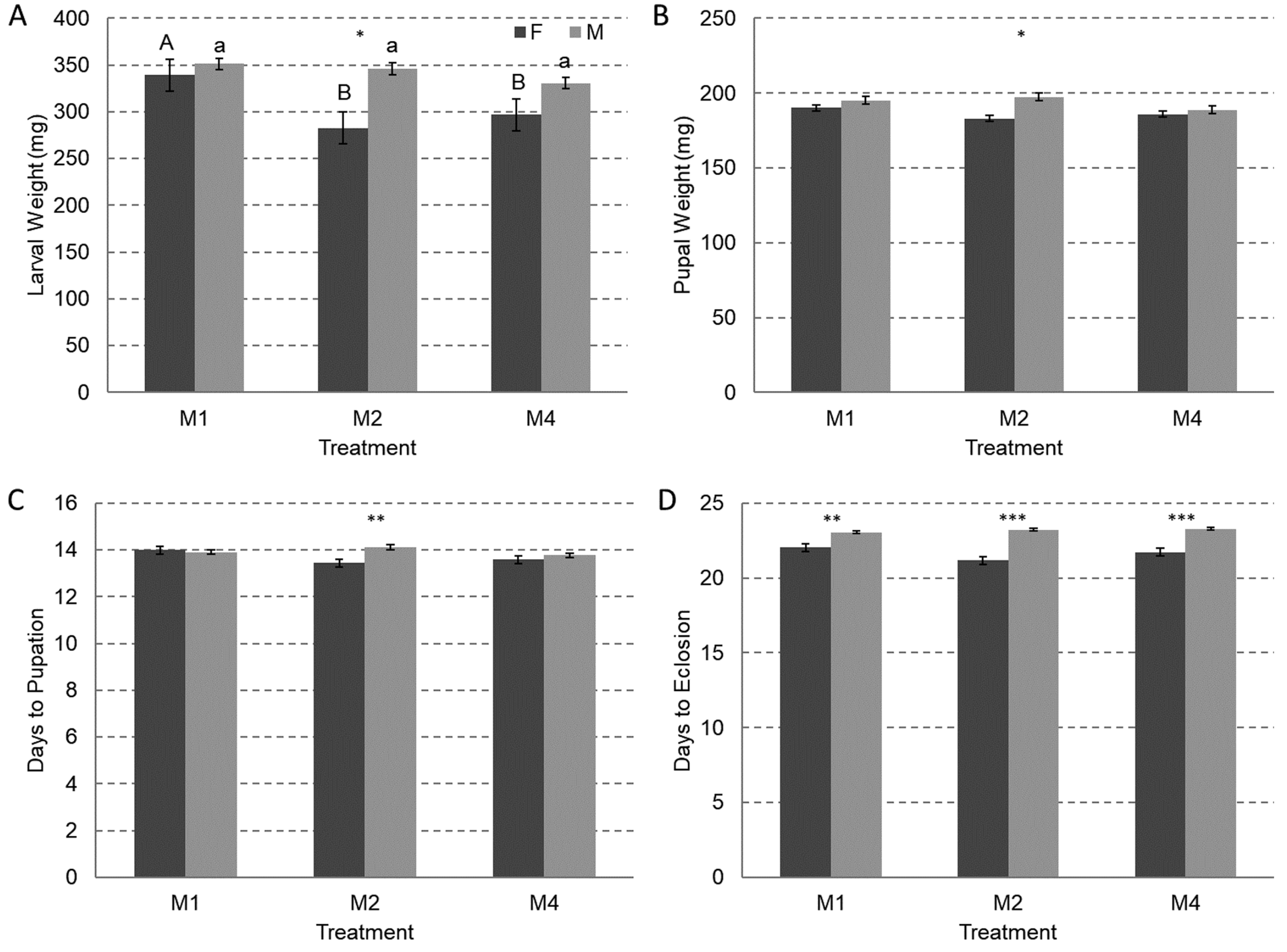

Fig. 2. Effects of *St. secundatum* cultivar diversity and *Sp. frugiperda* sex on fitness in no-choice experiments. Fitness measures include 9-d larval weight (A), pupal weight (B), days to pupation (C), and days to eclosion (D). Error bars represent SE. Different letters of the same case indicate statistical differences ($P < 0.05$). Asterisks over bars indicate a statistical difference between *Sp. frugiperda* sexes within a treatment. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Spodoptera frugiperda Host Choice

Spodoptera frugiperda larval host choice was significantly affected by cultivar diversity ($F_{2,478}$ = 47.0, P < 0.01) and this effect held true across all time points ($F_{3,480}$ = 0.2, P = 0.93) with no interaction ($F_{6,478}$ = 0.4, P = 0.87). More specifically, larval abundance significantly decreased with increasing cultivar diversity from M1 plantings to M2 and M4 plantings (Fig. 5).

On average, adult females deposited 74 egg masses per experimental replicate and two masses per planting. Egg mass weight averaged 11 mg and total egg mass weight per planting was 26 mg. There

Table 4. One-way ANOVA results for the effects of *St. secundatum* cultivar diversity (one, two, or four cultivars) on male and female *Sp. frugiperda* fitness measures in no-choice feeding experiments (larvae individually fed clippings)

Sex	Parameter	df	DFDen	*F* ratio	P-value
Male (*n* = 67)	Larval weight	2	63	0.4	0.70
	Pupal weight	2	62	1.3	0.29
	Days to pupation	2	61	0.7	0.50
	Days to eclosion	2	63	0.2	0.81
Female (*n* = 89)	Larval weight	2	83	5.4	0.01*
	Pupal weight	2	84	0.7	0.52
	Days to pupation	2	83	2.4	0.10
	Days to eclosion	2	83	1.9	0.16

Asterisks (*) indicate statistically significant results.

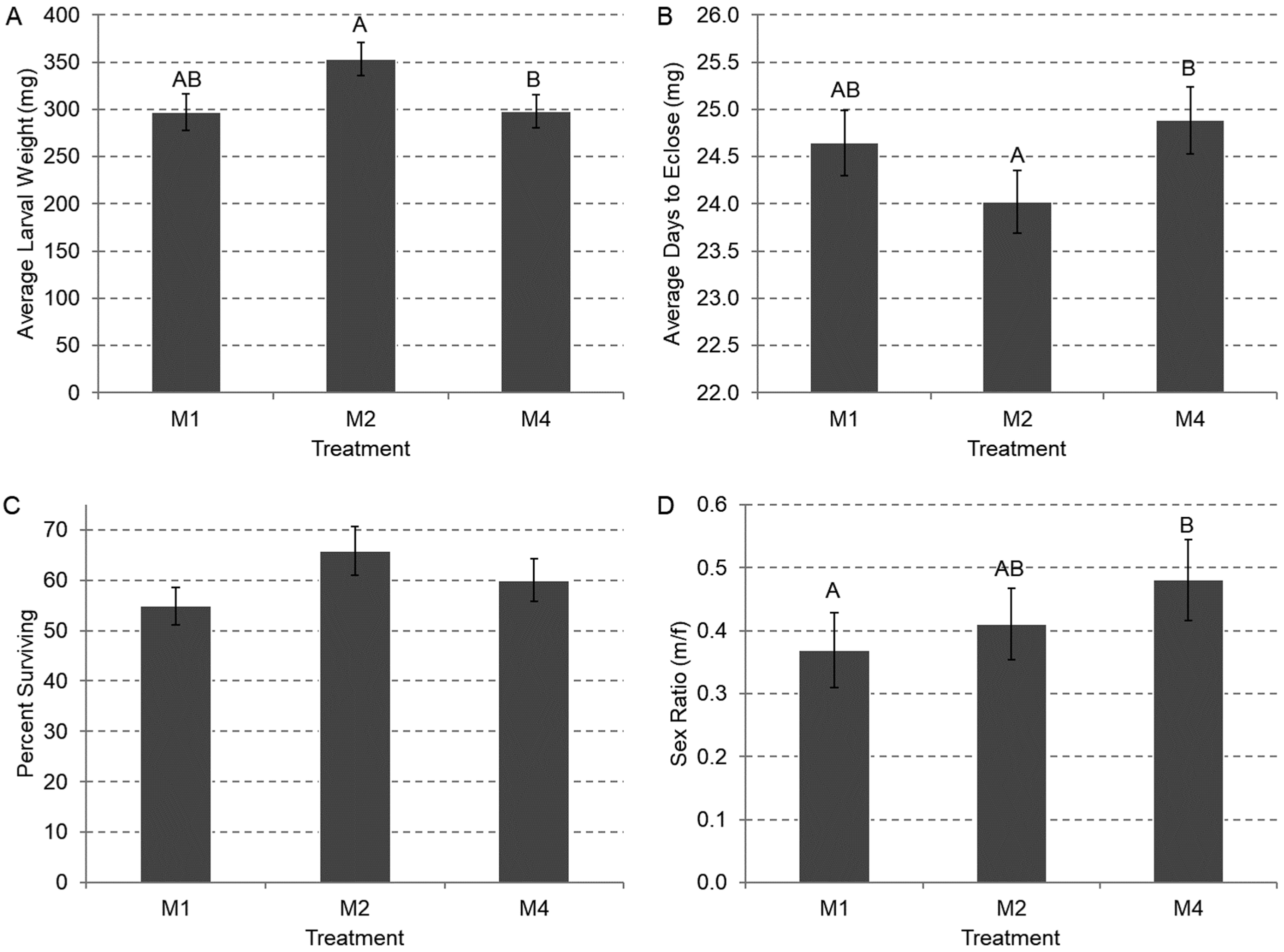

Fig. 3. Effects of *St. secundatum* cultivar diversity on *Sp. frugiperda* fitness and herbivory in limited-choice experiments (larvae provided rooted grasses in pots). The M1 pots are composed of St. Augustinegrass monocultures, M2 are pots composed of mixtures of two cultivars, and the M4 pots contain mixtures of four cultivars. Fitness measures include 11- to 12-d larval weight (A), days to eclosion (B), survival rate (C), and population sex ratio (D). Error bars represent SE. Different letters indicate statistical differences between treatments ($P < 0.05$).

were no apparent trends in egg number or mass across diversity levels. Thus, we did not detect an effect of cultivar diversity on the number ($F_{2,88} = 0.5$, $P = 0.59$), average weight ($F_{2,64} = 0.2$, $P = 0.81$), or total weight ($F_{2,70} = 0.04$, $P = 0.96$) of egg masses deposited by *Sp. frugiperda*.

Discussion

Greater adoption of insect pest-resistant grass species, cultivars, or mixtures could help reduce the need for chemical inputs to turfgrass lawns. Warm season turfgrasses, particularly *St. secundatum*, are ubiquitous to the most rapidly expanding land use type in Florida and the United States (Brown et al. 2005). Prior to this study, the relative resistance of commercially available *St. secundatum* cultivars to *Sp. frugiperda* was unknown. Based on the genotypic and morphological variation among cultivars and known effects on other insect herbivores (Casler and Duncan 2003, Rangasamy et al. 2009b, Reinert et al. 2009), we predicted that *St. secundatum* cultivars would differentially affect *Sp. frugiperda*. However, this was

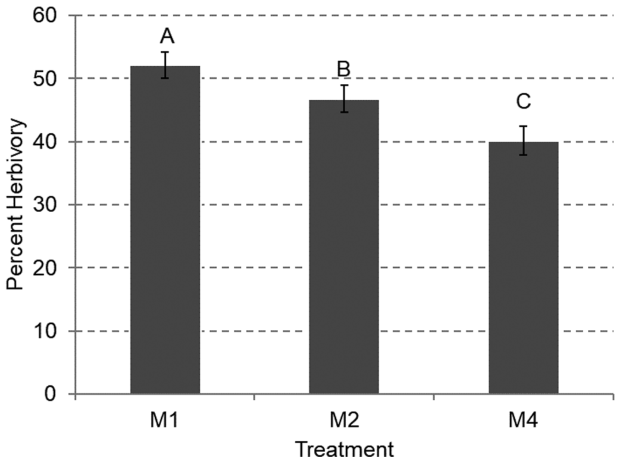

Fig. 4. Mean percent *Sp. frugiperda* herbivory across *St. secundatum* cultivar diversity treatment groups in the limited-choice experiment (larvae provided rooted grasses in pots). The M1 pots are composed of St. Augustinegrass monocultures, M2 are pots composed of mixtures of two cultivars, and the M4 pots contain mixtures of four cultivars. Error bars represent SE and different letters indicate statistical significance ($P < 0.05$).

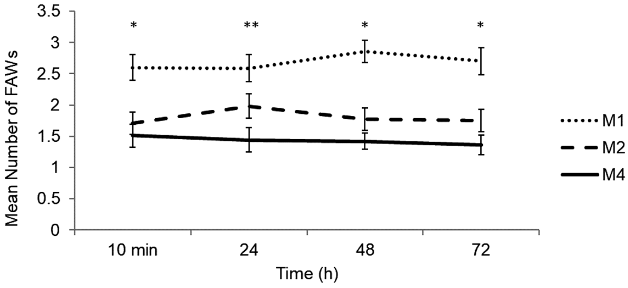

Fig. 5. Mean number of *Sp. frugiperda* on each *St. secundatum* cultivar diversity planting (M1, M2, M4). Error bars represent SE. One asterisk (*) indicates M1 is statistically different from M2 and M4. Two asterisks (**) indicates a statistical difference between all three treatment groups.

not supported, with the only difference being a slight developmental delay when fed 'Bitterblue' under no-choice conditions. Therefore, our results suggest that monoculture lawns of the six tested cultivars are equally susceptible to *Sp. frugiperda*.

Previous research has identified positive (Kotowska et al. 2010) and negative (Grettenberger and Tooker 2017) effects of increasing host plant diversity on herbivores via diet mixing and associational resistance, respectively. We pitted these hypotheses against each other to determine the methodological and biological significance of increasing genotypic diversity in an herbivore's diet. Interestingly, we found that experimental methodology (forced vs optional diet mixing) yielded different results. More importantly, we found that manipulating cultivar diversity affected herbivory and life history traits by changing body size, development rates, colonization rates, and sex ratios. Although we did not measure these effects over multiple generations, each of these results may have important implications for insect biology and pest management in turfgrass lawns.

Our results demonstrate that mixing susceptible cultivars may generate effects analogous to host plant resistance. We hypothesized that when *Sp. frugiperda* was forced to diet mix, its fitness would increase based on previous studies (Mody et al. 2007, Kotowska et al. 2010). Contrary to our prediction, increasing *St. secundatum* genotypic diversity affected *Sp. frugiperda* life history traits in ways that suggest reduced fitness. Our results mirror those of Wetzel and Thaler (2018), who found that diet mixing by a generalist herbivore, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), reduced body mass. Through diet mixing, *Sp. frugiperda* female larval weight decreased in the mixed plantings compared with monocultures. Increasing cultivar diversity also reduced development time from larva to adult, although this effect was only apparent when males and females were combined for analysis. Since female *Sp. frugiperda* eclose more quickly than males (Pashley et al. 1995), the overall effect on development rate may, in part, be driven by the female-biased sex ratios in the mixed cultivar treatments.

In our no-choice study, sex ratios became increasingly female-biased as cultivar diversity increased, which was driven by an increase in female survivorship and a decrease in male survivorship. When *Sp. frugiperda* developed on a monoculture diet under no-choice conditions, female larvae were larger, but fewer survived to adults. Male survivorship sharply declined in response to diet mixing and larval weight was unchanged. These results indicate that diet mixing creates female-biased populations composed of smaller individuals. Grettenberger and Tooker (2016, 2017) found similar results, where increased genotypic diversity reduced female aphid body size and population growth rates. However, our observed effects changed when larvae were not forced to diet mix through no-choice conditions and instead fed among diverse plantings.

With plantings, we hypothesized that increasing genotypic diversity would negatively affect life history traits through associational resistance (Barbosa et al. 2009). Interestingly, the effects of cultivar diversity did not become more apparent as cultivar diversity increased, but rather only when larvae developed on M2 plantings. Larvae in the M2 plantings were significantly larger and developed more rapidly than those in the M4 plantings, whereas neither cultivar diversity level was different than monoculture plantings. Therefore, our results suggest that a high level of cultivar diversity may be detrimental to *Sp. frugiperda* fitness, but low levels of genotypic diversity may benefit *Sp. frugiperda* by allowing them to select the relative cultivar composition of their diets. This pattern might have arisen due to diet optimizations in the M2 treatment that were not possible in the resource-limited M4 group. Further investigation into the mechanisms behind this pattern may help explain if these trends would persist in lawns.

The level of diet mixing that occurred within each treatment under no-choice and limited-choice conditions is one avenue for interpreting our results. Our no-choice experiment found that diet mixing at a 1:1 ratio (in M2) or a 1:1:1:1 ratio (in M4) reduced *Sp. frugiperda* fitness. However, we did not determine if diet mixing to a lesser degree (e.g., 3:1) has a different effect. It has been shown that when herbivores can choose hosts, they can reduce the negative effects of diet mixing. For example, Wetzel and Thaler (2018) found that when *L. decemlineata* was forced to feed on an inferior host, *Solanum lycopersicum* L. (Solanales: Solanaceae), its body mass decreased, and further decreased when forced to diet mix on *So. lycopersicum* and *S. tuberosum* L. (Solanales: Solanaceae) in equal portions. However, allowing it to choose its diet when feeding on both plant species mitigated the negative effects on body mass. Thus, within our limited-choice study, *Sp. frugiperda* may have selected an ideal balance in the M2 plantings, maximizing the beneficial effects of diet mixing by primarily feeding upon one cultivar and lightly feeding on a second. In the M4 treatment, which supports smaller quantities of more cultivars, feeding is more similar to the forced diet mixing experiment, effectively reducing any benefits of diet mixing. Unfortunately, due to limitations of our experimental design, we were unable to test this idea.

The resource concentration hypothesis predicts that reducing stand size of a preferred host by increasing plant diversity may reduce herbivore immigration, retention, and herbivory (Root 1973). Our results support this, as we observed reduced larval colonization and herbivory with increasing cultivar diversity. Although adult oviposition was not affected, *Sp. frugiperda* larvae preferentially colonized less diverse plantings of *St. secundatum* cultivars, which could translate to reduced lawn colonization rates. Adult *Sp. frugiperda* frequently oviposit on nonhost plants or structures adjacent to hosts (Thomson and All 1984), leaving larvae to disperse to colonize a host. Consequently, these generalist herbivores may avoid lawns of diverse cultivars and feed more ubiquitously on landscape plants, reducing concentrated herbivory and the need for pest control inputs. Moreover, we found that *Sp. frugiperda* herbivory declined with increasing cultivar diversity such that M4 plantings had 12% less damage than M1 plantings (Fig. 2). These results are particularly important for *St. secundatum* lawns because less herbivory translates to greater aesthetic quality and less need for supplemental inputs.

Our study suggests that lawns composed of mixed cultivars may have insect pest management benefits as indicated by our feeding trials, larval choice evaluation, and herbivory results. Preference of *Sp. frugiperda* for monoculture turf may translate to lower densities in more diverse mixed-cultivar lawns and reduce the need for insecticide treatments. In addition to plant diversity or richness, other studies have found that plant composition can be the most important factor affecting herbivores (Finch et al. 2003). Although beyond the scope of this study, further investigations may identify underlying factors contributing to our observed trends and lead to more targeted cultivar mixtures for implementation. Additionally, field studies should be conducted to evaluate the relative marketability of cultivar mixtures and determine effects on lawn quality. As it stands, our results show promise for increasing warm season turfgrass cultivar diversity as an effective IPM tactic that lawn managers and the turfgrass industry could implement to reduce the economic and environmental impact of insect pests and their management in urban ecosystems.

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