

**EVALUATING THE USE OF NATIVE ORNAMENTAL PLANT CULTIVARS
FOR INSECT HERBIVORES**

by

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ABSTRACT

Native plants are becoming more commonly used in ornamental gardening as a way to help combat the many environmental issues caused by urbanization. Designing anthropogenic habitats that promote insect diversity and abundance may be paramount for reconciliation efforts. Plant breeders have introduced many cultivars of native plants to improve the aesthetic value, disease resistance, or site adaption of the plant that may positively or negatively impact wildlife. There has been a debate as to whether or not native cultivars have the same ecological value as their wild type counterparts. This remains to be tested.

In this study I focus on the use of native plant cultivars for wildlife value, specifically for insect herbivore-driven food webs. These cultivars often have chemical or physical properties that have been altered from the straight species which may alter an insect's ability to locate and consume its host plant. I chose six cultivar traits that are commonly sought after in woody plant cultivar selections to compare insect feeding, abundance and species richness between the cultivars and the wild type plants. An experimental garden plot was established with cultivars and their parent species at the Mt. Cuba Center in Hockessin, Delaware. Three experiments explored the differences between the cultivars and their straight species. First, the garden was used to sample the insect community and abundance associated with each species and cultivar. Second, I conducted a feeding trial with the bagworm *Thyridopteryx ephemeraeformis* in which neonate caterpillars were offered a choice of the cultivars and parent plants and amount of feeding on each was compared. Lastly, I conducted

an end-of-season leaf damage analyses to compare the average amount of feeding damage that had accumulated on leaves in the garden plots by September.

Results showed a deterrence of feeding on cultivars that had leaves altered from green to red color. Results for the other traits varied from test to test and by plant species, but many often showed no difference from the straight species. In a few cases insects showed a preference for the cultivar over the straight species. Thus, the usefulness of native cultivars in restoring insect driven food webs may, in many situations, depend on the suitability of the cultivar trait and/or the plant species from which the selection was derived.

|Chapter 1

NATIVE CULTIVARS VERSUS STRAIGHT SPECIES

Introduction

Urbanization and agricultural practices have altered and in most cases degraded local ecosystems. Suburban and urban landscapes have only recently been evaluated as potential habitats for biodiversity. It has been well-documented that landscapes with introduced plant species do not support food webs well. This is due to the inability of insect herbivores to locate and exploit plants with lineages with which they do not share an evolutionary history (Zuefle et al. 2007, Burghardt et al. 2008, Tallamy and Shropshire 2009, Tallamy et al. 2009, Fortuna et al. 2013, Pearse et al. 2013). Insect herbivores typically comprise the first consumer level in terrestrial food webs and provide energy for many higher level consumers including birds, amphibians, reptiles, and many mammals (Tallamy 2004); thus, conservation of insect herbivores and the plants that sustain them is essential to the conservation of ecosystems as a whole (Wilson 1987). There is a strong positive correlation between native plant diversity, insect herbivore abundance and diversity, overall biodiversity, and community stability (MacArthur 1955, Hutchinson 1959, Wilson 1987, Kagata and Ohgushi 2006, Dyer et al. 2010).

Among the many reasons for using native plants in private gardens is to alleviate the biotic homogenization caused by urbanization across the globe (McKinney 2006). Urban and suburban areas make up much of the United States landscape and could provide potential habitat for both common and at risk wildlife if

properly landscaped (McKinney 2002, 2006, Rosenzweig 2003). When used appropriately, native plants also provide low maintenance gardening options because they are adapted to grow in their local area. Some argue that common gardening practices have disconnected society from the natural world and gardening with native plants can help rebuild this connection (McKinney 2002, Tallamy 2007).

Since 1974 and the Federal Noxious Weed Act there has been increased awareness of the negative impacts of non-native land management techniques (Reichard and Hamilton 1997); 85% of the woody invasive plants in North America are escapees from residential gardens (data derived from Kaufman and Kaufman 2013). The public has begun to recognize that plants are more than decorations and can perform essential ecosystem functions in home gardens (Nassauer 1988, Reichard and White 2001, Baskin 2002). This has resulted in growers, nurseries, and garden centers marketing plants labeled for their ecological characteristics as well as aesthetic value (Nassauer 1988, Reichard and White 2001).

With the increase in knowledge of the benefits of native plants, plant breeders and horticulturists have introduced many native cultivars to fulfill a visual or performance role in built landscapes that may also be beneficial to wildlife. *The International Code of Nomenclature for Cultivated Plants* offers the following definitions of a cultivar and a cultivated plant (Spooner et al. 2003).

“Cultivar. A systematic group of cultivated plants that is clearly distinct, uniform, and stable in its characteristics and which, when propagated by appropriate means, retains these characteristics.

Cultivated plant. One whose origin or selection is primarily due to the intentional activities of mankind. Such a plant may arise either by deliberate or, in cultivation, accidental hybridization, or by selection from existing cultivated stock, or may be a selection from minor

variants within a wild population and maintained as a recognizable entity solely by deliberate and continuous propagation.”

Cultivars may be useful in reconciling the fragmentation and habitat loss typical of built landscapes, but their ecological value has yet to be evaluated. Cultivars of native species may have altered chemical or physical properties such as changes in leaf color, habit, fruit size and abundance, flower shape, number or color, or disease resistance (Dirr 2011). Most cultivars are propagated as clones with no genetic diversity (Santamour 2004). This is predicted to be problematic as genetic diversity is a primary defense against disease epidemics. Moreover, slight changes in genotype may reduce herbivory in natural settings by preventing herbivores from breaking the defenses of potential host plants (Whitham and Slobodchikoff 1981).

Few studies have looked specifically at plant cultivars and their effects on insect behavior; however, many have examined how naturally occurring plant traits in the wild can affect herbivory. Plants have secondary metabolites that are not essential for growth and development but serve as defensive compounds (Chen 2008, Howe and Jander 2008, Gols 2014). Plant defensive chemicals include glucosinolates, cyanogenic glycosides, alkaloids, and anthocyanins. Physical defenses such as trichomes, thorns, and leaf toughness can also deter herbivores (Campitelli et al. 2008, Price et al. 2011, Dimarco et al. 2012). The amount of these defenses deployed in particular plant tissues depends on the evolutionary history of the relationships between a plant lineage and its insect herbivores (Ehrlich and Raven 1964, Becklin 2008, Campitelli et al. 2008, Price et al. 2011, Fürstenberg-Hägg et al. 2013, Gols 2014). An insect’s host plant selection is impacted by plant availability, phytochemistry, and physical characteristics and is not easily altered in ecological

time frames (Tallamy et al. 2009, Forister et al. 2012, Rasmann 2014, Fordyce et al. 2016).

Studies of how cultivars may alter the relationship between native plants and insects can be divided into two types: those that look at how changes in flower structure or color may impact pollinators and those that consider how changes in plant structure or color may impact insect herbivores. In this study I asked whether cultivars of native trees and shrubs change the way insect herbivores interact with these plants. While all cultivars are propagated to produce genetic uniformity to produce a guaranteed horticultural product, they can stem from two approaches. Some native cultivars are naturally occurring selections that are introduced to get an underused plant into the trade with no manipulation. They use cuttings to propagate. Others are produced by professional breeders that do deliberate crosses and reselection of the progeny. The later could be propagated by a cutting or inbreed parents producing an F-1 hybrid. They are both looking for garden performance and visual interest. Both approaches offer native cultivars assuming that these plants will provide the same ecological benefits as their wild type counter parts. From an ornamental perspective, the hope is that native plant cultivars do indeed provide exceptional ornamental displays while being low maintenance and benefiting wildlife. However, most insects are restricted to feeding on plants with which they share an evolutionary history and are sensitive to novel leaf chemistry and structure (Erhlich and Raven 1964, Tallamy and Shropshire 2009, Pearse et al. 2013). If cultivars of natives are not the ecological equivalents of their parent species, they may compromise the effort of planting for diverse food webs. Here I examined herbivore response to cultivars with six different selected traits compared to their parent species.

Materials and Methods

Test I. Garden Experiment/Insect Collection

I conducted my study at the Mt. Cuba Center; a botanical garden dedicated to native plant horticulture and research in Hockessin, Delaware. In 2014 Mt. Cuba staff and I established experimental plots within their nursery on the south east side of the property, located at 39°47'12.80" N, 75°38'49.77" W. The site has over 50 acres of gardens surrounded by a deer exclusion fence and 500 acres of natural land that provided a population of local insects with which to evaluate insect herbivore preference among plants within the experimental garden.

Working with the Mt. Cuba Center staff and various resources from the literature we selected 10 common ornamental trees and shrubs native to the Mid-Atlantic area that were available in the trade and also serve as host plants to a variety of common insects, particularly Lepidoptera species (Table 1) (Rehder 1940, Tallamy and Shropshire 2009, Dirr 2011). Because there are countless cultivars in the market and it would be impossible to test every one, we chose six commonly sought-after traits in ornamental plant cultivation: 1) red, purple, or blue leaf color, 2) variegated (white and green patterned) leaf color, 3) plants with growth habit modified to a low growing/compact forms, 4) disease resistance, 5) increased fruit size and yield, and 6) enhanced fall colors. For five of the plant species, we paired the straight species with a single cultivar that had one of the selected traits, while for the other five species we compared one planting of the straight species to two, three, or four different cultivars, each with one of the desired traits (Table 1). This allowed us to limit the number of plants we needed to purchase and plant in a limited space. In total, there were three

cultivars of different species representing each of the six traits. [for photographs of plants with visual differences see Appendix A]

In 2014 we established an experimental plot that was approximately 1,500 square feet. Plants were grouped by species with straight species and related cultivar(s) adjacent to each other in order to facilitate insect choice between host plants. Where more than one cultivar was paired with a single straight species, the cultivars were arranged around or next to the straight species. Five plants of each type were spaced 1.2 meters apart to allow for growth and to provide a larger target for herbivores to locate and populate. All plants were installed on May 20, 2014 and watered as needed for the next few weeks. Plots were maintained throughout 2014-2016 with regular weeding, watering, and pruning as needed. Leaf mulch was applied in the spring of 2014 and 2015 to limit weeding needs and to simulate common gardening practices.

Table 1 Treatments, plant species, and cultivars

Trait	Plant Species	Common Name	Cultivar Name	Trade Name
red/purple colored leaf	<i>Juniperus virginiana</i>	eastern red cedar	'CorCorCor'	Emerald Sentinal
	<i>Viburnum dentatum</i>	arrowwood viburnum	'JN Select'	Red Feather
	<i>Rhus copallina</i>	winged sumac	'Lanham's Purple'	
variegated leaf	<i>Cornus florida</i>	flowering dogwood	'Firecomz'	Firebird
	<i>Liquidambar styraciflua</i>	sweetgum	'Aurea'	
	<i>Cornus sericea</i>	redosier dogwood	'Silver and Gold'	
growth habit	<i>Cornus sericea</i>	redosier dogwood	'Farrow'	ARCTIC FIRE
	<i>Liquidambar styraciflua</i>	sweetgum	'Slender Silhouette'	
	<i>Juniperus virginiana</i>	eastern red cedar	'Gray Owl'	
disease resistance	<i>Ulmus americana</i>	American elm	'Princeton'	
	<i>Cornus florida</i>	flowering dogwood	'Appalachian Spring'	
	<i>Cornus sericea</i>	redosier dogwood	'Cardinal'	
fruit size and yield	<i>Vaccinium corymbosum</i>	highbush blueberry	'Chandler'	
	<i>Ilex verticillata</i>	winterberry	'Red Sprite'*	
	<i>Viburnum dentatum</i>	arrowwood viburnum	'Christom'	Blue Muffin
fall color	<i>Viburnum dentatum</i>	arrowwood viburnum	'KLMSIX'	Crimson Tide
	<i>Cornus sericea</i>	redosier dogwood	'Bailey'	
	<i>Acer rubrum</i>	red maple	'Franksred'	Red Sunset
			*'Jim Dandy' male pol.	

Insects were sampled once in June, July, and August of 2014, 2015, and 2016. This sampling regime covered seasonal shifts that drive insect abundance while preventing any excessive reduction of insect populations. Insects were collected via vacuum sampling and a total search technique, and standardized by time of sampling effort due to differences in size and growth pattern of plant species and cultivars. First we vacuumed plant foliage (30 seconds per sample) using a leaf-blower (Craftsman gasoline blow/vac, Item # 7179469) in vacuum mode fitted with a five-gallon paint strainer bag (Brook et al. 2008). The bags were labeled and put into jars containing ethyl acetate to kill the insects. After collection, samples were labeled and stored in vials of 85% ethanol for later identification. Suction samples were sorted in the lab where herbivores were separated, counted and identified to the lowest possible taxonomic unit. We then meticulously searched leaves and stems of target plants (5-

minutes per sample) for any caterpillars (larvae of Lepidoptera and Symphyta Hymenoptera) not removed by the reverse leaf-blower (Raimondo et al. 2004, Wagner 2005). Gall and leaf mines were also counted and collected, if necessary for identification, during the 5-minute search. Any caterpillars that could not be identified in the field were collected and lab reared on their respective host plants until the adult stage or until identification could be achieved. Caterpillars were also considered separately from the total herbivore data because of their importance in food webs.

Data Analysis

Data were analyzed with JMPpro 13 software. I used paired t tests to find differences of means in insect herbivore abundance (number of insects) and species richness (number of species) between wild type/parent plants and their cultivar counterparts. Control plants were the straight species (or wild type) and cultivars were grouped by treatment category (i.e. variegated, color change, etc.). The three years and three samples per year were pooled; thus, each t-test had an N of 27, with each “replicate” representing the difference between one of the treatment categories and its corresponding wild-type species. After conducting the paired t tests grouped by traits I re-ran the paired t-tests with each plant species separated within the group to see any differences in the reaction to the trait among individual plant species and their cultivar. I also subjectively examined differences in caterpillar species found on a specific plant species where a preference for or against a cultivar was apparent in the field, for one plant over another (analysis did not reflect this preference, but it was clear when visiting the site). [Refer to supplemental material for community comparisons of insect orders, families, and feeding guilds found on control and cultivar plants (Appendix B, C)].

Test II. Feeding Trials

To further compare insect preference for or against cultivars and their straight species, I quantified leaf area consumed by the Bagworm Moth, *Thyridopteryx ephemeraeformis* Haworth, a generalist lepidopteran species with host records on all of our study plants (Tallamy and Shropshire 2009, Moffis and Arthurs 2013). A few weeks before beginning the feeding trials I collected bagworm bags that had overwintered in the Northern Delaware area. Bags were monitored in a controlled environment (in a refrigerator with consistent cold temperatures) until neonate larvae were ready to emerge from the bags and plants had leafed out enough for the experiment to take place.

Leaves were collected after they had expanded to full size following bud break in the spring from our experimental garden at the Mount Cuba Center in Hockessin, Delaware in spring of 2015 and 2016. In 2015 bagworms hatched on May 19 and leaves were collected and fed to bagworms on May 20. In 2016 bagworms were removed from cold storage May 24. Bagworms hatched (early in the morning or overnight) and leaves were collected and fed to them on June 4; leaves appeared somewhat more mature in 2016 than in 2015. I collected 20 leaves from each plant type (4 extra to replace any ripped leaf disks) from southward facing branches. Leaves were selected from the fifth branch from ground or at breast height (depending on plant type/size, i.e. tree vs small shrub). I removed 4 leaves from each of the 5 plants, carefully selecting leaves that would be large enough to make 11.25 mm leaf disks (if not all 5 plants survived, an equal number of leaves was taken from the remaining plants).

The experiment was conducted in 4x4 cell well trays (BioServ well trays part number- 128 well trays: BAW128), 16 cells with leaf disks per plant type. 11.25 mm

leaf discs were cut, using a cork borer, from fresh plant material, being careful to avoid large veins that may contain higher amounts of defensive compounds. For *J. virginiana* plants the collected needles were flattened and cut with the cork borer enough so that just the bottoms of the wells were covered and amount missing was estimated. Three neonate bagworm larvae were gently placed on each leaf disk with a fine tip paintbrush and then covered with plastic well covers (BioServ Plastic 16 well covers for trays part number- BACV16) and left to feed for 48 hours. Temperature was not controlled, but all larvae for each straight species – cultivar pair each year were reared simultaneously in the same place. After the allotted time I removed the bagworm larvae and placed the leaf disks, by plant type and species, into labeled vials containing wetted paper towel, for rehydration. Once leaves were pliable, I placed them under a grid slide and microscope and estimated the percent of the disk that was eaten (Fig.1). For parts of the disks that had surface feeding (feeding that did not go all the way through the leaf) I halved the amount of the grid.

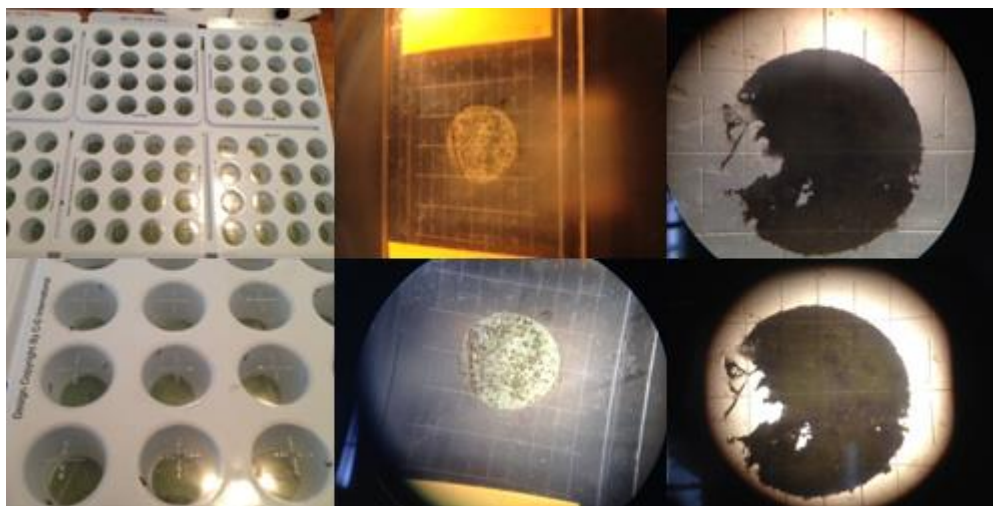


Figure 1 Leaf discs in cell well trays and under grid slides

Data Analysis

Data were analyzed using JMPpro13 software. Mean percent feeding was compared using two tailed t-tests for each wild type and its cultivar for each plant species. Each plant species and cultivar had 16 replicate leaf disks. Two-way ANOVAs were also conducted to compare the main effects of plant species and trait and the interaction effect between plant species and trait on the percent of leaf disk eaten by the bagworm caterpillars. Plant species included three levels (three species used for each trait type) and trait consisted of two levels (control/straight species and the trait change). Two-way ANOVAs were conducted for both years (2015 and 2016) and all six trait-changed groups. A post hoc Tukey HSD was also conducted for each ANOVA.

Test III. Leaf Damage Analysis

To assess cumulative seasonal use of cultivars and their straight species I conducted leaf damage analyses on our study plants in September of 2015 and 2016. Leaves were collected from plants at the Mt. Cuba Center study site and brought back to the laboratory at the University of Delaware. I compared end-of-season mandibulate feeding damage on leaves of wild type plants versus their cultivar counterparts. The end-of-season herbivory damage assessment helped us understand whether or not the number of insect herbivores collected during sampling provided an accurate measure of total leaf herbivory.

I collected 100 leaves from each plant type. Leaves were selected from southward facing branches, from the fifth branch from ground or at breast height (depending on plant type/size- i.e. tree vs small shrub). I removed all leaves from branch axil to terminal end, moving to the next branch up the trunk as needed until I

had 20 leaves from each of the 5 plants (if not all 5 plants survived, an equal number of leaves was taken from the remaining plants). Leaves were placed in plastic ziplock bags, labeled, and brought back to the lab. With a Xerox® DocuMate 510 scanner, I scanned images of all leaves and then uploaded each image onto ImageJ software for analysis. I estimated the area of each leaf that had been eaten using the precise tracing and measuring tools in ImageJ software. It is important to note that *J. virginiana* was left out of this test because of the inability to compare feeding damage on coniferous trees with deciduous trees with the ImageJ software.

Data analysis

Using ImageJ area estimates I found the average area (cm²) of herbivore damage for each plant type. Data were analyzed using JMPpro13 software. Area of leaf damage was compared for each wild type and respective cultivar for each plant species. Two-way ANOVAs were also conducted to compare the main effects of plant species and trait and the interaction effect between plant species and trait on the amount of insect damage at the end of the season. Plant species included three levels (three species used for each trait type) and trait consisted of two levels (control/straight species and the trait change). The two-way ANOVAs were conducted for both years (2015 and 2016) and all six trait-changed groups. A post hoc Tukey HSD was also conducted for each ANOVA. Two tailed t-tests were conducted as well to test for mean differences between parent species and respective cultivars for each plant species. Each plant species and cultivar had 100 leaf replicates.

Results

Garden Experiment/ Insect Collection

Species Richness

Figure 2 shows the paired t-test results for herbivore species richness (average number of species) sampled over the three-year study period. Cultivars with color-changed leaves supported significantly fewer herbivore species than the straight species ($t(26) = 3.1385$, $p = 0.0021$). Cultivars with disease resistance ($t(26) = -1.9908$, $p = 0.0286$) and those with variegated leaves ($t(26) = -5.0449$, $p < 0.0001$) supported significantly more herbivore species than the straight species. Cultivars with modified growth habit supported marginally more species than their straight species ($t(26) = -1.3825$, $p = 0.0893$). Cultivars with enhanced fall color or fruit production did not differ in species richness from the straight species ($t(26) = 0.5867$, $p = 0.5624$ and $t(26) = -0.8156$, $p = 0.4221$ respectively).

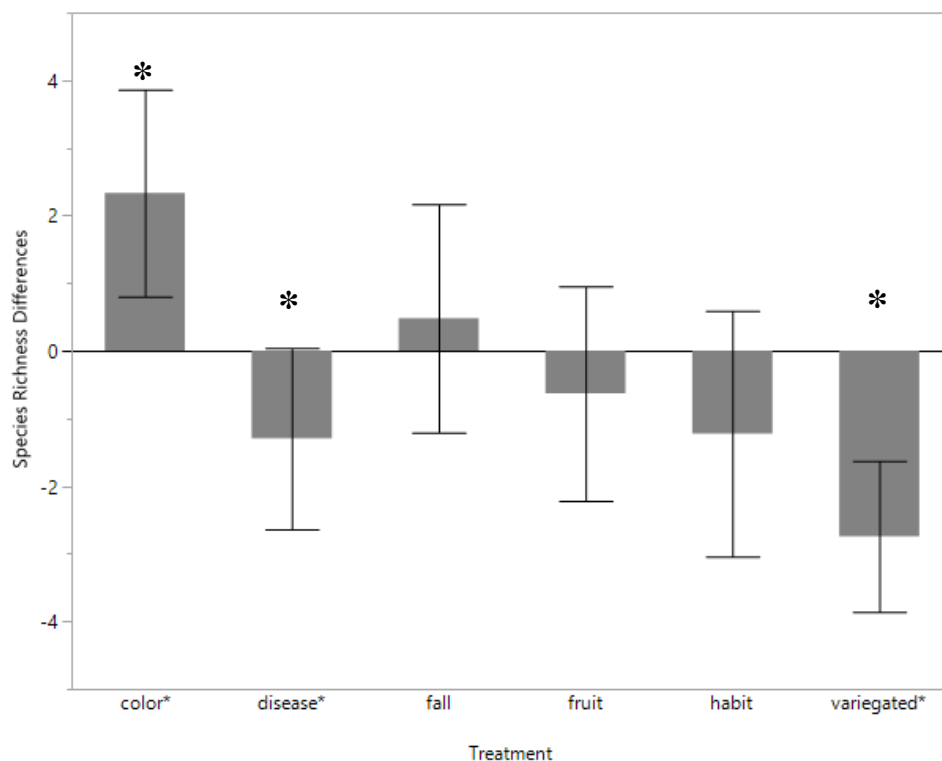


Figure 2 Average herbivore species richness difference of means. Error bars= 95% confidence intervals. Bars below 0 have more species on cultivars; bars above 0 have more species on straight species plants. *= significant differences (color, disease, and variegated).

Total Abundance (immatures plus adults)

Figure 3 shows the paired t-test results for herbivore abundance for the study period by treatment category. Cultivars with altered leaf color, disease resistance, increased fruit production, and leaf variegation all differed significantly from the straight species plants. As with species richness, cultivars with color-changed leaves supported significantly fewer herbivorous insects than the straight species counterparts ($t(26)= 3.1783$, $p= 0.0019$), while disease resistant cultivars ($t(26)= -1.7339$, $p= 0.0474$) and those with variegated leaves ($t(26)= -1.7555$, $p= 0.0455$) supported

significantly more herbivores than the controls. Increased fruiting cultivars also supported significantly more herbivores than the straight species ($t(26) = -1.9405$, $p = 0.0316$). Cultivars with enhanced fall color and modified growth habit did not differ in abundance from the straight species ($t(26) = 0.9997$, $p = 0.3267$ $t(26) = -0.1895$, and $p = 0.8511$ respectively).

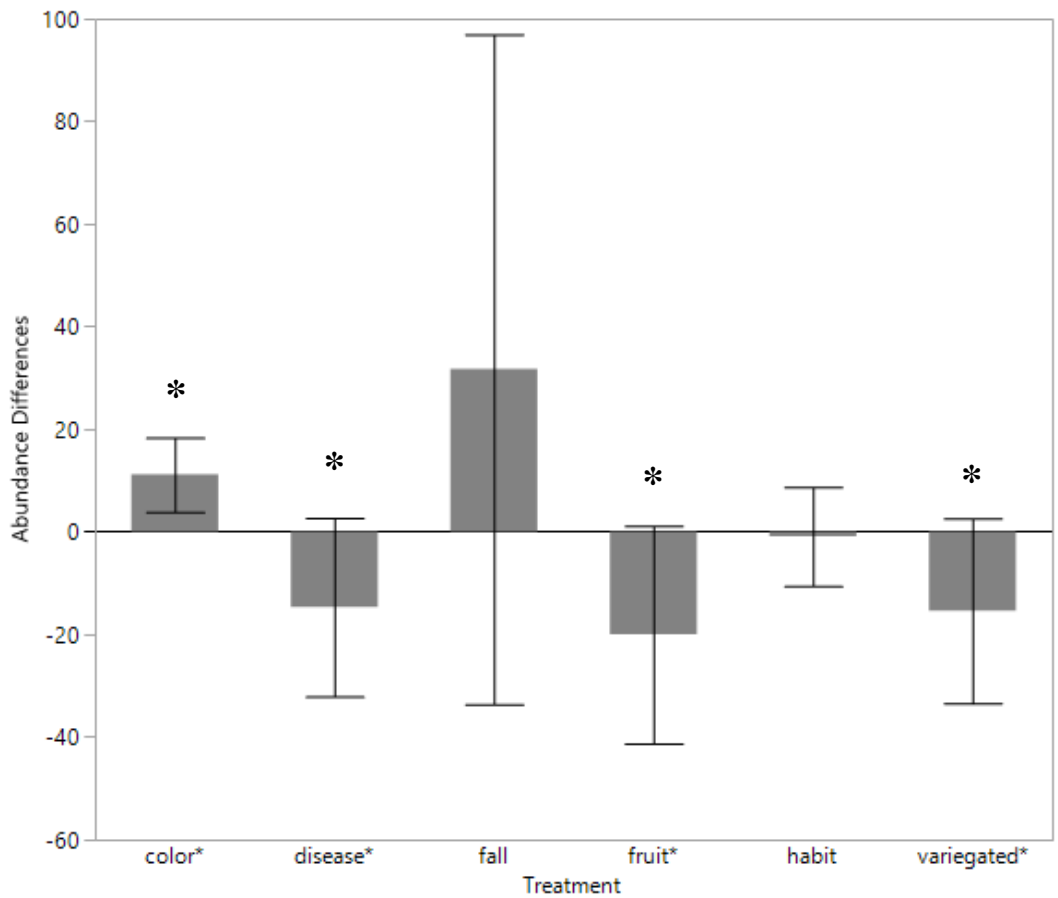


Figure 3 Average herbivore abundance difference of means. Error bars= 95% confidence intervals. Bars below 0 have more individuals on cultivars; bars above 0 have more individuals on straight species plants. *= significant differences (color, disease, fruit, and variegated).

Caterpillar Species Richness and Abundance (Fig.4, 5).

Due to their tendency to be host plant specialists, Lepidoptera and Symphyta sawfly larvae (hereafter caterpillars) were examined independently. To some extent these results paralleled those that included adults of all insect herbivore families in the analysis; however, some important differences are noted. There were significantly fewer caterpillar species on cultivars in which leaf color had been changed ($t(26)=2.4079$, $p=0.0117$) and significantly more caterpillar species on cultivars with variegated leaves ($t(26)=-3.5739$, $p=0.0007$). Contrary to the results that included adults of all insect species in the analysis, cultivars with increased fruiting ($t(26)=0.4507$, $p=0.6559$) and those with disease resistance ($t(26)=-0.7391$, $p=0.4665$) did not support more caterpillar species than the straight species. There were also no differences in the number of caterpillar species on cultivars with altered growth habits and cultivars with enhanced fall colors when compared to their straight species (Habit, $t(26)=-1.2433$, $p=0.2249$; Fall, $t(26)=1.2490$, $p=0.2228$).

Cultivars with changed leaf color supported significantly fewer caterpillars than the control plants ($t(26)=3.0392$, $p=0.0027$). This was the only significant difference in caterpillar abundance between cultivars and straight species across the groups. Contrary to the results that included all herbivore abundance cultivars with enhanced disease resistance ($t(26)=0.0307$, $p=0.9757$), variegated leaves ($t(26)=-1.0715$, $p=0.2938$) or larger fruits ($t(26)=-0.9678$, $p=0.3421$) did not, on average, support significantly more caterpillars than straight species. This may in some cases be due to low abundances of caterpillars making them difficult to compare. However when the plants species were separated in the paired t-tests *Cornus sericea* plants differed in some cases from the other species within their treatment groups in caterpillar responses to traits. There was also a notable preference for the variegated *L.*

styraciflua plants over the controls (Table 2). When individual plant species were compared *C. sericea* straight species attracted a higher abundance of caterpillars than their partnered cultivars sometimes giving the *C. sericea* plants a positive mean difference (more caterpillars on the straight species) contrasting the results of other species with the same trait change which often had a negative (or much smaller) mean difference (more caterpillars on the cultivar) (Table 2) influencing the significance of the overall abundance results.

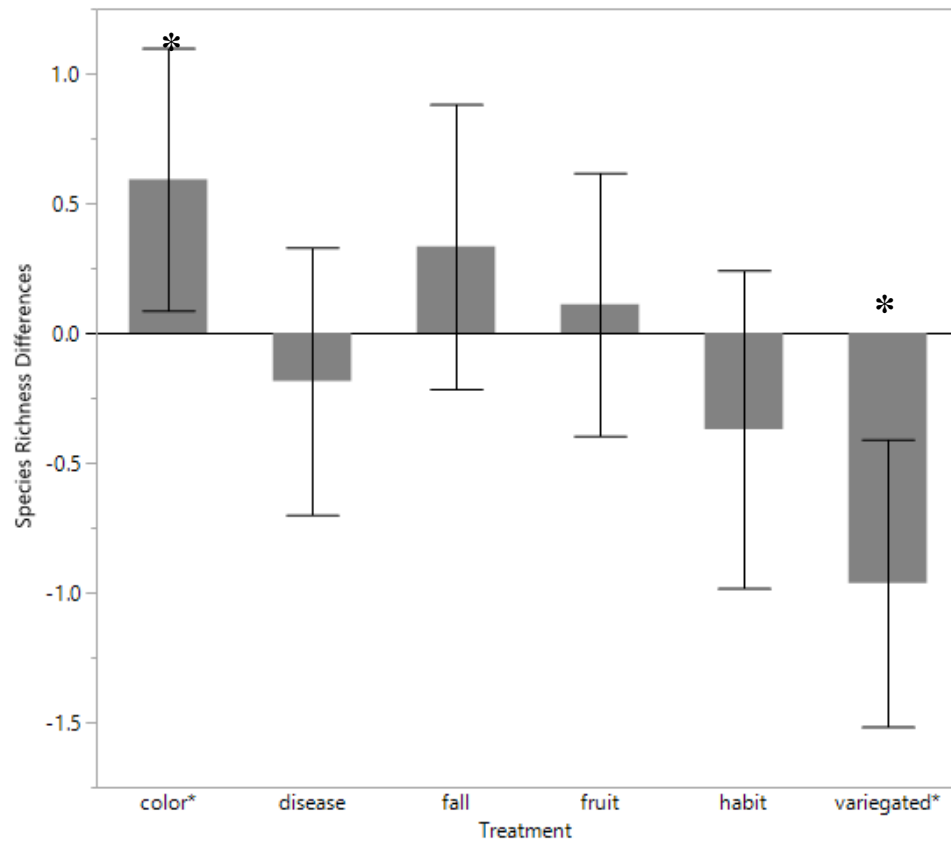


Figure 4 Average caterpillar species richness difference of means. Error bars= 95% confidence intervals. Bars below 0 have more species on cultivars; bars above 0 have more species on straight species plants. *= significant differences (color and variegated).

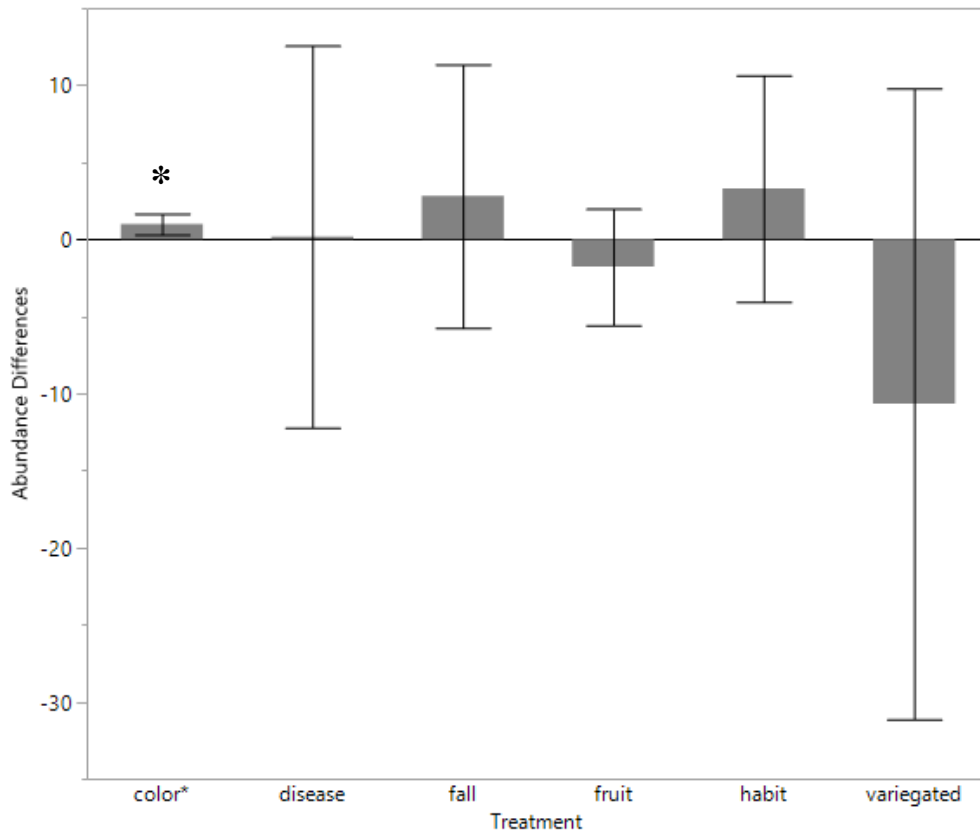


Figure 5 Average caterpillar abundance difference of means. Error bars= 95% confidence intervals. Bars below 0 have more individuals on cultivars; bars above 0 have more individuals on straight species plants. *= significant differences (color).

Table 2 Disease resistant, fall foliage, growth habit and variegated treatment groups, JMP paired t-test across species outputs of caterpillar abundance. *C. sericea* results (shown in red) differ from other species for disease, habit and variegated traits.

Disease Resistant						
Plant Species	Count	Mean Difference	Mean Mean	Test Across Groups	F Ratio	Prob>F
Cornus florida	9	-0.333	0.9444	Mean Difference	0.1387	0.8712
Cornus sericea	9	4.4444	16.667	Mean Mean	3.6992	0.0398*
Ulmus americana	9	-3.556	2.4444			
Fall Foliage						
Plant Species	Count	Mean Difference	Mean Mean	Test Across Groups	F Ratio	Prob>F
Acer rubrum	9	0.2222	2.2222	Mean Difference	0.2676	0.7675
Cornus sericea	9	7.2222	15.278	Mean Mean	2.3063	0.1213
Viburnum dentatum	9	1	0.9444			
Growth Habit						
Plant Species	Count	Mean Difference	Mean Mean	Test Across Groups	F Ratio	Prob>F
Cornus sericea	9	15.222	11.278	Mean Difference	3.7345	0.0387*
Juniperus virginiana	9	0.7778	0.3889	Mean Mean	1.7138	0.2015
Liquidambar styraciflua	9	-6.111	8.3889			
Variegated						
Plant Species	Count	Mean Difference	Mean Mean	Test Across Groups	F Ratio	Prob>F
Cornus florida	9	-1	1.2778	Mean Difference	5.0264	0.0150*
Cornus sericea	9	17.222	10.278	Mean Mean	3.7255	0.0390*
Liquidambar styraciflua	9	-48.22	29.444			

Feeding Trials

Two-way ANOVAs for both years for the altered leaf color group revealed that the plant species supported significantly different amounts of bagworm feeding (2015 $f(2,1)= 62.83$, $p<0.0001$; 2016 $f(2,1)= 74.71$, $p< 0.0001$). The post hoc Tukey HSD revealed that *Viburnum* had lower feeding than both *Rhus* and *Juniperus* plants in 2015, while in 2016 feeding was greater on *Rhus* than on the other two species. The main effect of leaf trait both years indicated a significant difference between the controls and color altered plants (2015 $f(2,1)=26.13$, $p<0.0001$; 2016 $f(2,1)=33.19$, $p<0.0001$). The interaction effect was significant in 2015 ($f(2,1)=5.02$, $p=0.0086$), but not in 2016 ($f(2,1)= 2.60$, $p=0.08$). In both 2015 and 2016 two tailed t-tests revealed that *T. ephemeraeformis* fed less on all cultivars with changed leaf color (Fig. 6; *J. virginiana*, 2015 $t(27.6)=2.97$, $p=0.0061$, 2016 $t(25.2)=6.65$, $p<0.0001$; *R. copallina*, 2015 $t(26.2)=3.94$, $p=0.0005$, 2016 $t(26.45)=3.23$, $p=0.003$; *V. dentatum*, 2015 $t(15)=1.86$, $p=0.08$, 2016 $t(22.26)= 2.25$, $p=0.035$).

Two-way ANOVAs for both years for the variegated plant group showed significant differences among plant species (2015 $f(2,1)=19.95$, $p<0.0001$; 2016 $f(2,1)=36.54$, $p<0.0001$), with significant interaction terms (2015 $f(2,1)=7.34$, $p=0.0011$; 2016 $f(2,1)=4.55$, $p=0.013$). The Tukey HSD showed that in 2015 there was greater bagworm feeding overall on *L. styraciflua* than on the two *Cornus* species, and in 2016 *C. florida* had less feeding than the other two species. Overall, the variegated trait effect was significant only in 2016 ($f(2,1)= 10.38$, $p= 0.0018$). Two-tailed t-tests showed that bagworms ate significantly more of the *L. styraciflua* with variegated leaves compared to the straight species both years (Fig. 7; 2015 $t(29.97)= 4.06$, $p= 0.0003$, 2016 $t(18.64)= 3.25$, $p=0.0043$). There were no differences in feeding amounts for *C. florida* and *C. sericea* species with variegated leaves compared to the controls

(Fig. 7; *C. florida* 2015 $t(26.6)=0.51$, $p=0.614$, 2016 $t(28.5)=0.096$, $p=0.924$; *C. sericea* 2015 $t(29.9)=-1.53$, $p=0.136$, 2016 $t(23.05)=1.46$, $p=0.158$).

In 2015 the two-way ANOVA for the enhanced fruiting plant group indicated that the plant species differed significantly ($f(2,1)= 32.57$, $p< 0.0001$), and the post hoc Tukey HSD revealed that bagworms fed most on *V. corymbosum*, significantly less on *I. verticillata*, and still less on *V. dentatum*. There was no difference between plant species in 2016. The enhanced fruiting trait had no significant effect in either year and the interaction effect was significant only in 2016 ($f(2,1)= 11.62$, $p< 0.0001$). Two-tailed t tests showed that the *V. corymbosum* increased fruiting cultivar was fed on significantly more than the straight species both years (Fig. 8; 2015 $t(29.29)=2.28$, $p=0.03$, 2016 $t(23.13)=3.41$, $p=0.0024$). In 2015 there were no differences in feeding amounts for *I. verticillata* and *V. dentatum* plants with increased fruiting compared to the straight species (Fig 8; $t(27.8)=0.13$, $p=0.897$ and $t(28.7)=1.17$, $p=0.253$ respectively). However, in 2016 the cultivar of *I. verticillata* with increased fruiting was fed on significantly less than the straight species; ($t(26.3)=-2.598$, $p=0.015$) and *V. dentatum* fruiting cultivars were fed on marginally more than the straight species ($t(29.8)=1.916$, $p=0.065$) (Fig. 8).

The two-way ANOVA for the disease resistant plant group showed no differences between plant species, no effect of disease resistance, and no significant interaction in 2015. In 2016 the disease resistant group showed significant differences among plant species ($f(2,1)= 28.14$, $p<0.0001$) and the interaction effect was significant ($f(2,1)= 3.17$, $p= 0.047$). The Tukey HSD test revealed that bagworms fed most on the *C. sericea* plants, significantly less on *U. americana*, and still less on *C. florida*. Two-tailed t tests revealed that disease resistant cultivars and controls had no

difference in feeding by bagworms in 2015 and 2016 for all species except *U. americana* in 2016, which was fed on less than the straight species (Fig. 9; *C. florida* 2015 $t(29.99)=1.28$, $p=0.209$, 2016 $t(25.2)=0.82$, $p=0.418$; *C. sericea* 2015 $t(28.6)=-0.57$, $p=0.5703$, 2016 $t(28.7)=0.72$, $p=0.475$; *U. americana* 2015 $t(21.5)=-0.525$, $p=0.6053$, 2016 $t(29.7)=-2.19$, $p=0.037$).

The two-way ANOVAs for the enhanced fall foliage plant group revealed that the plant species differed significantly in 2015 and 2016 (2015 $f(2,1)= 53.97$, $p<0.0001$; 2016 $f(2,1)= 15.25$, $p<0.0001$). The post hoc Tukey HSD revealed that *V. dentatum* plants supported significantly less feeding than *C. sericea* and *A. rubrum* plants both years. In 2016 the interaction effect was significant ($f(2,1)= 2.38$, $p=0.0062$). The enhanced fall foliage trait effect was not significant for either year. In 2015 and 2016 two-tailed t tests showed no difference between bagworm feeding on cultivars with enhanced fall foliage and on the controls for all species except *A. rubrum* in 2016, which had less feeding on the cultivar than the straight species (Fig. 10; *A. rubrum* 2015 $t(26.28)=0.54$, $p=0.596$, 2016 $t(28.6)=-3.43$, $p=0.0019$; *V. dentatum* 2015 $t(29.2)=-0.47$, $p=0.6396$, 2016 $t(27.3)=-0.511$, $p=0.614$; *C. sericea* 2015 $t(29.9)=1.70$, $p=0.099$, 2016 $t(20.5)=1.299$, $p=0.208$).

The two-way ANOVA for the altered growth habit plant group showed no differences in plant species, no effect by trait, and the interaction term was not significant in 2015. In 2016 the ANOVA showed differences between plant species ($f(2,1)= 12.22$, $p< 0.0001$) and the Tukey HSD revealed that bagworms fed on *J. virginiana* plants less than the other two species. The interaction effect was also significant in 2016 ($f(2,1)= 6.76$, $p= 0.0018$). In 2015 no cultivars with altered growth habits differed from the straight species (Fig. 11; *C. sericea* $t(29.9)=1.70$, $p=0.099$; *J.*

virginiana $t(27.3)=-0.13$, $p=0.898$; *L. styraciflua* $t(25.9)=-1.10$, $p=0.281$). In 2016 the *C. sericea* cultivar with altered growth habit did not differ from the straight species, the *J. virginiana* cultivar was fed on significantly less than the straight species, and the *L. styraciflua* cultivar was fed on significantly more than the straight species (Fig. 11; *C. sericea* $t(28.7)=0.72$, $p=0.475$; *J. virginiana* $t(29.7)=-2.05$, $p=0.049$; *L. styraciflua* $t(19.3)=2.795$, $p=0.011$).

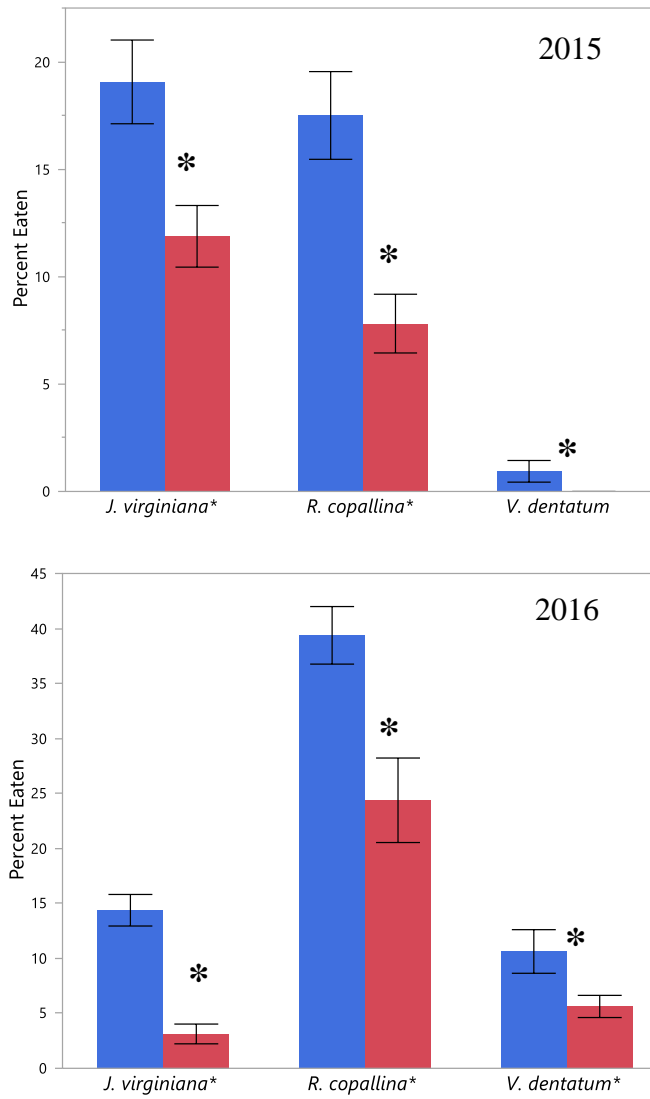


Figure 6 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of species with altered leaf color; cultivars= red, straight species= blue. Error bars = standard error from the mean. *=significant differences.

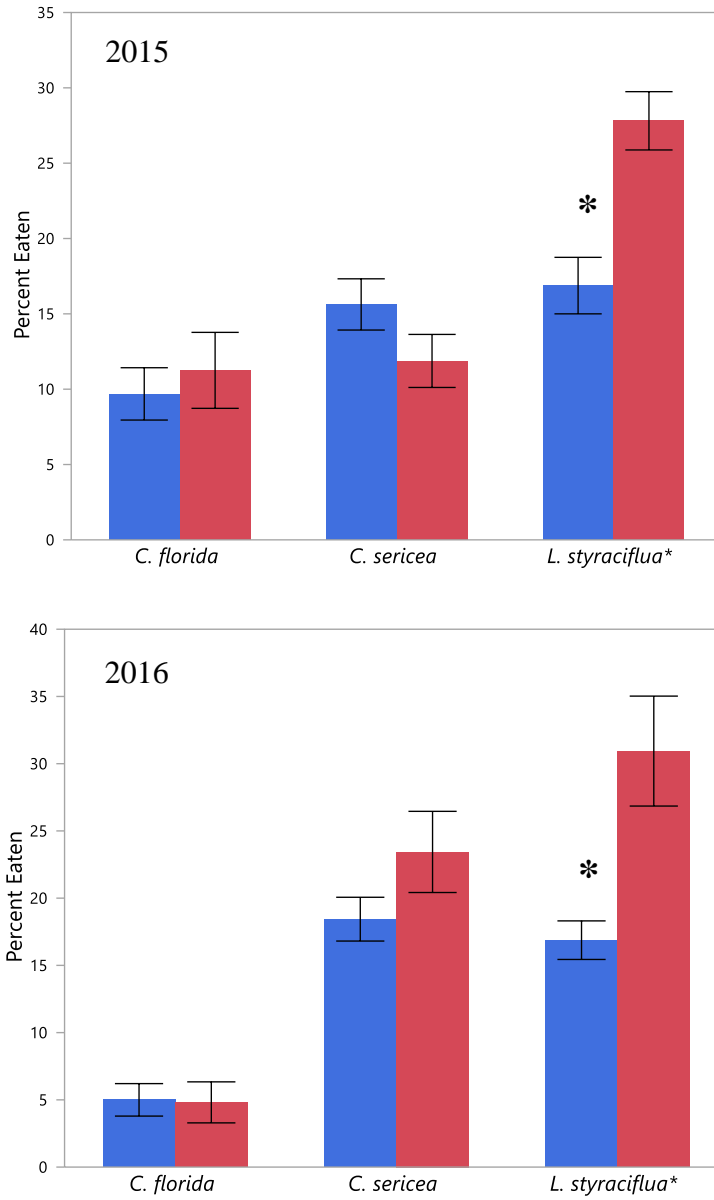


Figure 7 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of variegated species; cultivars= red, straight species= blue. Error bars = standard error from the mean. *=significant differences.

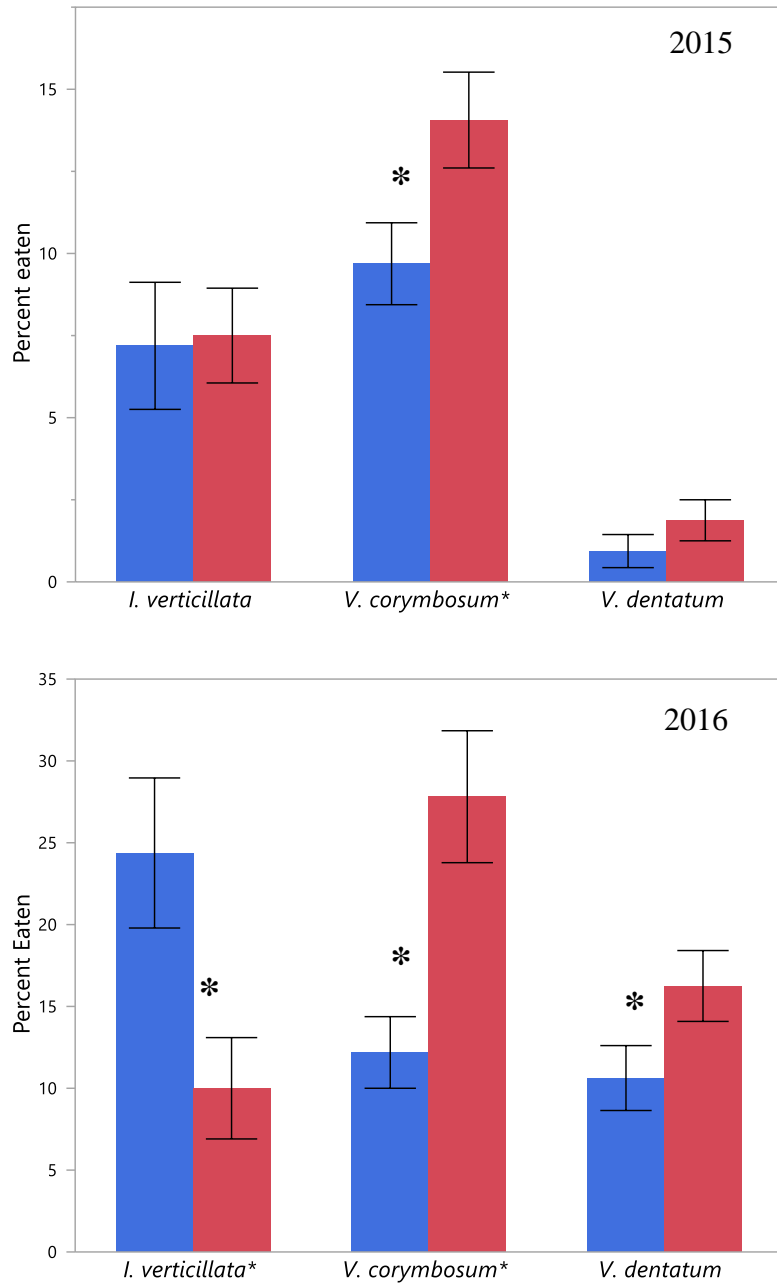


Figure 8 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of fruit altered species; cultivars= red, straight species= blue. Error bars = standard error from the mean. *=significant differences.

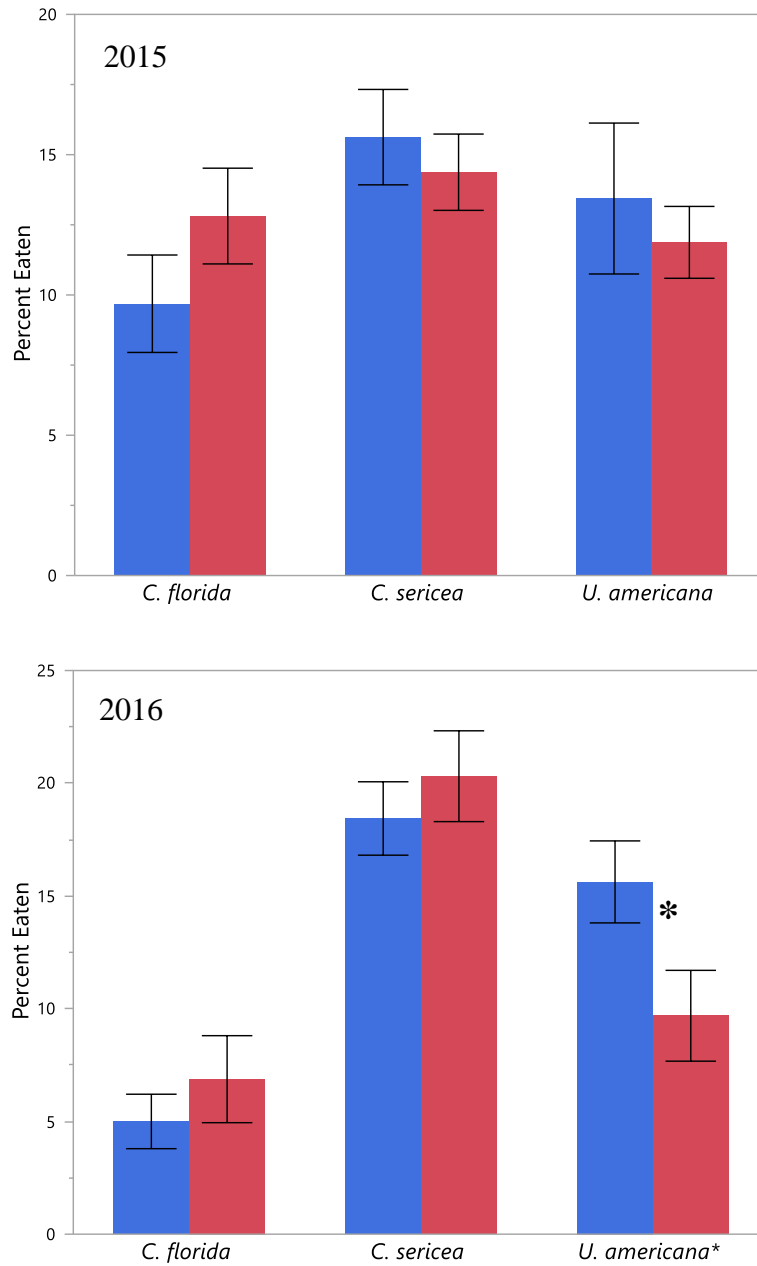


Figure 9 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of disease resistant species; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences

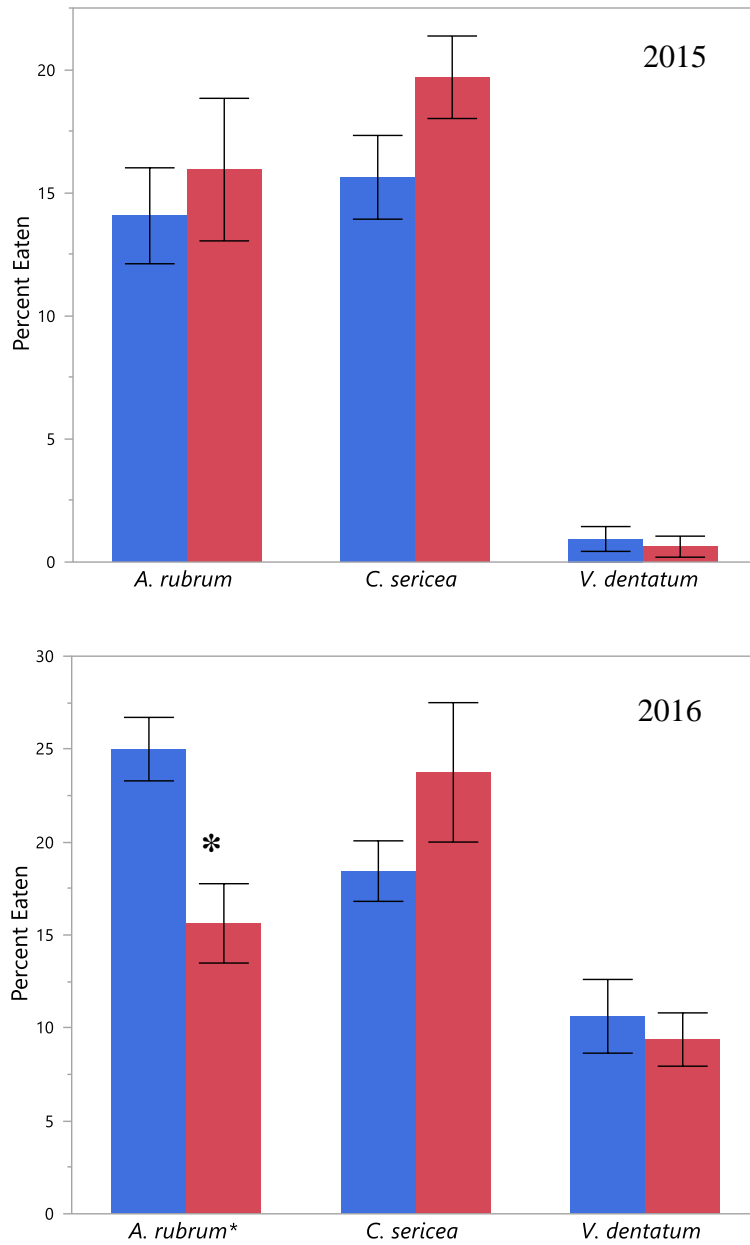


Figure 10 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of species with enhanced fall foliage; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

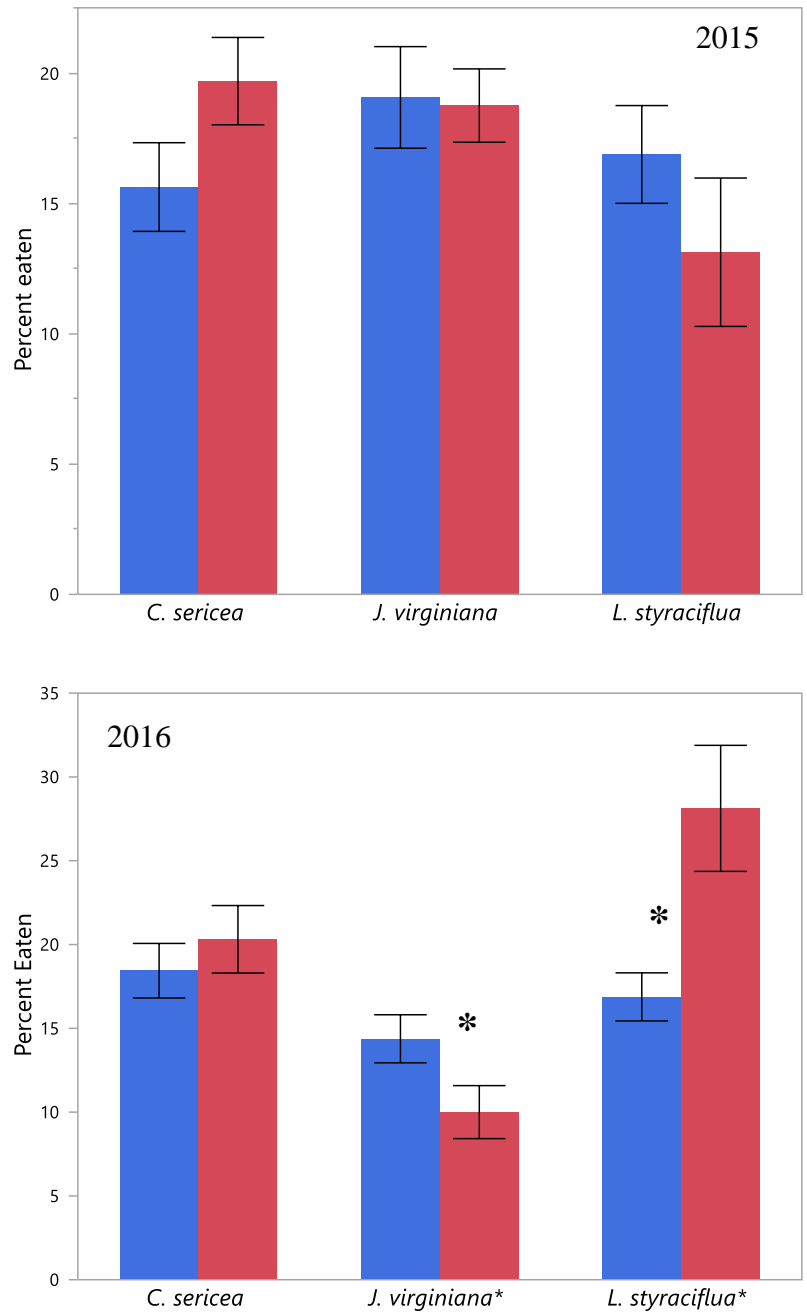


Figure 11 2015 and 2016 Bagworm feeding percent means of straight species and cultivars of species with altered growth habits; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

Seasonal Leaf Damage

The two-way ANOVA for the altered leaf color group revealed that the plant species differed significantly both years (2015 $f(2,1)= 9.12$, $p=0.0027$; 2016 $f(2,1)= 13.78$, $p=0.0002$) with more overall feeding damage on *V. dentatum* than *R. copallina* plants. The main effect of trait indicated a significant difference between the controls and the color altered plants (2015 $f(2,1)= 6.49$, $p= 0.0112$; 2016 $f(2,1)= 16.07$, $p<0.0001$). The interaction effect was significant in 2015 ($f(2,1)= 5.27$, $p= 0.022$), but not in 2016 ($f(2,1)= 2.49$, $p= 0.1152$). Two tailed t-tests revealed that insects fed significantly less on red leafed *V. dentatum* cultivars than the controls both years (Fig. 12; 2015 $t(118)= -2.56$, $p= 0.0116$, 2016 $t(122)= -2.96$, $p= 0.0037$). In 2015 there was no difference in seasonal insect feeding damage on *R. copallina* plants, but in 2016 the color altered cultivars were fed on significantly less than the green leafed controls (Fig. 12; 2015 $t(198)= -0.385$, $p= 0.701$; 2016 $t(106)= -3.67$, $p= 0.0004$).

Two-way ANOVAs for the variegated plant group showed significant differences in amount of seasonal insect damage among the plant species both years (2015 $f(2,1)= 21.74$, $p < 0.0001$; 2016 $f(2,1)= 14.31$, $p< 0.0001$) with significant interaction terms (2015 $f(2,1)= 19.68$, $p<0.0001$; 2016 $f(2,1)= 11.81$, $p<0.0001$). The post hoc Tukey HSD showed that in 2015 there was a greater amount of damage on *C. sericea* plants overall than on *L. styraciflua* and *C. florida*, and in 2016 *C. florida* had significantly less damage than the other two species. The variegated trait effect was significant only in 2015 ($f(2,1)= 40.89$, $p< 0.0001$). Two-tailed t tests showed that *C. sericea* had significantly more seasonal damage on the controls than the variegated cultivars both years (Fig. 13; 2015 $t(111.5)= -6.02$, $p< 0.0001$, 2016 $t(131)= -4.69$, $p< 0.0001$). In 2015 *C. florida* variegated cultivars had marginally less damage than the straight species and in 2016 there were no differences in damage (Fig. 13; 2015

$t(111) = -1.91, p = 0.0588$, 2016 $t(191) = 1.71, p = 0.089$). *L. sytraciflua* variegated cultivars in 2015 had no difference in damage from the control and in 2016 the cultivars had more damage than the controls (Fig. 13; 2015 $t(196) = -1.57, p = 0.117$, 2016 $t(196) = 2.04, p = 0.043$).

Two-way ANOVAs for the increased fruiting plant group revealed that the plant species differed significantly in amount of seasonal leaf damage both years (2015 $f(2,1) = 17.75, p < 0.0001$; 2016 $f(2,1) = 33.99, p < 0.0001$). The Tukey HSD revealed that *V. dentatum* plants had overall more damage than *I. verticillata* and *V. corymbosum* both years. The effect of the increased fruiting trait was significant only in 2016 ($f(2,1) = 6.99, p = 0.0084$) and the interaction terms were not significant in either year (2015 $f(2,1) = 0.524, p = 0.593$; 2016 $f(2,1) = 1.089, p = 0.337$). Two-tailed *t* tests showed no difference in seasonal insect damage between increased fruiting cultivars and controls for all species in 2015 (Fig. 14; *I. verticillata* $t(195) = -1.84, p = 0.07$, *V. corymbosum* $t(149.5) = 1.67, p = 0.097$, *V. dentatum* $t(169) = 0.158, p = 0.875$). In 2016 *I. verticillata* and *V. corymbosum* had significantly more damage on the leaves of increased fruiting cultivars than the straight species and *V. dentatum* showed no difference between cultivar and control (Fig. 14; *I. verticillata* $t(185.5) = 2.63, p = 0.0092$; *V. corymbosum* $t(126) = 3.87, p = 0.0002$; *V. dentatum* $t(187) = 1.628, p = 0.105$).

In 2015 and 2016 two-way ANOVAs for the disease resistant plant group indicated significant differences among plant species (2015 $f(2,1) = 13.36, p < 0.0001$; 2016 $f(2,1) = 24.92, p < 0.0001$), with significant interaction terms (2015 $f(2,1) = 6.58, p = 0.0015$; 2016 $f(2,1) = 4.276, p = 0.0143$). The post hoc Tukey HSD showed that in 2015 *C. sericea* had significantly more damage than *U. americana* and *C. florida* and

in 2016 there was the most damage on *C. sericea*, significantly less on *U. americana*, and still less on *C. florida*. The disease resistant trait effect was significant only in 2016 ($f(2,1)=9.94$, $p=0.0017$). Two-tailed t tests revealed that in both years *C. sericea* had significantly more seasonal damage on the control plants than the disease resistant cultivars (Fig. 15; 2015 $t(143)=-2.88$, $p=0.0046$, 2016 $t(169)=-3.33$, $p=0.0011$). There were no differences in amount of damage between cultivars and straight species for *U. americana* in either year (Fig. 15; 2015 $t(159)=0.495$, $p=0.621$, 2016 $t(195)=-0.196$, $p=0.845$). In 2015 *C. florida* disease resistant cultivars had significantly more damage than the controls and in 2016 the controls had more damage than the cultivars (Fig. 15; 2015 $t(177)=2.242$, $p=0.026$, 2016 $t(119)=-3.14$, $p=0.0021$).

The two-way ANOVAs for both years for the enhanced fall foliage plant group revealed that the plant species differed significantly (2015 $f(2,1)=14.46$, $p<0.0001$; 2016 $f(2,1)=17.26$, $p<0.0001$). The Tukey HSD showed that in 2015 *V. dentatum* had significantly less seasonal damage than *A. rubrum* and *C. sericea*, while in 2016 *C. sericea* had significantly more damage than the other two species. The main effect of trait both years indicated a significant difference between controls and cultivars with enhanced fall foliage (2015 $f(2,1)=7.36$, $p=0.0069$; 2016 $f(2,1)=12.895$, $p=0.0196$). The interaction effect was significant only in 2016 ($f(2,1)=3.96$, $p=0.0196$). In both 2015 and 2016 two-tailed t tests showed that *C. sericea* had significantly more seasonal leaf damage on the control plants than the cultivars with enhanced fall color (Fig. 16; 2015 $t(169)=-2.77$, $p=0.0063$, 2016 $t(155.5)=-3.38$, $p=0.0009$). There was no difference in amount of damage on *A. rubrum* plants in 2015, but in 2016 there was significantly more damage on the control plants compared to the cultivars (Fig. 16; 2015 $t(174)=-0.184$, $p=0.855$, 2016 $t(190)=-2.044$, $p=0.042$). In 2015 *V. dentatum*

controls had marginally more damage compared to the cultivars with enhanced fall foliage and in 2016 there was no difference between cultivars and controls (Fig. 16; 2015 $t(141) = -1.93$, $p = 0.0554$, 2016 $t(192) = -0.326$, $p = 0.744$).

Two-way ANOVAs for the plant group with altered growth habit indicated significant differences between plant species in 2015 and marginal differences between species in 2016 (2015 $f(2,1) = 9.87$, $p = 0.0018$; 2016 $f(2,1) = 3.82$, $p = 0.0514$) and the interaction term was significant only in 2015 ($f(2,1) = 14.815$, $p = 0.0001$). The LSD test showed that the *C. sericea* plants had overall more damage than *L. syraciflua* plants. The main effect for trait for both years indicated no difference between controls and cultivars with altered growth habits. Two-tailed t tests showed that only *C. sericea* cultivars with altered growth habits in 2015 differed from the control plants with significantly less insect damage (Fig. 17; *C. sericea* 2015 $t(142) = -3.47$, $p = 0.0007$, 2016 $t(193) = 0.253$, $p = 0.80$; *L. syraciflua* 2015 $t(133) = 1.86$, $p = 0.0651$; 2016 $t(191) = 0.814$, $p = 0.417$).

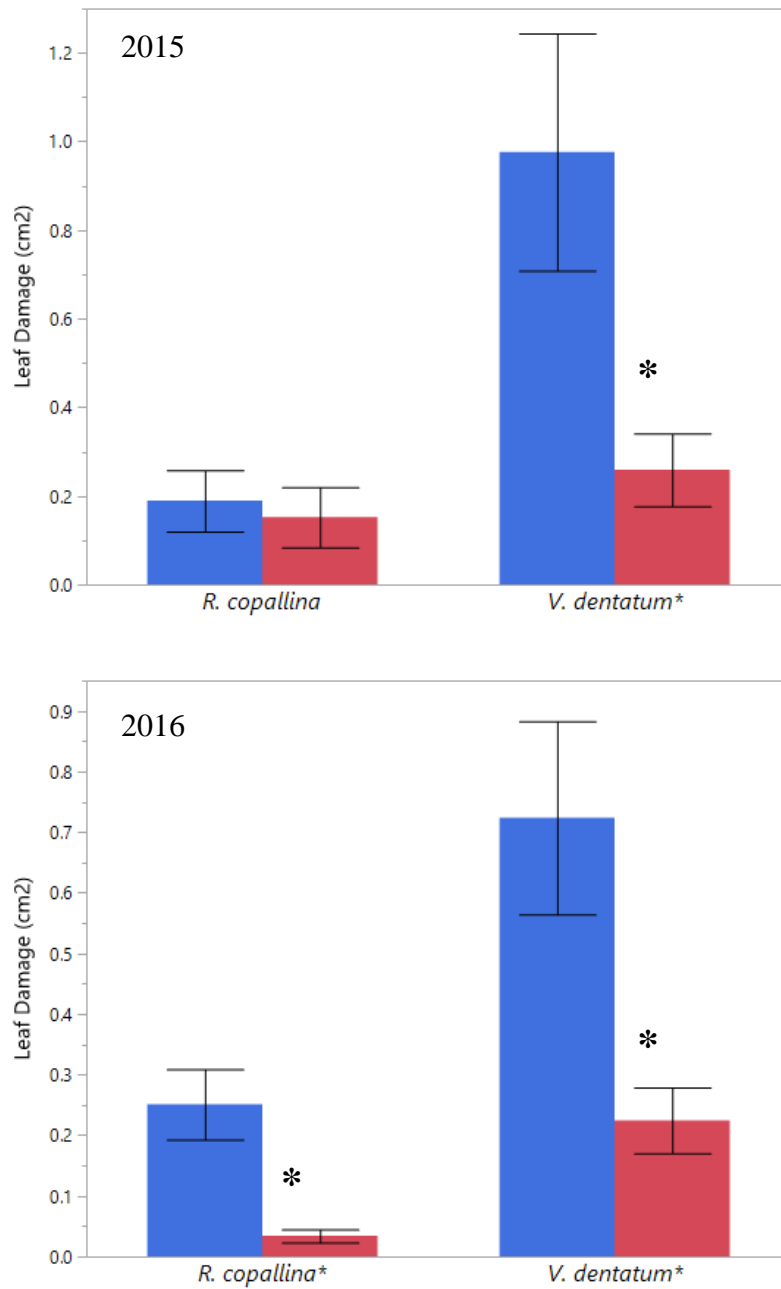


Figure 12 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the altered leaf color plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

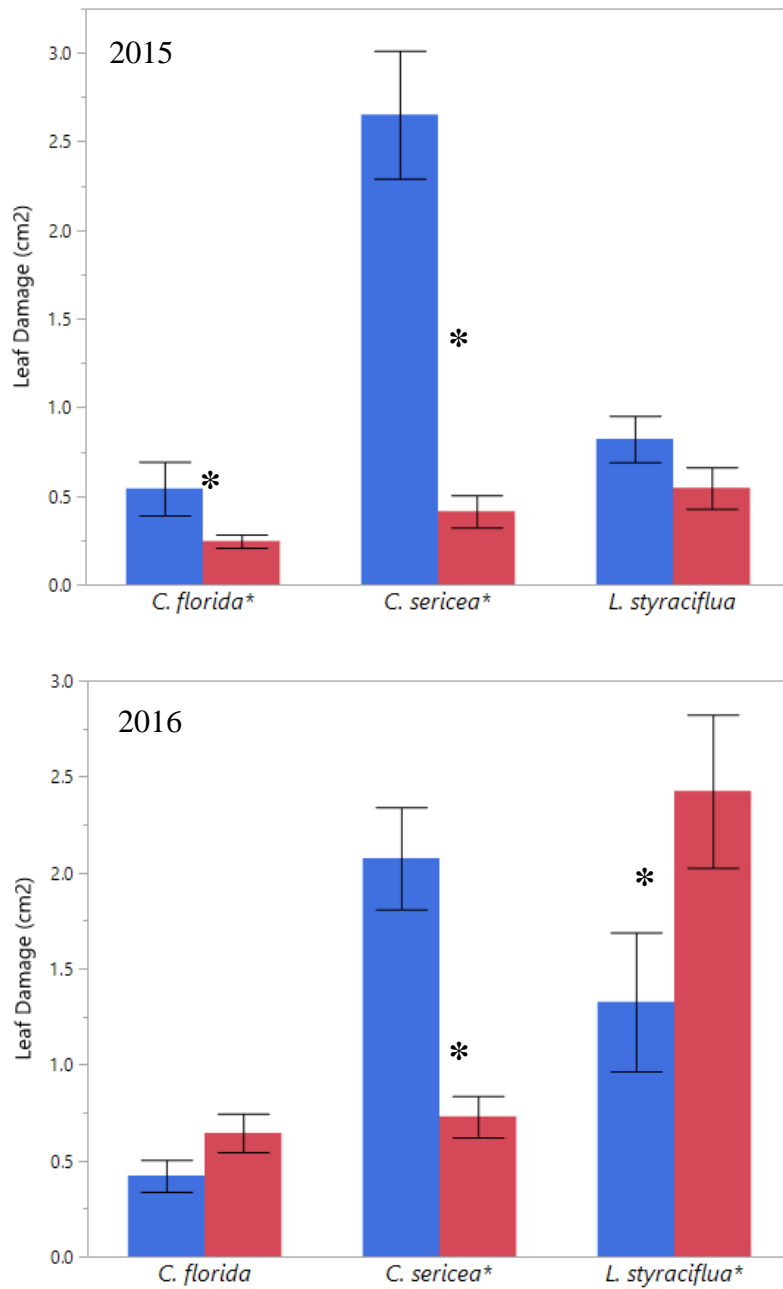


Figure 13 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the variegated plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

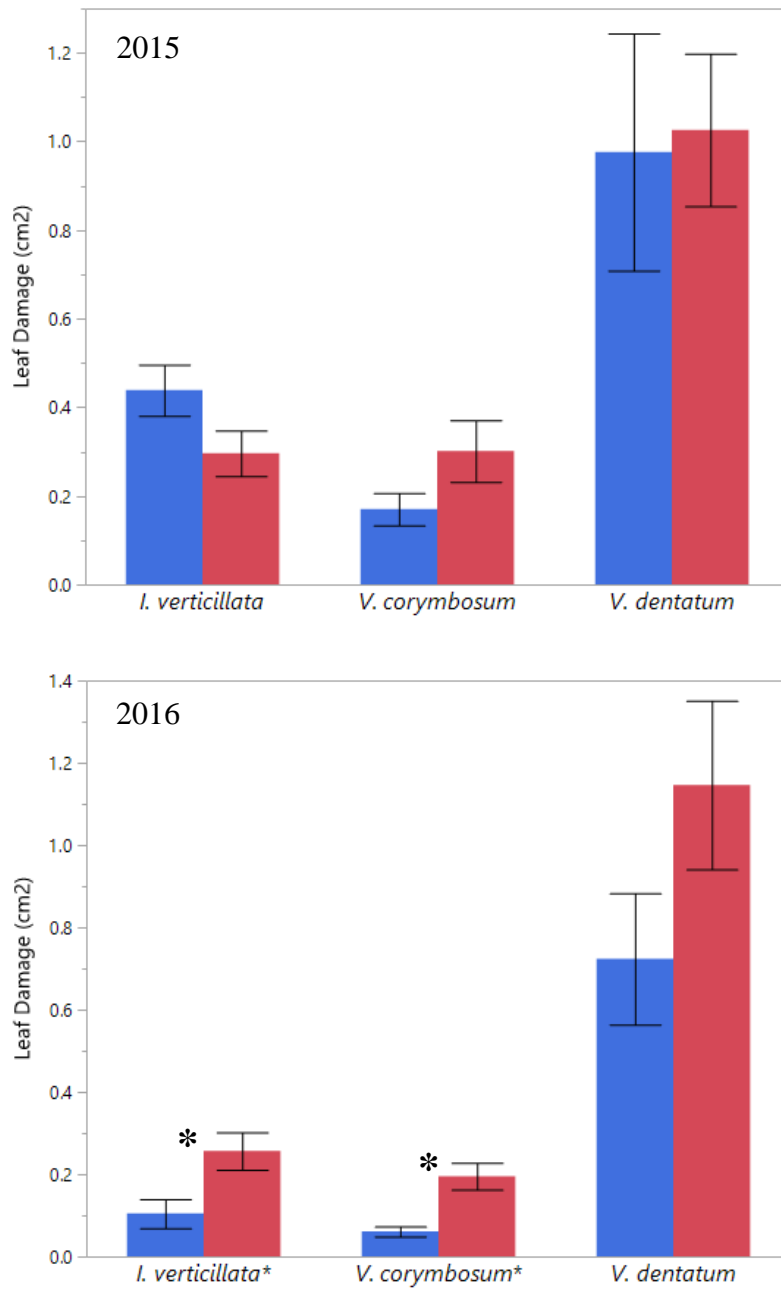


Figure 14 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the enhanced fruiting plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

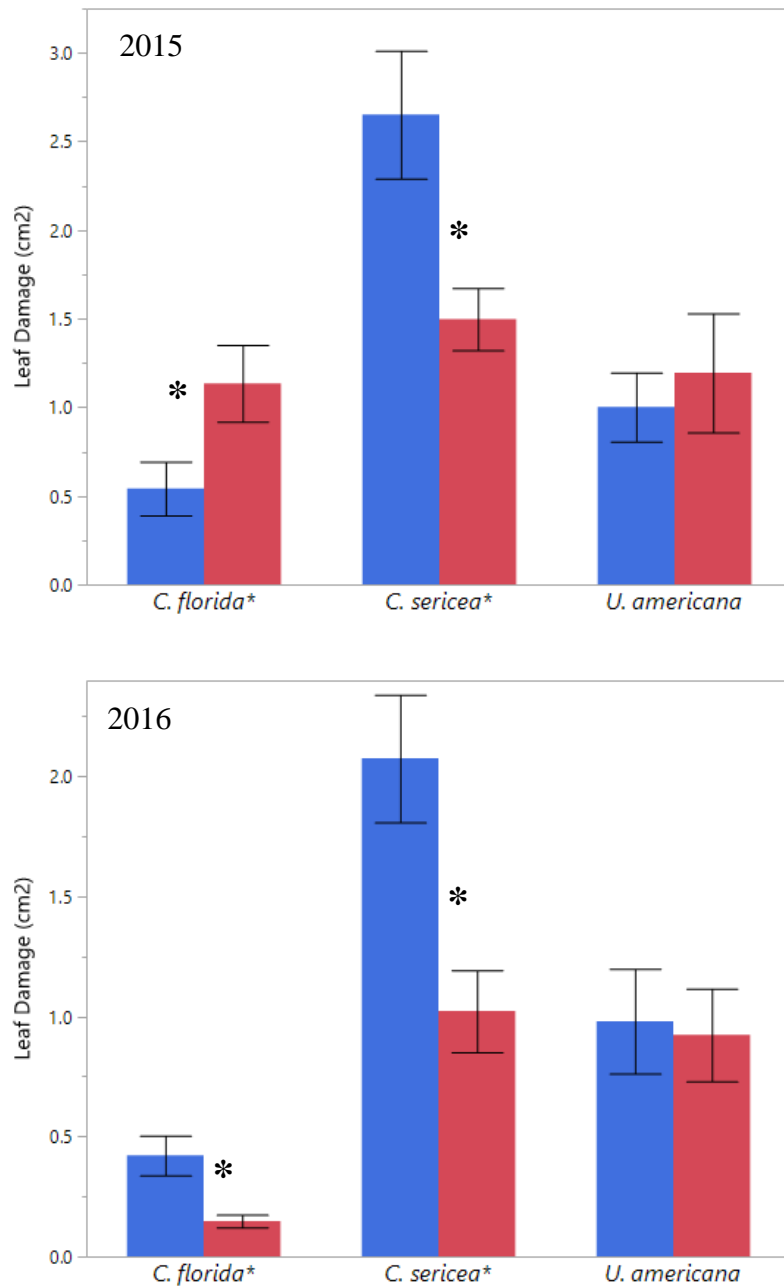


Figure 15 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the disease resistant plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

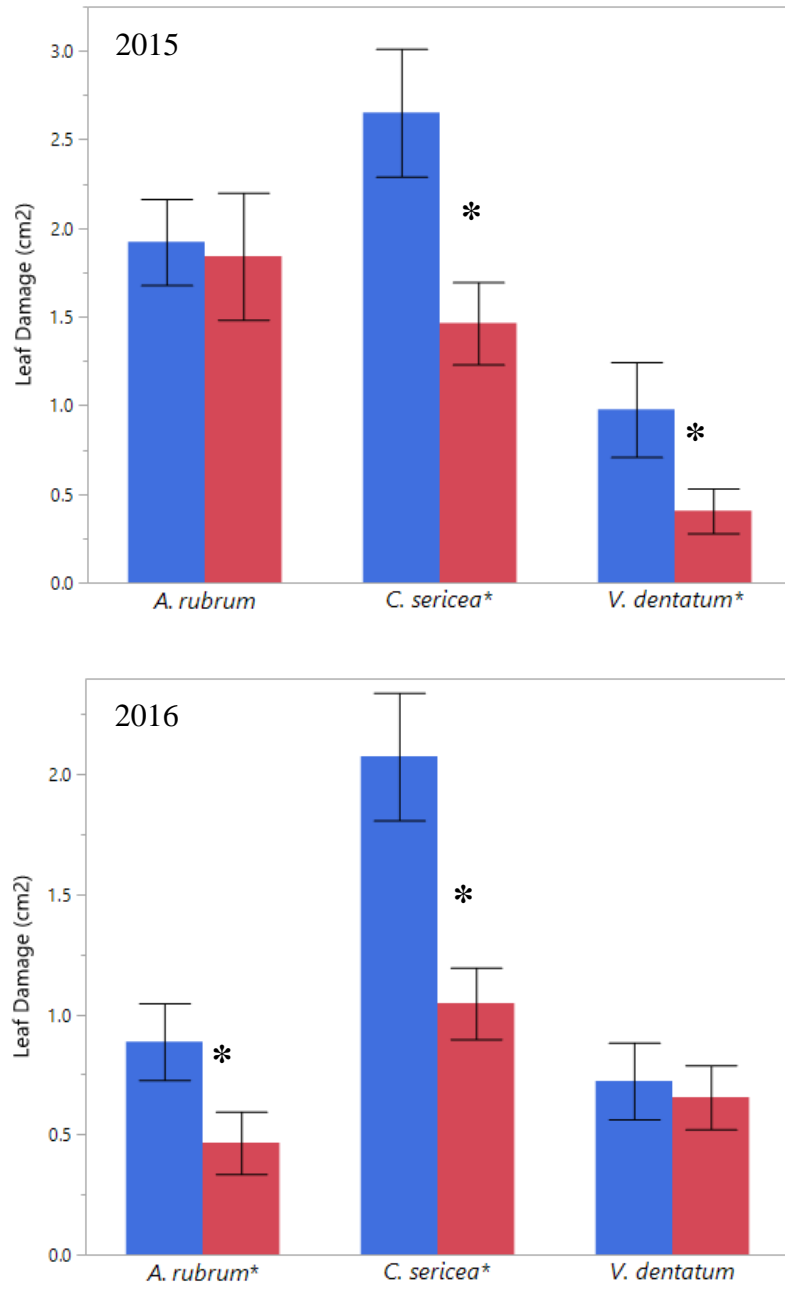


Figure 16 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the fall foliage plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

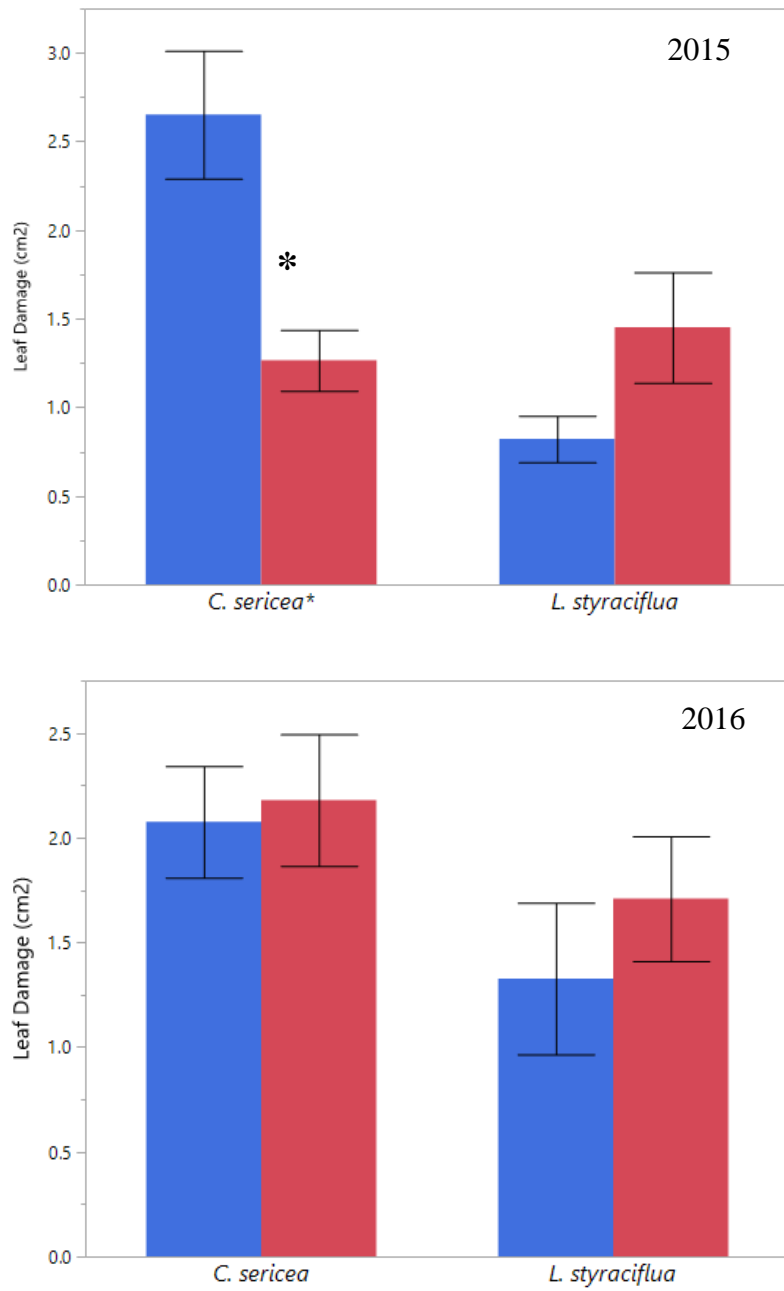


Figure 17 2015 and 2016 seasonal leaf damage means of straight species and cultivars of the altered growth habit plant group; cultivars= red, straight species= blue. Error bars = standard error from the mean. *= significant differences.

Discussion

This study addresses the potential use of native plant cultivars for wildlife value in a garden setting. I looked at the effects of six common traits in cultivar selection on insect herbivore feeding capabilities. To test these traits I set up three experiments; field collections, feeding trials using a known generalist caterpillar, and seasonal leaf damage analyses in the field. It is important to reiterate that plant species within the trait groups were expected to and often did differ from each other because of their different structures and chemistries; however, I was testing whether insects responded the same way to the trait changes on different plant species. Many traits did not show patterns of deterrence or preference overall while several traits differed significantly from the wild type control plants in almost every test. In some cases insect trait preferences differed by plant species, with one species' control plants being preferred when others' cultivars were preferred or showed no difference.

The effect of a plant trait on insect preferences in the seasonal leaf damage analyses may have been biased by the presence of one particularly abundant insect species. For example, *Cornus sericea* controls had more end of season leaf damage than their cultivar counterparts, but the other species within the same trait groups often showed a different or no response. *Cornus sericea* controls were also preferred by caterpillars in the field test (when other species within the same trait group had no difference or showed a preference for the cultivars), but were not shown to be overwhelmingly preferred by the total herbivores (caterpillars and adults) collected or by bagworm caterpillars. Though no single caterpillar species was significantly more abundant on the controls, a host-specific, species of Tenthredinid sawfly, the gregarious dogwood sawfly, *Macremphytus tarsatus* Say occurred in masses on control *C. sericea* plants throughout the growing seasons. *M. tarsatus* did not feed on

any species other than *C. sericea* in this study and caused obvious leaf damage. *M. tarsatus* secretes a defensive waxy coating that allows it to feed gregariously with little predation, causing significant aesthetic damage (Codella and Raffa 1993, Klingeman et al. 2007). In a study examining dogwood sawfly preferences on different *Cornus* species, Klingeman et al. (2007) found yellow-twig *Cornus sericea* ‘Flaviramea’ to be highly susceptible to the larvae compared to the red-twig form. They did not, however, compare other cultivars to wild type of the *Cornus* species. The only *C. sericea* with the yellow-twig form in my study was the variegated cultivar ‘silver and gold’ which was not attractive to the sawfly larvae. The overabundance of this sawfly on the controls in *C. sericea* may have biased the leaf damage analyses against cultivars for some of the traits considered. Furthermore, leaf damage tests may not be best indicator of host plant quality because insects may actually feed more on plants low in nutrient content (carbon and nitrogen) in order to acquire needed nutrients and less on highly nutritious plants because they acquire the required nutrients sooner (Awmack and Leather 2002).

Change in Leaf Color

In all tests, red, blue, or purple-leaved cultivars consistently deterred insect feeding. Many hypotheses have been presented as to why leaves with pigments other than green are avoided. Chemical defenses, such as feeding deterrents, digestibility inhibitors, and toxins, can alter palatability and deter herbivory (Becklin 2008, Dimarco et al. 2012, Fürstenberg-Hägg et al. 2013). Most plant pigments are secondary metabolic compounds which are not used in primary metabolism and do not participate in the growth of a plant, but may serve as physiological defenses against herbivore attacks (Schaefer and Rolshausen 2006, Manetas 2006, Lev-Yadun and

Gould 2009, Döring et al. 2009, Price et al. 2011, Cooney et al. 2012). It also is possible that red leaf coloration signals the presence of defensive compounds and/or serves as a warning of lack of nutrients that deters insect feeding behavior (Lev-Yadun and Gould 2009, Döring et al. 2009, Chen and Huang 2013).

The protective function of pigments such as anthocyanins and carotenoids has been a growing study subject over recent years. It is likely that pigmentation evolved in response to various stressors and provides defensive chemicals that influence the abundance and diversity of herbivorous insects (Schaefer and Rolshausen 2006, Lev-Yadun and Gould 2009, Döring et al. 2009). Schaefer and Rolshausen (2006) discuss three main pigment classes that control the coloration found in most plants; chlorophyll, anthocyanins, and carotenoids. Chlorophyll creates the green color of plants, responsible for light acquisition and photosynthesis. Anthocyanins create the reds, blues, purples, and other such colors, which were originally thought to only protect against UV radiation as well as cold temperatures (Schaefer and Rolshausen 2006). Carotenoids make up yellows and some reds and are thought to be important in light acquisition and photoprotection. Tannins, often in brownish plants, also protect against biotic and abiotic stresses and have been shown to be herbivore deterrents (Boeckler et al. 2014).

Anthocyanin pigmentation makes up the majority of color diversity in a variety of plant parts including roots, stems, leaves, and flowers. Schaefer and Rolshausen (2006) describe the likelihood that insect herbivores that can see the red spectrum would not attempt to eat a plant with anthocyanin pigmentations and those that cannot see red would leave after tasting the plant. They further discuss the correlation between the defensive strengths of plants and anthocyanin coloration. Ramírez et al.

(2007) showed aphid preference for green leaves over red colored leaves in autumn-leaved plants. Döring et al. (2009) investigated the response of aphids to different color pigments and found that even though aphids do not have red photoreceptors they still were able to differentiate red from green leaves and found that red leaves were much less attractive and actively avoided by winged aphids. Thus, some herbivores without the ability to actually see red pigments are still able to distinguish and avoid red leafed plants.

Whether the presence of anthocyanic pigments is a warning signal of increased defensive toxins or decreased leaf nutrition or mimicry of toxic compounds has been argued recently. It is likely that anthocyanins function in both capacities. Karageorou et al. (2008) discuss the strong positive correlation between plant redness and plant defensive potential and found that red signals are both honest and mimetic signals. Young red leaves were found to have a weak positive correlation with defensive chemical compounds, so they hypothesize that the young leaves may be using more of a mimicry strategy of toxic red leaves to avoid herbivory. Young leaves did not necessarily have the same defensive compounds as old leaves but still deterred feeding more than green young leaves.

Lev-Yadun and Gould (2009) discuss the broader capacity of a leaf's potential to impede insect feeding ability through mimicry; leaves with dark pigment spots may serve as anti-herbivore defenses by mimicking ant or aphid infestations that would be avoided by searching insects. They suggest a change in leaf color could reduce the ability of an herbivore to be cryptic as it eats. Red leaves could reduce the effectiveness of aposematic warning coloration in an insect, or the color could camouflage the plant against the landscape making it difficult for the insect to identify

it as a food source (Lev-Yadun and Gould 2009, Reeves 2011, Chen and Huang 2013). Cooney et al. (2012) found that red leaf coloration could be attributed to aposematic coloration. Their study species, *Pseudowintera colorata* (an evergreen shrub), was not eaten when it had red leaves or leaves with red margins. However, when the visual cues were removed in the lab experiment, insects did not avoid them. They concluded that visual cues of chemical defenses had a greater effect on feeding behavior than olfactory cues. They did, however, find that leaves with red coloration had higher concentrations of anthocyanins and concluded that these chemical compounds are likely a signal of higher investments in defensive compounds.

Regardless of whether shrubs and trees with red leaves are better chemically defended against herbivores, have poor nutritional content, or mimic plants with such traits; they are avoided by insect herbivores. Red-leafed cultivars, therefore, are not a good option when planting to support insect-based food webs.

Variegation

Cultivars with variegated leaves were preferred over wild type plants in the field tests for total herbivore abundance and species richness as well as caterpillar species richness; there were, however, no differences in overall caterpillar abundance. In some cases, insect preference depended on the species of plant. There was an overall preference for *Liquidambar styraciflua* variegated cultivars across almost every test (field trails, feeding trials, and 2016 leaf damage). *Cornus florida* and *Cornus sericea* variegated cultivars did not differ compared to straight species in the feeding trials. *C. sericea* (as stated above) had significantly more damage on the straight species plant in the seasonal leaf damage analysis, while the *C. florida* straight species had marginally more damage or no difference.

Leaf variegation occurs when local regions on the surface of the leaf have reduced chlorophyll, resulting in lightened patterns (Smith 1986, Campitelli et al. 2008). Studies of wild populations of naturally occurring leaf variegation have often shown a deterrence of herbivore feeding (Smith 1986, Lev-Yadun et al. 2004, Campitelli et al. 2008, Soltau et al. 2009, Lev-Yadun 2009, 2014). Campitelli et al. (2008) assessed whether variegation in wild populations of *Hydrophyllum virginianum* reduced herbivore damage. They found significantly more damage on non-variegated leaves. It is likely that a variegated plant would have lowered ability to photosynthesize due to its lack of chlorophyll and therefore lower productivity and nutrition (Smith 1986). I did not measure leaf nutritional quality or defensive compounds, but the results of my study suggest that reduced pigmentation may also have reduced defensive compounds in some plant species. Studies investigating the attractiveness of autumn leaves to aphids have shown an increased preference for yellowed leaves, with reduced chlorophyll, over red and green leaves (Döring et al. 2009, Holopainen et al. 2009). The nutrient-translocation hypothesis suggests that yellowing leaves improve the availability of nutrients in phloem sap after chlorophyll degradation, making them highly attractive to sucking insects (Holopainen et al. 2009) which may explain why I found higher amounts of herbivory on variegated plants.

Lack of color in variegated leaves may signal lack of nitrogen and poor nutritional quality for chewing insects but it may also signal fewer defensive compounds (Holopainen et al. 2009). Studies have shown that insects will often eat more of a plant with lower nutritional value to make up for what it missing in the diet (Hochuli 1996, Awmack and Leather 2002). This may account for excess feeding found on some of the variegated cultivars. A future study looking into the nutritional

quality of variegated cultivars compared to straight species plants would be useful in understanding whether variegated leaves, though eaten, impact herbivore fitness.

Fruit Enhancement

Cultivars with enhanced fruiting tended to perform no differently from the wild types or, in some cases, were preferred (with one case of deterrence). In 2016 the *I. verticillata* cultivar was the only plant species in the trait group to deter caterpillar feeding. Leaves collected in 2016 for the feeding trials were somewhat older than leaves in 2015. Leaf chemistry as well as leaf toughness will likely vary with leaf age and can have a strong influence on neonate caterpillars (Hough-Goldstein and Pimentel 1978) which may explain the deterrence on *I. verticillata* cultivars in 2016 and not in 2015. However there was more feeding on *I. verticillata* plants in 2016 overall than in 2015 so there may be other factors such as chemical differences involved in this case of deterrence. *V. corymbosum* cultivars were preferred by bagworms in 2015 and 2016 and had more damage in 2016 than the straight species. Increased fruiting cultivars also had higher herbivore abundance than straight species. Selection for enhanced fruiting seeks to create food plant cultivars that produce high yields and large palatable fruits (Plucknett and Smith 1986, White and Bus 1998). Because my study compared native plant cultivars with parent species it is not readily comparable to agricultural studies where crop plants are usually dramatically different from their wild types. In a study on cranberry cultivars (also a *Vaccinium* and native to the Northeast) compared to wild type cranberries, Rodriguez-Saona et al. (2011) found that caterpillars performed best on the highest yielding cultivars. They suggest that breeding for increased fruiting has compromised the plant's defenses.

It is important to note that my study only focused on foliage feeder responses to cultivars and did not measure the response of frugivorous insects to enhancing fruit production. In some cases excess damage to the leaves of fruiting plants causes induced responses that may reduce fruit palatability and development, and thus affect fruit-frugivore interactions (Whitehead and Poveda 2011). Studying the effect of fruit-enhanced cultivars on frugivores would be necessary to understand their overall ecological value.

Disease Resistance

In this study there was no pattern of preference or deterrence of herbivores by disease resistant cultivars across the tests or the plant species. In the field test total herbivore collections showed significantly higher abundance and species richness on the disease resistant cultivars and there was no difference in abundance or species richness of caterpillars. Feeding trials in 2015 showed no differences in bagworm feeding and in 2016 only the *U. americana* cultivar was shown to deter bagworm feeding. The deterrence in 2016 may be because the leaves were collected later in the growing season and the elms were more mature the second year. In the seasonal leaf damage analysis, as with other cases, *C. sericea* straight species had more damage than the disease resistant cultivars, most likely due to the presence of the gregarious dogwood sawfly, *M. tarsatus*. In 2015 *C. florida* cultivars attracted more insect feeding, but in 2016 the straight species supported more feeding. In both years *U. americana* cultivars had did not differ from the straight species in total seasonal insect use.

Previous studies have shown some connection between disease resistance in plants and insect deterrence. However, these studies tend to be vector-specific. Tree

pathogens are often spread by insect vectors such as the bark beetles *Scolytus multistriatus* Marsham and *Hylurgopinus rufipes* Eichhoff which spread Dutch Elm Disease (DED) (Smalley 1993). Some varieties of Asian Elms have been found to be highly resistant to DED and black leaf spot while simultaneously resistant to the elm-leaf beetle, *Xanthogaleruca luteola* Müller, an invasive defoliator (Smalley and Guries 1993, Smalley and Guries 2000). Since this discovery, there has been a push for breeding programs to combine disease defenses with insect resistance in elm cultivars due to the extremely detrimental effects DED has had on native elm populations (Townsend and Santamour 1993, Townsend and Douglass 2004, Merkle et al. 2007). Some American elm cultivars that are DED resistant have also shown some resistance to the elm-leaf beetle (Santamour and Bentz 1995).

Dogwood anthracnose is a disease that is caused by the fungus *Discula destructive* Redlin. It can have high mortality rates in *Cornus florida* plants, impacting native understories, and is also thought to be exotic in origin (Redlin 1991, Holzmueller et al. 2006, Merkle et al. 2007). Though there is no known vector, it is thought that spores are spread by splashing water and potentially birds and insects (Holzmueller et al. 2006). *Cornus* species in general, including *C. sericea* are prone to diseases such as powdery mildew, leaf spot, and spot anthracnose that tend not to be as detrimental to the species, but still cause reductions in the market value of infected shrubs (Mmbaga and Sauvé 2004). Many *Cornus* cultivars have been released that are effectively resistant to one or more of these diseases (Mmbaga and Sauvé 2004).

In my study, the *Ulmus* and *C. florida* disease resistant cultivars mostly did not deter herbivorous insects. This is an important result for elms and flowering dogwoods because of the more detrimental impacts of diseases that affect them than those

common on *Cornus* species. If disease resistant plants can deter the disease spreading vector without deterring other insect herbivores important to food web health, it would strengthen restoration efforts.

Enhanced Fall Color

Cultivars with enhanced fall color did not differ from wild type plants in the field trials or the 2015 feeding trials. In 2016 only *A. rubrum* differed, with more bagworm feeding on the control. This may be because leaf selection that year occurred somewhat later in the growing season and, as mentioned earlier, leaf chemistry and toughness can vary by leaf age and can have a strong influence on neonate caterpillars (Hough-Goldstein and Pimentel 1978). The trait difference may have not impacted feeding until later in the season. In seasonal leaf damage results, *C. sericea* cultivars had significantly less damage than the straight species due to the high number of *M. tarsatus* on wild type plants. However, enhanced fall color did have an effect both years indicating that the cultivars with enhanced fall foliage were not damaged as much as the control (in 2015 *Viburnum* controls had marginally more damage and in 2016 *Acer* controls had significantly more damage). The reason for this may parallel that of the reasons red leafed cultivars deter insect feeding. I did not quantify the amounts of reds, oranges or yellows in the leaves of our fall colored plants, but all insect collections were made prior to leaf senescence and color change. Any deterrence would most likely be due to a chemical difference in leaves that precedes fall color change.

Altered Growth Habit

Cultivars with altered growth habits rarely differed from the control plants. Only in the 2016 feeding trials did bagworms feed preferentially on *J. virginiana*

straight species and *L. styraciflua* cultivars; and in the 2015 seasonal damage test there was more damage on *C. sericea* straight species. The differences by year in the feeding trials may be due to the postponed leaf collection that year. Insect herbivores choose plants that they can recognize through a distinguishing trait (shape, color, smell, etc.) after extensive co-evolution (Ehrlich and Raven 1964, Lev-Yadun et al. 2004). Plant defenses may be expressed in traits that warn insects not to attempt to eat them, such as shape, color, or smell (Karageorou et al. 2008, Lev-Yadun and Gould 2009). Shape variation in leaves may reduce herbivory if it is not part of the insect's search image (Campitelli et al. 2008). My study, however, suggests that cultivars with changed growth habits are not altered in ways that deter insects from identifying and feeding on them which could be beneficial for plantings in limited space. This makes sense since young plants always have smaller habit than old plants, and that doesn't deter herbivory.

Conclusions

With the great diversity of plants and the insects that eat them, there is also a great diversity in the ways in which insects acquire nutrients and are affected by moderate to extreme trait changes. Some insects feed gregariously on many plant parts, while others feed specifically on parts of plants that are nutrient rich (Hochuli 1996, Awmack and Leather 2002). The amount of feeding damage may not be the best way to indicate host plant quality or at least should not be the sole justification of whether or not a plant will contribute to complex food webs. Further investigation into the nutritional quality, defensive chemicals, and mechanical properties (such as leaf toughness) of cultivars compared to straight species would be useful in understanding why in some cases insects showed a preference and/or deterrence for a trait and not in

others. Additional inquiry into the effect of traits on non-herbivorous species, such as frugivores, is also important to understanding any other potential impacts on food webs. This study asked whether certain types of trait selection in plants will influence insect feeding. Although different plant and insect species can respond differently to trait changes, my results suggest that when planting for complex food webs one should be cautious with cultivars that have been selected for red/purple/blue (anthocyanin pigment) leaves; other cultivar traits did not offer a consistent pattern that could be extrapolated to other plant species.

REFERENCES

- Awmack, C.S. and S.R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. *Annu.Rev.Entomol.* 47:817-844.
- Baskin, Y. 2002. The Greening of Horticulture: New Codes of Conduct Aim to Curb Plant Invasions. *BioScience* 52:464-471.
- Becklin, K.M. 2008. A coevolutionary arms race: understanding plant-herbivore interactions. *The American Biology Teacher* 70:288-292.
- Boeckler, G.A., M. Towns, S.B. Unsicker, R.D. Mellway, L. Yip, I. Hilke, J. Gershenzon, and P.C. Constabel. 2014. Transgenic upregulation of the condensed tannin pathway in poplar leads to dramatic shift on leaf palatability for two tree-feeding Lepidoptera. *Journal of Chemical Ecology* 40:150-158.
- Brzuszek, R.F. and R.L. Harkess. 2009. Green industry survey of native plant marketing in the southeastern United States. *HortTechnology* 19(1):168-172.
- Burghardt, K.T., D.W. Tallamy and W.G. Shriver. 2008. Impact of Native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology* 23:219-224.
- Campitelli, B.E., I. Stehlik and J.R. Stinchcombe. 2008. Leaf variegation is associated with reduced herbivore damage in *Hydrophyllum virginianum*. *Botany* 86:306-313.

- Chen, M.S. 2008. Inducible direct plant defense against insect herbivores: A review. *Insect Science* 15:101-114.
- Chen, Y.Z. and S.Q. Huang. 2013. Red young leaves have less mechanical defense than green young leaves. *Oikos* 122:1035-1041.
- Codella, S. G. and K. F. Raffa. 1993. "Defense strategies of folivorous sawflies." *Sawfly life history adaptations to woody plants. Academic Press, San Diego*: 261-294.
- Cooney, L.T., J.W. van Klink, N.M. Hughes, N.B. Perry, H.M. Schaefer, I.J. Menzies and K.S. Gould. 2012. Red leaf margins indicate increased polygodial content and function as visual signals to reduce herbivory in *Pseudowintera colorata*. *New Phytologist* 194:488-497.
- Dimarco, R.D., C.C. Nice and J.A. Fordyce. 2012. Family matters: effect of host plant variation in chemical and mechanical defenses on a sequestering specialist herbivore. *Oecologia* 170:687-693.
- Dirr, M.A. 2011. *Dirr's Encyclopedia of Tree & Shrubs*. Timber Press.
- Döring, T.F., M. Archetti and J. Hardie. 2009. Autumn Leaves Seen Through Herbivore Eyes. *Proceedings of the Royal Society B: Biological Sciences* 276.1654: 121-127.
- Dyer, L. A., T. R. Walla, H. F. Greeney, J. O. Stireman III and R. F. Hazen. 2010. Diversity of Interactions: A Metric for Studies of Biodiversity. *Biotropica* 42: 281-289.

- Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and Plants: A study in coevolution. *Evolution* 18:586-608.
- Fordyce, J.A., C.C. Nice, C.A. Hamm and M.L. Forister. 2016. Quantifying diet breadth through ordination of host association. *Ecology* 97(4):842-849.
- Forister, M.L., L.A. Dyer, M.S. Singer, J.O. Stireman III and J.T. Lill. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. *Ecology* 93:981-991.
- Fortuna, T.M., J.B. Woelke, C.A. Hordijk, J.J. Jansen, N.M. van Dam, L.E.M. Vet and J.A. Harvey. 2013. A tritrophic approach to the preference-performance hypothesis involving an exotic and a native plant. *BiolInvasions* 15:2387-2401.
- Fürstenberg-Hägg, J., M. Zagrobelny and S. Bak. 2013. Plant defense against insect herbivores. *International Journal of Molecular Sciences*. 14:10242-10297.
- Gols, R. 2014. Direct and indirect chemical defences against insects in a multitrophic framework. *Plant, Cell and Environment* 37:1741-1752.
- Hochuli, D.F. 1996. The Ecology of Plant/insect Interactions: Implications of Digestive Strategy for Feeding by Phytophagous Insects. *Oikos* 75:133-141.
- Holopainen, J.K., G. Semiz and J.D. Blande. 2009. Life-history strategies affect aphid preference for yellowing leaves. *Biology Letters* 5(5): 603-605.
- Holzmueller, E., S. Jose, M. Jenkins, A. Camp and A. Long. 2006. Dogwood anthracnose in Eastern hardwood forests: what is known and what can be done? *Journal of Forestry* 104(1):21-26.

- Hough-Goldstein, J.A. and D. Pimentel. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. *Environmental Entomology* 7:97-102.
- Howe, G.A. and G. Jander. 2008. Plant immunity to insect herbivores. *The Annual Review of Plant Biology* 59:41-66.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia; or, Why are there so many kinds of animals? *The American Naturalist* 93:145-159.
- Kagata, H. and T. Ohgushi. 2006. Bottom-up trophic cascades and material transfer in terrestrial food webs. *Ecol Res* 21:26-34.
- Karageorou, P., C. Buschmann and Y. Manetas. 2008. Red leaf color as a warning signal against insect herbivory: honest or mimetic? *Flora* 203:648-652.
- Kaufman, S.R. and W. Kaufman. 2013. *Invasive plants: a guide to identification, impacts, and control of common North American species*. Stackpole Books.
- Klingeman, W.E., F. Chen, J. Kim and P.C. Flanagan. 2007. Feeding Preferences of Dogwood Sawfly Larvae Indicate Resistance in *Cornus*. *Journal of Environmental Horticulture* 25(3): 134-138.
- Lev-Yadun, S. 2009. Müllerian and Batesian mimicry rings of white-variegated aposematic spiny and thorny plants: A hypothesis. *Israel Journal of Plant Science* 57:107-116.
- Lev-Yadun, S. 2014. Potential defense from herbivory by ‘dazzle effects’ and ‘trickery coloration’ of leaf variegation. *Biological Journal of the Linnean Society* 111:692-697.

- Lev-Yadun, S. and K.S. Gould. 2009. Role of anthocyanins in plant defense.
Anthocyanins Springer New York 22-28.
- Lev-Yadun, S., A. Dafni, M.A. Flaishman, M. Inbar, I. Izhaki, G. Katzir and G. Ne'eman. 2004. Plant coloration undermines herbivorous insect camouflage.
BioEssays 26:1126-1130.
- MacArthur, R. 1955. Fluctuations of Animal Populations and a Measure of
Community Stability. *Ecology* 36(3):533-536.
- Manetas, Y. 2006. Why some leaves are anthocyanic and why most anthocyanic
leaves are red? *Flora* 201:163-177.
- McKinney, M.L. 2002. Urbanization, Biodiversity, and Conservation. *BioScience*
52:883-890.
- McKinney, M.L. 2006. Urbanization as a major cause of biotic homogenization.
Biological Conservation 127: 247-260.
- Merkle, S.A., G.M. Andrade, C.J. Nairn, W.A. Powell and C.A. Maynard. 2007.
Restoration of threatened species: a noble cause for transgenic trees. *Tree*
Genetics & Genomes 3(2):111-118.
- Mmbaga, M.T. and R.J. Sauvé. 2004. Multiple disease resistance in dogwoods (*cornus*
spp.) to foliar pathogens. *Journal of Arboriculture*. 30(2):101-107.
- Moffis, B.L. and S.P. Arthurs. "[Bagworm - *Thyridopteryx ephemeraeformis*
Haworth](#)". *Creature Features*. University of Florida. EENY-548. February
2013. Revised March 2016.
<<http://entnemdept.ufl.edu/creatures/MISC/MOTHS/bagworm.htm>>

- Nassauer, J.I. 1988. The aesthetics of horticulture: neatness as a form of care:
HortScience 23:973-977.
- Pearse, I.S., D.J. Harris, R. Karban and A. Sih. 2013. Predicting novel herbivore-plant
interactions. Oikos 122:1554-1564.
- Plucknett, D.L. and N.J. Smith. 1986. Sustaining agricultural yields. *BioScience*
36:40-45.
- Price, P.W., R.F. Deno, M.D. Eubanks, D.L. Finke and I. Kaplan. 2011. Insect
Ecology Behavior, Populations and Communities. Cambridge University
Press. 99-180.
- Ramírez, C.C., B. Lavandero and M. Archetti. 2007. Coevolution and the adaptive
value of autumn tree colours: colour preference and growth rates of a southern
beech aphid. Journal of Evolutionary Biology 21:49-56.
- Rasmann, S. 2014. Fine-tuning of defenses and counter-defences in a specialized
plant-herbivore system. Ecological Entomology 39:382-390.
- Redlin, S.C. 1991. *Discula destructiva* sp. nov., cause of dogwood anthracnose.
Mycologia 83(5):633-642.
- Reeves, J.L. 2011. Vision should not be overlooked as an important sensory modality
for finding host plants. Environmental Entomology 40:855-863.
- Reichard, S.H. and C.W. Hamilton. 1997. Predicting Invasions of Woody Plants
Introduced into North America. Conservation Biology 11:193-203.
- Reichard, S.H. and P. White. 2001. Horticulture as a pathway of invasive plant
introductions in the United States. BioScience 51:103-113.

- Rodriguez-Saona, C., N. Vorsa, A.P. Singh, J. Johnson-Cicalese, Z. Szendrei, M.C. Mescher and C.J. Frost. 2011. Tracing the history of plant traits under domestication in cranberries: potential consequences on anti-herbivore defences. *Journal of Experimental Botany* 62(8): 2633-2644.
- Rosenzweig, M.L. 2003. Reconciliation ecology and the future of species diversity. *Oryx* 37(2):194–205.
- Santamour Jr, F.S. 2004. Trees for urban planting: diversity uniformity, and common sense. *The Overstory Book: Cultivating Connections with Trees. Permanent Agriculture Resources, Holualoa, Hawaii*, 396-399.
- Santamour Jr, F.S. and S.E. Bentz. 1995. Updated checklist of elm (*Ulmus*) cultivars for use in North America. *Journal of Arboriculture*, 21(3):122-131.
- Schaefer, M.H. and G. Rolshausen. 2006. Plants on red alert: Do insects pay attention? *BioEssays* 28:65-71.
- Smalley, E.B. and R.P. Guries. 1993. Breeding elms for resistance to Dutch elm disease. *Annual review of phytopathology*, 31(1):325-354.
- Smalley, E.B. and R.P. Guries. 2000. Asian elms: sources of disease and insect resistance. In *The Elms* 215-230. Springer US.
- Smith, A.P. 1986. Ecology of leaf color polymorphism in a tropical forest species: habitat segregation and herbivory. *Oecologia* 69:283-287.
- Soltau, U., S. Dötterl and S. Liede-Schumann. 2009. Leaf variegation in *Caladium steudneriifolium* (Araceae): a case of mimicry? *EvolEcol* 23:503-512.

- Spooner, D.M., W.L. Hetterscheid, R.G. van den Berg, W.A. Brandenburg. 2003. Plant nomenclature and taxonomy *Hortic Rev* 28:1-60.
- Tallamy, D.W. 2004. Do Alien Plants Reduce Insect Biomass? *Conservation Biology* 18(6):1689-1692.
- Tallamy, D.W. 2007. *Bringing Nature Home*. Portland, Oregon. Timber Press.
- Tallamy, D.W. and K.J. Shropshire. 2009. Ranking Lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941-947.
- Tallamy, D.W., M. Ballard and V. D'Amico. 2009. Can alien plants support generalist insect herbivores? *Biol Invasions* 12:2285-2292.
- Townsend, A.M. and F.S. Santamour Jr. 1993. Progress in the development of disease-resistant elms. In *Dutch Elm Disease Research* 46-50. Springer New York.
- Townsend, A.M. and L.W. Douglass. 2004. Evaluation of elm clones for tolerance to Dutch elm disease. *Journal of Arboriculture*, 179-184.
- White, A.G. and V.G. Bus. 1996. Breeding commercial apple cultivars in New Zealand with resistances to pests and diseases. *Eucarpia Symposium on Fruit Breeding and Genetics* 484:157-162.
- Whitehead, S.R and K. Poveda. 2011. Herbivore-induced changes in fruit-frugivore interactions. *Journal of Ecology* 99: 946-969.
- Whitman, T.G. and Slobodchikoff. 1981. Evolution by individuals, Plant-Herbivore Interactions and Mosaics of Genetic Variability: The Adaptive Significance of Somatic Mutations in Plants. *Oecologia* 49:287-292.

Wilson, E.O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1:344-346.

Zuefle, M.E., W.P. Brown and D.W. Tallamy. 2007. Effects of non-native plants on the native insect community of Delaware. *Biol Invasions* 10:1159-1169.

Appendix A

STRAIGHT SPECIES AND CULTIVAR PHOTOGRAPHS WITH VISUAL DIFFERENCES



Figure 18 *Ilex verticillata*- straight species, Accessed March 15, 2017 from Missouri Botanical Garden
<<http://www.missouribotanicalgarden.org/PlantFinder/FullImageDisplay.aspx?documentid=9254>>



Figure 19 *Ilex verticillata*- 'Red Sprite'



Figure 20 *Vaccinium corymbosum*- straight species photo by Arthur Haines 2017
Accessed March 15, 2017 from New England Wild Flower Society
<<https://gobotany.newenglandwild.org/species/vaccinium/corymbosum/>>



Figure 21 *Vaccinium corymbosum*- ‘Chandler’ Accessed March 15, 2017 from http://m.bloomingadvantage.com/info.asp?code=9188&utm_source=avail-retail&utm_medium=plant-info&utm_campaign=excel-link



Figure 22 *Viburnum dentatum*- straight species, Aug. 4, 2016. Department of Horticulture, Cornell University. Accessed March, 15, 2017 <<http://www.hort.cornell.edu/vlb/images/vibdentfrlg.jpg>>



Figure 23 *Viburnum dentatum*- 'Christom' BLUE MUFFIN Accessed March 15, 2017 from Missouri Botanical Garden
<<http://www.missouribotanicalgarden.org/PlantFinder/FullImageDisplay.aspx?documentid=23035>>



Figure 24 *Viburnum dentatum*- 'J.N. Select,' Red Feather®



Figure 25 *Juniperus virginiana*- straight species



Figure 26 *Juniperus virginiana*- 'Gray Owl'



Figure 27 *Juniperus virginiana*- 'Corcorcor' Emerald Sentinel™ Accessed March 15, 2017 from Longwood Gardens Plant Explorer
<https://plantexplorer.longwoodgardens.org/webui/oecgi2.exe/INET_ECM_DisPI?NAMENUM=10930&DETAIL=&startpage=1#images>



Figure 28 *Cornus sericea*- Straight Species photo by Peter M. Dziuk 2003
Accessed March 15, 2017 from Minnesota Wildflowers a field guide to
the flora of Minnesota
<<https://www.minnesotawildflowers.info/shrub/red-osier-dogwood>>



Figure 29 *Cornus sericea*- 'Silver and Gold'



Figure 30 *Rhus copallina*- Straight Species [top] and 'Lanham's Purple' [bottom]



Figure 31 *Cornus florida*- Straight Species Accessed March 15, 2017 from Missouri Botanical Garden
<<http://www.missouribotanicalgarden.org/PlantFinder/FullImageDisplay.aspx?documentid=8391>>



Figure 32 *Cornus florida*- 'Fircomz' Firebird



Figure 33 *Liquidambar styraciflua*- straight species Accessed March 15, 2017 from Missouri Botanical Garden
<<http://www.missouribotanicalgarden.org/PlantFinder/PlantFinderDetails.aspx?kempercode=c116#AllImages>>



Figure 34 *Liquidambar styraciflua*- 'Aurea'

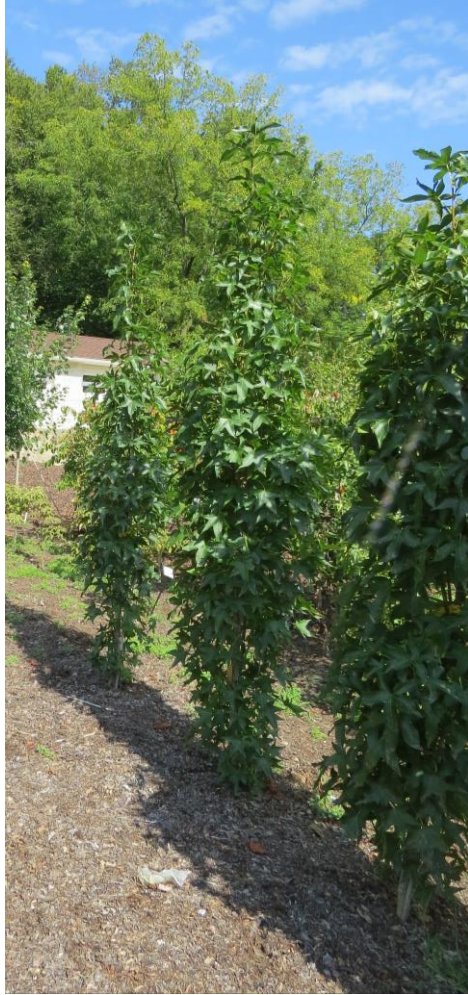


Figure 35 *Liquidambar styraciflua*- 'Slender Silhouette'

Appendix B

PRINCIPAL COMPONENT ANALYSIS OF PLANT TRAITS, INSECT ORDERS AND FEEDING GUILDS

I ran a principal component analysis for each of the six trait groups to look for correlations between the cultivars and controls in terms of the major insects orders sampled as well as the feeding guilds that they [broadly] fit into. The loadings plot graphs, which indicate correlations between variables and the components, are presented below. Feeding guilds include; chewers, sucker, gall makers, and leaf miners. Chewers are comprised of Lepidoptera, Orthoptera, Coleoptera, and Hymenoptera; suckers include Hemiptera and Thysanoptera; and gall makers and leaf miners are Dipteran. The trait type (cultivar group and control or cultivar) is represented as supplemental variables in blue. In the loading plot graphs when points are close together and relatively far from the origin (center of the plot) they are correlated. Points clustered close together but close to the origin are not correlated. Variable lines with angles that are less than 90 degrees are positively correlated and variable lines that make angles that are greater than 90 degrees are negatively correlated. So if the angle made by a control group and the sucker group lines is less than 90 degrees there is a positive correlation between the control group and the suckers.

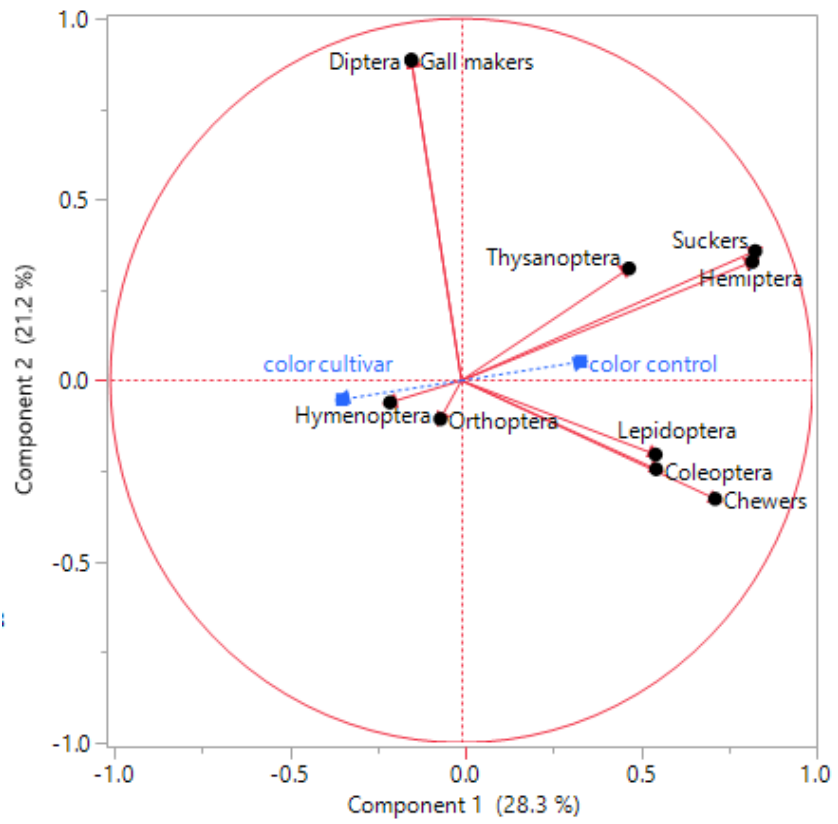


Figure 36 Loading plot graph for the altered leaf color cultivar group (*J. virginiana*, *R. copallina*, and *V. dentatum*).

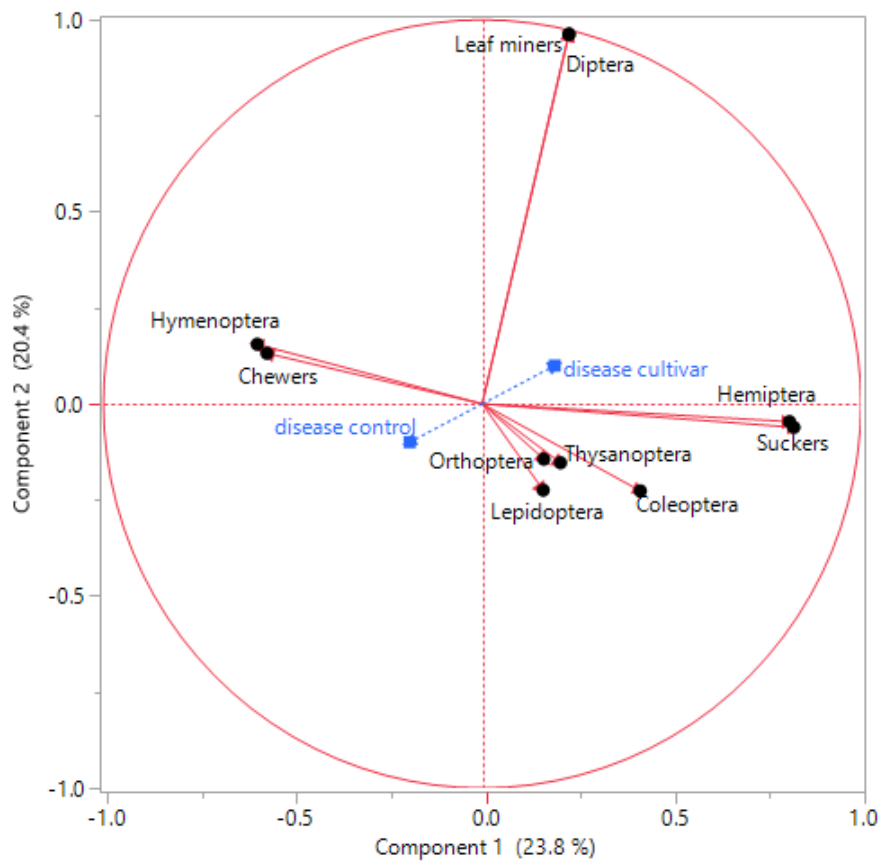


Figure 37 Loading plot graph for the disease resistant cultivar group (*C. florida*, *U. americana*, and *C. sericea*).

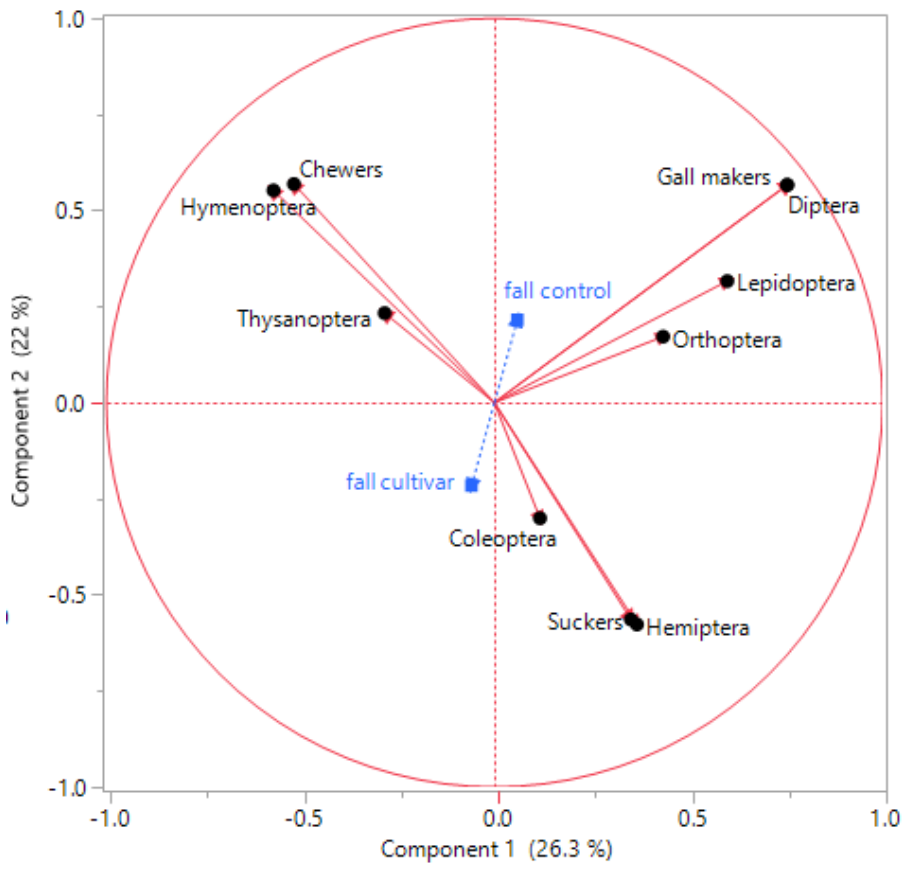


Figure 38 Loading plot graph for the enhanced fall foliage cultivar group (*A. rubrum*, *V. dentatum*, and *C. sericea*).

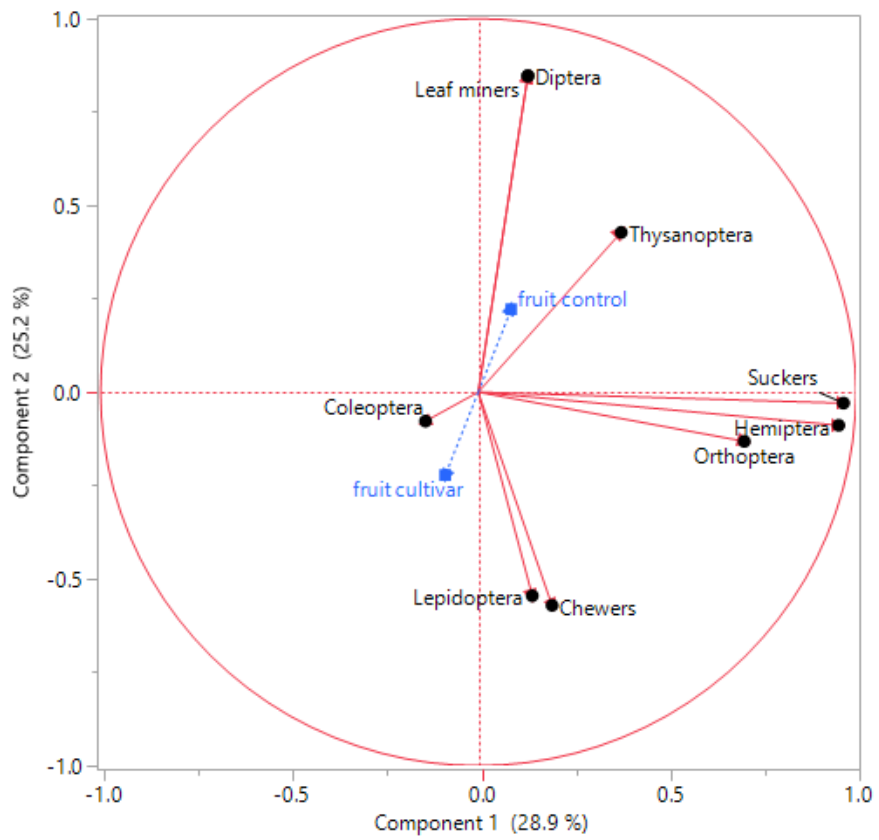


Figure 39 Loading plot graph for the enhanced fruiting cultivar group (*I. verticillata*, *V. dentatum*, and *V. corymbosum*).

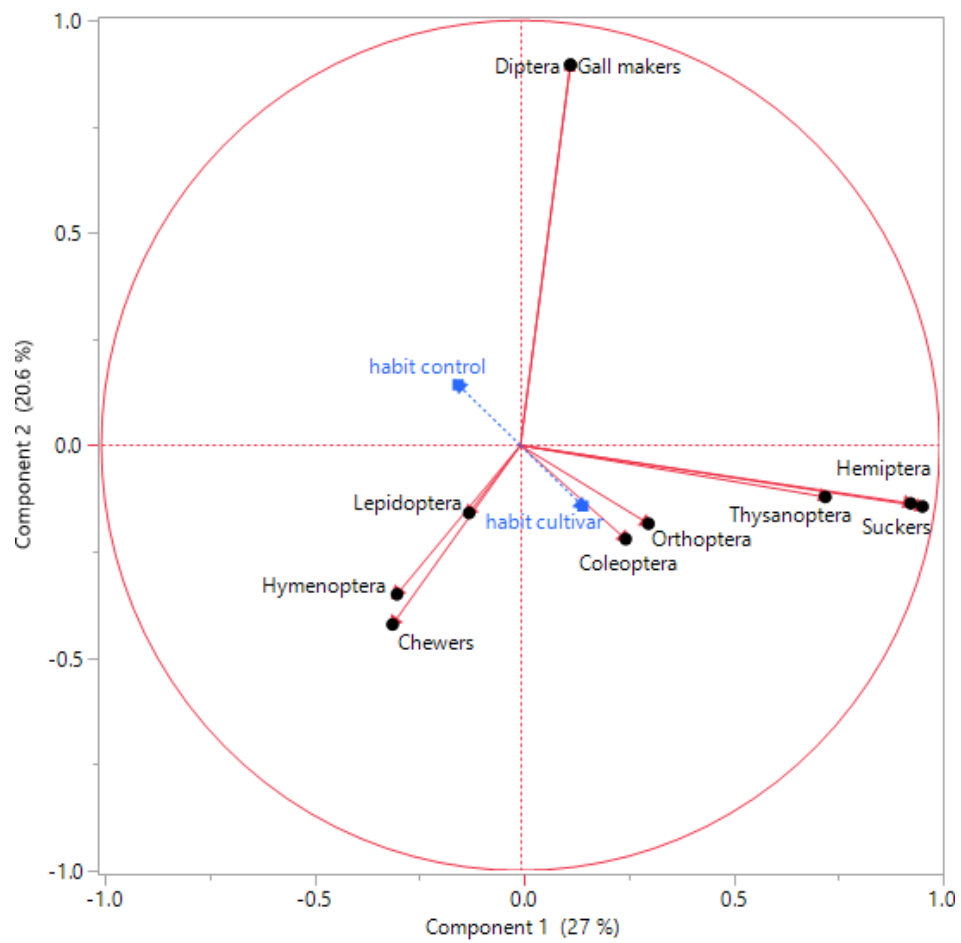


Figure 40 Loading plot graph for the altered growth habit cultivar group (*C. sericea*, *J. virginiana*, and *L. styraciflua*).

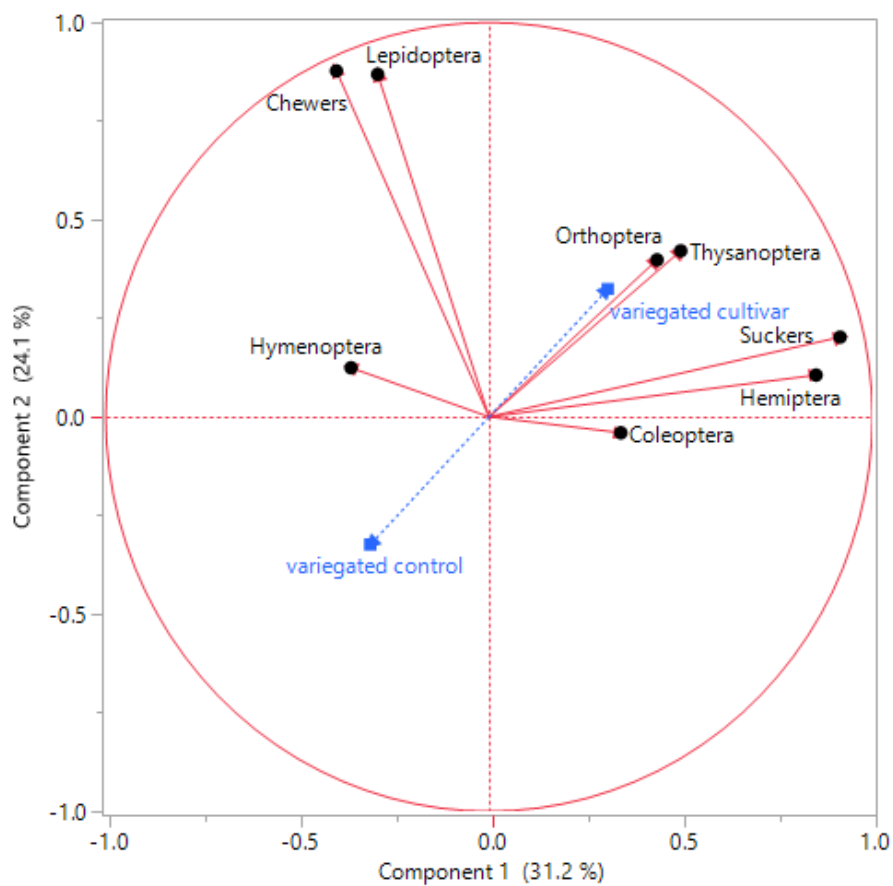


Figure 41 Loading plot graph for the variegated cultivar group (*C. sericea*, *C. florida*, and *L. styraciflua*)

Appendix C

PROPORTIONAL INDEX OF COMMUNITY SIMILARITY- INSECT FAMILY LEVEL

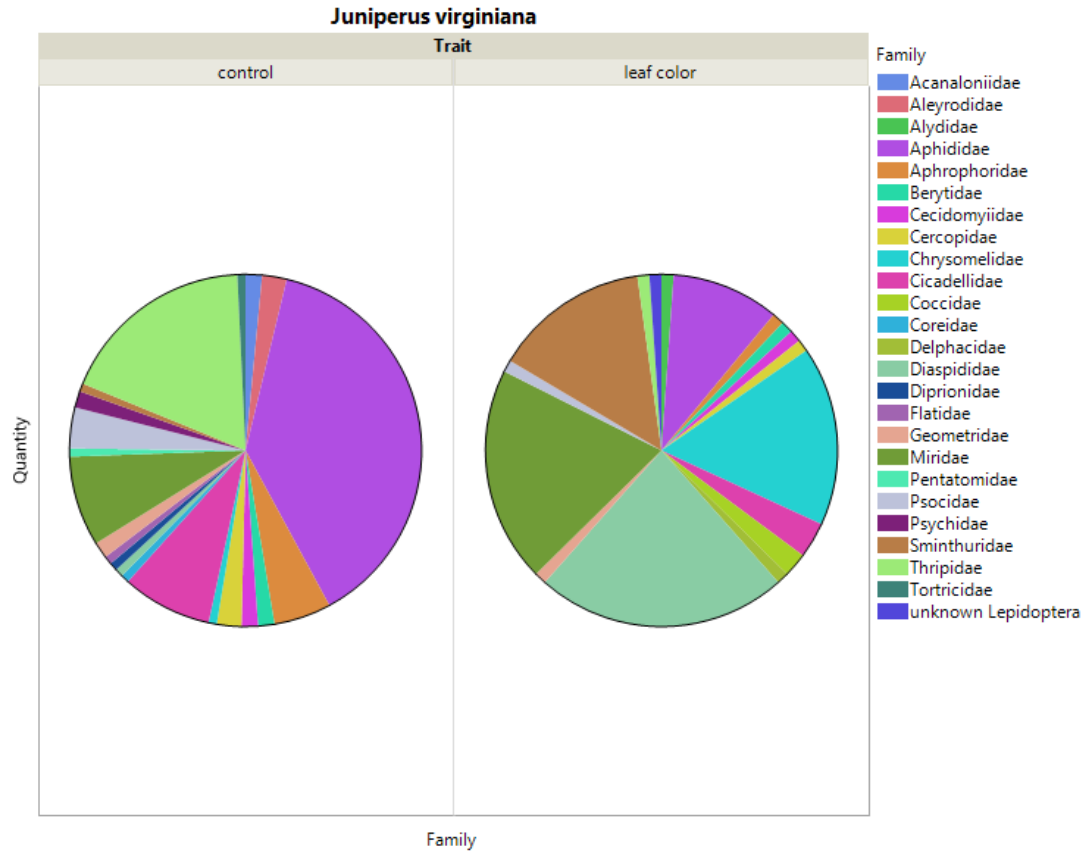


Figure 42 *Juniperus virginiana* insect family comparisons; altered leaf color cultivar and straight species. 31.45 % similarity.

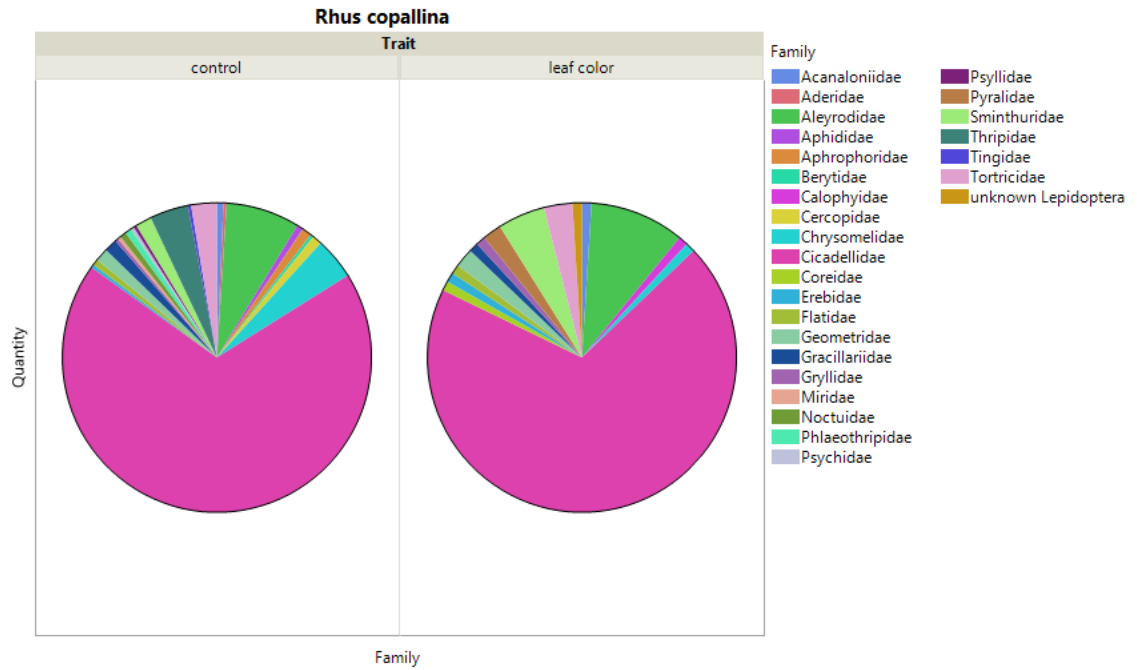


Figure 43 *Rhus copallina* insect family comparisons; altered leaf color cultivar and straight species. 86.2 % similarity.

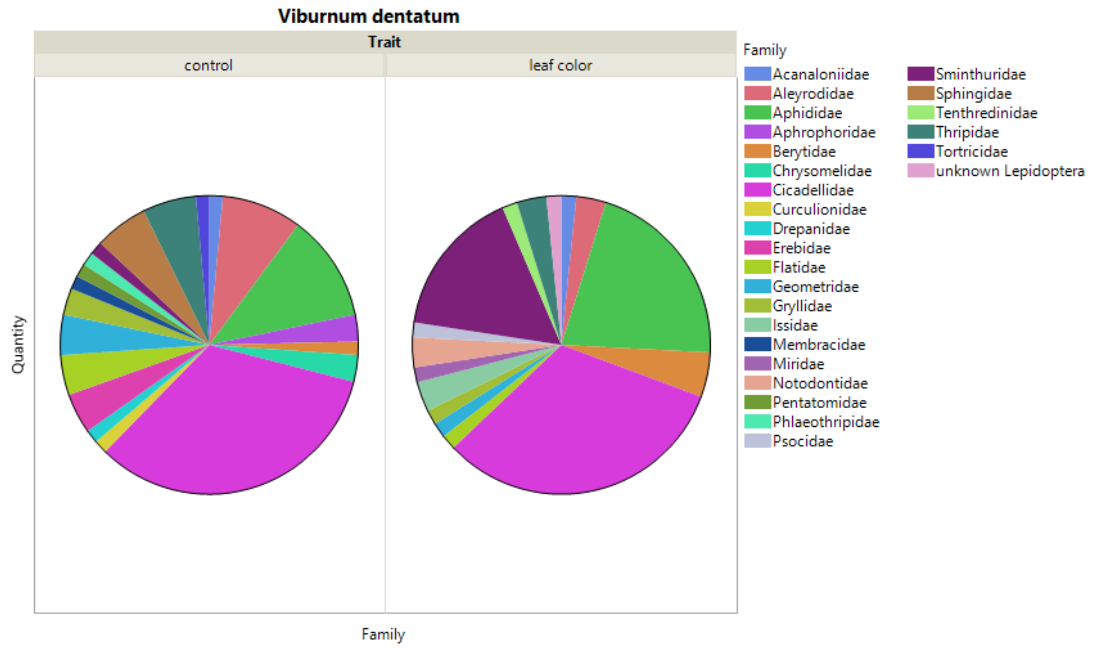


Figure 44 *Viburnum dentatum* insect family comparisons; altered leaf color cultivar and straight species. 59.6 % similarity.

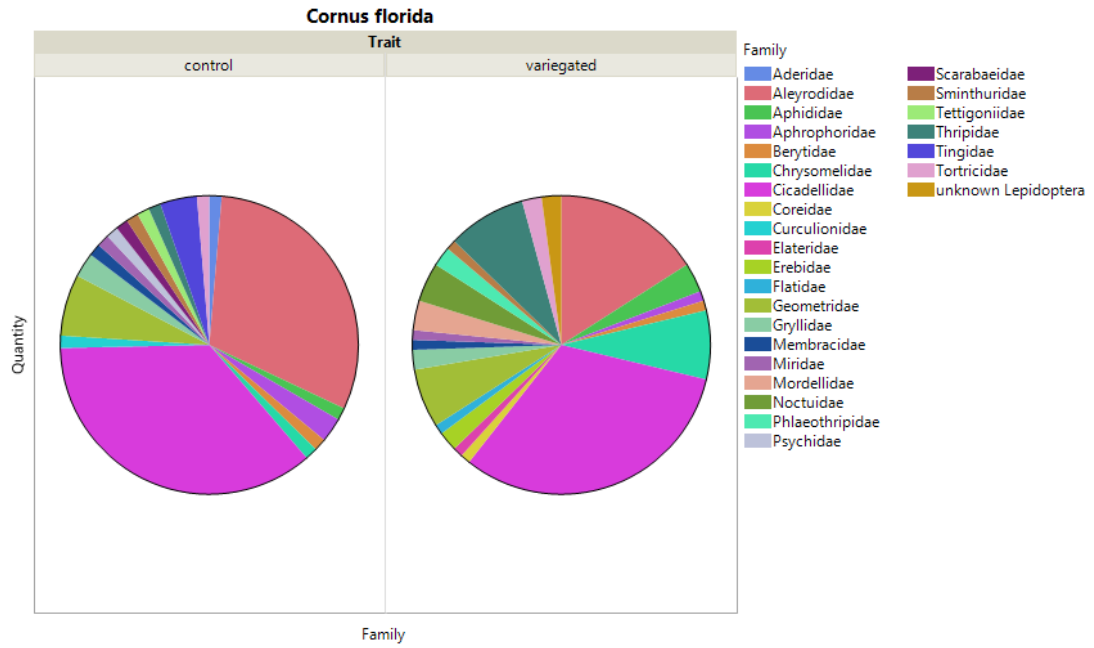


Figure 45 *Cornus florida* insect family comparisons; variegated cultivar and straight species. 67 % similarity.

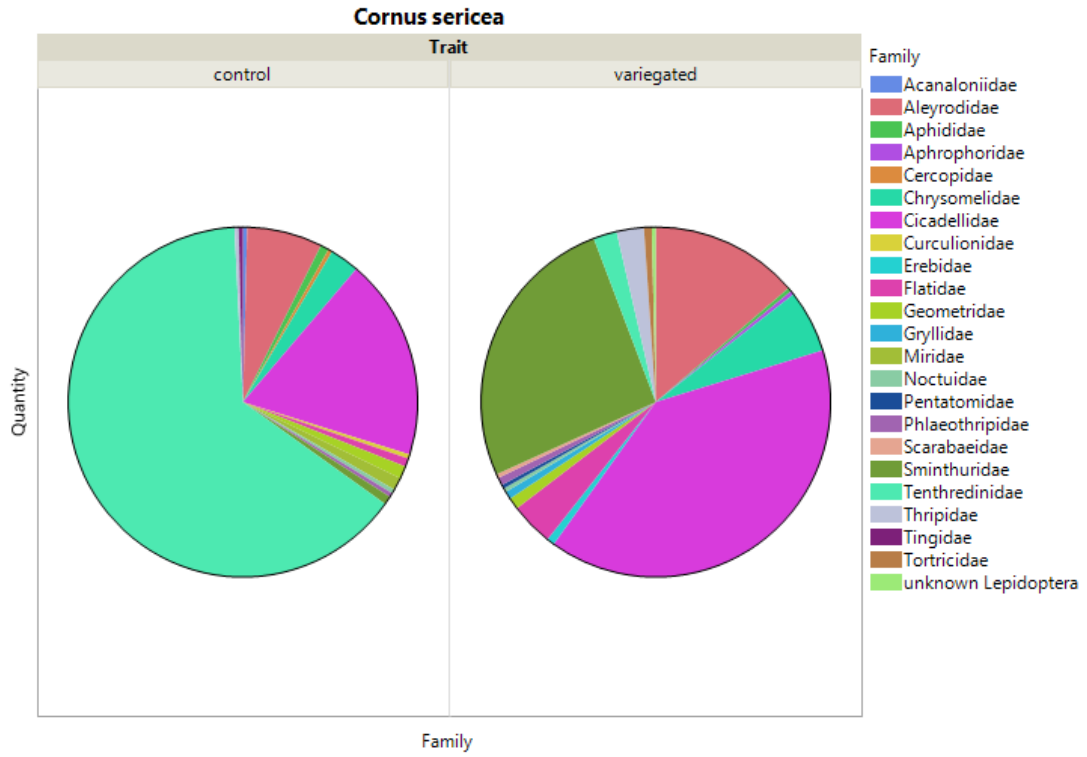


Figure 46 *Cornus sericea* insect family comparisons; variegated cultivar and straight species. 34.56 % similarity.

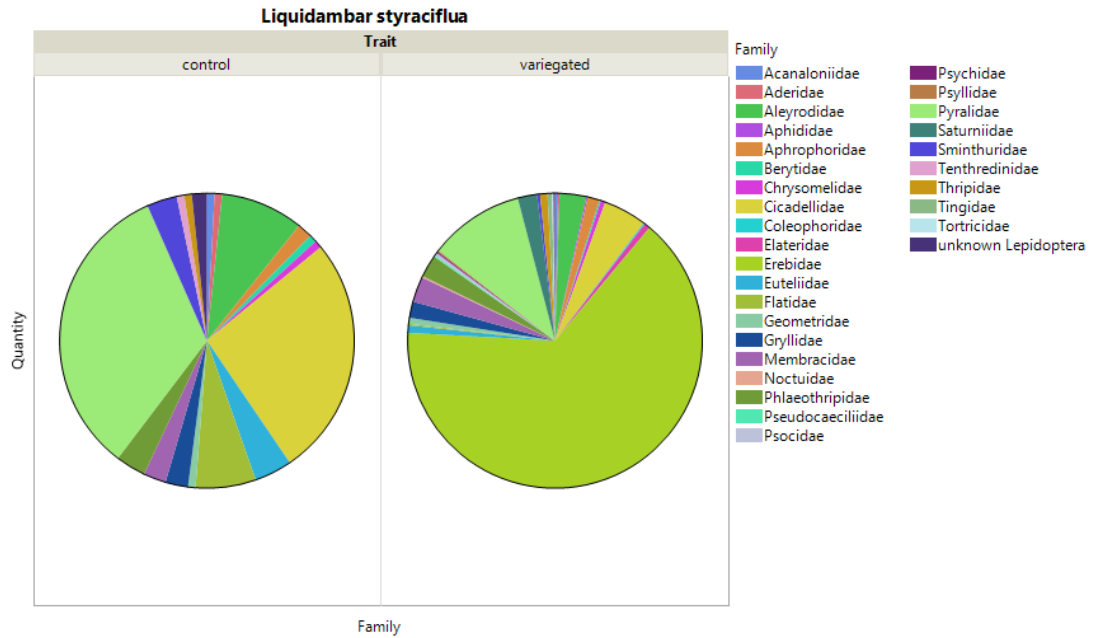


Figure 47 *Liquidambar styraciflua* insect family comparisons; variegated cultivar and straight species. 30.18 % similarity.

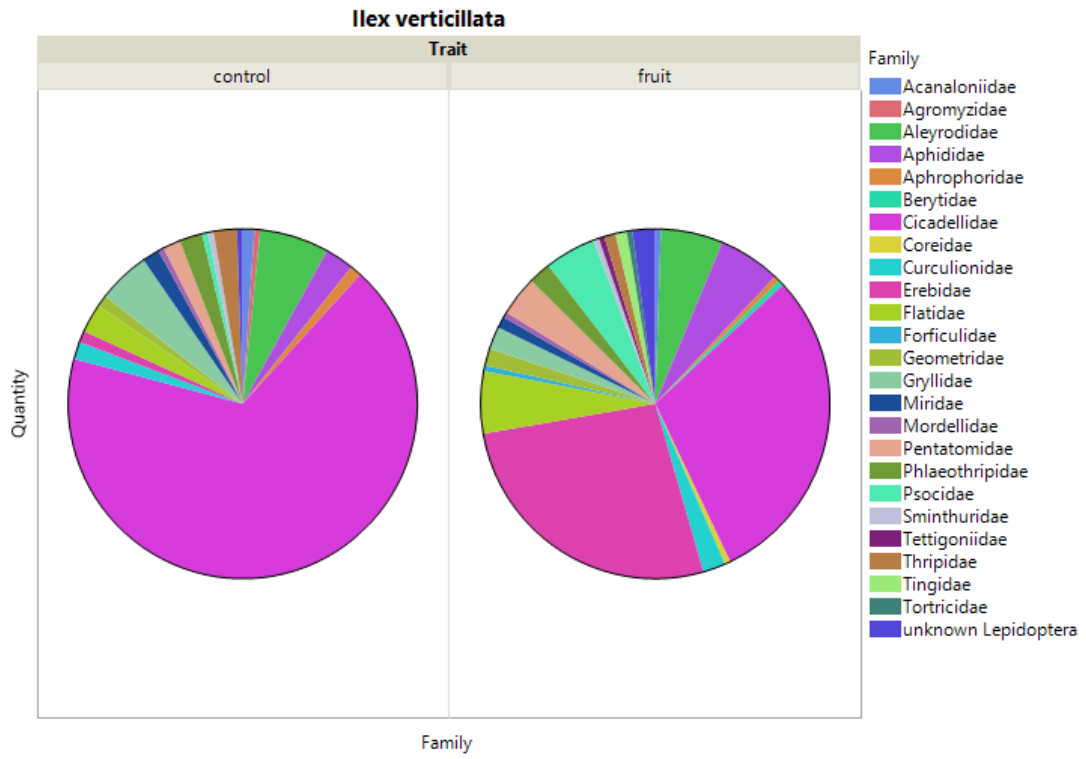


Figure 48 *Ilex verticillata* insect family comparisons; enhanced fruiting cultivar and straight species. 55.96 % similarity.

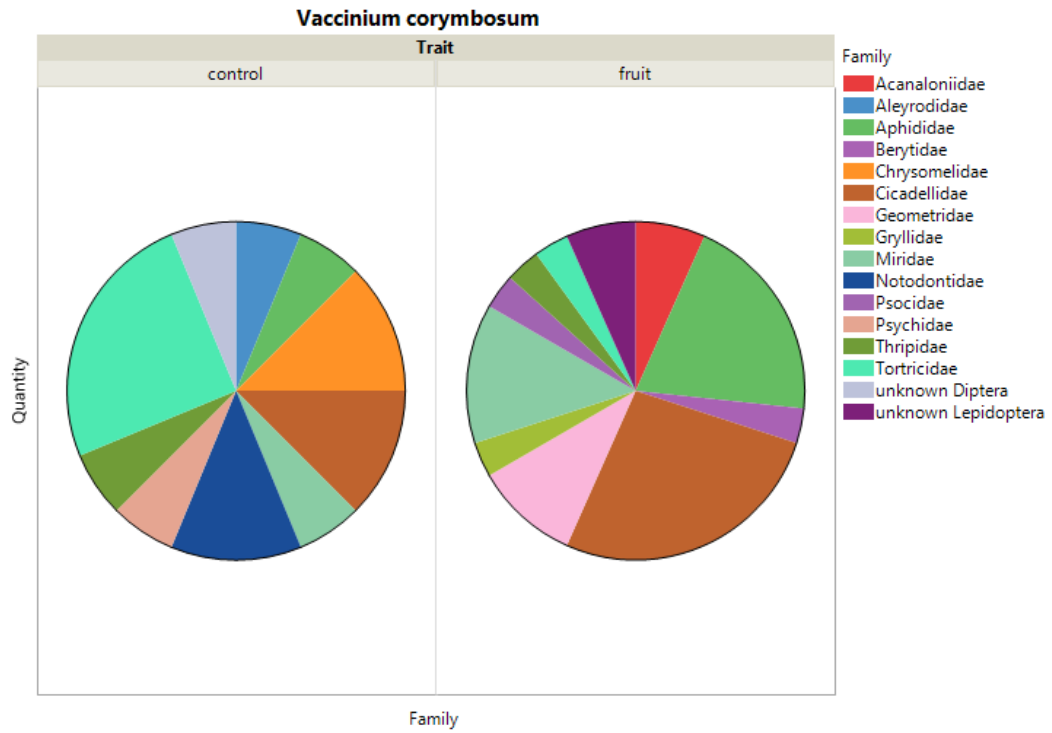


Figure 49 *Vaccinium corymbosum* insect family comparisons; enhanced fruiting cultivar and straight species. 31.7 % similarity.

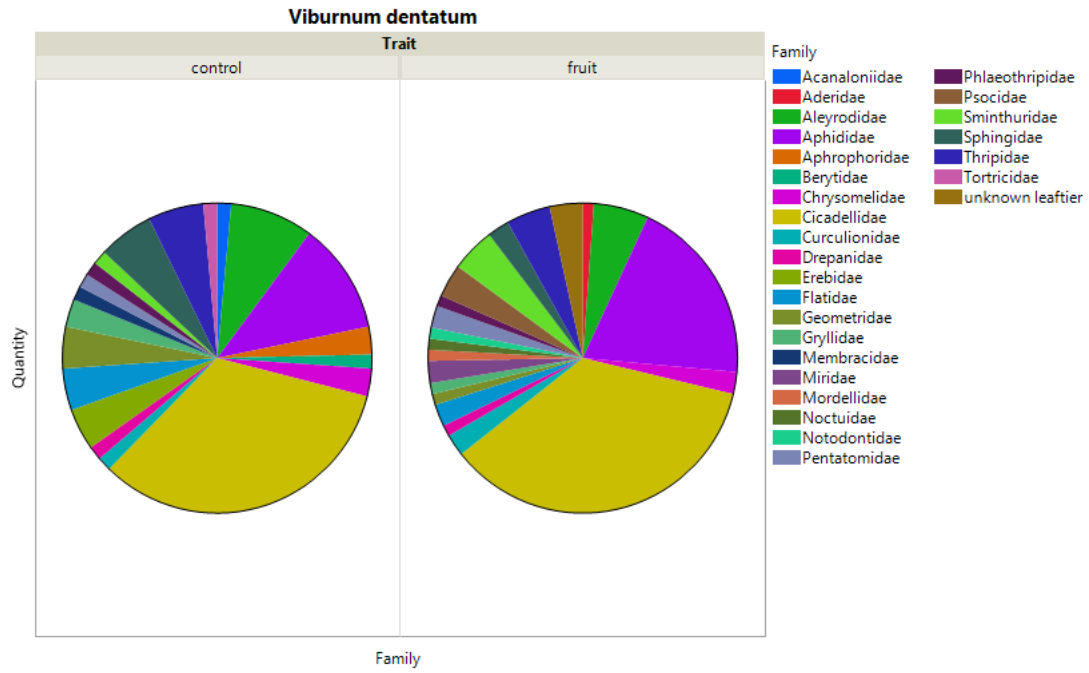


Figure 50 *Viburnum dentatum* insect family comparisons; enhanced fruiting cultivar and straight species. 71.8 % similarity.

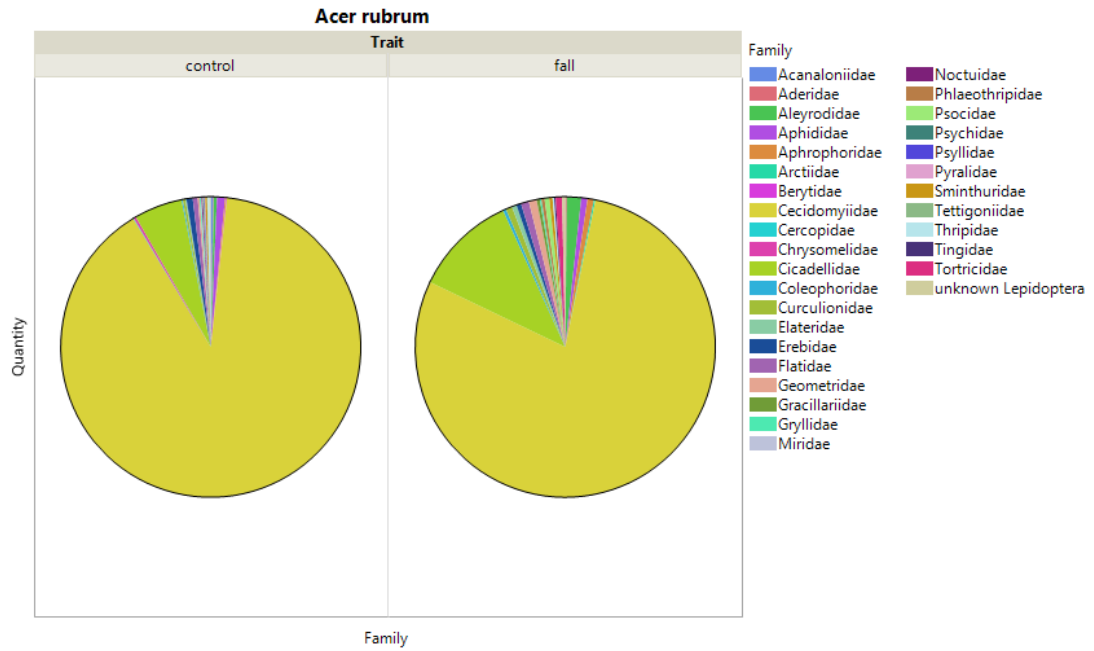


Figure 51 *Acer rubrum* insect family comparisons; enhanced fall foliage cultivar and straight species. 87.78 % similarity.

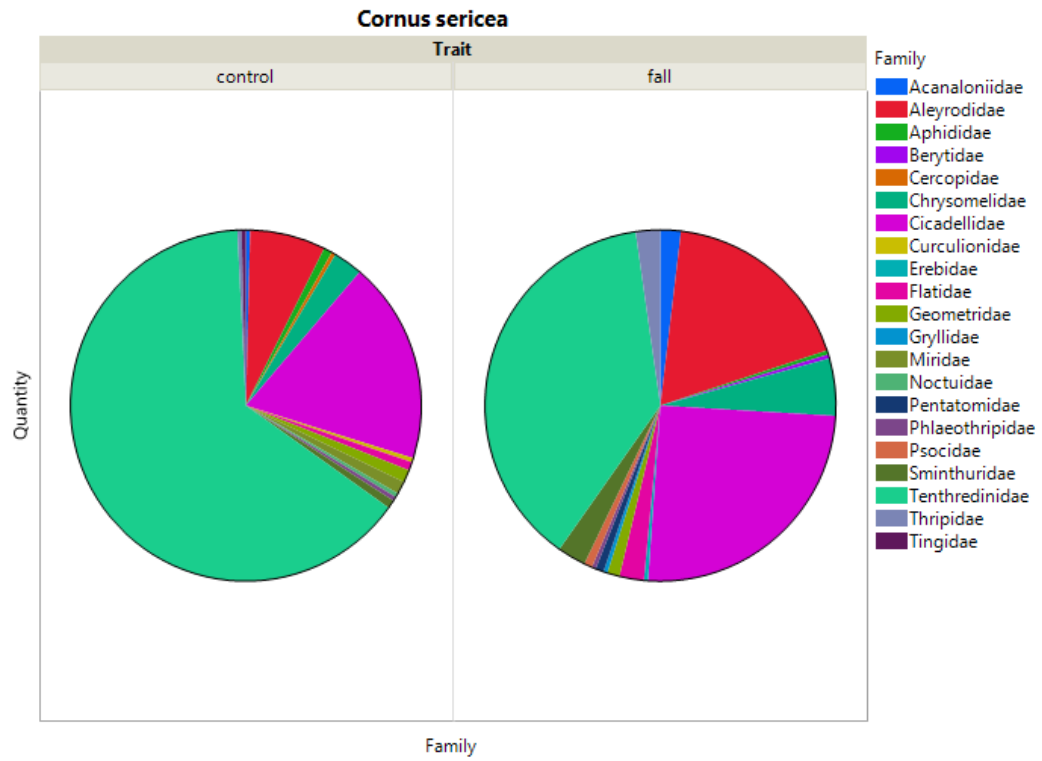


Figure 52 *Cornus sericea* insect family comparisons; enhanced fall foliage cultivar and straight species. 70.5 % similarity.

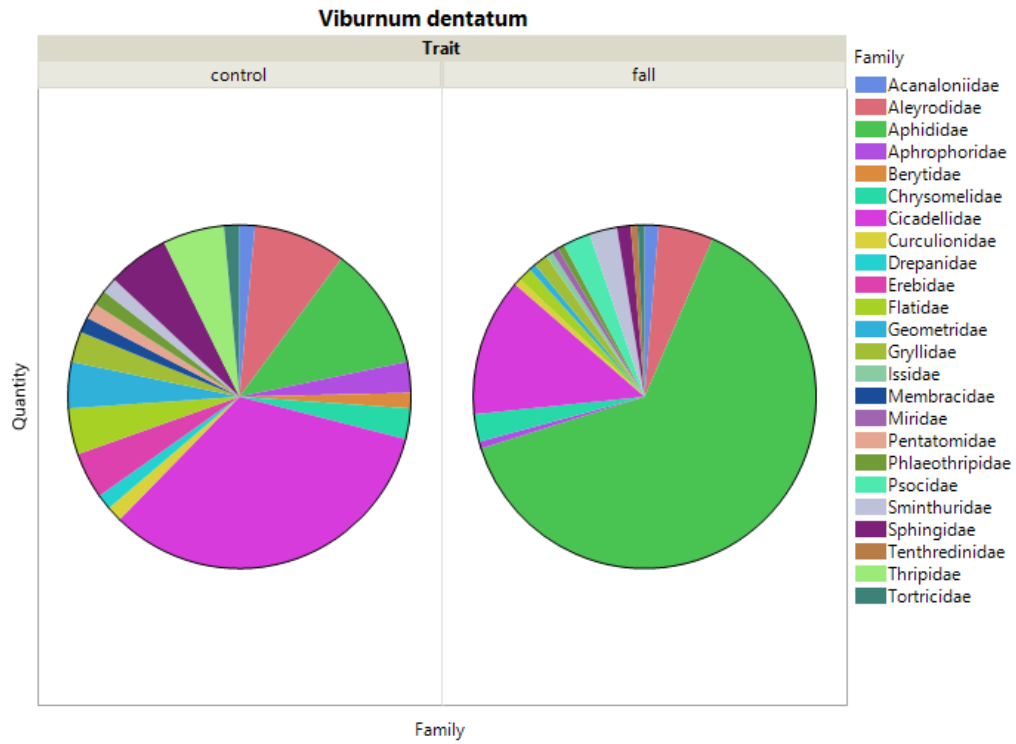


Figure 53 *Viburnum dentatum* insect family comparisons; enhanced fall foliage cultivar and straight species. 42.35 % similarity.

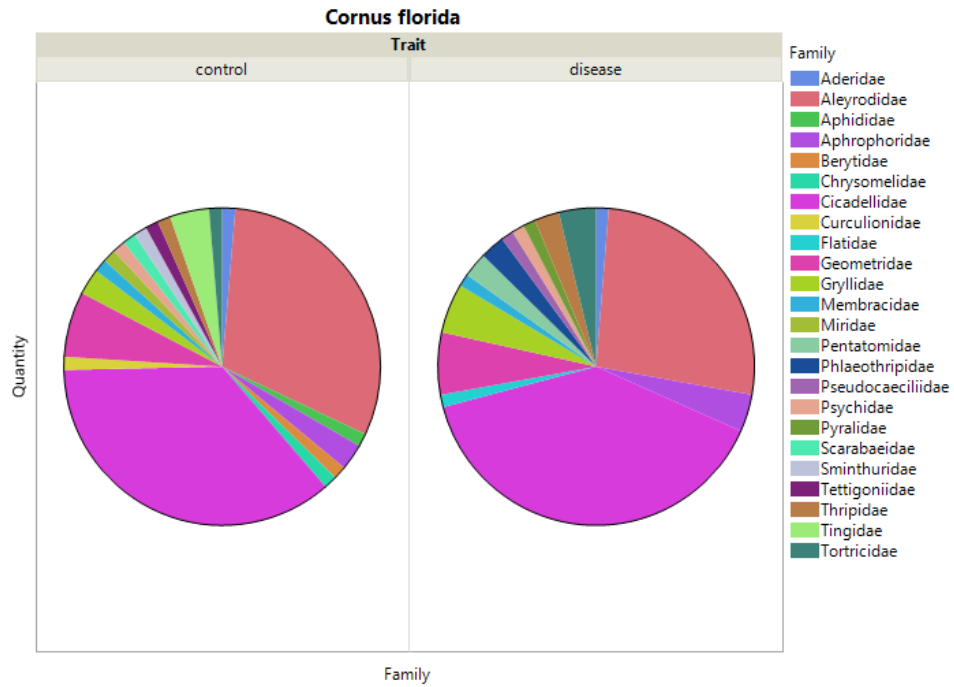


Figure 54 *Cornus florida* insect family comparisons; disease resistant cultivar and straight species. 80.8 % similarity.

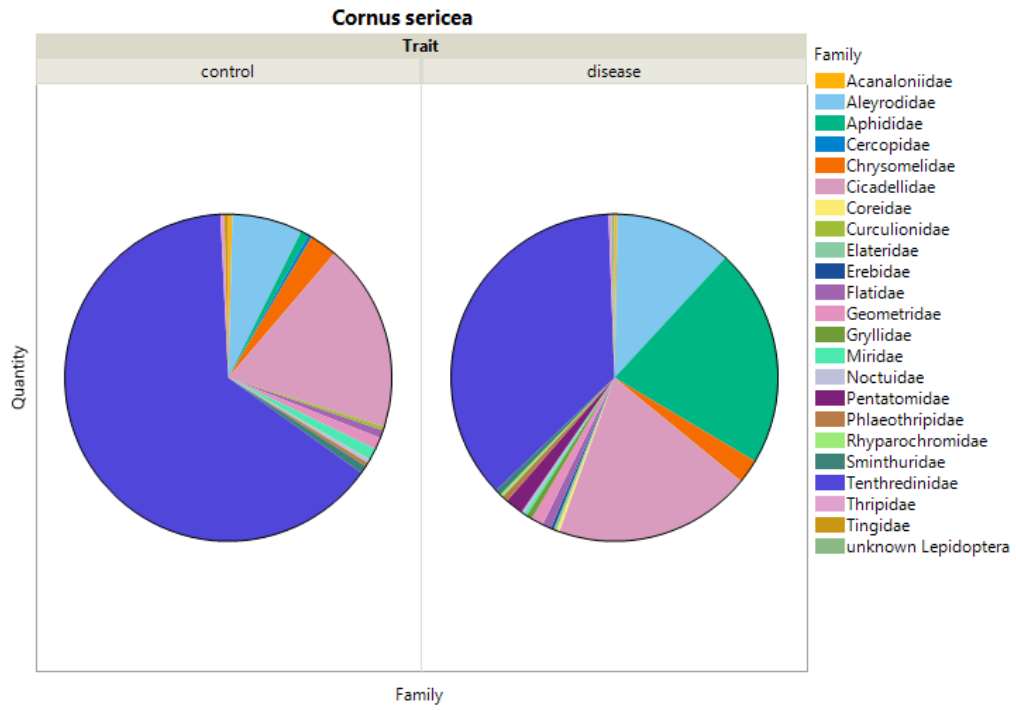


Figure 55 *Cornus sericea* insect family comparisons; disease resistant cultivar and straight species. 69.44 % similarity.

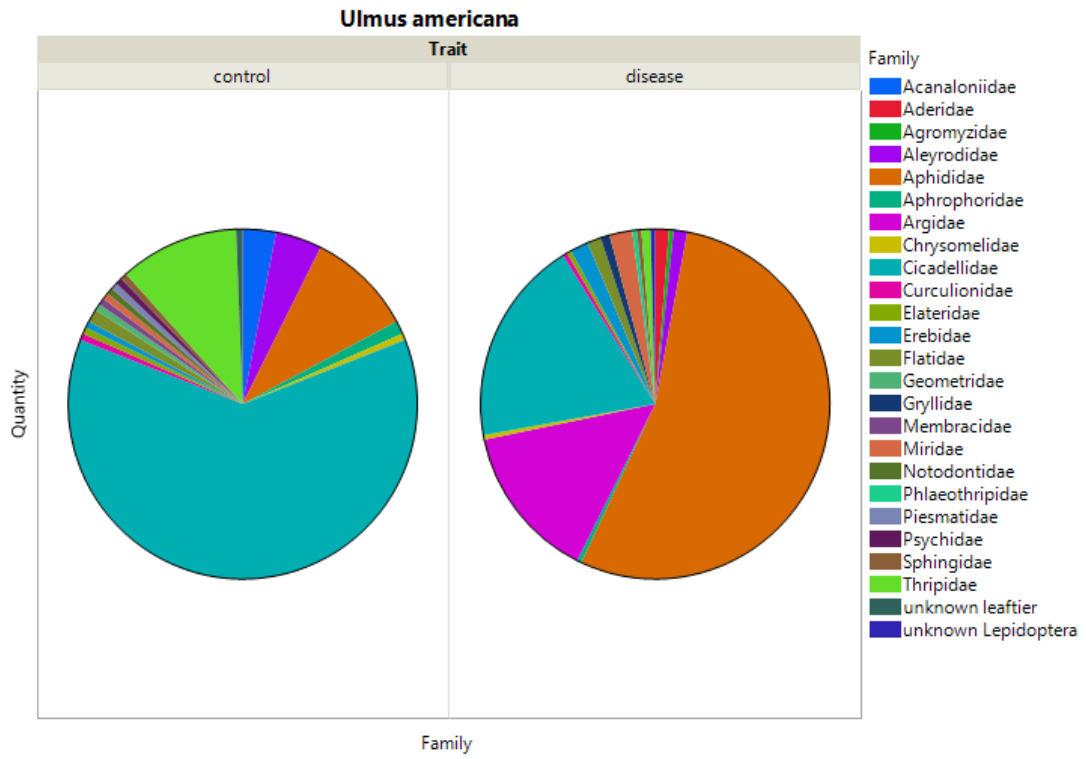


Figure 56 *Ulmus americana* insect family comparisons; disease resistant cultivar and straight species. 35.46 % similarity.

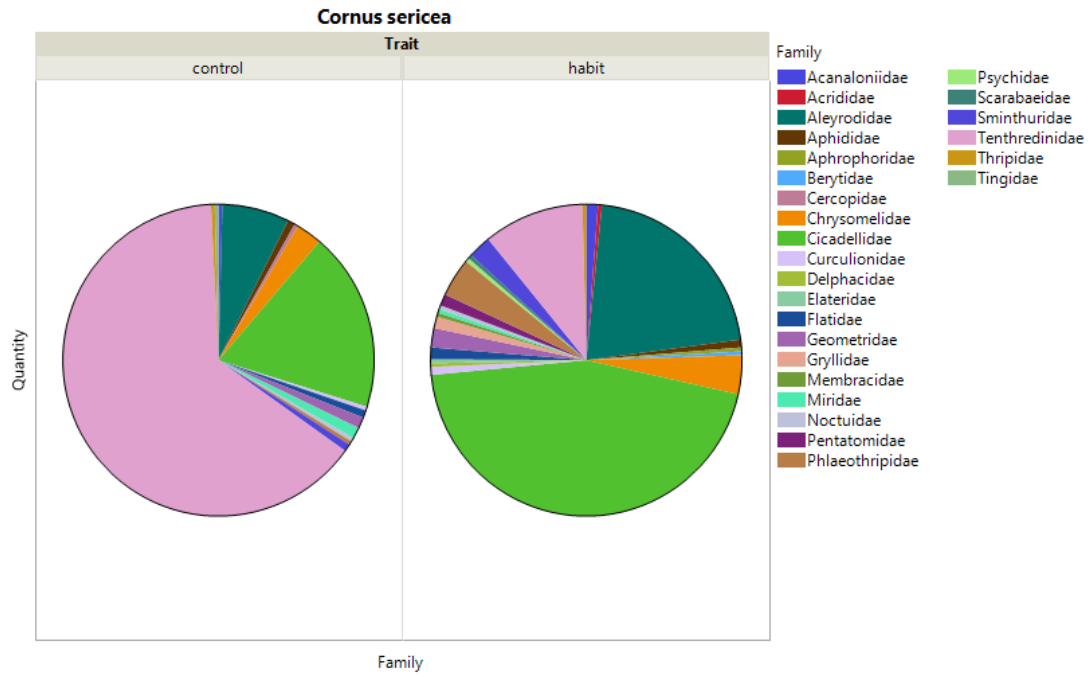


Figure 57 *Cornus sericea* insect family comparisons; altered growth habit cultivar and straight species. 44.59 % similarity.

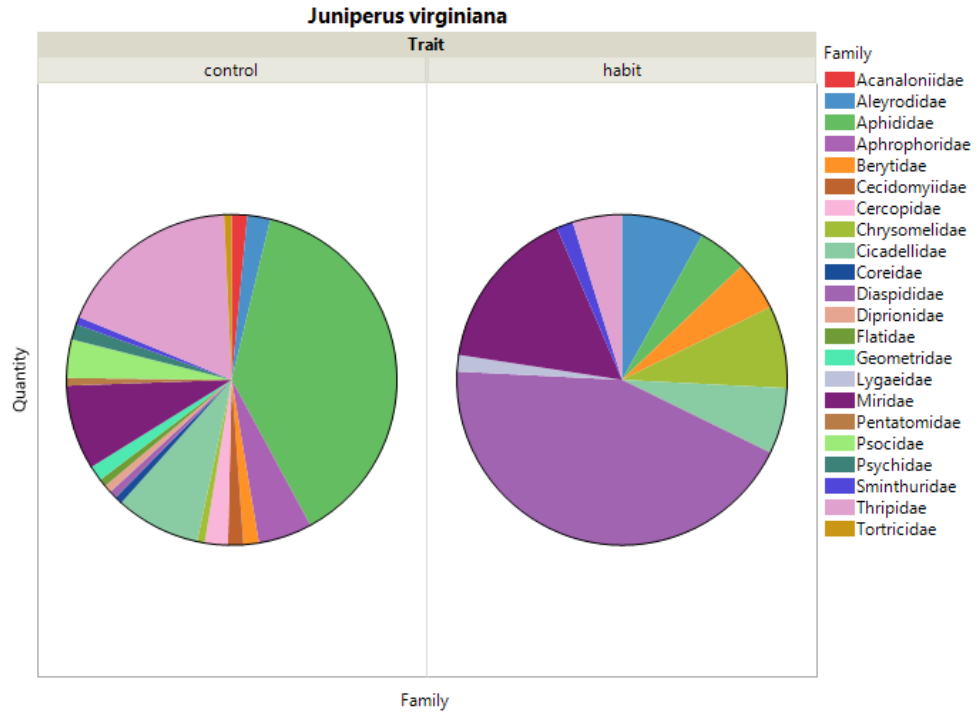


Figure 58 *Juniperus virginiana* insect family comparisons; altered growth habit cultivar and straight species. 30.45 % similarity.

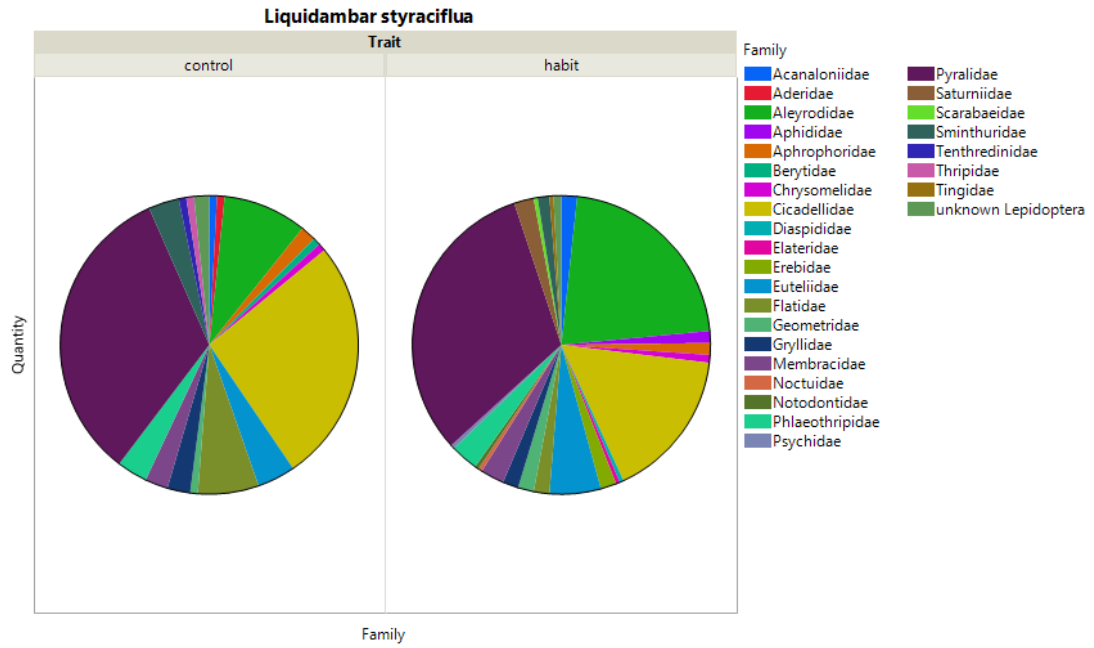


Figure 59 *Liquidambar styraciflua* insect family comparisons; altered growth habit cultivar and straight species. 75.85 % similarity.