

Insect Herbivory across Varying Leaf Morphology:
Comparative Analysis of Four Tree Species in a Northern Hardwood Forest

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ABSTRACT

The severity of five types of insect leaf herbivory damage—discoloration, chew, leaf roll, galls, and epidermal feeding— and occurrence frequency of Coleoptera, Lepidoptera, and Hemiptera were evaluated across four tree species in the Northern Hardwood forest of the Upper Peninsula of Michigan. Herbivory damage and insect occurrence frequency was compared across two deciduous and two coniferous tree species— balsam fir (*Abies Balsamea*), northern white cedar (*Thuja occidentalis*), speckled alder (*Alnus incana*), and sugar maple (*Acer saccharum*)— in order to evaluate insect herbivory on leaves with varying morphology. A secondary experiment evaluated the effect of restricted insect crawling access on sugar maple in relation to insect leaf herbivory by application of Tanglefoot to branch bases. Damage was measured by percent leaf area effected by each damage type. Significant differences were found between all guild type damage and all insect occurrence frequencies except Lepidoptera. There were several significant differences in both damage severity and composition and insect frequency between speckled alder and sugar maple and between cedar and balsam fir. This supports the hypothesis that there is significant variance of insect herbivore damage between both deciduous and coniferous trees and in different leaf morphologies.

INTRODUCTION

Insect herbivores can alter plant community composition by influencing plant competition through variable per capita competitive effects and intrinsic growth rates (Kim, 2013). Specializations in tree-insect symbiotic and parasitic relationships develop differently across varied species and habitat types. By linking herbivory patterns with specific tree traits, it should be possible to predict future associations between tree species and insect herbivores as communities change. These patterns could also be used to focus in on aspects of the phylogenetic history and specialization/niche partitioning between insect herbivores and plants. The concept of niche differentiation suggests evolutionary adaptations of insects towards food sources, this study aims to evaluate how variances in leaf morphology can cause or explain this type of speciation (Jung, 2010).

Insect herbivores employ a variety of general approaches to use plant tissues to obtain nutrients, known as feeding guilds. Feeding guilds utilize different aspects of plant tissue and damage from them can manifest differently, depending on various plant structures and compounds. This can have a significant effect on ecological interactions between these insects and trees, potentially cascading up or down to further ecological effects.

Gianoli and Hannunen (2000) found that leaf expression plasticity—variance in shape, size, and chemical content—within a tree species can affect insect herbivory in varied environmental conditions. For example, deciduous leaf loss in winter has been shown to decrease insect herbivory in the following spring across individuals of valley oak (*Quercus lobata*) (Karban, 2007). Herve (2007) found reduced insect herbivory in areas of higher tree diversity and taxonomically more distant species in a worldwide data set. It is unclear what mechanisms are responsible for this outcome; certain plant types or species may be targeted more heavily or herbivory may be disbursed more evenly across all species in a population.

Carmona (2011) found, in a study across 19 plant families, that secondary metabolites do not have a significant impact on insect herbivore susceptibility of plants while physical traits—trichomes, plant size, etc.—do have significant impact on this susceptibility. Morphological attributes impact feeding patterns and susceptibility to insect herbivores differently across each guild type (Carmona, 2011). This study aims to evaluate the potential effects of variation in leaf morphology on feeding damage of insects across different guilds through an analysis of tree/insect ecological interactions. The associations between insect herbivore communities and four tree species common to Northern hardwood forests: balsam fir (*Abies Balsamea*), northern white cedar (*Thuja occidentalis*), speckled alder (*Alnus incana*), and sugar maple (*Acer saccharum*) were evaluated.

These species were selected to maximize the diversity of leaf morphology as a method of identifying potential correlations between leaf traits and herbivore resource selection. Niche differentiation by insects into different guilds is a display of evolutionary adaptations towards food types (Jung, 2010). This study aims to link specific morphological traits and insect herbivore communities in Northern Hardwood forests of the Upper Peninsula of Michigan and begin to explain how these types of adaptations occurred.

By linking herbivory patterns with specific tree traits, it should be possible to predict future associations between tree species and herbivores, allowing us to predict potential shifts in community dynamics. This analysis can be applied to recovery efforts and insect damage control following outbreaks or in response to invasive plants and insects. This may also provide a foundation for further research aimed towards understanding how these dynamics affect the health of these plants and if responses vary across different tree species. This could lead to new methods of biological controls in agriculture and other efforts meant to mimic or restore natural conditions.

The objective of this study is to identify leaf traits associated with tree species that affect life time and evolutionary preference and patterns of insect herbivores. This research focuses specifically on evaluating: (1) how frequency and severity of each herbivore guild damage and total insect leaf herbivory damage varies across four tree species, (2) how insect occurrence frequency

varies across four tree species and (3) how restriction of movement onto leaves by crawling herbivores (Tanglefoot application to branch bases) affect herbivore leaf damage on sugar maple.

-----*Expected Results*

It is expected that the varied leaf morphology will alter the guild types of insect herbivores that utilize each tree as a resource and that certain guilds will dominate and vary across each morphology type (Carmona, 2011). Closer proximity and overlapping leaf/branch distribution are expected to attract more herbivores to sugar maple due to higher resource density. This could also allow insects to more easily move from leaf to leaf while feeding, which may favor certain guild types. Increased leaf dispersal may favor flying insect encounters while close proximity will favor all insect herbivores by increasing resource density, raising the potential for increased herbivory and nesting damage (Zytynska, 2011). It is therefore hypothesized that sugar maple will experience the most damage, specifically gall damage which is a common form of damage from flying insects. Increased leaf area and malleability are expected to increase the likelihood of leaf rollers but decrease other forms of herbivory due to increased chance of disturbance. This hypothesizes that sugar maple will also experience the most severe rolling damage.

MATERIALS AND METHODS

The associations between insect herbivore communities and four tree species in northern hardwood forests were evaluated in relation to insect caused leaf damage. Leaf damage observed for each species was measured and compared. The variation between total damage and damage within each herbivore guild type was evaluated.

Four tree species—speckled alder, balsam fir, sugar maple, and northern white cedar-- were evaluated for insect herbivory damage categorically by guild type. Insect leaf herbivory damage was assessed on a categorical percent damage ranges (Table 1A, 1B).

Data was collected from four branches per tree and twelve trees per species, except for northern white cedar, which had nine sampled trees due to limited plot selection. Sampling took place by random selection on the University of Notre Dame Environmental Research Center (UNDERC) property, located in Gogebic County of the Upper Peninsula of Michigan (Fig. 1, Table 2). Two lower canopy branches and two upper canopy branches, each pair on opposing sides of the tree from one another, were randomly selected for damage sampling. For branches with 15-40 leaves on a branch, all leaves were sampled. For branches with >40 leaves, every other leaf was sampled from branch tip towards base until 25 leaves were sampled. For balsam fir, leaves were defined as one annual section

of growth and for northern white cedar, leaves were defined as a section with tertiary scale branching. During this sampling, all insect occurrences on each surveyed branch were recorded.

Damage was transformed into percent damage of leaf area per leaf and compared across tree species by guild and total damage. Data was tested using a Shapiro Wilkes Normality test and transformed as necessary to yield normally distributed data. An ANOVA was used to compare guild type damage and total damage across species. ANOVA tests with p-values <0.05 were considered significant and further tested with a Tukey Post Hoc: Multiple comparisons of means between each species pair in 95% family-wise confidence level to determine specific differences between species. The same statistical analyses were applied to frequency of each insect order and total insect frequency to transformed data represented as a ratio of individuals seen per 100 leaves sampled. The frequencies of insect occurrences across each order and total insects seen were compared across tree species, transformed into data in terms of individuals seen per 100 leaves sampled. These evaluations were done using ANOVA, Shapiro Wilkes Normality test, and Tukey Post Hoc Multiple comparison tests in the same manner as herbivore damage. These analyses had three degrees of freedom in respect to ANOVA comparisons and 41 degrees of freedom from experimental replication.

Three adjacent maple stands were selected from previous sampling sites in a second experiment looking at insect damage on maple. This experiment aimed to evaluate the effect of limiting access to leaves by insects that climb to leaves by walking from the trunk of the tree. Two branches at the same canopy level were randomly selected on each tree. Tanglefoot was applied to 3 inches at the base of one branch and another branch was left untreated to act as a control. Insect leaf herbivory damage was collected for every leaf on each branch both before treatment and nine days after treatment (Table 1A, 1B). The change in damage of each guild type during this time was compared between the Tanglefoot and control branches. A student's t-test was run to determine significant difference between the control and Tanglefoot treated branches for each damage guild. Data found to have a non-normal distribution using the Shapiro-Wilkes were then analyzed using a Mann-Whitney U test (non-parametric). These analyses had three degrees of freedom in respect to comparisons and six degrees of freedom from experimental replication.

RESULTS

Variation in Herbivore Damage among Tree Species

Total Leaf Damage. The highest average total leaf damage was 26.63% seen on northern white cedar. Balsam fir, speckled alder, and sugar maple followed in decreasing order with total leaf damage of 22.54%, 14.48%, and

14.45%, respectively (Table 4, Fig. 2). Northern white cedar and speckled alder showed a significant difference ($p= 0.0153$, $df= 3$, $F\text{-value}= 5.10$) in total leaf damage, as did northern white cedar and sugar maple ($p= 0.0150$, $df= 3$, $F\text{-value}= 5.10$)(Table A1).

Discoloration Damage. Northern white cedar and balsam fir had a mean discoloration of 14.4% and 8.9% respectively, while sugar maple and alder did not display discoloration damage (Table 4 and Fig. 3). Northern white cedar and balsam fir showed significant difference ($p= 3.74e-5$, $df= 3$, $F\text{-value}= 34.7$) (Table A2).

Leaf Chewing Damage. The highest average leaf chewer damage was 12.53% seen on balsam fir. Northern white cedar, speckled alder, and sugar maple followed in decreasing order with leaf chewer damage of 12.24%, 6.93%, and 9.02% respectively (Table 4 and Fig. 4). Balsam fir and sugar maple showed a significant difference ($p= 0.035$, $df= 3$, $F\text{-value}= 3.49$) in leaf chewing damage, as did northern white cedar and sugar maple ($p= 0.078$, $df= 3$, $F\text{-value}= 3.49$) (Table A3).

Leaf Roller Damage. The highest average leaf roller damage was $2.52\pm 0.37\%$ seen on speckled alder. Balsam fir, sugar maple, and northern white cedar followed in decreasing order with leaf roller damage of 1.22%, 0.83%, and 0% respectively (Table 4 and Fig. 5). Northern white cedar and speckled alder

showed a significant difference ($p=2.85E-4$, $df= 3$, $F\text{-value}= 7.41$) in, as did speckled alder and balsam fir ($p= 0.0772$, $df= 3$, $F\text{-value}= 7.41$) and speckled alder and sugar maple ($p= 0.0116$, $df= 3$, $F\text{-value}=7.41$) (Table A4).

Gall Damage. The highest average gall damage was 3.50% seen on sugar maple. Balsam fir, speckled alder, and northern white cedar followed in decreasing order with of 2.75%, 0.77%, and 0% respectively (Table 4 and Fig. 6). Sugar maple and speckled alder showed a significant difference ($p= 0.0793$, $df= 3$, $F\text{-value}= 3.97$) in, as did sugar maple and northern white cedar ($p= 0.0267$, $df= 3$, $F\text{-value}= 3.97$) (Table A5).

Epidermal Feeding Damage. The highest average epidermal feeding damage was 3.18% seen on sugar maple. Speckled alder had less, 2.17%, epidermal feeding damage with none in balsam fir or northern white cedar (Table 4 and Fig. 7). Sugar maple and balsam fir showed a significant difference ($p= 0.0187$, $df= 3$, $F\text{-value}= 4.48$) in, as did Sugar maple and northern white cedar ($p= 0.0332$, $df= 3$, $F\text{-value}= 4.48$) (Table A6).

Variation in Insect Abundance among Tree Species

Significant differences were indicated in total insect, Coleoptera, and Hemiptera occurrence frequency, where p values were $1.56E-4$, 0.0115, and

0.0011, respectively (Table 5). Lepidoptera showed no significant difference in occurrence frequency across tree species ($p= 0.9834$) (Table 5).

Total Insects. The highest average total insect occurrence frequency was 6.6 ± 1.58 individuals per 100 leaves (#/100L) seen on speckled alder (Table 6). Balsam fir, northern white cedar, and sugar maple had total insect occurrence frequencies of 1.2 ± 0.24 (#/100L), 1.5 ± 0.87 (#/100L), and 1.2 ± 0.38 (#/100L) respectively (Table 6, Fig. 8). Speckled alder showed a significant difference in total insect occurrence frequency with balsam fir ($p= 8.52E-4$, $df= 3$, $F\text{-value}= 8.56$), northern white cedar ($p= 1.05 E-3$, $df= 3$, $F\text{-value}= 8.56$), and sugar maple ($p= 1.03 E-3$, $df= 3$, $F\text{-value}= 8.56$)(Table A7).

Coleoptera. The highest average Coleoptera occurrence frequency was (#/100L) seen on speckled alder (Table 6). Balsam fir, northern white cedar, and sugar maple had Coleoptera occurrence frequencies of (#/100L), (#/100L), and $1.2 \pm$ (#/100L) respectively (Table 6 and Fig. 9). Speckled alder showed a significant difference of Coleoptera occurrence frequency with balsam fir ($p= 2.13E-2$, $df= 3$, $F\text{-value}= 4.17$), northern white cedar ($p= 7.17 E-2$, $df= 3$, $F\text{-value}= 4.17$), and sugar maple ($p= 2.68E-2$, $df= 3$, $F\text{-value}= 4.17$)(Table A8).

Hemiptera. The highest average Hemiptera occurrence frequency was (#/100L) seen on speckled alder (Table 6). Balsam fir, northern white cedar, and sugar maple had Hemiptera occurrence frequencies of (#/100L), (#/100L), and

1.2± (#/100L) respectively (Table 6 and Fig. 10). Speckled alder showed a significant difference of Hemiptera occurrence frequency with balsam fir ($p=9.20E-3$, $df=3$, $F\text{-value}=6.44$), northern white cedar ($p=2.89E-3$, $df=3$, $F\text{-value}=6.44$), and sugar maple ($p=9.20E-3$, $df=3$, $F\text{-value}=6.44$)(Table A8).

Lepidoptera. No significant difference was shown across species in the frequency of Lepidoptera larvae (Table 5 and Fig. 11).

Insect Herbivore Movement-Restriction Experiment

In the Tanglefoot treatment experiment, the average leaf suffered between 0.30%- 4.0% increase in all insect herbivore guild damages in both the control and Tanglefoot branches (Table 16). Comparisons of change in cumulative chewer ($p=0.457$), gall ($p=0.263$), roller ($p=0.887$), and epidermal ($p=0.664$) damage severity between Tanglefoot and control group showed that they were not statistically different (Table 8). There was a higher increase of insect herbivore damage in all insect herbivore guilds in the sugar maple control branch average than in the Tanglefoot treatment, but none were shown to be statistically different than the Tanglefoot treatment (Table 17).

DISCUSSION

Plant susceptibility to insect leaf herbivory has been shown to be affected by phenotypic expression of leaf traits—size, shape, etc. (Gianoli, 2000). Galling

damage patterns were the most profoundly variable across different species. This damage was significantly highest and most diverse in sugar maple leaves across four types of gall: Bladder Gall, Spindle Gall, Gouty Vein Gall, and erineum (Table 9). Balsam fir showed Gall midge damage, which occurred only on new growth but was severe (26-75%) when present. Speckled alder showed gall damage by bladder and erineum gall and no gall activity was found on northern white cedar. This pattern may be partially due to habitat conditions, since both Alder and Cedar grow in in swampy, high sunlight environments while Maple and Balsam tend to grow in more well drained soil and cast more shade (Barnes, 1981). Habitat characteristics and their fluctuations, such as changes in soil moisture, can vary the phenotypic expression of leaf traits, supporting this trend (Gianoli, 2000). This could suggest that species with similar habitat preferences will be similarly vulnerable to galling damage. It is possible that patch dynamics and species proximity had an effect on gall damage, since these two pairs were found growing near each other in many sample sites, and may be a driving force in this pattern (Miller, 2007).

Yamazaki (2006) showed that gall forming insects displayed a host use preference towards larger leaf area compared to linear shaped leaves, such as willow species, which was shown to be a critical factor for non-use in galling insects. This pattern is not displayed in balsam fir in this study due to a

specialized insect herbivore, the Balsam Gall Midge, which is unique and adapted to balsam and fraser fir. The pattern described by Yamazaki (2006) does, however, explain the trend of higher severity of gall on sugar maple (larger leaf area) versus speckled alder (smaller leaf area). This tendency for gall forming insects to favor sugar also explains the higher diversity of gall types found in sugar maple.

Karban (2007) found that valley oak (*Quercus lobata*) individuals that lost their leaves in the winter faced reduced insect herbivory the following summer and spring. The trend Karban (2007) found is supported by this study, suggesting deciduous leaf drop and regrowth provides stronger leaf defense against insect herbivores by renewal of leaf health and defensive capacities. This could also be attributed to foliage regrowth removing insect damage from prior years while coniferous species do not. The trend of balsam fir and northern white cedar to have higher insect herbivore damage may be due to the accumulation of damage over several years while that on maple and speckled alder are only from current year and potentially one or two years past. The tendency for insects to be found most commonly on speckled alder while most damage is seen on balsam fir and northern white cedar support that the damage seen in the two later species is cumulative damage from past years.

Balsam fir had high levels of galling behavior, discoloration, and missing foliage (Table 3). All of the galls formed on balsam fir were on new growth leaves and identified as the Balsam Gall Midge, which infests new growth needles and causes discoloration and missing foliage. The missing foliage on balsam fir often did not provide suitable evidence with which to identify the cause; therefore some damage on balsam fir may also be due to causes other than the gall midge and chewing damage or misattributed between these two causes. The comparison of other types of guild damage are more reliable to identify and measure than that of chewing damage, to which both northern white cedar and balsam fir damage was attributed. Chewing damage was determined to be reliable only on broad leaf species where patterns of chewing evidence have been well documented and are easily identifiable. Coniferous leaves are not reliable in this way due to small leaves which do not allow for trademark chewing patterns to be left by the insect as often and as visibly as on broad leaves.

The highest total percent of leaf area damaged by insect herbivory was found on northern white cedar (Fig. 2). There has been little research done on herbivory patterns and damage in this species and discoloration and missing foliage were the only notable leaf damage. Markings on leaf scales indicate that at least part of the missing foliage was due to chewing damage, although some observed leaf damage may have been misidentified or from other causes.

Patch effects such as neighboring vegetation and species diversity can also raise or lower herbivory by insects (Miller, 2007, Morath 2013). Leaf miner activity was not found across any species in this study, which was unexpected due to data from a concurrent study showed frequent miner damage on Quaking Aspen trees across a two mile radius of the study sites (Harrow, 2014). This may be due to specialization in the leaf miners towards Quaking Aspen, however, all trees surveyed in this study were found in Quaking Aspen dominated stands. Since leaf miner damage has been shown to decrease in mixed stands, where most trees in this study were found, the lack of leaf miner activity could also be due to patch dynamics (Morath, 2013).

The access restriction maple experiment showed no significant difference of damage in any guild type or total leaf percent damage between the Tanglefoot treated and control branches. This could also reflect the time period limitation. Since this experiment had time restrictions to nine days, the length of treatment may need to be expanded before true effects can be seen. This may indicate that the majority of insect herbivores on this species are flying insects and mites that were already present. Insects could have also traveled to the experimental branch from adjacent branches, especially on windy days when branches and leaves were pushed together. To evaluate which is the cause, this experiment could be redone and begun immediately following foliage flushing of the year, when there is no prior insect damage—specifically mite or gall damage—and evaluated over the

entire course of the summer until leaf loss in autumn. This experiment could also be suitable for identifying the source of damage across coniferous trees and could provide solutions to some of the aforementioned problems concerning reliable identification and measurement of balsam fir and northern white cedar damage.

Speckled alder and sugar maple showed no statistical difference in total insect herbivory damage or epidermal or chewer feeding, however, there were variances in where the majority of damage was allocated (Tables A1-A6). In sugar maple, more damage was due to gall activity more damage seen on speckled alder was roller damage (Figure 10). Leaf thickness has been shown to increase beetle herbivory (Gianoli, 2000). This trend was supported by this study, since the highest beetle (Coleoptera) occurrence frequency was seen in speckled alder, which has the thickest leaf morphology of the four studied species (Barnes, 1981). Beetles are known epidermal and roller herbivores, two types of damage found in speckled alder.

Significant differences were found in the severity by leaf percent of all guild type damage and all insect occurrence frequencies except Lepidoptera. Tukey Post Hoc Multiple Comparison showed variance in severity of damage between speckled alder and sugar maple and between cedar and balsam fir. This supports the hypothesis that there is significant variance of insect occurrence frequency and herbivore damage not only between deciduous and coniferous trees, but between two species expressing different leaf morphologies within

deciduous and coniferous classifications. This supports the hypothesis that leaf morphology affects the type and severity of insect herbivore damage across tree species.

Non-specialized galling damage has been shown to be more severe in broad leaf species with higher leaf dispersal than smaller leaf species and not present in those with scale leaves (Fig. 12, Table 9). Leaf roller damage has been shown to occur more frequently in thicker leaf species with more overlapping leaf distribution (speckled alder and balsam fir) than those with more dispersed leaf distribution (sugar maple) and was found to not occur in scale leaves (Barnes, 1981). Epidermal feeding has been shown to be limited to broad leaf, deciduous species and not present in coniferous needle species. Carmona's research in 2011 also strongly supports leaf morphology variation as a primary factor of variation in insect herbivore damage, also showing differences in attributes' effects across different herbivory guilds.

These trends can offer the ability to predict how introduced insects may affect present plants through herbivory or how introduced plants will react to native insect herbivores. This could be applied for predicting methods of remedy efforts for outbreak or invasive species situations or to new methods of bio-control in which the effect of an insect on plants would allow for the avoidance of unintended damage. These trends can also be used in phylogeny and speciation

studies to evaluate how and why changes occurred in plants and insect and their interactions or predict how this could occur in the future.

TABLES

Table 1A: Severity ranking system for leaf herbivore damage

Severity Ranking	Leaf Area Damage (%)
1	0 – 5
2	6 – 25
3	26 – 50
4	51 – 75
5	76 – 99

Table 1B: Severity ranking system for leaf roller damage

Severity Ranking	Extent of Rolling (%)
1	0 – 5
2	6 – 33
3	34 – 66
4	67 – 99 (<%5 other damage in rolled area)
5	67 – 99 (>%5 damage in rolled area)

Table 2: Locations of Surveyed Trees, by species, across UNDERC Property (Figure 1).

Species	Location
Speckled Alder	A B C D H I K L M N W R
Balsam Fir	A B C D H I J K L M R X
Northern White Cedar	A B C D J I L R X
Sugar Maple	A B C D E F G H I K L R

Table 3: ANOVA comparison of damages across species: P Value of <0.05 indicates statistically significant differences in comparisons; Tukey Post Hoc in shows which comparisons (Tables 5-10). Significant difference seen in all guilds and in total leaf herbivory.

Damage Type	ANOVA P-Value
Total Leaf Herbivory	0.00433
Discoloration	2.509E-11
Leaf Chewer	0.0240
Leaf Roller	0.00045
Gall	0.0143
Epidermal Feeder	0.00830

Table 4: Mean insect leaf herbivory damage/leaf (%) across each guild type and total damage for each evaluated tree species (mean \pm standard error).

Species	Leaf Chewer Damage (%)	Discoloration (%)	Gall (%)	Leaf Roller Damage (%)	Epidermal Feeding (%)	Total Damage (%)
Cedar	12.24 \pm 01.30	14.4 \pm 2.48	0	0	0	26.63 \pm 3.49
Balsam	12.53 \pm 01.80	8.9 \pm 0.89	2.75 \pm 1.08	1.22 \pm 0.52	0	22.54 \pm 3.00
Maple	6.93 \pm 0.82	0	3.50 \pm 1.03	0.83 \pm 0.28	3.18 \pm 1.25	14.45 \pm 2.06
Alder	9.02 \pm 1.58	0	0.77 \pm 0.26	2.52 \pm 0.37	2.17 \pm 0.68	14.48 \pm 1.97

Table 5: ANOVA comparison of Insects Occurrence Frequencies across tree species: P

Value of <0.05 indicates the potential for statistically significant differences in comparisons; Tukey Post Hoc shows which comparisons (Tables 13-15).

Damage Type	ANOVA P-Value
Total Insects	0.000156
Coleoptera	0.0115
Hemiptera	0.0011
Lepidoptera*	0.9834

*Only larvae

Table 6: Mean Insect Occurrence frequencies, individuals/100 leaves, across tree species (mean \pm standard error).

Species	Coleoptera	Hemiptera	Lepidoptera*	Total
Alder	2.9 \pm 1.18	3.4 \pm 1.00	0.3 \pm 0.14	6.6 \pm 1.58
Balsam	0.2 \pm 0.12	0.8 \pm 0.28	0.3 \pm 0.18	1.2 \pm 0.24
Cedar	0.1 \pm 0.50	0.4 \pm 0.12	1.0 \pm 0.26	1.5 \pm 0.87
Maple	0.2 \pm 0.12	0.7 \pm 0.29	0.2 \pm 0.12	1.2 \pm 0.38

*Only larvae

Table 7: Average changes in damage by percent of each leaf damaged.

Treatment	Chewer (%)	Gall	Roller	Epidermal
Control	1.12	1.93	0.58	3.71
Tanglefoot	0.30	0.92	0.16	3.14

Table 8: Statistical (Mann-Whitney U: non-parametric or T-Test: parametric) tests for statistical difference of leaf herbivory damage by guild type between untreated control branch with a branch treated with Tanglefoot. Comparisons with p-values <0.05 were determined to be significantly different.

Guild Damage	P-Value
Chewer	0.457
Gall	0.263
Roller	0.887
Epidermal	0.664

Table 9: Gall types across tree species

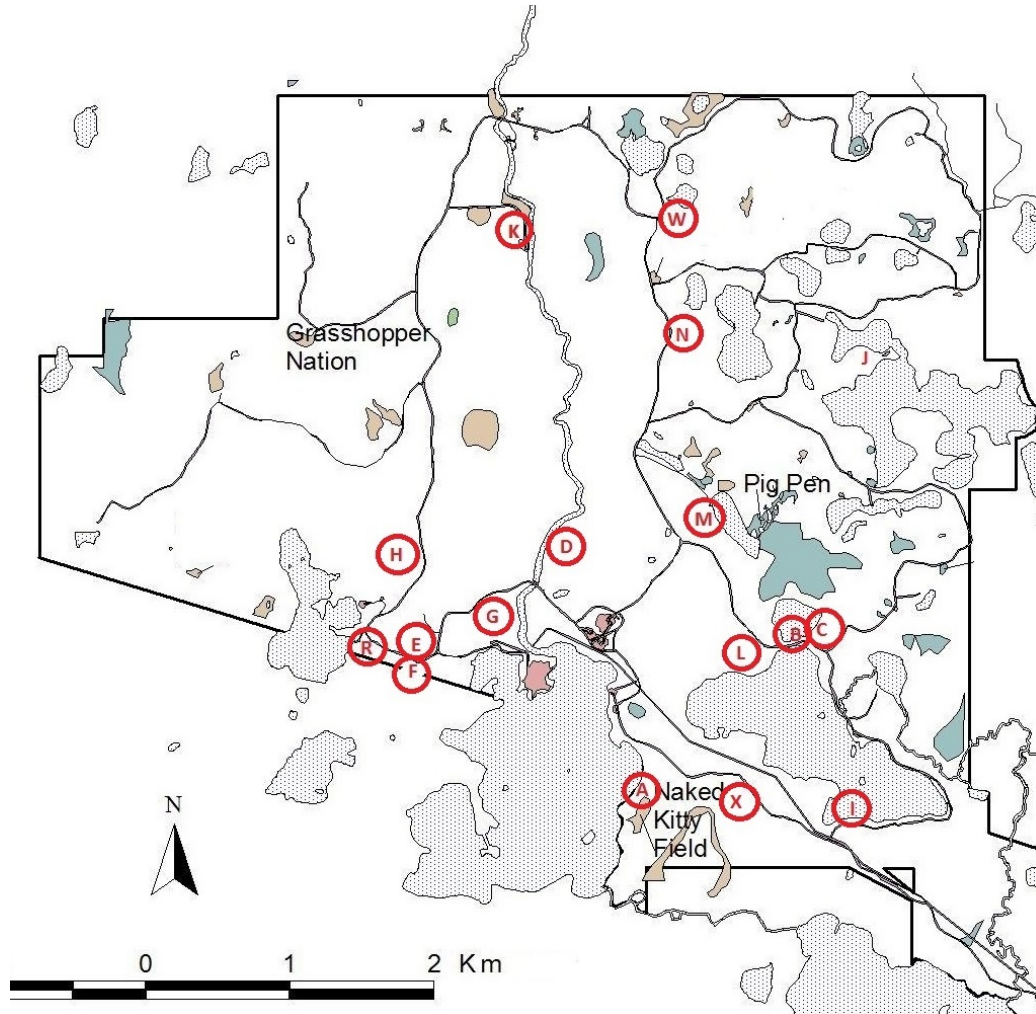
Species	Gall type
speckled alder	Bladder gall, erineum
sugar maple	Bladder gall, erineum, spindle gall, gouty vein gall
balsam fir	balsam gall midge*
northern white cedar	N/A

*specialized gall type (specific to species)

FIGURES

Figure 1: University of Notre Dame Environmental Research Facility: Tree

Locations



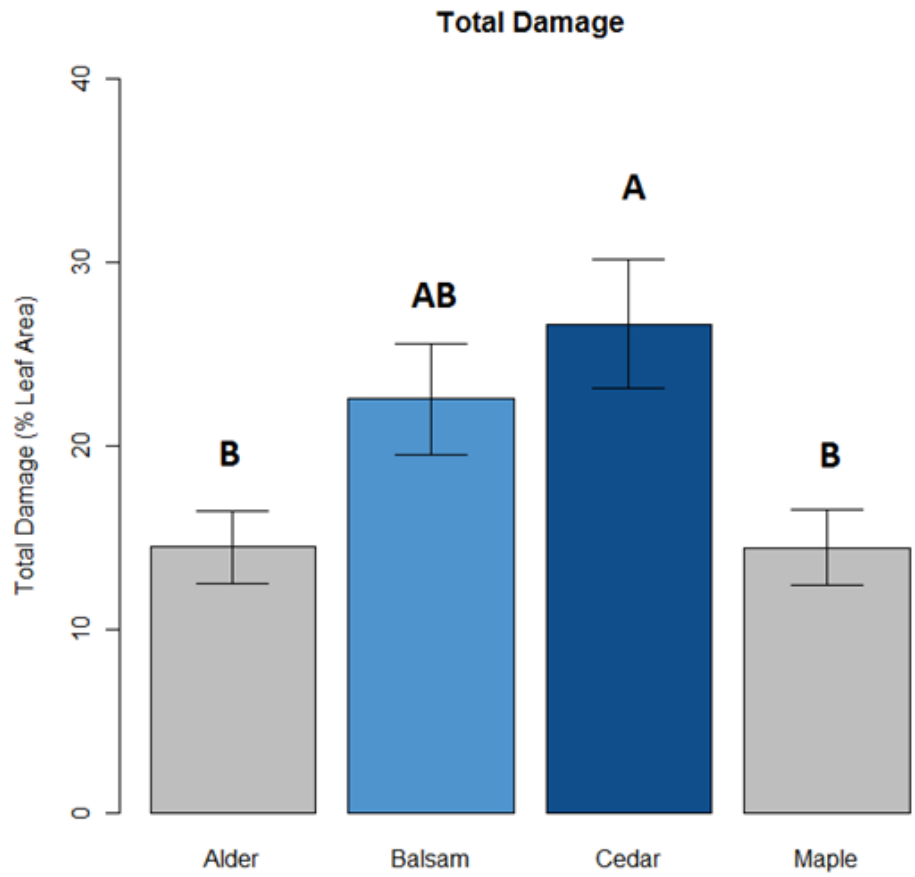


Figure 2: Comparative Total Leaf Herbivory Damage % across four Northern Hardwood tree species (mean +/- standard error). Letters and colors indicate differences found in Tukey Multiple Comparison Test.

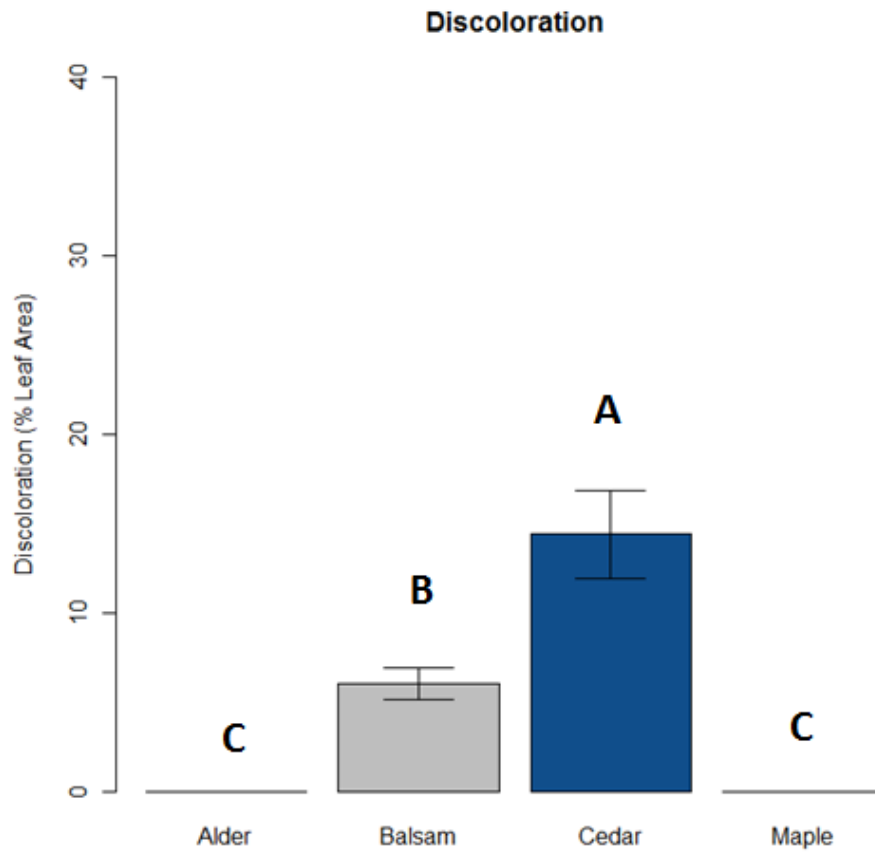


Figure 3: Comparative Discoloration % across four Northern Hardwood tree species (mean +/- standard error). Letters and colors indicate differences found in Tukey Multiple Comparison Test.

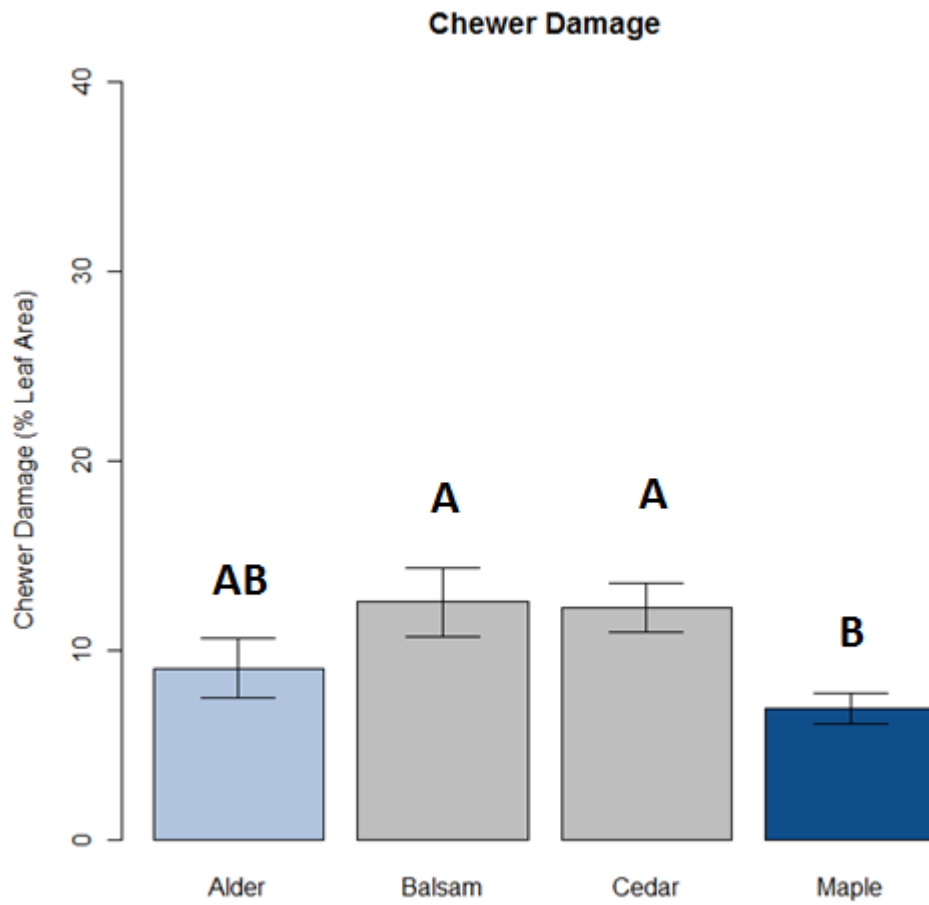


Figure 4: Comparative Leaf Chewer Damage % across four Northern Hardwood tree species (mean +/- standard error). Letters and colors indicate differences found in Tukey Multiple Comparison Test.

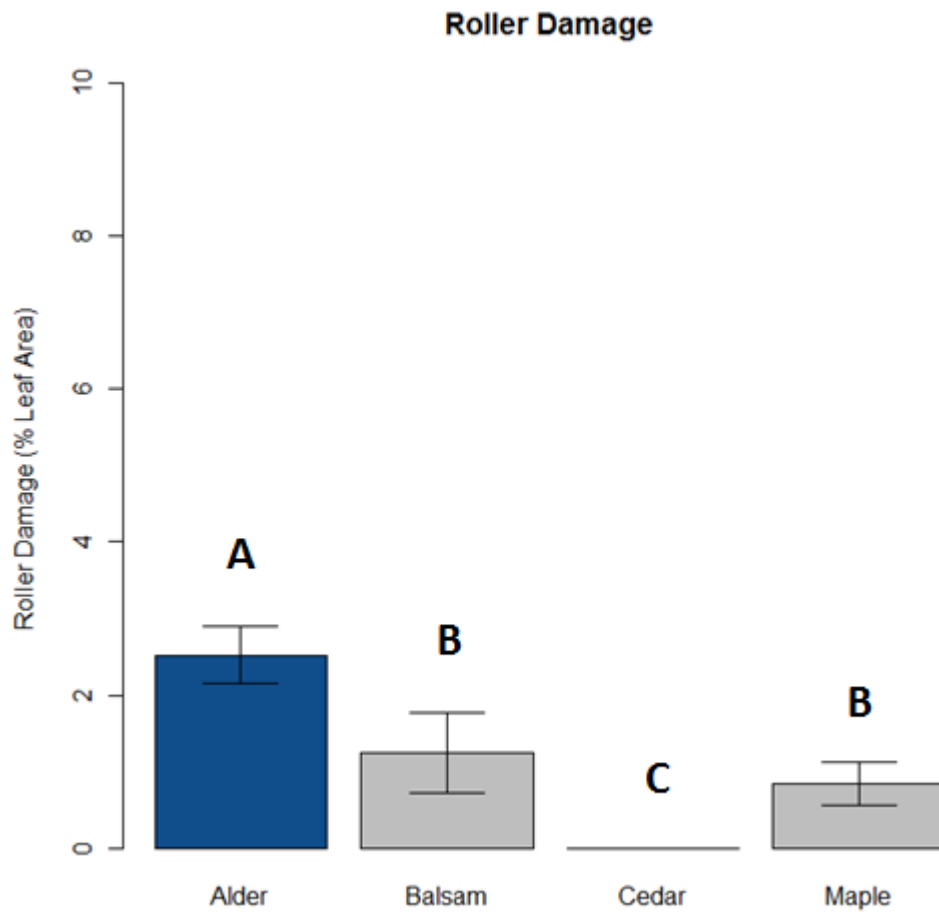


Figure 5: Comparative Leaf Roller Damage % across four Northern Hardwood tree species (mean +/- standard error).

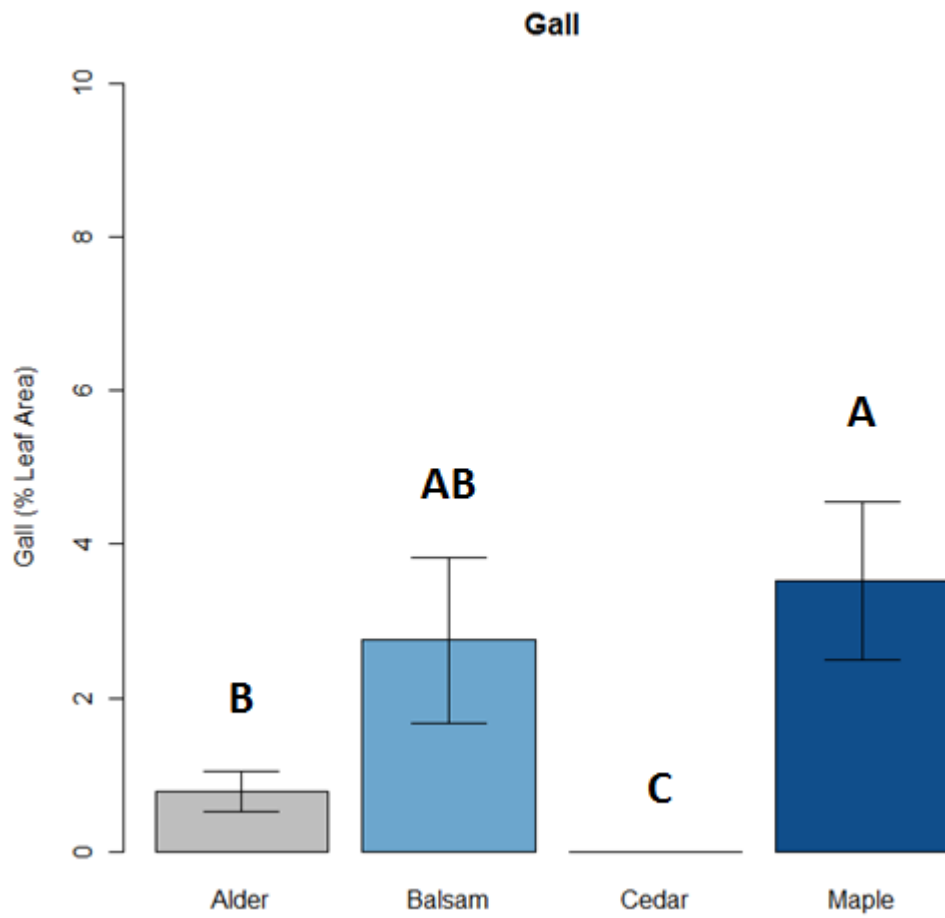


Figure 6: Comparative Gall Damage % across four Northern Hardwood tree species (mean +/- standard error).

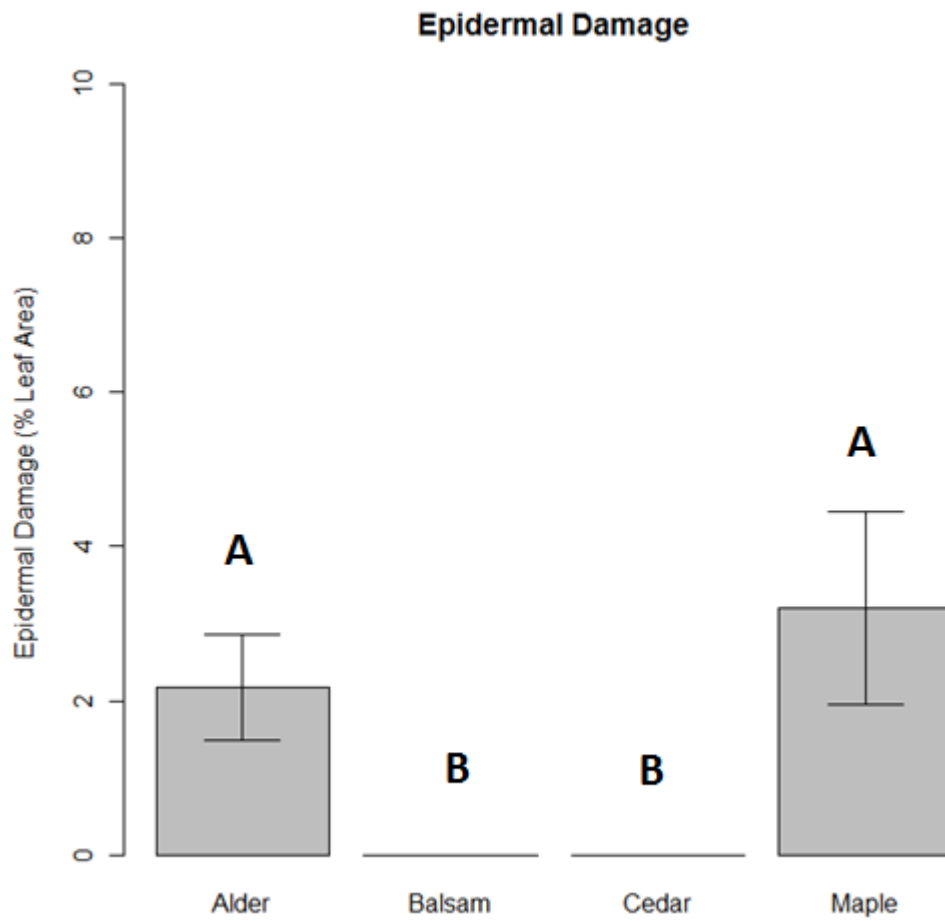


Figure 7: Comparative Epidermal Feeder Damage % across four Northern Hardwood tree species (mean +/- standard error).

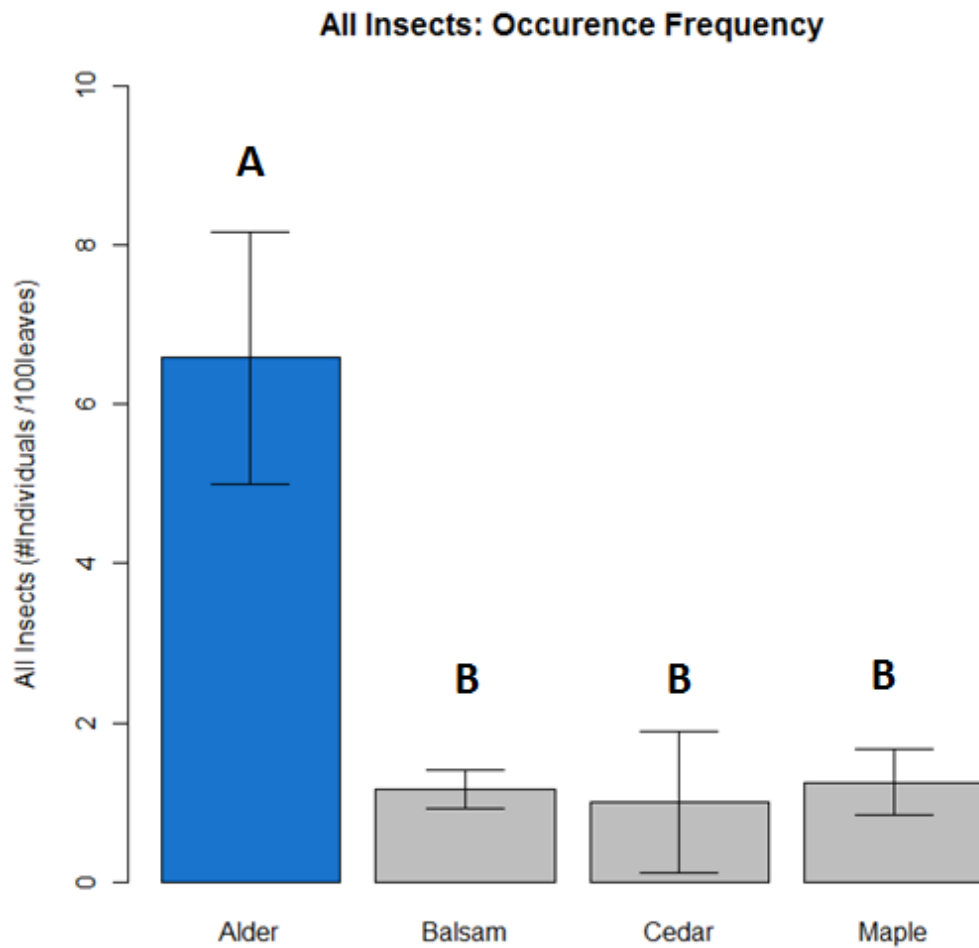


Figure 8: Comparative Total Insect Occurrence Frequency across four Northern Hardwood tree species (mean +/- standard error).

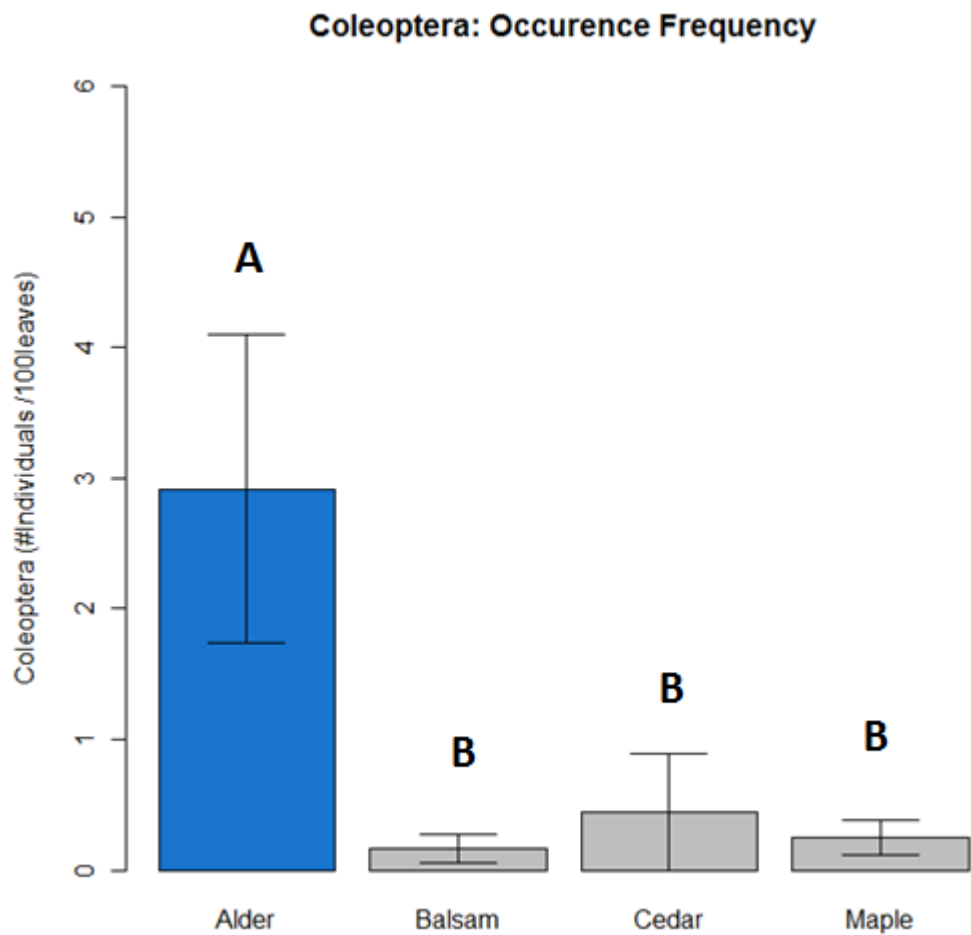


Figure 9: Comparative Coleoptera Occurrence Frequency across four Northern Hardwood tree species (mean +/- standard error).

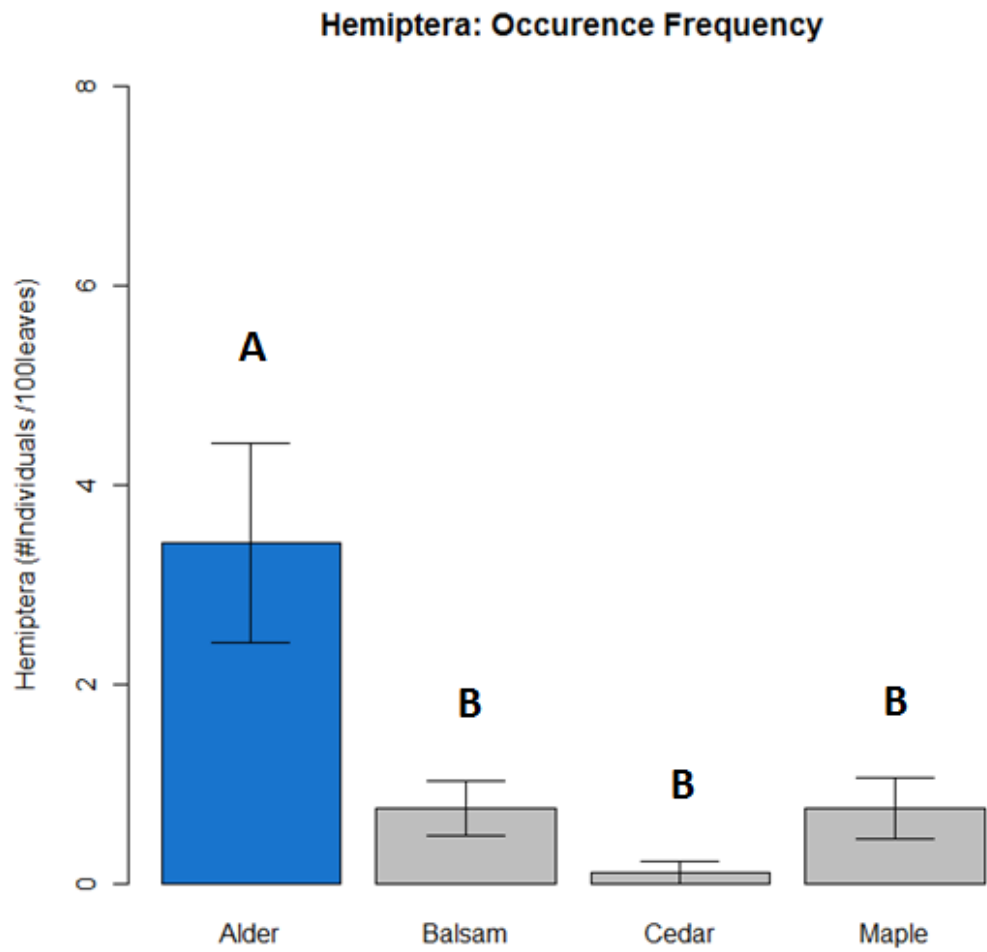


Figure 10: Comparative Hemiptera Occurrence Frequency across four Northern Hardwood tree species (mean +/- standard error).

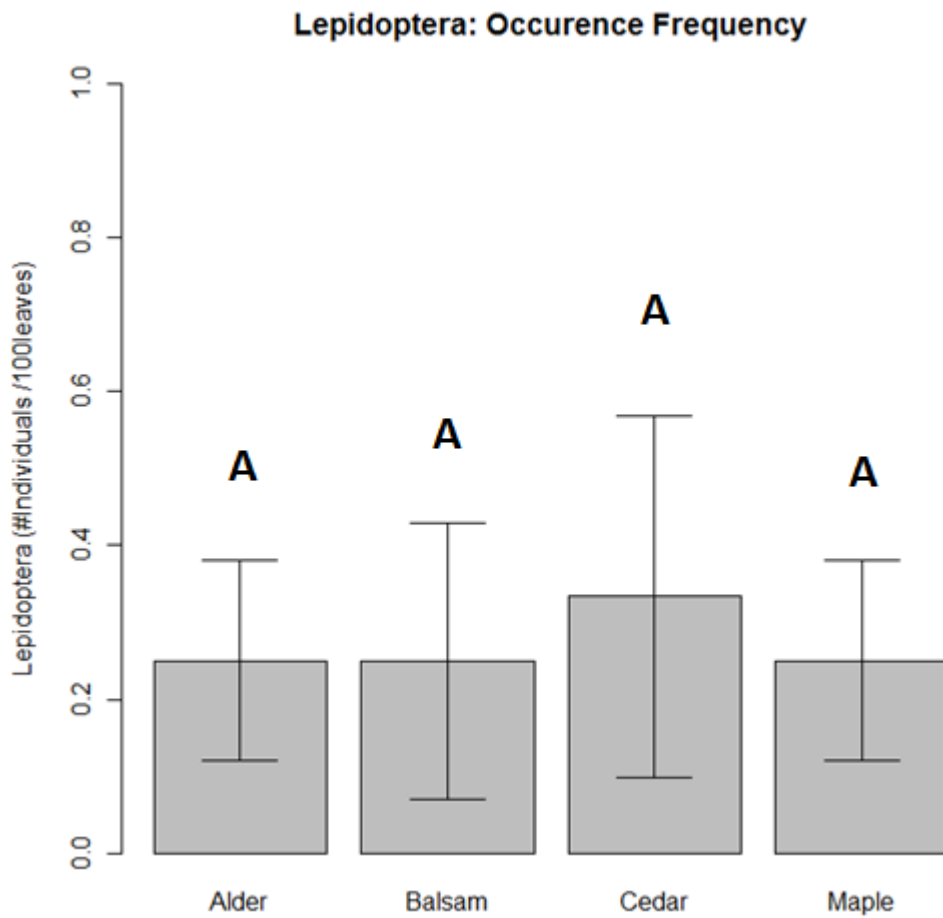


Figure 11: Comparative Lepidoptera (larvae and pupae only) Occurrence Frequency across four Northern Hardwood tree species (mean +/- standard error).

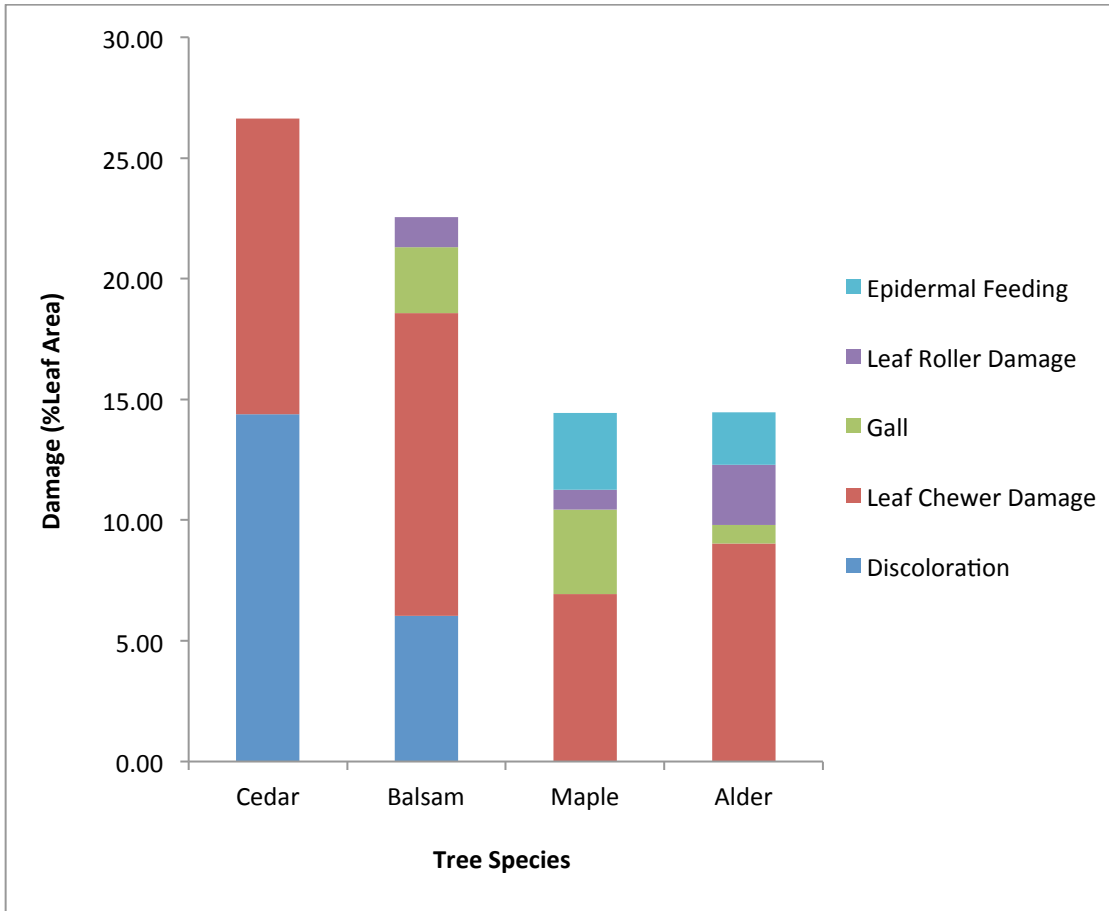


Figure 12: Average Total Insect Herbivore Damage by showing percent composition type across species

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APENDIX

Table A1: Total Leaf Herbivory Damage Tukey Multiple Comparison Post Hoc between tree species: Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	8.05833333	-1.505207	17.621873	0.1253933
CEDAR-ALDER	12.16111111	1.831307	22.490915	0.0153986
MAPLE-ALDER	-0.04166667	-9.605207	9.521873	0.9999994
CEDAR-BALSAM	4.10277778	-6.227026	14.432582	0.7133363
MAPLE-BALSAM	-8.10000000	-17.663540	1.463540	0.1224658
MAPLE-CEDAR	-12.20277778	-22.532582	-1.872974	0.0149690

Table A2: Discoloration Tukey Multiple Comparison Post Hoc between tree species:

Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	6.041667	2.039419	10.043914	0.0012562
CEDAR-ALDER	14.388889	10.065968	18.711810	0.0000000
MAPLE-ALDER	0.000000	-4.002247	4.002247	1.0000000
CEDAR-BALSAM	8.347222	4.024301	12.670143	0.0000374
MAPLE-BALSAM	-6.041667	-10.043914	-2.039419	0.0012562
MAPLE-CEDAR	-14.388889	-18.711810	-10.065968	0.0000000

Table A3: Chewer Damage Tukey Multiple Comparison Post Hoc between tree species:

Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	3.5250000	-1.785136	8.8351359	0.2985971
CEDAR-ALDER	3.2277778	-2.507825	8.9633801	0.4427766
MAPLE-ALDER	-2.0833333	-7.393469	3.2268026	0.7209913
CEDAR-BALSAM	-0.2972222	-6.032825	5.4383801	0.9990306
MAPLE-BALSAM	-5.6083333	-10.918469	-0.2981974	0.0349448
MAPLE-CEDAR	-5.3111111	-11.046713	0.4244912	0.0783167

Table A4: Roller Damage Tukey Multiple Comparison Post Hoc between tree species:

Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	-1.2833333	-2.6656373	0.09897067	0.0772141
CEDAR-ALDER	-2.5250000	-4.0180590	-1.03194103	0.0002851
MAPLE-ALDER	-1.6833333	-3.0656373	-0.30102933	0.0115591
CEDAR-BALSAM	-1.2416667	-2.7347256	0.25139230	0.1330227
MAPLE-BALSAM	-0.4000000	-1.7823040	0.98230400	0.8653617
MAPLE-CEDAR	0.8416667	-0.6513923	2.33472564	0.4412825

Table A5: Gall Damage Tukey Multiple Comparison Post Hoc between tree species:

Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	1.9750000	-0.9925089	4.942509	0.2964176
CEDAR-ALDER	-0.7750000	-3.9802760	2.430276	0.9158475
MAPLE-ALDER	2.7416667	-0.2258423	5.709176	0.0792854
CEDAR-BALSAM	-2.7500000	-5.9552760	0.455276	0.1153225
MAPLE-BALSAM	0.7666667	-2.2008423	3.734176	0.8996503
MAPLE-CEDAR	3.5166667	0.3113907	6.721943	0.0266627

Table A6: Epidermal Damage Tukey Multiple Comparison Post Hoc between tree

species: Comparisons between tree species with p adj of <0.05 are considered

significant.

	diff	lwr	upr	p adj
BALSAM-ALDER	-2.17500e+00	-4.9596664	0.6096664	0.1729649
CEDAR-ALDER	-2.17500e+00	-5.1827834	0.8327834	0.2291319
MAPLE-ALDER	1.02500e+00	-1.7596664	3.8096664	0.7583798
CEDAR-BALSAM	-3.94746e-16	-3.0077834	3.0077834	1.0000000
MAPLE-BALSAM	3.20000e+00	0.4153336	5.9846664	0.0187264
MAPLE-CEDAR	3.20000e+00	0.1922166	6.2077834	0.0332214

Table A7: All Insects Occurrence Frequency Tukey Multiple Comparison Post Hoc

between tree species: Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
Balsam-Alder	-5.41666667	-8.893774	-1.939559	0.0008524
Cedar-Alder	-5.58333333	-9.339039	-1.827628	0.0015080
Maple-Alder	-5.33333333	-8.810441	-1.856226	0.0010341
Cedar-Balsam	-0.16666667	-3.922372	3.589039	0.9993899
Maple-Balsam	0.08333333	-3.393774	3.560441	0.9999035
Maple-Cedar	0.25000000	-3.505706	4.005706	0.9979556

Table A8: Coleoptera Occurrence Frequency Tukey Multiple Comparison Post Hoc

between tree species: Comparisons between tree species with p adj of <0.05 are considered significant.

	diff	lwr	upr	p adj
Balsam-Alder	-2.75000000	-5.182701	-0.3172988	0.0212934
Cedar-Alder	-2.47222222	-5.099840	0.1553954	0.0717251
Maple-Alder	-2.66666667	-5.099368	-0.2339655	0.0268370
Cedar-Balsam	0.27777778	-2.349840	2.9053954	0.9919678
Maple-Balsam	0.08333333	-2.349368	2.5160345	0.9997188
Maple-Cedar	-0.19444444	-2.822062	2.4331732	0.9971996

Table A9: Hemiptera Occurrence Frequency Tukey Multiple Comparison Post Hoc

between tree species: Comparisons between tree species with p adj of <0.05 are

considered significant.

	diff	lwr	upr	p adj
Balsam-Alder	-2.666667e+00	-4.801031	-0.5323024	0.0092017
Cedar-Alder	-3.305556e+00	-5.610932	-1.0001787	0.0022850
Maple-Alder	-2.666667e+00	-4.801031	-0.5323024	0.0092017
Cedar-Balsam	-6.388889e-01	-2.944266	1.6664880	0.8794934
Maple-Balsam	2.220446e-16	-2.134364	2.1343643	1.0000000
Maple-Cedar	6.388889e-01	-1.666488	2.9442658	0.8794934