

**Variation of Leaf Area Index with Forest Structure
in Mixed Temperate Forest of Upper Peninsula Michigan**

BIOS 35502-01: Practicum in Field Biology

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2015

Abstract

Forests of northern Wisconsin and the southwestern Upper Peninsula of Michigan are undergoing significant change during their recovery after historical logging, burning, and agriculture. The composition and structure of forests have climatic repercussions through variations in albedo, latent heat flux, sensible heat, and carbon sequestration. One metric that has understood relationships with these climatic effects is leaf area index (LAI); this study aimed to discover how LAI was related to temperate mixed forest species composition, age structure, and edge effects. Species composition, species diversity, stand basal area, average stand age, tree density, canopy heterogeneity, distance from nearest edge, and LAI were all assessed for 18 forest stands across a gradient of species compositions and ages, and analyzed with Pearson correlations and 1-way ANOVA. LAI measurements followed a normal distribution with a low mean ($\bar{x}_{LAI}=4.468$, $SD_{LAI} = 1.035$). Species specific effects on LAI explained 98.15% of the variation in LAI between monoculture sites, confirming Asner et al. 2003. LAI was strongly correlated with average site age ($r=0.856$, $p<0.001$) and strongly correlated with distance from nearest edge ($r=0.701$, $p=0.001$). LAI was approaching a significant correlation with species diversity, stand basal area, and tree density. These results suggest that species-specific effects in monocultures, average stand age, and edge effects are the major determinants of LAI in temperate mixed forests. Because of the relatively young, even-aged state of the northern Wisconsin and UP forests from historical logging, stands appear to be structured into mixtures of one-species clumps, making LAI modeling across landscapes feasible.

Introduction

Prior to European settlement in the mid 1800's, northern Wisconsin and the Upper Peninsula of Michigan (UP) were densely forested with *Tsuga canadensis* (eastern hemlock), *Pinus resinosa* (red pine), *Pinus strobus* (white pine), *Thuja occidentalis* (northern white-cedar), *Populus tremuloides* (quaking aspen), *Betula alleghaniensis* (yellow birch), *Betula papyrifera* (paper birch), *Acer saccharum* (sugar maple), and *Acer rubrum* (red maple). After heavy logging and repeated burning by colonizing Europeans, forests were decimated from 96% land cover to 56% in half a century (Rhemtulla et al. 2009). Most logged areas were allowed to regrow naturally; however, from the 1930's to 2000, northern Wisconsin and UP forests did not recover entirely, and the species composition shifted, favoring *Populus spp.*, *Betula spp.*, and northern hardwoods over *T. canadensis*, *T. occidentalis*, and *P. strobus* (Rhemtulla et al. 2009).

The change in both density and composition of the forests in northern Wisconsin and the UP will have climatic repercussions, due to forest biophysical properties. First and foremost, forests behave as a carbon sink, sequestering atmospheric carbon dioxide (CO₂) as biological carbon and helping to mitigate climate change. Numerous studies have linearly related species diversity to the carbon sequestration ability of ecosystems; if composition changes and reduces species diversity, the carbon sequestration ability of a forest will decrease (Kirby & Potvin 2007). Secondly, forests influence local and regional climate through transpiration and solar radiation absorption or reflection (Anderson et al. 2010). Canopy density and the species composition of a forest influence the degree of albedo (solar radiation reflected back to space), sensible heat (absorbed solar radiation), and the rate of transpiration/latent heat flux (Bonan 2008). Latent heat flux - the energy used to transpire - helps mitigate solar energy by transforming it to work without the emission of heat. Transpiration also forms clouds in humid

climates, which increases albedo (Anderson et al. 2010). Using knowledge of how different forests affect local climate through these traits, forestry practices like afforestation (planting forests where none have historically existed), reforestation, and forest management are becoming major climate change mitigation strategies. In areas like northern Wisconsin and the UP where forests are just beginning to recover from rapid deforestation, forest recovery could be guided to maximize climate change mitigation effects.

Leaf area index (LAI), an analog for canopy density, quantifies the leaf surface available in a forest stand for transpiration, CO₂ exchange, and latent heat flux (Asner et al. 2003). LAI measures the amount of one-sided leaf area of broadleaves or the hemi-surface area of evergreen needles in m² divided by m² ground area (Chen & Black 1992). LAI also characterizes albedo and indicates the forests' ability to interrupt precipitation and wind (Baldocchi 2012). As such, LAI is an “essential climate variable” in climate change modeling (World Meteorological Organization 2003), because it quantifies how a forest will affect local and regional climates.

LAI is influenced by composition, forest structure, and edge effects. A synthesis of global LAI measurements by Asner et al. (2003) found LAI was linked to climate (temperate, tropical, boreal), stand type (needle leaf/broadleaf, evergreen/deciduous), and species composition (significant variation between *Acer*, *Helianthus*, *Pinus*, etc.). Northern Wisconsin and UP forests are temperate mixed forests with highly variable species composition, so it is not clearly understood what elements of forest structure and species composition in the area affect LAI. Because forests in northern Wisconsin and the UP are fragmented by common bogs and lakes, LAI may be influenced by edge effects.

In this study, I investigated the relationship between LAI and maturity, species composition, and fragmentation in the mixed temperate forests of northern Wisconsin and the

UP. I evaluated the species composition, species diversity, average age, stand basal area, canopy heterogeneity, tree density, and distance to nearest edge (a lake, large bog, or road) of 18 forest stands. I hypothesized:

I. Temperate mixed forest would have an average LAI intermediate to the global average LAI of temperate deciduous broadleaf forest (mean = 5.1, SD = 1.8) and temperate evergreen needle leaf forest (mean = 6.7, SD = 6.0), with higher variability than either (Asner et al. 2003).

II. Each stand would have higher species diversity than temperate hardwood forests ($1.49 < H' < 1.66$) (Elliott & Hewitt 1997), with a high frequency of *Acer saccharum*, *P. tremuloides*, *Betula spp.*, and *Abies balsamea*, with some *T. canadensis*, *T. occidentalis*, and *Pinus spp.* (Rhemtulla et al. 2009).

III. Lower species diversity would correlate with higher LAI.

IV. Species composition would be a significant factor: coniferous sites would have a significantly higher LAI than hardwood sites, and monoculture sites would have significantly higher LAI than mixed sites.

V. Increased average age of a stand would be related to lower tree density, higher stand basal area (Johnson & Abrams 2009), and lower canopy heterogeneity.

VI. Average age and all related characteristics would be correlated to lower LAI, since some studies suggest that LAI gradually declines with stand age (Kram 1998, Wood 2005).

VII. Canopy heterogeneity would predict higher LAI due to the overlapping of different canopy layers.

VIII. Distance from nearest edge (lake, large bog, or road) would positively correlate with LAI due to edge effects (Chen et al. 1992).

Methods

Study Sites

I selected sixteen study sites in the southwestern Upper Peninsula of Michigan and northern Wisconsin on the property of the University of Notre Dame Environmental Research Center (UNDERC). I selected two additional study sites in the nearby Guido Rahr Sr. Tenderfoot Forest Reserve owned by The Nature Conservancy (TNC), with a sampling permit issued by TNC to Bethany Blakely. Both properties are part of the “northern Wisconsin highland lakes country” ecoregion (50i), which contains outwash plains, shallow glacial lakes, extensive wetlands, and supports both northern hardwood-hemlock forests as well as white, red, and jack pine barrens (U.S. EPA 2015a & 2015b). Both the UNDERC and TNC properties are impacted by current and historical human disturbances, including roads, motorized vehicles, and recreation, with some history of agriculture and logging (Rhemtulla et al. 2009).

I chose study sites of 50 meters by 50 meters to represent a gradient of forest ages, including young (20 – 40 years old), middle aged (40 – 100 years old), and old growth (100+ years old), as well as a variety of species compositions. I accessed data for twelve sites, gathered in previous surveys by Sam Pecoraro, through the Jason McLachlan lab archive. Of these 12 sites (notated KRSP1 – KRSP12), site KRSP10 was discarded due to a critical data deficit. I surveyed seven sites, two in TNC (notated KRC1 and KRC2) and five in UNDERC (notated KR1 – KR5). I analyzed a total of 18 sites (Fig. 1): the 11 KRSP sites were surveyed by Sam

Pecoraro with one square plot of 500 m² and I surveyed each of the 2 KRC and 5 KR sites with one circular plot of radius 10 meters.

Surveys

I geo-tagged the center of each plot using a GPS device for later GIS analysis. In each circular plot I took a census of the trees with a diameter at breast height (DBH) greater than 5 cm including snags. I noted the species of each tree for species composition and diversity calculations. I did not record the species of snags. I measured azimuth and distance from the center of the plot (m) to construct plot diagrams. I measured DBH (cm) using a diameter tape for basal area calculations. I used a clinometer to determine the angle from the center of the plot to the top of the tree. I used the cline and distance between the center and the tree to calculate the height of the tree and inform my qualitative assignment of canopy classifications (dominant, co-dominant, intermediate, or suppressed). I assigned height cutoffs for canopy classification qualitatively. The cutoffs varied by site depending on the co-dominant layer's height.

I chose to core the two trees with the lowest azimuths in each of the four ranges (0-90°, 90-180°, 180-270°, and 270-360°), in order to minimize bias in core ages. If a tree selected for coring was part of a tree that split into multiple trunks below breast height or if it was a snag too rotten to core, I did not core the tree and did not select an alternate tree. I dried the cores in their sample tubes in a drying oven set at 36°C for between two and four weeks. I mounted the dried cores on boards and adhered them in place. I allowed the mounted cores to dry at room temperature between five days and three weeks. I sanded the mounted cores to ease reading if necessary and used a microscope to read the core ages. In sites KRSP1 – KRSP5, 8 – 20 trees were randomly sampled for coring, and most trees were cored twice to account for errors in

coring and age-reading. Sites KRSP6 – KRSP12 were not cored, and were excluded in age analyses.

Leaf Area Index Measurements

I measured LAI using a Li-COR LAI-2200C optical sensor unit which includes a main console and two wands. One wand was used to autonomously measure background sky brightness, known as the above canopy (A) reading, every 15 or 30 seconds. The other wand was used in conjunction with the main console to record the below canopy (B) readings in the 50 meter by 50 meter sites that were surveyed. I established eight A sites. Each A site was paired with one to four B sites, all of which were within 1 km of the A site (Fig. 1). When I established an A site, I recorded the bearing of the wand for both later scattering correction analysis and to replicate the same measurement direction for the B readings. All A and B readings were taken with a 90° view cap on the optical sensor.

For each site, I started the auto-logging feature on the A wand before going to measure B readings. As recommended by the Li-COR LAI-2200C manual, I took a K record (AAA) with the B wand at the A site before making B measurements for later LAI scattering corrections. At the B site I took 25 B readings in a 5 x 5 grid approximately centered on the 500 m² square plot or 10 m radius circular plot (Fig. 2). For each B reading I had the wand facing the same bearing as the A wand. I moved as necessary to avoid recording a B measurement within 1 m directly below any leaves. I recorded LAI measurements on days with clear blue sky or fairly uniform overcast sky. On days that were less uniformly overcast, I took a second K record (AAA) at the A site after I made B measurements as well.

Leaf Area Index Corrections

I used Li-COR FV2200 software (version 2.1.1) to make corrections to the LAI data. Of the five optical sensor rings, I masked the outside two rings, which had view angles of 53° and 68° (Fig. 3). I excluded these two wide-angled rings from LAI calculation because of the high probability they would sense tree trunks, underbrush, and branches and produce an inaccurate LAI.

I imported A readings from the related A site file using a Match 90° view cap file, pairing A and B readings by closest in time. I created K records from the AAA sequence(s) in the B file and applied scattering corrections with the recorded bearing. Some files were missing K records, so I formed K records from the A files and imported them. I applied all changes to calculate the corrected LAI.

ArcGIS Analysis

The GPS coordinates of each site were used to pin sites in an ArcGIS Online map accessible at arcg.is/1Kfb0A8 (Fig. 4). The map includes a layer of wetlands location data from the U.S. Fish and Wildlife Service Wetlands Project. I used ArcGIS to measure the distance in meters from the center of each plot to the nearest edge: a lake, bog (“freshwater pond”), or road. Wooded wetlands were not included as bogs/edges.

Statistical Analysis

I tested the LAI data for normality using a normal probability plot and confirmed the data could be used in parametric tests. In all statistical tests, I used a significance level of $\alpha = 0.05$. I performed descriptive statistics on the LAI data.

I used the census of tree species in each plot to calculate the percentage of trees of each species per plot. If a species was more than 80% of the composition of a site, I classified the site as a monoculture of that species. There were seven monoculture sites of four different species: *T.*

canadensis (1 site), *Picea mariana* (1 site), *P. tremuloides* (1 site), and *A. saccharum* (4 sites). I compared the LAI by monoculture species using 1-way ANOVA. I compared all of the monoculture sites against all of the non-monoculture (mixed) sites using 1-way ANOVA. Post-hoc analysis (Tukey's test) was run on any significant ANOVA results.

I then classified sites as one of six species composition categories: "hardwood monoculture" contained $\geq 80\%$ of one hardwood species, "hardwoods" contained $\geq 80\%$ of trees as a few hardwood species, "hardwood mixed" contained a mix of hardwood and coniferous species dominated by hardwood species, "even mixed" contained a fairly even mixture of hardwood and coniferous species, "conifer mixed" contained a mix of hardwood and coniferous species dominated by coniferous species, and "conifer monoculture" contained $\geq 80\%$ of one coniferous species. I compared the LAI between the six species composition classifications using 1-way ANOVA.

I calculated species diversity of each site using the Shannon diversity index. I ran descriptive statistics on the species diversity data. I ran Pearson correlation analysis on species diversity with LAI.

I calculated the mean of the core age data from all the trees in a site to get the average site age. Because KRSP6 – KRSP12 were not cored, all average age statistical analyses had $n=12$. I ran Pearson correlation analysis on average site age with LAI. I also compared average site age to stand basal area, tree density per hectare, and canopy heterogeneity using three separate Pearson correlation analyses. I classified each site by age into "young" (20 – 40 yrs.), "mid" (40 – 100 yrs.), and "old" (100+ yrs.) and performed a 1-way ANOVA between age classification and LAI. A Tukey's post-hoc test was run on significant ANOVA results.

I calculated basal area in m^2 of each tree using the following formula:

$$\text{Basal Area} = \frac{\pi}{4 \times 10000} * \text{DBH}^2$$

I calculated site basal area (m²/ha) using the following formula:

$$\frac{\sum \text{Tree Basal Areas}}{\text{Plot Area in hectares}}$$

I compared site basal area to LAI using a Pearson correlation analysis. I calculated tree density (trees/ha) and compared it to LAI using a Pearson correlation analysis. Snags were included in basal area and density calculations.

I calculated canopy heterogeneity for each site by calculating the Shannon diversity index, treating each canopy class as a species. I ran a Pearson correlation analyses for Shannon diversity of canopy with LAI. Snags were not included in canopy heterogeneity calculations.

I ran a Pearson correlation analysis on the distance to nearest edge in meters and LAI.

Results

Species composition, composition classification, and species diversity data are reported in (Fig. 5). Census data on species present in each site are located in (Fig. 6). Among all sites, *A. saccharum* was most abundant (n = 303; 42.3% of all trees), followed by *P. tremuloides* (n = 114; 15.8%) and *A. balsamea* (n = 112; 15.6%). Species in lower abundance included *T. canadensis* (n = 26; 3.6%), *P. mariana* (n = 51; 7.1%), *A. rubrum* (n = 45; 6.3%), *P. resinosa* (n = 22; 3.1%), and *Fraxinus americana* (n = 13, 1.8%). Rare species included *Picea glauca* (n = 5; 0.7%), *Populus grandidentata* (n = 1; 0.1%), *B. alleghaniensis* (n = 9; 1.3%), *B. papyrifera* (n = 2; 0.3%), *Amelanchier arborea* (n = 1; 0.1%), *Prunus serotina* (n = 8; 1.1%), *Pinus strobus* (n = 2; 0.3%), and *T. americana* (n = 3; 0.4%).

One-way ANOVA found a significant difference between the LAIs of the seven monoculture species sites (df=6, F=53.11, p=0.004). Post-hoc analysis revealed that the *A.*

saccharum sites ($\bar{x}_{LAI}=5.088$) and the *T. canadensis* site ($\bar{x}_{LAI}=6.270$) were not significantly different from one another but were significantly higher than the *P. mariana* ($\bar{x}_{LAI}=3.050$) and *P. tremuloides* ($\bar{x}_{LAI}=2.870$) sites. The *P. mariana* and *P. tremuloides* sites were not significantly different from one another. This model (Fig. 7) accounted for 98.15% of the variation in LAI between the seven sites.

The 1-way ANOVA comparing monoculture sites to mixed sites failed to find a significant difference in LAI (df=17, F=1.23, p=0.285). The 1-way ANOVA of six different species composition classifications also failed to find a significant difference in LAI (df=17, F=1.01, p=0.453).

Calculated site basal area (m²/ha), density (trees/ha), canopy heterogeneity (Shannon diversity index), distance from nearest edge (m), the type of the nearest edge, and LAI are reported in Table 2. The Pearson correlation analysis found a significant correlation of -0.444 between average site age and LAI (p<0.001). The Pearson correlation of 0.786 between average site age and site basal area was also significant (p=0.002). The Pearson correlations between species diversity and LAI, stand basal area and LAI, and tree density and LAI were all approaching significance (Table 2). The correlations between average site age and density, canopy heterogeneity and LAI, and average site age and canopy heterogeneity were not significant (Table 3). The Pearson correlation analysis of distance to nearest edge (m) with LAI found the correlation of 0.701 was significant (p=0.001).

The 1-way ANOVA comparing young, mid, and old age classes (Table 4) found a significant difference in LAI (df=11, F=6.94, p=0.015). Post-hoc analysis revealed that old growth sites had significantly higher LAIs than the young and mid-aged sites and that the young

and mid-aged sites did not have significantly different LAIs. The model (Fig. 8) explains 60.67% of the variation in LAI between the twelve sites.

Discussion

Hypothesis I predicted the LAI distribution of my study sites would be $5.1 < \bar{x}_{LAI} < 6.7$ with a standard deviation > 6.0 . Contrary to expectation, the study sites had a lower mean LAI ($\bar{x}_{LAI}=4.468$) with less variation ($SD_{LAI} = 1.035$) than either temperate deciduous broadleaf forest or temperate evergreen needle leaf forest. The low standard deviation is likely a result of the small sample plots, which selected only a small section of the true variation of a stand. It is possible that another metric measured in this study can explain the uncharacteristically low LAI mean.

Hypothesis II predicted that the temperate mixed forests of my study area would have a higher mean species diversity than the temperate hardwood forests of Elliott & Hewitt (1997); but the distribution of Shannon species diversity of $\bar{x}_{div}=0.797$, $SD_{div} = 0.110$ was lower than that of Elliott & Hewitt ($1.49 < H' < 1.66$). Species diversity may have been lower than I expected because so many of my plots were monocultures or groups of two to three species. Qualitatively, it appeared that sections of the mixed forests in my study region were mixed clumps of near-monoculture stands, rather than being well mixed throughout. This may be an artifact of historical logging. Once logged, species composition would depend on which species was best suited to grow quickly given the abiotic conditions of the area, which probably would be one or two species per small area. The study forests may not be old enough for significant disturbances

to have created new niches within near-pure stands and allowed for the development of truly mixed forests.

For species composition, I expected to find a higher abundance of *A. saccharum*, *P. tremuloides*, *Betula spp.*, and *A. balsamea* than other species, with moderate abundance of *T. canadensis*, *T. occidentalis*, and *Pinus spp.* I found an overabundance of *A. saccharum*, *P. tremuloides*, and *A. balsamea* and shortage of *Pinus spp.* (3.3%) and *T. canadensis*, as expected according to Rhemtulla et al. (2009). However, I found an unexpectedly low abundance of *Betula spp.* (1.5%), which generally grows together with *P. tremuloides* (Rhemtulla et al. 2009). The low abundance of *Betula spp.* may have originated from repeated clonal reproduction by *P. tremuloides* due to an environmental factor. If *P. tremuloides* reproduces clonally, the stand will generally be a monoculture (Little 1980), potentially driving the exclusion of *Betula spp.* I found no *T. occidentalis* in my plots, which may have been due to chance, since I saw *T. occidentalis* near my plots. It is also possible that the study area is becoming unfavorable habitat for *T. occidentalis* due to climate change or land use (Rhemtulla et al. 2009). *Picea spp.*, *Prunus spp.*, and *T. americana* were rare, as expected.

I expected lower species diversity would be correlated with higher LAI because I subjectively observed that (near-) monoculture stands have dense canopy layers, whereas mixed forests appeared to have open canopies (hypothesis III). Although the Pearson correlation was only approaching significance, I found a negative relationship; therefore, the data suggest that less diverse forest stands, like monocultures, could be expected to have higher LAIs. This effect may stem from species-specific shade tolerances or some similar species-monoculture efficiency effect. For instance, I qualitatively observed a tendency of *T. canadensis* to grow in pure stands, most likely due to shading out potential competitors. This shade tolerance can come from the

dense layering of needles to draw the most amount of sunlight, leading to a higher LAI. If a *T. canadensis* site is mixed with other species, the dense layering of needles and branches may not occur, leading to a lower LAI.

I hypothesized (IV) that species composition would be significantly correlated with differences in LAI. I expected conifers to have higher LAIs than hardwoods due to their apparent tendency to grow in dense clumps; I also expected monocultures to have significantly higher LAI than mixed sites, due to the same reasoning for hypothesis III. Monocultures, whether they were distinguished by coniferous/hardwood or not, did not differ significantly in LAI from any variety of mixed forest. However, among monocultures, dominant species did make a significant difference. *T. canadensis* and *A. saccharum* monocultures have high LAI while *P. mariana* and *P. tremuloides* monocultures have extremely low LAIs. Because these results were not grouped by type (conifer or hardwood), it suggests that the effect of these monocultures on LAI is species-specific, confirming Asner et al. (2003). *T. canadensis* has long been known to grow branches very densely due to its high shade tolerance (Baker 1949), probably leading to the observed high LAI, whereas *P. mariana* tends to extensively self-prune lower branches (Little 1980), potentially leading to very low LAI. Qualitatively, *A. saccharum* sites appeared to grow dense canopies with wide fluted branching, whereas *P. tremuloides* stands grew trees spaced farther apart with narrower fluted vertical tree structure. With *A. saccharum* and *P. tremuloides* expected to become more abundant and *T. canadensis* expected to become less abundant in the study area (Rhemtulla et al. 2009), there may be a further decrease in LAI in the future. However, this effect appears to only be significant in monocultures. There was no significant difference between monocultures and mixed forests, possibly because the species-specific differences in LAI caused unpredictable changes in the LAI of mixed forests; therefore, using

species-specific effects on LAI may not prove to be a useful method of predicting the influence of mixed forests on LAI in large scale modeling.

I hypothesized (V) that average age of a site would be directly related to stand basal area and inversely related to tree density and canopy heterogeneity. My analysis confirmed a positive correlation between average age and basal area, but did not confirm a correlation between age and tree density or canopy heterogeneity. The relationship between age and basal area makes sense because as trees get older, their DBH increases, thereby increasing their individual basal area. Age may not have been related to tree density due to my minimum DBH cutoff. Young sites ought to have more stems because they have not hit the stem exclusion phase yet (Kocher & Harris 2007). However, the young trees have rather small DBHs. By setting a DBH cutoff at 5 cm, I excluded many young trees from analysis in the younger sites, possibly creating a skew in the density data. Similarly, canopy heterogeneity may not have been significantly correlated with any other variables due to the method of calculation. Canopy heterogeneity is generally evaluated with spatial remote sensing techniques (Rich et al. 2010) or not dealt with at the stand level (ex: U.S. Forest Service), so using Shannon's diversity index may not have been an accurate way to assess diversity. There was very little variation in the canopy heterogeneity values ($SD = 0.17$) even though there subjectively appeared to be a large difference in heterogeneity between sites. Part of the error may also have come from excluding snags in canopy heterogeneity analyses because snags were often a majority of the suppressed canopy layer. The error may have also stemmed from how young and even-aged the forests are; mortality has not had the chance to diversify the canopy yet.

I predicted (hypothesis VI) average age and related characteristics would be correlated to lower LAI. The data suggest the opposite is true: there was a strong positive correlation (0.856)

between age and LAI ($p < 0.001$), confirmed also by the ANOVA run by age group. Older stands may have had higher LAIs due to the establishment of a dense, efficient canopy layer, rather than a young or middle-age stand with canopy gaps. The related trait stand basal area approached significance in a positive correlation with LAI, as might be expected from how basal area is positively correlated with age. Tree density approached a significant negative correlation with LAI; this suggests the idea that higher density is related to younger ages. More analysis would help to determine why tree density has this effect on LAI.

Canopy heterogeneity may not have been correlated with LAI (hypothesis VII) due to the low variation between canopy heterogeneity values or due to confounding by species composition effects. Some sites with low heterogeneity – like the *A. saccharum* and *T. canadensis* monocultures – had unexpectedly high LAI due to the dense co-dominant canopy cohort and their species-specific shade tolerance. Monocultures of different species (*P. mariana*, *P. tremuloides*) that did not form the dense co-dominant cohort expressed the expected low LAI. Further research with a canopy heterogeneity index that more accurately reflects the variation of a site would be useful in teasing out possible relationships.

I found that distance from the nearest edge had a significant, strong positive correlation with LAI (hypothesis VIII). This supports the hypothesis that LAI in the forests in the northern Wisconsin/southwestern UP are impacted by edge effects from lakes, bogs, and roads. This may be due to any of the usual road-edge canopy thinning effects (Chen et al. 1992) or possible lake- and bog-specific effects: edges along bodies of water supporting a different tree species composition, extreme bog pH supporting fewer individuals for a thinner canopy, or strong winds that carry across open water causing tree falls. Due to the high prevalence of bogs and lakes in northern temperate mixed forests, future research should explore bogs and lakes as a potential

cause of severe edge effects in northern forests. It may be a major factor in the unusually low mean LAI of my study sites.

Overall, the studied sites had a lower diversity than temperate broadleaf forests and also a lower average LAI, contrary to the inverse relationship I found between of diversity and LAI. It's possible that the low LAI was caused by masking too many rings, or that the comparison data from Asner et al. (2003) did not mask any rings and therefore had an inaccurately high LAI. More likely, this was the result of confounding by one of the three most significant factors effecting LAI: species composition, age, and edge effects. The species-specific variation in monoculture LAI most likely confounded the species diversity data. Similarly, old growth stands – which tended to be monocultures – had high LAI, further confounding the diversity relationship. Perhaps most importantly, edge effects were correlated with a significant strong depression of LAI values.

Modeling how temperate mixed forests like those of northern Wisconsin and southwestern UP Michigan will change in respect to LAI may be difficult due to unknown species-specific effects. The next steps to learning how to effectively model LAI may include understanding how each major species effects LAI in pure stands and how the species composition of the forests are changing over time. The subjectively-observed pure-stand clumping model of species distribution should be explored. If the model is accurate in some areas, it should attempt to predict how certain species may have a tendency to clump together.

It would be helpful to model how LAI and transpiration are related varying by species. This could predict how changes to LAI from species composition would affect the productive value of northern temperate mixed forests. Once these factors are understood, forest management could be an extremely viable and effective approach to optimize the climate change mitigation

effects of forests. This is especially important while northern Wisconsin and UP Michigan forests recover and change after historical logging, burning, and road building.

Tables

Abbrev.	Scientific name	Common name
TC	<i>Tsuga canadensis</i>	Eastern hemlock
PR	<i>Pinus resinosa</i>	Red pine
PS	<i>Pinus strobus</i>	White pine
PG	<i>Picea glauca</i>	White spruce
PM	<i>Picea mariana</i>	Black spruce
AB	<i>Abies balsamea</i>	Balsam fir
PT	<i>Populus tremuloides</i>	Quaking aspen
PtG	<i>Populus grandidentata</i>	Bigtooth aspen
BA	<i>Betula alleghaniensis</i>	Yellow birch
BP	<i>Betula papyrifera</i>	Paper birch
AS	<i>Acer saccharum</i>	Sugar maple
AR	<i>Acer rubrum</i>	Red maple
TA	<i>Tilia americana</i>	American basswood
PrS	<i>Prunus serotina</i>	Black cherry
FA	<i>Fraxinus americana</i>	White ash
AA	<i>Amelanchier arborea</i>	Downy serviceberry

Table 1: All tables and figures use the tree species abbreviations from the above table.

Site	Basal Area	Density (trees/ha)	Canopy Heterogeneity	Distance to Edge (m)	Edge Type	LAI
KRC1	65.41125	477.4637128	1.078	371.1	Lake	6.27
KRC2	39.59885	572.9564553	1.168	193.7	Bog	4.83
KR1	43.33655	1718.869366	1.318	32.0	Lake	3.64
KR2	66.930975	859.434683	1.106	190.4	Road	5.87
KR3	40.197277	1878.023937	1.232	29.5	Road	3.05
KR4	38.09825	700.280112	1.11	68.0	Road	2.87
KR5	49.31476	1750.70028	1.164	74.0	Road	2.46
KRSP1	41.4	1100	0.9785	280.8	Bog	4.95
KRSP2	41.383343	1260	1.12	18.4	Road	3.94
KRSP3	24.335847	2360	0.6692	176.1	Road	4.36
KRSP4	31.4	820	1.155	79.6	Road	3.80
KRSP5	38.1	2300	1.154	123.3	Road	4.90
KRSP6	36.6	1160	1.265	72.3	Road	4.31
KRSP7	29.145536	1060	1.34	120.9	Road	4.26
KRSP8	32.675612	960	1.384	109.1	Lake	5.03
KRSP9	35.870663	1180	1.128	362.3	Lake	5.35
KRSP11	49.7	580	0.8578	80	Road	5.22
KRSP12	61.491589	580	1.229	136.9	Road	5.31

Table 1 reports the site basal area (m^2/ha), tree density (trees/ha), canopy heterogeneity (Shannon index value), distance to the nearest edge (m), the type of edge, and the corrected LAI value for each site.

Pearson Correlation Results			
Variable 1	Variable 2	Correlation (r)	p-value
Spp diversity	LAI	-0.444	0.065~
Average site age	LAI	0.856	0.000*
Average site age	Site basal area	0.786	0.002*
Average site age	Tree density	-0.484	0.111
Average site age	Canopy heterogeneity	0.012	0.970
Site basal area	LAI	0.435	0.071~
Tree density	LAI	-0.414	0.087~
Canopy heterogeneity	LAI	-0.172	0.494
Distance from edge	LAI	0.701	0.001*

Table 2 reports the results of the Pearson correlation analyses, including the two factors tested for a relationship, the Pearson correlation coefficient, and the p-value. A tilde (~) signifies that the p-value is approaching significance, while an asterisk (*) signifies that the p-value is significant at $\alpha = 0.05$.

Site	Avg Age	Age Classification
KRC1	115	Old
KRC2	63.25	Mid
KR1	41.625	Mid
KR2	110.5	Old
KR3	37.5556	Young
KR4	43.5	Mid
KR5	34.75	Young
KRSP1	72.2273	Mid
KRSP2	26.375	Young
KRSP3	30.5682	Young
KRSP4	40.6875	Mid
KRSP5	68.6591	Mid

Table 3 reports the average site age and assigned age classification for each site.

Figures

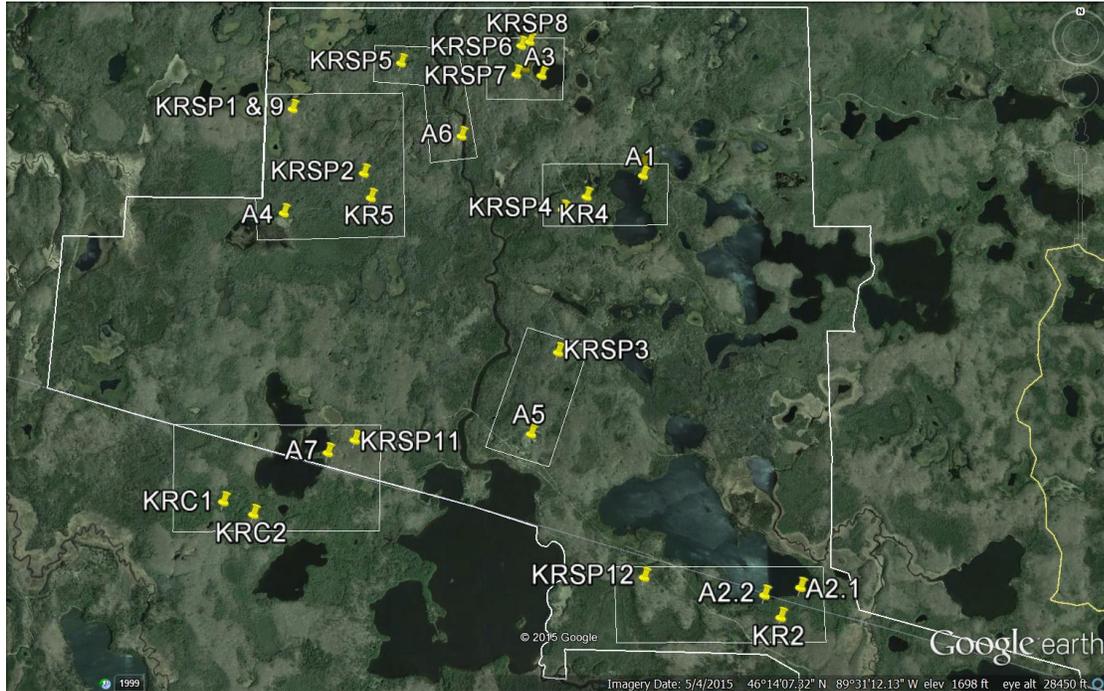


Figure 1 depicts the 18 study sites and 7 A sites. Note, site A2 had two locations (2.1 and 2.2) because it needed to be moved to avoid heavy sun in the view area on one day. Grouping boxes are drawn around sites that all referred to the same A site.

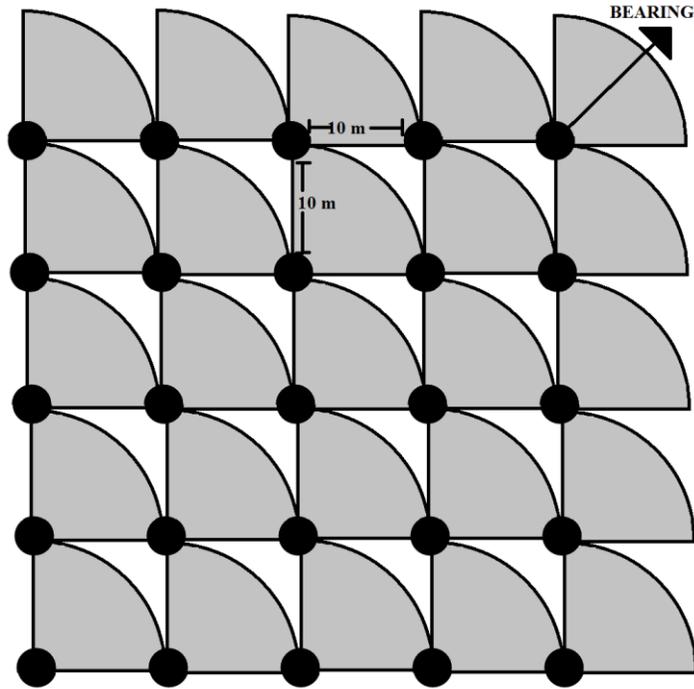


Figure 2 depicts the LAI sampling scheme. Each measurement point is 10 m away from the next. The area measured by the LAI sensor is represented by the gray area. The measurement bearing is represented by the arrow in the top right corner.

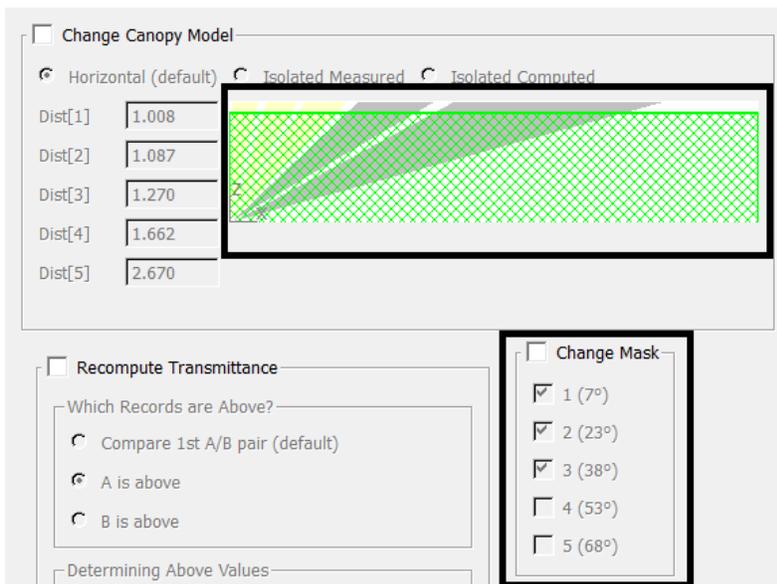


Figure 3 depicts the masking recalculation in FV2200 2.1.1. The grey shaded triangles in the green checked box represent the two ignored rings. The yellow triangles represent the three included rings.

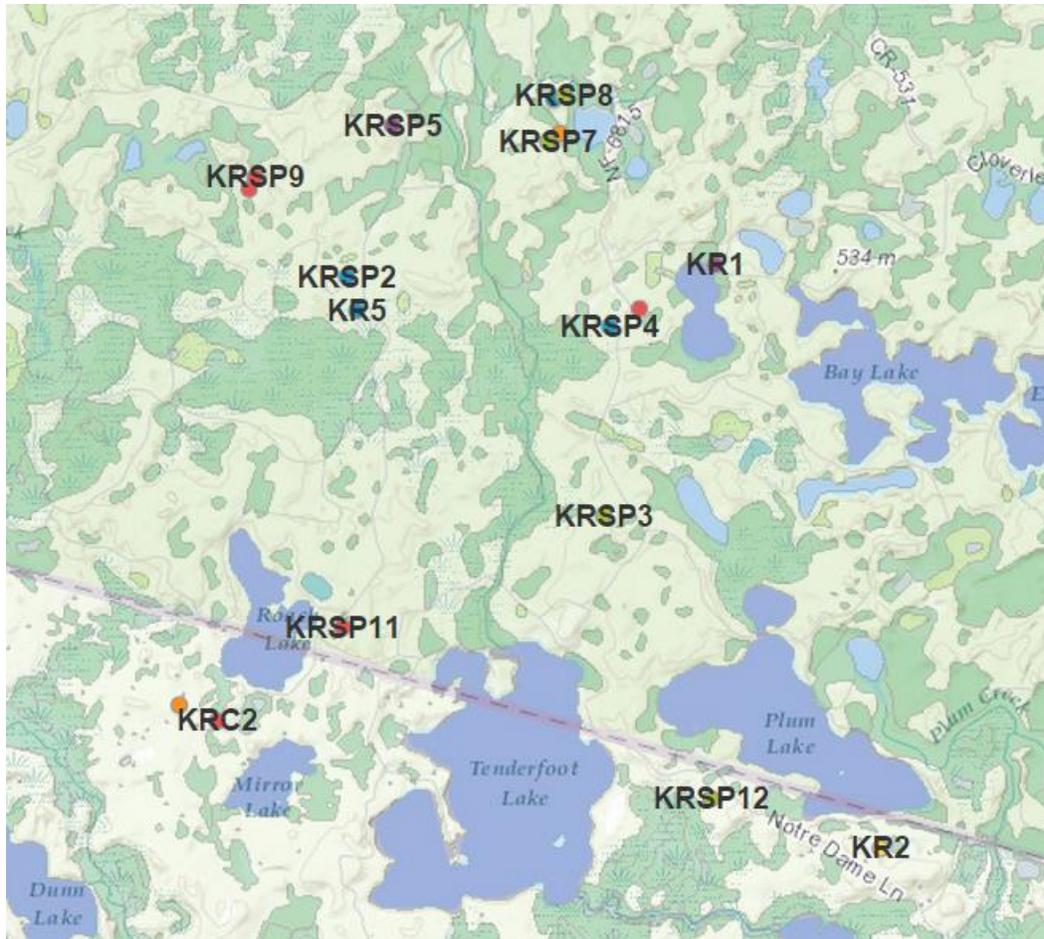


Figure 4 depicts the ArcGIS map available online, which includes the 18 study sites and the U.S.F.W.S. Wetlands layer. Each of the 18 sites are color coded by their assigned species composition classification.

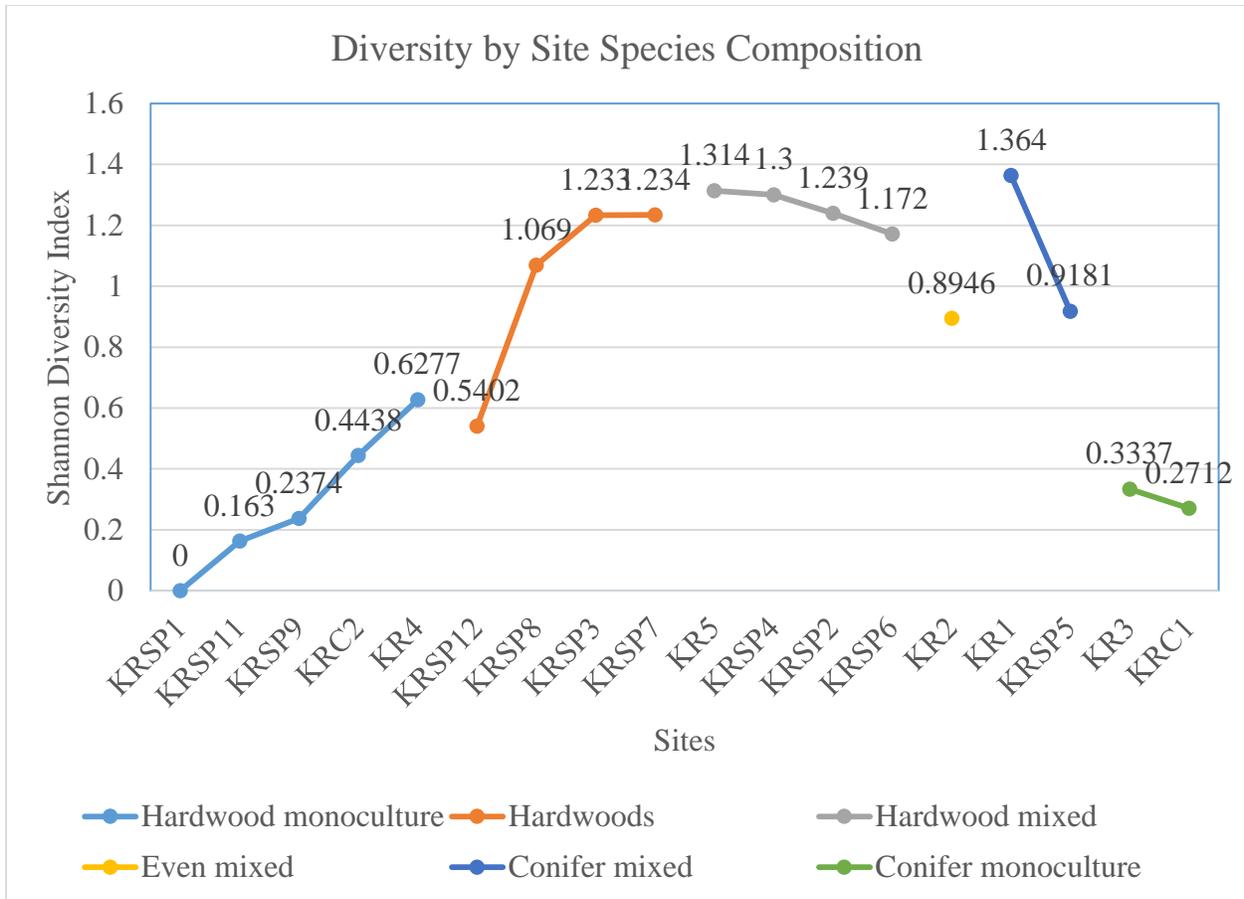


Figure 5 depicts the species diversity (Shannon diversity index) for each site, which are grouped by their species composition classifications. Species diversity increases as species composition becomes more mixed, as is intuitively expected.

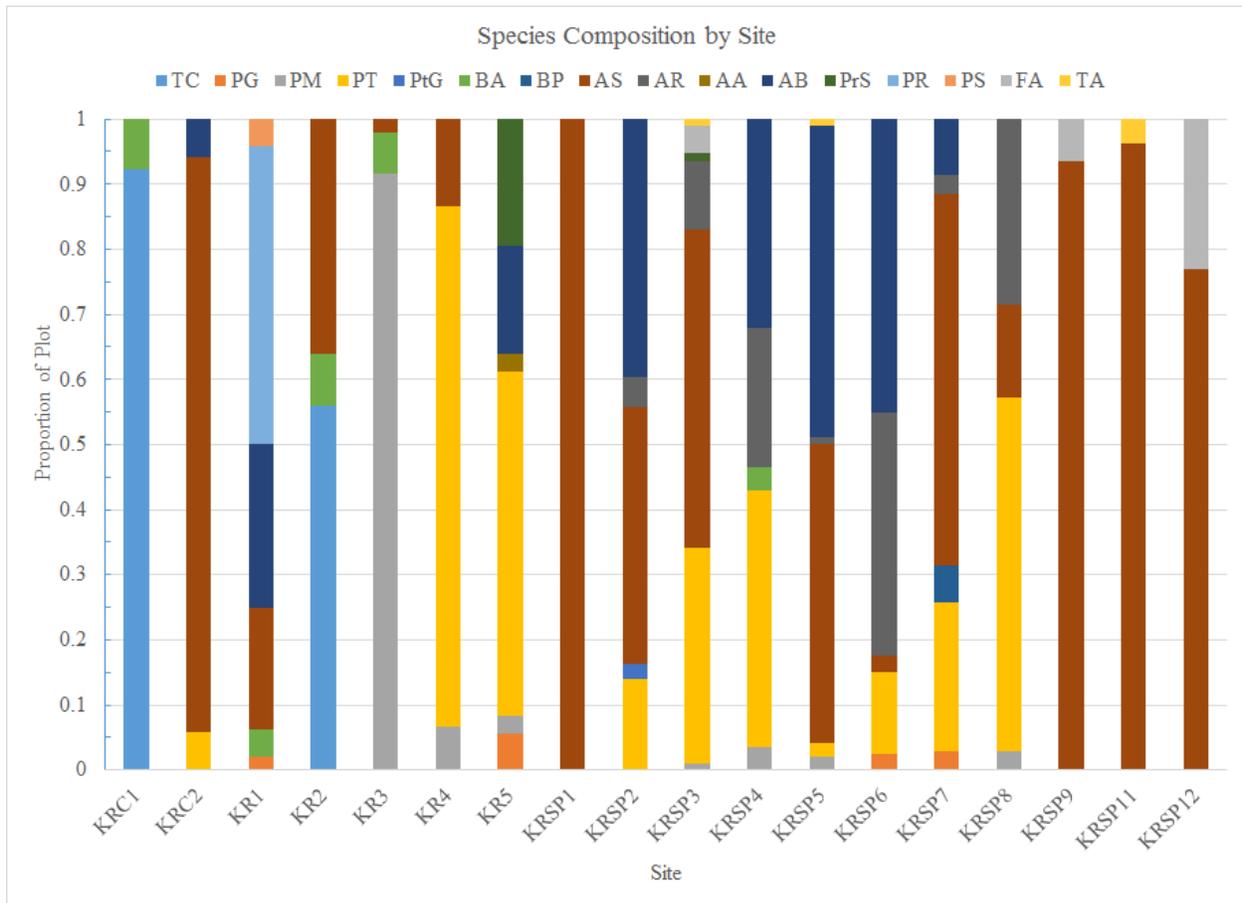


Figure 6 depicts the species composition of each of the sites by proportion. The species abbreviations used in this figure are defined in Table 1.

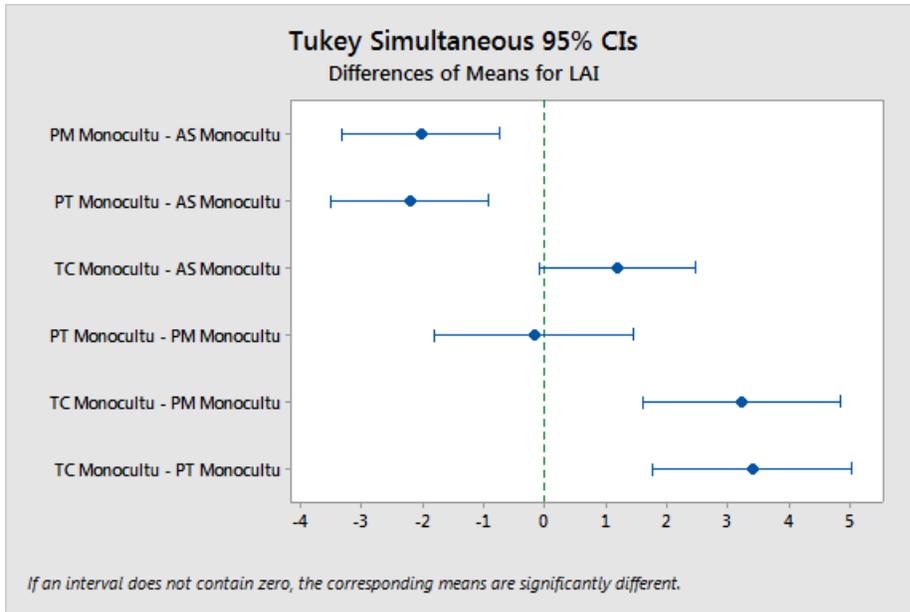


Figure 7 depicts the results of the Tukey's post-hoc analysis of the monoculture species comparison 1-way ANOVA. The species abbreviations used in this figure are defined in Table 1.

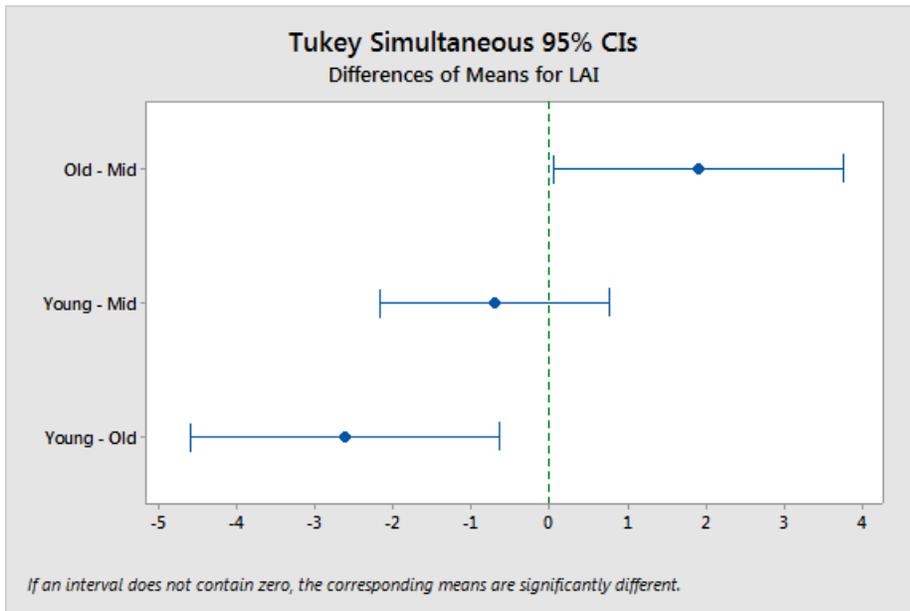


Figure 8 depicts the results of the Tukey's post-hoc analysis of the age class comparison 1-way ANOVA.

Acknowledgements

First and foremost, I would like to thank the Bernard J. Hank Family Endowment for the funding and support that made my experience and research possible. I would also like to thank the University of Notre Dame Environmental Research Center for the opportunity to be a part of the UNDERC program and a part of the property's rich history of research. I would like to thank Dr. Gary Belovsky, Hannah Madison, Julia Hart, and Sarah Small for their direction, teaching, and logistical support, as well as Dr. Rose-Marie Muzika, Dr. Walter Carson, Dr. Todd Crawl, and Dr. Michael Cramer for the opportunity to learn about ecology, field research, graduate school, and life from them. Sincere thanks to Bethany Blakely for guidance, technical instruction, and a lot of extra effort in all aspects of this project. Thank you to Sam Pecoraro for access to his data from the Jason McLachlan lab archive. I would also like to thank CeCe Graff, Carly Olson, Katie Georgi, Mariel Cueller, Patrick Lunn, Caitlin Broderick, Leah Ellman, Lorena Cortés, Sharlo Bayless, and Annika Kohler and for help collecting data and company in the field. My deep thanks go to the entire UNDERC-East 2015 class for the wonderful experience and memories.

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