EVALUATING INTER AND INTRA-SPECIFIC VARIATION IN LEAF MASS AND AREA

By

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ABSTRACT

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Tree leaf area and mass are small but important components of forest ecosystems. There have been many efforts to model leaf mass, but face challenges in doing so because leaf mass varies within and between tree species, location, and time. Often leaf mass models are limited to species-specific, empirical models, which predict intra-specific variation from diameter at breast height (DBH). Such models have limited potential; there are many other factors than tree girth that can lead to varying tree leaf mass, and models cannot be applied to species which lack foliage mass data. We conducted destructive sampling of trees of 17 different species, covering multiple life history traits, across Michigan, in order to generate a 'trans-species' model for foliage biomass which can be used across species. In addition, four species destructively sampled were subjected to canopy stratified sampling of specific leaf area (SLA) to capture an additional species-related life history trait contrasted by shade tolerance.

Our results identified the most important variables for predicting foliage mass, which were non-species-specific variables: diameter at breast height, five year basal area increment, crown class, and competition index, and species-related traits: leaf longevity and shade tolerance. Collectively, these variables describing tree size, life-history traits, and competitive environment allowed for a generalized leaf mass model with potential application to many tree species. The study of tree SLA identified a mechanism explaining why shade tolerant species might hold a greater leaf mass in the trans-species leaf biomass model. Shade tolerant trees maintained greater leaf area and leaf number and also expressed greater SLA and SLA plasticity.

This thesis is dedicated to my parents Gary and Tammy Dettmann.

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KEY TO ABBREVIATIONS

DBH	Diameter at Breast Height
SLA	Specific Leaf Area
LL	Leaf Longevity
ST	Shade Tolerance
FIA	Forest Inventory and Analysis
CA	Crown Area
LCR	Live Crown Ratio
CC	Crown Class
CI	Competition Index
DPI	Dots Per Inch
DLB	Diameter of the Largest Branch
BAI	Basal Area Increment
AIC	Akaike's Information Criterion
VIF	Variable Inflation Factor
RSE	Residual Standard Error
ANOVA	Analysis of Variance

CHAPTER 1

INTRODUCTION

1.1 Importance of Leaves

Leaves are a relatively small, but vital component of the biomass of forest ecosystems, which play a major role in global biogeochemical cycles (Lake et al. 2001). Leaves carry out the primary energy production process (photosynthesis) that supports the trees that bear them and many other forest life forms (Wright et al. 2004; Waring and Runing 2007). Leaves also provide energy inputs into neighboring systems, such as streams or wetlands (Fisher and Likens 1973), and form important ecosystem structures (Bilby and Likens 1980). Facelli and Pickett (1991) emphasized that leaf litter is an important factor affecting community organization and dynamics and can alter the physical and chemical environment. Globally, foliage in leaf decomposition, leaf litter chemistry, and climate form strong relationships that effect one another in turn (Aerts 1997). At the forest ecosystem level, leaf litter plays an important role in nutrient cycling (Gosz, Likens, and Bormann 1973; Cornwell et al. 2008) and soil production within the forest ecosystem (Facelli and Pickett 1991). Modeling forest ecosystem nutrients requires estimates or measures leaf mass and turnover, due to the strong relationships between tree leaves and ecosystem cycles (Blanco et al. 2005). With leaves being so critical to the vitality of trees (Gehrig 2004), forests and related ecosystems (Innes 1993), it is important to continue to improve methods to quantify the leaf components of forest ecosystems.

1.2 Leaf Mass and its Links to Specific Leaf Area and Other Functional Traits

Studies have shown that leaf mass is critically related to key functional attributes of plants (Wright et al. 2004; Atkinson et al. 2010). Many leaf traits are linked to mass including

leaf longevity (LL), specific leaf area (SLA), photosynthetic capacity, dark respiration rate, leaf nitrogen, and leaf phosphorus which are all correlated with one another (Wright et al. 2004). SLA relates to both the light environment in which the tree grows (Reich et al. 1998), and is correlated with shade-tolerance of the tree (Lusk and Warton 2007). SLA can thus be an important corollary of a species' strategy (Westoby et al. 2002; Grime 2006). Species related traits such as SLA, LL, and shade tolerance (ST) prove a useful and ordinal measurable traits related to leaf mass which place trees into groups relating to their function rather than into taxonomic groups (Lavorel et al. 1997; Weiher et al. 1999).

1.3 Previous Work on Leaf Biomass Estimation

Major efforts to improve tree / forest biomass estimates have placed most of the emphasis on improving estimating total tree mass (e.g., for forest carbon inventories, Chave et al. 2014) or on aboveground woody components that make up the bulk of observable forest biomass and which have known commercial value (e.g., main stem mass, MacFarlane 2015). So, there is a need to develop better estimates of leaf mass to improve forest ecosystems inventories (Weiskittel et al. 2015; Clough et al. 2016).

Leaf mass has proven challenging to model because it varies by tree species, age, and health, and varies seasonally along environmental gradients reflecting differences in climate and geography (Niinemets 2001; Wirth et al. 2004; Rance et al. 2014; Reich et al., 2014). A range of approaches have been employed, including partitioning methods that models leaf mass as a component ratio of the whole tree (e.g. Bartelink 1998; Domke et al. 2012) or more direct approaches that predict mass directly from variables. Empirical models often use common tree measurements (tree diameter at breast height (DBH), or crown length) and stand variables such as stand age (Weiskittel et al. 2006) or stand conditions (Wirth, Schumacher, and Schulze 2004).

There has been much less effort on developing biologically-motivated models, such as predicting tree foliar mass from the amount of conductive tissue at the base of the live crown (Valentine 1985) or sapwood area (Schneider et al. 2011).

Most approaches employ species-specific leaf mass models (Poudel and Temesgen 2016; Clough et al. 2016) because species have suites of leaf functional attributes related to their lifehistory (Wright et al. 2004; Reich et al. 2014). However, there is considerable intra-specific variation in leaf mass, as recently demonstrated by Wutzler et al. (2008), who documented the large degree of intraspecific variation of Fagus sylvatica across Central Europe. From a practical perspective, developing species-specific models for the many species that occupy a region has been highly problematic. It is costly and difficult to obtain accurate leaf mass data over many locations and trees, covering many orders of magnitude in size, which generally requires destructive sampling (Weiskittel et al. 2015). Even with over 250 tree mass studies conducted within the United States, less than half of the tree species listed within the Forest Inventory and Analysis (FIA) database have published mass models and even fewer species have had leaf mass included in those models (Weiskittel et al. 2015). To address this issue for US national mass equations, Jenkins et al. (2003) and Chojnackey et al. (2013) combined species into taxonomic groups, but Clough et al. (2016) found large uncertainties in leaf mass estimation with these groupings; the groupings chosen may have ignored important differences between species in the same taxonomic groups.

1.4 Study Intent

This thesis seeks to investigate the possibility of creating a single, generalized "transspecies" model for estimating leaf mass, meaning a single model that works across multiple trees species. The idea was to identify key functional traits of trees that can predict leaf mass over a

wide range of species and forest conditions, which could then possibly be applied to other species, even ones for which there is little to no data. A mixed-modeling approach was used, combining tree traits known to be correlated with leaf mass with two species-specific traits (LL and ST) that could be measured on a continuous scale, with indices of crowding and shading from other trees and a random variable indicating the effect of location. SLA was then used with tree leaf biomass in calculation of tree leaf area, an important modeling variable in forest functions including net primary production (Running and Coughlan 1987; Gower et al. 1999). Additionally, SLA was examined for linkages to species functional groupings.

CHAPTER 2

METHODS

2.1 Study Area and Data

Tree data for this study were collected from 22 forest sites across Michigan, 21 located in the Lower Peninsula, and one in the Upper Peninsula, including the Michigan counties of Schoolcraft, Allegan, Gogebic, Kent, Missaukee, Jackson, Cass, Crawford, and Oakland (Figure 1). The region is cool-temperate with an average annual temperature of 9°C and about 800 mm of rainfall per year, supporting both broad-leaved deciduous and mixed coniferous-deciduous forests (Dickmann 2004).

Figure 1. Study site locations within Michigan.



2.2 Sample Tree Selection

Our goal was to develop a sample of trees to capture both within and between species variation in tree functional attributes. Trees of regionally-important, broad-leaved, deciduous and needle-leaved, coniferous species, representing varying degrees of shade tolerance and levels of leaf longevity, were selected to fulfill a matrix of stem diameter at breast height (DBH) classes (from 2 to 80 cm, Table 1). One species, *Larix laricina*, which is a needle-leaved, deciduous species, was included to see if it differed from the other two taxonomic groups. ST ratings were determined for species based on a scale of 0 (shade intolerant) to 5 (shade tolerant) using published values from Niinemets and Valadares (2006). LL values were based on published LL averages from the GLOPNET database (Wright et al. 2004) as well as published values from Hallik et al. (2009) and Niinemets and Lukjanova (2003) (Table 1). Trees were selected from a diversity of upland and wetland forests with various mixtures of deciduous and coniferous trees. A subset of the trees sampled were selected for SLA sampling. These trees were grouped to represent shade intolerant (Prunus serotina and Populus tremuloides) and shade tolerant (Acer saccharum and Acer nigrum) species (Table 2). All trees selected for this study were live trees that did not exhibit any obvious signs of decline or major crown damage, and had complete leaf sampling and standing measurements taken (see below).

Species	N	DBH (cm.)*	Leaf Mass (kg.)*	Shade	Leaf Longevity	Leaf Type
				Tolerance	(mo.)	
Acer nigrum	4	35.31	19.69	3	5.50	Broad-leaved De-
(Black Maple)		[28.22; (4.06, 67.06)]	[21.55; (0.55, 45.22)			ciduous
Acer platanoides	2	9.02	1.52	4.20	6	Broad-leaved De-
(Norway Maple)		[3.77; (6.35, 11.68)]	[1.1; (0.74, 2.29)]			ciduous
Acer rubrum	5	38	15.29	3.44	5.57	Broad-leaved De-
(Red Maple)		[26.87; (10.16, 76.96)]	[15.9; (1.28, 37.58)]			ciduous
Acer saccharum	18	41.43	24.57	4.76	5.50	Broad-leaved De-
(Sugar Maple)		[23.87; (6.86, 83.31)]	[22.68; (0.4, 79.63)]			ciduous
Fagus grandifolia	16	42.67	22.39	4.75	6	Broad-leaved De-
(American Beech)		[24.02; (5.59, 79.76)]	[18.46; (0.67, 63.04)]			ciduous
Liriodendron tulipifera	14	43.62	14.31	2.07	5.30	Broad-leaved De-
(Tulip Poplar)		[22.36 ; (9.65, 80.52)]	[9.83; (0.98, 32.75)]			ciduous
Populus tremuloides	8	23.24	5.12	1.21	5.48	Broad-leaved De-
(Quaking Aspen)		[12.16; (7.11, 41.66)]	[7.09; (0.69, 22.19)]			ciduous
Prunus serotina	3	23.88	6.26	2.46	5.50	Broad-leaved De-
(Black Cherry)		[12.37; (10.92, 35.56)]	[4.63; (1.2, 10.28)]			ciduous
Quercus alba	16	42.53	19.85	2.85	5.50	Broad-leaved De-
(White Oak)		[23.34; (6.35, 80.01)]	[18.13; (0.53, 59.26)]			ciduous
Quercus rubra	15	45.18	21.12	2.75	6	Broad-leaved De-
(Northern Red Oak)		[23.56; (4.83, 83.31)]	[19.61; (0.26, 67.31)]			ciduous
Tilia americana	15	38	12.22	3.98	5.50	Broad-leaved De-
(American Basswood)		[20.64; (6.6, 71.37)]	[11.71; (0.41, 43.41)]			ciduous
Larix laricina	6	16.64	8.76	0.98	6	Needle-leaved
(Tamarack)		[8.53; (5.33, 28.19)]	[7.76; (0.71, 21.69)]			Deciduous
Abies balsamea	14	18.72	11.98	5.01	110	Needle-leaved
(Balsam Fir)		[11.11; (3.3, 40.64)]	[8.84; (0.66, 27.66)]			Evergreen
Pinus resinosa	11	34.59	18.55	1.89	36	Needle-leaved
(Red Pine)		[18.53; (5.33, 61.98)]	[20.88; (0.77, 65.15)]			Evergreen
Pinus strobus	16	44.1	36.4	3.21	19.95	Needle-leaved
(Eastern White Pine)		[24.37; (6.6, 81.28)]	[35; (0.79, 107.05)]			Evergreen
Thuja occidentalis	10	28.22	19.04	3.45	29.39	Needle-leaved
(Northern White Cedar)		[15.16;(5.84, 50.29)]	[20.02; (0.58, 56.09)]			Evergreen
Tsuga canadensis	15	45.48	37.54	4.83	60	Needle-leaved
(Eastern Hemlock)		[23.39; (5.59, 82.04)]	[38.2; (0.35, 145.24)]			Evergreen

*Mean [Standard Deviation (Minimum, Maximum)]

Table 2.	Summary	, of a	lata for	trees san	npled for	r SLA.
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Species	Ν	DBH (cm)*	SLA (cm²/g)*	Shade Tolerance
Acer nigrum (Black Maple)	4	35.30 [28.22 (4.06, 67.06)]	53.50 [17.91 (36.09, 74.67)]	Tolerant
Acer saccharum (Sugar Maple)	16	43.30 [24.31 (6.86, 88.17)]	57.88 [15.57 (29.36, 88.17)]	Tolerant
Populus tremuloides (Quaking Aspen)	8	23.24 [12.16 (7.11,41.65)]	175.57 [114.84 (38.62, 297.46)]	Intolerant
Prunus serotina (Black Cherry)	3	23.88 [12.37 (10.92, 35.56)]	42.49 [4.78 (39.54, 48.00)]	Intolerant

*Mean [Standard Deviation (Minimum, Maximum)]

2.3 Pre-destructive Measurements

Based on other published studies (e.g., Mäkelä and Valentine 2006, Clough et al. 2016), we expected that dimensional variables relating to the size of the tree or its crown would be positively correlated with its leaf mass, because larger trees can support and would need to be supported by more leaves. Prior to felling, dimensional measurements were taken on each standing tree included DBH (cm), tree height (m), crown height (base to lowest live branch, m), and crown width (m). The crown width was sampled by measuring the crown in two directions, 90 degrees from one another, and taking the average. The average crown radius was used to estimate the average crown area (CA, m²). The live crown ratio (LCR) was calculated from the length of the crown (tree height – crown height), divided by the total height of the tree.

We used two methods to capture competition from neighboring trees, because we hypothesized that, at any given dimensions, competition would affect allocation to leaf mass. First, each study tree was assigned to a crown class (CC), based on the position of the tree in the canopy: (i) overtopped, (ii) intermediate, (iii) co-dominant, or (iv) dominant, to indicate shading experienced by the tree (MacFarlane and Kane 2017). Second, the general crowding experienced from surrounding trees was assessed by tallying trees with a DBH greater than 10 cm around the subject tree in a 7.3 m radius plot (these specifications were chosen to match plot guidelines from the US FIA program). The DBH of each surrounding tree and distance to the subject tree were recorded and used to compute a Competition Index (CI) suggested by Hegyi (1974).

$$CI = \sum_{i=1}^{n} \left[\frac{d_i / d_j}{D_{ij}} \right]$$

eq. 1

where d_j is the DBH of the subject tree, d_i is the DBH of the competitor, and D_{ij} is the distance between the subject tree and its competitor.

2.4 Destructive Sampling - Leaf Area Data Collection

Each tree selected for SLA sampling was felled into a cleared area to prevent as much damage to the branches as possible and to prevent inclusion of leaves and branches from neighboring trees. The crown was then split into three equal portions: the lower, middle, and upper section. Then three leaf samples, consisting of enough leaves to obtain a five gram green weight sample, were taken from each of these sections. Each sample location was spaced evenly out to obtain a stratification of sampling within each section. The leaves in each sample were immediately weighed, counted, and scanned on a color scanner at 400 dots per inch (DPI). The single sided area of the leaves were calculated using the software ImageJ (Schindelin et al. 2015) from these scans. The leaf samples were then taken back to the lab to be oven dried at 70° C until they reached a 0% moisture content determined by reweighing the samples until their weight was constant. The SLA for each sample was then calculated by dividing the green area of the sample by the dry weight. The plasticity of the expressed SLA was calculated as the absolute difference between the maximum expressed SLA and the minimum expressed SLA divided by the maximum SLA multiplied by 100 (Valladares et al. 2000). Following the SLA sampling each tree was destructively sampled for leaf mass (see below). A total leaf number was calculated by dividing the total tree foliage dry mass by the average leaf dry mass. Total leaf area coverage was calculated by taking the average leaf SLA and multiplying it by the total tree foliage dry mass.

2.5 Destructive Sampling - Leaf Mass Data Collection

Each subject tree was felled into a cleared area to prevent as much damage to the crown as possible and to prevent inclusion of leaves and branches from neighboring trees. After felling, branches were systematically stripped from the stem for branch and leaf mass estimates. The diameter of the largest branch (DLB, cm) at its base was recorded, as we hypothesized that this might be a useful predictor variable for leaf mass, based on prior work by MacFarlane (2011), which showed greater allocation to branches versus the trunk for trees with a larger DLB.

The branch sampling method for deciduous and coniferous trees differed slightly. For deciduous species, any live branch greater than 2.5 cm in diameter was weighed green with the leaves still attached. The leaves were then clipped off and weighed for each branch to obtain the green weight of the leaves for that branch. A representative subsample of about 10% of leaves from each branch was then taken back to the lab to then be dried to obtain dry weight to green weight ratios, for computing dry leaf mass. Any branches that were less than 2.5 cm in diameter were collected and weighed together, and otherwise treated in the same manner as the individual branches described previously. For coniferous species, the felled tree was divided up into 1.2 m sections from the base to the top of the tree. The living branches in each section were weighed together to obtain total green branch weight. Then, one live branch was selected randomly from each section. If the selected branch for that section was less than 2.5 cm in diameter, the whole branch was taken back to the lab to be dried, and to obtain a total needle mass dry weight. If the

branch was greater than 2.5 cm in diameter, the needles were clipped off and weighed green and a sample of these separated needles for each sample branch was brought back to the lab for drying to obtain the dry-weight to green weight ratios.

Fresh leaf samples collected were oven dried at 70° C until they reach a stable weight, determined by reweighing the samples until their weights were constant. Leaf dry weight to green weight ratios from samples were multiplied by the field-measured green weights of the leaves, so the total leaf mass of each tree was the sum of all green leaf mass from all branches multiplied by the corresponding dry-weight to green weight ratios for leaves from each branch. All weights were measured to three significant figures of precision.

2.6 Tree Wood Density Measurement

We expected that wood density should correlate with leaf mass based on work by Forrester et al. (2017), so after branch removal, an approximately 5 cm thick disk was removed from each tree's stem at breast height (1.3 m from the ground) to be used for wood density calculations. This location on the tree was chosen because this is the place where tree wood density is typically assessed in published literature (e.g., Chave et al. 2009, MacFarlane 2015). The disks were measured for thickness to the nearest 0.01 cm at 4 locations, each 90° from one another, to obtain an average disk thickness. Two diameters were also taken to the nearest 0.1 cm to obtain an average diameter. These diameters along with the thicknesses were then used to calculate the volume of the disks taken. The disks were then dried at 105°C for 48 hours until a stable weight was obtained. Density was calculated using the disk weight and volume for each tree and then standardized to wood specific gravity (Williamson and Wiemann 2010).

2.7 Measurements of Tree Growth as an Indicator of Vigor

We expected leaf mass to be affected by the vigor of the tree, and the vigor of the tree to be correlated positively with growth rate, as the latter has been recognized as an indicator of tree health (Duchesne et al. 2003) or vitality (Dobbertin 2005). The sample disks, taken from breast height for density calculations, were also used for tree growth and age calculations. Exceptions were made where the breast height disk were decayed to the point where dendrochronological analyses were prohibited. In these cases, a disk sampled from stump height (0.15 m above ground) or a disk from 2.4 m above-ground was used instead, whichever was the least decayed.

Disks were first planed with a router to remove chainsaw marks and level the disks, and then sanded, with increasing steps in grit up to 600 grit sandpaper, to obtain a smooth and even surface for better scanning and viewing under the microscope. After the sanding process, two radii on each disk were marked that were at least 90° apart from one another to be used in our growth analysis; care was taken to avoid any pockets of severe decay or ring distortion. Each of these radii were scanned, using a color scanner at 2400 DPI, and in any location where the resolution was unable to pick up the rings were then also imaged using a microscope using a magnification from 0.7 at 4650 DPI to 4.5 at 33000 DPI in order to obtain accurate ring widths. These images were then uploaded to a software called *CooRecorder* (www.cybis.se) to mark the ring locations of the rings and obtain ring widths. Then, using *CDendro* software (www.cybis.se), the two radii for each tree were checked for accuracy against one another and then the ring widths were averaged.

From the tree ring analyses, we determined the average change in stem cross-sectional area at breast height, also known as basal area increment (BAI, mm² y⁻¹), which is one of the most commonly used estimators of tree growth/vigor (Leblanc 1994, Voelker et al. 2008). Bigler and Bugmann (2003) suggested that recent growth may be a better indicator of tree health,

so we computed five different BAI values for each tree; average lifetime increment (basal area / age) and the mean BAI over the most recent 50, 25, 10, and 5 years.

2.8 Model Formulation and Fitting

We hypothesized that a single model containing the best combination of these variables would provide a "trans-species" equation, which would be accurate for trees of all the species. We began by identifying all the key variables that we expected to be positively correlated with leaf mass (Table 3) and defined them as "fixed" effects variables. We assumed that dimensional variables, vigor, and competitive effects would affect all trees regardless of species and that key differences between species could be represented by two quantitative variables: shade tolerance and leaf longevity, both of which would be positively correlated with leaf mass. In the first stage of model development, all variables of interest were fit using linear regression to predict the dry mass of leaves. All variables in the modeling were log transformed, as the relationships between leaf mass and predictors were generally observed to be heteroscedastic. Variables that had p-values over 0.05 were removed from the model in a progressive manner until all variables left were significant ($\alpha = 0.05$) (Table 4).

Table 3. Summary statistics of fixed effects variables used in modeling: diameter at breast height (DBH), competition index (unitless), crown area, live crown ratio (LCR), diameter of the largest branch (DLB), leaf mass (dry basis), shade tolerance, lifetime basal area increment (BAI, mm2 y-1), wood specific gravity (unitless) and leaf longevity (mo) for all of the destructively sampled trees from 12 different species and 188 individuals at 22 different sites.

Summary (Species = 12) N = 188							
Statistic	Mean	Standard Deviation	Min	Max			
DBH (cm)	37.16	22.41	3.30	83.31			
Competition Index	0.78	1.71	0.00	16.63			
Crown Area (m ²)	81.81	84.74	1.98	468.63			
LCR (unitless)	0.67	0.15	0.26	0.95			
DLB (cm)	14.48	12.38	0.95	51.56			
Dry Leaf Mass (kg)	20.19	22.40	0.26	145.24			
Shade Tolerance (unitless)	3.44	1.21	0.98	5.01			
Lifetime BAI (mm ² y ⁻¹)	1,363.30	1,202.73	23.34	5,816.67			
Wood Specific Gravity (unitless)	0.47	0.12	0.19	0.76			
Leaf Longevity (mo)	22.01	29.75	5.30	110.00			

Table 4. Coefficients and standard deviations for predictor variables in a log-log linear model: log (leaf mass) = intercept + log(variable1) + log(variable2), etc. Initial model fits were without random effects. All variables were used in an initial model and then progressively removed until a subset were identified where all variables were statistically significant (α = 0.05).

	All variables	Significant subset
Log DDU (am)	1.261***	1.281***
	(0.156)	(0.082)
Log Lorgest Pronch Diameter (am)	-0.051	
Log Largest Branch Diameter (Chi)	(0.100)	
Los Crown Datio	0.574***	0.598***
Log Clowii Ratio	(0.134)	(0.131)
Log Wood Specific Crewity (unitless)	0.281*	0.292**
Log wood specific Gravity (unitiess)	(0.144)	(0.141)
$L_{\alpha\alpha}$ Crown Area (m^2)	0.062	
Log Crown Area (m)	(0.063)	
Las Competition Index (unitless)	-0.513***	-0.530***
Log Competition Index (unitiess)	(0.118)	(0.111)
Los Chada Talaranaa (unitlass)	0.246***	0.251***
Log Shade Tolerance (unitiess)	(0.084)	(0.082)
	0.277***	0.279***
Log Lear Longevity (mo)	(0.051)	(0.037)
Codominant Crown Close	-0.075**	-0.079**
Codominant Crown Class	(0.036)	(0.035)
Intermediate Creary Class	-0.118**	-0.119**
Intermediate Crown Class	(0.049)	(0.048)
Overteened Creeve Class	-0.212***	-0.208***
Overtopped Crown Class	(0.068)	(0.067)
Dominant Crown Class (Intercont)	-0.932***	-0.901***
Dominant Crown Class (Intercept)	(0.148)	(0.142)
*p<0.1; **p<0.05; ***p<0.01; (Standard I	Deviation)	

In the second stage, we investigated how BAI changed from mean lifetime to successively more recent time periods and which measure of BAI was most related to leaf mass. So, models with variables selected in the first stage were each fit separately with the lifetime, 50, 25, 10, and 5 year BAI as variables. These models with different growth rate measures were then compared to one another, to determine if any of the BAI means were significant, and if so, the model with the highest adjusted r^2 and lowest Akaike's information criterion (AIC) was selected for the third stage of modeling (Table 5).

The remaining model variables after the second stage were inspected for high collinearity by calculating their variance inflation factor (VIF) (Gregoire et al. 1995) (Table 6). While recommended acceptable maximum VIF values vary in the literature (Hair et al. 1995; Rogerson 2001; Pan and Jackson 2008), we chose the criterion that any variable with an extreme VIF of 10 or over would be unacceptable for our model and would be subsequently removed. The final set of fixed-effects variables were placed into a mixed-effects framework specifying location as a random effect to help us evaluate whether the location where trees were sampled explained any significant portion of the residual variation (Table 7). Relative importance of each variable in the final model was then calculated using dominance analysis (Budescu 1993; Johnson and Lebreton 2004).

Table 5. Comparison of different models using the significant variables from Table 3 with varying time periods for computing mean BAI: (a)

lifetime BAI, most recent: (b) 50 years, (c) 25 years, (d) 10 years, and (e) 5 years.

	Dependent variable: Log Dry Leaf Mass (kg)				
	(a)	(b)	(c)	(d)	(e)
Log DBH (cm)	1.273*** (0.108)	1.203*** (0.120)	1.122*** (0.110)	1.092*** (0.098)	1.116*** (0.094)
Log Leaf Longevity (mo)	$0.274^{***}(0.037)$	0.277*** (0.037)	0.289*** (0.037)	0.307*** (0.037)	0.302*** (0.037)
Log Competition Index (unitless)	-0.531*** (0.114)	-0.510*** (0.114)	-0.485*** (0.112)	-0.460*** (0.110)	-0.447*** (0.111)
Log Crown Ratio	0.614*** (0.130)	0.604*** (0.130)	0.589*** (0.129)	0.585*** (0.126)	0.582*** (0.126)
Log Wood Specific Gravity (unitless)	0.279*(0.146)	0.294** (0.142)	0.319** (0.141)	0.360** (0.139)	0.341** (0.138)
Log Shade Tolerance (unitless)	$0.263^{***}(0.086)$	0.272*** (0.083)	0.273*** (0.081)	$0.290^{***}(0.080)$	0.296*** (0.080)
Log Total BAI (mm ² y ⁻¹)	0.005 (0.066)				
Log 50yr BAI ($mm^2 y^{-1}$)		0.061 (0.070)			
Log 25yr BAI (mm ² y ⁻¹)			0.125** (0.060)		
Log 10yr BAI ($mm^2 y^{-1}$)				0.156*** (0.048)	
Log 5yr BAI (mm ² y ⁻¹)					0.147*** (0.045)
Codominant Crown Class	-0.082** (0.035)	-0.081** (0.035)	-0.081** (0.035)	-0.087** (0.034)	-0.086** (0.034)
Intermediate Crown Class	-0.120** (0.048)	-0.120** (0.048)	-0.121** (0.047)	-0.123*** (0.047)	-0.121*** (0.047)
Overtopped Crown Class	-0.209*** (0.068)	-0.201*** (0.068)	-0.195*** (0.067)	-0.198*** (0.066)	-0.197*** (0.065)
Dominant Crown Class (Intercept)	-0.904*** (0.174)	-0.982*** (0.173)	-1.079*** (0.166)	-1.148*** (0.158)	-1.159*** (0.160)
Adjusted r ²	0.919	0.919	0.921	0.923	0.923
AIC	-114.75	-115.54	-119.31	-125.63	-125.79

p*<0.1; *p***<0.05; ******p*<0.01; (Standard Deviation)

Table 6. Variable inflation factors (VIF) for the ordinary least squares model with the selected variables of diameter at breast height (DBH), leaf longevity, competition index, live crown ratio, wood specific gravity, shade tolerance, recent 5 year basal area increment (BAI), and crown class.

	VIF Score
DBH (cm)	6.62
Leaf Longevity (mo)	1.89
Competition Index (unitless)	2.95
Crown Ratio	1.14
Specific Gravity (unitless)	1.70
5yr Mean BAI (mm ² y ⁻¹)	4.45
Log Shade Tolerance (unitless)	1.45
Codominant Crown Class	1.74
Intermediate Crown Class	2.40
Overtopped Crown Class	4.45

Table 7. Comparison of fixed-effects only ordinary least squares (OLS) model and linear mixedeffects model with the same fixed effects variables, but with location as a random intercept

effect. Conditional r² computed from Nakagawa and Schielzeth (2013) includes location's effect.

	OLS	Linear Mixed-effects with Location (random intercept)
Log DBH (cm)	1.116***	1.042***
	(0.094)	(0.099)
Log Leaf Longevity (mo)	0.302***	0.218***
	(0.037)	(0.048)
Log Competition Index	-0.447***	-0.440***
(unitless)	(0.111)	(0.107)
Log Crown Ratio	0.582***	0.463***
	(0.126)	(0.125)
Log Specific Gravity	0.341**	
(unitless)	(0.138)	
Log 5yr Mean BAI (mm ² y ⁻¹)	0.147***	0.210***
	(0.045)	(0.043)
Log Shade Tolerance	0.296***	0.280**
(unitless)	(0.080)	(0.114)
Codominant Crown Class	-0.086**	-0.063*
	(0.034)	(0.032)
Intermediate Crown Class	-0.121***	-0.098**
	(0.047)	(0.046)
Overtopped Crown Class	-0.197***	-0.176***
	(0.065)	(0.066)
Dominant (Intercept)	-1.159***	-1.302***
	(0.160)	(0.184)
AIC	-125.788	-134.801
	Adjusted r ² : 0.923	Conditional r ² : 0.942

All model development and statistical analyses were carried out using the R software version 3.3.1 (R Core Team 2016). With the help of packages car (Fox and Weisberg 2011), MASS (Venables and Ripley 2002), lme4 (Bates et. al. 2015), ggplot2 (Wickham 2009), psych (Revelle 2016), stargazer (Hlavac 2015), piecewiseSEM (Lefcheck 2015), relaimpo (Grömping 2006), and coefplot (Lander 2016) in model creation, evaluation, and plotting. Models were compared to one another using r^2 , AIC, and residual standard error (RSE) to determine the models with the best fit.

2.9 SLA - Analysis of Variance Testing

With the SLA data, tests of Analysis of Variance (ANOVA) were done to identify differences between species, strata, and plasticity. Testing was carried out using the R software version 3.3.2 (R Core Team 2016) and the packages MASS (Venables and Ripley 2002), ggplot2 (Wickham 2009), stargazer (Hlavac 2015) in evaluation, and plotting.

CHAPTER 3

TRANS-SPECIES PREDICTORS OF TREE LEAF MASS

3.1 Trans-species Model Results

3.1.1 Key Attributes Influencing Leaf Mass

Our initial variable selection analysis selected DBH, LCR, wood specific gravity, shade tolerance, leaf longevity, CI and CC as predictors of leaf mass (Table 4). Larger (DBH) trees, with relatively larger crowns (LCR) had greater amounts of leaf mass, as hypothesized. Shade tolerance, leaf longevity and wood density were all also positively related to leaf mass (Table 4). Predictors related to shading (CC) and general crowding experienced by the tree (CI) were negatively correlated with leaf mass (Table 4). With regards to CC, each progressively inferior crown position lead to lower leaf mass holding other factors constant (Table 4). The DLB had a negative relationship with leaf mass and CA a positive relationship, but neither was found to be statistically significant given other variables in the model (Table 4) and they were dropped in the next stage of modeling. Removing these variables did not have any major effects on the remaining coefficients after removal (Table 4).

For the vigor analyses (Table 5), only the BAI of the most recent (5 or 10 years) had a significant effect on leaf mass. The overall best model was a model fit with the most recent, 5-year BAI with the highest r^2 and lowest AIC, though it was very similar to the 10-year BAI model with equivalent r^2 values (Table 5). All the variables in the model with the 5-year BAI exhibited VIF scores under 10 and were retained into the final stage of modeling.

3.1.2 Residual Error from Location

When location was added to the final fixed-effects model, wood specific gravity lost

significance and was dropped from the fixed-effects model (Table 7). When the final fixedeffects model (the 5-year model above) was compared to a mixed-effects model with location as a random effect, the mixed-effects model was superior, as judged by AIC (Table 7). After accounting for stem girth, crown size, tree vigor, shade tolerance, leaf lifespan and the shading and crowding experienced by the tree, location explained a relatively small portion of the remaining variability in leaf mass (which was about $6\% = 1 - r^2$). Most of the residual error was explained by location (about 25% of 8% = 2%). The addition of the location effect and removal of the wood specific gravity also influenced the magnitude of the other effects.

3.1.3 Relative Importance of Variables Influencing Tree Leaf Mass

The most important predictors of leaf mass across many species and locations were independent of species (Fig. 2). Tree size (DBH) was the most important explaining about 31% of relative importance, followed by its vigor (BAI, 19%), its position in the canopy (crown class, 18%) and competition from larger neighbors, in general (CI, 17%). Live crown ratio turned out to be of relatively little importance and the two variables that quantified key functional leaf traits for species accounted for only a small percent of relative importance (6% combined, Fig. 2).

Figure 2. Relative importance of variables calculated using dominance analysis (Budescu 1993; Johnson and Lebreton 2004) predicting tree leaf mass (rounded to the nearest 1%) of the mixedeffects model with location as a random effect and diameter at breast height (DBH), competition index, live crown ratio, shade tolerance, recent 5 year basal area increment, crown class and leaf longevity as fixed effects in the prediction of dry leaf mass.



3.1.4 Trans-species Mass Equation.

Based on our analyses, we recommend the following trans-species leaf mass equation model:

$$\log(DW) = \beta_0 + \theta_{loc} + \beta_1 \log(DBH) + \beta_2 \log(LL) + \beta_3 \log(ST) + \beta_4 \log(LCR) + \beta_5 \log(CI)$$
eq. 2

where β_0 is a variable intercept based on *CC* (see Table 7) and θ_{loc} is a random variable that allows the addition of a local, site-specific modifier based on location.

The results show that eq. 2 gives accurate estimates of leaf mass over a diverse range of tree sizes and species, sampled a different locations (Fig. 3a) and performs about equally well for deciduous and evergreen trees (Fig. 3b). Looking at the predictions for individual species we see that for most species the trans-species model appears to give accurate estimates of leaf mass over a wide mass range after correcting for location effects (Fig. 3c). *Larix laricina* was the only species which showed a serious prediction bias (from a 1:1 line of measured vs predicted, Fig. 4) if location effects were not included in the model; leaf mass was significantly underestimated for trees or all sizes.

Figure 3. Plots of measured versus predicted leaf dry mass (kg) on a log-log scale in a mixed effects model with location as a random effect with (a) all species pooled together, (b) trees separated out by decidiousness, and (c) separated by species.



Figure 4. Plots of measured versus predicted leaf dry mass (kg) on a log-log scale in (a) a fixed effects model without location and including specific gravity, and (b) mixed effects model with location as a random effect after specific gravity was removed from the model for Larix laricina.



3.2 Trans-species Model Discussion

3.2.1 General Tree Traits Related to Leaf Mass

Our study of multiple tree species, covering a wide range of functional attributes, revealed a set of four important attributes of trees or their competitive environments, that have a general influence on leaf mass regardless of species, DBH, BAI, CC and CI. The most important was DBH, which was not surprising that larger (DBH) trees carried more leaf mass than smaller trees, as it is well documented that DBH is a good predictor of tree foliar mass (Wirth, Schumacher, and Schulze 2004, Chojnacky et al. 2013, Clough et al. 2016). However, it only accounted for about 31% on a relative importance scale, meaning that this variable alone is not very reliable.

The second most important variable was BAI over the last five years (Fig. 2) and the results showed that trees with faster growth rates retained greater leaf mass. This corroborates an earlier finding by Albrektson (1984) who found that trees with narrower rings in their sapwood maintained a lower leaf mass. The fact that the most recent BAI was the best predictor among BAI values examined, suggests that it is an indicator of current tree health (Voelker, Muzika, and Guyette 2008). Dobbertin (2004) showed that BAI relates to crown sparseness, which should be related to stresses to the tree and which should be related to leaf mass (Weiskittel et al. 2006).

CI and CC were the third and fourth most important predictors of leaf mass in the model, respectively, which aligns with the findings of Le Goff et al. (2004) that measures of competitive status are correlated with leaf mass. However, Bigler and Bugmann (2003) suggested that the recent BAI increment reflects the competitive status of the tree, so the fact that CI and CC were also retained as important variables in the model indicates that competitive effects go beyond reducing tree vigor.

We know that trees alter the resources available to their neighbors (Palik et al. 1997) and that a tree's position in the canopy as well as general crowding from neighbors may result in depletion of resources (Canham et al. 2004). This competitive environment for light around the tree influences leaf traits, such as leaf mass per area (Ellsworth and Reich 1993). For example, leaves growing in high light conditions also tend to have a higher specific mass than those in shade (Abrams and Kubiske 1990). Depletion of light resources is also known to influence crown shape (Muth and Bazzaz 2003, MacFarlane et al. 2003), and the light environment can be quite complex, especially in mixed species stands where crown shapes of different species may respond plastically to minimize competitive effects (Pretzsch 2014). It is well-known that

shading and crowding reduces the length of the live crown of a tree (Antos et al. 2010), which might explain the relatively low importance of live crown ratio, relative to the other non-species-specific variables (Fig. 2). Though our variable inflation factor suggest that LCR be retained (Table 6), these other variables might capture most of what was important about LCR. This does not mean that LCR is not important; it is known to influence the scaling between leaf and woody mass in trees (Mäkelä and Valentine 2006) and has been shown to be useful in leaf mass prediction (Loomis et al. 1966, Temesgen et al. 2011). However, we expect that this dimensional variable is highly influenced by the canopy position of the tree and crowding and should be most useful when these are absent.

3.2.2 Shade Tolerance and Leaf Longevity-Modifiers of Otherwise Plastic Leaf Mass Allocation

One of the most interesting aspects of our analyses was that fact that the two variables that accounted for inter-specific differences in tree leaf mass (shade tolerance and LL) were of relatively small importance (6% combined). This means for any tree there are very large intra-specific variations in leaf mass allocation which are primarily dependent on the allometry, vigor of the tree, and growing space it has to operate in. This suggests that a "trans-species" model for leaf mass is justified. However, it is useful to discuss how the key leaf functional traits of shade tolerance and leaf longevity contribute as a means of drawing relevant and important distinctions between trees of different species holding size, vigor and competitive environment constant.

Shade tolerance, while only holding a 3% relative importance within our model, allowed leaf mass prediction to be modified to represent the tendency of shade tolerant trees to retain more leaf mass, under any given condition and vice versa. Shade tolerance has been much studied as an aspect of tree biology and others have found more shade tolerant trees should hold

a greater leaf mass (Callaway et al. 2000). The mechanism is presumably that shade tolerant species are able to maintain leaves with a positive carbon balance in areas of lower light availability in locations deeper within the crown, or on lower branches that experience a greater shading effect (Valladares and Niinemets 2008). Shade tolerant trees have been shown to have deeper crowns (Canham et al. 1994), with strong lateral branch growth and more efficient leaf display in lower canopy positions (Canham 1988). Lower maintenance costs and more efficient leaf display in lower light conditions should allow shade tolerant trees to retain a greater leaf mass than shade intolerant species (Abrams and Kubiske 1990).

Leaf longevity (which also only held a relative importance value of 3%) served as another means of placing species on a meaningful continuous scale for estimation of leaf mass. Two species with very different life-histories can have the same leaf life span (e.g., *Nothofagus nitida* and *Banksia menziesii*) and such convergence can inform us about leaf strategy tradeoffs across a spectrum of leaf traits (Wright et al. 2004). For example, trees with greater average leaf longevity have been shown to maintain a greater leaf mass in mature stands (Reich et al. 1992), due to the strong positive robust LL to leaf mass per area correlation (Osnas et al. 2013). Trees with longer LL need to maintain leaves for a longer period of time to achieve a positive carbon balance for their leaves (Reich 1987; Reich et al. 1991).

Our results show that leaf life span and shade tolerance work together to localize a trees allocation to leaf mass, holding other species-independent traits constant. Deciduous trees in our study all had LLs less than year and needle-leaved ("evergreen") trees had a wide range of LLs a range greater than a year (except *Larix laricina*), but both deciduous and evergreen LL groups covered the full range or shade tolerance (Table 1). The fact that this is possible for different species growing in the same forest ecosystems within the same geographic region, shows the general independence of these two traits as predictors. So, the trans-species model shows that

Fagus grandifolia and *Acer saccharum* trees have very similar amounts of leaf mass at a similar size, vigor, and competition level because they have about the same ST and LL. *Tsuga canadensis* trees have nearly the same ST as the former two species, but *T. canadensis* has leaves that live an order of magnitude longer on average; this increased investment in leaves with a longer LL results in a higher total leaf mass.

3.2.3 Wood Specific Gravity and Residual Site-to-site Variation.

The initial analysis showed that trees with higher specific gravity (denser wood) tended to carry more leaves when other tree traits are accounted for. However, when a site-specific random effect was included in the model, specific gravity was no longer a significant predictor (Table 3). Due to the study design limitations, location is confounded with species and time, and as we see here, specific gravity. One interpretation for the confounding of location with specific gravity in particular, is that when location-specific effects (Muller-Landau 2004) that moderate leaf mass (Ketterings et al. 2001) are included in the model, the density of the wood is accounted for. A number of studies support the notion that specific gravity varies both within (Lei et al. 1996) and between species (Chave et al. 2006), but studies of tree wood density variation across different sites, regions and past silvicutural practices are rare (Paul 1963). Since we measured the specific gravity of the wood of each tree, both inter and intra-specific variation in specific gravity was accounted for.

The largest bias without including this "site" effect was for *Larix laricina*. We expected this species to be the most divergent species from the trans-species model, because it was the only needle-leaved, deciduous species we included in our study. But, it appears that the reason for its divergence is confounded with its site, because it was only sampled at one wetland site and was one of only a few wetland species included. Kunstler et al. (2016) noted a possible

relationship where denser species indicate an increased tolerance to competition, but before location was added both competition measures and wood specific gravity were retained in the model. Other environmental factors such as soil conditions may also account for variations in leaf mass via leaf morphological traits which could result in the site effects seen (Wright et al. 2001). However, we are left with no clear answer and need more research to identify specific site characteristics that influence leaf mass variation beyond what we have found here.

3.2.4 Potential Applications for a Trans-species Leaf Mass Equation

Producing reliable leaf mass estimates is important for modeling carbon stocks and fluxes (Kirschbaum and Paul 2002) and modeling other aspects of the forested environment, such as leaf-area index (Thornton et. al. 2002). As noted by Weiskittel et al. (2015), there are many knowledge gaps with respect to leaf mass. Most of the published models for leaf estimation are generally based on small datasets (Chojnacky et al. 2013). The intense cost and effort that would be required to fill these data gaps necessitates the need for modeling approaches that can encompass many species.

The trans-species model developed here has the potential to accurately predict tree leaf mass from variables describing the tree's size, health, competitive status and two leaf functional traits over a range of species and forest ecosystems. Of these variables DBH, CC, and LCR are already regularly measured during forest inventories (for example the US FIA). The CI we used requires measuring the distance and size of neighboring trees immediately around the tree, so it not typically available, except in situations where stem maps are available, but could be obtained with some additional effort. It may also be possible to get similar results from distance-independent CIs, which only require knowing the number and sizes of trees occurring on the same plot. Of the most important predictors, BAI of the most recent 5 years requires much more

effort to know for each tree; it generally requires a core to be extracted from the tree, but such cores can also be used to estimate stem specific gravity. A possible substitution may also be available for BAI where repeated measurements of tree diameter are recorded over 5 years.

Our model can be applied to any species where there are published values for ST (Niinemets and Valadares 2006) and LL (Wright et al. 2004). This means, theoretically, the transspecies model could be used to predict leaf mass for trees of species for which no leaf mass data exist. This could be very important in areas such as tropical forests, which have enormous numbers of species, with limited capacity to obtain leaf mass for species where no data may be available (Cháve et al. 2014). However, more testing of the importance of the variables examined here is needed before one could confidently apply the model over many more species and biomes. Such testing should also include climatic as well as site effects, as recent research indicates that changing climates might affect the total proportion of mass in leaves (Reich et al. 2014) and leaf morphology and growth (Vitasse et al. 2014) for species. With the emergence of new technologies, such as TLS (terrestrial laser scanning, Moskal and Zheng 2011, Kankare et al. 2013) it may be possible to non-destructively calibrate models such as ours (Srinivasan et al. 2014) to estimate changes in leaf mass across a range of years and times of year.

Another way to use the knowledge gained from the trans-species modeling work we've shown here, is to use it to define species groups for fitting leaf mass equations, should one want to use multiple models, instead of a single, trans-species model. With LL and ST, the model defines a biologically- meaningful way to group species on a continuous scale of leaf mass allocation based on key functional traits, rather than using taxonomic groupings. For example, the US national tree mass equations currently use species groupings based on broad taxonomic associations to deal with data limitations at the species level (Chojnacky et al. 2013; Jenkins et al. 2003), but these have been found to be unhelpful in producing better leaf mass equations

(Clough et al. 2016).

CHAPTER 4

SLA VARIABILITY BETWEEN SPECIES AND CANOPY STRATA

4.1 SLA Variation Results

4.1.1 Early SLA sampling

The first few *P. tremuloides* trees sampled in the field season were seen to exhibit a high variability and range in leaf area, specific leaf area, and weight overall compared to other trees sampled of the same species (Table 6 and Fig. 5). During the destructive analysis, it was noted that these trees did not show signs of full leaf out at the times they were sampled, and were subsequently removed from further analysis related to SLA.

4.1.2 Observed SLA Trends

With all species grouped together, average SLA within the canopy increases as canopy position decreases (significance at $\alpha = 0.05$). This pattern remains significant for each individual species as well (Fig. 6). In addition when comparing shade tolerant species to shade intolerant, shade tolerant species exhibited a significant ($\alpha = 0.05$) and greater plasticity in SLA (Fig. 7). By combining the average leaf weight with total tree foliage mass and SLA averages with total tree foliage mass we can estimate the number of leaves and the total leaf area on a tree. Shade tolerant trees carried significantly more leaves and had a greater total leaf area. (Fig. 8)

Figure 5. Boxplots of individual tree averages for P. tremuloides specific leaf area (a), leaf area (b), and leaf mass per leaf (c). Each tree was sampled at a different time with those sampled earlier in the growing season on the left.



Figure 6. Boxplots of specific leaf area (cm^2/g) within sections of the canopy for all trees sampled (a), and separated out by each species sampled (b).



Figure 7. Boxplots of expressed plasticity in specific leaf area (SLA) for shade intolerant species and shade tolerant species.



Figure 8. Boxplots of number of leaves (a) and total leaf area (b) for shade intolerant and shade tolerant species sampled.



4.2 Discussion on SLA Variation

4.2.1 SLA Variation Seen by Early Sampling

We added SLA after a significant amount of the destructive sampling was accomplished, so that we only had SLA values on a subset of the total trees sampled for the trans-species leaf biomass model. However, we were able to learn some important things about SLA – tree foliage mass relationships.

We learned about the temporal variation in SLA by inadvertently sampling too early in the growing season, for the first species sampled for SLA (*P. tremuloides*). While the trees were standing they were observed to have their foliage fully initiated. After felling, however, the first few sampled were later noted as not having full leaf initiation throughout the crown. This caused trees sampled earlier on in the growing season to have lighter leaves and a higher SLA than their counterparts sampled later on even though they were only sampled a few days apart from the same stand (Fig. 5).

Leaf unfolding typically initiates from the lower part of the crown (Koike et al. 2001). Shade leaves also tend to have a larger surface area than sun leaves (Koike et al. 2001). If we sampled trees prior to full leaf establishment then our average surface area should be larger than expected for the species since the shade leaves which should be larger would be more fully developed and folded out. Additionally, we would expect abnormally low average leaf mass, since they are not fully developed. Combining these two factors, SLA should be abnormally high for a tree before the leaves are fully formed. Our data supports the anecdotal observations of the field crew after felling, that these trees were sampled prior to full leaf establishment, since those sampled earlier saw extremely high SLA, low mass, and larger surface area (Fig. 5). This early sampling however did not appear to create outliers with respect to total leaf mass with the early sampled *P. tremuloides* compared to the other trees sampled (Fig. 9). So, most of the

difference was likely in the distribution of the mass over the area of the leaf.

Figure 9. Plot of measured versus predicted leaf dry mass (kg) on a log-log scale in a mixed effects model with location as a random effect of the early sampled Populus tremuloides and the later sampled Populus tremuloides with all other species.



4.2.2 SLA and its Expressed Plasticity in Shade Tolerant Trees

Leaves, growing in the shade, experience an environment where light is a limiting resource. Shade leaves therefore have a high chlorophyll content per mass basis which puts them on par with sun leaves for chlorophyll content per unit area compared to sun leaves to achieve a similar light capture to sun leaves with a lower biomass investment (Chazdon et al. 1996; Poorter et al. 2000). Within the canopy, shade leaves are expected to have increased efficiency of light capture via a higher SLA compared to sun leaves (Evans and Poorter 2001). Koike et al. (2001) also observed this relationship where SLA continuously increased as one moved down the canopy profile across many species. Here, we note the same trend with the species we sampled, where no matter the species the further down the crown, SLA increased (Fig. 6).

Studies on tree leaf trait plasticity often find differences between shade-tolerant versus shade intolerant species. Some studies fine plasticity higher in early successional species (shade intolerant) due to resource rich heterogeneous environments they grow in (Strauss-Debenedetti and Bazzaz 1996; Valladares et al. 2000). Other studies have found a similar plasticity between shade tolerant and intolerant species where the overall range of physiological and morphological plasticity of leaves differed irrespective of shade tolerance (Sims and Pearcy 1989; Kitajima 1994). Additionally others have found leaf plasticity to be greater in shade tolerant species (Popma et al. 1992; Rozendaal et al. 2006). Within our study shade tolerant species exhibited a greater expressed plasticity in SLA (Fig. 7). This agrees with other studies which found a higher plasticity in SLA for shade tolerant species such as Rozendaal et al. (2006). This also supports the idea that species adapted for low light environments would have a higher plasticity in traits important in harvesting light (eg. SLA) (Valladares et al. 2002). We must note however that within our sampling of SLA, sampling between shade tolerance levels and canopy positions was not evenly distributed. Due to this, the expressed SLA sampled may not fully encompass the possible SLA values for each species.

CHAPTER 5

SUMMARY AND RECOMMENDATIONS

5.1 Summary of Research

Our new trans-species model enabled us to predict foliage mass accurately over trees of many trees of different sizes and species over many locations in Michigan. We were able to do this by selecting important variables that capture the dimensions of the tree (DBH and LCR) its competitive environment (CC and CI), its vigor (BAI), and its species related traits (LL and ST) which correlate with leaf biomass. This combination of species-independent allometric variables and species-dependent attributes allow us to fit a model capable of working across species. This model makes it possible to estimate leaf biomass on tree species that do not currently have leaf biomass given you know these variables which has expanded the possibilities for modeling and estimation.

Our trans-species model also showed that shade tolerant trees hold a greater leaf mass than shade intolerant species. Shade tolerant species are able to do this by maintaining leaves with a positive carbon balance in areas of lower light availability (Valladares and Niinemets 2008). As such shade tolerant trees have been shown to hold deeper crowns (Canham et al. 1994), and more efficient leaf display in lower canopy positions (Canham 1988). With this we expected shade tolerant trees to maintain a higher leaf area and number of leaves overall compared to shade intolerant species. In our study shade tolerant species were also able to maintain a larger total leaf area and number of leaves (Fig. 8) which strengthens our inference by which shade tolerant trees held a greater leaf mass. In addition, this agrees with other studies where shade tolerant trees maintained a greater overall leaf area to survive in lower light conditions (Lusk 2002), and where canopy trees of shade tolerant species accumulate more leaf

area and denser crowns (Valladares and Niinemets 2008).

Finally, studying leaf area as well as mass enhanced our understanding of variation in tree allocation to foliage. Though sampling of SLA was not comprehensive enough to include within the framework of the trans-species model, it helped inform our interpretation of model results. By exploring SLA within our study, we were able obtain data demonstrating that shade tolerant trees had on average greater SLA, plasticity in expressed SLA, leaf area, and leaf number. We must note, however, that the SLA sampled was what was expressed on the sampled trees. Our measures of SLA due to the small diversity of sample trees taken from may be confounded with tree age (England and Attiwill 2006) or shading (Walters and Field 1987, Reich et al. 1998).

5.2 Areas of Future Research

Here, we have presented a trans-species model with potential for estimating tree leaf mass, and have shown some useful correlations between SLA, SLA plasticity, species traits and leaf mass. However, we can see that it is possible to combine leaf mass estimations with measures of SLA, which opens new avenues for exploring other aspects of the forest such as leaf-area index (Thornton et al. 2002). Leaf area index is a valuable forest metric, because of its influence on the exchange of energy, water vapor, and carbon dioxide between terrestrial ecosystems and the atmosphere (Bonan 1993). Leaf area has also been shown to change with many of the conditions that affect leaf mass as well such as tree size and species (Gower et al. 1999), and so further exploration of leaf mass, SLA, and leaf area should be done. Rozendaal et al. (2006) also notes that plasticity in SLA has had limited investigation in the past, which is an avenue which could be explored with continuation of sampling of SLA. Additionally, measuring of SLA allows us to fill in knowledge gaps due to our destructive sampling targeting a wide range of tree species.

Our trans-species model also identified a novel variable for relating recent growth to leaf mass (i.e., the most recent 5 year BAI). Our model was fitted with many species, but differences in nutrient storage between ring porous and diffuse porous trees (Barbaroux and Bréda 2002) may be a basis for using different year BAI depending on wood anatomy. The trans-species model could be further tested on different trees with differing wood anatomy to see if wood anatomy gives further insight into which years of BAI were important for determining leaf mass.

Finally, our trans-species model remains to be tested at a larger spatial scale, with more species and environments and against unseen data and species, to see if the patterns observed here hold more generally. This model could be tested with data from other sources such as the LegacyTreeDatabase (http://www.legacytreedata.org/). With this large comprehensive historical dataset and other data, the trans-species model could be tested across many regions and species. A larger dataset would also allow the model to be tested against 'reduced' versions of itself. These reduced models would contain subsets of predictors that were less costly to obtain or which were aligned with current protocols such as methods used in the Forest Inventory and Analysis national program (FIA), which already uses most of the variables used here. The FIA program could benefit by using its many other already measured variables to provide estimates of leaf biomass across the large range of environments and tree species found in the ecosystems of the United States. We expect that this methodology is general enough that it could be calibrated to tree data sets worldwide.

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