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# Production Ecology and Stand Dynamics of Young Acadian Forest Stands in Response to Silvicultural Intensity and Compositional Objectives

Andrew S. Nelson

# PRODUCTION ECOLOGY AND STAND DYNAMICS OF YOUNG ACADIAN

# FOREST STANDS IN RESPONSE TO SILVICULTURAL INTENSITY

# AND COMPOSITIONAL OBJECTIVES

By

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# PRODUCTION ECOLOGY AND STAND DYNAMICS OF YOUNG ACADIAN FOREST STANDS IN RESPONSE TO SILVICULTURAL INTENSITY AND COMPOSITIONAL OBJECTIVES

By Andrew S. Nelson

Dissertation Advisor:  Dr. Robert G. Wagner

An Abstract of the Dissertation Presented
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Early successional stands are common across the Acadian forests of eastern Canada and the Northeastern US. However, productivity and dynamics of these stands, as well as the underlying mechanisms influencing these processes, under different management scenarios are poorly understood. To address this need, I used a factorial experiment that controlled silvicultural intensity and species composition to quantify the effects of varying treatments on early stand dynamics, and the physiological and morphological factors influencing tree performance . Specifically, I studied: 1) species differences in aboveground allometrics, 2) light capture, light-use efficiency (LUE; growth/light capture), and foliar carbon isotope composition ($\delta^{13}$C) of white spruce across a range of growing conditions, and 3) stand growth and yield in response to combinations of silvicultural intensity and compositional objectives. In Chapter 1, a new set of aboveground component biomass equations were developed for sapling-sized trees. In addition, I found that the Forest Inventory and Analysis (FIA) sapling biomass equations underestimated biomass between 10% and 36%, which corresponded to the loss of forest

biomass in Maine when FIA switched to new equations. In Chapter 2, I found that aboveground productivity of white spruce seedlings was negatively correlated to competition and positively correlated to light capture. LUE was not correlated with inter-tree competition, suggesting the stands had not reached a density-dependent sorting stage, where use-efficiency tends to increase for dominant trees. $\delta^{13}$C was negatively correlated with competition suggesting that assimilation declined as trees became more light-limited. In Chapter 3, I found that a *Populus nigra* × *P. maximowiczii* clone outperformed three *P. deltoides* × *P. nigra* clones at the rocky, somewhat poorly drained site, while white spruce yield was negatively correlated with hybrid poplar yield in mixed plantations. Compositional objectives strongly influenced the productivity of naturally regenerated stands over a seven-year period after treatment in Chapter 4, indicating that stands can be directed into distinctly different trajectories depending on the silvicultural treatment. The approach used to study forest productivity in this experiment revealed that hierarchical responses (physiological, tree, and stand) to silviculture-induced growing conditions may influence the long-term trajectories of young Acadian forest stands in the region.

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# PROLOGUE

Early-successional forest composition in northeastern North America is prevalent across the landscape due to the diversity of historic land-use practices in the region. For instance, 13% (936 thousand ha) of forestlands in Maine are dominated by early-successional hardwood species and 24% (1.7 million ha) of forestlands are dominated by saplings (McWilliams et al. 2005). Intermediate stand tending of early successional mixedwood stands is uncommon, with crop-tree release and precommercial thinning (PCT) operations accounting for only 1% of the annual harvested area (Maine Forest Service 2010). Past research in the region has shown that species composition can be shifted early in stand development (Nelson and Wagner 2011; Newton et al. 1992) and crop-trees can be selected to substantially increase long-term growth, yield, and financial value (Bataineh et al. 2013; Olson et al. 2012; Pitt and Lanteigne 2008), but the stand-level responses and underlying mechanisms driving the responses of early successional stands in the region to different intensities of silviculture are still poorly understood.

Early successional stands in the Acadian region typically develop following large-scale disturbances, such as fire, wind, spruce budworm (*Choristoneura fumiferana* (Clemens)),and harvesting (Lorimer and White 2003). During the first couple of decades after disturbance, early-successional Acadian stands are typically dominated by rapidly growing shade intolerant hardwood species that form an upper stratum over slower growing shade tolerant advance regeneration of conifer and hardwood species. Common hardwood species in these early successional stands include: trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), gray birch (*Betula*

*populifolia* Marsh.), paper birch (*Betula papyrifera* Marsh.), and red maple (*Acer rubrum*
L.). The aspen and birch species are considered shade intolerant while red maple is
moderately shade tolerant, but may be a dominant species because of its ability to
prolifically stump sprout (Walters and Yawney 1990). Common conifer species
occupying understories of early successional stands include: balsam fir (*Abies
balsamifera* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and red spruce
(*Picea rubens* Sarg.). The diversity of tree species in these young stands can often be
high and the species composition will generally depend on the complex of species
available in the seed and bud bank prior to disturbance. For instance, aspen species
commonly regenerate at recently disturbed sites by suckering from roots systems of killed
or harvested trees (Domke et al. 2008).

Recent evidence suggests that the land area of early successional forests in the Northeast
is declining due to a shift almost exclusively to partial harvesting practices as well as
land-use conversion (Brooks 2003). For instance, clearcutting in Maine comprises only
4% of the area harvested annually (Maine Forest Service 2010). Prior to the Maine Forest
Practices Act in 1989, clearcutting was a common practice to salvage wood from stands
attacked by spruce budworm during the large-scale outbreak in the 1970's and 1980's
(Seymour 1992). Following harvest, many of these stands became dominated by an early
successional composition of shade intolerant hardwood species and advance regeneration
of conifer species. Stands that were sprayed with herbicides were generally shifted to
conifer dominance, while hardwood composition persisted in unsprayed stands (Olson et
al. 2012). More recently, partial harvesting practices have maintained more mid- to late-
successional species composition (Brissette 1996). Residual stands rarely receive

intermediate treatments to increase growing space of residual trees and promote desired species composition.

Species composition in early successional Acadian stands can be shifted onto a wide variety of long-term trajectories using different silvicultural strategies. Historically, many intermediate silvicultural practices in Maine were designed to promote conifer dominance (Seymour 1992). More recently, however, there is increased interest in favoring hardwood species to diversify stands ecologically and the types of forest products available in the region. Unfortunately, there is limited information about the responses of young hardwood and mixedwood stands to early thinning prescriptions to increase residual tree growth and enhance species composition.

One major objective of intermediate silvicultural treatments is to manipulate stand structure and composition to enhance resource capture of residual trees and increase growth (Smith et al. 1997). Underlying the response of trees and stands to different intermediate silvicultural treatments are various physiological, morphological, ecological (e.g., within stand competition), and abiotic factors. Compared to forest biometrics, which often focuses solely on quantifying tree and stand growth and yield, testing various mechanistic hypotheses can help answer "how" and "why" forests respond to various silvicultural treatments.

Mechanistic factors influencing forest responses to silvicultural treatments have been studied for many years. For instance, leaf area production and distribution throughout the crown and canopy have been used to examine tree and stand light capture (Brunner 1998), because leaf area represents a tree's investment in light harvesting structures.

Since light is a key resource required by forests for growth, leaf area is often strongly related to growth across a range of species (DeRose and Seymour 2009; Gersonde and O'Hara 2005; Seymour and Kenefic 2002). Growth efficiency (the ratio of growth per unit of leaf area) is considered a metric of tree vigor (Waring et al. 1980), and has been used extensively to study tree responses to variation in stand structure (Mainwaring and Maguire 2004), nutrient and water inputs (Albaugh et al. 1998), and species composition (Gersonde and O'Hara 2005; Stancioiu and O'Hara 2006). For instance, Gersonde and O'Hara (2005) compared growth efficiency among species with different shade tolerances in mixed species conifer stands, and found that volume production for smaller trees was substantially greater for shade intolerant species, possibly as a shade avoidance strategy.

Mechanistic approaches to studying forest productivity have also attempted to measure or model resource availability, resource capture, and the efficiency that captured resources are converted into growth to understand forest responses to silvicultural treatments. The product of these three factors comprise the production ecology equation hypothesis, initially developed for agricultural crops by Monteith (1977), and recently refined for forested systems by Binkley et al. (2004):

$$GPP = \frac{R_{available}}{time} \times \frac{R_{captured}}{R_{available}} \times \frac{Growth}{R_{captured}}$$

where GPP is gross primary productivity (net primary productivity + respiration), $R_{available}$ is the availability of resources, and $R_{captured}$ is resources captured by trees or stands. Components of the production ecology equation, especially resource-use efficiency (growth per unit of $R_{captured}$), have been used extensively to study forest responses to

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silvicultural treatments (Binkley et al. 2010; Campoe et al. 2013a; Gspaltl et al. 2013) and changes in tree growth patterns with age to elucidate potential mechanisms influencing dominance of individual trees within stands (Binkley 2004; Binkley et al. 2013b).

The overall goal of this dissertation was to increase our understanding about the productivity and dynamics of early successional stands, as well as the underlying mechanisms influencing these processes, under factorial combinations of silvicultural intensity and compositional objectives. The specific objectives, which are addressed in the four chapters of this dissertation, included quantifying: (1) aboveground biomass allometry of selected hardwood species, by developing a set of new component aboveground biomass equations, and comparing their performance to published biomass equations, (2) white spruce light capture, light-use efficiency, stable carbon isotope composition, and aboveground productivity in relation to contrasting growing conditions, (3) growth and yield of white spruce and four hybrid poplar clones in pure and mixed-species plantations, and (4) growth, yield, and compositional changes of naturally-regenerated stands in response to factorial combinations of silvicultural intensity (thinning, thinning plus enrichment) and species compositional objectives (conifer, mixedwood, hardwood), as well as no silvicultural intervention.

# CHAPTER 1

# DEVELOPMENT AND VERIFICATION OF ABOVEGROUND SAPLING BIOMASS EQUATIONS FOR NATURALLY REGENERATED AND PLANTED TREE SPECIES IN EASTERN MAINE

## 1.1. Abstract

Numerous equations are available in northeastern North America to estimate aboveground tree biomass, yet most biomass studies have focused on trees >25.4 cm diameter, and these equations are often poor predictors of sapling biomass (<12.5 cm diameter). Additionally, equations available to estimate sapling biomass often lack independent verification with field data. We developed a new set of additive biomass component (foliage, branch, and bole) equations for five naturally regenerated hardwood species, four hybrid poplar (*Populus* sp.) clones and planted white spruce (*Picea glauca* (Moench.), from trees in eastern Maine. Biomass measurements were used to verify national and regional equations for naturally regenerated species, and species specific equations for planted stock. Results showed that the regional and national equations provided similar fits for total biomass across all species. Moreover, the sapling biomass equations currently used nationwide to predict woody biomass substantially underestimated biomass from 19.0% to 36.6% for all of the naturally regenerated hardwood species at our site. This substantial underestimation of sapling biomass may have contributed to the recent 34% decrease in estimated sapling woody biomass, and 15% decrease in aboveground biomass of all living trees in Maine, where nearly one-quarter of the 70,000 $km^2$ forestlands are dominated by saplings. This problem may exist in other regions of the United States if substantial proportions of forestlands are

dominated by saplings. Further model verification is warranted to assess the performance of the current equations.

## 1.2. Introduction

Numerous equations are available to predict aboveground biomass of tree species in northeastern North America (Jenkins et al. 2003; Monteith 1979; Wharton and Griffith 1998; Young et al. 1980), yet the majority of these equations were developed for medium and large size trees ($\geq$ 12.5 cm diameter at breast height [DBH]). Sapling (< 12.5 cm DBH) biomass estimates in the region are limited to a few set of equations, and their predictions have not been well verified using data from controlled experiments. Therefore, biomass predictions may be inaccurate when naturally regenerated understories and juvenile plantations are common. For instance, alternative equations were recently found to produce substantially different estimates of tree biomass in northeastern North America (Westfall 2012) , but there is general lack of data to verify biomass equations and investigate potentially different estimates. Reliable sapling biomass equations are especially important in the state of Maine where nearly 24% of the forested area (17,000 km$^2$ out of 70,000 km$^2$) is dominated by sapling-sized stands (McWilliams et al. 2005). Although different equations may produce variable sapling biomass estimates in the region, the scope of the problem may extend across the United States, particularly in regions with large proportions of stands dominated by saplings.

Only a few equations are currently available to estimate sapling biomass in northeastern North America, including the national Jenkins et al. (2003, 2004) (Jenkins) equations, the regional Young et al. (1980) (Young) equations, and compilation of equations in Ter-

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Mikaelian and Korzukhin (1997) (TMK). The Jenkins, Young, and TMK equations were developed to predict total aboveground biomass (foliage, branch, bole, and stump) but also present equations to predict estimates of individual component biomass. The Jenkins equations were developed from a large database of published biomass equations and condensed into nine equations for all trees species across the United States. The Jenkins equations apply to a wide range of tree sizes, but were only fit to trees $\geq 2.5$ cm diameter at breast height (DBH). The Young equations were developed for many tree species in Maine and estimate total aboveground biomass of trees down to 0.1 cm DBH. The Young equations have been used to predict aboveground biomass extensively in the northeastern US and were used for regional sapling biomass estimates by the US Forest Service, Forest Inventory and Analysis (FIA) program from 1998 to 2009 (Wharton and Griffith 1998). Like the Jenkins equations, the TMK equations are compiled biomass equations of common North American tree species from multiple sources, but their work has received less attention.

In 2009, the FIA program switched from estimating forest biomass using regional equations to a nationally-consistent approach termed the component ratio method (CRM). The CRM estimates woody aboveground biomass as the sum of the biomass of branches, bole, and stump, but is only valid for trees $\geq 12.5$ cm DBH (minimum merchantability threshold) (Heath et al. 2009; Woodall et al. 2011). The CRM is not applicable for saplings since it relies on estimates of merchantable volume, which is considered zero for trees $< 12.5$ cm DBH. Instead, the FIA aboveground sapling (FAS) equations were developed to estimate woody (branches, bole, and stump) biomass of trees ranging from 2.5 cm to 12.4 cm DBH. The FAS equations multiply the Jenkins woody biomass

prediction (total aboveground – foliage) by a species-specific adjustment factor to ensure a smooth transition into larger size-class estimates by the CRM (Woodall et al. 2011; Woudenberg et al. 2011). Even though the FAS equations have not been verified with field data in northeastern North America, they are the only equations used by FIA to estimate sapling woody biomass across the United States (Woudenberg et al. 2011). Without verification of the FAS biomass equations, it is difficult to determine whether current estimates accurately represent sapling biomass in northeastern North America. For instance, in Maine, McWilliams et al. (2005) reported that sapling density was 18,560 million stems and sapling biomass was 169,603 thousand Mg in 2003 using the FIA regional equation approach. Comparatively, sapling density in 2010 was estimated as 20,920 million stems and sapling biomass as 112,128 thousand Mg using the FAS equations (USDA FIA Program 2012). The result was an 11% increase in sapling density but a 34% decrease in sapling woody biomass in Maine over the seven year period.

Inconsistencies in the prediction of sapling total and woody aboveground biomass in northeastern North America and the selection of appropriate equations to refine predictions can be addressed by verifying published equations with independent data and fitting new equations to field measurements. In particular, no biomass equations for Northeast tree species were fit with statistical techniques that force additivity of aboveground components, where predictions from component equations sum to predictions from total aboveground equations. Therefore, the objectives of this study were to: (1) develop a new set of additive aboveground component (foliage, branch, bole [including stump]) and total aboveground biomass equations for five naturally regenerated hardwood species (red maple [*Acer rubrum* L.], paper birch [*Betula*

*papyrifera* Marsh.], gray birch [*Betula populifolia* Marsh.], bigtooth aspen [*Populus grandidentata* Michx.] and trembling aspen [*Populus tremuloides* Michx.]), four planted hybrid poplar clones (D51, DN10, DN70 – *Populus deltoides* x *P. nigra*, NM6 – *P. nigra* x *P. maximowiczii*), and planted white spruce (*Picea glauca* (Moench) Voss) in eastern Maine, (2) compare the partitioning of total aboveground biomass to various components of naturally regenerated hardwood species, hybrid poplar, and white spruce early in stand development, (3) verify and compare total aboveground oven-dry sapling biomass estimates of national and regional equations for naturally regenerated hardwood species, hybrid poplar clones, and planted white spruce, and (4) verify and compare aboveground woody (branches, bole, stump) oven-dry biomass estimates of the Jenkins et al. (2003) and FAS (Heath et al. 2009) equations currently used by the FIA program for five naturally regenerated species .

## 1.3. Methods

### 1.3.1. Study Design

Five naturally regenerated hardwood species (red maple, paper birch, gray birch, bigtooth aspen, and trembling aspen), four planted hybrid poplar clones (D51, DN10, DN70, and NM6), and planted white spruce were destructively sampled to estimate aboveground component oven-dry biomass. Trees were part of an experiment established in 2004 on the Penobscot Experimental Forest in eastern Maine (44° 49' N, 68° 38' W). A detailed description of the experiment, including treatments and planting stock are given in Nelson et al. (2012; 2013). Briefly, the experiment is a $3 \times 3 + 1$ factorial array of three silvicultural intensities (thinning, thinning plus enrichment planting, and intensively

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managed plantations) and three species compositional objectives (hardwood, mixedwood, and conifer), plus an untreated control, each replicated four times. The experiment was installed at a 9.2-ha site that was clearcut in 1995. Therefore, trees were destructively sampled sixteen years after harvest and seven years after the experiment was initiated. Natural species composition at the site when the trees were sampled was dominated by a mixture of young shade intolerant hardwood and shade tolerant conifer species.

### 1.3.2. Measurements

Trees were cut at the root collar in the summer of 2011 during peak leaf-out (late June to early August) to ensure accurate estimates of hardwood foliage biomass. For each species, trees were sampled from five DBH classes estimated from observed DBH distributions of the 2010 inventory. For the naturally regenerated hardwood species, between 12 and 17 individuals (3 to 6 in each DBH class) were sampled per species. Five individuals per hybrid poplar clone were sampled from plantations for a total of 20 trees. Ten planted white spruce were sampled (5 from plantations and 5 from naturally-regenerated treatments with enrichment planting). A total of 102 (72 naturally-regenerated and 30 planted) were sampled with a median DBH between 1.2 and 6.8 cm (Table 1.1).

DBH, height, and length of live crown were measured for all sample trees. Foliage and branch components were separated from boles in the field and dried in the lab. Foliage and branches were dried at 65°C for a minimum of two weeks. Boles were cut into approximately 25 cm segments and dried at 65° C for a minimum of six weeks. While drying, weight was checked periodically to ensure samples dried to constant mass. After

drying, foliage and branch components were separated and weighed to the nearest 10 mg.

Bole dry weight was measured to the nearest 10 g.

### 1.3.3. Analytical Approach

### 1.3.3.1. Additive Biomass Equations

Since saplings were sampled from different silvicultural treatments, we investigated whether accounting for treatment effects in the model influenced the fit of the component biomass equations. Biomass equations by species and component were fit with nonlinear mixed-effects models with treatment as a random effect and compared to models fit without random effects with likelihood ratio tests. If the likelihood ratio tests were significant at $\alpha = 0.05$, the mixed-effects model had a superior fit to the fixed-effects model (Pinheiro and Bates 2000). Natural hardwood species were tested across three silvicultural intensities (untreated control, thinning, thinning plus enrichment planting), planted white spruce across two treatments (thinning plus enrichment planting and plantations), and hybrid poplar equations were tested for differences among the four clones.

Table 1.1. Descriptive statistics of destructively sampled trees used to fit the additive aboveground biomass equations and verify published equations. The number of individuals per species (n), median values and ranges of DBH (cm), foliage biomass (kg), branch biomass (kg) and bole biomass (kg) are shown.

| Species | n | DBH median (cm) | DBH range (cm) | Foliage median (kg) | Foliage range (kg) | Branch median (kg) | Branch range (kg) | Bole median (kg) | Bole range (kg) |
|---|---|---|---|---|---|---|---|---|---|
| Red maple | 12 | 2.4 | 0.3-6.0 | 0.12 | 0.01-0.92 | 0.27 | 0.01-0.99 | 0.73 | 0.01-7.11 |
| Paper birch | 13 | 1.2 | 0.5-3.9 | 0.05 | 0.01-0.32 | 0.04 | 0.01-0.42 | 0.17 | 0.02-2.38 |
| Gray birch | 15 | 1.2 | 0.5-6.9 | 0.04 | 0.01-0.54 | 0.05 | 0.01-1.50 | 0.14 | 0.04-10.02 |
| Bigtooth aspen | 17 | 5.6 | 1.1-13.1 | 0.41 | 0.01-4.08 | 1.06 | 0.02-9.46 | 5.77 | 0.13-32.33 |
| Trembling aspen | 15 | 5.2 | 2.6-12 | 0.38 | 0.04-7.39 | 0.76 | 0.07-18.62 | 4.03 | 0.78-29.63 |
| Hybrid poplar (D51) | 5 | 4.3 | 1.4-7.5 | 0.56 | 0.06-1.46 | 0.72 | 0.11-2.39 | 2.52 | 0.33-7.98 |
| Hybrid poplar (DN10) | 5 | 4.6 | 2.3-10.9 | 0.45 | 0.11-2.67 | 0.77 | 0.16-4.70 | 3.08 | 0.70-14.94 |
| Hybrid poplar (DN70) | 5 | 4.1 | 0.7-8.7 | 0.66 | 0.02-1.53 | 1.45 | 0.04-2.67 | 2.51 | 0.10-9.69 |
| Hybrid poplar (NM6) | 5 | 6.8 | 3-13.7 | 1.32 | 0.30-4.12 | 2.48 | 0.52-14.99 | 7.06 | 1.01-27.89 |
| White spruce | 10 | 1.6 | 0.3-5.1 | 0.78 | 0.20-2.74 | 0.44 | 0.12-1.70 | 0.43 | 0.13-2.22 |

When additivity of component biomass equations is not forced, summed component biomass estimates may not equal estimated total biomass (Parresol 2001). Therefore, a system of component aboveground biomass equations were fit by species using nonlinear seemingly-unrelated regression (NSUR;Table 1.2) (Parresol 2001; Srivastava and Giles 1987). Compared to other additive approaches, such as weighted least squares regression, which assume independence among observations, NSUR is preferred since it accounts for autocorrelation among components of the same tree resulting in lower variance (Parresol 1999). Additive biomass models were fit using the MODEL procedure in SAS software version 9.2 (SAS 2009).

Multiple model forms, including various combinations of DBH, height, and length of live crown were explored, but did not improve predictions compared to a two-parameter power function with DBH as the sole independent variable (Biomass = $\beta_0 DBH^{\beta_1}$). Although numerous equation forms can represent exponential relationships common to sapling diameter and biomass, the power function is common because the scaling parameter ($\beta_1$) has biological interpretation (Niklas 1994) and estimated biomass is restricted to positive values.

### 1.3.3.2. Published Equations

Several different sets of published equations were verified with the field data (Table 1.2). For naturally regenerated hardwoods, the Jenkins, Young, and TMK equations were used. The Jenkins equations were not developed from field measurements, but instead parameters were estimated using a generalized regression approach (Pastor et al. 1984), where biomass was predicted with many individual equations and then generalized

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parameters were estimated from the pseudo-data. Comparatively, the Young and TMK equations were fit with field measurements. The Young equations do not include weight of a 15.2 cm stump length for trees > 2.5 cm DBH. Therefore, the weight of the 15 cm stump of the sampled trees was subtracted from the observed total aboveground biomass to verify the Young equations. The TMK equations selected for this investigation were fit with data proximate to our study site, namely New Brunswick and Nova Scotia, Canada, and included: Freedman et al. (1982) for bigtooth aspen; Ker (1980) for gray birch; and Ker (1984) for red maple, paper birch, and trembling aspen. In addition, these five TMK equations were fit with data that included DBH ranges similar to the measurements used in the current investigation.

Table 1.2. Equations forms of the seven equations used for verification with data from eastern Maine. M is oven-dry biomass (kg) for foliage, branch, and bole components, and total aboveground biomass. DBH is diameter at breast height in cm. $A_s$ is the species specific sapling adjustment factor that is multiplied by woody biomass for the FIA aboveground sapling (FAS) equations. $\beta i$'s are species or group specific parameters of the models.

| Equation | Form | Species | Citation |
|---|---|---|---|
| Additive | $M_{foliage} = \beta_{10} DBH^{\beta_{11}}$ <br> $M_{branch} = \beta_{20} DBH^{\beta_{21}}$ <br> $M_{bole} = \beta_{30} DBH^{\beta_{31}}$ <br> $M_{total} = \sum_{i=1}^{3} \beta_{i0} DBH^{\beta_{i1}}$ | ALL | This investigation |
| Jenkins | $M_{total} = e^{(\beta_0 + \beta_1 \times \ln(DBH))}$ | ALL | Jenkins et al. (2003) |
| FAS | $M_{total} = e^{(\beta_0 + \beta_1 \times \ln(DBH))}$ <br> $M_{foliage} = M_{total} \left[ e^{\left( \beta_0 + \frac{\beta_1}{DBH} \right)} \right]$ <br> $M_{FAS} = \left( M_{total} - M_{foliage} \right) \times A_s$ | Natural hardwood species | Heath et al. (2009) |
| Young | $M_{total} = e^{(\beta_0 + \beta_1 \times \ln(DBH))}$ | ALL | Young et al. (1980) |
| TMK | $M_{total} = \beta_0 DBH^{\beta_1}$ | Natural hardwood species | Ter-Mikaelian and Korzukhin (1997) |
| Netzer | $M_{total} = \beta_0 + \beta_1 DBH + \beta_2 DBH^2$ | Hybrid poplar clones | Netzer et al. (2002) |
| Pitt | $M_{total} = \beta_0 + \beta_1 DBH^{\beta_2}$ | Improved white spruce | Pitt and Bell (2005) |

White spruce total aboveground biomass was predicted with the Jenkins, Young, and Pitt and Bell (2005) (Pitt) equations (Table 1.2). The Pitt equation was developed for juvenile plantation white spruce in Ontario, Canada ranging from 0.6 cm to 7.1 cm DBH. Hybrid poplar total aboveground biomass was predicted using the Jenkins, Young, and Netzer et al. (Netzer et al. 2002) (Netzer) equations. Jenkins and Young equations for aspen species were used for this investigation, since specific hybrid poplar parameters were not available. The Netzer hybrid poplar equation was developed from 152 plantation-grown trees in the north central United States. The majority of trees used for the Netzer equation were crosses of *P. deltoides* × *P. nigra*, ranging in age from 3 to 10 years old and 1.6 cm to 22.2 cm DBH. All of the aforementioned equations were selected because they used DBH as the only predictor variable, but model form differed by equation (Table 1.2). For consistency and to investigate extrapolation potential of all equations, total biomass was predicted for all observed data, even if the measured DBH was below the lower limit of the DBH range used to develop the equation.

Woody aboveground biomass estimates of the FAS (Heath et al. 2009) and Jenkins (Jenkins et al. 2003) equations were verified with the field measurements. Woody aboveground woody biomass was estimated by the FAS and Jenkins equations by subtracting foliage biomass from total aboveground biomass. Then, for the FAS equations, a species-specific adjustment factor was multiplied by estimated woody biomass. The FAS adjustment factor varied by species (0.7-0.8) and was the ratio of the average CRM and Jenkins woody biomass estimates for all 12.5 cm DBH trees in the FIA database (Heath et al. 2009).

### 1.3.3.3. Model Performance

This investigation comprised three phases of model verification: (1) total aboveground biomass of naturally regenerated hardwood trees for the Jenkins, Young, TMK, and additive equations; (2) total aboveground biomass of hybrid poplar clones and white spruce for the Jenkins, Young, Netzer, Pitt, and additive equations; and (3) woody aboveground biomass for the naturally regenerated species using the FAS, Jenkins, and additive equations. Predictions were verified using root mean square error (RMSE) to assess model accuracy, and mean bias (MBIAS) and absolute bias (ABIAS) to assess model precision (Huang et al. 2009; Newton and Amponsah 2007). RMSE was calculated as:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n}}$$

where $y_i$ are the observed values, $\hat{y}_i$ are the predicted values, and $n$ is the number of observations. MBIAS was calculated as:

$$MBIAS = \frac{\sum_{i=1}^{n} y_i - \hat{y}_i}{n}$$

and ABIAS was calculated as:

$$ABIAS = \frac{\sum_{i=1}^{n}|y_i - \hat{y}_i|}{n}$$

Additionally, the minimum detectable negligible difference (MDND) equivalence test

proposed by Parkhurst (2001) and refined for model verification by Radtke and Robinson

(2006) was used to assess prediction accuracy. Similar to other equivalence tests, the null

hypothesis was the observed and predicted values were not equal (Robinson and Froese

2004). MDND was calculated from the equation:

$$P\left( t \leq \frac{\left( \mu_{obs} - \mu_{pred} \right) - MDND}{\sigma_{\mu_{obs} - \mu_{pred}}} \right) = \alpha$$

where $t$ is the critical t-value for the respective degrees of freedom and significance level

($\alpha = 0.05$ for this investigation), $\mu_{obs}$ and $\mu_{pred}$ were the observed and predicted mean

biomass, and $\sigma_{\mu\,obs\,-\,\mu\,pred}$ was the standard deviation of the difference between the

observed and predicted values. If the prediction relative to the observed (PRO) value (i.e.

negative or positive percent deviation of predictions from the observed values) was

within the bounds of $\mu_{obs} \pm$ MDND, the null hypothesis of the equivalence test was

rejected and the predicted values were considered similar to the observed values.

Equivalence tests generally set a pre-determined equivalence region for model

verification, such as 10% (Leites et al. 2009), where predictions greater than or less than

10% of the observed mean result in not rejecting the null hypothesis. Comparatively, we

estimated the MDND to define the upper and lower limits of the equivalence region, as

the value can vary among models due to absolute differences between observed and

predicted values. The MDND can also be used to infer the range of mean predictions

where equivalence is assumed between the observed and predicted values. Since the

sample of trees in this investigation was dominated by small sized trees, a slight

difference between the observed and predicted mean biomass can result in an inflated estimate of the percent MDND. Therefore, absolute MDND estimate (kg) was also calculated. Model verification analyses were performed in R version 2.14.0 (R Development Core Team 2011).

**1.4. Results**

**1.4.1. Silvicultural Effects on Biomass Estimation**

Likelihood ratio tests were not significant for 17 of the 21 equations examined. Significant results were found for the bole equations of red maple (p=0.028) and bigtooth aspen (p=0.016) as well as branch equations of gray birch (p=0.002) and hybrid poplar (p<0.001) (Table 1.3). For the bole equations, the red maple percent mean difference of predictions among treatment intensities ranged from 8.4% to 34.6%, and ranged from 9.2% to 18.4% among treatments for bigtooth aspen (Figure 1.1). For the branch equations, the percent mean difference of gray birch predictions ranged from 36.2% and 60.0%, while the range of percent mean difference between the hybrid poplar clones was between 8.5% and 46.9%. Given that the majority of the component equations were not influenced by silviculture, and due to the logical and statistical constraints of having only one equation with random effects in a system of equations, all additive component biomass equations were fit with NSUR assuming no difference among treatment or hybrid poplar clone.

Table 1.3. Likelihood ratios and associated p-values for the likelihood ratio tests comparing the fit of component equations with and without silvicultural treatment / hybrid poplar clone as a random effect. P-values <0.05 were considered significant and indicate the inclusion of treatment / clone as a random effect significantly improved the fit of the models. ΔAIC is the difference in AIC between the two models. ΔAIC values < -2 indicate that inclusion of treatment / clone as a random effect improved the fit of the model.

| Species | Component | Likelihood ratio | p-value | ΔAIC |
|---|---|---|---|---|
| Red maple | Foliage | <0.001 | 0.998 | 5.860 |
| | Branch | 0.101 | 0.751 | 2.101 |
| | Bole | 14.081 | 0.003 | -8.081 |
| Paper birch | Foliage | 7.419 | 0.060 | -1.419 |
| | Branch | 0.001 | 0.994 | 6.000 |
| | Bole | 5.062 | 0.167 | 0.938 |
| Gray birch | Foliage | 0.885 | 0.829 | 5.115 |
| | Branch | 15.282 | 0.002 | -9.282 |
| | Bole | 0.001 | 0.994 | 2.000 |
| Bigtooth aspen | Foliage | <0.001 | 0.998 | 2.000 |
| | Branch | 0.670 | 0.413 | 1.330 |
| | Bole | 5.805 | 0.016 | -3.805 |
| Trembling aspen | Foliage | 0.983 | 0.322 | 1.017 |
| | Branch | <0.001 | 0.998 | 2.000 |
| | Bole | <0.001 | 0.998 | 6.000 |
| White spruce | Foliage | 0.483 | 0.923 | 5.517 |
| | Branch | <0.001 | 0.998 | 6.000 |
| | Bole | <0.001 | 0.998 | 6.000 |
| Hybrid poplar | Foliage | <0.001 | 0.998 | 2.000 |
| | Branch | 24.025 | <0.001 | -18.025 |
| | Bole | 0.001 | 0.998 | 5.999 |
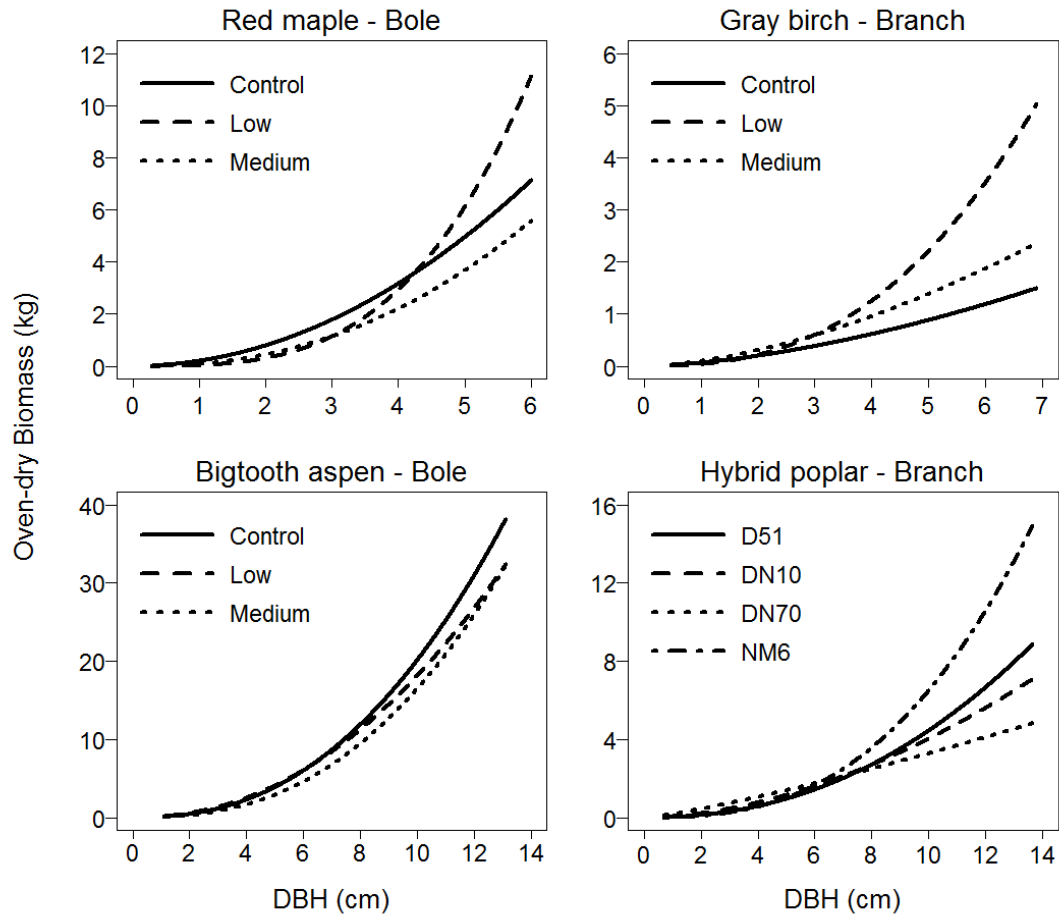
Figure 1.1. Oven-dry biomass (kg) vs. DBH (cm) of select species and aboveground component equations where likelihood ratio tests indicated including silvicultural treatment / hybrid poplar clone as a random effect significantly improved model fit. Shown are bole equations for red maple and bigtooth aspen, and branch equations for gray birch and hybrid poplar for each of the three silvicultural intensities (control – untreated control, low – thinning/conifer release, and medium – thinning/conifer release plus enrichment planting of white spruce and hybrid poplar), and four hybrid poplar clones (D51, DN10, and DN70 – *Populus deltoides* × *P. nigra*, and NM6 – *P. nigra* × *P. maximowiczii*).

### 1.4.2. Additive Component Biomass Equations

Aboveground component and total oven-dry biomass additive equations provided a good fit for the majority of the five naturally regenerated hardwood species (Table 1.4), with the exception of red maple foliage ($R^2 = 0.47$). Scaling exponents ($\beta_1$) were similar among the red maple component equations, ranging from $3.079 \pm 0.390$ (estimate $\pm$ SE; foliage) to $3.515 \pm 0.101$ (bole). Comparatively, the scaling exponents were more variable among the trembling aspen component equations, with estimates of $5.126 \pm 0.257$ and $2.272 \pm 0.107$ for foliage and bole biomass, respectively. For all naturally regenerated hardwood species, constant parameters ($\beta_0$) were greater for bole biomass than foliage or branch biomass, but the difference was most pronounced for the aspen species, where $\beta_0$ for bole equations were $0.116 \pm 0.018$ and $0.107 \pm 0.026$ for bigtooth aspen and trembling aspen, respectively.

Hybrid poplar additive component equations also provided a good fit to the data ($R^2 \geq 0.94$; Table 1.5). Component scaling exponents ranged from $1.829 \pm 0.077$ for foliage to $3.272 \pm 0.241$ for branch biomass, while the constant parameters ranged from $0.003 \pm 0.002$ for branch biomass to $0.112 \pm 0.038$ for bole biomass. Compared to the other species investigated, white spruce component equations had a poor fit to the data, with $R^2$ values of 0.73 and 0.80 for foliage and branch biomass, respectively. The scaling exponents for white spruce were similar among equations, ranging from $1.289 \pm 0.202$ to $1.596 \pm 0.128$ for branch and bole biomass, respectively.

Table 1.4. Parameter estimates (Est.), standard error (SE), p-values, and fit statistics of additive component oven-dry biomass (kg) equations for the five naturally-regenerated hardwood species. Component (Comp.) biomass equations were fit with nonlinear seemingly-unrelated regression to restrict the sum of component biomass to total aboveground biomass. Mean-square error (MSE) and $R^2$ are shown to demonstrate the fit of the models to the observed data.

| Species | Comp. | $\beta_0$ Est. | SE | p-value | $\beta_1$ Est. | SE | p-value | Fit Statistics MSE | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| Red maple | Foliage | 0.135 | 0.069 | 0.079 | 0.811 | 0.366 | 0.051 | 0.045 | 0.466 |
| | Branch | 0.132 | 0.040 | 0.008 | 1.148 | 0.200 | 0.001 | 0.023 | 0.830 |
| | Bole | 0.091 | 0.022 | 0.002 | 2.421 | 0.140 | <0.001 | 0.079 | 0.981 |
| | Total | | | | | | | 0.169 | 0.979 |
| Paper birch | Foliage | 0.042 | 0.009 | 0.001 | 1.519 | 0.175 | <0.001 | 0.001 | 0.906 |
| | Branch | 0.039 | 0.014 | 0.015 | 1.742 | 0.287 | <0.001 | 0.003 | 0.844 |
| | Bole | 0.100 | 0.006 | <0.001 | 2.323 | 0.044 | <0.001 | 0.003 | 0.999 |
| | Total | | | | | | | 0.008 | 0.992 |
| Gray birch | Foliage | 0.101 | 0.019 | 0.001 | 0.913 | 0.122 | <0.001 | 0.008 | 0.792 |
| | Branch | 0.109 | 0.029 | 0.002 | 1.418 | 0.149 | <0.001 | 0.017 | 0.933 |
| | Bole | 0.088 | 0.003 | <0.001 | 2.449 | 0.017 | <0.001 | 0.001 | 0.998 |
| | Total | | | | | | | 0.039 | 0.997 |
| Bigtooth aspen | Foliage | 0.001 | 0.001 | 0.055 | 3.264 | 0.194 | <0.001 | 0.032 | 0.966 |
| | Branch | 0.001 | 0.001 | 0.095 | 3.612 | 0.225 | <0.001 | 0.167 | 0.996 |
| | Bole | 0.116 | 0.018 | <0.001 | 2.191 | 0.064 | <0.001 | 0.643 | 0.991 |
| | Total | | | | | | | 0.985 | 0.993 |
| Trembling aspen | Foliage | 0.001 | 0.001 | 0.137 | 5.126 | 0.257 | <0.001 | 0.044 | 0.987 |
| | Branch | 0.001 | 0.001 | 0.132 | 4.848 | 0.254 | <0.001 | 0.356 | 0.984 |
| | Bole | 0.107 | 0.026 | 0.001 | 2.272 | 0.107 | <0.001 | 1.567 | 0.976 |
| | Total | | | | | | | 1.580 | 0.992 |

Table 1.5. Parameter estimates (Est.), standard error (SE), p-values, and fit statistics of additive component oven-dry biomass (kg) equations for hybrid poplar and white spruce. The four hybrid poplar clones were combined for a single equation. Component biomass equations were fit with nonlinear seemingly-unrelated regression to restrict the sum of component biomass to total aboveground biomass. Mean-square error (MSE) and $R^2$ are shown to demonstrate the fit of the models to the observed data.

| Species | Component | $\beta_0$ | | | $\beta_1$ | | | Fit Statistics | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | Est. | SE | p-value | Est. | SE | p-value | MSE | $R^2$ |
| Hybrid poplar | Foliage | 0.034 | 0.006 | <0.001 | 1.829 | 0.077 | <0.001 | 0.026 | 0.975 |
| | Branch | 0.003 | 0.002 | 0.118 | 3.272 | 0.241 | <0.001 | 0.642 | 0.941 |
| | Bole | 0.112 | 0.038 | 0.009 | 2.112 | 0.141 | <0.001 | 2.682 | 0.944 |
| | Total | | | | | | | 5.415 | 0.960 |
| White spruce | Foliage | 0.299 | 0.090 | 0.010 | 1.346 | 0.209 | 0.001 | 0.133 | 0.733 |
| | Branch | 0.211 | 0.060 | 0.008 | 1.289 | 0.202 | 0.001 | 0.046 | 0.801 |
| | Bole | 0.163 | 0.031 | 0.001 | 1.596 | 0.128 | <0.001 | 0.022 | 0.940 |
| | Total | | | | | | | 0.612 | 0.847 |

For DBH < 4 cm, white spruce, gray birch, paper birch, and red maple were respectively the four species with the greatest proportion of total aboveground biomass in foliage; while gray birch and white spruce had the greatest proportion of biomass in branch material; and bigtooth aspen, trembling aspen, hybrid poplar, and red maple had the greatest proportion of biomass in the bole (Figure 1.2). Across the range of DBH sampled, the proportion of foliage biomass increased for the aspen species, but decreased for all the other species. Conversely, the proportion of bole biomass decreased with greater DBH for the aspen species and hybrid poplar but increased for the other species.
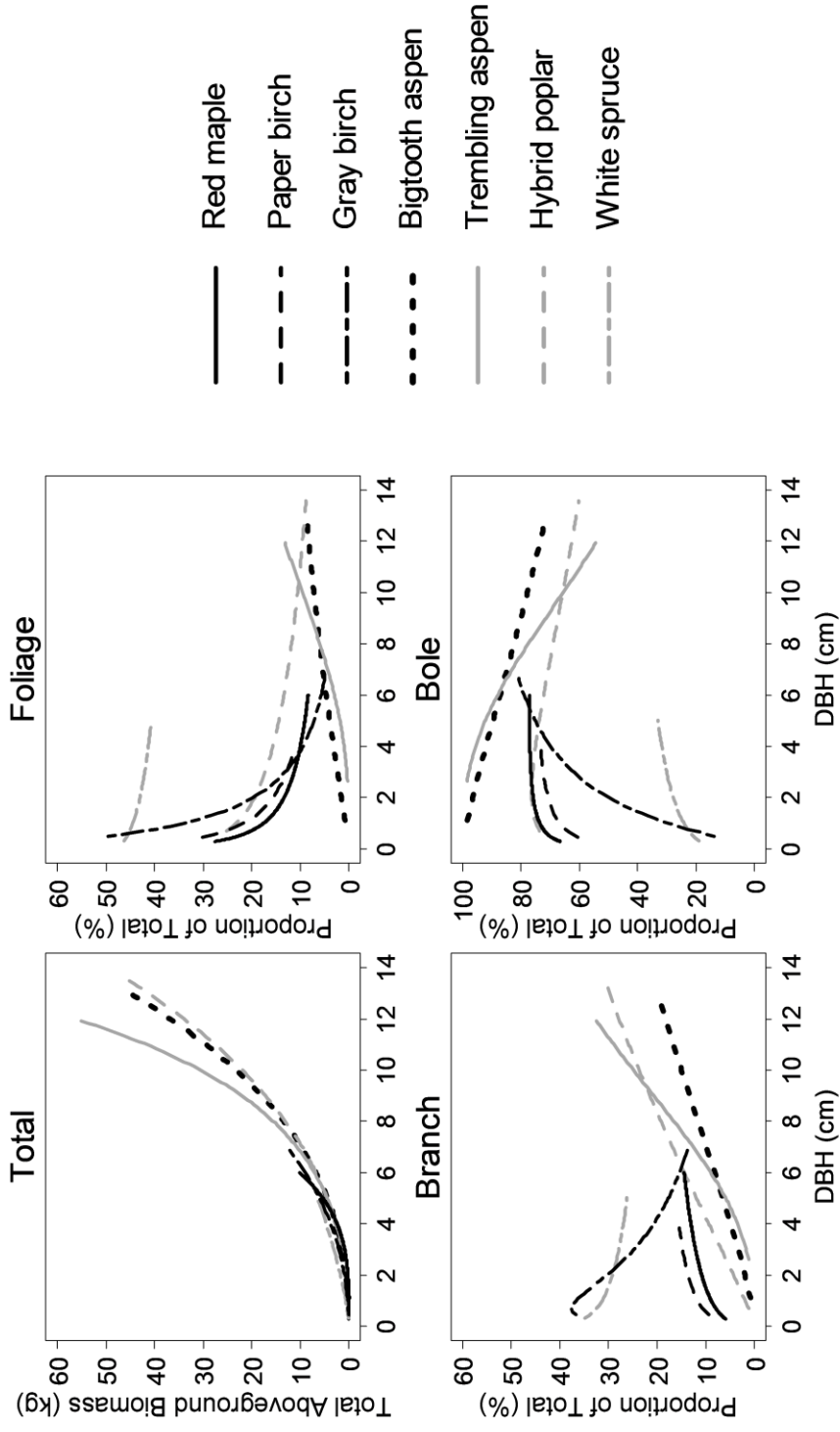
Figure 1.2. Total aboveground biomass (kg) and the proportion of total biomass (%) by component (foliage, branch, and bole) predicted from the additive equations for red maple, paper birch, gray birch, bigtooth aspen, trembling aspen, hybrid poplar, and white spruce.

### 1.4.3. Verification of Total Aboveground Biomass Equations

Among the different equations verified for the naturally regenerated species, the Jenkins and Young equations overestimated total aboveground biomass of red maple, paper birch, and gray birch, while the TMK equations underestimated biomass for these three species (Figure 1.3). For red maple, RMSE and ABIAS of the Young equation were 44% and 77% lower than the TMK equation (Table 1.6). The Young and Jenkins equations produced similar total aboveground biomass estimates for both aspen species, overestimating bigtooth aspen total aboveground biomass by 12.3% and 13.3%, respectively, and underestimated trembling aspen biomass by 11.3% and 8.0%, respectively (Table 1.6). The RMSE and ABIAS of the TMK bigtooth equation were 0.98 kg and 0.60 kg, respectively, while the RMSE and ABIAS of the Jenkins equations were 2.15 kg and 1.39 kg, respectively. The null hypothesis of the equivalence test was not rejected for the TMK equations for red maple, paper birch, gray birch, and trembling aspen, while the null hypothesis of the Young equations was only not rejected for trembling aspen.

Figure 1.3. Total aboveground oven-dry biomass (kg) versus DBH (cm) for the five naturally regenerated hardwood species. Observed data are shown as solid circles, while each of the four lines represents a different biomass equation. The equations are: Additive – this investigation, Young (Young et al. 1980), Jenkins (Jenkins et al. 2003) and Ter-Mikaelian (Ter-Mikaelian and Korzukhin 1997). Note the difference in the X- and Y-axis values.

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Table 1.6. Root mean square error (RMSE), mean bias (MBIAS), absolute bias (ABIAS) and equivalence test results for natural hardwood total aboveground oven-dry biomass (foliage, branch, bole, and stump) for the four compared models. Data used to verify the Young equations excluded the 15 cm stump weight for trees >2.5 cm DBH. The number of observations (n), observed and predicted means, predicted mean relative to observed (PRO), minimum detectable negligible difference (MDND), expressed as a percent and in absolute values, and the result of the equivalence test are shown. The Additive models were developed from the field data, while the other equations were: Young -Young et al. (1980), Jenkins - Jenkins et al. (2003), and TMK - Ter-Mikaelian and Korzukhin (1997).

| Species | n | RMSE (kg) | MBIAS (kg) | ABIAS (kg) | Obs. mean (kg) | Pred. mean (kg) | PRO (%) | MDND (%) | MDND (kg) | Null |
|---|---|---|---|---|---|---|---|---|---|---|
| **Red maple** | | | | | | | | | | |
| Additive | 12 | 0.36 | -0.02 | 0.24 | 2.01 | 2.06 | 2.73 | 14.48 | 0.29 | reject |
| Young | 12 | 0.48 | -0.02 | 0.32 | 1.92 | 1.94 | 1.02 | 17.07 | 0.33 | reject |
| Jenkins | 12 | 0.59 | -0.11 | 0.35 | 2.01 | 2.11 | 5.31 | 24.02 | 0.48 | reject |
| TMK | 12 | 0.86 | 0.56 | 0.56 | 2.01 | 1.45 | -27.84 | 7.65 | 0.15 | not reject |
| **Paper birch** | | | | | | | | | | |
| Additive | 13 | 0.08 | 0.00 | 0.10 | 0.65 | 0.65 | -0.03 | 7.57 | 0.05 | reject |
| Young | 13 | 0.32 | -0.03 | 0.23 | 0.63 | 0.66 | 4.86 | 35.78 | 0.23 | reject |
| Jenkins | 13 | 0.20 | -0.05 | 0.10 | 0.65 | 0.70 | 7.73 | 26.16 | 0.17 | reject |
| TMK | 13 | 0.26 | 0.17 | 0.17 | 0.65 | 0.48 | -26.57 | 8.85 | 0.06 | not reject |
| **Gray birch** | | | | | | | | | | |
| Additive | 15 | 0.18 | -0.04 | 0.14 | 1.60 | 1.64 | 2.81 | 8.99 | 0.14 | reject |
| Young | 15 | 0.65 | -0.28 | 0.36 | 1.53 | 1.82 | 18.35 | 39.44 | 0.61 | reject |
| Jenkins | 15 | 0.61 | -0.09 | 0.25 | 1.60 | 1.69 | 5.63 | 26.50 | 0.42 | reject |
| TMK | 15 | 0.85 | 0.44 | 0.44 | 1.60 | 1.16 | -27.44 | 2.57 | 0.04 | not reject |
| **Bigtooth aspen** | | | | | | | | | | |
| Additive | 17 | 0.93 | 0.09 | 0.59 | 9.39 | 9.30 | -0.96 | 4.12 | 0.39 | reject |
| Young | 17 | 2.53 | -1.09 | 1.37 | 8.92 | 10.02 | 12.26 | 25.35 | 2.26 | reject |
| Jenkins | 17 | 2.15 | -1.25 | 1.39 | 9.39 | 10.64 | 13.30 | 22.78 | 2.14 | reject |
| TMK | 17 | 0.98 | -0.06 | 0.60 | 9.39 | 9.45 | 0.64 | 6.01 | 0.56 | reject |
| **Trembling aspen** | | | | | | | | | | |
| Additive | 15 | 1.17 | 0.12 | 0.70 | 11.12 | 11.00 | -1.09 | 4.73 | 0.53 | reject |
| Young | 15 | 3.61 | 1.20 | 1.49 | 10.65 | 9.45 | -11.26 | 6.51 | 0.69 | not reject |
| Jenkins | 15 | 4.01 | 0.89 | 1.63 | 11.12 | 10.23 | -7.99 | 11.58 | 1.29 | reject |
| TMK | 15 | 5.40 | 2.03 | 2.26 | 11.12 | 9.10 | -18.22 | 6.75 | 0.75 | not reject |

The Young and Jenkins aspen equations produced similar total aboveground biomass estimates for hybrid poplar (Figure 1.4), overestimating observed biomass by 10.6% and 11.5%, respectively (Table 1.7). The null hypothesis of the equivalence test null hypothesis was not rejected for the Netzer equation where biomass was underestimated by 9.4%. White spruce total aboveground biomass was underestimated by 52.4%, 12.8%, and 2.1% by the Jenkins, Additive, and Young equations, and overestimated by 15.0% by the Pitt equation (Table 1.7). The null hypothesis for the white spruce equivalence test was not rejected for the Additive and Jenkins equations.
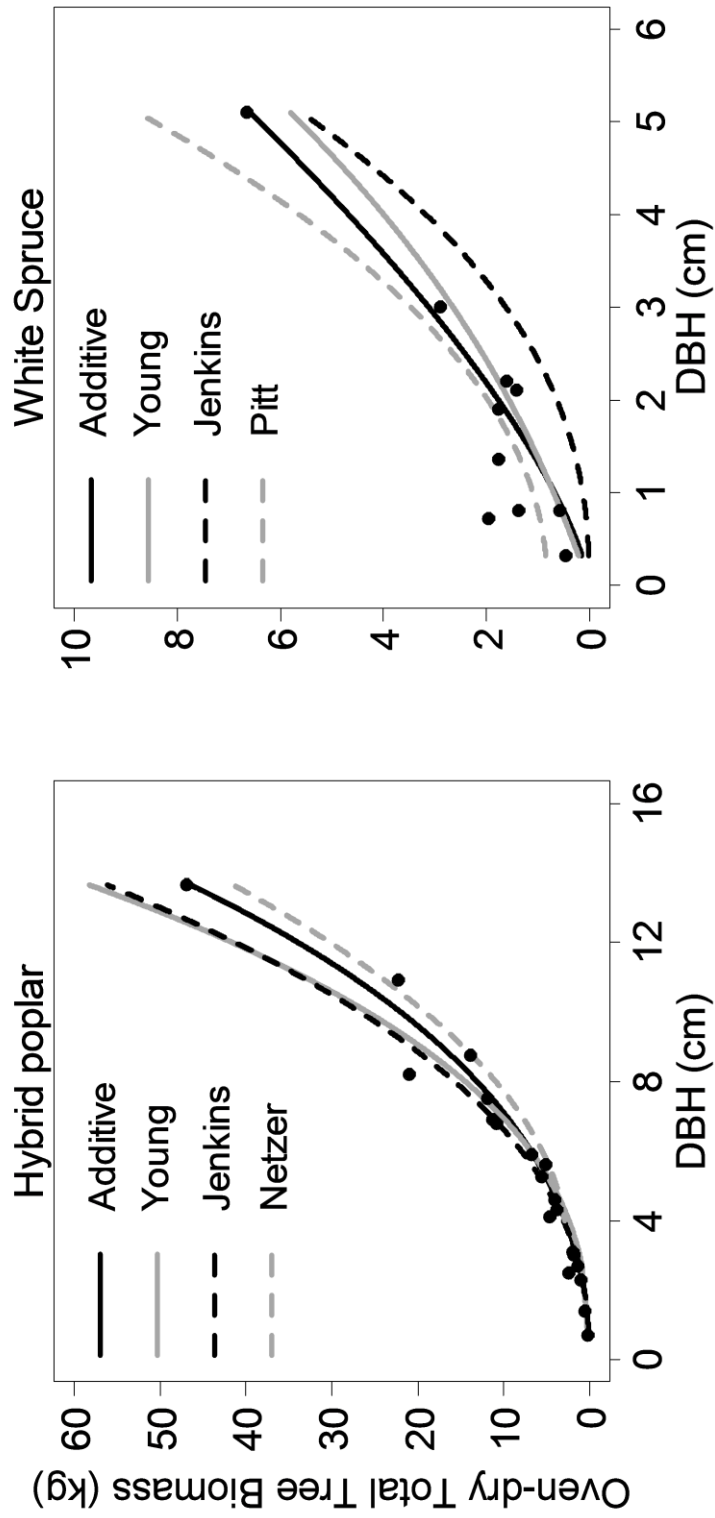
Figure 1.4. Total aboveground oven-dry biomass (kg) versus DBH (cm) for hybrid poplar and white spruce. The observed data are shown as solid circles, while each of the four lines represents a different biomass equation. The equations are: Additive – this investigation, Young (Young et al. 1980), Jenkins (Jenkins et al. 2003), Netzer (Netzer et al. 2002), and Pitt (Pitt and Bell 2005). Note the difference in the X- and Y-axis values.

Table 1.7. Root mean square error (RMSE), mean bias (MBIAS), absolute bias (ABIAS) and equivalence test results for hybrid poplar and white spruce total aboveground oven-dry biomass (kg). The number of observations (n), observed and predicted means, predicted mean relative to observed (PRO), minimum detectable negligible difference (MDND) expressed as a percent and in absolute values, and the result of the equivalence test are shown. The Additive models were developed from the field data, while the other equations were: Young (Young et al. 1980), Jenkins (Jenkins et al. 2003), Netzer (Netzer et al. 2002), and Pitt (Pitt and Bell 2005).

| Species | n | RMSE (kg) | MBIAS (kg) | ABIAS (kg) | Obs. mean (kg) | Pred. mean (kg) | PRO (%) | MDND (%) | MDND (kg) | Null |
|---|---|---|---|---|---|---|---|---|---|---|
| **Hybrid poplar** | | | | | | | | | | |
| Additive | 20 | 1.35 | -0.17 | 0.97 | 8.87 | 9.04 | 1.93 | 9.04 | 0.80 | reject |
| Young | 20 | 4.31 | -0.90 | 2.26 | 8.45 | 9.35 | 10.64 | 34.05 | 2.88 | reject |
| Jenkins | 20 | 3.67 | -1.01 | 1.94 | 8.87 | 9.88 | 11.45 | 30.09 | 2.67 | reject |
| Netzer | 20 | 3.25 | 0.84 | 2.29 | 8.87 | 8.03 | -9.44 | 7.17 | 0.64 | not reject |
| **White spruce** | | | | | | | | | | |
| Additive | 10 | 0.69 | 0.26 | 0.49 | 2.05 | 1.79 | -12.75 | 9.78 | 0.20 | not reject |
| Young | 10 | 0.94 | 0.04 | 0.75 | 2.01 | 1.96 | -2.10 | 31.93 | 0.64 | reject |
| Jenkins | 10 | 1.22 | 1.07 | 1.07 | 2.05 | 0.98 | -52.37 | 35.94 | 0.74 | not reject |
| Pitt | 10 | 0.90 | -0.31 | 0.67 | 2.05 | 2.36 | 15.04 | 45.07 | 0.92 | reject |

## 1.4.4. Aboveground Woody Biomass Verification

Paper birch and gray birch were combined for verification of the woody biomass equations because of the small sample size for both species within the valid DBH range of the FAS equations ( 2.5 cm and 12.4 cm DBH), and since woody biomass was estimated with the same Jenkins equation and FAS adjustment factor. The FAS equations substantially underestimated aboveground woody biomass relative to the observed data for all four naturally regenerated hardwood species (Figure 1.5), from 36.6% for trembling aspen to 19.0% for the birch species (Table 1.8). Similarly, the equivalence test of the FAS equation was not rejected for any of the species. Comparatively, the Jenkins

equations overestimated woody biomass by 8.4%, 11.3%, and 17.0% for red maple, birch

species, and bigtooth aspen, respectively, and underestimated trembling aspen woody

biomass by 3.4%. The Jenkins equation equivalence test was rejected for all species.
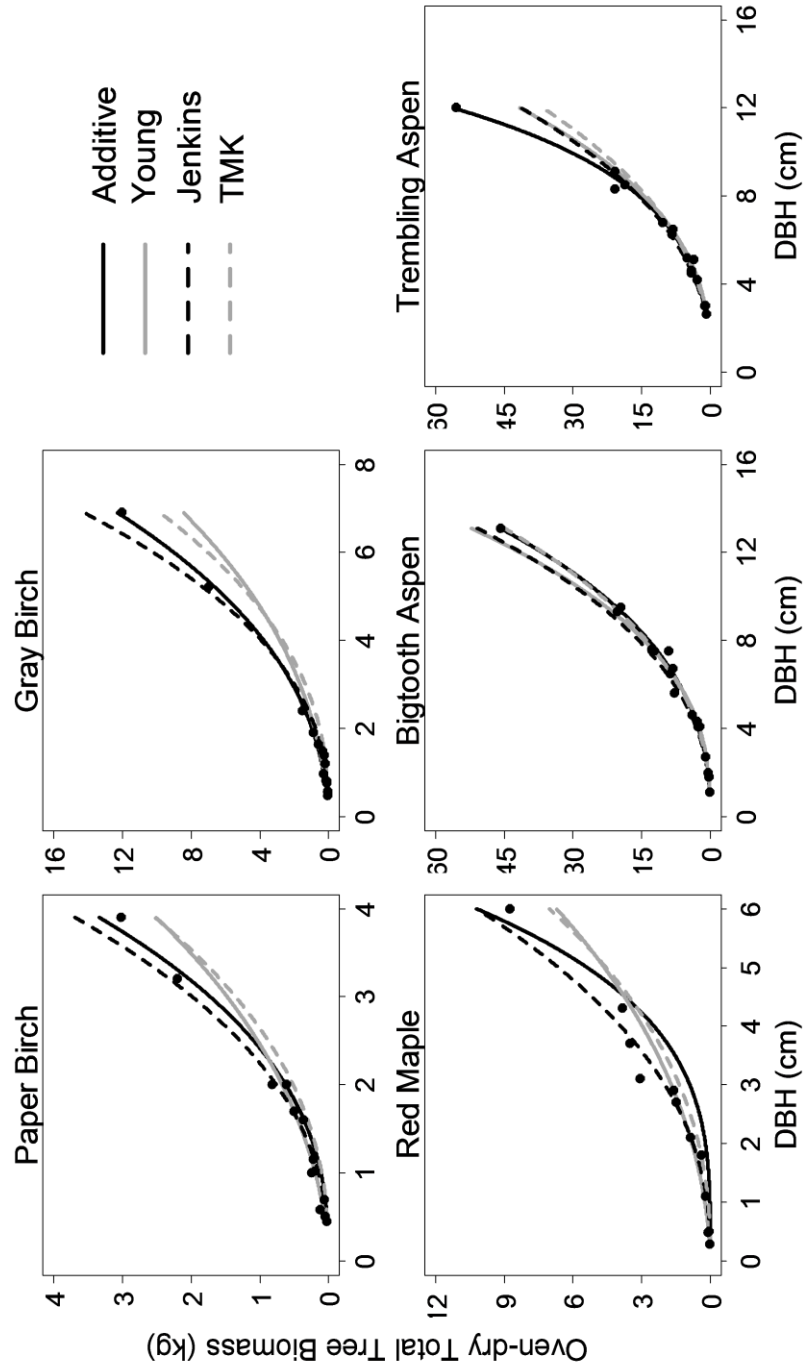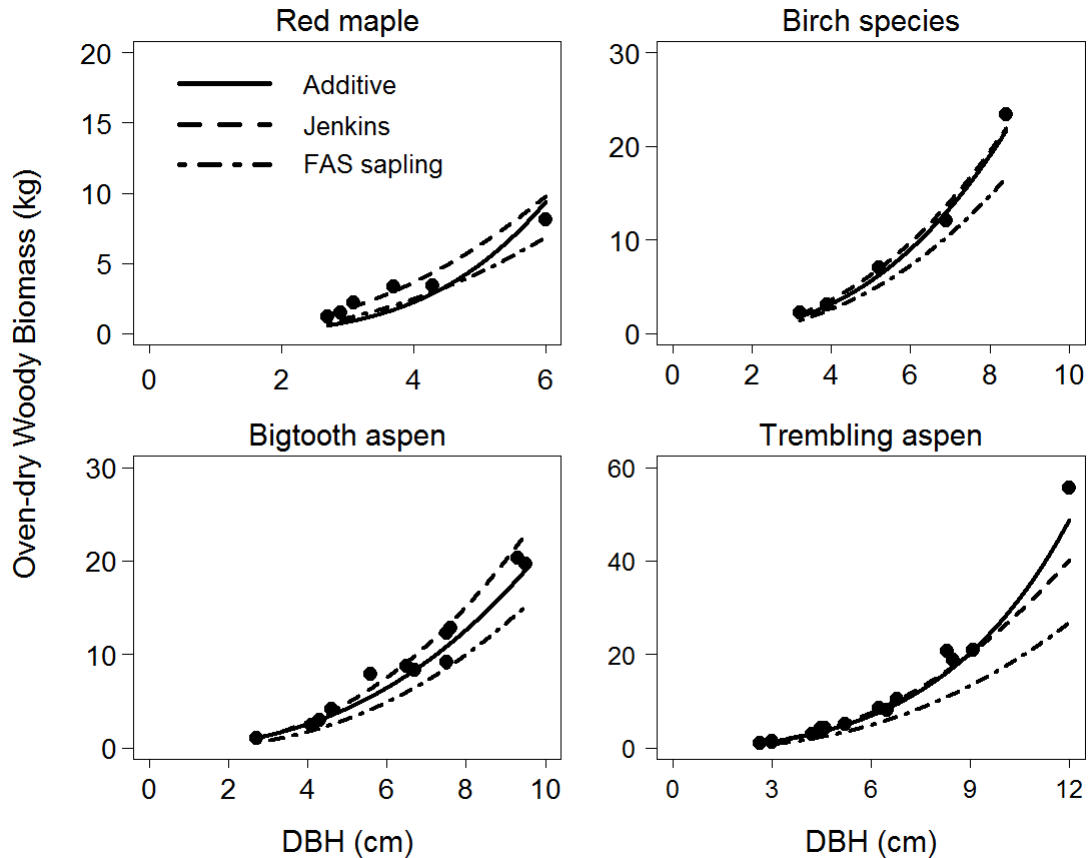


Figure 1.5. Woody aboveground oven-dry biomass (kg) versus DBH (cm) for the five naturally regenerated hardwood species (paper birch and gray birch combined). The observed data are shown as solid circles, while the three lines represent predictions of the different equations. The equations were: Additive – this investigation, Jenkins (Jenkins et al. 2003) and FIA aboveground sapling (Heath et al. 2009). Note the difference in the X- and Y-axis values.

Table 1.8. Root mean square error (RMSE), mean bias (MBIAS), absolute bias (ABIAS) and equivalence test results for natural hardwood oven-dry woody biomass (branch, bole, and stump) equations. The equations were: Additive – this investigation, Jenkins – Jenkins et al. (Jenkins et al. 2003), and FIA aboveground sapling - FAS (Heath et al. 2009). The number of observations (n), observed and predicted means, predicted mean relative to observed (PRO), minimum detectable negligible difference (MDND) expressed as a percent and in absolute values, and the result of the equivalence test are shown. Paper birch and gray birch were combined and referred as birch species.

| Species | n | RMSE (kg) | MBIAS (kg) | ABIAS (kg) | Obs. mean (kg) | Pred. mean (kg) | PRO (%) | MDND (%) | MDND (kg) | Null |
|---|---|---|---|---|---|---|---|---|---|---|
| **Red maple** | | | | | | | | | | |
| Additive | 6 | 0.362 | 0.012 | 0.289 | 3.28 | 3.27 | -0.38 | 12.12 | 0.40 | reject |
| Jenkins | 6 | 0.876 | -0.371 | 0.575 | 3.28 | 3.65 | 11.31 | 38.11 | 1.25 | reject |
| FAS | 6 | 0.997 | 0.825 | 0.825 | 3.28 | 2.46 | -25.13 | 10.63 | 0.35 | not reject |
| **Birch species** | | | | | | | | | | |
| Additive | 5 | 3.010 | 1.242 | 1.336 | 8.85 | 7.61 | -14.03 | 28.86 | 2.55 | reject |
| Jenkins | 5 | 1.162 | -0.743 | 0.743 | 8.85 | 9.59 | 8.39 | 21.47 | 1.90 | reject |
| FAS | 5 | 2.686 | 1.681 | 1.681 | 8.85 | 7.17 | -18.99 | 11.88 | 1.05 | not reject |
| **Bigtooth aspen** | | | | | | | | | | |
| Additive | 13 | 0.947 | 0.070 | 0.742 | 8.12 | 8.05 | -0.86 | 6.23 | 0.51 | reject |
| Jenkins | 13 | 2.152 | -1.382 | 1.508 | 8.12 | 9.51 | 17.02 | 29.04 | 2.36 | reject |
| FAS | 13 | 2.427 | 1.889 | 1.889 | 8.12 | 6.23 | -23.26 | 12.57 | 1.02 | not reject |
| **Trembling aspen** | | | | | | | | | | |
| Additive | 15 | 1.097 | 0.045 | 0.655 | 10.18 | 10.13 | -0.44 | 5.57 | 0.57 | reject |
| Jenkins | 15 | 2.413 | 0.347 | 1.208 | 10.18 | 9.83 | -3.41 | 9.67 | 0.98 | reject |
| FAS | 15 | 6.711 | 3.722 | 3.722 | 10.18 | 6.45 | -36.57 | 6.45 | 0.66 | not reject |

## 1.5. Discussion

### 1.5.1. Additive Component Equations

A total of 21 component equations were fit as nonlinear mixed-effects models, where silvicultural treatment/hybrid poplar clone were included as random effects, but only 4 of the mixed-effects model were significantly improved compared to models without random effects. Overall, this suggests that silvicultural treatment/clone were not important factors to account for in the additive component biomass equations and DBH alone was sufficient to account for their influence. The juvenile age of the trees is one likely reason why the majority of the mixed-effects models did not have better fits. For instance, the trees may not have developed for long enough to differentiate within the stands. Other biomass studies have also found that including treatment characteristics, such as density, basal area, and pruning effects did not increase the fit of aboveground biomass models (Antonio et al. 2007; Bond-Lamberty et al. 2002; Forrester et al. 2012; Pitt and Bell 2005; Zhang et al. 2004). Comparatively, treatment effects may be significant in some biomass models (Reed and Tomé 1998). Although silvicultural treatments may influence aboveground biomass partitioning, accounting for treatment effects may not substantially increase the amount of variation explained by the model due to the strong allometric relationships between tree dimensions and biomass components (Niklas 1994). This was demonstrated by the additive biomass models in this investigation with DBH as the sole predictor since $R^2$ values were generally greater than 0.90 except for red maple foliage and branch equations, the paper birch branch equation, and the gray birch foliage equation.

The additive aboveground component biomass equations (foliage, branch, and bole) were fit using NSUR, which restricted the sum of the components to total biomass. Additivity of component biomass estimates is often desirable since it is logical to assume the sum of component biomass estimates equal the predicted total biomass and to account for the inherent correlation among components on the same tree (Kozak 1970). Often, when component biomass equations are not fit as a system, there is disagreement between the total biomass estimates from summing component predictions and predictions from a total biomass equation (Bi et al. 2004). For instance, when sapling (2.5 cm – 12.4 cm DBH) total aboveground biomass was estimated using the Young equations for the naturally regenerated hardwood species in this investigation, estimates from the total aboveground biomass equation were between 3.2% and 10.1% greater than estimates obtained by summing component biomass. Fitting additive component biomass equations is becoming more common due to the ease of fitting the equations with available statistical software and the recognition of the greater statistical efficiency (Parresol 2001). The technique has been used to fit additive biomass equations in Canada (Lambert et al. 2005), Portugal (Antonio et al. 2007), and the southern hemisphere (Bi et al. 2010; Bi et al. 2004).

Even though other covariates and model forms were investigated, a two-parameter power function was found to provide a good fit to the observed exponential relationship between DBH and component biomass for all of the species. The power function is a common form for biomass equations (Crow and Schlaegel 1988; Ketterings et al. 2001) and the parameters have biological interpretation, where the scaling parameter ($\beta_1$) is the ratio of the relative growth rate of component biomass to the relative growth rate of DBH (Niklas

2004). Sometimes, height is included as a covariate in biomass models when equations are fit to trees from multiple sites (Lambert et al. 2005), as height growth tends to be more sensitive to site conditions than diameter. It is likely that including height in the biomass equations did not substantially improve model fit in this investigation because all of the trees were sampled from the same site.

Component biomass prediction are often required for investigations of ecosystem productivity (Waring and Running 1998) and financial analyses requiring estimates of merchantable biomass. Our results showed that the additive equations adequately fit the observed biomass component data. Agreement between the predicted and observed values was verified using a MDND equivalence test, and the null hypothesis of dissimilarity was rejected for all species except planted white spruce. The additive equations only underestimated trembling aspen mean total aboveground biomass by 1.1% and overestimated gray birch biomass by 2.8%. Similarly, the additive equations provided a good fit to the hybrid poplar data, as the equation only slightly overestimated biomass by 1.9%. In contrast, the additive equation underestimated white spruce total aboveground biomass by 12.7%. The underestimation was likely due to the lack of relationship between DBH and biomass of young spruce trees (Pitt and Bell 2005), since the trees were young and likely were at a height of DBH for only a short time. Although the equations were fit to trees from a single site, the method of forcing additivity of component biomass equations is novel in northeastern North America. In order to refine predictions and investigate differences among sites, more field data are needed that encompass the diversity of tree species and sizes in the region.

Although total aboveground biomass at a given diameter may be similar among species, partitioning of the various aboveground components differed. For instance, at the median DBH of 3 cm across all species, planted white spruce had the greatest proportion of biomass partitioned to foliage (42%), followed by hybrid poplar (17%), gray birch (13%), paper birch (13%), red maple (11%), bigtooth aspen (2%), and trembling aspen (0.5%). A similar pattern was found for branch biomass indicating the proportion of crown biomass (foliage + branch) tended to be lower for the aspen species than red maple and the birch species. In contrast, at the median DBH of 3 cm trembling aspen had the greatest proportion of biomass partitioned to the bole (98%), followed by bigtooth aspen (94%), red maple (77%), hybrid poplar (76%), paper birch (72%), gray birch (62%), and white spruce (30%). It was expected that the majority of biomass of shade intolerant aspen species was partitioned to the bole due to fast early growth rates and dominance in the overstory (Laidly 1990; Perala 1990), and greater partitioning to crown biomass for mid-tolerant red maple and white spruce that commonly occupy mid- and understories in natural stands where there is often high competition for light. Therefore, greater crown biomass may facilitate increased light interception in low light conditions (Niinemets 2010). Interestingly, the birch species and hybrid poplar had a greater proportion of crown biomass than the aspen species, even though they are also considered shade intolerant.

## 1.5.2. Verification of Total Aboveground Biomass Equations

Although the Jenkins, Young, and TMK equations were not fit with techniques that force additivity of component equations, the Jenkins and Young total aboveground biomass equations both had good agreement with the observed data of the naturally regenerated species. It was hypothesized that of all the compared equations, the Young equations would have the best fit to the data since they were fit with data collected in Maine. The results showed that the Jenkins equation produced similar or better estimates than the Young equations as RMSE was lower for paper birch, gray birch, and bigtooth aspen. Even though the equivalence tests provided evidence whether the predicted values were similar to the observed values, the test has some limitations. For instance, due to low sample sizes and the skewness of the data towards small diameter saplings, the standard deviation between the observed and predicted values were often large. The MDND statistic requires an estimate of the standard deviation, and if the value is large, the MDND value can also be large, resulting in a wide equivalence region to reject the null hypothesis. With greater sample sizes, the standard deviation should be lower, providing a more conservative estimate of the MDND.

The equivalence test null hypothesis of the TMK equations was not rejected for all species except bigtooth aspen, suggesting the predicted values were not within an acceptable range to consider them similar to the observed values. In particular, the TMK equations underestimated total aboveground biomass by more than 25% for red maple, paper birch, and gray birch. Data used to fit the equations in TMK for these species were collected from Nova Scotia and New Brunswick, Canada, and included trees with DBH <1 cm (Ker 1980, 1984). The poor fit of these models were unexpected because of the

close geographic proximity, number of observations (44, 196, and 197 for gray birch, paper birch, and trembling aspen, respectively) and similar DBH ranges to the trees in the current investigation. It is possible that the number of saplings used to fit the TMK equations were small relative to the total sample size.

The Jenkins equations were developed to encompass all tree species across the United States and are currently part of the CRM methods used by the FIA program to estimate woody biomass on all forestlands, yet the equations were fit using generalized regression of pseudo-data (Pastor et al. 1984) and have not been well verified with actual field data. In this investigation, null hypotheses of the equivalence tests were rejected for the Jenkins total aboveground biomass predictions for all naturally regenerated species and hybrid poplar (using the aspen/birch equation). It was hypothesized that the Jenkins equations would provide poor estimates of biomass in this investigation because the equations were only developed for trees $\geq 2.5$ cm DBH, while we extrapolated predictions down to 0.3 cm DBH. Extrapolation of estimates beyond the range of the data used to fit the models or across sites is typically discouraged since erroneous results can occur (Crow and Schlaegel 1988). In this investigation, testing the lower extremes of the Jenkins equations was important to assess their accuracy in estimating biomass of trees < 2.5 cm DBH since a substantial proportion of stands in Maine are dominated by small trees (McWilliams et al. 2005). Although further validation of the Jenkins equations is warranted across a wider range of tree size and geographic location, the results from this investigation suggest the Jenkins equations provided adequate estimates of total aboveground biomass of the species investigated at this particular site.

Supplementing commercial forest production with planted stock to increase growth rates in northeastern North America has been proposed to accommodate increasing wood fiber demands (Wagner et al. 2003). Planting tree species, such as hybrid poplar and white spruce, to enrich naturally regenerated stands is not well studied in the region and without verification of biomass models it is difficult to predict potential gains in productivity. We compared the fit of the Jenkins, Young, Netzer, and additive equations to 7-year-old plantation hybrid poplar clones and the results showed that predictions of total aboveground biomass were similar to the observed values for all equations except the Netzer equation, with the additive equation outperforming the Jenkins and Young equations. Even though the Netzer equation was developed for hybrid poplar the majority of the trees used to develop the equation were *P. deltoides* × *P. nigra* clones, and our sample included a *P. nigra* × *P. maximowiczii* clone. This is a likely reason for the substantial underestimation by the equation (9.4%). Additionally, the hybrid poplar used to fit the Netzer equation were grown on better quality sites (post-agriculture) than the site in our investigation where rocky, poorly-drained conditions were prevalent (Nelson et al. 2012), which may have influenced the prediction ability of the equation. However, compared to other equations investigated, component biomass cannot be predicted using the Netzer equation, a key feature for hybrid poplar species that are grown primarily for wood fiber.

Total aboveground biomass estimates are often expressed at a stand-level as this is the typical management unit in most forestry applications and financial analyses. Natural stands often have diverse species composition and stand structure, which may cause alternate biomass equations to produce different stand-level biomass estimates. One

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likely reason is that the precision of different equations developed in an investigation may vary by species and across the range of sampled tree sizes. To demonstrate stand-level predictions of the different sets of equations in this investigation, total aboveground biomass was predicted for stands in the experiment where trees were destructively sampled. The stands were approaching self-thinning and dominated by the five naturally regenerated species that were fit with additive equations. Total aboveground biomass estimates from the equations were: Jenkins - $512.0 \pm 118.2$ Mg km$^{-2}$ (mean $\pm$ SD), Young - $470.6 \pm 110.4$ Mg km$^{-2}$, TMK - $437.7 \pm 100.1$ Mg km$^{-2}$, and the additive equations - $460.2 \pm 89.3$ Mg km$^{-2}$. Although mean stand-level biomass estimates were slightly different among the equations, the standard deviations indicated similar estimates. The TMK mean stand estimate was the lowest among equations, which is similar to the results of the model verification exercise where the equations substantially underestimated total aboveground biomass of red maple, birch sp., and trembling aspen.

### 1.5.3. Woody Aboveground Biomass Model Verification

Oven-dry aboveground woody biomass was predicted by the FAS, Jenkins, and additive equations for the five naturally regenerated hardwood species. The FAS equations reduced Jenkins woody biomass estimates for all species, resulting in the underestimation of mean biomass between 19.0% and 36.6% for the natural hardwood species. The FAS equations are used to ensure a smooth transition of sapling biomass estimates to CRM estimated biomass of trees $\geq 12.5$ cm in the FIA database (Heath et al. 2009). Similar to the Jenkins equations, the FAS equations lack verification with field data in northeastern North America. In stands dominated by saplings, such as 24% of the forested area in Maine, our results suggest aboveground woody biomass may be substantially

underestimated. The underestimation of sapling biomass with the FAS is likely a cause for the estimated 34% reduction in sapling biomass in the state of Maine when FIA switched from regional equations to the current methods, as shown by the change in biomass and density between 2003 and 2010 (McWilliams et al. 2005; USDA FIA Program 2012). Since nearly one-quarter of forestlands in Maine are dominated by saplings, the switch to the FAS equations has also influenced aboveground biomass predictions of all living trees in the state. For instance, aboveground biomass of all living trees > 2.5 cm DBH decreased by 15% between 2003 and 2010 (USDA FIA Program 2012), likely due to a combination of biomass removal, the change to the CRM for estimating biomass of tree >12.5 cm DBH, and the switch to the FAS equations for sapling biomass. The inability of the FAS equations to accurately estimate biomass of saplings may pose problems for producing landscape biomass estimates by the FIA program across the nation for stands dominated by trees < 12.5 cm DBH, and warrants further verification with field data.

## 1.6. Conclusion

We investigated the fit of various total (foliage, branches, bole) and woody (total − foliage) aboveground biomass equations to data collected from a controlled experiment in eastern Maine. The results suggested that the national Jenkins and regional Young equations predicted biomass within an acceptable range of the observed data, while the TMK and FAS equations provided poor fits to the data. Even though many of these equations can predict biomass of individual aboveground components, one major limitation is that they were not fit with statistical techniques that force additivity of the component predictions to predictions obtained with a total aboveground equation.

Therefore, we developed a new set of additive component equations for naturally

regenerated hardwood species and planted stock saplings in Maine. These additive

equations are simple in form and only require DBH as a predictor variable but provided a

good fit to the observed data. Additionally, biomass equations and aboveground biomass

partitioning of sapling-sized hardwood species have not received much attention in the

literature, including aspen and birch. There is increasing national interest in accurately

estimating forest biomass for carbon accounting and potential bioenergy purposes. The

uncertainties of landscape biomass estimation in Maine have been driven primarily by the

high proportion of sapling-sized stands in the region and the unknown performance of the

sapling biomass equations. We propose that the current FAS equations may be

inadequate for providing reliable sapling biomass estimates in Maine, and that new

techniques be developed, such as similar additive equations presented in this

investigation, using field data spanning various species and across multiple sites to

account for heterogeneous growing conditions.

# CHAPTER 2

# EFFECTS OF CONTRASTING GROWING CONDITIONS ON

# ABOVEGROUND NET PRIMARY PRODUCTIVITY,

# LIGHT-USE EFFICIENCY, AND FOLIAR

# $\delta^{13}$C COMPOSITION OF JUVENILE

# WHITE SPRUCE

## 2.1. Abstract

Aboveground net primary productivity (ANPP) of trees is influenced primarily by resource availability, resource capture, and conversion efficiency of captured resources into biomass. These tree-level mechanisms are underlain by physiological processes that influence responses to heterogeneous growing conditions. In this investigation, ANPP, light-use efficiency (LUE; ANPP/absorbed photosynthetically active radiation (APAR)), leaf area efficiency (LAE; ANPP/leaf area), and foliar stable carbon isotope composition ($\delta^{13}$C) of white spruce (*Picea glauca* (Moench) Voss) trees were compared between naturally-regenerated stands and plantations. ANPP was linearly correlated with APAR, where ANPP was 56.0% higher in natural stands than within plantations at the mean APAR. LUE was 80.0% greater, on average, in natural stands, but LUE differed between the smallest tree and largest tree by only 1.4%, and between the lowest level of an inter-tree competition index and the highest level of the competition index by only 5.4%. Comparatively, $\delta^{13}$C increased with tree size by 1.5‰, and declined by 1.7‰ with greater competition in the natural stands. $\delta^{13}$C was not correlated with ANPP, LUE or LAE, possibly due to photosynthate allocation to other sinks, including root growth, storage, and respiration. Overall, APAR had the strongest influence on ANPP, suggesting that

within natural stands, where crown closure is likely to occur sooner than within plantations, ANPP and LUE of white spruce trees will likely decline due to earlier differentiation in resource-use efficiency.

## 2.2. Introduction

Aboveground net primary productivity (ANPP) of trees is influenced primarily by resource availability, resource capture, and the conversion efficiency of captured resources into biomass (Binkley et al. 2004). In particular, ANPP is often linearly related to light interception (Jarvis and Leverenz 1983; Monteith 1977) since light is one of the key drivers of photosynthesis. Light interception by individual trees and the associated ANPP can vary among trees due to interspecific differences in crown form, leaf area distribution, and photosynthetic productivity (Ishii and Asano 2010; Niinemets 2010), but can also be influenced by stand composition and structure (Canham et al. 1994; Chen et al. 1996; Pacala et al. 1994). Many of the investigations that have examined the efficiency of light conversion into ANPP have focused on mature trees in plantations, where differentiation in resource-use efficiency often leads to divergence in growth among trees (Binkley et al. 2013a; Binkley et al. 2010; Campoe et al. 2013b). Comparatively, resource-use efficiency and the underlying physiological mechanisms influencing resource-use efficiency of juvenile trees in natural stands with diverse species composition have received less attention.

Resource availability for individual trees can be manipulated by controlling species composition and stand density, especially during the early stages of tree development (Finzi and Canham 2000). In addition, resource capture can be enhanced by increasing

availability of other limiting resources (Allen et al. 2005; Balster and Marshall 2000; Campoe et al. 2013a; Dalla-Tea and Jokela 1991). For instance, greater nitrogen (N) availability can increase leaf area production, carbon assimilation, and subsequently, light absorption (Campoe et al. 2013a; Lambers et al. 2008). Consequently, in naturally-regenerated stands one may expect that lower asymmetric and symmetric competition would increase absorbed photosynthetically active radiation (APAR) and ANPP of individual trees.

Even though ANPP is strongly related to light interception, it is often difficult to obtain accurate estimates of diurnal and seasonal light interception with field measurements. Therefore, leaf area often is used as a surrogate for light interception (Brunner 1998), since leaf area represents a tree's investment in light harvesting structures. Therefore, leaf area and APAR are strongly correlated (Binkley et al. 2002; Forrester et al. 2013; Gspaltl et al. 2013; Niinemets et al. 2001). Measures of leaf area, however, often do not account for photosynthetic efficiency based on self-shading, foliar display, or position within the canopy. Accounting for these factors can be particularly important in natural stands with complex species composition, stand structure, and heterogeneous light conditions.

Photosynthesis is a major driver of ANPP, but the amount of intercepted light is not the only factor influencing productivity. Numerous biochemical reactions occur within the foliage that convert carbon dioxide ($CO_2$) into carbohydrates for growth (Lambers et al. 2008). Therefore, various techniques have been developed to study photosynthetic productivity, including stable carbon isotope composition ($\delta^{13}C$) as a ratio of $^{13}C$ to $^{12}C$. $\delta^{13}C$ provides a time-integrated measure of carbon assimilation (A) to stomatal conductance ($g_s$) (Farquhar et al. 1982), and is strongly related to intrinsic water-use

efficiency (iWUE = A/$g_s$) (Livingston et al. 2002; Ripullone et al. 2004; Sun et al. 2006). Therefore, $\delta^{13}C$ can be used to investigate physiological responses to competition for both above- and below-ground resources. For instance, the response of $\delta^{13}C$ has been shown to be influenced by stem density (Bladon et al. 2007), mineral nutrition (Choi et al. 2005; Davis et al. 2004; Hobbie and Colpaert 2004; Walia et al. 2010) and soil moisture (Choi et al. 2005; Staples et al. 2001). When growing conditions favor the opening of stomata (i.e., reduced moisture stress), rapid uptake of atmospheric $CO_2$ often occurs, and the lighter isotope, $^{12}C$ is preferentially fixed (Farquhar et al. 1989). Comparatively, when $g_s$ is reduced, more $^{13}C$ is incorporated into photosynthate due to increased $CO_2$ diffusion resistance, thereby increasing $\delta^{13}C$ (Farquhar et al. 1989). Therefore, greater competition for resources during early stages of tree development can lead to reductions in net photosynthetic rates (Reynolds et al. 2000), potentially influencing the allocation of photosynthates to aboveground growth.

The mechanisms influencing tree responses to heterogeneous growing conditions are integrated across multiple scales including both the physiological processes that affect $CO_2$ conversion into carbohydrates and the effects of these mechanisms on tree-level efficiency of captured resource conversion into ANPP. These two factors, in particular, have not been jointly investigated to understand the mechanisms influencing the productivity of juvenile conifer trees. Therefore, the overall goal of this investigation was to examine ANPP, light-use efficiency (LUE = ANPP/APAR), leaf area efficiency (LAE = ANPP/leaf area), and foliar $\delta^{13}C$ of planted juvenile (7-8 years old) white spruce (*Picea glauca* (Moench) Voss) in relation to contrasting growing conditions (natural stands and plantations). The specific study objectives were to determine the: (1) relation between

APAR and leaf area, and ANPP, (2) relation between tree size and neighborhood

competition intensity, and LUE, LAE, $\delta^{13}$C, and ANPP, and (3) correlation between

foliar $\delta^{13}$C, and ANPP, LUE, and LAE.

## 2.3. Methods

### 2.3.1. Study Site

The study was conducted at a post-clearcut harvested site on the Penobscot Experimental

Forest (PEF) in east-central Maine (44° 50' 37" N, 68° 37' 39" W). The PEF is in the

Acadian forest region of North America, which is a transitional region between the

eastern hardwood forests to the south and boreal forests to the north, with species

composition similar to both (Braun 1950). Natural forest composition at the site is

dominated by trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus*

*grandidentata* Michx.), paper birch (*Betula papyifera* Marsh.), gray birch (*Betula*

*populifolia* Marshall), red maple (*Acer rubrum* L.), balsam fir (*Abies balsamifera* (L.)

Mill.), eastern hemlock (*Tsuga canadensis* L.), and red spruce (*Picea rubens* Sarg.)

(Nelson et al. 2013).

Climate at the PEF is classified as cool and humid. The 30-year (1951-1980) mean

annual temperature at Bangor, Maine (~16 km from the site) was 6.6 °C, with an average

low of -7.0 °C in February and average high of 20.0 °C in July. Precipitation averages

106 cm per year with 48% occurring between May and October. Annual snowfall

averages 239 cm, and the frost-free period in the region is between 140 and 160 days per

year. A weather station at the study site during the 2011 and 2012 growing seasons (May

to September) recorded a mean air temperature of 16.8 °C, mean soil temperature (10 cm

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mineral soil) of 16.8 °C, mean volumetric soil water content of 0.10 $m^3$ $m^{-3}$, and mean above-canopy, daytime photosynthetic active radiation (400-700 nm) of 640.3 μmol $m^{-2}$ $sec^{-1}$. Soils at the study site are Wisconsian till origin and range from loamy, mixed, active, acid, frigid, shallow, Aeric Endoquepts to coarse-loamy, isotic, frigid, Aquic Haplothods. The seasonal high water table averages 34 cm and large rock fragments are common in the upper soil layers across the site.

The 9.2 ha site was harvested in 1995 with 2.3 $m^2$ $ha^{-1}$ of residual basal area scattered across the site. The site regenerated to a mixture of shade intolerant hardwood species and shade tolerant conifer species. In 2004, a 3 x 3 +1 factorial experiment of management intensity and species composition, plus an untreated control, was replicated four times on the site. Treatments included thinning, thinning plus enrichment planting, and plantations, all across a compositional gradient ranging from pure hardwood to nearly pure conifer (Nelson et al. 2012; Nelson et al. 2013). The growing stock used for enrichment planting and plantations were 2+0 half-sib white spruce seedlings and cuttings of four different hybrid poplar (*Populus* species) clones. White spruce seedlings were provided by a J.D. Irving, LLC tree nursery in New Brunswick, Canada, with 65-$m^3$ rooting volume, mean height of 15.5 cm (range 7.5 – 28.0 cm), and mean ground line diameter of 2.6 mm (range 1.0 – 9.0 mm) at the time of planting.

**2.3.2. Study Design**

The current investigation focused on planted white spruce in 4 of the 10 treatments. The four treatments included: two white spruce enrichment treatments shifted to conifer (EC) and mixedwood (EM) composition, and two plantation treatments planted either in pure

white spruce (PC) or 67% white spruce and 33% hybrid poplar crop trees mixtures (PM).

All trees were planted at a 2 m x 2 m spacing. In the EC and EM treatments, naturally

regenerated trees were thinned to a 2 m x 2 m crop-tree spacing using herbicides and

brush saws, and 50% of the crop-trees were planted with white spruce (EC) or white

spruce and hybrid poplar (EM). In the PM treatment, hybrid poplar cuttings were planted

in clumps to minimize asymmetric competition and the probability of mortality of the

white spruce seedlings. Basal area in 2011 among the treatments were $0.78 \pm 0.44$ m$^2$ ha$^{-1}$, $3.40 \pm 1.28$ m$^2$ ha$^{-1}$, $6.97 \pm 2.73$ m$^2$ ha$^{-1}$, $10.12 \pm 4.54$ m$^2$ ha$^{-1}$ in the PC, PM, EC, and

EM treatment, respectively (Table 2.1). Seasonal high water table depth varied widely

between treatments and replicate plots (Table 2.1).

Table 2.1. Mean (standard deviation) and range of stand-level characteristics and seasonal high water table (SHWT) depth in the four different treatments (EC - conifer enrichment, EM - mixedwood enrichment, PC - conifer plantation, PM - mixedwood plantation). Stand variables include: basal area, proportion of hardwood (Hardwood Comp) and conifer (Conifer Comp) density, distant-weighted competition (DWC), and seasonally high water table (SHWT).

| Treatment | Basal area $(m^2 ha^{-1})$ | Hardwood Comp (%) | Conifer Comp (%) | DWC $(cm\ cm^{-1}\ m^{-1})$ | SHWT (cm) |
|---|---|---|---|---|---|
| EC | | | | | |
| mean (sd) | 6.97 (2.73) | 37.7 (24.0) | 62.3 (24.0) | 22.8 (13.0) | 37 (13) |
| range | 5.17 - 11.59 | 12.7 - 69.8 | 30.2 - 87.3 | 9.8 - 57.9 | 19 - 53 |
| EM | | | | | |
| mean (sd) | 10.12 (4.54) | 55.9 (18.3) | 44.1 (18.3) | 24.6 (16.1) | 26 (10) |
| range | 5.09 - 15.79 | 36.2 - 75.0 | 25.0 - 63.8 | 9.5 - 64.2 | 8 - 35 |
| PC | | | | | |
| mean (sd) | 0.78 (0.44) | 0.0 (0.0) | 100.0 (0.0) | 2.3 (1.2) | 24 (19) |
| range | 0.23 - 1.29 | 0.0 - 0.0 | 100.0-100.0 | 0.4 - 3.8 | 10 - 58 |
| PM | | | | | |
| mean (sd) | 3.40 (1.28) | 25.8 (6.4) | 74.2 (6.4) | 7.1 (7.8) | 27 (14) |
| range | 1.80 - 4.74 | 19.1 - 32.9 | 67.1 - 81.0 | 1.7 - 29.9 | 24 - 60 |

In each treatment replicate (16 total), three planted white spruce trees were selected from three stratified height classes (height 1: <1.7 m, height 2: 1.8 - 4.2 m, and height 3: >4.2 m) to ensure adequate representation of tree size (48 trees total). The search cone method (Biging and Dobbertin 1992; Pretzsch 2009) with a 60° angle from the base of the crown was used to select competitor trees around each white spruce tree. This method ensured that both asymmetric and symmetric competition was accounted for. Competitors were limited to a horizontal distance of 6 m due to high stem densities in the EC and EM treatments.

## 2.3.3. Variables Measured

### 2.3.3.1. Tree Measurements

All white spruce and competitor trees were measured at the end of the growing season in September of 2011 (age 7) and 2012 (age 8). For each tree, diameter at breast height (DBH; cm), basal diameter (BD; cm), total height (HT; m), live crown length (CL; m), and crown radius (CR; m) in the four cardinal directions were measured. In addition, the spatial location of all trees was measured using a Haglof Postex stem mapping unit. Across the treatments, HT and BD of white spruce trees ranged from 60 - 460 cm, and 1.4 – 6.2 cm, respectively (Table 2.2).

Table 2.2. Tree attributes for the sampled white spruce in the four different treatments (EC - conifer enrichment, EM - mixedwood enrichment, PC - conifer plantation, PM - mixedwood plantation). Mean, standard deviation, and range of total height (HT), stem diameter 10 cm above the root collar (BD), total aboveground biomass (TAB), aboveground net primary productivity (ANPP), leaf area (LA), absorbed photosynthetically active radiation (APAR), and $\delta^{13}C$ are shown.

| Treatment | HT (cm) | BD (cm) | TAB (kg) | ANPP (kg year$^{-1}$) | LA (m$^2$) | APAR (MJ year$^{-1}$) | $\delta^{13}C$ (‰) |
|---|---|---|---|---|---|---|---|
| **EC** | | | | | | | |
| mean (sd) | 191 (73) | 3.7 (1.1) | 1.19 (0.72) | 0.25 (0.15) | 2.25 (1.29) | 198.5 (129.4) | -29.6 (0.8) |
| range | 75 - 330 | 1.9 - 5.3 | 0.19 - 2.55 | 0.03 - 0.50 | 0.44 - 4.60 | 30.8 - 470.4 | -30.5 - -27.6 |
| **EM** | | | | | | | |
| mean (sd) | 189 (80) | 3.5 (1.3) | 1.11 (0.75) | 0.23 (0.18) | 2.11 (1.35) | 192.1 (137.6) | -29.8 (1.0) |
| range | 60 - 360 | 1.4 - 5.3 | 0.09 - 2.63 | 0.02 - 0.47 | 0.20 - 4.60 | 16.1 - 540.8 | -31.6 - -28.2 |
| **PC** | | | | | | | |
| mean (sd) | 268 (93) | 4.9 (1.0) | 2.19 (1.04) | 0.33 (0.24) | 4.01 (1.71) | 516.2 (243.8) | -29.2 (0.7) |
| range | 130 - 460 | 3.0 - 6.2 | 0.71 - 4.11 | 0.05 - 0.86 | 1.52 - 6.89 | 155.1 - 973.3 | -30.5 - -28.1 |
| **PM** | | | | | | | |
| mean (sd) | 280 (92) | 4.9 (1.1) | 2.27 (1.01) | 0.35 (0.23) | 4.13 (1.69) | 505.3 (240.2) | -29.4 (0.8) |
| range | 90 - 420 | 2.2 - 6.1 | 0.26 - 3.74 | 0.04 - 0.87 | 0.59 - 6.39 | 51.7 - 885.3 | -31.2 - -28.4 |

### 2.3.3.2. Foliage Stable Carbon Isotope Composition

In September 2011 and 2012, current-year foliage was sampled from the vertical middle one-third of the live crown and on the south side of each white spruce tree. Samples were collected from 5 branches on each tree, washed with deionized water, dried at 65 °C for a minimum of 96 hours, and ground and homogenized with a Wiley mill to pass through a 40 mesh screen. Samples were prepared in triplicate for stable isotope analysis. Approximately 4 mg of material was sealed in a tin capsule and analyzed at the University of California, Davis Stable Isotope Facility. $\delta^{13}C$ was analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were combusted at 1000°C in a reactor of chromium oxide and silvered copper oxide. During analysis, samples were interspersed with reference samples of known isotopic composition, including nylon, bovine liver, USGS-41 glutamic acid, and peach leaves. In addition, blank tin capsules were interspersed among the samples to measure trace detection of $\delta^{13}C$. The standard deviation of replicate samples within trees ranged from 0.01‰ to 0.17‰.

### 2.3.4. Analysis

### 2.3.4.1. Estimating ANPP and Leaf Area

Juvenile white spruce trees typically have slow growth rates (Cole et al. 2003; Nelson et al. 2013; Nienstaedt and Zasada 1990), and the foliage often comprises a substantial proportion of the total aboveground biomass (Claveau et al. 2005; Claveau et al. 2002). Therefore, ANPP was defined as the annual change in total aboveground oven-dry biomass (stem, stump, branches, and foliage). Component (foliage, branch, and

stem+stump) oven-dry biomass was estimated from measured BD, HT, and CR using regression equations developed for juvenile white spruce trees (Pitt and Bell 2005). Total aboveground biomass was then estimated as the sum of these aboveground components. Woody growth fraction (WGF) was calculated as the proportion of ANPP partitioned to branches, stem, and stump. White spruce foliage biomass was converted to leaf area using the study-wide mean specific leaf area ($m^2$ $kg^{-1}$) estimated from white spruce trees at the site. Specific leaf area ranged from 3.4 $m^2$ $kg^{-1}$ to 5.4 $m^2$ $kg^{-1}$, with a mean of 4.2 $m^2$ $kg^{-1}$.

## 2.3.4.2. Modeled Light Absorption

Total growing season APAR of each white spruce tree was estimated for 2011 and 2012 using the MAESTRA model (Medlyn 2004; Wang and Jarvis 1990). The growing season was defined as the period when hardwood foliage had completed its annual expansion (May 15 to September 20), since there is a substantial hardwood component at the site (Nelson et al. 2013). Tree measurement data were used to specify the location and dimensions of each tree. Leaf area of red maple, paper birch, bigtooth aspen, trembling aspen, and hybrid poplar was estimated using equations developed from trees at the site (Nelson et al. *In review*). Leaf area of balsam fir, eastern white pine (*Pinus strobus* L.), and red spruce were estimated using the equations of Weiskittel et al. (2009), while leaf area of American beech (*Fagus grandifolia* Ehrh.) and northern red oak (*Quercus rubra* L.) were estimated by predicting foliage biomass using the equations in Jenkins et al. (2003), and converted to leaf area using specific leaf area estimates presented by Beaudet and Messier (1998) and Gower et al. (1993), respectively.

All conifer species were assumed to have cone crown shapes in MAESTRA. Paper birch, gray birch, and American beech were assumed to have half-ellipsoid crown shapes, while red maple, hybrid poplar, bigtooth aspen, trembling aspen, and northern red oak were assumed to have parabaloid crown shapes. MAESTRA estimates bivariate vertical and horizontal leaf area density (LAD; $m^2$ $m^{-3}$) using a beta distribution. The vertical LAD parameters for red maple, paper birch, gray birch, bigtooth aspen, trembling aspen, hybrid poplar, and white spruce were estimated using data from destructively sampled trees collected at the site (Nelson et al. *In review*), while the horizontal distribution of LAD was assumed uniform for these species. Beta parameters were not available for the other species in the investigation, so a uniform LAD distribution was assumed in both dimensions. Average leaf inclination angle was estimated for each species by measuring three to five randomly selected leaves per species using a clinometer. These leaf angle measurements were used to specify the average leaf angle by species in MAESTRA. In addition, a single leaf angle class was assumed for all species, and leaf angle was assumed to follow an ellipsoidal distribution.

Light that is intercepted by a leaf has three potential fates: transmittance, reflectance, and absorbance (Lambers et al. 2008). To account for light not absorbed by the foliage, leaf transmittance and reflectance were specified for three wavebands (PAR, near infra-red, and thermal) using the optical parameters for boreal conifer and hardwood species used in the National Center for Atmospheric Research Land Surface Model (Bonan 1996, 1998). Default MAESTRA values were used for all other physiological parameters since only APAR was of interest in this investigation. Within MAESTRA, the crown of each white spruce tree was separated into 6 vertical layers, and APAR was calculated for 12

grid points per layer at 1-hour intervals. These 72 hourly APAR estimates were then summed by tree over the specified growing season to obtain total APAR estimates.

Meteorological data were specified in MAESTRA as hourly means over the duration of the 2 simulation periods, including above-canopy PAR, aboveground temperature, relative humidity, mineral soil temperature (10 cm mineral soil), and volumetric soil water content (0-10 cm B-horizon). These data were obtained from a weather station at the study site. The default value of 0 was used for the distribution of diffuse radiation incident from the sky, while atmospheric carbon dioxide ($CO_2$) concentration was assumed constant over the growing season at 380 mmol mol$^{-1}$.

### 2.3.4.3. Distance-Weighted Competition

Distance-weighted competition (DWC) indices that incorporate tree size and location were used to quantify neighborhood competition around each white spruce tree. Multiple indices were investigated, including area potentially available, but this method was not suitable due to the small plot size and large edge effects. The distance-weighted, size ratio index developed by Hegyi (1974) was found best suited for this investigation. The radius varied for each sample plot due to the competitor selection method, but was defined as the distance of the furthest competitor from the focal tree. Numerous tree metrics have been used to calculate size-distance, competition indices (Weiskittel et al. 2011), but for this investigation CL was chosen due to the potential influence on light interception. The DWC index was defined as:

$$DWC = \sum_{j=1}^{n} \frac{CL_j}{CL_i} \div dist_{ij}$$

where DWC is the competition index ($m^{-1}$), $CL_j$ is the CL of each competitor tree, $CL_i$ is the CL of the white spruce tree, and $dist_{ij}$ is the distance between the competitor and white spruce tree. Larger DWC values correspond to greater competition.

### 2.3.4.4. Statistical Analysis

Analysis of covariance (ANCOVA) was used to analyze the relationships between: (1) leaf area and APAR, (2) APAR and ANPP, (3) leaf area and ANPP, (4) total aboveground biomass and ANPP, LUE, LAE, and $\delta^{13}C$, and (5) DWC and ANPP, LUE, LAE, and $\delta^{13}C$. Preliminary analysis found that year was not a significant factor in any of the models ($p > 0.811$). Therefore, year was dropped as a fixed effect. In addition, mean separation with Tukey's Honest Significant Difference showed that significant differences were not found between treatments within growing condition (EC-EM and PC-PM) ($p > 0.396$). Therefore, models were simplified to investigate differences between the two growing conditions (natural stands and plantations). In all ANCOVA models, the interaction between the continuous variables and growing condition were used to test for different slopes. If slopes were not significantly different and growing condition was not a significant factor in the models at $\alpha = 0.05$, linear regression was used to investigate the relationships. The analysis used linear hierarchical models with constant slopes and with intercepts that varied by year, and treatment plot nested within year (Gelman and Hill 2007). A conditional autoregressive of order 1 (CAR1) term was included in the ANCOVA models to account for the dependence among the within-group errors due to the repeated measures on the same tree (Pinheiro and Bates 2000). Statistical significance in the ANCOVA models was assessed at the $\alpha = 0.05$ level.

When nonlinear relationships were evident among variables, nonlinear hierarchical

models with indicator variables for the two growing conditions were fit to the data. The

nonlinear models were fit using maximum likelihood (Pinheiro and Bates 2000). The

amount of variation explained by the ANCOVA and nonlinear models was assessed with

the generalized $R^2$ statistic. $R^2$ was calculated as $1 - \left[ \sum (y - \hat{y})^2 / \sum (y - \bar{y})^2 \right]$, where $y$ are

observed values, $\hat{y}$ are values predicted from the model, and $\bar{y}$ is the mean of observed

values (Kvålseth 1985). All analyses were conducted using functions in the nlme package

(Pinheiro et al. 2013) with the R statistical software version 3.0.0 (R Core Team 2013).

## 2.4. Results

### 2.4.1. ANPP and Efficiency in Relation to Growing Condition

Tree APAR increased linearly with leaf area ($R^2 = 0.961$) (Figure 2.1), and the slopes

between the two growing conditions were different ($p < 0.001$). At the mean leaf area of

3.1 $m^2$ tree$^{-1}$, the ANCOVA model predicted APAR of 281.9 ± 7.3 MJ tree$^{-1}$ and 375.5 ±

9.9 MJ tree$^{-1}$ for the natural stands and plantations, respectively.
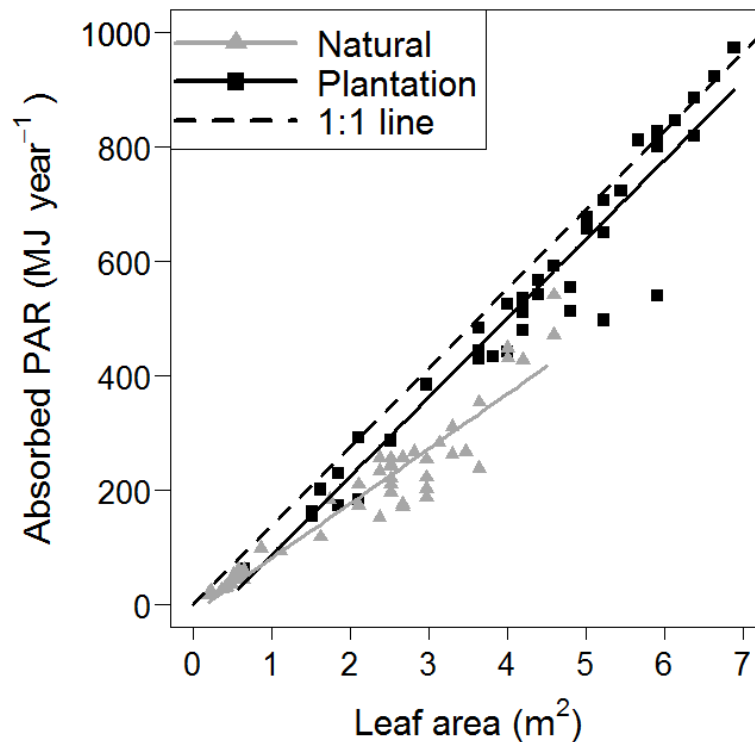
Figure 2.1. Relationship between absorbed photosynthetically active radiation (PAR; MJ year$^{-1}$) and individual tree leaf area (m$^2$) fit with ANCOVA ($R^2 = 0.960$). Data are shown for white spruce in two contrasting growing conditions: planted in naturally regenerated stands (Natural), and planted in plantations (Plantation). A 1:1 line through the origin is also shown.

ANPP was positively related to APAR ($R^2 = 0.503$), with slopes that differed by growing condition ($p = 0.015$) (Figure 2.2). At the mean APAR of 349.5 MJ tree$^{-1}$, predicted ANPP was $0.39 \pm 0.04$ kg year$^{-1}$ and $0.25 \pm 0.05$ kg year$^{-1}$ for the natural stands and plantations, respectively. WGF was also positively related to APAR, but the pattern was nonlinear and best fit with a two-parameter power function accounting for differences in growing condition ($R^2 = 0.434$) as $WGF_{Natural} = 0.320 \times ANPP^{0.113}$ and $WGF_{Plantation} = 0.325 \times ANPP^{0.113}$. ANPP was also positively correlated with leaf area ($R^2 = 0.534$), but

the slopes of the two growing conditions not different (p = 0.215). For example, at the mean leaf area of 3.1 $m^2$ tree$^{-1}$, predicted ANPP was 0.34 ± 0.04 kg tree$^{-1}$ in the natural stands and 0.26 ± 0.05 kg tree$^{-1}$ in the plantations. The relationship between WGF and leaf area was positive and nonlinear ($R^2 = 0.450$), where WGF was on average 4.7% greater in the plantations than in the natural stands. The nonlinear models were $WGF_{Natural} = 0.526 \times$ leaf area$^{0.123}$ and $WGF_{Plantation} = 0.551 \times$ leaf area$^{.123}$ for the natural stands and plantations, respectively.

## 2.4.2. ANPP and Efficiency in Relation to Tree Size and Competition

The ratio of APAR to leaf area (APAR:LA) was positively related to total aboveground biomass in both growing conditions ($R^2 = 0.661$) (Figure 2.3). The slopes of this relationship were not different (p = 0.312), but APAR:LA was 30.6% greater in the plantations than the natural stands at the mean biomass of 1.68 kg. In addition, the relationships between biomass, LUE, and LAE differed by growing condition (p < 0.001 and p = 0.007, respectively). LUE did not change substantially across the size range of sampled trees, where predicted LUE was 0.74 ± 0.17 g MJ$^{-1}$ for 1 kg tree$^{-1}$ and 0.68 ± 0.17 g MJ$^{-1}$ for 3 kg tree$^{-1}$ in the plantations. ANPP and WGF were significantly and positively correlated with biomass ($R^2 = 0.534$ and $R^2 = 0.455$, respectively), where ANPP was 35.3% greater in the natural stands and WGF was 4.7% greater in the plantations, on average. The relationship between $\delta^{13}C$ and biomass was nonlinear and positive, but did not differ between growing conditions. Therefore, a single power function of the form $\delta^{13}C = -29.6 \times$ Biomass$^{-0.013}$ was found to best fit the data ($R^2 = 0.229$).
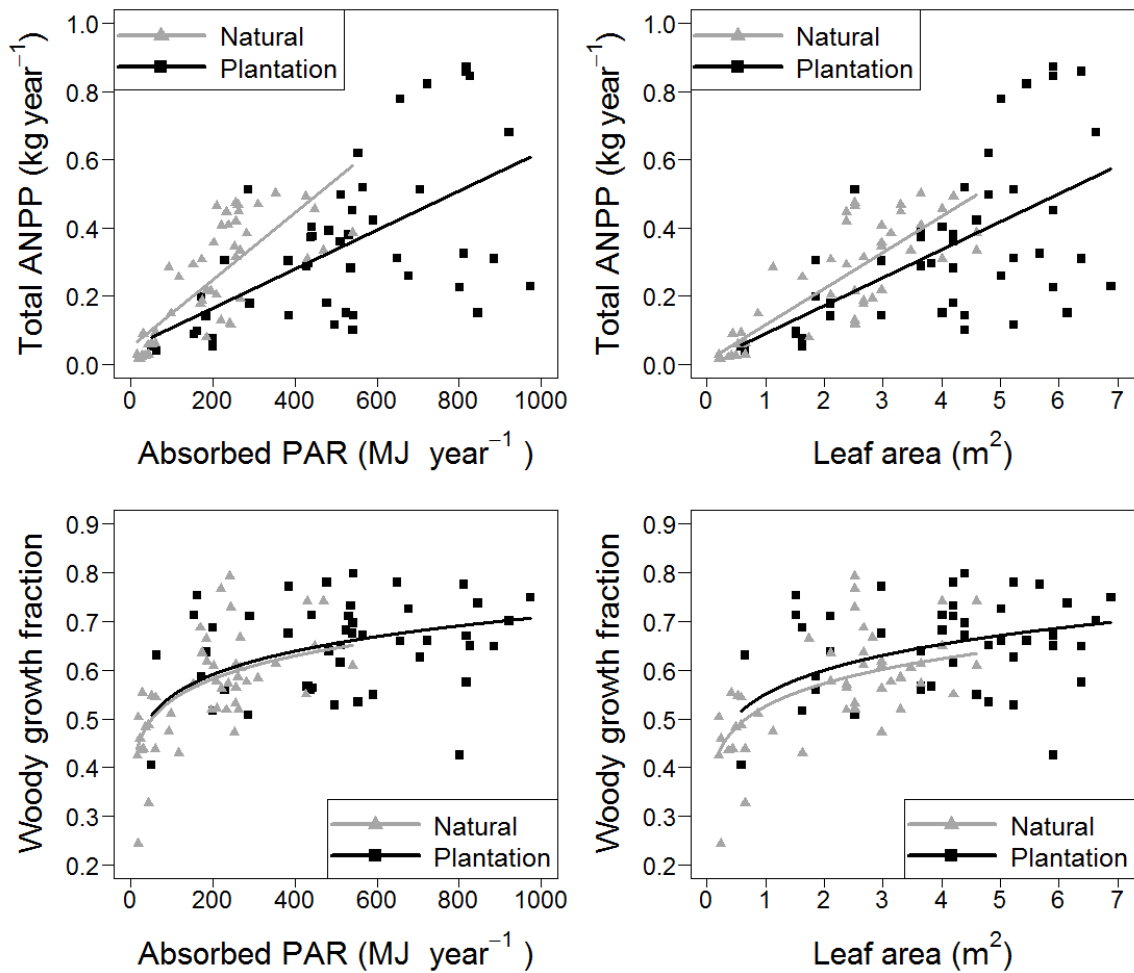
Figure 2.2. Relationship between total aboveground net primary productivity (ANPP) and absorbed photosynthetically active radiation (PAR) ($R^2 = 0.503$) and tree leaf area ($R^2 = 0.534$) fit with ANCOVA models. The relationship between woody growth fraction (fraction of ANPP partitioned to stem and branch growth) and PAR ($R^2 = 0.434$) and leaf area ($R^2 = 0.450$) were fit with nonlinear power functions with indicator variables accounting for the two growing conditions. Data points represent white spruce trees planted in naturally regenerated stands (Natural) and in plantations (Plantation).
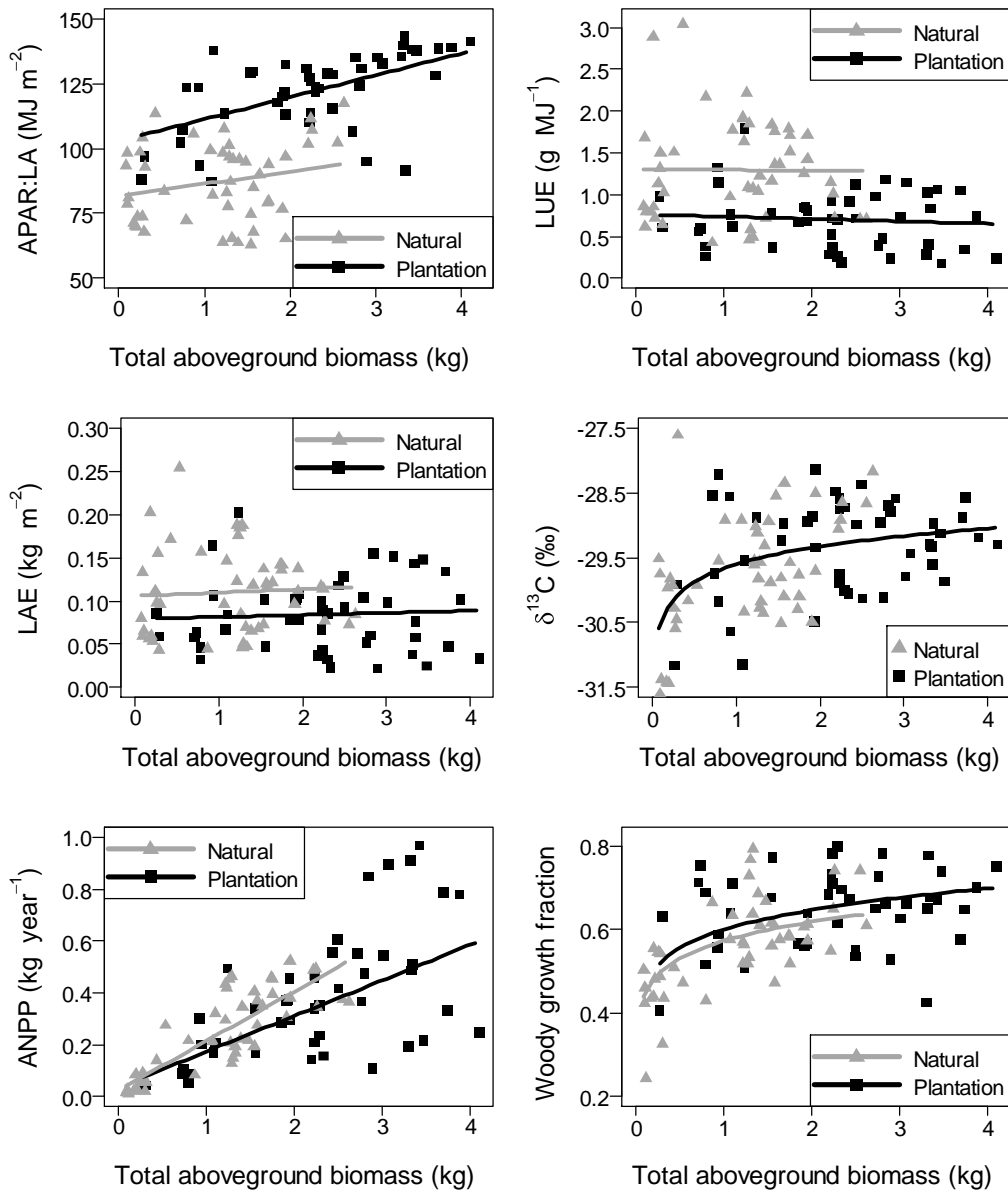
Figure 2.3. Relationship between total aboveground biomass and (a) ratio of absorbed photosynthetically active radiation (APAR) to leaf area (LA) ($R^2 = 0.661$), (b) light-use efficiency (LUE; aboveground net primary productivity (ANPP)/APAR) ($R^2 = 0.366$), (c) leaf area efficiency (LAE; ANPP/LA) ($R^2 = 0.215$), (d) foliar $\delta^{13}C$ composition ($R^2 = 0.229$), (e) ANPP ($R^2 = 0.534$), and (f) woody growth fraction (fraction of ANPP in branches and stem) ($R^2 = 0.455$). Data are shown for white spruce trees planted in naturally regenerated stands (Natural) and in plantations (Plantation). APAR:LA, LUE, LAE, and ANPP models were fit with ANCOVA, while $\delta^{13}C$ and woody growth fraction were fit with nonlinear power functions accounting for the two growing conditions with indicator variables.

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The relationship between APAR and $\delta^{13}$C was nonlinear and positive ($R^2 = 0.288$)

(Figure 2.4), where $\delta^{13}$C increased rapidly between 10 and 200 MJ tree$^{-1}$. For instance,

between 10.0 and 200.0 MJ tree$^{-1}$ APAR, $\delta^{13}$C increased by 1.3‰, but only increased by

0.4‰ between at 300.0 MJ tree$^{-1}$ and 800.0 MJ tree$^{-1}$.
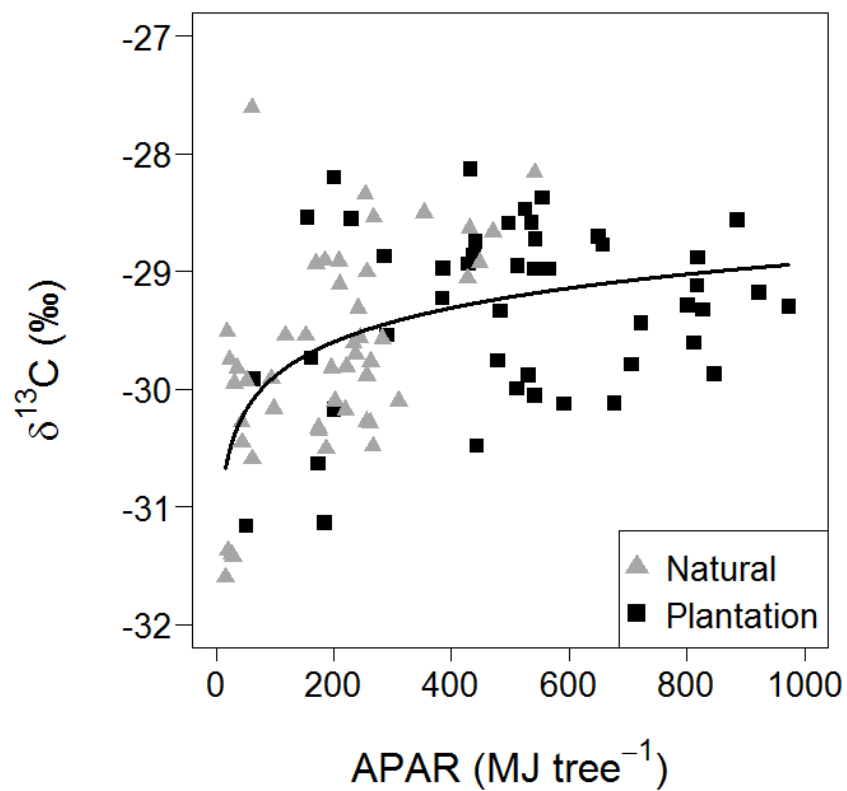


Figure 2.4. Relationship between absorbed photosynthetically active radiation (APAR) and foliar $\delta^{13}$C composition ($R^2 = 0.288$) fit with a nonlinear power function. Data are shown for white spruce trees planted in naturally regenerated stands (Natural) and in plantations (Plantation).

DWC ranged from 0.4 to 29.9 $m^{-1}$ in the plantations, and from 9.5 to 64.2 $m^{-1}$ in the natural stands (Figure 2.5). A negative, nonlinear relationship was found between APAR:LA and DWC for both growing conditions ($R^2 = 0.682$), where APAR:LA was greater in the plantations. For instance, at the mean DWC of 14.5 $m^{-1}$, APAR:LA was 18.1% greater in the plantations than the natural stands. LUE was significantly related to DWC ($p < 0.001$), but the slopes between plantations and natural stands were not different ($p = 0.631$). Overall, LUE did not change substantially over the range of DWC in the natural stands, ranging from $1.35 \pm 0.22$ g $MJ^{-1}$ at the minimum DWC to $1.27 \pm 0.28$ g $MJ^{-1}$ at the maximum DWC. LAE decreased slightly with increased DWC in both growing conditions ($R^2 = 0.218$), even though competition was not a significant factor in the model ($p = 0.535$). For instance, in the natural stands, LAE ranged from $0.12 \pm 0.02$ kg $m^{-2}$ at the minimum DWC to $0.09 \pm 0.02$ kg $m^{-2}$ at the maximum DWC. As DWC increased, $\delta^{13}C$ decreased ($R^2 = 0.330$), but with similar slopes for the two growing conditions ($p = 0.107$). Across the range of DWC in the enrichment intensity, predicted $\delta^{13}C$ decreased from $-28.98 \pm 0.20$ to $-31.00 \pm 0.32$

A negative nonlinear relationship between ANPP and DWC was found for both growing conditions ($R^2 = 0.415$) (Figure 2.5). The final model form of the relationships were $ANPP_{Natural} = 0.750 \times DWC^{-0.057}$ and $ANPP_{Plantation} = 0.476 \times DWC^{-0.055}$. The relation between WGF and DWC did not differ between growing conditions ($p = 0.795$), but overall WGF decreased with increasing DWC ($R^2 = 0.447$). For instance, WGF decreased by 46.8% from the minimum DWC of 0.42 $m^{-1}$ to the maximum DWC of 64.25 $m^{-1}$.

Foliar $\delta^{13}C$ was not correlated with ANPP (p = 0.080), WGF (p = 0.306), LUE (p = 0.930), or LAE (p = 0.389), for white spruce trees in either growing condition (Figure 2.6).
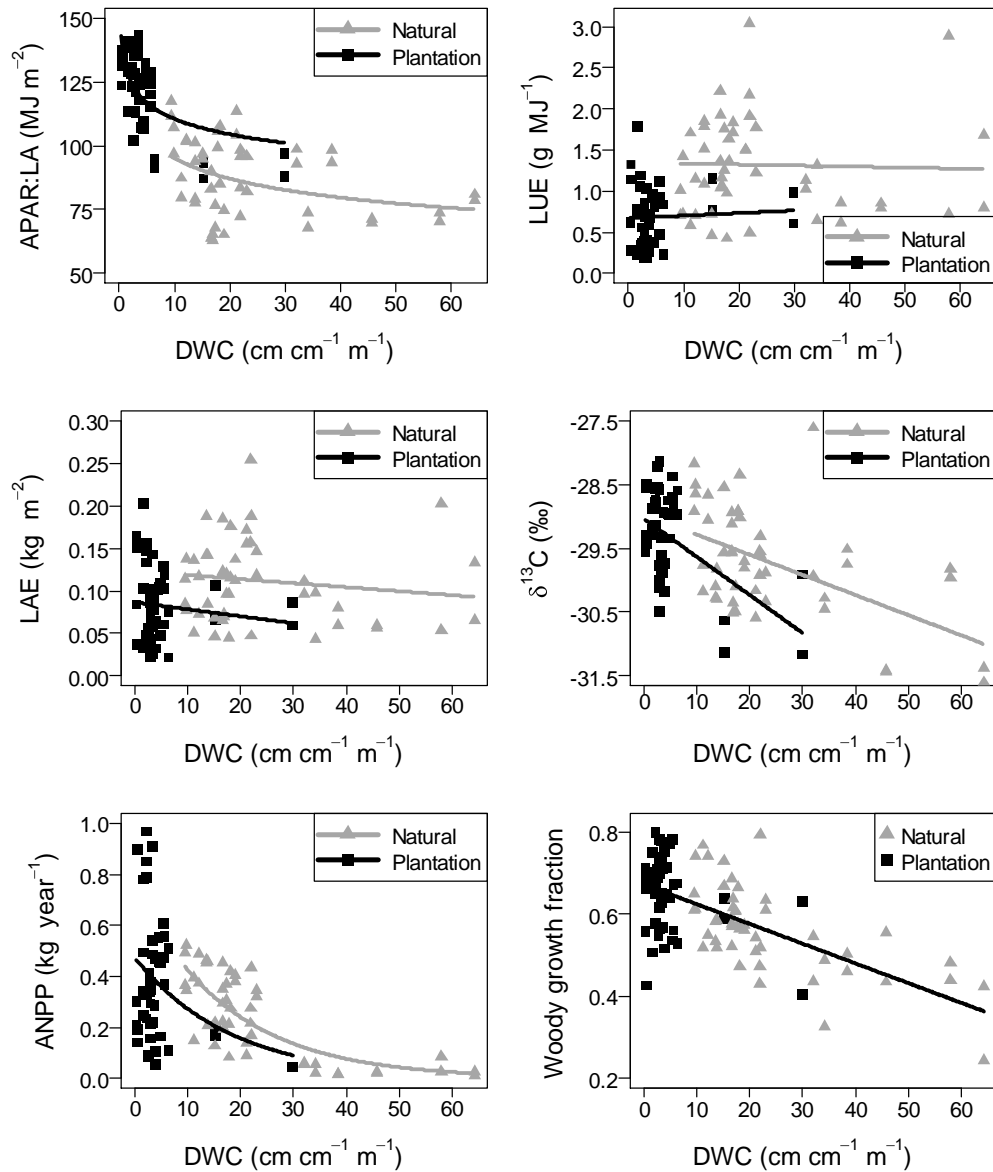
Figure 2.5. Relationship between distance-weighted competition (DWC) and (a) ratio of absorbed photosynthetically active radiation (APAR) to leaf area (LA) ($R^2 = 0.682$), (b) light-use efficiency (LUE; aboveground net primary productivity (ANPP)/APAR) ($R^2 = 0.363$), (c) leaf area efficiency (LAE; ANPP/LA) ($R^2 = 0.218$), (d) foliar $\delta^{13}C$ composition ($R^2 = 0.330$), (e) ANPP ($R^2 = 0.415$), and (f) woody growth fraction (fraction of ANPP in branches and stem) ($R^2 = 0.448$). Data are shown for white spruce trees planted in naturally regenerated stands (Natural) and in plantations (Plantation). LUE, LAE, and $\delta^{13}C$ models were fit with ANCOVA, APAR:LA and ANPP models were fit with nonlinear power functions accounting for growing conditions with indicator variables, and woody growth fraction was fit with linear regression.
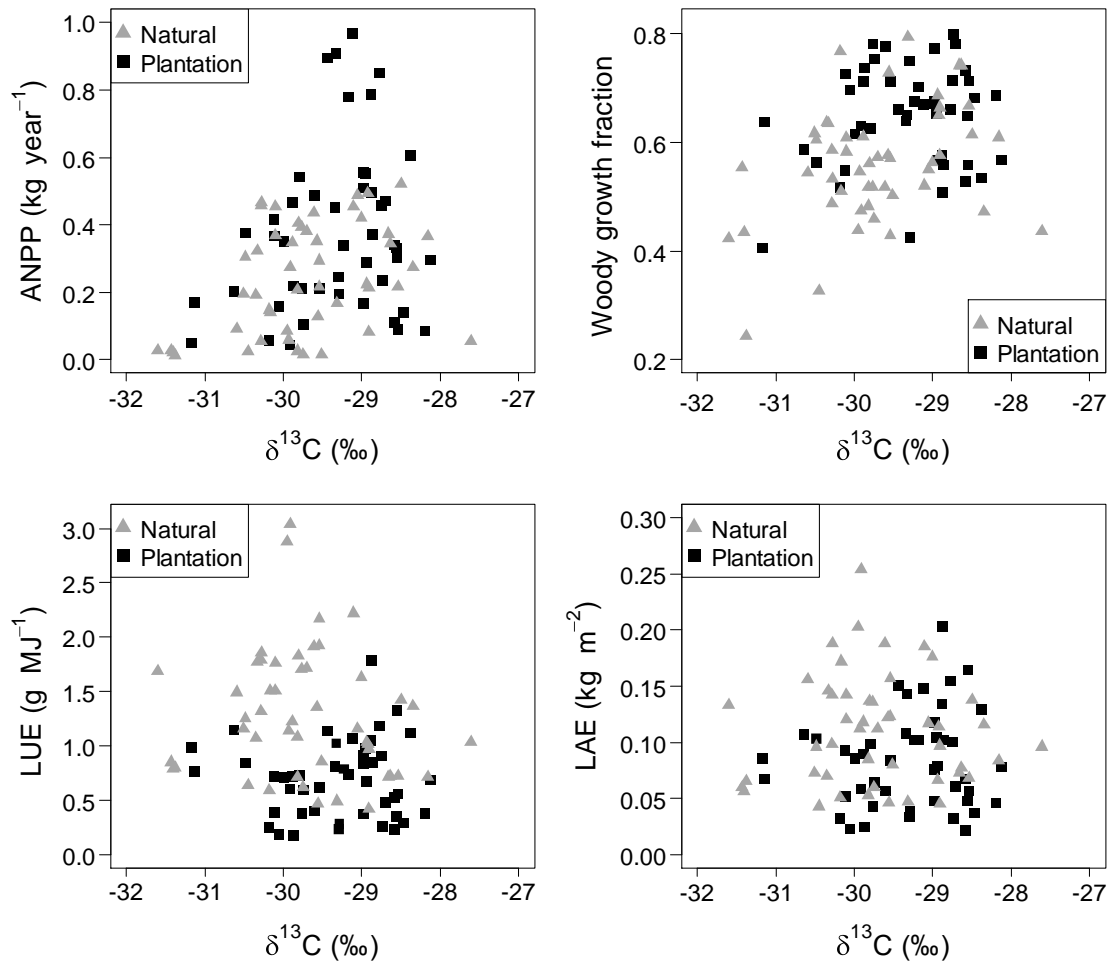
Figure 2.6. Scatterplots of foliar $\delta^{13}C$ composition, and aboveground net primary productivity (ANPP), woody growth fraction (fraction of ANPP in branches and stem), light-use efficiency (LUE), and leaf area efficiency (LAE). None of the relationships were significant ($p > 0.101$) with ANCOVA or nonlinear models. Data are shown for white spruce trees planted in naturally regenerated stands (Natural) and in plantations (Plantation).

## 2.5. Discussion

### 2.5.1. Relationship between Leaf Area and APAR

A strong positive relationship was found between leaf area and APAR ($R^2 = 0.961$), and both the slope and intercept differed between white spruce trees growing in natural stands and plantations. For example, APAR increased by 56.3% on average for each additional square meter of leaf area in the plantations and by 48.9% in the natural stands. The percentage gain in APAR per unit of leaf area was not constant across the sampled range of leaf area in either growing condition (Figure 2.1), likely a consequence of increased vertical foliage stacking that occurs as trees increase in size and produce more leaf area (Valladares and Niinemets 2007). Vertical foliage stacking in conifer species is common due to strong apical dominance (Parker et al. 2002), which tends to enhance self-shading within a tree (Duursma et al. 2010; Oker-Blom et al. 1989). The result is an exponential decline of light interception deeper into the crown, as predicted by the Beer-Lambert law of light extinction. The shallower regression slope for the natural stands compared to the plantations was also likely influenced by neighborhood competition, as the relationship between APAR and leaf area can also be affected by stand structure (Kim et al. 2011) through light capture by neighboring, competing trees.

Incident leaf angle and clumping can also influence light interception within a tree crown (Valladares and Niinemets 2007). MAESTRA was calibrated by using a small sample of foliage angles collected from trees across the site, but the proportion of leaf area in each foliage age class was not specified and horizontal LAD was assumed uniform, since neither data were available. It is likely that using default values for these factors in

MAESTRA influenced predictions of seasonal APAR, since leaf angle can vary substantially among species (Falster and Westoby 2003) and at different depths within a tree crown (Pearcy et al. 2005).

Leaf area is often used as a surrogate of APAR (Brunner 1998) since accurately measuring APAR over the course of a growing season can be time consuming, expensive, and prone to uncertainty due to diurnal and seasonal changes in light intensity and phenology. Gspaltl et al. (2013), for instance, reported relationships between leaf area and APAR, leaf area and ANPP, and APAR and ANPP for juvenile Norway spruce (*Picea abies* L.) trees that were similar to those observed in this study. Leaf area, therefore, may be a suitable surrogate for APAR in juvenile stands of white spruce (Figure 2.1). Furthermore, since leaf area accounted for 3.1% more of the explained variation in ANPP than APAR, leaf area is a robust predictor of ANPP as well.

### 2.5.2. Relationship between APAR/Leaf Area and ANPP

ANPP was positively related to APAR and leaf area in both natural stands and plantations, but ANPP in the natural stands was greater per unit of APAR and leaf area. For instance, ANPP in the natural stands was 46.7%, 56.0%, and 60.0% greater than the plantations at the 1st quartile, mean, and 3rd quartile APAR, respectively. The substantial differences between the natural stand and plantation conditions were likely due to differences in aboveground biomass allocation. For instance, WGF was greater for trees in the plantations than the natural stands across the range of APAR. Comparatively, the lower WGF of trees in the natural stands suggests that a greater proportion of ANPP was allocated to foliage production. This would be expected since moderately shade tolerant

species (such as white spruce) growing in reduced light environments tends to allocate more aboveground biomass to foliage production in order to increase light interception (Chan et al. 2003). In contrast, changes in allocation patterns are not as pronounced for shade tolerant species across environments with contrasting light availability (Claveau et al. 2005). Results from our investigation are consistent with results found for juvenile Norway spruce trees following thinning, where unthinned trees had greater aboveground growth per unit of APAR (Gspaltl et al. 2013). Annual stem volume increment per unit of APAR was slightly greater for thinned trees in mature Norway spruce stands (Gspaltl et al. 2013) and in *Eucalyptus nitens* (H. Deane & Maiden) Maiden stands (Forrester et al. 2013), suggesting ontogenetic changes in aboveground biomass allocation.

APAR was only estimated for white spruce trees during the portion of the growing season when hardwood leaves ceased annual expansion (mid-May to mid-September). This time period was specified in both treatments because of the substantial hardwood component at the site (Nelson et al. 2013), and to accurately account for light interception of white spruce trees in the natural stands during the most active period of growth. Evergreen habits of many conifer species allows for potential photosynthesis throughout the year, even though many conifers become dormant during the parts of the winter in temperate regions (Kozlowski et al. 1991). It is likely that white spruce APAR was underestimated, since conifer species can absorb light and photosynthesize during the spring and fall as long as soil and air temperatures are above freezing (Schwarz et al. 1997). This may be one possible reason that APAR explained only 50.3% of the variation in ANPP, since ANPP represented cumulative annual growth.

## 2.5.3. Relationship between Tree Size / Competition and ANPP

Overall, ANPP increased with tree biomass in both the natural stands and plantations. For example, ANPP increased by 117.0% from the smallest (0.1 kg) to largest (2.6 kg) observed biomass in the natural stands. The increase in ANPP with tree size was expected due to relatively open canopy conditions in both treatments and the young age of the trees. Tree and stand ANPP typically increase until crown closure, when ANPP declines because of density-dependent competition (Oliver and Larson 1996). Within the natural stands, the lower ANPP of smaller trees may be attributed to greater neighborhood competition. Similar results were found by Pitt et al. (2010) where gains in white spruce wood volume between 167% and 1,166% were documented when herbaceous and woody competition was reduced, respectively, compared to plots without competition control. Similar gains in overall tree size were found for white spruce with vegetation control, soil scarification, and fertilization in New Brunswick, Canada (Burgess et al. 2010), suggesting that lower competition and greater resource availability strongly influenced ANPP. ANPP increased with tree biomass in the natural stands, but these stands had not reached crown closure and had much higher species diversity than the plantations. Therefore, as these stands mature, it is likely that white spruce ANPP will decline, and potentially result in lower productivity than the trees in the plantations. For instance, Sutton (1995) found that greater competition early in stand development can result in lower long-term white spruce productivity that can persist up to three decades after treatment without subsequent competition control.

Within the plantations, DWC was relatively low (0.4-29.9 m$^{-1}$), where the upper range of DWC represented a few white spruce trees growing in close proximity to hybrid poplar trees. Therefore, the variability in plantation-grown white spruce ANPP across the range of tree biomass suggests that other factors besides APAR, such as micro-site soil conditions, may be influencing tree productivity. For instance, McKinnon et al. (1998) found reduced aboveground growth of white spruce when soil fertility and soil moisture were limiting, leading to lower foliar N concentrations. Similarly, Munson et al. (1995) found that vegetation control, soil scarification, and N-P-K fertilization increased foliar N content, with an associated increase in ANPP. Soil drainage may also be influencing white spruce ANPP in the plantations, since there was a large range in the seasonal high water table depth (indicator of rooting depth and seasonal soil saturation), from 17-58 cm. Some of the smaller trees in the plantations were selected in poorly-drained areas to encompass the diverse growing conditions and tree sizes at the site. Root development of these smaller trees may be inhibited by to poor soil aeration (Heineman et al. 1999), which can reduce ANPP (Wang and Klinka 1996).

## 2.5.4. Relationship between Tree Size / Competition and LUE, LAE and $\delta^{13}C$

Even though APAR and leaf area were positively correlated with total ANPP, LUE and LAE were relatively constant across the range of tree biomass and DWC. For instance, white spruce LUE decreased by only 1.4% and 2.7% in the natural stands and plantations, respectively, across the range of biomass. The majority of studies using MAESTRA to estimate APAR have found that LUE increases with tree size (Binkley et al. 2010; Campoe et al. 2013b; Forrester et al. 2013). However, Gspaltl et al. (2013) found a slight decrease in LUE with increasing tree size for juvenile Norway spruce, which they

attributed to the open canopy conditions and the lack of resource limitation in these stands due to low levels of competition. In contrast, when stands reach crown closure, differentiation in resource-use efficiency among trees is common, where larger trees become more efficient at utilizing available resources, while smaller trees often senesce from the inability to acquire necessary resources to sustain growth (Binkley et al. 2004). Therefore, the slight decreasing patterns of LUE observed for white spruce may be due to the relatively open-canopy conditions in both growing conditions and the corresponding low intensities of density-dependent resource competition.

LUE and LAE provide integrated tree-level measures of resource conversion to ANPP, but physiological mechanisms underlie these observed responses. For this investigation, $\delta^{13}C$ of current-year foliage was measured to study the influence of the growing conditions, tree size, and competition on the ratio of A to $g_s$. $\delta^{13}C$ is inversely proportional to the ratio of foliage intercellular $[CO_2]$ ($c_i$) to atmospheric $[CO_2]$ ($c_a$) (Farquhar et al. 1982), since Rubisco tends to discriminate against the heavier $^{13}C$ isotope. Hence when $c_i$ declines, the rate of discrimination against $^{13}C$ tends to decline (Park and Epstein 1961). Since the ratio of A to $g_s$ (iWUE) is the major influence of $c_i$, $\delta^{13}C$ is often correlated with iWUE (Farquhar et al. 1989). The results from this investigation indicated that foliar $\delta^{13}C$ increased with greater tree biomass (Figure 2.3). The increase was rapid for small trees, where between 0.1 kg and 1 kg, $\delta^{13}C$ increased by 0.9‰ while between 2 kg and 3 kg, $\delta^{13}C$ increased by only 0.2‰. The increase of $\delta^{13}C$ with tree size for these juvenile trees was likely due to an increase in A potentially enhancing aboveground growth. The positive relationship between tree size and $\delta^{13}C$ was

also found for hardwood species in Japan, where $\delta^{13}C$ increased by ~2.5‰ with height for *Fagus crenata* Blume and *Quercus crispula* Blume (Osada et al. 2004).

In the plantations, white spruce trees with greater biomass were likely growing in more favorable micro-environments, such as better drained soils, since light was not a limiting resource. Therefore, it would be expected that factors hypothesized to increase ANPP, such as better drainage and greater nutrient availability may have also influenced the observed $\delta^{13}C$ increase. For instance, foliar $\delta^{13}C$ has been shown to increase with greater soil fertility (Hobbie and Colpaert 2004; Matsushima et al. 2012; Staples et al. 2001) and water availability (Garten and Taylor 1992; Peri et al. 2011). In comparison, the white spruce trees growing in poorly drained soils may have exhibited lower $\delta^{13}C$ because hypoxic soil conditions reduce soil oxygen diffusion rates, which can increase diffusive resistance of leaf gas exchange, resulting in a decrease in both A and $g_s$ (Sojka et al. 2005). For instance, Gardiner and Hodges (1996) found that $\delta^{13}C$ of oak (*Quercus*) species was 1‰ more negative when induced with hypoxic soil conditions compared to individuals growing in nonhypoxic soils. Similarly, A was 7.33 μmol m$^{-2}$s$^{-1}$ lower, and $g_s$ was 0.27 cm s$^{-1}$ lower for seeding growing in hypoxic conditions, suggesting that the more negative $\delta^{13}C$ was correlated with reductions in both A and $g_s$ but with a disproportionate decline in A (Gardiner and Hodges 1996).

Foliar $\delta^{13}C$ was found to decrease with greater DWC in both treatments, while $\delta^{13}C$ increased with APAR, similar to other species (Bladon et al. 2007; Broadmeadow and Griffiths 1993; Ponton et al. 2002). Farquhar et al. (1982) suggest that increases in $\delta^{13}C$ could result from three potential mechanisms: (i) increase in A, (ii) decrease in $g_s$, or (iii) declines in both A and $g_s$, but with a disproportional decline in $g_s$. Light-saturated

photosynthetic rates of juvenile conifer trees are often greater in open conditions than beneath closed canopies (Dumais and Prevost 2008; Pothier and Prévost 2002). Therefore, it is likely that the associated increase in $\delta^{13}$C with lower DWC and greater APAR is due to an increase in A. In order to test whether increases in A or decreases in $g_s$ were responsible for observed patterns $\delta^{13}$C patterns, a dual-isotope approach would be necessary. The dual isotope approach combines the isotope fraction of $^{18}$O/$^{16}$O ($\delta^{18}$O) with $\delta^{13}$C, since $\delta^{18}$O is related to $g_s$ but not A. The increase in foliar $\delta^{13}$C with greater APAR in this investigation suggests that iWUE was greater for trees that intercepted more light. This result may partially explain some of the observed differences in ANPP and LUE between the growing conditions.

Foliar $\delta^{13}$C composition of white spruce was not related to ANPP, WGF, LUE, or LAE in either of the growing conditions. Assuming the increase in $\delta^{13}$C was more strongly related to an increase in A, the lack of relationship between $\delta^{13}$C and ANPP would be expected due to the various sinks for photosynthate besides aboveground growth, including root growth, carbohydrate storage, and respiration (Lambers et al. 2008). Similarly, the lack of relationship between $\delta^{13}$C and LUE was expected since LUE did not change substantially across the range of sampled tree size and competition, while $\delta^{13}$C increased slightly with tree size and decreased with greater competition. Therefore, with no detectable patterns between ANPP and $\delta^{13}$C, it was unlikely that a significant relationship between foliar $\delta^{13}$C composition and the conversion of light capture into ANPP at the tree-level would be detected.

## 2.6. Conclusion

The goal of this investigation was to explore the relationships between potential environmental and physiological mechanisms (APAR, LUE/LAE, foliar $\delta^{13}$C) and ANPP of juvenile white spruce trees in stand with contrasting species composition and varying levels of aboveground competition (natural stands versus plantations). ANPP was positively correlated with APAR and declined with greater neighborhood competition. This result suggests that neighborhood species composition and stand structure can strongly influence aboveground productivity of this moderately shade tolerant species. In contrast, LUE and LAE did not change over a range of tree sizes or neighborhood competition. Therefore, it is reasonable to assume that leaf area production, and consequently APAR, in both the natural stands and plantations was also related to other factors, such as belowground resource availability. One objective was to test whether foliar $\delta^{13}$C was related to tree-level processes influenced by the contrasting environments. Foliar $\delta^{13}$C increased with tree size and light capture, and decreased with greater inter-tree competition, but was not related to either LUE or ANPP. Therefore, even though photosynthetic capacity and carbon assimilation likely increased with lower competition and greater light interception, other physiological mechanisms (photosynthate allocation to nonstructural carbohydrates and roots), belowground resource availability and resource capture may also have had a strong influence on aboveground tree-level productivity. Overall, APAR had the strongest influence on ANPP, suggesting that in natural stands where crown closure is likely to occur sooner than in plantations, ANPP and LUE of white spruce trees will likely decline due to earlier differentiation in resource-use efficiency.

# CHAPTER 3

## EARLY STAND PRODUCTION OF HYBRID POPLAR AND WHITE SPRUCE IN MIXED AND MONOSPECIFIC PLANTATIONS IN EASTERN MAINE[1]

### 3.1. Abstract

Forest plantations in the northeastern United States comprise a small proportion of the total forest area. Most plantations are typically softwood dominated and managed for sawlog and pulpwood production, while high-yield hardwood plantations for bioenergy feedstocks have not been as widely investigated. The objective of this study was to compare the biomass production of planted white spruce (*Picea glauca* (Moench) Voss) and hybrid poplar (*Populus spp.*) plantations (four clones) in monoculture, and in mixture of the two on a typical reforestation site in Maine. Three years following planting, hybrid poplar height and ground line diameter growth rates began to diverge among clones, and by six years, the *P. nigra* x *P. maximowiczii* (NM6) clone clearly outperformed three *P. deltoides* x *P. nigra* clones (D51, DN10 and DN70) both in pure stands and in mixtures with white spruce. In mixture, we found the yield of white spruce to decline as the yield of hybrid poplar increased. Overall, yields of the white spruce monocultures were comparable to those reported in eastern Canada, while the hybrid poplar biomass yields were substantially lower than those reported from studies on abandoned agricultural lands, likely due to the harsher soil conditions at our site. The dominance of rocky and

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poorly drained sites (like the one tested in this study) across Maine will likely limit the feasibility of widespread hybrid poplar plantations, and thus constrains their potential use as a bioenergy feedstock.

## 3.2. Introduction

Forest plantations in northeastern United States comprise a relatively small proportion of the landscape. For example, only 4% of the total forested land in the state of Maine is plantations (McWilliams et al. 2005), even though increasing the proportion of plantations has been proposed both to improve wood supplies (Wagner et al. 2003) and increase the amount of land set aside for unmanaged reserves (Seymour and Hunter 1999) in that state. The majority of stands in the region are extensively managed with naturally regenerated hardwood-softwood mixtures (or mixedwoods). As such, many of these mixedwood stands rarely receive intermediate treatments, such as thinning, leading to relatively poor growth and low yields. Increasing the intensity of silvicultural practices, particularly by planting more area with softwood, hardwood and mixed-species plantations as well as developing improved thinning regimes, could help increase biomass supply and still provide multiple silvicultural benefits.

White spruce (*Picea glauca* (Moench) Voss) is a commonly planted species in the region. It is moderately shade-tolerant with high growth rates in open conditions (Nienstaedt and Zasada 1990), but is also the most vulnerable and susceptible of the spruce species to spruce budworm (*Choristoneura fumiferana* (Clemens)) defoliation. A budworm outbreak may cause a significant reduction in landscape level growing stock when white spruce is a common plantation species (Hennigar and MacLean 2010), but desirability of

the species has encouraged the development of various proposed defenses, including anti-insectant endophytes (Miller et al. 2002; Miller et al. 2008; Sumarah et al. 2005) and transgenic *Bacillus thuringiensis* individuals (Lachance et al. 2007). These advances decrease the risks of planting improved white spruce in northeastern North America. However, early white spruce plantation performance on rocky, poorly-drained sites, which dominate in Maine and much of the northeastern US has not been thoroughly investigated.

Although white and other spruce species dominate the plantings in the region, there may be potential to grow high-yield hybrid poplar plantations to supplement current regional and national bioenergy production efforts. For example, Yuan et al. (2008) reported a net positive energy balance of 10 to 20%, or approximately 150-250 GJ ha$^{-1}$ yr$^{-1}$, in hybrid poplar plantations; this included the offset of silvicultural inputs required to maximize yields. In addition, hybrid poplar has recently been shown to be marketable for pulp, lumber and composite wood products (Balatinecz et al. 2001; Stanton et al. 2002).

In North America, the majority of hybrid poplar crosses are derived from four species: black cottonwood (*Populus trichocarpa* Torr. & Gray), eastern cottonwood (*P. deltoides* Bartr. Ex Marsh.), Japanese poplar (*P. maximowiczii* A. Henry) and European black poplar (*P.nigra* L.) (Stanton et al. 2002). Yields among clones with similar parentages may be substantially different (Coyle et al. 2006; Laureysens et al. 2004; Lo and Abrahamson 1996). In the northeastern United States, the best performing clones have been found to be crosses of *P. deltoides* x *P. nigra* and *P. nigra* x *P. maximowiczii* (Lo and Abrahamson 1996). In other regions of the United States, clones with different and similar parentages can have substantially different performance on single sites (Devine et

al. 2010). However, experimentation with hybrid poplar plantations on sub-optimal sites in the northeastern US has been limited, and therefore it is unclear whether such plantations could contribute to regional efforts to increase bioenergy and byproduct demands. Sub-optimal sites for hybrid poplar production dominate much of the Northeast, including glacial-till derived soils with densic layers and poor soil aeration that may limit hybrid poplar growth (Weiskittel and Timmons unpublished data). In one of the few published studies in Maine, Czapowskyj and Safford (1993) reported no growth difference between two full sib clones of *P. maximowiczii* x *P. trichocarpa*, but found that the overall growth of the clones was poor without fertilizer amendments. Additionally, it has been shown that a clone of *P. deltoides* x *P. petrowskyana* production was predicted to be greatest on sites with high sand content, moderate acidity and relatively fertile soils (Pinno et al. 2010). Hybrid poplar tend to consume large quantities of water and nutrients, growing best in deep (>1 m) soils where root growth is not prohibited by densic layers or poor aeration (Dickmann and Stuart 1983). For these reasons, hybrid poplar plantations are typically established on high-quality agricultural or pasture lands where soils are relatively homogenous and water and nutrient availability can be intensively managed.

Large-scale plantings of hybrid poplar or other conifer and hardwood species can be susceptible to insect and disease outbreaks, downturns in timber markets, and public criticism. Mixed-species plantations composed of complementary species, such as those with contrasting shade tolerances and growth rates (Kelty 2006; Richards and Schmidt 2010) that may minimize competitive interference, may be a better approach. For example, mixed-species plantations of hybrid poplar and white spruce may be an

approach to provide both short-rotation biomass and longer-rotation sawlog production. Theoretically, hybrid poplar could be coppiced every six to ten years to provide periodic monetary returns, while allowing white spruce to grow to sawlog size in 60 to 70 years. Another strategy may be to grow hybrid poplar on a 20 year rotation and perform a commercial thinning of the white spruce at the same time. One of the complications with this species mixture is that hybrid poplar is intolerant of shade while white spruce is moderately tolerant (Lieffers and Stadt 1994), so novel planting designs (Vanclay 2006) may be necessary to ensure plantation success.

Here we report six-year results from a replicated experiment comparing the early growth of pure white spruce, pure hybrid poplar, and white spruce-hybrid poplar mixed-species plantations on a typical reforestation site in eastern Maine. Our hypotheses were: (1) hardwood plantations would out yield conifer plantations, with mixed-species plantations intermediate in aboveground biomass yields; (2) aboveground biomass yield among four hybrid clones would not differ in either pure or mixed-species plantings, but the yields of individual clones would be greater in the pure plantings because of higher densities, and (3) aboveground biomass yield of improved white spruce would not differ among pure or mixed-species plantings.

## 3.3. Methods

### 3.3.1. Study Site

This study is installed within the Penobscot Experimental Forest (PEF) in eastern Maine, near the towns of Bradley and Eddington (44° 49' N, 68° 38' W). Natural forest composition is dominated by shade tolerant conifer species, including balsam fir (*Abies balsamea* L.), eastern hemlock (*Tsuga canadensis* L.), and red spruce (*Picea rubens* Sarg.), and shade-intolerant hardwood species, including trembling aspen (*P. tremuloides* Michx.), bigtooth aspen (*P. grandidentata* Michx.), red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marsh.) (Sendak et al. 2003). Soils are of Wisconsian glacial till origin and the classifications range from well-drained coarse-loamy, isotic, frigid Oxyaquic Haplorthods to poorly-drained loamy, mixed, active, acid, frigid, shallow Aeric Endoaquepts. Across the experiment site, B-horizon characteristics, nutrient availability, and other soil factors were variable (Table 3.1). In 1995, the 9.2 ha site was clearcut with approximately 2.3 $m^2$ $ha^{-1}$ of residual basal area. Following harvest, the site naturally regenerated primarily to shade-intolerant hardwoods (trembling aspen, bigtooth aspen, red maple, and paper birch), with an understory of balsam fir, red spruce, white pine (*Pinus strobus* L.) and white spruce.

Table 3.1. Raw mean, standard error of the mean (SE), and range of soil conditions and mineral soil chemistry at the study site measured by 20-40 samples taken from across the study site. Depth to redoximorphic features is a measure of the seasonally-high water table (low soil aeration and root growth). All B-horizon characteristics were measured in the top 20 cm of the horizon unless indicated.

| | Mean ± SE | Range |
|---|---|---|
| Depth to redoximorphic features (cm) | 33.8 ± 5.3 | 10.0 – 95.0 |
| Depth of organic horizon (cm) | 5.2 ± 0.5 | 2.2 – 9.2 |
| **B-horizon characteristics** | | |
| Soil texture (%) | | |
| Sand | 46.4 ± 0.9 | 36.4 – 63.6 |
| Silt | 35.5 ± 0.9 | 19.6 – 46.2 |
| Clay | 18.1 ± 0.6 | 12.5 – 32.5 |
| Coarse rock fragments > 2 mm diameter (%) | | |
| 0-10 cm | 26.9 ± 3.7 | 6.2 – 60.0 |
| 10-20 cm | 33.9 ± 4.0 | 6.2 – 60.0 |
| 20-30 cm | 51.2 ± 6.4 | 8.8 – 88.3 |
| Coarse and fine roots (%) | | |
| 0-10 cm | 21 ± 4.9 | 0 – 74 |
| 10-20 cm | 11 ± 2.8 | 0 – 36 |
| 20-30 cm | 3 ± 1.1 | 0 – 15 |
| Organic matter (%) | 6.0 ± 0.4 | 2.0 – 13.1 |
| pH | 5.1 ± 0.1 | 4.6 – 5.7 |
| Chemical Concentrations (mg kg$^{-1}$) | | |
| $NO_3$ | 3.6 ± 1.2 | 0.2 – 27.6 |
| $NH_4$ | 10.0 ± 1.2 | 1.9 – 39.0 |
| P | 3.8 ± 0.2 | 0.5 – 7.9 |
| K | 52.9 ± 3.8 | 30.8 – 132.5 |

### 3.3.2. Experimental design

Between 2003 and 2004, six to seven years following harvest, the experiment was installed that included three whole plot treatments replicated four times and randomly assigned across the site: Pure Spruce – pure white spruce, Mixture– species' proportion of 0.68 and 0.32 for white spruce and hybrid poplar clones, respectively, and Pure Poplar – pure hybrid poplar (Figure 3.1). Each of the whole plots are 30 m x 30 m. In the center of each whole plot, a 20 m x 20 m measurement plot containing a total of 100 crop trees on a 2 m x 2 m spacing was established (i.e., 2500 trees per ha [tph]). The Mixture and Pure Poplar whole plots were split into four 15 m x 15 m quarter plots and each quarter plot was planted with one of four different hybrid poplar clones. The four clones were selected based on performance in earlier research trials in cooler Northeast climates, and included three *Populus deltoides* x *P. nigra* clones (D51, DN10 and DN70), and one *P. nigra* x *P. maximowczii* clone (NM6). The hybrid poplar clones were planted as cuttings (mean length = 25 cm; mean ground line diameter = 1.2 cm) obtained from the Short-Rotation Woody Crops Program at the State University of New York's College of Environmental Science and Forestry (SUNY-ESF). Two-year old white spruce seedlings were planted in the Pure Spruce and Mixture treatments. In the Mixture treatment, the white spruce seedlings were planted as groups in each hybrid poplar quarter plot. The Pure Spruce whole plots were not split and considered as a single group. The white spruce seedlings were 2+0 half-sib individuals provided by a J.D. Irving, LLC. tree nursery in New Brunswick, Canada. White spruce seedlings were grown in MP67 multi-pots with a 65-cm$^3$ rooting volume. The average seedling height was 15 cm and the mean ground line diameter was 2.6 mm at the time of planting. Thus the Pure Spruce

measurement plots included 100 white spruce seedlings, the Pure Poplar plots included 25 individuals of each of the four clones randomly assigned to one of the four quarter plots, and the Mixture plots included 68 white spruce individuals and 8 individuals of each of the four clones. The Mixture treatment included a higher proportion of spruce and spatial clumping of hybrid poplar to increase the chance that the slower growing spruce could compete with hybrid poplar to produce a mixed stand. Within the Mixture plantings, hybrid poplar were clustered in groups of 4-10 individuals with each clone randomly assigned to each quarter plot. Ground line diameter above the root collar was measured for all trees to the nearest millimeter, while height was measured to the nearest tenth of a meter.

The whole plots were initially prepared in June of 2003 by controlling all shrub and hardwood stems with a basal application of 20% triclopyr as Garlon 4® in Bark Oil EC Blue®, followed by brushsawing to remove the dead biomass from the plots. In mid-August 2003, the remaining woody and herbaceous vegetation was controlled with a broadcast application of 2.8 kg ha$^{-1}$ acid equivalent (a.e.) glyphosate as Accord Concentrate®. In May 2004, the white spruce seedlings and hybrid poplar cuttings were planted on a 2 m x 2 m spacing and caged to prevent browsing. Because of low initial survival (approximately 51%) of poplar after the first year, largely due to an unusually cool spring and summer, all plots were replanted (filling in holes of dead individuals) before the start of the second growing season (May 2005) to ensure that all the measurement plots had the same starting densities. No replanting of spruce was needed due to high survival. The replanted population were not followed separately since mean ground line diameter and height of the survivors were not different than the stems planted

the previous year (p = 0.1). In the years following planting, herbaceous and woody

vegetation were controlled in early summer (early to mid-June) using spot applications of

glyphosate (1.7 kg ha$^{-1}$ a.e.) ensuring that the crop trees were not contacted. During the

first two years after planting, crop-trees were protected from herbicide by covering with

plastic bags.
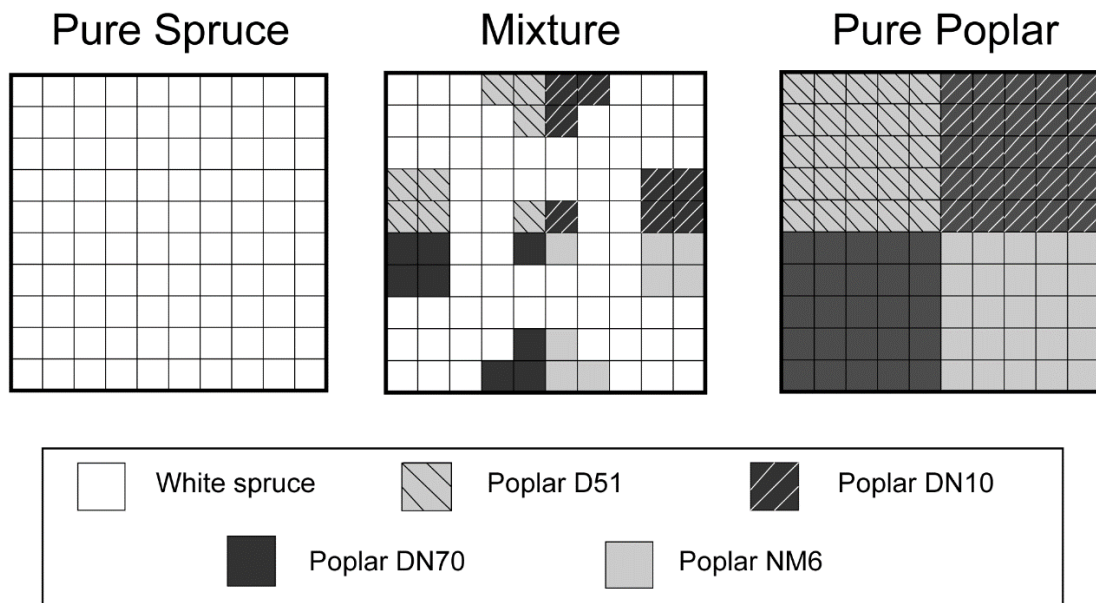


Figure 3.1. Design of the three 0.09-ha whole-plot treatments in the study. Pure Spruce are pure white spruce plantations, Mixture are plantations with 68 white spruce and 32 hybrid poplar individuals (8 of each clone), and Pure Poplar plantations are 25 of each hybrid poplar clone in quarter plots. Four poplar clones were planted: *Populus deltoides × P. nigra* (D51, DN10 & DN70) and *P. nigra × P. maximowiczii* (NM6).

### 3.3.3. Analytical approach

The Pure Spruce whole plots were not split, so in order to compare the performance of white spruce in the Pure Spruce and Mixture treatments, one-way analysis of variance (ANOVA) was used. White spruce in the quarter plots of the Mixture treatment were treated as separate groups, each associated with one of the four different hybrid poplar clones while the Pure Spruce treatment was considered a single group. Split-plot ANOVA was used to test for differences in the whole plots (Pure Poplar and Mixture) and quarter plots within whole plots for hybrid poplar (one for each clone). Biomass index ($m^3 \, ha^{-1}$), calculated as ground line diameter$^2$ x height was used to estimate stand yields. Additionally, mean height, ground line diameter and individual tree biomass index were used to compare individual tree attributes. Height and diameter growth rates were calculated as the difference between two measurement periods divided by the number of years.

Both the spruce and hybrid poplar analyses used mixed-effects ANOVA to test for differences in stand level biomass index ($m^3 \, ha^{-1}$), mean biomass index ($m^3$), mean height (m), mean ground line diameter (cm), and mean survival (%) after six years of growth. Preliminary analysis of maximum plot values suggested differences among the clones consistent with mean values. Therefore we decided to use mean plot values to address the three hypotheses. Hypothesis 1 was tested using a one-way mixed-effects ANOVA of whole plot means with treatment as fixed effect and whole plot replicate as a random effect. Hypothesis 2 was investigated using a mixed-effects split-plot ANOVA to test for difference in hybrid poplar performance. The fixed effects of the model consisted of: treatment (whole plot), clone (split-plot) and their interaction, while replicate within

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whole plot and the clone x replicate within whole plot interaction were the random effects. Hypothesis 3 was tested using a one-way mixed-effects ANOVA for spruce and consisted of the treatment fixed effects: Mixture-D51, Mixture-DN10, Mixture-DN70, Mixture-NM6 and Pure Spruce, while whole plot replicate was the random effect. Significance of fixed effects in the linear models was evaluated at the $\alpha = 0.05$ level for all of the analyses. We used standard linear models for one-way and split-plot ANOVA (Quinn and Keough 2002). Multiple comparison tests were performed using Tukey's Honest Significant Difference at $\alpha = 0.05$. Additionally, the models were modified for repeated measures ANOVA to analyze height (cm $yr^{-1}$) and basal diameter (cm $yr^{-1}$) growth rates. Since autocorrelation among observation is common in time-series analyses (Neter and Wasserman 1974), a power error structure was added to the repeated measures models. Based on model fit statistics, inclusion of the power error structure improved the model fits. All ANOVA analyses were performed with the MIXED procedure in SAS software version 9.2 (SAS 2009). The relationship between white spruce and hybrid poplar yield in the Mixture treatment was analyzed with nonlinear mixed-effects models using the nlme library (Pinheiro et al. 2013) in R version 2.13.0 (R Core Team 2013), where whole-plot replicate was the random effect. The data were fit to the following model form:

$$Y = \beta_0 + \beta_1 e^{(-\beta_2 X)}$$

where the $\beta_i$'s are parameters to be estimated, Y is white spruce biomass index and X is hybrid poplar biomass index. The normality and constant variance assumptions of the

ANOVA and regression analyses were analyzed using the Shapiro-Wilks normality test and plots of fitted versus predicted values, respectively.

## 3.4. Results

### 3.4.1. Individual tree characteristics

In general, the growth rates of the four clones were similar for the first three growing seasons (Figure 3.2). Following this year, the height and diameter growth rates of clone NM6 were superior to the other three clones in the Mixture treatment ($p < 0.05$). During the sixth growing season, height growth of NM6 was $2.0 \pm 0.2$ m yr$^{-1}$ while the three *P. deltoides* x *P. nigra* clones ranged from $0.9 \pm 0.2$ m yr$^{-1}$ (clone D51) to $1.1 \pm 0.2$ m yr$^{-1}$ (clone DN70). Similarly, diameter growth of clone NM6 was $2.6 \pm 0.3$ cm yr$^{-1}$, a greater rate than clone D51 growing at $1.2 \pm 0.3$ cm yr$^{-1}$ ($p = 0.002$). In the Pure Poplar treatment, clone NM6 had a greater height growth rate than the other three clones, but their diameter growth rates were similar. After the third growing season, clone DN10 consistently had the lowest height and diameter growth rates in the pure plantations. Height growth of DN10 in the sixth season was $0.9 \pm 0.2$ m yr$^{-1}$ compared to the $1.6 \pm 0.2$ m yr$^{-1}$ rate of NM6 ($p = 0.001$). Comparatively, the diameter growth of DN10 was $1.6 \pm 0.3$ cm $^{-1}$ while NM6 was growing at $2.2 \pm 0.3$ cm yr$^{-1}$ ($p = 0.12$).
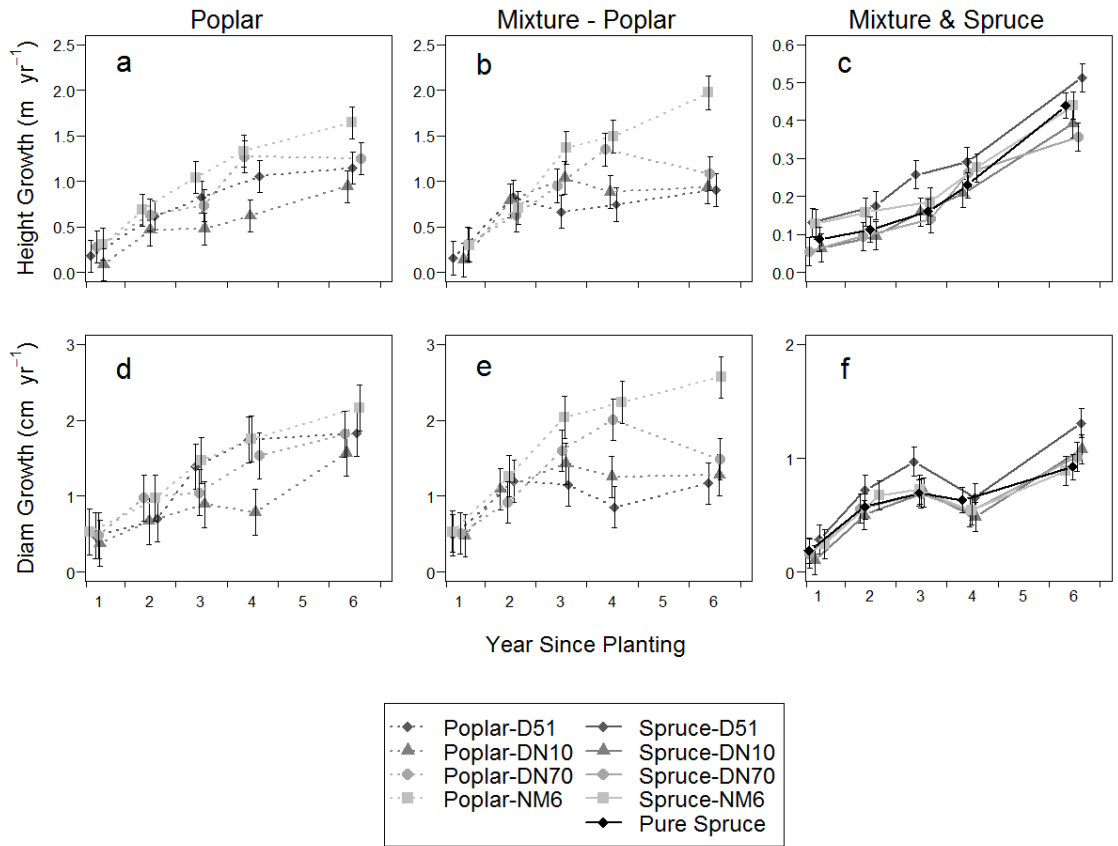
Figure 3.2. Species-specific least square mean growth rates of height (m yr$^{-1}$) and ground line diameter (cm yr$^{-1}$) by year following planting of the four hybrid poplar clones in the Pure Poplar (a, d) and Mixture (b, e) stands and for white spruce in Mixture and Pure Spruce stands (c, f). Error bars represent ± 1 standard error. Note that the y-axis scale on graphs (c) and (f) are different than the other graphs.

The superior growth rates of clone NM6 resulted in the greatest individual tree performance by the sixth growing season (Table 3.2). Although the growth rates and size of the three *P. deltoides* x *P. nigra* clones were similar, biomass index of DN70 was 27% and 2% greater than DN10 and D51, respectively, in the Pure Poplar treatment and 46% and 95% greater in the Mixture treatment after six years. By the sixth season, the height of clone NM6 in the Pure Poplar treatment ($6.9 \pm 0.9$ m) was 60% greater than clone DN10 ($3.7 \pm 0.9$ m). In addition to being the smallest clone in the Pure Poplar treatment, DN10 had the poorest survival ($20 \pm 11\%$), substantially lower than the $75 \pm 11\%$ survival of NM6 ($p = 0.001$). In the Mixture treatment, the height, ground line diameter and biomass index of clone NM6 was greater than the other three clones ($p < 0.03$). For instance, the mean height of NM6 ($8.1 \pm 0.9$ m) and mean diameter ($11.5 \pm 1.3$ cm) in mixture were 47% greater than clone DN10 ($p < 0.009$). Additionally, the survival of clone NM6 in the Mixture treatment ($91 \pm 11\%$) was 25%, 35% and 31% greater than clones DN70, DN10 and D51 respectively.

Table 3.2. Least square means (± 1 standard error) of tree height, ground line diameter, biomass index and survival six years following planting for the four hybrid *Populus* clones in the Pure Poplar (Poplar) and Mixture treatments. The four clones were: *P. deltoides x P. nigra* (D51, DN10, DN70) and *P. nigra x P. maximowczii* (NM6). Within each column and across both treatments, clones with the same letters indicate factors that were not significantly different at α = 0.05 using Tukey's HSD test.

| | Height (m) | Diameter (cm) | Biomass Index (m$^3$) | Survival (%) |
|---|---|---|---|---|
| Poplar - D51 | $5.2 \pm 0.9^{bc}$ | $7.9 \pm 1.3^{b}$ | $0.05 \pm 0.02^{bc}$ | $41 \pm 11^{cd}$ |
| Poplar - DN10 | $3.7 \pm 0.9^{c}$ | $5.9 \pm 1.3^{b}$ | $0.04 \pm 0.02^{bc}$ | $20 \pm 11^{d}$ |
| Poplar – DN70 | $5.6 \pm 0.9^{bc}$ | $7.5 \pm 1.3^{b}$ | $0.05 \pm 0.02^{bc}$ | $63 \pm 11^{abc}$ |
| Poplar – NM6 | $6.9 \pm 0.9^{ab}$ | $9.0 \pm 1.3^{ab}$ | $0.09 \pm 0.02^{b}$ | $75 \pm 11^{ab}$ |
| Mixture - D51 | $4.4 \pm 0.9^{c}$ | $6.0 \pm 1.3^{b}$ | $0.02 \pm 0.02^{c}$ | $60 \pm 11^{bc}$ |
| Mixture - DN10 | $5.1 \pm 0.9^{bc}$ | $7.1 \pm 1.3^{b}$ | $0.04 \pm 0.02^{bc}$ | $56 \pm 11^{bc}$ |
| Mixture - DN70 | $5.6 \pm 0.9^{bc}$ | $7.9 \pm 1.3^{b}$ | $0.06 \pm 0.02^{bc}$ | $66 \pm 11^{abc}$ |
| Mixture - NM6 | $8.1 \pm 0.9^{a}$ | $11.5 \pm 1.3^{a}$ | $0.14 \pm 0.02^{a}$ | $91 \pm 11^{a}$ |

Between the two whole plot treatments, intra-clonal hybrid poplar performance was similar (p > 0.05). For instance, the mean height of NM6 in the Mixture treatment was 8.1 ± 0.9 m, while the height of the clone in the Pure Poplar treatment was 6.9 ± 0.9 m (p = 0.21). Additionally, intra-clonal survival was similar between the treatments (p = 0.25). The only noticeable difference in the performance ranking of the clones between the two treatments was that clone D51 was a poorer performer than DN10 in Mixture, while DN10 was the poorest performer in the Pure Poplar treatment.

In contrast to the hybrid poplar, height and diameter growth rates were similar among the four white spruce groups in the Mixture treatment and the Pure Spruce group (Figure 3.2). The five groups all experienced a slight dip in diameter growth during the fourth growing season, while height growth rates continued to increase. By the sixth growing season, height growth of the D51 group in mixture ($0.5 \pm 0.1$ m yr$^{-1}$) was 36% greater than the DN70 group, 27% greater than the DN10 group and 15% greater than the Pure Spruce treatment ($p < 0.04$). Additionally the diameter growth of the D51 group in mixture ($1.3 \pm 0.1$ cm yr$^{-1}$) was greater than the NM6 group and the Pure Spruce treatment (both $0.9 \pm 0.1$ cm yr$^{-1}$) ($p<0.02$). Although the D51 white spruce group had greater height growth than the other Mixture groups, mean heights were similar in the sixth season (Table 3.3; $p = 0.52$). The results indicate that the ground line diameter of the NM6 group ($3.7 \pm 0.4$ cm) was lower than the $5.0 \pm 0.4$ cm diameter of the D51 group ($p = 0.02$). Coincidently, D51 was the poorest performing hybrid poplar clone in the Mixture treatment. Survival was similar among the four Mixture groups, but the $97 \pm 7$% survival of the D51 group was greater than the $78 \pm 7$% of the Pure Spruce treatment ($p = 0.03$).

Table 3.3. Least square means (± 1 standard error) of tree height, ground line diameter, biomass index and survival of improved white spruce six years following planting in the Pure Spruce and Mixture treatments. Within the Mixture treatment, the corresponding *Populus* clone is listed. Within columns and across both treatments, populations with the same letters in each column indicate factors that were not significantly different at α = 0.05 using Tukey's HSD test.

| | Height (m) | Diameter (cm) | Biomass Index (m³) | Survival (%) |
|---|---|---|---|---|
| Pure Spruce | $1.6 \pm 1.3^a$ | $4.2 \pm 0.4^{ab}$ | $0.004 \pm 0.001^{ab}$ | $78 \pm 7^b$ |
| Mixture – D51 | $1.8 \pm 1.3^a$ | $5.0 \pm 0.4^a$ | $0.005 \pm 0.001^a$ | $97 \pm 7^a$ |
| Mixture – DN10 | $1.7 \pm 1.3^a$ | $4.8 \pm 0.4^{ab}$ | $0.004 \pm 0.001^{ab}$ | $94 \pm 7^{ab}$ |
| Mixture – DN70 | $1.7 \pm 1.3^a$ | $4.5 \pm 0.4^{ab}$ | $0.004 \pm 0.001^{ab}$ | $90 \pm 7^{ab}$ |
| Mixture – NM6 | $1.5 \pm 1.3^a$ | $3.7 \pm 0.4^b$ | $0.003 \pm 0.001^b$ | $87 \pm 7^{ab}$ |

### 3.4.2. Stand-level Production

Total stand biomass index after six years was greatest in the Pure Poplar treatment ($86.1 \pm 16.6$ m³ ha⁻¹), followed by the Mixture treatment ($50.2 \pm 16.6$ m³ ha⁻¹), and lastly the Pure Spruce treatment. Within the Pure Poplar treatment, clone NM6 contributed the most to total stand yield with $151.0 \pm 28.1$ m³ ha⁻¹ (Figure 3.3a), which was 134% greater than the $29.6 \pm 28.1$ m³ ha⁻¹ contribution of DN10 (p =0.01) and 98% greater than the $51.8 \pm 28.1$ m³ ha⁻¹ contribution of D51 (p = 0.01). Similarly, NM6 had the greatest contribution in the Mixture treatment ($101.8 \pm 28.1$ m³ ha⁻¹) followed by DN70, DN10 and lastly D51. Between the whole plot treatments, clones D51, DN10 and NM6 had similar contributions to overall treatment yield. Clone NM6 contributed 44% to hybrid poplar yield in the Pure Poplar treatment and 58% in Mixture, while the DN10 contribution was 9% and 13% respectively.
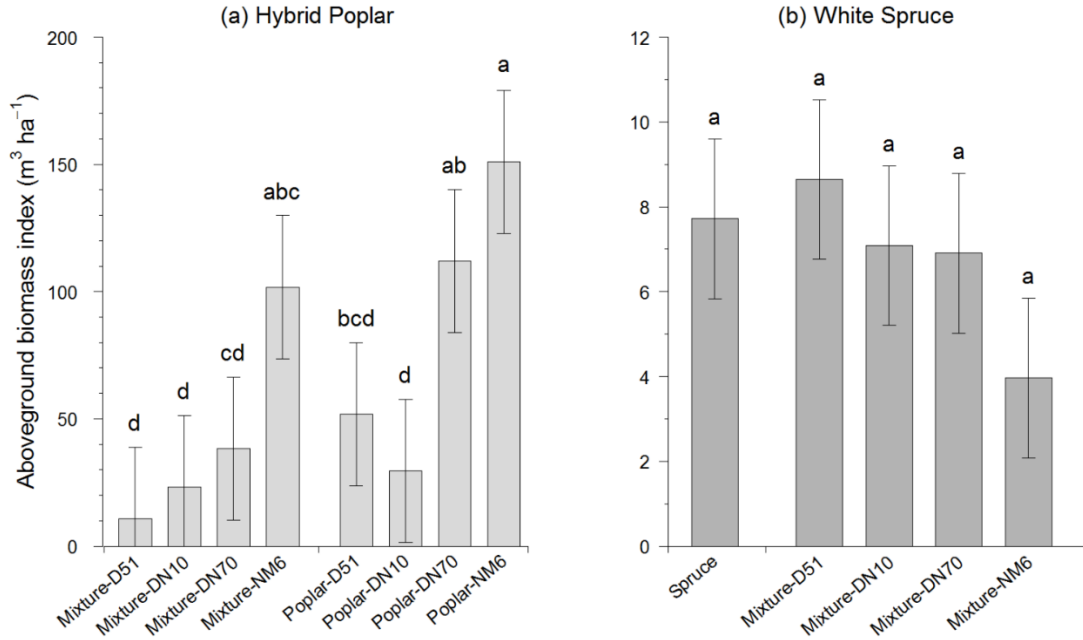
Figure 3.3. Least square mean total biomass index (m³ ha⁻¹) by species after six years of growth of hybrid poplar (a) and white spruce (b) in each of the respective treatments (hybrid poplar – Pure Poplar (Poplar) and Mixture, white spruce – Pure Spruce and Mixture), and the four hybrid poplar clones (D51, DN10, DN70 and NM6). Error bars represent ± 1 standard error. Mean separation was performed using Tukey's HSD test at $\alpha = 0.05$. Clones or white spruce groups with the same letter were not significantly different.

White spruce stand biomass index was similar among the Mixture groups and the Pure Spruce treatment (p = 0.38) (Figure 3.3b). The D51 group biomass index was 8.6 ± 1.9 m³ ha⁻¹ while the biomass index of the NM6 group was 4.0 ± 1.9 m³ ha⁻¹ (p = 0.07). In the Mixture treatment, a nonlinear exponential decay relationship was found between white spruce and hybrid poplar biomass index (Figure 3.4). The analysis demonstrated that the white spruce group growing with clone NM6 had lower biomass index than the group growing with D51, similar to the results of the individual tree measurements. The final model found to best represent the relationship was:

$$Y = 1.678 + 8.644e^{(-0.019X)}$$

with an $R^2$ of 0.68 for the fixed effect of poplar biomass index.
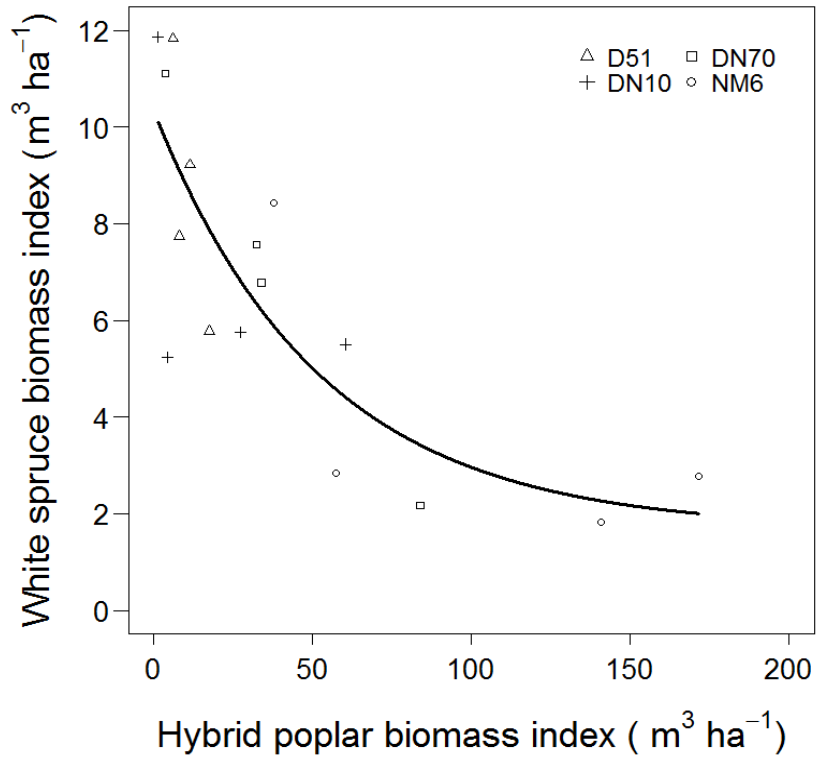


Figure 3.4. Nonlinear relationship between white spruce biomass index and hybrid poplar biomass index in the Mixture treatment. The different symbols represent the four hybrid poplar clones. The regression was developed from the pooled data of the four replicates. The $R^2$ of the model fit was 0.68.

## 3.5. Discussion

Among the three whole plot treatments, the biomass index ranking was Pure Poplar > Mixture > Pure Spruce as would be expected with the substantially different growth rates between the hybrid polar and spruce and their respective planting densities. Thus, we confirmed our first hypothesis regarding the ordering of the treatments in respect to stand biomass index. These results occurred because of the inherent rapid growth rates of intensively managed hybrid poplar, and the relatively slower growth rates of white spruce (Figure 3.2). Further, we saw little evidence of overyielding in the Mixture treatment; yields appeared nearly proportional to the pure yields of each species or clone but at their respective planting densities.

After six growing seasons, clone NM6 consistently had the greatest height and diameter growth rates among the four clones tested which resulted in the clone being the largest individual and contributing the greatest to stand yields in both treatments. Hence, we rejected our second hypothesis of no clonal differences. This result was unexpected as all four clones have been successful in earlier field trials in the Northeast and were thought to perform similarly. Lo and Abrahamson (1996) found that these four clones ranked in the top 7 of 54 clones tested in northern New York, but their site was afforested agricultural lands with soils high in base saturation. Among the clones in the Pure Poplar treatment, DN10 and D51 had lower yields than clone NM6, and also slightly lower mean height and diameter growth rates. The stand level difference in biomass index between the clones is likely due to both the lower survival of DN10 and D51 and their inherent lower growth rates. Overall, clones D51 and DN10 produced lower total stand biomass, had lower survival, and slightly lower growth rates than clones DN70 and NM6. These

differences suggest that factors not accounted for within this study may have influenced

clone expression, such as site conditions and site × genotype interactions. Although our

site is typical for many reforestation sites in northeastern United States, it is stony, with

relatively poorly drained soils, two undesirable site characteristics for hybrid poplar

plantations (Dickmann and Stuart 1983).

Hybrid poplar plantations produce highest yields when grown on uniform sites with deep

soils of moderate texture, good aeration, and high nutrient concentrations (Dickmann and

Stuart 1983). Measurements of soil resources and conditions at our study site indicated

the opposite: heterogeneous, stony, and poorly drained conditions (Table 3.1), which

likely accounts for the substantially lower performance than those documented in other

studies of hybrid poplar. For example, Labrecque and Teodorescu (2005) found that

clone NM6 (obtained from the same source – SUNY-ESF) had a total aboveground

biomass yield of 72.2 Mg ha$^{-1}$ after three years of growth when planted at a density of

18,000 tph on an abandoned agricultural site. Compared to upper mineral horizon soil

analyses at their site, concentrations of P and K, and percent organic matter were much

lower at our site. Additionally, our site had a much higher proportion of sand and lower

proportion of clay than their site. Greater yields on agricultural lands were found in many

other regions, including the upper Great Plains of the United States (Tuskan and Rensema

1992) and southern Sweden (Karacic et al. 2003).

The yields observed in this study were comparable to those reported from other sub-

optimal sites, particularly for DN70 and NM6, our best performing clones. For instance,

Laureysens et al. (2004) compared the performance of three *P. deltoides × P. nigra*

clones on anthropogenic soils in Belgium, and found that after four years, the yield of

their best performing clone ("Primo") was slightly greater than our best performing clone of the same species cross (DN70) after six years of growth, although they planted 10,000 tph compared to our 2,500 tph. Additionally, Czapowskyj and Safford (1993) found that after six years of growth of two *P. maximowiczii x P. trichocarpa* clones planted at 2,500 tph in eastern Maine, yields of approximately 7 Mg ha$^{-1}$ were achieved when interspecific competition was controlled but no soil amendments were applied. Their yields were slightly greater than those observed in our study, but still low compared to studies on agricultural lands, suggesting that the limitations to hybrid poplar production at our site was strongly influenced by the soil conditions.

Although the total stand contributions of the four white spruce populations in mixture were not different, individual tree measurements indicated that the ground line diameter and mean biomass index of the D51 group was greater than the NM6 group. Therefore, we rejected our hypothesis that there would be no differences among the white spruce groups. The lack of differences in contribution to stand yields likely occurred because both Pure Spruce and Mixture treatments were designed to minimize early intra- and interspecific competition, and because the genetics differences were minimized by planting half-sib seedlings. The difference in the mean diameters between the D51 group and the NM6 group is likely due to multiple factors, including the lower survival of the D51 clone in mixture and greater light availability to the spruce. White spruce has been found to maintain high height growth rates at light levels at or above 40% (Lieffers and Stadt 1994), which likely are available to the D51 group due to the clone's low survival. Similarly, it has been shown that reducing woody competition around white spruce individuals tended to increase mean diameter when grown in mixture with trembling

aspen, while height growth was relatively unaffected (Pitt et al. 2010). In a comparison of the gap light environments below *P. deltoides × P. nigra* and *P. nigra × P. maximowiczii* clones, Paquette et al. (2008) found that the light transmittance through a NM6 clone was lower than through *P. deltoides × P. nigra* clone, which they attribute to clonal differences in crown allometrics. Therefore, the greater survival and allometrics of clone NM6 in our study may be a reason for the lower mean diameter of the NM6 white spruce group.

White spruce plantations generally have been shown to exhibit peak performance at a particular site when woody and herbaceous competition are controlled early in plantation development (Cole et al. 2003; Pitt and Bell 2005; Pitt et al. 2010), and we can assume that the yields found for the Pure Spruce treatment at our site was at a maximum without the addition of fertilization or soil site preparation. Compared to plantations of young planted white spruce from the same nursery and with the same planting density, Burgess et al. (2010) found that after nine years of growth the mean height and ground line diameter of white spruce in their intensive herbicide treatment was similar to the results we found after six years of growth. Their white spruce stands likely had already closed canopy when individual trees typically begin to slow growth rates due to inter-tree competition while our plantations had not, which may be why the mean height and diameters were similar. Additionally, the white spruce biomass yield in the Pure Spruce treatment was found to be lower than those estimated for nine year old planted white spruce plantations in northern Ontario (Pitt and Bell 2005) even though their planting density was 1,700 tph (Bell et al. 1997). Similar to the low performance of the hybrid poplar clones, the lower spruce yield may be due to the poorer site conditions, and also

possibly due to differences in plantation age. Mean survival of spruce in the Pure Spruce treatment was 78% (range of 58-98%), which we suspect is largely due to the lower quality soils since aboveground competition was minimal and the plantations had yet to reach crown closure. At our site, we feel that differences in soil drainage may have driven variation in survival. Depth to redoximorphic features is a quantitative measure of soil drainage, roughly equivalent to the seasonal high water table, and can be related to tree growth in the region because it infers a limitation to root growth (Briggs 1994; Meng and Seymour 1992). Redoximorphic depth was highly variable across our site ($10 - 95$ cm, Table 3.1). This and other soil conditions such as coarse rock fragments, within and between the Pure Spruce treatment replicates, may be a reason for the variation survival and resulting stand yields after six years.

We found no intra-clonal differences in size or yield between the Pure Poplar and Mixture treatments except for clone DN70 (Table 3.2, Figure 3.3a), which was surprising since the planting density in the Mixture treatment was 1700 tph lower than the Pure Poplar treatment. Similarly, the only difference found for the white spruce groups was the mean diameters in the D51 and NM6 groups, but the nonlinear regression analysis revealed a relationship of lower spruce yield to higher poplar yield in mixture (Figure 3.4). This result suggests that the presence of vigorous hybrid poplar clones negatively influenced the performance of white spruce. Mixture of species with similar aboveground requirements, such as moderately shade-tolerant white spruce and shade-intolerant hybrid poplar, are not typically recommended (Kelty 2006) since the two species may have similar resource demands, potentially resulting in single-species dominance. Interspecific competition theory suggests that competition for resource availability tends to be

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asymmetric with larger individuals capturing a greater proportion of the resources (Goldberg 1990; Weiner 1990). Additionally, different strategies of resource capture and efficiencies at using the resources (Binkley et al. 2004) can influence how the individual species perform in mixture and affect the overall stand productivity. For these reasons, plantation mixtures are often composed of complementary species (Bergqvist 1999; Simard and Hannam 2000) or mixtures where one species provides facilitative benefits, neither of which characterizes hybrid poplar-white spruce mixtures. Therefore, the inherently faster growth rates of the hybrid poplar would require a novel planting scheme design to minimize early interspecific interaction of the two species. Early results from this study suggest that clumping the hybrid poplar planting locations in the Mixture treatment rather than even dispersion achieved the goal of minimizing the pre-crown closure interaction of the two. This relationship may change in the future as the spruce performance may decrease with increasing size of the hybrid poplars.

The planting design in the Mixture treatment may seem operationally infeasible since the rotation length of the two species will obviously differ. The hybrid poplar under the no fertilization silvicultural regime will likely mature around age 20. Around the age the hybrid poplars mature, the planted white spruce should be sufficient in size to warrant commercial thinning. Pelletier and Pitt (2008) found a single early (age 19 – 24) commercial thinning in white spruce plantations increased merchantable volume by 24% over unthinned stands, suggesting that an early thin of the residual white spruce stands may increase volume growth rates and potentially reduce the final rotation age of the stands. The commercial thinning operation could occur at the same time the hybrid poplars are harvested which would minimize the number of entries into the stands and

therefore reduce damage to the residual white spruce crop-trees. An alternative design to manage these two species in mixture may be to "unmix to mixtures" and plant pure groupings of spruce and hybrid poplar in larger blocks. Comeau et al. (2005) suggest this may be an appropriate strategy for sites that are of low productivity and relatively inaccessible since the maintenance costs are low once the plantations are established. Additionally, splitting the species into discrete blocks helps meet multiple wood supply objectives, while minimizing damage to residual trees.

In contrast to the Pure Spruce or Pure Poplar treatments which will likely only provide a single product, the Mixture treatment can potentially provide multiple products. For instance, if the hybrid poplar clones are grown to an age of 20 years they could be harvested for biomass or pulp while the white spruce from the commercial thin could be used for pulp or small sawlogs. By age 20, the hybrid poplars in the Pure Poplar treatment may produce yields of $300 - 400$ $m^3$ $ha^{-1}$ (Wilson et al. 2000), and since the Mixture treatment has 33% lower densities we would suspect a proportionally lower yield of $100 - 130$ $m^3$ $ha^{-1}$. At the same time, the white spruce commercial thin may remove $20\text{-}35$ $m^3$ $ha^{-1}$ potentially resulting in yields of $180 - 275$ $m^3$ $ha^{-1}$ after 40 years of growth in the Mixture treatment (Pelletier and Pitt 2008).

### 3.6. Conclusion

Forest management in northeastern North America could benefit from increasing intensities of silviculture and establishing more plantations, especially with increasing interests in providing a greater diversity of forest products and enhancing forest carbon sequestration in North America. Current plantation silviculture in the region typically

relies on growing softwood species, commonly in monospecific stands. Although our results demonstrate this is an effective strategy for maximizing early growth of white spruce plantations, it may be possible to diversify compositional objectives and forest products by planting both white spruce and hybrid poplar plantations. Unfortunately, research on the performance of different hybrid poplar clones in Maine is limited, and our results suggest that a *P. nigra* × *P. maximowiczii* had the greatest individual tree and stand performance among the four clones tested. Additionally, in comparison with other studies of hybrid poplar in North America, the yields from our experiment were much lower, possibly due to the harsh soil conditions at the site. Many forested areas in the region have similar site conditions which may limit large scale establishment of hybrid poplar plantations. We found that the performance of hybrid poplar and white spruce was similar between pure plantings and mixture suggesting that if this strategy was desired for landowners with similar site conditions that it may be possible to mix a vigorous clone with white spruce on a larger scale, or plant a mosaic of pure stands. These stands could be managed by performing an early commercial thinning of the white spruce while harvesting the hybrid poplar. This strategy would reduce the number of intermediate entries and minimize damage to the residual white spruce crop-trees. Therefore, we believe that the three strategies presented here contribute to the silvicultural options in the region and may be useful for landowners interested in diversifying their wood supplies and forest products.

# CHAPTER 4

# INFLUENCE OF MANAGEMENT INTENSITY ON THE PRODUCTIVITY
# OF EARLY SUCCESSIONAL ACADIAN STANDS
# IN EASTERN MAINE[2]

## 4.1. Abstract

Early successional stands composed of naturally regenerated hardwood and conifer

species are abundant in the forests of northeastern North America. Substantial

improvements in the composition and growth of these stands may be possible with early

management intervention. Unfortunately, stand responses to early management inputs are

poorly understood since many of these stands are rarely manipulated. We examined the

response of early successional stands to combinations of two management intensities

(with and without enrichment planting and different levels of vegetation control) and

three compositional objectives (hardwood, mixedwood, and conifer). The treatments

were designed to represent management options available in the region including

hardwood thinning, conifer release, and a combination of treatments to promote

hardwood-conifer mixedwood stands. Seven years after treatment, yields of the two

hardwood thinning treatments ranged from 43.4 to 56.6 Mg ha$^{-1}$, which were similar to

the 52.9 Mg ha$^{-1}$ yield of the untreated control but with 17 and 46% lower densities,

respectively. In the conifer release treatments, removal of hardwoods promoted conifer

dominance and resulted in yields between 19.9 and 30.4 Mg ha$^{-1}$ seven years after

treatment. The conifer release treatments will likely be dominated by conifers in the future with varying hardwood densities due to hardwoods establishing in gaps without conifers. After seven years, yields of the mixedwood treatments were between 19% and 47% greater than the conifer release treatments due to the retention of thinned hardwood stems and represent stands that dominate much of the forestland in the region. Results from this study demonstrated that early successional stands can be effectively managed during early stand development to improve growth and the longer-term composition.

## 4.2. Introduction

Early-successional vegetation is common across northeastern North America due to historic land-use practices (Lorimer and White 2003). The majority of these stands are naturally regenerated and often composed of a mixture of desirable and undesirable conifer and hardwood species that could be manipulated to improve species composition and growth over the longer term. The management opportunity is particularly important in the Acadian forest region of Maine and eastern Canada – a transitional forest between the eastern hardwood forest to the south and the boreal forest to the north (Braun 1950). For example, 0.9 million ha (13%) of forestlands are dominated by early successional hardwood species and 1.7 million ha (24%) are dominated by saplings in the state of Maine (McWilliams et al. 2005). The majority of these stands generally go untreated even though shifting species composition early in stand development can lead to long-term dominance of desirable species with greater growth rates (Olson et al. 2012). In addition, there are increasing regional demands to harvest trees for energy production (Benjamin et al. 2010) and early successional forests are often dominated by rapidly growing hardwood species that may be used to supply these demands. Therefore, early

successional forests in the region may be managed to meet more diverse management objectives. Unfortunately, there are few long-term experiments documenting the response of early successional stands to management, such as thinning hardwood species or releasing conifer regeneration from overtopping hardwood cover.

In northeastern North America, early successional forests arise following disturbances that remove most or all of the pre-existing overstory. One such disturbance, large clearcuts, were common in Maine following the large-scale spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreak in the 1970's and 1980's that left hundreds of thousands of hectares of standing dead conifer trees (Seymour 1992). Without management, many of these clearcut stands regenerated to overstories dominated by shade intolerant hardwood species with understories of shade tolerant conifer. These mixedwood stands continue to shift further toward hardwood dominance over time unless hardwood cover is removed to promote the slower growing, shade tolerant conifers (Newton et al. 1992; Olson et al. 2012). In recent years, clearcutting has accounted for < 4% of the annual harvest (Maine Forest Service 2010) and harvesting practices have shifted to selective partial harvesting with little or no management of composition or density after harvest. This extensive management promotes hardwood-conifer mixedwood composition, often with high residual densities and a large proportion of noncommercial species that will continue to shift in dominance towards lower quality hardwoods over time (Olson and Wagner 2010; Saunders and Wagner 2008). These changing harvesting practices are likely contributing to the decline in juvenile conifer-dominated forests that may have negative consequences for wildlife habitat (Hoving et al. 2004). Further, lack of compositional and density management in many mixedwood

stands leads to slower growth and a higher prevalence of noncommerical species, which together may reduce the regional capacity to increase yields for energy production.

Multiple options are available to manage early successional mixedwood stands during stand development across the region. Unfortunately, since many of the conifer species in the region have slow juvenile growth rates, early release from competition is often necessary to maintain conifer composition throughout stand development. With a moderate investment, desirable conifer species can be promoted during stand initiation and very early stem exclusion with conifer release treatments (Newton et al. 1992; Olson et al. 2012). Likewise, a higher proportion of desirable hardwood species can be promoted through precommercial crop tree release, cleaning, and weeding (Nelson and Wagner 2011; Ward 2009; Zenner and Puettmann 2008). Later, during the self-thinning stage of stand development, precommercial thinning (PCT) and commercial thinning can be used to increase hardwood growth (Gilmore et al. 2006; Miller 2000; Rice et al. 2001), or reduce hardwood density and increase residual conifer growth (Olson et al. 2012). Further investment, such as enrichment planting, may enhance stand growth, and allow for greater control over the stocking of desirable species (Greene et al. 2002; Kabzems et al. 2007; Paquette et al. 2006a, b). With the exception of conifer release treatments, many of these management options have not been investigated with well-controlled experiments. Therefore, it has been difficult to speculate on stand responses from these treatments.

Manipulating early successional stands in the stand initiation and early stem exclusion stages can direct long-term species composition and may enhance growth rates of the residual stand. Fortunately in northeastern North America, natural regeneration is prolific

and diverse (Brissette 1996) allowing flexibility to shift composition in directions that can meet diverse product mixes and create multiple habitat needs from these mixedwood stands. Therefore, the overall goal of this investigation was to document the response of early successional stands to a wide range of management inputs designed to shift species composition to hardwood, mixedwood, or conifer at two intensities of silviculture (with and without enrichment planting and different levels of vegetation control). The treatments were designed to represent management options currently available in the region including conifer release treatments, hardwood PCT, and a combination of the two to promote continued mixedwood stand development. The specific objectives of this investigation were to: (1) document the initial differences in stand productivity among the three compositional objectives, and (2) determine whether increased silvicultural intensity, including vegetation control and enrichment planting increased productivity of stands for all three compositional objectives.

## 4.3. Methods

### 4.3.1. Study Site

The experiment was installed on the Penobscot Experimental Forest (PEF) in eastern Maine, near the towns of Bradley and Eddington (44° 49' N, 68° 38' W). The PEF is in the Acadian region. Lying between the eastern hardwood and boreal forest, the Acadian forest region has characteristics of both, commonly composed of both hardwoods and conifers. Natural forest composition on the PEF is dominated by shade tolerant conifer species, including balsam fir (*Abies balsamifera* (L.) Mill.), eastern hemlock (*Tsuga canadensis* L.), and red spruce (*Picea rubens* Sarg.), and shade intolerant hardwood

species, including trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*Populus grandidentata* Michx.), and paper birch (*Betula papyifera* Marsh.), and mid-tolerant red maple (*Acer rubrum* L.) (Sendak et al. 2003). The PEF is located in eastern Maine where the climate is cool and humid. February is the coldest month on average (-7.1°C) while July is typically the warmest (20.0 °C). Mean precipitation is 1070 mm, and the average growing season last approximately 160 days (Sendak et al. 2003). Soils at the PEF are of Wisconsian glacial till origin (Sendak et al. 2003) and the soil classifications at the study site range from loamy, mixed, active, acid, frigid, shallow, Aeric Endoquepts to coarse-loamy, isotic, frigid, Aquic Haplothods. The soils are rocky with a shallow seasonal water table (about 30 cm) across the site (Nelson et al. 2012).

The experiment was installed in 2004 on a 9.2 ha site that was clearcut in 1995 with approximately 2.3 $m^2$ $ha^{-1}$ of residual basal area. Following harvest, the site naturally regenerated to shade intolerant hardwoods (trembling aspen, bigtooth aspen, paper birch, and gray birch (*Betula populifolia* Marsh.)) and mid-tolerant red maple, with an understory of balsam fir, red spruce, white pine (*Pinus strobus* L.) and white spruce (*Picea glauca* (Moench) Voss). Shortly after harvest, Norway (*Picea abies* (L.) Karst.), red, black (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and white spruce were planted to increase the density of desirable conifer species, but nearly all of the planting failed due to hare clipping during the first winter (Robert Seymour *personal communication*).

## 4.3.2. Experimental Design

The experimental design included two silvicultural intensities (low and medium) and three compositional objectives (hardwood, mixedwood, and conifer), plus an untreated control. Abbreviations for the array of treatments are: Low Conifer (LC), Low Mixedwood (LM), Low Hardwood (LH), Medium Conifer (MC), Medium Mixedwood (MM), Medium Hardwood (MH), and Untreated Control (UC). Each of the seven treatments was replicated four times in a randomized design across twenty-eight 30 m x 30 m treatment plots.

In each treatment plot, crop trees were selected within each 2 m x 2 m growing space (i.e., an average of 225 spaces per plot). Depending on treatment, these growing spaces were assigned one of four crop tree types: naturally regenerated hardwood, planted hybrid poplar (*Populus* clones), naturally regenerated conifer, or planted white spruce (Table 4.1). Compositional targets of hardwood treatments were 100% hardwood, the conifer treatments 100% conifer, and mixedwood treatments 67% conifer and 33% hardwood.

For both naturally regenerated crop tree types, all woody vegetation within a 1-m radius around crop trees was controlled. Hardwood competitors around conifer trees were controlled using a basal-bark application of 20% Garlon 4® (triclopyr ester) mixed with Bark Oil Blue® (Table 4.2) applied by backpack sprayer to all sides of the bottom 20-30 cm of each stem. Since aspen stems originating from root-suckering were common across the site, hardwood competitors around hardwood crop trees were controlled using motorized brushsaws to avoid potential herbicide damage to crop trees through shared

root systems with controlled trees (i.e., flashback). All conifer competitors were controlled using motorized brushsaws. The medium intensity treatments differed from the low intensity treatment by enrichment planting and a follow-up control of competing vegetation as a backpack herbicide treatment using glyphosate herbicide in a 1-m radius around each crop tree.

Table 4.1. Mean density (stems per hectare) ± one standard deviation of natural hardwood, planted hybrid poplar, natural conifer, and planted white spruce crop trees in each of the seven treatments at the start of the experiment. The proportion (%) ± one standard deviation of crop-trees is shown in parentheses, and n.a. indicates crop trees not available in a treatment.

| Treatment | Natural hardwood | Hybrid poplar | Natural conifer | Planted white spruce |
|---|---|---|---|---|
| Untreated Control | 2,256 ± 270 (87 ± 16) | n.a. | 238 ± 181 (14 ± 3) | n.a. |
| Low Conifer | 769 ± 249 (30 ± 3) | n.a. | 1,681 ± 301 (70 ± 8) | n.a. |
| Medium Conifer | n.a. | n.a. | 1,356 ± 72 (54 ± 4) | 1,356 ± 72 (46 ± 3) |
| Low Mixedwood | 1,363 ± 113 (52 ± 7) | n.a. | 1,169 ± 128 (45 ± 7) | n.a. |
| Medium Mixedwood | 419 ± 13 (17 ± 3) | 425 ± 20 (17 ± 2) | 850 ± 35 (34 ± 4) | 819 ± 13 (33 ± 1) |
| Low Hardwood | 2,394 ± 232 (89 ± 11) | n.a. | 217 ± 118 (6 ± 2) | n.a. |
| Medium Hardwood | 1,288 ± 43 (51 ± 9) | 1,244 ± 31 (49 ± 11) | n.a. | n.a. |

Table 4.2. Description of the vegetation control methods used to achieve the desired species composition (hardwood, mixedwood, and conifer) and level of silvicultural intensity (low & medium).

| Treatment | Herbaceous Control | | Shrub & Hardwood Control | | Conifer Control | |
|---|---|---|---|---|---|---|
| | Method | Duration | Method | Duration | Method | Duration |
| Untreated Control | - | - | - | - | - | - |
| Low Conifer | - | - | Triclopyr bark application | 1 year | - | - |
| Medium Conifer | Glyphosate foliar spot-treatment | 2 years | Triclopyr bark application | 2 years | - | - |
| Low Mixedwood | - | - | Triclopyr bark application and brushsaw | 1 year | - | - |
| Medium Mixedwood | Glyphosate foliar spot-treatment | 2 years | Triclopyr bark application and brushsaw | 2 years | - | - |
| Low Hardwood | - | - | Brushsaw | 1 year | Brushsaw | 1 year |
| Medium Hardwood | Glyphosate foliar spot-treatment | 2 years | Brushsaw | 2 years | Brushsaw | 1 year |

Growing spaces assigned to fill-planted hybrid poplar and white spruce in the medium intensity treatments were treated with herbicides (triclopyr bark applications and glyphosate foliar treatments) and manually cleared of all preexisting woody and herbaceous vegetation. The four hybrid poplar clones included three *Populus deltoides* x *Populus nigra* clones (D51, DN10 and DN70), and one *Populus nigra* x *Populus maximowiczii* clone (NM6). Each treatment plot planted with hybrid poplar was divided into four quarter plots, and one clone was randomly assigned to each. The hybrid poplar cuttings were obtained from the Short-Rotation Woody Crops Programs at the State University of New York's College of Environmental Science and Forestry. The white spruce seedlings were 2+0 half-sib individuals grown in MP67 multi-pots with a 65-cm$^3$ rooting volume. White spruce seedlings were obtained from a J.D. Irving, LLC tree nursery in New Brunswick, Canada.

When summed across all growing spaces, the low-intensity treatments represent a combination of PCT and crop tree release to favor conifer domination (LC), hardwood domination (LH), or mixedwood composition (LM). The medium intensity treatments have the same compositional goals and basic treatment, but also included herbaceous vegetation control and enrichment planting to increase stocking with white spruce with 1,250 trees per hectare (tph) (MC), 312 tph per hybrid poplar clone (MH), or 367 tph white spruce and 44 tph of each hybrid poplar clone (MM).

### 4.3.3. Variable Measured

To track overall changes in composition and structure within treatments, five 16-m$^2$ circular sample plots were located in each treatment plot. Four of these plots were centered 12.7 m from the center of the plot towards the four corners. The fifth plot was located directly in the center of each treatment plot. Diameter at breast height (DBH) of all trees ≥ 1.37 m in height were measured and identified by species in each sample plot. Measurements were collected prior to treatment in 2003, two immediate post-treatment measurements (2004 & 2005) and the sixth and seven years after treatment (2009 & 2010). Measurements were collected at the start of the subsequent growing seasons when hardwood leaves were beginning to flush in late May and early June.

### 4.3.4. Analytical Approach

Changes in tree composition were analyzed using relative importance value (%), which is an index of a species importance in a plant community (Curtis and McIntosh 1951) and was calculated as the average of relative frequency, relative density, and relative dominance of a given species. Relative frequency was calculated as the number of sample plots where a species was present divided by the total number of sample plots in each treatment plot (5 sample plots in each treatment plot). Relative density was calculated as the trees per hectare of a species divided by the cumulative stem density in each treatment plot. Relative dominance was calculated as the species-specific, oven-dry mass (kg ha$^{-1}$) divided by the cumulative oven-dry mass of all species in each treatment plot.

Species were grouped into one of three categories: desirable hardwood – aspen, paper birch, yellow birch (*Betula alleghaniensis* Britton), red maple, ash (*Fraxinus* sp.) and northern red oak (*Quercus rubra* L.); undesirable hardwood – gray birch (*Betula populifolia* Marsh.), cherry (*Prunus* sp.), and willow (*Salix* sp.); and conifer – balsam fir, spruce sp., eastern white pine, and eastern hemlock. Total aboveground dry mass (foliage plus wood) of the most common hardwood species (red maple, gray birch, paper birch, trembling aspen and bigtooth aspen) and the planted white spruce were estimated using site-specific dry mass equations fit to data spanning the DBH distributions of the experiment (Chapter 1). Total aboveground dry mass of the remaining species was estimated using the equations of Ter-Mikaelian and Korzukhin (1997). All of the equations estimated dry mass using the power function:

$$M = \beta_0 DBH^{\beta_1}$$

where M is oven-dry total aboveground biomass (kg) and $\beta_i$'s were species-specific parameters. Dry mass was then summed for each treatment plot and scaled to per hectare values.

Stand structure was analyzed by calculating stand dry mass (Mg ha$^{-1}$) and current annual increment (CAI; Mg ha$^{-1}$ yr$^{-1}$). Additionally, DBH (cm) distribution was analyzed by fitting a Weibull function, and estimating shape and scale parameters using maximum likelihood (Robinson 2004). Dry mass was analyzed for each of the 5 measurement years (pre-treatment, 1,2,6,7 years after treatment), while CAI was only analyzed for measurement years 2, 6, and 7. CAI could not be calculated for the 1st measurement year because the metric required two consecutive post treatment measurements. Diameter

distributions were only analyzed for pre-treatment, 2 and 7 years after treatment

measurements to simplify interpretation. The two-parameter Weibull probability density

function used to model DBH distributions had the form (Bailey and Dell 1973):

$$f(x) = \frac{c}{b} \times \frac{x^{c-1}}{b} \times e^{-\left(\frac{x}{b}\right)^c} ; x \geq 0, b > 0, c > 0$$

where x is the value of interest, in this case DBH, b is the scale parameter and c is the

shape parameter to be estimated. A shape parameter less than 1 results in a reverse J-

shaped distribution; if the shape parameter is equal to one then the function resembles an

exponential distribution; and if the shape parameter is near 3.6, the function approximates

a normal distribution (Bailey and Dell 1973).

Stand structure variables (cumulative dry mass, CAI, Weibull shape & scale parameters)

were analyzed using repeated measures analysis of variance (ANOVA) to test for

differences among treatments, years, and treatment × year interactions. Extended mixed-

effects models (Pinheiro and Bates 2000) were used to account for serial correlation

among years by including a random replicate within treatment term as well as a

continuous time autoregressive correlation function of order 1 ($\psi$; CAR1). The CAR1

function accounts for the correlation of the within-year error, which is common in

repeated-measures analysis (Pinheiro and Bates 2000). Additionally, preliminary

examination of the models suggested heteroscedastic residual variance, where variance

increased with greater fitted values. This result was expected because following treatment

application, within-treatment heterogeneity was initially reduced by the management

activities. In subsequent years, within-treatment heterogeneity increased as stand

structure diversified. Rather than transforming the dependent variables to rectify

heterescedastic residuals, the models were improved by including an estimated within-

year variance parameter for each inventory with the form:

$$Var(\varepsilon_{ij}) = \sigma^2 \delta_{sij}^2$$

where $Var(\varepsilon_{ij})$ is variance for each measurement, $\sigma^2$ is the standard error and $\delta_{sij}^2$ is the

estimated variance parameter for each measurement. Including this function in the model

provided different estimates of least-square standard errors for each inventory. All

ANOVA models were fit using the nlme package (Pinheiro et al. 2013) in R version

2.13.2 (R Core Team 2013). Least-squares means and standard errors of all models were

calculated using the lsmeans package in R (Lenth 2013). Incorporating within-year and

within-treatment variance and accounting for serial correlation among inventories vastly

improved model performance and homogenized overall residual variance. Similar models

were used to analyze importance value, but species group and its interactions with year

and treatment were included.

## 4.4. Results

### 4.4.1. Species Composition

Stem densities of trees $\geq 1.37$ m tall in the UC treatment were dominated by aspen

species (56 $\pm$ 9%), birch species (20 $\pm$ 15%), and red maple (13 $\pm$ 18%) prior to

treatment, while conifers were only 4% of the total density (Table 4.3). After seven years,

the proportion of hardwood density in the UC treatment was 93 $\pm$ 11%, while conifer

density increased to 7 $\pm$ 11%. In the LH treatment, hardwood density was reduced from

17,045 ± 1069 tph prior to treatment to 4,456 ± 2,477 tph two years after treatment, and increased to 10,750 ± 6,565 tph after seven years, mostly from increases in red maple and birch densities through stump sprouting and ingrowth. Similarly in the MH treatment, hardwood density was reduced from 13,648 ± 4,702 tph to 3,802 ± 3,596 two year after treatment, and increased to 7,416 ± 3,873 tph after seven years. Comparatively, the conifer treatments (LC and MC), substantially reduced hardwood density from 16,110 ± 4,380 tph to 1,558 ± 360 tph in the LC treatment and from 15,144 ± 1,545 tph to 717 ± 605 tph in the MC treatment two years after treatment, while balsam fir density increased three-fold in the LC treatment and four-fold in the MC treatment seven years after treatment (Table 4.4). Hardwood species accounted for over 90% of the total density prior to treatment in the LM and MM treatments, but were reduced from 14,022 ± 5,709 tph to 1,215 ± 542 tph and 13,991 ± 3,789 tph to 1,184 ± 388 tph in the LM and MM treatments, respectively, two years after treatment (Table 4.5). Seven years after treatment, hardwood density increased to 2,991 ± 1,666 tph and 3,677 ± 1,050 tph, while conifer density increased to 4,331 ± 2,487 tph and 2,836 ± 1,645 tph, in the LM and MM treatments, respectively.

Table 4.3. Stem density of hardwood and conifer species greater than 1.37 m tall in the untreated control, low (without enrichment planting) and medium (with enrichment planting) hardwood treatments. Mean ± one standard deviation in hundreds of stems per hectare are shown for the pre-treatment measurement (Pre-Trt), 2 and 7 years after the establishment of the study. n.p. indicates enrichment planted species not planted in a particular treatment. The Other Hardwood group includes: cherry species, willow species, northern red oak, and ash species.

| | Untreated Control | | | Low Hardwood | | | Medium Hardwood | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Pre-Trt | 2 | 7 | Pre-Trt | 2 | 7 | Pre-Trt | 2 | 7 |
| Red maple | 25.9 ± 38.0 | 22.4 ± 18.1 | 23.1 ± 20.7 | 38.6 ± 7.8 | 5.3 ± 1.2 | 21.5 ± 8.9 | 28.0 ± 32.6 | 17.8 ± 24.7 | 24.9 ± 25.6 |
| Birch species | 30.5 ± 29.7 | 29.6 ± 20.1 | 37.7 ± 25.2 | 24.6 ± 38.8 | 15.3 ± 27.3 | 46.1 ± 74.9 | 18.7 ± 23.1 | 3.1 ± 5.4 | 18.4 ± 16.6 |
| Aspen species | 86.0 ± 17.1 | 63.3 ± 8.3 | 46.7 ± 9.0 | 96.9 ± 25.6 | 22.1 ± 4.8 | 18.1 ± 2.6 | 78.5 ± 8.3 | 17.1 ± 12.1 | 18.4 ± 11.6 |
| American beech | 6.9 ± 12.9 | 9.3 ± 14.2 | 10.9 ± 15.3 | 2.5 ± 5.0 | 0.0 ± 0.0 | 6.2 ± 11.6 | 8.7 ± 16.6 | 0.0 ± 0.0 | 7.2 ± 11.1 |
| Other Hardwood | 2.8 ± 4.8 | 4.1 ± 4.9 | 6.2 ± 7.4 | 7.8 ± 10.3 | 1.9 ± 1.6 | 15.6 ± 14.6 | 2.5 ± 3.1 | 0.0 ± 0.0 | 4.4 ± 3.3 |
| Hybrid poplar | n.p. | n.p. | n.p. | n.p. | n.p. | n.p. | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.9 ± 1.2 |
| Balsam fir | 6.2 ± 7.4 | 6.5 ± 8.5 | 12.8 ± 13.8 | 5.9 ± 5.4 | 2.2 ± 2.8 | 7.8 ± 6.9 | 0.9 ± 1.2 | 0.0 ± 0.0 | 0.9 ± 1.2 |
| Spruce species | 0.0 ± 0.0 | 1.2 ± 1.8 | 2.5 ± 4.2 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.3 ± 2.8 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.3 ± 0.6 |

Table 4.4. Stem density of hardwood and conifer species greater than 1.37 m tall in the low (without enrichment planting) and medium (with enrichment planting) conifer treatments. Mean ± one standard deviation in hundreds of stems per hectare are shown for the pre-treatment measurement (Pre-Trt), 2 and 7 years after the establishment of the study. n.p. indicates enrichment planted species not planted in a particular treatment. The Other Hardwood group includes: cherry species, willow species, northern red oak, and ash species.

| Species | Low Conifer | | | Medium Conifer | | |
|---|---|---|---|---|---|---|
| | Pre-Trt | 2 | 7 | Pre-Trt | 2 | 7 |
| Red maple | 31.8 ± 3.3 | 5.9 ± 8.8 | 11.8 ± 14.3 | 25.6 ± 20.7 | 0.0 ± 0.0 | 4.1 ± 4.5 |
| Birch species | 12.5 ± 23.3 | 0.0 ± 0.0 | 3.4 ± 2.6 | 4.1 ± 4.2 | 1.9 ± 3.7 | 9.7 ± 9.9 |
| Aspen species | 73.2 ± 37.2 | 5.3 ± 4.2 | 9.0 ± 4.1 | 84.8 ± 33.6 | 1.2 ± 1.8 | 6.2 ± 8.4 |
| American beech | 39.0 ± 62.5 | 3.4 ± 5.3 | 7.5 ± 11.9 | 22.4 ± 21.0 | 1.9 ± 2.2 | 4.1 ± 2.6 |
| Other Hardwood | 4.7 ± 5.6 | 0.9 ± 1.9 | 2.2 ± 2.1 | 14.6 ± 1.2 | 2.2 ± 1.6 | 10.6 ± 11.5 |
| Balsam fir | 13.1 ± 10.9 | 19.9 ± 10.9 | 35.5 ± 18.5 | 7.8 ± 8.0 | 15.0 ± 14.6 | 35.2 ± 20.5 |
| Spruce species | 0.0 ± 0.0 | 0.6 ± 1.2 | 3.1 ± 1.6 | 0.0 ± 0.0 | 0.3 ± 0.6 | 6.5 ± 7.3 |
| Planted white spruce | n.p. | n.p. | n.p. | 0.0 ± 0.0 | 0.0 ± 0.0 | 6.9 ± 8.0 |

Table 4.5. Stem density of hardwood and conifer species greater than 1.37 m tall in the low (without enrichment planting) and medium (with enrichment planting) mixedwood treatments. Mean ± one standard deviation in hundreds of stems per hectare are shown for the pre-treatment measurement (Pre-Trt), 2 and 7 years after the establishment of the study. n.p. indicates enrichment planted species not planted in a particular treatment. The Other Hardwood group includes: cherry species, willow species, northern red oak, and ash species.

| Species | Low Mixedwood | | | Medium Mixedwood | | |
|---|---|---|---|---|---|---|
| | Pre-Trt | 2 | 7 | Pre-Trt | 2 | 7 |
| Red maple | 30.2 ± 13.0 | 1.9 ± 2.4 | 6.5 ± 7.6 | 22.7 ± 17.4 | 0.3 ± 0.6 | 8.4 ± 7.7 |
| Birch species | 12.2 ± 17.8 | 0.9 ± 1.2 | 4.4 ± 4.4 | 35.5 ± 52.8 | 4.1 ± 5.0 | 16.5 ± 21.8 |
| Aspen species | 80.7 ± 44.2 | 8.4 ± 3.3 | 10.3 ± 2.9 | 65.7 ± 18.5 | 4.1 ± 1.9 | 4.4 ± 0.7 |
| American beech | 9.3 ± 6.8 | 0.6 ± 0.7 | 3.4 ± 2.9 | 14.0 ± 19.4 | 1.9 ± 3.0 | 4.1 ± 4.9 |
| Other Hardwood | 7.8 ± 8.5 | 0.3 ± 0.6 | 5.3 ± 6.6 | 1.9 ± 3.0 | 1.6 ± 2.4 | 3.1 ± 3.9 |
| Hybrid poplar | n.p. | n.p. | n.p. | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.3 ± 0.6 |
| Balsam fir | 10.3 ± 9.0 | 18.7 ± 17.2 | 40.5 ± 25.1 | 7.5 ± 7.4 | 10.6 ± 8.8 | 23.4 ± 17.4 |
| Spruce species | 0.0 ± 0.0 | 1.9 ± 0.7 | 2.8 ± 2.1 | 0.0 ± 0.0 | 1.2 ± 1.4 | 2.8 ± 2.8 |
| planted white spruce | n.p. | n.p. | n.p. | 0.0 ± 0.0 | 0.0 ± 0.0 | 2.2 ± 1.2 |

All fixed-effects in the importance value model were significant, including the species group × treatment × year interaction (p<0.001), but the within-measurement year variance was greater in the second ($\delta$ = 1.510) and seventh ($\delta$ = 1.225) measurements than the pre-treatment measurement (Table 4.6). Correlation among measurements was negligible ($\psi$ < 0.001). Importance value in the UC, LH and MH treatments was dominated by desirable hardwood species throughout the seven years of development (Figure 4.1). Desirable conifer importance value in the LH treatment was initially 12.6 ± 4.1% but was reduced to 8.7 ± 6.8% two years after treatments, while desirable hardwood

importance value increased from 67.8 ± 4.1% to 74.1 ± 6.8%. Similarly, conifer

importance value in the MH treatment was 4.5 ± 4.4% before treatment and was reduced

to 0.1 ± 4.4% two years after treatment, but had increased to 9.6 ± 5.1% seven years after

treatment. Additionally, undesirable hardwood importance value was reduced from 16.3

± 4.1% to 4.9 ± 6.8% two years after treatment, but increased to 18.1 ± 5.1% seven years

post-treatment in the MH treatment. The mixedwood treatments (LM & MM) initially

had hardwood importance values > 70%, but the silvicultural prescriptions reduced the

importance value of hardwoods to 54.0 ± 4.4% and 55.6 ± 4.4% respectively, and

increased conifer importance value from 16.6 ± 4.1% and 13.5 ± 4.1% to 46.0 ± 4.4%

and 44.4 ± 4.4%, in the LM and MM treatments, respectively. The LC and MC

treatments were dominated by desirable hardwood species prior to treatment with

importance value values of 59.9 ± 4.1% and 63.1 ± 4.1%, respectively. Two years after

treatment, desirable hardwood importance value was reduced to 38.0 ± 4.4% in the LC

treatment and 16.6 ± 4.4% in the MC treatment. Seven years after treatment, conifer

importance value in the LC treatment was 49.5 ± 5.1% and 61.8 ± 5.1% in the MC

treatment.

Table 4.6. P-values of the fixed-effects, CAR(1) autocorrelation parameter estimates, replicate random effects, and within-year estimated variance parameters of the extended mixed-effects analysis of variance. Dependent variables in the models were importance value (%), Weibull diameter distribution shape and scale parameters, current annual increment (CAI; Mg ha$^{-1}$ yr$^{-1}$), and cumulative dry mass (Mg ha$^{-1}$).

| Factor | Importance Value | Weibull scale | Weibull shape | CAI | Dry Mass |
|---|---|---|---|---|---|
| Treatment | < 0.001 | 0.689 | 0.008 | < 0.001 | < 0.001 |
| Year | 0.060 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |
| Treatment x Year | < 0.001 | 0.051 | 0.043 | 0.615 | < 0.001 |
| Species group x Treatment | < 0.001 | | | | |
| Species group x Year | < 0.001 | | | | |
| Species group x Treatment x Year | < 0.001 | | | | |
| | | | | | |
| CAR(1) $\psi$[3] | < 0.001 | < 0.001 | < 0.001 | 0.068 | < 0.001 |
| Replicate random effect | 0.001 | 0.027 | < 0.001 | 1.020 | 1.827 |
| With-measurement year variance parameter[4] | | | | | |
| Pre-Treatment | 1.000 | 1.000 | 1.000 | | 1.000 |
| Measurement 1 | | | | | 0.687 |
| Measurement 2 | 1.510 | 3.138 | 2.608 | 1.000 | 0.534 |
| Measurement 6 | | | | 0.802 | 2.715 |
| Measurement 7 | 1.225 | 1.661 | 0.659 | 0. | 2.718 |

[3] The continuous-time autoregressive correlation parameter estimate ($\psi$) representing the between-measurement year correlation among observations. Default to zero, deviation from zero represents the strength of the within-group correlation.

[4] Variance parameter estimates ($\delta$) obtained by modeling different variances per stratum for each of the measurements in the analysis. For the pre-treatment (Pre-Trt), $\delta = 1$ to achieve identifiability of variance structure. Subsequent $\delta_i$ estimates represent the ratio between the standard deviation of the ith stratum and the pre-treatment stratum.
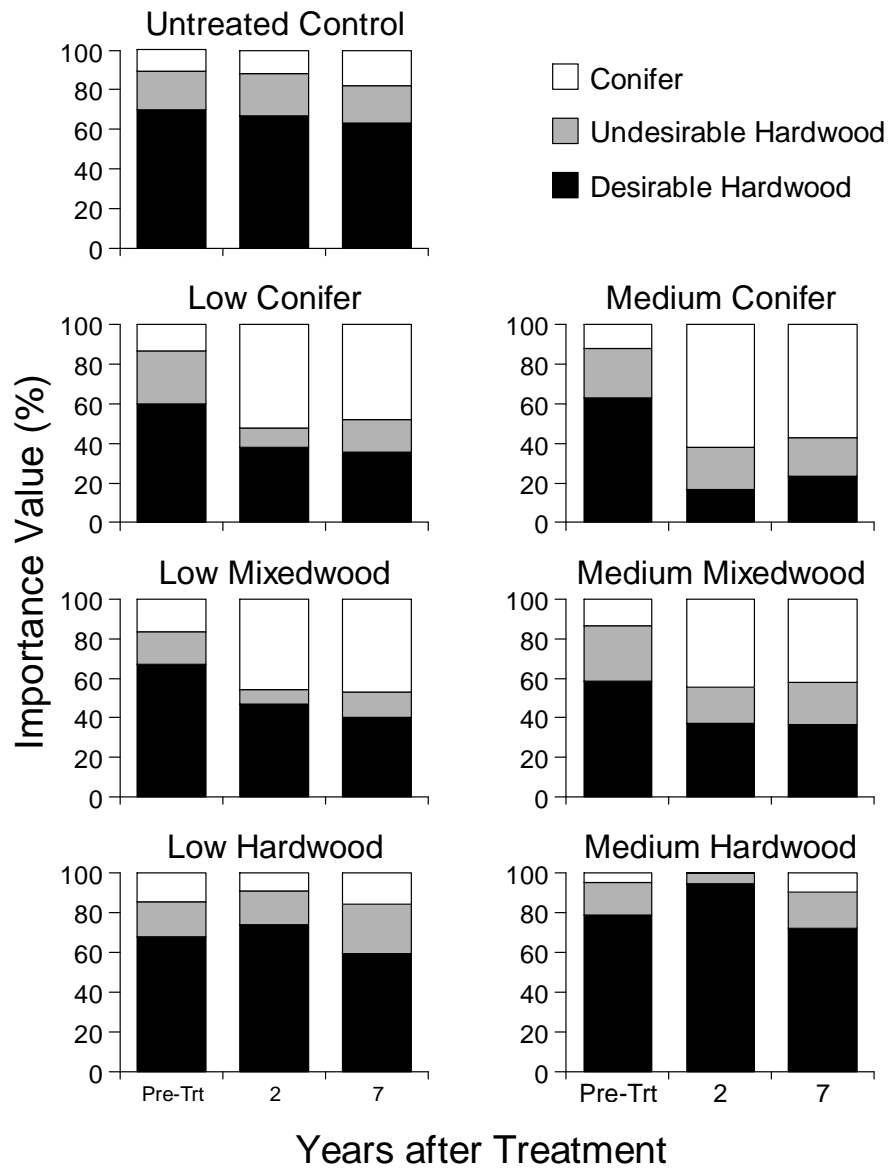
Figure 4.1. Importance value (sum of relative frequency, relative density and relative dominance) of the three species groups in the experiment (desirable hardwood, undesirable hardwood, and conifer). Three measurement years are shown: Pre-Trt – pre-treatment, 2 & 7 – two and seven years after treatment.

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## 4.4.2. Diameter Distributions

The treatment × year interaction was marginally significant for the Weibull scale (p = 0.051) and shape parameters (p = 0.043), while the within-measurement year variance was greater in the second (scale δ = 1.510; shape δ = 2.608) and seventh (scale δ = 1.661; shape δ = 0.659) post-treatment measurements than the pre-treatment measurement (Table 4.6). Prior to treatment, DBH distributions were similar among treatments, with the majority of stems between 0.1 cm and 4.0 cm DBH (Figure 4.2), and estimates of the Weibull shape parameters were lowest for the MM treatment (1.27 ± 0.13) and the highest being the LH and MH treatments (1.55 ± 0.13) (Table 4.7). Two year after treatment, overlapping standard errors suggested that the shape parameters were similar between the two silvicultural intensities for each of the compositional objectives, but by seven years after treatment, shape parameters were different with 1.48 ± 0.08 and 1.37 ± 0.8 in the LC and MC treatments, respectively, and 1.31 ± 0.08 and 1.19 ± 0.08 in the LM and MM treatments, respectively.

The majority of stems in the LH and MH treatments were between 2 and 6 cm two years after treatment. By seven years after treatment, most stems were less than 2 cm DBH, but the number of trees greater than 8 cm DBH had increased. The majority of stems in the LM and MM treatments remained in the smaller diameter classes after treatment, but similar to the hardwood treatments, the number of large trees increased by seven years after treatment. Similarly, in the LC and MC treatments, the majority of stems remained between 0.1 and 4 cm after treatment, where higher densities of large trees were found after seven years.
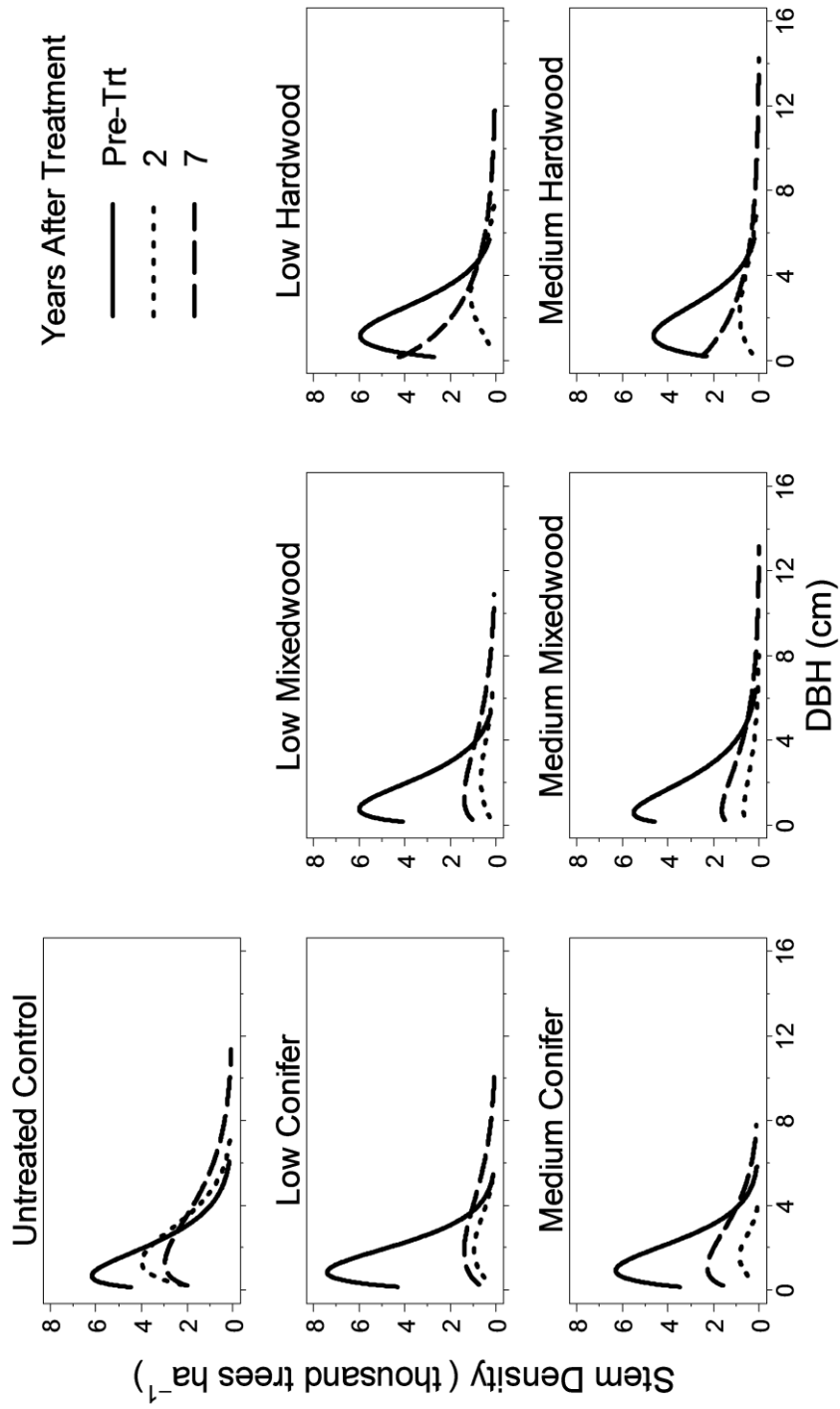
Figure 4.2. DBH distributions fit by the two-parameter Weibull function for each of the 7 treatments over three measurements: pre-treatment, 2 and 7 years post treatment.

Table 4.7. Least-square mean estimates of Weibull scale and shape parameters for each of the seven treatments. The within column least-square standard error is shown at the bottom of the table. Estimates are shown for the pre-treatment (Pre-Trt), 2nd year after treatment (2) and 7th year after treatment (7) measurements.

| Treatment | scale | | | shape | | |
|---|---|---|---|---|---|---|
| | Pre-Trt | 2 | 7 | Pre-Trt | 2 | 7 |
| Untreated Control | 1.9 | 2.61 | 3.54 | 1.33 | 1.54 | 1.34 |
| Low Conifer | 1.77 | 2.82 | 3.91 | 1.49 | 1.90 | 1.48 |
| Medium Conifer | 1.91 | 2.08 | 2.82 | 1.91 | 2.20 | 1.37 |
| Low Mixedwood | 1.87 | 3.48 | 3.91 | 1.39 | 1.73 | 1.31 |
| Medium Mixedwood | 2.00 | 2.58 | 3.2 | 1.27 | 1.24 | 1.19 |
| Low Hardwood | 2.24 | 3.94 | 2.77 | 1.55 | 2.31 | 0.97 |
| Medium Hardwood | 2.23 | 3.59 | 2.97 | 1.55 | 1.73 | 0.99 |
| Group standard error | 0.19 | 0.60 | 0.32 | 0.13 | 0.34 | 0.08 |

## 4.4.3. Dry Mass

The treatment $\times$ year interaction in the annual dry mass model, expressed as CAI, was not significant (p = 0.615), but there was correlation between the measurement years ($\psi$ = 0.068) and the standard deviation of the replicate random effect was 1.020 (Table 4.6). Two years after treatment, CAIs of the LH and MH treatments were 3.6 $\pm$ 1.4 and 0.9 $\pm$ 1.4 Mg ha$^{-1}$ yr$^{-1}$, respectively, while the CAI of the UC treatment was -1.1 $\pm$ 1.4 Mg ha$^{-1}$ yr$^{-1}$ (Figure 4.3). CAI of the hardwood treatments increased after the second year and by seven years after treatment, the CAIs of the LH, MH and UC treatments were 7.0 $\pm$ 1.0 Mg ha$^{-1}$ yr$^{-1}$, 6.2 $\pm$ 1.0 Mg ha$^{-1}$ yr$^{-1}$ and 5.4 $\pm$ 1.0 Mg ha$^{-1}$ yr$^{-1}$, respectively. CAI of the LM and MM treatments were similar two years after treatment (2.0 $\pm$ 1.4 and 2.2 $\pm$ 1.4 Mg ha$^{-1}$ yr$^{-1}$, respectively), and after seven years, the CAI of the LM treatment was only

14% greater than the MM treatment. CAI of the LC and MC treatments were similar to the other treatments two years after treatment, but after seven years, CAI of the LC treatment was $4.3 \pm 1.0$ Mg ha$^{-1}$ yr$^{-1}$ and $3.2 \pm 1.0$ Mg ha$^{-1}$ yr$^{-1}$ for the MC treatment.

The dry mass ANOVA model indicated that the treatment $\times$ year interaction was significant ($p < 0.001$) and the standard deviation of the replicate random effect was 1.827 (Table 4.6). Additionally, the within-measurement year variance ($\delta$) increased after treatment from 0.687 in the first measurement year to 2.718 in the seventh measurement year. Seven years after treatment, cumulative dry mass of the hardwood treatments were similar to the UC treatment, while the mixedwood and conifer treatments were much lower (Figure 4.3). For instance, cumulative dry mass yield of the LH treatment was 52.6 $\pm$ 5.9 Mg ha$^{-1}$ and the MH treatment yield was $43.4 \pm 5.9$ Mg ha$^{-1}$, only 0.7% and 22% lower, respectively, than the UC treatment. After seven years, the yields of the LM and MM treatments were $36.0 \pm 5.9$ Mg ha$^{-1}$ and $30.0 \pm 5.9$ Mg ha$^{-1,}$ respectively. Comparatively, yields of the LC and MC treatments were 74% and 165% lower than the UC treatment, respectively. Dry mass yields after seven years of development were similar between the low and medium intensity treatments for all three compositional treatments (p>0.05).
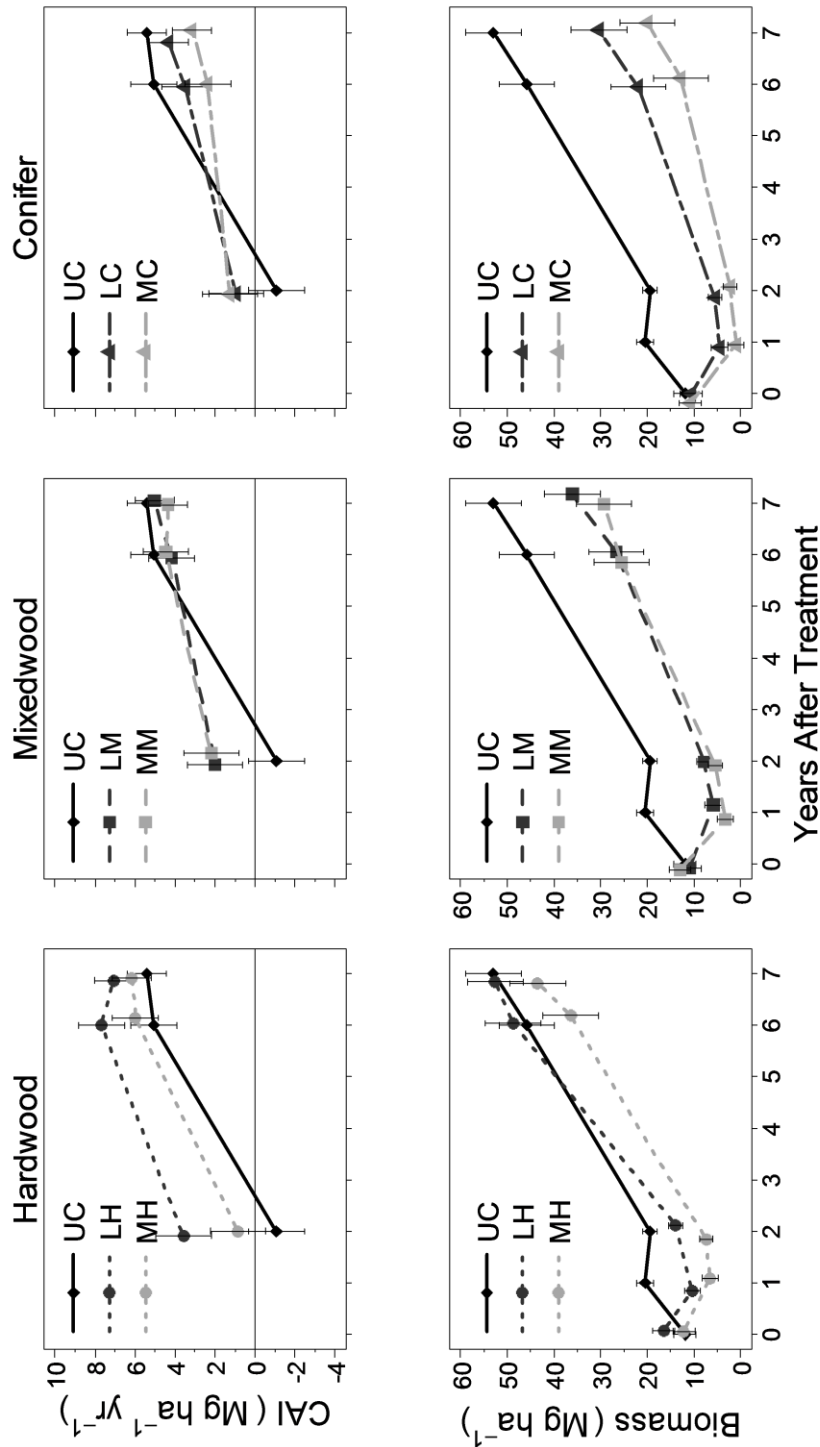
Figure 4.3. Current annual increment (CAI) in Mg ha$^{-1}$ yr$^{-1}$ and cumulative biomass in Mg ha$^{-1}$ for the hardwood, mixedwood, and conifer species composition treatments and the two different silvicultural intensities for each species composition. Growth of the Untreated Control (UC) is shown as reference for each of the three species composition. The other treatments are: Low Hardwood (LH), Low Mixedwood (LM), Low Conifer (LC), Medium Hardwood (MH), Medium Mixedwood (MM), and Medium Conifer (MC).

## 4.5. Discussion

In this investigation the developmental response through the first seven years are presented from an experiment designed to shift early successional stands in different trajectories with a variety of treatments. Three treatments were applied to promote hardwood, conifer, or mixedwood dominance, and after seven years of development the target composition and structure of the treatments have been achieved. Below, the results of each of the treatments and their applicability to early successional stands in northeastern North America are discussed. The three main treatments were: (1) thinning early successional hardwood species, (2) conifer release to promote late successional composition, and (3) a combination of the two to promote hardwood-conifer mixedwoods.

### 4.5.1. Hardwood Thinning

Hardwood composition was easily maintained in the hardwood thinning treatments (LH and MH) since this was the dominant composition prior to treatment. Additionally, yields in the LH and MH treatments were similar to the UC treatment even though densities were 19% and 45% lower, respectively. Increasing growth of residual crop trees is the goal of thinning (Smith et al. 1997; Ward 2009), but the majority of thinning research in the Acadian region has been limited to spruce-fir dominated stands (Meyer et al. 2007; Olson et al. 2012; Pitt and Lanteigne 2008; Saunders et al. 2007). Results from these investigations suggest positive responses from early thinning, increasing growth rates and merchantable volume. Our results suggest early successional hardwoods can have similar growth responses following PCT, but the financial value of the stands may be much

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lower than spruce-fir stands grown for sawlogs since the final product in hardwood stands will likely be wood chips for pulp and energy production. If, however, early successional hardwood species are being grown for products other than pulp and energy, such as low-defect sawlogs, thinning in hardwood stands may be warranted. For instance, in northern Ontario seventeen years after thinning aspen stands to various densities, Rice et al. (2001) showed that mean height and diameter growth of trembling aspen was greater with increased spacing up to 5 m x 5 m. Therefore, a possible management scenario could harvest small diameter aspen trees in a thinning for pulp and/or energy (Gilmore et al. 2006), assuming harvest costs are low enough to allow for net revenue. This would then promote the growth of the residual stand. This management system is becoming more feasible since the diversity of products such as wood composites from aspen has recently increased (Balatinecz et al. 2001; Einspahr and Wykoff 1990).

One of the consequences of thinning young hardwood stands is the ability of many species to sprout and increase small diameter tree density. Our results demonstrate that although thinning initially reduced hardwood density of stands, birch and red maple densities rebounded to densities similar to those found prior to treatment in the low intensity hardwood treatment. The increase of red maple stems are likely due to stump sprouts (Walters and Yawney 1990), which can develop soon after stems are cut and often have greater shoot growth than seed-origin individuals (Wilson 1968). Similarly, gray birch, an undesirable, noncommercial species, typically occurs in sprout clumps with high growth rates (Farrar 2006). These results show that the rapid sprout growth of these two species were the largest contributors to increased densities seven years after treatment in the LH treatment and likely contributed to the increase in yield over this time

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period. Comparatively, densities of red maple and gray birch did not increase as much in the MH treatment, likely because two consecutive years of hardwood control was performed, which removed many of stems that sprouted after the initial stems were cut.

### 4.5.2. Conifer Release

Balsam fir and spruce species are abundant in mature canopies and understories in the region, and the species are typically dominant species following various silvicultural treatments (Arseneault et al. 2011; Brissette 1996; Olson and Wagner 2010; Sendak et al. 2003). Stands that regenerate following clearcutting in the region typically require combinations of herbicide application and PCT to promote conifer dominance. Without early conifer release, the conifer understory may persist in the understory with slow growth, even though the stands may eventually convert to conifer dominance following the senescence of the overtopping hardwood species after several decades. Management that removes this overtopping hardwood cover early in the rotation can accelerate growth and development of the conifer understory, and when combined with a later rotation PCT, can increase merchantable volume growth, thus shortening the time until final harvest (Newton et al. 1992; Olson et al. 2012). For instance, Pitt et al. (2004) found that a single release of juvenile spruce from overtopping aspen cover in boreal forests increased diameter by 43% and proportional conifer basal area from 12% to 75% five years after treatment.

The conifer release treatments in our study increased conifer density, largely from ingrowth into the measurement height class (1.37 m) and early growth rates, but the stands have yet to reach crown closure. As a result, hardwood stems developed in the

available growing spaces that were initially not stocked with conifers; these hardwoods have increased in density and importance values over time. Therefore, these stands will likely maintain conifer-dominance, but still contain hardwoods until they senesce or are removed with thinning. Similar results were found in a northern Maine study, where different hardwood species showed selectivity to the different herbicide compounds tested in a conifer release trial (Olson et al. 2012). In that study, red maple was more susceptible to triclopyr and aspen was more susceptible to glyphosate resulting in mixedwood stands with different hardwood composition after forty years of development (Olson et al. 2012). Similarly, Pitt et al. (2004) found that spruce released from aspen cover increased conifer volume three-fold, but the stands still were still conifer-hardwood mixtures five years after hardwood control. In order to shift composition to nearly pure conifer composition and further increase crop tree growth, PCT may be a viable option to eliminate the residual hardwood composition after crown closure (Olson et al. 2012).

### 4.5.3. Mixedwood Treatments

Seven years after treatment, conifer and hardwood importance values were similar in the conifer and mixedwood treatments, but growth and cumulative dry mass were slightly greater in the mixedwood treatments than the conifer treatments due to the greater retention of hardwood trees. Although the importance values were similar between the treatments, the increased hardwood composition in the conifer treatments was likely from sprouting, since red maple, American beech (*Fagus grandifolia* Ehrh.), and paper and gray birch densities all increased after treatment in both conifer treatments. Although the mixedwood treatments had a one-third hardwood compositional target, the LM treatment had 18% greater dry mass than the LC treatment, and the MM treatment had 47% greater

mass than the MC treatment. Therefore, the hardwood retention in the mixedwood treatments was able to create stands structurally different than the conifer treatments. These differences will likely persist and create mature heterogeneous mixedwood stands.

Due to past harvesting practices in the region, the majority of commercial stands reflect the composition and structure in the mixedwood treatments (e.g. intimately mixed conifer and hardwood species in various size classes). Little is known about potential management strategies for these often complex mixedwood stands, but the majority are managed with some form of partial harvesting (Maine Forest Service 2010). Partial harvesting typically removes trees that have reached merchantable size and leaves the remainder of the stand untreated creating multi-cohort structures often with high densities of undesirable species. Partial harvesting is common because it is an efficient method for removing large volumes, which is often required due to the small size of many of the trees and because many stands are harvested for pulp due to the lack of significant volumes of high-value, sawlog-quality stems. Although this practice is widespread, our results present an alternative management option for young Acadian mixedwood stands, including conifer release and thinning to favor valuable species and reduce densities of defective and suppressed trees.

Even though this study should be considered preliminary in respect to the long-term effects of treatment on mixedwood composition, it is possible that intimate mixtures of aspen, birch and conifer species may have greater productivity throughout the rotation than the hardwood or conifer treatments. For instance, in the boreal forests of Canada, mixedwood composition of aspen, birch and conifers are common (Towill 1996). Experiments have demonstrated that by retaining aspen stems intermixed with planted

spruce trees, early spruce growth is typically lower than in pure plantations, but total

yield projections indicate that total stand yield could be increased by 21% (Kabzems et

al. 2007). Additionally, Pitt et al. (2010) showed that the removal of woody vegetation

(including aspen) around white spruce crop trees, reduced spruce performance because of

increased competition from herbaceous species, but hardwood composition will likely

reduce spruce diameter growth and delay sawlog production. Similar responses of

increased productivity with hardwood components in conifer stands have been

documented in Scandinavia (Bergqvist 1999).

# EPILOGUE

## Overall Findings

The novelty of this thesis is that I used a combination of production ecology, and forest biometrics to increase our understanding about the responses of early successional stands to factorial combinations of silvicultural intensities and compositional objectives. All four investigations presented here used the Silvicultural Intensity and Species Composition (SIComp) experiment on the University of Maine's Penobscot Experimental Forest (PEF). The SIComp experimental design consists of various silvicultural prescriptions designed to create stands with diverse species composition (hardwood, mixedwood, and conifer) and stand structures. The diversity of treatments in the SIComp experiment allowed for detailed exploration of aboveground growth and underlying mechanistic responses to a range of growing conditions.

This thesis begins with tree-level investigations of aboveground biomass allometrics of naturally-regenerated hardwood species, hybrid poplar clones, and planted white spruce (Chapter 1), followed by white spruce light capture, light-use efficiency (LUE; growth per unit of light capture), and foliar stable carbon isotope composition ($\delta^{13}$C) of trees planted in naturally-regenerated stands and plantations (Chapter 2). The final two chapters present results on tree- and stand level growth, yield, and compositional change of white spruce and hybrid poplar plantations (Chapter 3), and naturally-regenerated stands shifted to hardwood, mixedwood, and conifer composition at two different silvicultural intensities (one-time thinning, thinning plus enrichment planting) (Chapter 4). Major findings from each of the four chapters are:

**Chapter 1**

Aboveground biomass partitioning and the performance of various published biomass equations for juvenile hardwood trees and white spruce were examined in Chapter 1. A new set of additive component (foliage, branches, stem) sapling biomass equations were fit with a two-parameter power function, with stem diameter as the sole predictor variable. Additive equations ensured that predictions of component equations sum to predictions of total biomass, and these equations were the first set of additive component biomass equations for juvenile trees in the region. I found that as stem diameter increased, the proportion of biomass partitioned to foliage declined for red maple, paper birch, and gray birch, but increased for bigtooth aspen and trembling aspen. Comparatively, the proportion of biomass partitioned to the main stem decreased with stem diameter for the aspen species. When comparing my equations with published equations, I found total aboveground biomass predictions were similar for most of the equations, with the exception of the equations developed by Ter-Mikaelain and Korzukhin (1997). These equations substantially underestimated biomass of red maple, paper birch, gray birch, and trembling aspen. I addition, I found that the sapling woody biomass equations used by the US Forest Service's Forest Inventory and Analysis program underestimated biomass between 10% and 36% across naturally-regenerated hardwood species.

**Chapter 2**

In Chapter 2, white spruce mechanistic responses to a range of aboveground growing conditions were investigated by modeling light capture, estimating LUE, and measuring foliar $\delta^{13}C$. Overall, leaf area was found to be a suitable surrogate for estimates of light

capture, as the two variables were linearly correlated. In addition, aboveground annual growth was linearly related to light capture and leaf area. These two factors only accounted for ~50% of the variation in growth, while the remainder of unexplained variation in growth was likely influenced by unmeasured factors such as microsite soil drainage and nutrient availability. LUE did not vary across the range of neighborhood competition conditions, likely because stands have yet to reach crown closure when density-dependent competition for resources (including light) causes competitive sorting. In contrast, $\delta^{13}C$ declined with greater competition, potentially due to lower light interception and carbon assimilation.

**Chapter 3**

Chapter 3 presents the growth and yield results of pure and mixed plantations of white spruce and hybrid poplar trees. Out of the four hybrid poplar clones planted at the site, the *Populus nigra* × *Populus maximowiczii* clone outperformed the three *Populus deltoides* × *Populus nigra* clones at this rocky and somewhat poorly-drained site. Significant differences in stand production were not found among the white spruce populations in pure plantations or in mixture with the four hybrid poplar clones. But when stand yields of white spruce were regressed against hybrid poplar yields in the mixed plantations, an exponential decay pattern was found, suggesting asymmetric competition from the faster growing hybrid poplar clones negatively influenced white spruce yields.

**Chapter 4**

Stand-level responses of hardwood, conifer, and conifer-dominated mixedwood stands to a range of silvicultural intensities (untreated controls, thinned crop-trees, and thinned

crop-tree plus enrichment planting with white spruce and hybrid poplar clones) were

examined in Chapter 4. Seven years following treatment application, stand yields of the

two hardwood thinning treatments were similar to the untreated control but with

substantially lower stem densities. In contrast, yields of the conifer and mixedwood

treatments were substantially lower than the hardwood treatments and untreated controls

due to the slower growth rates of the conifer species even after release. Overall, I found

that depending on the silvicultural intensity and compositional objectives, naturally

regenerated early successional stands in the Acadian forest can be shifted towards

distinctly different long-term trajectories.

**Strengths and Limitations**

**Sapling Aboveground Biomass Models**

Chapter 1 was the first investigation to explore the performance of various published

sapling biomass equations for juvenile hardwood species and white spruce in Maine. One

of the major findings was that the sapling biomass equations used by the Forest Inventory

and Analysis (FIA) program substantially underestimated sapling woody (branches plus

stem) biomass compared to the observed data collected from the SIComp experiment. I

initially hypothesized that the FIA equations would underestimate sapling woody

biomass since between 2003 and 2009, when FIA switched their biomass estimation

methods, Maine lost nearly 35% of its sapling biomass. The corresponding

underestimation of sapling biomass between 10% and 36% for the trees in this

investigation suggested that the change to the new estimation method was the likely

culprit for the estimated declines in biomass by the US Forest Service. Accurate forest

biomass estimation in Maine and across the country is necessary to study forest growth

and estimate forest capacity to store carbon. The results showed that the new FIA

equations are not suitable for sapling hardwood species in Maine, and I recommend that

the FIA program revise their estimation methods for sapling trees.

I also developed a new set of aboveground component biomass models with the field data

from the SIComp experiment. I used a regression technique that fit the component and

total biomass equations simultaneously, which forced additivity of component biomass

predictions. Although this technique has been widely used in other regions, these are the

first set of additive component biomass equations for early hardwood species and white

spruce in the Northeast. The equations provided a good fit to the data, but one of the

major limitations is that the equations were fit to a small sample size (13-17 trees per

species) from a single site. The small sample size, especially of larger diameter trees may

limit the applicability of these equations to trees across a wider range in diameter, since

the behavior of the equations beyond the sampled tree sizes could not be evaluated. In

addition, since the trees were only sampled from the SIComp site, it is difficult to

determine the accuracy of the equations at other sites with different soil and climate

conditions, and stand composition and structure.

**White Spruce Efficiency and Carbon Isotope Composition**

One of the major objectives of Chapter 2 was to investigate the relationship between

modeled light interception and aboveground growth of white spruce sapling planted in

naturally regenerated stands and in plantations. This was the first investigation to

calibrate the MAESTRA model for naturally regenerated stands with complex species

composition in the Northeast. Most other studies that have used MAESTRA to estimate

light capture were conducted in pure and mixed species plantations with relatively uniform spacing. Comparatively, the naturally regenerated stands in the SIComp experiment were dominated by species with inherently different growth habits, and often with non-uniform spacing among trees. This condition required extensive data collection of all competitor trees in the study. Since it was infeasible to measure light interception over the course of the growing season for all 48 white spruce trees, it was not possible to test whether the model accurately estimated the amount of light intercepted by each tree. In addition, MAESTRA only provides estimates of light capture (assuming loss to reflectance and transmission) and not light interception. Therefore, I had to select average optical parameters for boreal conifer species from the literature, since these parameters were not measured. This constraint was another possible limitation to the study since the average optical parameters may not have best represented the white spruce trees at the SIComp site. Besides model calibration limitations, plot sizes around white spruce trees were limited to 6 m. Stem densities were relatively high in the naturally regenerated stands (~6,500 stems ha$^{-1}$), and taller trees outside the 6 m plots were likely interfering with light interception of the white spruce crop trees. It would have been very difficult to collect detailed measurements on all trees interfering with light interception of the white spruce trees due to time and monetary constraints, and this may have affected the results in this investigation.

Many of the studies that have investigated variation in light capture and light-use efficiency have only focused on these tree-level phenomena as potential mechanisms influencing responses to heterogeneous growing conditions. A major strength of Chapter 2 is that in addition to these tree-level factors, foliar $\delta^{13}C$ was also measured, to

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determine whether this physiological parameter was related to tree-level efficiency and aboveground productivity. I found that $\delta^{13}C$ decreased with greater neighborhood competition and lower light capture, suggesting reductions in carbon assimilation for more light-limited trees. Comparatively, light-use efficiency was not related to $\delta^{13}C$, suggesting that other potential biochemical and abiotic factors were also likely influencing light-use efficiency and aboveground productivity. Therefore, one of the main limitations of this investigation was that belowground conditions were not controlled and the amount of variation in LUE and aboveground productivity influenced by nutrient and water availability could not be investigated.

In addition, although relationships between competition, tree size, and light capture, and $\delta^{13}C$ were found, it was difficult to determine whether the physiological responses were driven more by changes in carbon assimilation or stomatal conductance. In order to determine which factor was more responsible for the variation in $\delta^{13}C$, a simultaneous measure of oxygen isotope composition ($\delta^{18}O$) would have been necessary, as $\delta^{18}O$ is only related to stomatal conductance and not carbon assimilation. Therefore, an additional limitation of this investigation was that I could only speculate as to whether changes in $\delta^{13}C$ were driven more by changes in carbon assimilation or stomatal conductance.

**Growth and Yield of the SIComp Experimental Plots**

One of the major strengths of the SIComp experiment is that all of the treatments were implemented at the same site on the PEF. Since there was only a single 9.2-ha site, site-level factors, such as soil type, climate, and topography were unlikely to be confounding

in the analyses of tree and stand growth and yield. Therefore, in both Chapters 3 and 4, I was able to demonstrate that early successional stands can be shifted onto distinctly different trajectories depending on the compositional objective and the level of silvicultural investment at a single site with similar starting conditions.

Numerous investigations in the region have studied the response of young stands to intermediate silvicultural treatments, but many of the silvicultural prescriptions were focused on promoting conifer dominance. The unique experimental design of the SIComp study allowed us to investigate multiple different silvicultural options for young stands. For instance, this is one of the first investigations to study the response of early successional hardwood species to precommercial thinning. This management strategy could be used in stands with similar composition and structure to increase growth of residual trees and promote the dominance of merchantable species, such as aspen, paper birch, and red maple. In addition, the mixedwood treatments of the SIComp experiment demonstrated an alternative management technique to enhance conifer and hardwood growth while maintaining diverse species composition. In addition, Chapter 3 showed that with greater silvicultural investment, stands can be shifted to high-yield plantations. Overall, Maine has diverse forest composition and management practices, and results from the SIComp experiment demonstrate different options for managing young early successional forests.

Although having all of the treatments plots replicated on the same site was one of the major strengths of the SIComp experiment, the lack of replication on other sites is a major limitation. Lack of replication across sites limits the scope of inference of the results to other stands in the region. For instance, few stands in Maine are currently

managed with clearcutting. It would be difficult to implement the same experimental

design in partially harvested stands because the practice typically creates stands with a

diversity of age and size structures. In addition, the mixedwood composition of many

partially harvested stands would make it difficult to use precommercial thinning to

promote dominance of early successional hardwoods. If the SIComp experimental design

were replicated at partially harvested sites, the initial starting conditions would be

substantially different. In particular, there would likely be a greater proportion of conifer

species in the larger diameter size classes, something that was not observed at the

SIComp site. Nonetheless, the SIComp study is unique in its experimental design, and

somewhat homogenous starting conditions allowed for the detailed exploration of early

stands responses to a variety of silvicultural treatments. If the study had been

implemented across multiple sites, financial and labor limitations would likely have

limited implementing the rigorous silvicultural prescriptions on a much larger scale.

**Future Research Directions and Opportunities**

The research presented in this dissertation was the first attempt to integrate the

investigation of mechanistic factors influencing tree and stand responses, and stand

dynamics of young Acadian forest stands to different silvicultural intensities and species

compositional objectives. In particular, I investigated species differences in aboveground

biomass allometrics, the effects of light capture on white spruce productivity in

contrasting growing conditions, and stand-level growth and yield responses to different

silvicultural treatments. Results from this dissertation revealed that multiple other factors,

including belowground growth and soil factors (e.g. soil chemistry, drainage), and

underlying physiological processes (e.g. assimilated carbon allocation) were likely also

influencing the development of the often complex young stands. Below, I discuss a few of the potential future projects to undertake to build on the results presented in this dissertation

**Biomass Equations in Northeastern North America**

As mentioned above, one of the major limitations of Chapter 1 was the small dataset used to develop the additive component biomass equations and verify the published regional and national biomass equations. The data was only collected from a single site and for a select number of dominant hardwood species at the site. Future projects might consider collecting biomass data from a wider range of species and tree sizes, and from multiple sites. It is worthwhile to collect data from multiple sites, as stand composition and structure may influence aboveground allometrics, particularly partitioning of foliage and branch biomass. In addition, this investigation only focused on sapling-sized (< 12.5 cm DBH) trees since sapling dominated the SIComp site. Future biomass modeling efforts should focus on encompass trees from across a range of tree sizes common on the landscape, especially since harvesting practices in the region have resulted in multi-cohort stands with diverse mixedwood species composition. It will be important to identify the dominant tree species in the region, and focus data collection efforts on those species (e.g. balsam fir, red spruce, sugar maple, yellow birch), as the biomass from these species will have the greatest influence on landscape-level estimation.

In addition to assembling more robust biomass datasets, I would suggest future biomass models should explore refined model fitting techniques. For instance, similar to the additive component biomass models presented in Chapter 1, I would suggest that all future component biomass models be fit as a system of equations to force additivity of

component predictions. Statistical software currently available makes it relatively easy to force additivity of models. One future approach would attempt to develop fitting technique that force additivity of component biomass equations but allow for the inclusion of random effects in the models. Random effects of site, plots within site, and tree within plot within sites could then be specified to examine the variability at these hierarchical level. It would also be possible to include species as a random effect in a regional biomass model, accounting for species variability within a single model instead of the current methods where separate models are often fit for each species. Another potential approach would be to use Bayesian techniques and incorporate climate and soil factors into biomass models.

A larger biomass dataset could then be used to perform a more thorough verification analysis of published biomass models. One of the limitations of the verification of the FIA sapling equations in Chapter 1 was the small amount of data points and species examined. A larger dataset would allow for verification of the FIA sapling equations, but also for the component ratio method currently used for merchantable trees ($\geq$12.5 cm DBH). Similar statistical tools, including root mean square error, mean absolute bias, and the minimum detectible negligible difference, could be used for validation. The current FIA estimation techniques have not been well verified with independent data, so such an analysis would be warranted and would provide a more holistic study of biomass prediction in the region.

**Juvenile Forest Stand Light Capture and Aboveground Productivity**

Chapter 2 examined individual white spruce light capture, light-use efficiency, and aboveground productivity in two contrasting growing conditions (plantations and

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naturally regenerated stands). Future directions of this project may including (1)

incorporating the effects of microsite belowground conditions (e.g. depth to

redoximorphic features, soil chemistry) and foliar nutrient content, (2) scaling estimates

of light interception to the stand level across the suite of SIComp treatments, (3) Link

light interception estimates with a growth model to project stand development into the

future and examine the relationship between annual light interception and productivity,

(4) refine the phonological sub-model of MAESTRA to estimate conifer light

interception during periods of the year without hardwood foliage cover, (5) further

parameterize MAESTRA to estimate annual photosynthesis to investigate the effects of

biochemical processes on aboveground productivity, and (6) examine the performance of

the recently developed MAESPA model, which combines the aboveground routines of

MAESTRA and a stand-level water balance model to examine the effects of water

availability or soil saturation on aboveground productivity.

**Stand-level Forest Development**

The stand-level growth, yield, and compositional changes of the SIComp treatments

examined in Chapters 3 and 4 are just a small portion of the long-term data. The

experiment was designed to investigate the effects of the factorial combinations of

silvicultural intensity and compositional objectives on individual crop-tree response.

Within each treatment replicate, 100 crop-trees were selected, and manual and chemical

silvicultural treatments were applied to promote the dominance of each crop-tree. The

crop-trees were measured annually from 2004 to 2011, including stem diameter, total

height, and crown length, plus periodic crown width measurements. One future research

opportunity is to analyze the crop-tree data by examining the changes in tree size and

mortality in relation to the various treatments. Energy inputs (petroleum, labor, and herbicide) required to meet the silvicultural objectives have been tracked since the experiment began. Energy input could be used as a covariate in the analysis to examine the potential trade-off associated with each of the ten treatments.

Another opportunity to pursue with the crop-tree data is the development of a growth and yield model for pre-crown closure early successional stands incorporating the effects of the different silvicultural treatments. Potential model components could include equations to predict future height, diameter, crown width, mortality, and ingrowth. The model could be parameterized to account for one-sided (e.g. basal area in larger trees) and two-sided competition (e.g. total stand basal area, stem density), the effects of different silvicultural treatments (e.g. proportion of basal area removed), and annual variability in growth by including time since treatment application. The crop-tree model could then be used to simulate tree development and examine future stand dynamics.

It might be worthwhile to select a few of the treatments and implement them on a larger, more operational scale in the region. In particular, I would focus on implementing the hardwood thinning, conifer release, and mixedwood treatments, and potentially the white spruce plantations. The majority of Maine forestlands are naturally regenerated, and based on the early results from the SIComp experiment, the thinning plus enrichment treatment would likely not be a feasible silvicultural technique due to the cost of planting and intermediate tending required to enhance the growth of the enrichment stock. Comparatively, precommercial thinning, conifer release, and conifer plantations are already part of the silvicultural toolbox in the region. Precommercial thinning is typically implemented in conifer-dominated stands, while the response of hardwood species has

received less attention. I would expand the investigation to northern hardwood dominated

stands and investigate the response of species such as sugar maple and yellow birch.

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