Early Growth as a Predictor of Canopy Class

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Abstract

A tree's position in the forest canopy is determined by its growth rate. Fast growth can secure a dominant position, which can ensure a tree acquisition of the full available light resources. A spot in the dominant canopy class is a necessity for shade intolerant species like quaking aspen (*Populus tremuloides)* because they cannot survive under the shade of overstory trees. Fast early growth in both shade intolerant and shade tolerant species can aid a tree in escaping suppression and attaining a spot in the canopy. This study sought to determine whether early growth rates differed between the four canopy classes (dominant, codominant, intermediate, and suppressed) and between different species. Significant differences between early growth rates and species were found between aspen (*Populus tremuloides)* and sugar maple (*Acer saccharum*). Significant differences between early growth rates of sugar maple and canopy classes were found. Early growth rates of sugar maple in dominant and codominant canopy classes differed from early growth rates in intermediate and suppressed, but dominant and codominant did not differ, nor did intermediate and suppressed. Early growth rates of dominant and codominant sugar maples were greater than those of intermediate and suppressed sugar maples, which was consistent with the hypothesis. Understanding the effects of early growth on canopy class can be valuable for ensuring canopy complexity, which is important for forest productivity and environmental health as a whole.

Introduction

Attainment of a dominant position in the forest canopy layer can be a result of several factors including water availability, shade tolerance and the presence or absence of canopy gaps. A tree's ability to reach the dominant canopy layer is also strongly related to its growth rate

(King 1986). Fast early growth can give a tree an advantage and allow it to secure a spot in the canopy above the others. By growing fast in the early years of a tree's life it is able to overcome suppression from surrounding trees and take advantage of available light resources (Landis and Peart 2005).

Tree growth is a combination of vertical and lateral growth. Vertical growth is the extension of height due to apical cell division and elongation at the meristem. Lateral growth is an increase in girth due to cell division in the cambium (Srivastava 1973). Both types of growth are needed to give trees a competitive advantage in their juvenile stages. Lateral growth allows for greater acquisition of water and nutrient resources and vertical growth allows trees to obtain more of the available light resources. Increased size and growth rates in the early growth stages can increase developing trees' ability to acquire resources (Wyckoff and Clark 2005).

Shade tolerant species such as sugar maple have begun to dominate the northern hardwood forests in which the UNDERC property is located. Land use changes and timber harvests have been a major contributor to the changes in forest composition in northern hardwood forests. Many of the previously dominant species like aspen have begun to decline and overstory has become dominated by sugar maple (Hardiman et al. 2011; Rhemtulla et al. 2009). Shade intolerant species like aspen in closed canopy forests are unable to have fast enough growth early on to attain a position in the canopy. This is causing the composition of the canopies of the northern hardwood forests to become less diverse (Landis and Peart 2005).

Shade by neighboring trees greatly affects the growth of developing trees. Light availability is often used to divide trees stands into one of four different canopy classes. Dominant canopy class trees emerge above the canopy, acquire full sunlight on all sides and cast shade on understory trees. Codominant trees acquire light resources primarily from the top while creating a single canopy layer above the understory trees. Intermediate trees do not emerge above the canopy but do still gain partial sunlight for at least part of the day. Suppressed trees are fully shaded by overstory trees and are rarely exposed to the sun. Because of this they acquire the least amount of light resources.

It is especially important for shade intolerant species like quaking aspen (*Populus tremuloides*) to gain as much height early on in development in order to reach the top of the canopy. They are much more susceptible to mortality via slow growth and shading. Slow growth can make aspens more susceptible to being shaded out by more shade tolerant trees that will exclude them from gaining available light (Landis and Peart 2005). Shade tolerant species like sugar maple (*Acer saccharum*) can persist under the shade suppression of other trees for longer periods of time. They are able to do this because they do not require as much sunlight to survive under the suppression of other trees. They can then take advantage of releases from suppression when canopy gaps form after by the death of overstory trees. This gives them an advantage over shade-intolerant species in a closed forest because intolerant species must secure their canopy position early on in growth (Lorimer 1981). Although shade tolerant species are able to persist in low light levels and therefore do not require as rapid of early growth as shade intolerant species, Landis and Peart (2005) found that even shade tolerant species have greater early growth in canopy trees than understory trees.

In order to take full advantage of available light, trees must not only be tall, but must be taller than the other trees around them to give them a competitive advantage (Bonser and Aarssen 1994). Dominant trees are able to acquire the most light because they shade out understory trees. Suppressed trees, on the other hand, are unable to acquire much light at all because they are excluded by the shade of the dominant trees. Therefore, it is advantageous for trees to have fast early growth and obtain a dominant spot in the canopy in order to gain full access to light.

Many long-term studies have compared growth rates of saplings to their ability to attain a dominant spot in the canopy. This study, however, uses a retrospective approach using tree rings to compare early growth to canopy class to determine if early growth can predict which canopy class a tree will eventually fall into. Because early growth is important for canopy attainment only those trees that are able to grow fast early on will be able to reach the dominant canopy class. We predict that shade intolerant species like quaking aspen would be more likely to have faster early growth rates because they must attain a dominant position in the canopy in order to escape suppression from shade tolerant species like sugar maple. We tested early growth rates of five different species northern hardwood species, which included sugar maple (*Acer saccharum),* red maple (*Acer rubrum),* balsam fir (*Abies balsamea)*, quaking aspen (*Populus tremuloides)*, and black cherry (*Prunus serotina)*. We hypothesized that there will be a difference in mean early growth rates between trees in different canopy classes as well as different species.

Methods

Study site

The study site was located within the nearly 7,500 acres of northern hardwood forest on the University of Notre Dame Environmental Research Center (UNDERC) property located in Land O' Lakes, WI in the Ottawa National Forest. These forests are dominated by species such as sugar maple (*Acer saccharum*), red maple (*Acer rubrum),* balsam fir (*Abies balsamea*), and quaking aspen (*Populus tremuloides).* Three 0.05 ha (22.36 m X 22.36 m) plots were chosen so as to span the compositional gradient within the UNDERC property. One study plot was located within an even-aged sugar maple monoculture. The second and third were located within mixed deciduous forest stands with heterogeneous composition and canopy classes.

Field Methods

The three plots were completely mapped using the "Interpoint method" outlined by Boose et al. (1998). This method uses the diameter at breast height of each tree and the distances of each tree to three surrounding trees to map tree locations. Measurements are put into the INTERPNT computer program, which performs triangulation, detects errors, and provides coordinates for each tree (Boose et al. 1998). Within each plot each tree species was recorded, and each tree was tagged and classified into one of four canopy classes: dominant, codominant, intermediate, or suppressed. The diameter at breast height was measured for each tree as well. To obtain tree ring samples, trees with stems of ≥5 cm dbh were cored twice on opposite sides of the stem in order to obtain rings from the full diameter of the tree. Cores were not collected from standing dead trees but these trees were included in the stand maps.

Ring width measurements

Cores were analyzed by counting and measuring ring widths. To count and measure ring widths cores were mounted and sanded using progressively finer sandpaper up to 600 grit. Ring widths were measured using a dissecting microscope and a Velmex measuring system (Velmex Inc., Bloomfield, New York, USA), which measures each ring to 1μm. Since samples were not cross-dated we had to assume that there were no missing rings and no false rings. Missing rings could cause a potential bias in our data because it would cause an underestimation of tree age and an overestimation of growth, and false rings would have the opposite effect.

Data Analysis

Cores from each of the dominant tree species (sugar maple, red maple, balsam fir, and quaking aspen) and each of the four canopy classes were randomly selected for measuring and analysis. Analysis of core samples focused on the measurements of early growth rings, which were defined as the rings prior to first suppression. Suppression was defined as periods in which there were 4 or more years with growth less than 1.5mm/year based on the criteria of Canham (1985). The criterion was modified for the location of the study because the trees in the sampling location had faster growth rates and therefore would not fit the original criteria. The growth rates of all of our samples were greater than 0.5 mm/year, therefore, the threshold was increased to 1.5 mm/year in order to have a suitable sample for analysis. Early growth rates were calculated by summing the ring widths up to the first year of suppression and dividing by the number of years those rings represented. Statistical analysis of the early growth included a General Linear Model and a two-way ANOVA test with species and canopy class as the predictor/independent variables and early growth rate as the dependent/response variable and a one-way ANOVA using only sugar maple with canopy class as the predictor/independent variable and early growth as the dependent/response variable.

Results

To determine if the early growth rates differed between trees of the five most abundant species (*Acer saccharum, Acer rubrum, Abies balsamea, Populus tremuloides, and Prunus serotina*) and among the four different canopy classes differed a General Linear Model test was used with average ring width per year as the predictor variable and species and canopy class as the response variables. There was a significant difference between canopy class and early growth rates (p-value<0.001, F-statistic=8.7351 on (3, 40) df) (Figure 1). There was also a significant difference in early growth rates among the different species (p-value= 0.011, F-statistic= 3.7572 on (4, 40) df) (Figure 1). Since there were not trees in each canopy class for each of the five species we were unable to determine the interactions between species and canopy class.

Aspen had overall greater mean early growth rates than sugar maple. The mean early growth rate of aspen was 2.0818 mm/year and the mean early growth rate of sugar maple was 1.7132 mm/year. Aspen also had greater mean early growth rates than sugar maple in each of the canopy classes (Table 1). This does not include suppressed, however, because there were no suppressed aspen trees. To determine differences in early growth within the different canopy classes between sugar maple and aspen a two-way ANOVA was used, however, it only tested the differences in three of the four canopy classes (dominant, codominant and intermediate) since none of the three plots contained suppressed aspen trees. There was insignificant difference in the early growth rates between the different canopy classes (p-value= 0.0647, F-statistic= 3.0034 on (2, 30) df). However, there was a significant difference in the early growth rates between the two species. (p-value= 0.0421, F-statistic= 4.5099 on (1, 30) df) (Figure 2).

A third ANOVA was used to determine how early growth differed in the four canopy classes. Only sugar maple trees were used because they were they only species in any plot that had individuals in all four canopy classes. This test resulted in a significant p-value of <0.001 (F-statistic= 11.6944 on (3,31) df). The pair-wise comparison indicated that there was no difference between codominant and dominant trees or between intermediate and suppressed. There was a significant difference between codominant and intermediate (p-value= 0.0299) as well as between codominant and suppressed (p-value <0.001). There was also a significant difference between dominant and intermediate (p-value= 0.0174) as well as between dominant and suppressed (p-value <0.001) (Figure 3).

Discussion

The overstory canopy, which consisted of trees in the dominant and codominant canopy classes, was primarily composed of sugar maple and aspen in both of the mixed deciduous plots that were sampled. The sugar maple monoculture was composed almost completely of codominant sugar maples. The only species sampled that contained individuals in all four canopy classes was sugar maple. The General Linear Model test determining the differences in early growth between the four canopy classes and among the five species resulted in significant p-values for both canopy class and species. This test, however, is inconclusive because not all species had a representative samples from each of the four canopy classes. Though each of the three plots that were sampled from were selected to be heterogeneous both in composition and canopy class, and each of the plots were completely mapped with samples were take from every tree in the plot we were still unable to obtain samples from all four canopy classes for any species other than sugar maple. Sugar maple is the most predominant species in the forests within the UNDERC property.

The differences in early growth within the different canopy classes between aspen and sugar maple were tested because these two species had the most representative samples each of the four canopy classes excluding suppressed since there were no suppressed aspen trees. They also lie on opposite sides of the shade tolerance spectrum. The test showed growth rate was insignificantly related to canopy class and significantly related to species type. This indicates that early growth was not significantly different between the four canopy classes, which is contrary to our hypothesis. It was, however, significantly different between the two species. Aspen have a much higher growth rate than sugar maple. The average early growth rate of aspen was greater than sugar maple in all three of the canopy classes aspen was present in (Table 1). Aspen, therefore, grow faster than sugar maple, and the lack of data for is likely a result of its extreme shade intolerance.

Even though the early growth was not significantly different within the different canopy classes, the fact that there was not one suppressed aspen in any of the plots has some importance. Aspen is an extremely shade intolerant species. If aspen are unable to grow large enough to escape suppression they are most likely doomed to die. Competition with other species in higher canopy classes will limit a suppressed aspen's light resources leading to mortality (Smith and Smith 2005). Unless a canopy gap forms, a suppressed aspen will not survive to make it to a dominant position in the canopy.

Testing the differences in early growth between the different canopy classes for only sugar maple resulted in a significant p-value, which suggests that there can be different early growth rates in the different canopy classes. While dominant and codominant canopy classes were not significantly different and intermediate and suppressed canopy classes were not significantly different, codominant and dominant were significantly different from both intermediate and suppressed. (Figure X) Both codominant and dominant canopy class trees are frequently exposed to sunlight so they would have similar growth rates. Intermediate and suppressed canopy class trees do not emerge above the canopy and are shaded by the overstory dominant or codominant trees. They are excluded by the overstory and do not receive full light resources. Intermediate and suppressed, therefore would have similar growth rates but different growth rates from dominant and codominant trees, which is apparent just from visual observation of forest structure. Dominant and codominant canopy class trees had greater early growth than intermediate and suppressed canopy class trees, which is consistent with the hypothesis that dominant trees would have fast early growth and suppressed would have slow early growth.

While it can be stated that there is a difference in early growth within the different canopy classes for sugar maples, this cannot be said for all species. One potential problem was that there was not enough replication because there were no other species besides sugar maple that had trees in every canopy class. With more samples from more compositionally and structurally heterogeneous forest stands more conclusive results may be obtained.

Although it cannot be concluded for all species, early growth rates have an affect on canopy attainment of sugar maple. With further studies on more species we could better understand how early growth rates impact canopy class. The fact that the canopies of the sampled plots were composed of predominantly sugar maple and aspen does indicate that there is very little structural complexity to the canopy. The structural complexity of the canopy has importance for the productivity of forests as well as species diversity (Hardiman et al. 2011). Understanding the relationship between early growth and canopy class can aid in the maintenance of canopy complexity and therefore productivity. This, in turn, can have larger scale environmental impacts such as increased carbon sequestration, which can aid in decreasing rates of global climate change.

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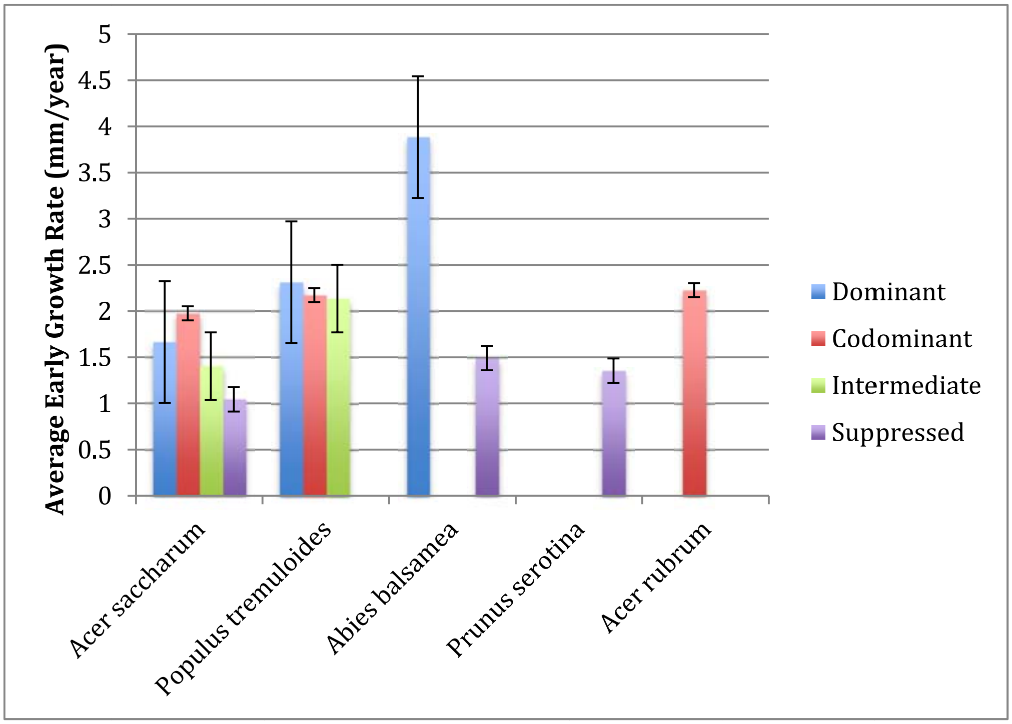

Figure 1. Average early growth rates between canopy classes for each of the five most prevalent species.

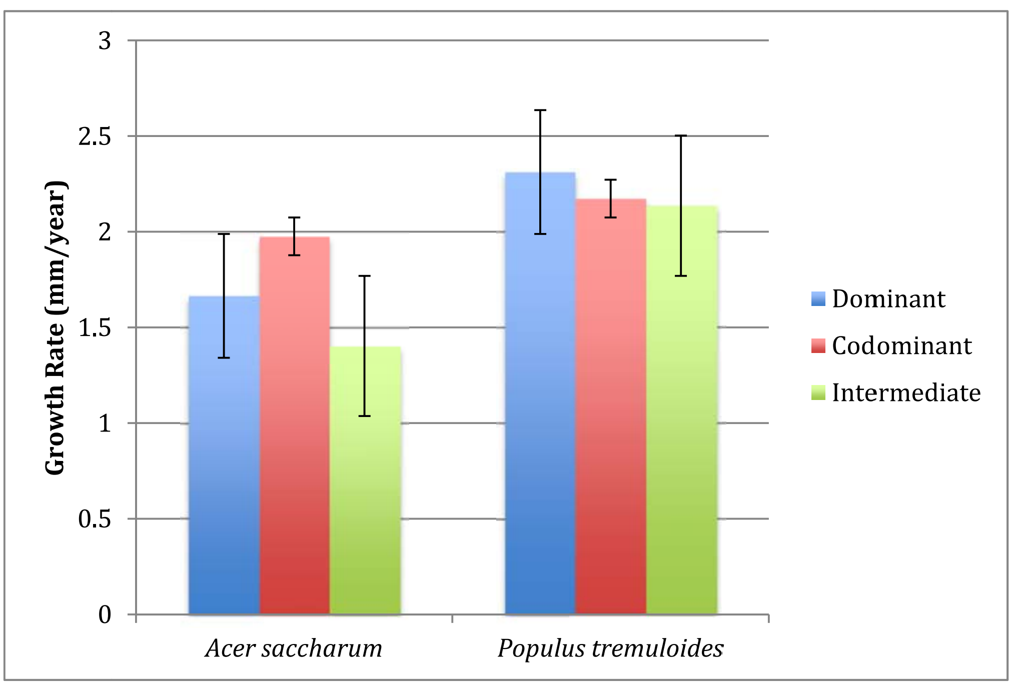

Figure 2. Average early growth rates between canopy classes for *A. saccharum* and *P. tremuloides.*

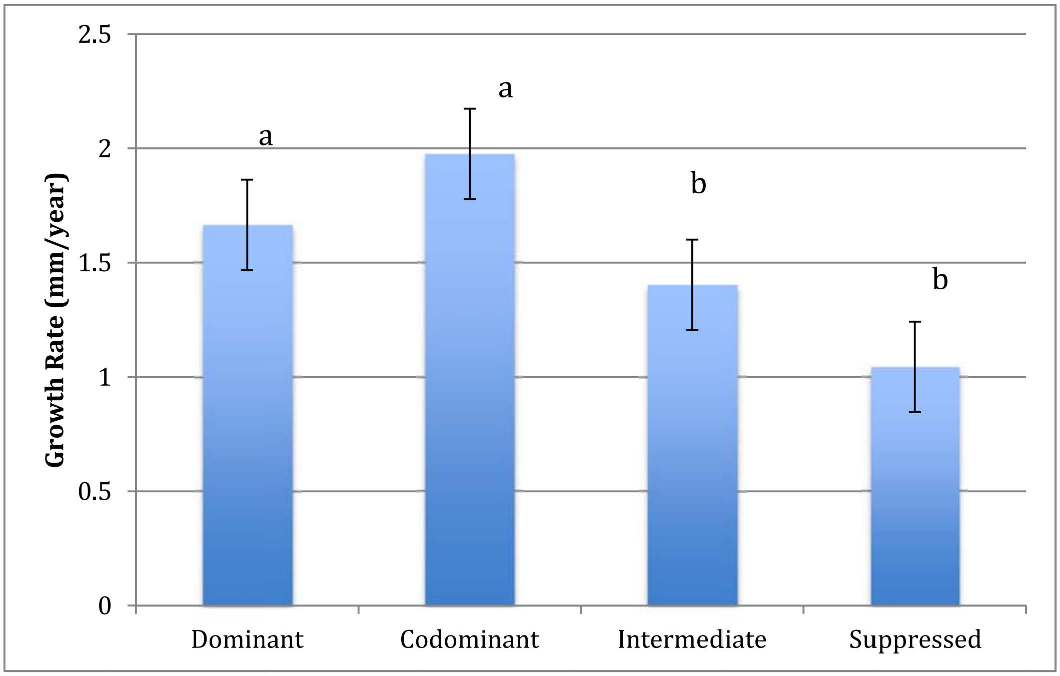

Figure 3. Average early growth rates between canopy classes for *A. saccharum*. “a” and “b” denote variable that are statistically the same

Table 1. Average growth rates per year between different canopy classes for *A. saccharum* and *P. tremuloides*

Average growth rate (mm/year)				
	Dominant	Codominant	Intermediate	Suppressed
A. saccharum	1.665	1.976	1.403	1.044
P. tremuloides	2.312	2.173	2.136	N/A