2009

Species vs. Height as Predictors of Increased Growth Rate in New England Canopy Trees

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An Honors Project Submitted in Partial Fulfillment

of the Requirements for Honors

in

The Department of Biology

The Faculty of Arts and Sciences

Rhode Island College

2009

Abstract

This study is part of a larger study on the effect of an experimentally-created gap on adult canopy trees. The results of a non-linear regression model showed that within ten meters of the gap edge the tree species that showed the greatest significant growth response to the gap was *Acer saccharum* (sugar maple), a shade tolerant species. My question was whether this response in growth rate was due to a species effect or due to a height effect. Tree radial growth response to the gap was calculated for a total of fifty trees within all four transects next to an experimentally-created large gap. A two-way ANOVA was conducted with the predictors being species and height class, and the response being tree radial growth. A two-way ANOVA was also conducted with the same predictors and response, but with data for only trees within the first ten meters from the gap. The results of both two-way ANOVAs showed that species was a predictor of tree radial growth response and that height was not. Thus, it appears that whether a tree is of canopy or subcanopy height does not affect its radial growth response to a gap. However, the species of a tree does affect its radial growth response.

Introduction

Deforestation is a well-documented worldwide issue of increasing importance, with many important consequences for forest ecosystems, including on the biodiversity of those forests. Deforestation creates new forest edges, which change many environmental factors for the trees at the edge. A few of those factors are the amount of sunlight available, soil moisture, and wind (Mourelle 2001, Harper 2005). Experimentally-created gaps within a forest can be used to study the effects of new forest edges on the surrounding trees. Conclusions made about how these new edges affect the surrounding forest could be used to predict the effects of deforestation on forests (Harper 2005). Few studies that have used experimentally created gaps have focused on adult canopy trees.

The canopy of a forest consists of the uppermost layer in a forest, and is formed by the crowns of trees. Adult canopy trees represent both the future of the forest by being the main source of seedlings, and also a large part of the current ecosystem. The focus of the “Species specific growth response of canopy trees to an experimental gap” study (henceforth “main study”), which this research is a part of, is on the effect of an experimentally created gap on adult canopy trees. This study (RIC Biology honors research henceforth referred to as “this study”) focused on the possible effect of tree height on radial growth response to gap creation.

For the main study, data were collected and analyzed for fifty trees in four belt transects perpendicular to an experimental gap that was created in the winter of 1999-2000. Annual tree growth was measured from tree cores, and the ratio of the mean annual growth from 2000-2006 (seven years after gap creation) to the mean annual growth from 1993-1999 (seven years before gap creation) was calculated. This ratio, “*ratio-G*”, was used as an indicator of tree radial growth response to the gap. If the ratio was close to one, there was no change in growth rate between the seven pre-gap and seven post-gap years, and the gap did not have an effect on tree growth.

The results of a non-linear regression model from the main study (Figure 1) showed that within ten meters of the gap edge the tree species that showed the greatest significant radial growth response to the gap was *Acer saccharum* (sugar maple), a shade tolerant species. The next greatest growth response was seen in *Quercus rubra* (red oak), which is an intermediately shade tolerant species. The mean *ratio-Gs* were 4.99 for sugar maple, 3.93 for eastern white pine, 2.99 for sweet birch, 1.49 for black oak, 1.18 for red oak, and 1.18 for red maple. A one-way ANOVA (a statistical model used to analyze data) conducted as a part of this study showed that there was a very significant difference between the mean *ratio-Gs* of these species (p= 0.002). Sugar maple was significantly different from red oak and red maple, as determined by post-hoc tests.

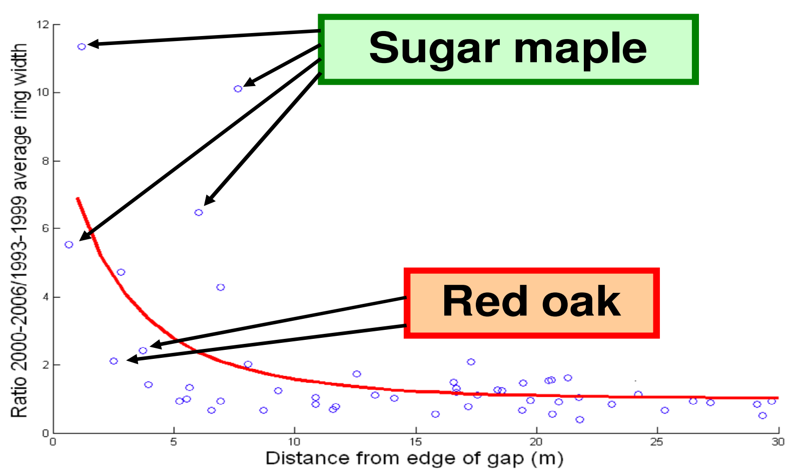

Figure 1: Graph of non-linear regression model, with *ratio-G* on y-axis and distance from edge on x-axis. *Acer saccharum* showed the greatest significant increase in growth.

My question was whether this unequal response in growth rate was due to a tree species effect or due to a tree height effect. The height of a tree influences the amount of sunlight available to that tree. The crown of a tree already at canopy height has almost full exposure to the sun, and thus gap creation would minimally affect the amount of sunlight it receives, which could lessen any tree growth response. On the other hand, the crown of a tree shorter than the canopy (a subcanopy tree) receives less sunlight than the crowns of trees at canopy height because the taller canopy trees block most of the direct sunlight. If subcanopy sugar maple trees had a lower average height, they might show more of a response to gap creation than trees that were at canopy height. The mean heights (in meters) of the different species were 11.05 for sugar maple, 12.05 for sweet birch, 12.96 for eastern white pine, 13.04 for red maple, 20.61 for red oak, and 22.1 for black oak. A one-way ANOVA showed that there was a very significant difference between the mean heights of these species ($p = 0.000$), with the two oak species being significantly different from sugar maple, red maple, and eastern white pine, as determined by post-hoc tests.

Several studies have shown that there is some species-specific growth response to gap creation (Takahashi and Lechowicz 2008, Canham 1988). Takahashi and Lechowicz (2008) investigated the differences in growth response of beech and sugar maple in saplings. Canham (1988) showed that sugar maples less than four meters in height had a high degree of phenotypic plasticity, and were able to respond quickly to gap creation. On the other hand, Pederson and Howard

(2004) found marginal support for their hypothesis that smaller trees would show a greater increase in growth response to gap creation. Muth and Bazzaz (2002) found that subcanopy trees expanded their crowns towards a gap significantly more than canopy trees. However, they also found a species effect in regards to crown displacement. I hypothesized that the radial growth response observed in this study was a result of a species effect, and not a height effect. However, because Takahashi and Lechowicz (2008) and Canham's (1988) studies mostly focused on juvenile trees, it was important for this study to statistically test the growth response of canopy trees as a function of both species and height. This was in order to determine if either species, height, or both were predictors of growth response following the creation of the gap.

Along with investigating whether species and/or height influenced the observed growth response, I had also hypothesized that age influenced *ratio-G*. My hypothesis was that any height effect would correlate with an age effect, based solely on the observation that shorter trees were usually younger. However, a one-way ANOVA for age conducted for this study showed no significant mean age difference between the different species (p=0.263).

Materials and Methods

A. Main study methods (for background only)

The main study and this study were conducted in the Yale-Myers Experimental Forest in Connecticut, where a 20 x 100 m gap was created in the winter of

1999-2000, by removing all above-ground trees, shrubs, and seedlings. In 2007, four 30 x 10 m belt transects were established, starting at randomly chosen points and running perpendicular to the forest edge. The transects are at least 10 m apart from each other. For all of the trees within the belt transects that were at least one cm in diameter at breast height (dbh), the tree height, species, diameter and distance from the gap edge (d-edge) were recorded. Tree cores were collected from trees that were at least 10 cm in dbh, for a total of 50 trees. Two cores were taken per tree and these were mounted in the lab. The distance between tree rings was marked with a fine pencil and measured with a Velvex® instrument. Tree ring width data were transferred to excel data sheets.

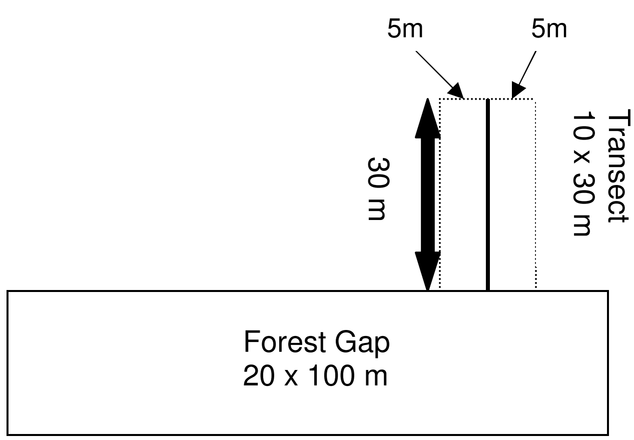

Figure 2: General layout of the study site.

B. Methods used in this study

Ratio-G was calculated for a combined total of fifty trees within all four transects next to an experimentally-created large gap. SPSS®, which is a computer program used for statistical analysis, was used to conduct a two-way ANOVA with the predictors being species and height class, and the response being *ratio-G*. The results of a two-way ANOVA in SPSS® only show for each variable if one of the categories of that variable (i.e. one species or one class height) is significantly different from the other categories. In order to determine which of those categories are actually significantly different from the others, Student-Newman-Keuls (SNK) and Tukey Post-Hoc tests were conducted on the results of the two-way ANOVAs. The purpose was to see which species or which height classes were a predictor of *ratio-G*. Of the fifty trees four were *Acer saccharum*, three were *Quercus velutina*, sixteen were *Quercus rubra*, twenty were *Acer rubrum*, two were *Betula lenta* and five were *Pinus strobus*. These were divided into three height classes (1-9.9 m, 10-19.9 m, and 20-29.9 m) with 10, 27 and 13 trees, respectively, in each class.

SPSS® was also used to conduct a two-way ANOVA with the same predictors and response, but using only data for trees within ten meters from the gap. For this second two-way ANOVA there were a total of sixteen trees, two of which were *Acer saccharum*, two were *Quercus velutina*, three were *Quercus rubra*, seven were *Acer rubrum* and two were *Pinus strobus*. *Betula lenta* was not used in the two-way ANOVA within ten meters because there was only one *Betula lenta* tree within ten meters of the gap, and Post-Hoc tests could not be performed with only one datum. The height classes were the same, and there were four trees in the 1-9.9 m class, ten trees in the 10-19.9 m class and two in the 20-29.9 m class.

Results

The results of the two-way ANOVA for all of the trees with *ratio-G* data within the four transects showed that height class was not a significant predictor of *ratio-G* (*p*-value=0.838) and that species was a significant predictor of *ratio-G* (*p*-value=0.005) (Table 1). The results of the Tukey Post-Hoc test showed that *Acer saccharum* was significantly different from *Quercus rubra* (*p*-value=0.013) and from *Acer rubrum* (*p*-value=0.010) (Table 2). There was no significant difference between *Quercus rubra* and *Acer rubrum*, or between any of the other tree species.

The results of the two-way ANOVA for the trees within ten meters again showed that height class was not a significant predictor of *ratio-G* (*p*-value=0.652) and that species was a significant predictor of *ratio-G* (*p*-value=0.010) (Table 1). The results of the Tukey Post-Hoc test showed that *Acer saccharum* was significantly different from *Quercus velutina* (*p*-value=0.024), from *Quercus rubra* (*p*-value=0.012) and from *Acer rubrum* (*p*-value=0.007) (Table 3). There were no other significant differences between the other trees.

Table 1: Two-way ANOVA results with predictors being species and height class and response being *ratio-G*. The "all trees" data are from a two-way ANOVA using data from all cored trees. The "all trees w/in 10 m" data are from a two-way ANOVA using only data from cored trees within ten meters of the gap. Significant values are noted with an asterisk.

Predictor	*p*-value All trees	*p*-value All trees w/in 10 m
Species	0.005*	0.010*
Height	0.838	0.652

Table 2: *P*-values from Tukey Post-Hoc test between species for species-height two-way ANOVA using data from all of the trees with a *ratio-G* within all four transects. Significant values are noted with an asterisk. ACSA= *Acer saccharum*; QUVE= *Quercus velutina*; QURU= *Quercus rubra*; ACRU= *Acer rubrum*; BELA= *Betula lanta*; PIST= *Pinus strobus*.

	ACSA	QUVE	QURU	ACRU	BELA	PIST
ACSA	-----	0.191	0.013*	0.010*	0.837	0.963
QUVE	0.191	-----	1.0	1.0	0.957	0.522
QURU	0.013*	1.0	-----	1.0	0.814	0.083
ACRU	0.010*	1.0	1.0	-----	0.808	0.071
BELA	0.837	0.957	0.814	0.808	-----	0.992
PIST	0.963	0.522	0.083	0.071	0.992	-----

Table 3: *P*-values from Tukey Post-Hoc test between species for species-height two-way ANOVA using data only from trees with a *ratio-G* within the first ten meters from the gap within all four transects. Significant values are noted with an asterisk. Abbreviations used are the same as listed for figure 4.

	ACSA	QUVE	QURU	ACRU	PIST
ACSA	-----	0.024*	0.012*	0.007*	0.071
QUVE	0.024*	-----	1.0	1.0	0.941
QURU	0.012*	1.0	-----	1.0	0.881
ACRU	0.007*	1.0	1.0	-----	0.887
PIST	0.071	0.941	0.881	0.887	-----

Discussion

The results of both two-way ANOVAs showed that species was a predictor of *ratio-G* and that height was not. Thus, it appears that whether a tree is at or below canopy height does not affect its growth response to a gap. However, the species of a tree does affect its growth response.

Post-Hoc tests were performed for both two-way ANOVAs, and in both of these *Acer saccharum* was the only species that was significantly different from any of the other species in its radial growth response to gap creation. In the two-way ANOVA for all of the trees, *Acer saccharum* (sugar maple) was significantly different from *Acer rubrum* (red maple) and *Quercus rubra* (red oak). These differences are among the same species that had differences in the one-way ANOVA for *ratio-G*. In the two-way ANOVA for all of the trees within ten meters of the gap, *Acer saccharum* was significantly different from *Quercus velutina* (black oak), *Acer rubrum* and *Quercus rubra*. Thus, the observed species effect was even more dramatic within ten meters of the gap. This was expected based on the results of the main study. As the non-linear regression model showed, the most dramatic growth response was seen within ten meters of the gap. Both Canham (1989) and Mourelle (2001) also suggested that effects from gap creation extend into the forest. Canham (1989) suggested that sunlight reaches the canopy understory farther into the forest than the line between the gap and the edge of the forest suggests, and thus the distinction between gap and nongap is blurred. This is indeed what was seen, both in the main study and in this study, with edge effects reaching ten meters into the forest.

Pederson and Howard (2004) were unable to make any species specific conclusions about tree growth response to gap creation, due to small sample sizes. The results of their study showed only marginal support for the hypothesis that smaller trees will show a greater growth response. This study continued to diminish the already marginal support from their results for that hypothesis by showing that in this case height was not a predictor of growth response. Poage and Peart's (1993) study focused solely on beech trees, so species effects can not be taken into account, but they found that greater radial growth rates after gap creation in subcanopy beech trees were not due to individual tree size. Thus, the results of this study agree with their study that height did not play a factor in radial growth response to gaps.

As predicted based on Canham (1988), sugar maple has shown the most dramatic response in the relatively short amount of time since gap creation. Sugar maple is considered to be a small-gap specialist due to its phenotypic plasticity (Canham, 1988). However, previous literature focused on juvenile trees, and the phenotypic plasticity found in other literature could be the result of the younger age of the tree. Thus, the results of this study show that adult sugar maples also display a species effect plasticity in the radial growth response.

The results of this study add to the results of the main study. The focus of the main study is the effects of gap formation on adult canopy trees. While this study showed that species is a significant predictor of growth response to gap formation and provided more evidence for a species effect, particularly in sugar maple trees, it is important that other variables such as soil data, light data, and canopy architecture be investigated.

In “The Red Maple Paradox”, Abrams (1998) states that whether sugar maple or red maple is the dominant maple species at a site depends on the soil. Kobe (1995) found that sugar maple mortality varies depending on the soil variables. Thus another two-way ANOVA with soil data should probably be performed in order to determine if there is a soil effect, along with the species effect. On a different note, Canham (1988) found that there was no correlation between the relative amount of light that reached saplings and height growth, but there was a correlation between amount of light and lateral growth. Thus, more research should also be done on canopy architecture. Potential predictor variables of tree radial growth must be identified and then tested, in order to determine how much each variable may have contributed. As these growth responses and the factors behind them become better understood, the knowledge gained from studying this experimentally created gap could be used to predict the response of other forests actually facing deforestation.

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