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Relationships Between Overstory and Understory Tree Composition and Light Environment in an Old Growth Forest, Adirondacks, NY

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Relationships Between Overstory and Understory Tree Composition and Light
Environment in an Old Growth Forest, Adirondacks, NY

by

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Abstract

Density of tree seedlings and saplings can be considerably influenced by light availability and the overstory canopy composition. We examined whether forest understory light environment could be predicted by overstory composition in an old growth northern hardwood forest at Huntington Wildlife Forest in the central Adirondacks, NY. We also tested whether the overstory composition and light environment could be used to predict the understory tree composition. Existing continuous forest inventory data were used to quantify the overstory and we collected additional data on tree seedlings and saplings. We characterized the light environment using hemispherical canopy photography. Percent canopy openness was positively correlated with the proportion of American beech (*Fagus grandifolia*) in the overstory. Understory tree species richness was not predicted by light environment or by the overstory. Yet seedling and sapling density of certain tree species could be predicted by certain overstory characteristics. Density of understory beech was positively correlated with the proportion of overstory beech basal area; however, the densities of other tree species in the understory were not as well correlated with the proportion of overstory conspecifics. Understanding these relationships may help shed light on factors influencing regeneration dynamics in this Adirondack old growth forest. Additionally, since forests in the region have been impacted by beech bark disease the results of this study help elucidate the overstory-understory dynamics in the presence of this disturbance.

Table of Contents

Acknowledgements.....	i
Introduction.....	1
Methods.....	4
Results.....	11
Discussion.....	18
References.....	24
Appendix 1: Mean Density and Frequency of Understory Trees	25
Appendix 2: Species Level Size Class Distributions	26

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Introduction

Forest succession is a complex process influenced by multiple factors. In the absence of major large-scale disturbances, small gaps in the canopy may provide suitable sites for tree regeneration (Runkle, 1981). Additionally, trees may regenerate under a closed canopy. Two important factors influencing regeneration of tree seedlings and saplings are canopy composition and light environment (Ricard et al., 2003; Woods, 1984; Roberts, 1992). Neighborhood effects are processes driven by overstory trees which influence the replacement of conspecific or heterospecific trees in the understory and are important drivers of forest dynamics (Frelich et al., 1998; Frelich and Reich, 1995; Frelich and Reich, 1999).

Distributions of understory tree saplings and seedlings relative to nearby canopy trees have been documented to be non-random, indicating a correlation between canopy trees and understory regeneration (Woods, 1984). Various factors have been proposed as affecting understory tree seedling and sapling communities, including seed dispersal, shade tolerance, and soil moisture characteristics (Woods, 1979; Roberts, 1992; Arie and Lechowicz, 2002). Canopy species may facilitate or inhibit seedlings and saplings of the same or different species. For instance, American beech (*Fagus grandifolia*) may be less likely to establish under Eastern hemlock (*Tsuga canadensis*) than other species. However, under sugar maple (*Acer saccharum*) canopies, beech saplings may be favored relative to other species (Woods, 1984). Similarly, maple may preferentially regenerate under beech, indicating a reciprocal replacement. Saplings under conspecific canopies can have higher mortalities than under other species, possibly as a result of greater intraspecific competition (Woods, 1979). In contrast other studies have found spatial

aggregation of conspecifics, while interspecific autocorrelation of trees was generally neutral or negative, suggesting that trees of one species did not generally favor the recruitment of other species (Friedman et al. 2001; Frelich et al., 1993). These findings indicate that in some instances overstory composition can be useful in predicting the understory structure. Although beech root sprouts were uncommon, Woods (1979) found that beech sprouts did not follow the same pattern of reciprocal replacement as the seedlings. The increase in beech sprouts because of beech bark disease (Houston, 1994), may alter overstory-understory interactions found in previous studies.

Canopy structure influences the amount of light available for tree seedling and sapling growth (Canham et al., 1994). Since light is one of the most limiting factors for understory tree growth (Ricard et al., 2003), the amount of light reaching the forest floor could affect understory tree composition. The response of tree seedlings to light may vary between species. For example, growth of yellow birch (*Betula alleghaniensis*) responds more strongly to increases in light than more shade tolerant species such as beech (Beaudet and Messier, 1998). Similarly, Pacala et al. (1994), studying tree saplings in New England, found that certain species grew quickly under high light environments and slowly under low light conditions, with the opposite being true for other species, indicating trees differ with regard to how they respond to light. The light environment in a forest can vary based on height of canopy trees and by gaps in the overstory (Canham et al., 1990). Different species of trees also allow varying levels of light to pass through the canopy, with shade tolerant species blocking the most light (Canham et al., 1994), indicating that the influences of light environment and canopy composition on the understory are interrelated.

Because light can influence tree seedlings and saplings, the light environment in a forest may be a predictor of the understory community. If light environment influences the understory trees, there may be a relationship between the density and diversity of the understory trees and the light environment in the forest. Understanding the ways in which light environment and overstory influence the understory tree seedling and sapling communities will increase our knowledge of forest succession. Detecting the overstory-understory relationships is essential for better understanding neighborhood effects. Since neighborhood effects can differ between forest types (Frelich and Reich, 1995), studying a particular forest community might yield results that highlight processes that differ from similar investigations of other systems. The highest concentration of beech in the United States is in the Adirondacks (Randall et al., 2007) and thus beech likely plays an important role influencing neighborhood dynamics in the region. Beech bark disease has altered forest structure in the Adirondacks (McNulty and Masters, 2004), which could in turn further impact overstory-understory relationships. Certain studies on neighborhood effects or light environment have focused on forest communities lacking beech (e.g. Frelich et al., 1993; Frelich and Reich, 1995), while some others have not addressed beech bark disease as a disturbance that could be mediating relationships (e.g. Woods, 1979; Woods, 1984; Canham, 1988; Canham 1990; Arie and Lechowicz; Roberts, 1992; Zhao et al., 2006). Therefore, specifically investigating the relationships between the overstory and understory in an Adirondack old-growth forest may help us better understand neighborhood dynamics that are likely mediated by beech bark disease in a system that otherwise has had little human disturbance.

Objectives

The goal of our study was to gain a better understanding of the relationships between light environment, and overstory and understory tree communities in an old growth forest in Adirondacks, NY. More specifically our objectives were to (1) determine whether total overstory basal area and overstory composition can be used to predict light environment and (2) to test whether overstory species richness, overstory composition and light environment can be used to predict understory tree species richness and composition in an old growth forest at the Huntington Wildlife Forest, Adirondacks, NY.

Methods

Study Site Description

Research was conducted at the Huntington Wildlife Forest, which is a 6000 ha property managed by SUNY College of Environmental Science and Forestry near Newcomb, New York, in the central Adirondacks (latitude 44°00'N, longitude 74°13'W). Elevation of the property ranges from 475-820 m (Cook et al., 1989). Climate in the Adirondacks is characterized by mean temperatures of -12°C to -7°C during winter months and 21°C to 27°C during the summer. Monthly mean precipitation is around 7.6 cm to 10.2 cm (Jenkins and Keal, 2004). Most of the soils in the Adirondacks were derived from glacial till and moraine parent material, as well as glacial outwash and lake sediments. Muck and peat soils have also developed in swamps and bogs (Jenkins and Keal, 2004). The Huntington Wildlife Forest is composed largely of northern hardwood as well as hardwood/conifer and conifer forests (Glennon, 1994). Parts of the forest are old growth but the majority has been managed in various ways including use of the shelterwood method and selection systems, and there are both even and uneven aged

stands (R. Nyland, personal communication). This research was conducted in a >400 ha old-growth forest on the property, known as the “natural area,” located on the western shore of Catlin Lake (Figure 1).

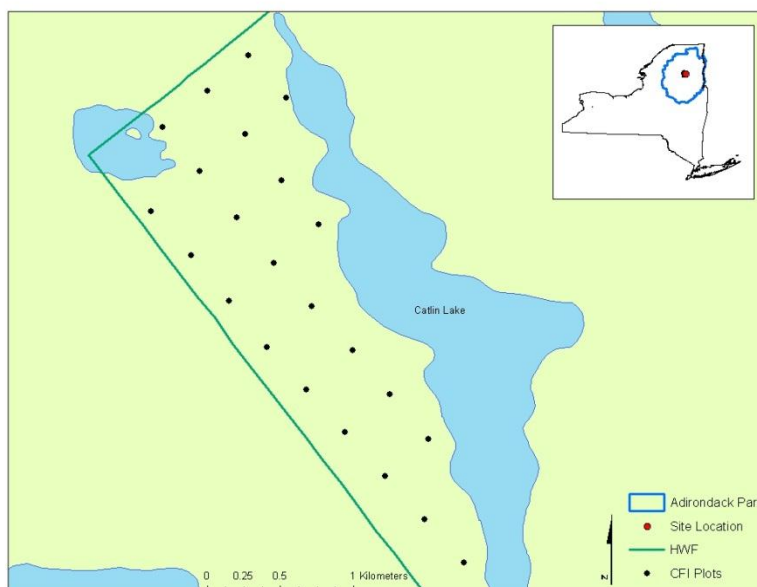


Figure 1. Continuous Forest Inventory plots sampled in the northwestern portion of Huntington Wildlife Forest, central Adirondacks, NY.

Continuous Forest Inventory Plots

A grid of 288 Continuous Forest Inventory (CFI) plots has been established at Huntington Wildlife Forest to measure structure and composition of forest tree communities. Since 1970 the plots were sampled about every ten years and they were re-sampled again during the summer of 2011 by a forest inventory crew. The >400 ha old growth forest located on the property contains 23 CFI plots. For this study, 2011 overstory CFI data from these 23 plots was used. CFI plots are circular and cover an area of 0.081 ha, with a 16.05 m radius and are 402 m apart. As part of the forest inventory, all trees and stumps with a dbh ≥ 26.92 cm were measured over the entire area of CFI plots,

while all smaller trees and stumps with a dbh between 11.68 cm and 26.67 cm were measured only in the northeastern quarter of each CFI plot. Currently no data on understory trees or shrubs are collected as part of the inventory. However, for this study data on smaller trees, saplings, seedlings and shrubs were collected at the 23 CFI plots in the natural area (old-growth) section of the property during June-August, 2011.

Understory Trees and Shrubs

One 2 m radius plot containing one nested 1×1 m sub-plot was located in each of the four quadrants of the CFI plots (Figure 2). The centers of each 2 m radius plot and 1×1 m sub-plot were located 8 m from the center of the CFI plot at angles of 45°, 135°, 225°, and 315° respectively. The plots located 45° from the center coincided with the northeastern corner of the CFI plot where data on midstory trees was collected as part of the CFI.

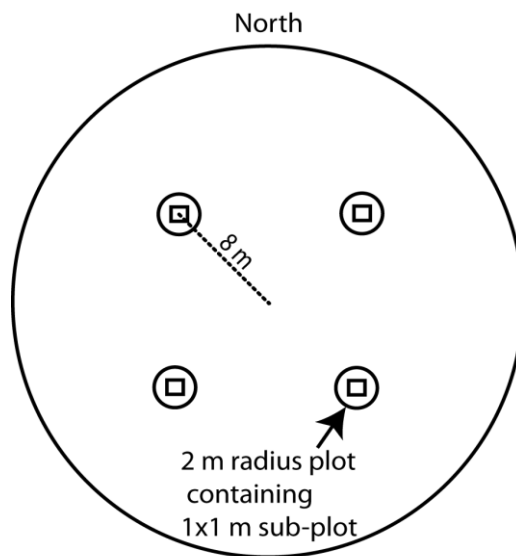


Figure 2. Continuous Forest Inventory plot (0.081 ha area, 16.05 m radius) containing four 2 m radius plots and 1x1 m sub-plots (not to scale).

In each 1x1 m sub-plot tree seedlings, saplings and shrubs were counted and identified to species whenever possible. They were classified as current year germinants, one year old to <30 cm tall, 30 cm to <1 m, and 1 to 2 m. For most analyses involving the understory these categories were pooled together to include all stems ≤ 2 m tall. Current year germinants were identified by the presence of cotyledons, absence of bud scale scars and lack of woody growth. In the 1x1 m plots, trees >2 m tall were also identified, and their dbh measured. Dbh was measured using guidelines presented by Avery and Burkhart (1983). Trees >2 m tall were classified according to dbh increments of 0-2 cm, 2-5 cm, 5-8 cm and 8-11.68 cm. Trees with a dbh >11.68 cm were measured exactly to the nearest 0.1 cm, so these data are comparable to the CFI data.

Beech seedlings and beech root sprouts were differentiated from each other and counted separately when the seedlings/root sprouts were <30 cm tall. This was determined by digging to see if the shoot originated from a parent root. However, because for many individuals the origin could not be determined, root sprouts and seedlings were lumped together for the analyses. For shrubs/trees >2 m tall with stems/boles that branched below 1.37 m, the dbh of each stem/bole was measured separately, but it was noted that they belonged to the same individual.

Within the 2 m radius plots, all saplings and larger trees over 2 m tall were counted, identified and dbh measured (using the same system as for the 1x1 m plots). Inclusion of woody vegetation that fell on the boundary of a plot was determined based on the location of the base of the stem/bole in a manner recommended by Elzinga et al. (2001). Snags and standing dead shrubs and saplings were measured and counted in the same manner as was done for living woody vegetation.

Percent Cover Estimation

Percent cover of woody vegetation less than 1 m tall was visually estimated in the 1×1 m sub-plots. The percent cover estimation was based on the percent woody vegetation above the plot, regardless of whether the stems originated inside or outside of the plot. Percent cover of woody vegetation <1 m tall was recorded separately for each species present. Total woody plant cover <1 m was also recorded. The percent cover of coarse woody debris (CWD) was estimated at the 1x1 m plots. Only sticks/logs >3 cm in diameter, within 5 cm of the ground and tree stumps <1 m tall, were included in the CWD category. CWD was categorized into three decay classes (modified from Stevens, 1997): (1) little if any decay, bark intact, some twigs still present, wood hard, (2) partly decayed, bark partially intact, twigs absent, wood slightly soft and (3) well decayed/partly integrated into the soil, wood very soft. Percent cover was estimated separately for each decay class and for all decay classes combined. Percent cover was also estimated for the following categories at the 1x1 m sub-plots: herbaceous vegetation, leaf litter, bare soil, bare rocks and moss. Six cover classes were used: (1) <1%, (2) 1-5%, (3) 5-25%, (4) 25-50%, (5) 50-75% and (6) 75-100%. Midpoints of these cover classes were used for analyses.

Canopy Photography

Four canopy photographs were taken in each of the CFI plots included in this study to measure the light environment at the plots. Photographs were taken 1 m off the ground at the center of each 1 m radius sub-plot, during July and early August 2011. The photographs were taken around sunrise, sunset or when the sky was overcast to minimize the effects of direct sunlight penetrating into the forest canopy. A Nikon Coolpix 4500

camera with a Nikon LC-ER1 fish-eye lens was used. Camera settings including shutter speed were determined in a way similar to as suggested by Zhang et al. (2005). However, in instances when light conditions changed substantially between when the reference photo was taken and when the photos were taken at the plots, photographs with the least overexposure that still made the sky bright, were selected for analysis. Gap Light Analyzer version 2.0 was used to calculate percent openness, direct light and diffuse light from the photographs. The monthly average solar radiation values were calculated using hourly measurements taken at Huntington Wildlife Forest over the past 10 years (CASTNET, n.d.). These average solar radiation values were used to calculate cloudiness index, spectral fraction and beam fraction as described by Frazer et al. (1999). These three parameters were then input into GLA for the direct and diffuse light calculations.

Data Analysis

For the analyses understory was defined as saplings and seedlings ≤ 2 m tall, and overstory was defined as trees with a dbh ≥ 11.68 cm. For analyses of the understory or overstory, tree species were only analyzed if they occurred at over 30% of the plots in the understory or overstory, respectively. Percent canopy openness, percent cover and understory density measurements were averaged across the sub-plots for each CFI plot ($n = 23$), unless otherwise noted. In the overstory, for each species the proportion of basal area and actual basal area were strongly correlated ($r > 0.91$). Therefore, analyses using either proportion of basal area or actual basal area for a species yielded very similar results and only the results of analyses using proportion basal area are presented.

Correlation, ordinary least squares linear regression and stepwise regression analyses were used to determine the relationships between overstory, light environment, and understory variables. The following a priori model was fit to the data

$$(\text{sp. } i \text{ understory}) = \beta_0 + \beta_1(\text{sp. } i \text{ overstory}) + \beta_2(\% \text{ canopy openness}) + \varepsilon \quad [1]$$

where “sp. *i* understory” is the understory density of species *i*, “sp. *i* overstory” is the proportion overstory basal area for species *i*, and *i* represents any of the tree species that occur at > 30% of the plots in both the understory and overstory. Thus the model represents regeneration of a species as a function overstory conspecifics and light environment.

For the stepwise regression analyses the significance level to enter (forward selection) was set at $\alpha = 0.15$ and the significance level to stay (backwards elimination) was also set at $\alpha = 0.15$. Stepwise regression analyses were done using various understory response variables including understory tree species richness and density by trees species in the understory. Predictor variables included in these analyses were canopy openness, total overstory basal area, and the proportion basal area of each overstory tree species. An additional stepwise regression analysis was done with percent canopy openness as the response variable, and total overstory basal area and the proportion basal area of each overstory species as predictor variables. The proportion basal area was calculated based on data from live trees only. Similarly, hereafter “total basal area” refers to the total basal area of all living trees (with $\text{dbh} \geq 11.68$). All analyses were done using Minitab 16 statistical software.

Results

Overstory and Understory Characteristics

Total mean (\pm S.D.) basal area of living overstory trees (defined as trees with a dbh over 11.68 cm) was found to be 29.9 (\pm 6.7) m²/ha. Yellow birch (*Betula alleghaniensis*) was the most dominant tree (25% of overstory basal area) followed by Eastern hemlock (*Tsuga canadensis*, 24%), American beech (*Fagus grandifolia*, 22%), sugar maple (*Acer saccharum*, 19%), red maple (*Acer rubrum*, 7%), red spruce (*Picea rubens*, 3%), balsam fir (*Abies balsamea*, <1%) and white ash (*Fraxinus americana*, <1%). All of these tree species, as well as striped maple (*Acer pensylvanicum*) were also found in the understory (defined as trees \leq 2 m tall). The most abundant woody plant in the understory was hobblebush (*Viburnum lantanoides*) which occurred at 91% of CFI plots sampled, and had a higher mean density than any tree species in the understory (Appendix 1).

The size class distributions differed between tree species (Appendix 2). There were high densities of beech saplings and small trees, with much lower densities of larger beech. Other species including yellow birch, red maple and sugar maple had a different size class distribution with very high densities of seedlings and small saplings (<30 cm tall) but larger saplings and small trees were mostly absent. However, larger trees were relatively abundant. Additionally, dominance of certain tree species differed between plots with high and low total basal area (Figure 3). Beech was more dominant at plots with low basal area. This relationship is also reflected by the negative correlation between total overstory basal area and the proportion of overstory beech basal area ($r = -0.632$, $p = 0.001$).

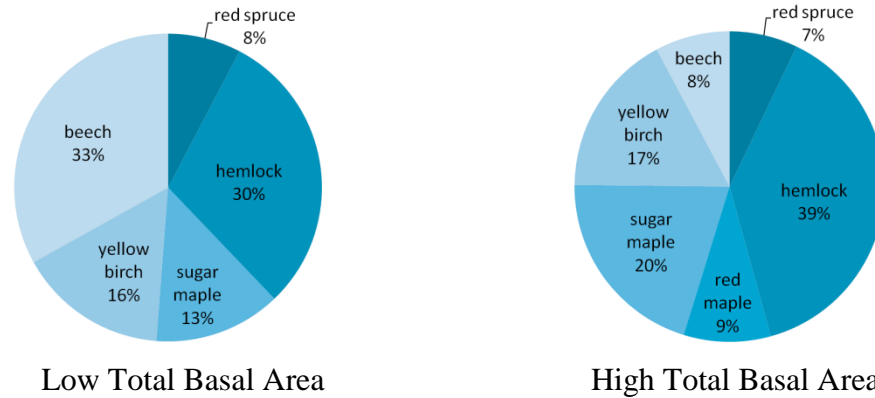
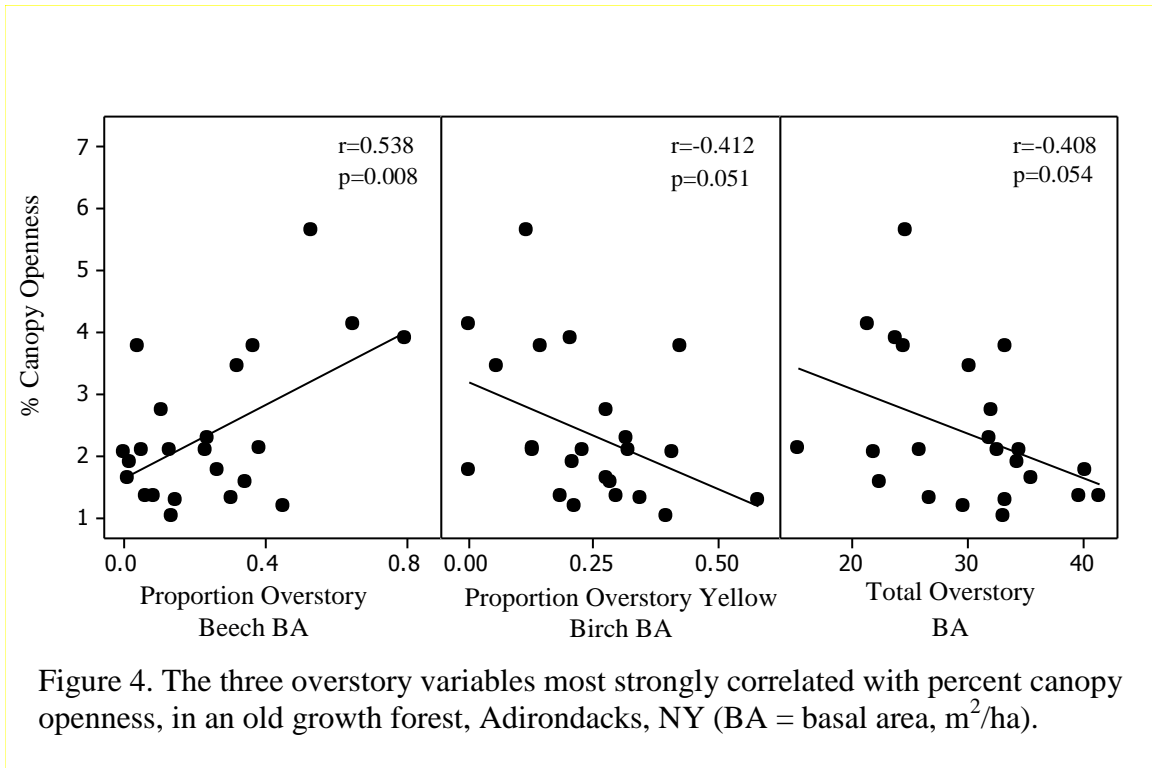


Figure 3. Percent of overstory basal area by species for the five plots with the lowest total basal area and the five plots with the highest total basal area.

Overstory-Light Environment Relationships

Mean (\pm S.D.) percent canopy openness was found to be 2.4 (\pm 1.2) %. The proportion of overstory beech basal area was the overstory variable most strongly correlated with percent canopy openness ($r = 0.538$, $p = 0.008$, Figure 4). The stepwise regression analysis showed that the proportion overstory yellow birch basal area and total basal area were the next best predictors of percent canopy openness. Overstory beech was positively correlated with canopy openness while yellow birch ($r = -0.412$, $p = 0.051$) and total live basal area ($r = -0.408$, $p = 0.054$) were negatively correlated with canopy openness (Figure 4).



Overstory-Understory Relationships

Total basal area of live overstory trees was not found to be significantly correlated with understory tree species richness ($r = -0.030$, $p = 0.891$). The stepwise regression analysis showed that other overstory variables including percent canopy openness, overstory species richness, and the proportion of overstory basal area by species were also not significant predictors of understory species richness ($p > 0.11$).

Total live overstory basal area was significantly correlated with understory beech density ($r = -0.470$, $p = 0.024$), but not with the densities of other tree species ($p > 0.12$). The proportion of overstory beech basal area was positively correlated with understory beech density ($r = 0.696$, $p < 0.001$, Figure 5). The proportion of overstory sugar maple was positively correlated with understory sugar maple ($r = 0.411$, $p = 0.051$, Figure 5). In comparison, both the densities of understory red maple and yellow birch were not significantly correlated with the proportion of overstory conspecifics ($p > 0.39$).

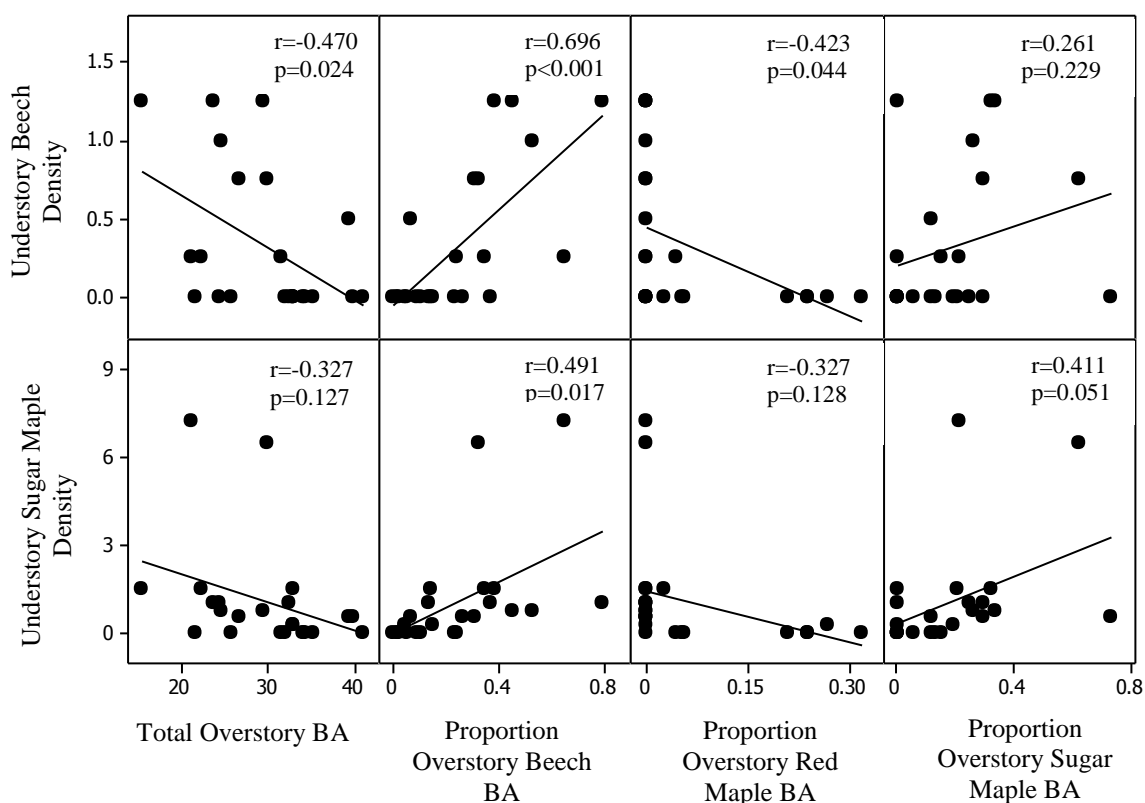


Figure 5. The relationships between the density (stems/m²) of understory (≤ 2 m tall) beech and sugar maple, and total basal area (BA, m²/ha) of living overstory trees, and proportion overstory basal area of beech, red maple and sugar maple, in an old growth forest, Adirondacks, NY. The understory was defined as trees ≤ 2 m tall, and the overstory was defined as trees with a dbh ≥ 11.68 cm.

The proportion of overstory hemlock basal area and understory beech density were negatively correlated ($r = -0.489$, $p = 0.018$, Figure 6). The proportion of overstory hemlock was positively correlated with understory red maple density ($r = 0.487$, $p = 0.018$), and moderately significantly negatively correlated with understory sugar maple density ($r = -0.375$, $p = 0.078$) (note that there were strong outliers in both instances). A negative correlation between the proportion of overstory yellow birch and understory sugar maple density was found ($r = -0.498$, $p = 0.016$, Figure 6). In contrast, understory sugar maple density was positively correlated with the proportion of overstory beech ($r =$

0.491, $p = 0.017$, Figure 5). Additionally, the stepwise regression analysis showed that understory yellow birch was not significantly predicted by any overstory variables including percent canopy openness, total overstory basal area, and the proportion basal area by species in the overstory ($p > 0.11$ in all instances). Note that yellow birch also had very poor recruitment, as indicated by the lack of saplings ≥ 30 cm tall (Appendix 2).

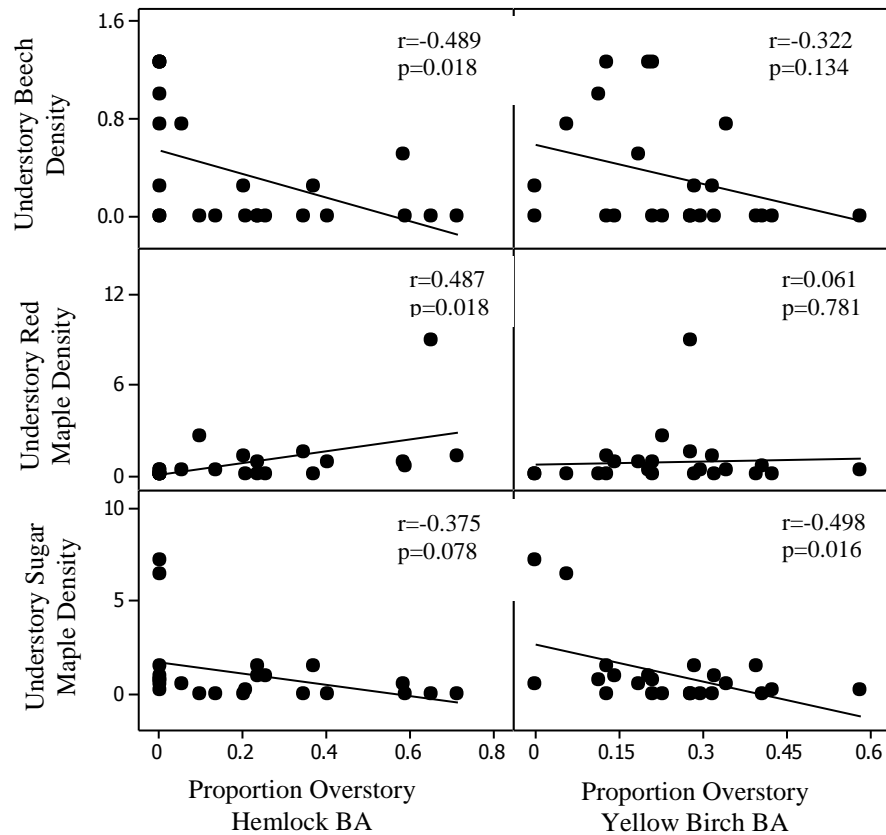


Figure 6. The relationships between the density (stems/m²) of understory beech, red maple and sugar maple, and the proportion overstory basal area (BA) of hemlock and yellow birch, in an old growth forest, Adirondacks, NY. The understory was defined as trees ≤ 2 m tall, and the overstory was defined as trees with a dbh ≥ 11.68 cm.

The density of hobblebush was not found to be significantly correlated with understory tree species richness, or with the understory density of any tree species (in all cases $p > 0.2$). Percent cover of herbaceous vegetation was significantly positively correlated with understory beech density ($p = 0.037$, $r = 0.437$) and with understory

yellow birch density ($p = 0.012$, $r = 0.517$). Understory density of all other tree species was not significantly correlated with percent cover of herbaceous vegetation (in all cases $p > 0.38$).

Light Environment-Understory Relationships

Percent canopy openness was not found to be significantly correlated with tree species richness ($r = 0.023$, $p = 0.917$), or with total density of understory trees ($r = 0.217$, $p = 0.320$). A moderately significant positive correlation was found between percent canopy openness and understory sugar maple density ($r = 0.384$, $p = 0.071$, Figure 7). Percent canopy openness did not significantly correlate with understory density of other tree species ($p > 0.12$ in all instances). However, when the data were analyzed on the sub-plot level (i.e. data not averaged across the four subplots of the CFI, so $n = 92$ instead of 23), the results differed somewhat. When using this subplot level data ($n = 92$), percent canopy openness was not significantly correlated with understory sugar maple density ($r = 0.131$, $p = 0.213$) and it was significantly correlated with yellow birch density ($r = 0.203$, $p = 0.052$).

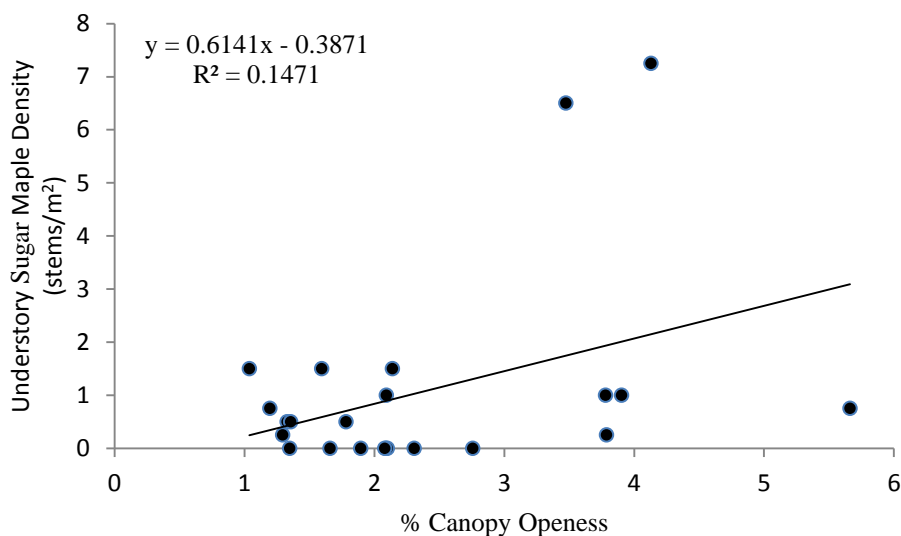


Figure 7. The relationship between the density of understory sugar maple ≤ 2 m tall and percent canopy openness in an old growth forest, Adirondacks, NY ($r = 0.384$, $p = 0.071$).

Understory vs. light environment and overstory conspecifics

Model [1] could only be fit for beech, sugar maple, red maple, red spruce, and yellow birch because these were the only species occurred at over 30% of the plots in both the understory and overstory. This linear model was fit such that the density of a species in the understory was a function of the proportion overstory basal area of conspecifics and light environment.

Table 1. Fitted ordinary least squares regression models with understory density (stems/m²) of a species as the response variable and percent canopy openness and the proportion overstory basal area of conspecifics as the two predictor variables. The understory was defined as trees ≤ 2 m tall, and the overstory was defined as trees with a dbh ≥ 11.68 cm.

Response Variable	Predictors	Coefficient Estimate	t	p (from t-test)	F	p (from F-test)	R ² adjusted
Understory beech density	Constant (y-intercept)	0.0545	0.33	0.74	10.18	0.001	0.45
	% Canopy Openness	-0.06549	-0.89	0.38			
	Proportion overstory beech	1.7188	4.21	<0.001			
Understory sugar maple density	Constant (y-intercept)	-0.8852	-1.05	0.307	3.93	0.036	0.21
	% Canopy Openness	0.5423	1.77	0.091			
	Proportion overstory sugar maple	3.619	1.94	0.067			
Understory red maple density	Constant (y-intercept)	1.094	1.05	0.31	0.49	0.62	0.0
	% Canopy Openness	-0.1814	-0.50	0.62			
	Proportion overstory red maple	2.789	0.69	0.50			
Understory red spruce density	Constant (y-intercept)	0.2481	2.90	0.009	1.39	0.27	0.034
	% Canopy Openness	-0.05533	-1.66	0.11			
	Proportion overstory red spruce	-0.3909	0.54	0.59			
Understory yellow birch density	Constant (y-intercept)	-0.122	-0.12	0.91	1.13	0.34	0.011
	% Canopy Openness	0.3930	1.44	0.17			
	Proportion overstory yellow birch	0.453	0.20	0.85			

Overall the model of understory beech density as a function proportion overstory beech and canopy openness was significant (Table 1, F = 10.18, p = 0.001). However, overstory beech was the only significant predictor variable in the model (Table 1). In the model of understory sugar maple, both canopy openness (p = 0.091) and proportion

overstory sugar maple ($p = 0.067$) were marginally significant predictors (note that overall the model was significant, $F = 3.93$, $p = 0.036$). The models of red maple, red spruce and yellow birch were not significant ($p \geq 0.27$, Table 1).

Discussion

The overstory variable that most strongly predicted canopy openness was the proportion of overstory beech basal area. Canham (1994) found that beech and hemlock cast deeper shade than other species such as red maple, sugar maple, and yellow birch and that this was largely due to crown depth. Since all these species were present in the old growth forest studied, one might expect that the proportion of beech would be negatively correlated with canopy openness, however, a positive correlation was found. A confounding factor is that total overstory basal area was negatively correlated with the proportion of beech, meaning beech tended to be more dominant in the overstory when there was less total basal area (i.e. fewer or smaller trees in the overstory). Beech was also most abundant in smaller size classes, which may be a reflection of beech bark disease which causes mortality of larger beech trees and increases root sprouting (Houston, 1994). Thus in certain parts of the forest where relatively small beech trees are dominant canopy openness may be higher because there is not as much shading as might be caused by a deeper canopy created by larger trees.

The proportion of yellow birch and total overstory basal area of living trees were the next best predictors of canopy openness. There was a moderately significant negative correlation between the proportion of overstory yellow birch and canopy openness. The observation that yellow birch and canopy openness were negatively correlated while beech and canopy openness were positively correlated may be due to the different size

distributions of the species. Glennon (1994) conducted a study in the same old growth forest of Huntington Wildlife Forest and presented data indicating that beech had a smaller average dbh than yellow birch, which is corroborated by our data (see size class distributions, Appendix 2), and this shift toward smaller beech commonly occurs due to beech bark disease (McNulty and Masters, 2004). Perhaps because yellow birch are larger on average, they tend to block more light, thereby explaining the marginally significant negative correlation between proportion of yellow birch and canopy openness. Total overstory basal area was found to be negatively correlated with canopy openness. This relationship could be due to higher total basal area reflecting a greater number of trees and or larger trees, which in turn might be responsible for creating a more closed canopy.

The overstory tree community might influence the understory tree community for different reasons. As indicated by the correlation between the proportion of overstory beech and canopy openness, light environment and the overstory tree community are not independent of each other. Light can be a limiting resource for trees and thus help shape succession (Roberts, 1992), and may therefore impact understory composition. A moderately significant positive correlation between understory density of sugar maple and canopy openness was found. However, understory densities of the other tree species were not significantly correlated with canopy openness. A similar trend was found when the model [1] of understory density as function of canopy openness and overstory conspecifics was fit. In this case the canopy openness slope coefficient was moderately significant for the model of sugar maple, but was not significant in the models of the other species. Ricard et al. (2003) found that sugar maple growth responded more

strongly to light availability than either yellow birch or beech. Canham (1988) also found sugar maple growth to be more strongly affected by light levels than beech. Therefore the weak positive correlation between understory sugar maple density and canopy openness may be due to this species' greater sensitivity to the light environment. However, this relationship must be considered tentatively because canopy openness and understory sugar maple were not found to be significantly correlated when the data were analyzed on a sub-plot basis (not averaged across the CFI plot).

The overstory tree community may also affect understory trees in ways other than by influencing the light environment. For instance, overstory trees might impact nearby growing conditions through altering leaf litter quality or competitive effects such as nutrient use (Woods 1984) and also act as sources of seeds or root sprouting. These neighborhood effects can be either positive, neutral, or negative (Frelich and Reich, 1995). Total overstory basal area was negatively correlated with the understory density of sugar maple and also with the understory density of beech. This could be an expression of the competitive effect of the overstory, with greater overstory basal area resulting in a higher use of resources thereby reducing the understory density of sugar maple and beech.

Other possibly competitive interactions observed, were the negative correlations between the proportion of overstory hemlock and density of understory beech, as well as between proportion of overstory hemlock and density of understory sugar maple. Woods (1984) found a similar trend and suggested that beech and sugar maple seedlings may have higher mortality under hemlock canopies. Hemlocks produce poor quality litter

(high C:N ratio)(Pastor et al., 1984) and transmit little light (Canham et al. 1994), and thereby may inhibit recruitment of other species.

Positive correlations may be expected between the density of seedlings and saplings of a species in the understory and the proportion of conspecifics in the overstory, which act as a seed source. The strongest predictor of the density of understory beech was the proportion of overstory beech. Root sprouting is an important means of regeneration for beech and Beaudet et al. (1999) found that over half of beech saplings were of root sprout origin, and that the root sprouts were relatively more abundant at larger size classes indicating they could survive better than seedlings. If root sprouting were the primary means of beech regeneration in the old growth forest studied, that may help explain why understory beech density was more strongly positively correlated with the proportion of nearby overstory conspecifics than other species were. This is because root sprouts tend to grow nearby their parent tree (Jones and Raynal, 1986), while seeds may be dispersed a further distance from their source.

In addition to being correlated with understory beech, overstory beech was also correlated with understory sugar maple. The positive correlation between understory sugar maple and the proportion of overstory beech is a similar finding to that reported by Woods (1984).

The relationships between overstory or canopy openness and understory tree composition need to be interpreted with caution because many of the overstory relationships are correlated with each other. Additionally, for several species including yellow birch, red maple and sugar maple, the vast majority of the seedlings and saplings were <30 cm tall, and very few large saplings and small trees were present (beech being a

notable exception). Therefore, many of the understory trends documented may be more a reflection of the relationships relating to the establishment of seedlings and small saplings and less related to the recruitment of these trees into the overstory. Nonetheless, the results indicate that there are interactions between the overstory and understory tree communities. Several of the relationships found were related to the abundances of particular tree species in the overstory or understory and these species specific relationships may be due to factors unique to the tree species in question. Certain species seemed to have positive neighborhood effects on conspecifics and/or heterospecifics in the understory, while others appear to have neutral or negative effects.

While the forest studied has not experienced strong direct human disturbance such as logging, it has been affected by beech bark disease. By shifting the distribution of beech trees toward smaller size classes, this disease may likely have influenced many of the overstory-understory relationships observed. Loss of large beech probably altered canopy structure, thus impacting the light environment and increased densities of beech saplings may have impacted the understory competition dynamics. Thus this study provides insight into the relationships that occur between the light environment and overstory and understory tree composition in a system that has been disturbed by beech bark disease but is otherwise relatively pristine. However, additional studies are needed to help further elucidate what role beech bark disease plays in mediating neighborhood dynamics in northern hardwood forests.

References

- Arii, K. and M. J. Lechowicz. (2002). The influence of overstory trees and abiotic factors on the sapling community in an old-growth *Fagus-Acer* forest. *Ecoscience*, 9(3): 386-396.
- Avery, T. E. and H. E. Burkhart. (1995). *Forest Measurements*. (3rd Ed.). New York: McGraw-Hill Book Company.
- Beaudet, M., C. Messier, and D. Paré. (1999). Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-de-Muir old-growth forest, Québec. *Ecoscience*, 6(2): 264-271.
- Beaudet, M. and C. Messier. (1998). Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Canadian Journal of Forest Research*, 28: 1007-1015.
- Canham, C. D. (1988). Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, 69(3): 786-795.
- Canham, C. D., A. C. Finzi, S. W. Pacala and D. H. Burbank. (1994). Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, 24: 337-349.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, 20: 620-631.
- CASTNET. (n. d.). Hourly raw meteorological data (2001-2011) from Huntington Wildlife Forest. Retrieved from http://java.epa.gov/castnet/datatypepage.do?reportTypeId=REP_001
- Cook, E. A., L. R. Iverson, and R. L. Graham. (1989). Estimating forest productivity with Thematic Mapper and biogeographical data. *Remote Sensing of Environment*, 28: 131-141.
- Elzinga, C. L., D. W. Salzer, J. W. Willoughby, and J. P. Gibbs. (2001). *Monitoring Plant and Animal Populations*. Malden: Blackwell Science, Inc.
- Frazer, G. W., C. D. Canham, and K. P. Lertzman. (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Frelich, L. E. and P. B. Reich. (1995). Neighborhood effects, disturbance, and succession in forests of the western Great Lakes Region. *Ecosystems*, 2(2): 148-158.
- Frelich, L. E. and P. B. Reich. (1999). Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems*, 2: 151-166.
- Frelich, L. E., R. R. Calcote and M. B. Davis. (1993). Patch formation and maintenance in an old-growth hemlock-hardwood forest. *Ecology*, 74(2): 513-527.
- Frelich, L. E., S. Sugita, P. B. Reich, M. B. Davis and S. K. Friedman. (1998). Neighbourhood effects in forests: implications for within-stand patch structure. *Journal of Ecology*, 86: 149-161.
- Friedman, S. K., P. B. Reich and L. E. Frelich. (2001). Multiple scale composition and spatial distribution patterns of the north-eastern Minnesota presettlement forest. *Journal of Ecology*, 89: 538-554.

- Glennon, M. (1994). Forty-five years of change in the old-growth northern hardwood stands of the HWF Natural Area. SUNY-ESF Adirondack Ecological Center Special Report 81. Adirondack Ecological Center, Newcomb, New York, USA.
- Houston, D. R. (1994). Major new tree disease epidemics: beech bark disease. *Annual Review of Phytopathology*, 32: 75-87.
- Jenkins, J. and A. Keal. (2004). *The Adirondack atlas: A geographic portrait of the Adirondack Park*. Syracuse: Syracuse University Press.
- Jones, R. H., and D. J. Raynal. (1986). Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). *American Journal of Botany*, 73(12): 1723-1731.
- McNulty, A. S and R. D. Masters (2004). Changes to the Adirondack forest: implications of beech bark disease on forest structure and seed production. *Beech bark disease: proceedings of the beech bark disease symposium*. USDA Forest Service General Technical Report NE-331, 52-57.
- Pastor, J., J. D. Aber, C. A. McLaugherty and J. m. Melillo. (1984). Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology*, 65(1): 256-268.
- Pacala, S. W., C. D. Canham, J. A. Silander, and R. K. Kobe. (1994). Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research*, 24(11): 2172-2183.
- Morin, S. R., A. M. Liebhold, P. C. Tobin, K. W. Gottschalk and E. Luzader. (2007). Spread of beech bark disease in the eastern United States and its relationship to regional forest composition. *Canadian Journal of Forest Research*, 37: 726-736.
- Ricard, J. P., C. Messier, S. Delagrange, and M. Beaudet. (2003). Do understory saplings respond to both light and below-ground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. *Annals of Forest Science*, 60: 749-756.
- Roberts, M. R. (1992). Stand development and the overstory-understory interaction in an aspen-northern hardwoods stand. *Forest Ecology and Management*, 54: 157-174.
- Runkle, J. R. (1981). Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, 62(4): 1041-1051.
- Stevens, V. (1997). The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. Res. Br., B.C. Min. For., Victoria, B.C. Work. Pap. 30/1997.
- Woods, K. D. (1979). Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *OIKOS*, 33: 31-39.
- Woods, K. D. (1984). Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. *Vegetatio*, 87-107.
- Zhang, Y., J. M. Chen, and J. R. Miller. (2005). Determining digital hemispherical photograph exposure for leaf area index estimation. *Agricultural and Forest Meteorology*, 133: 166-181.
- Zhao, D., B. Borders, M. Wilson and S. Rathbun. (2006). Modeling neighborhood effects on the growth and survival of individual trees in a natural temperate species-rich forest. *Ecological Modelling*, 196: 90-102.

Appendix 1.

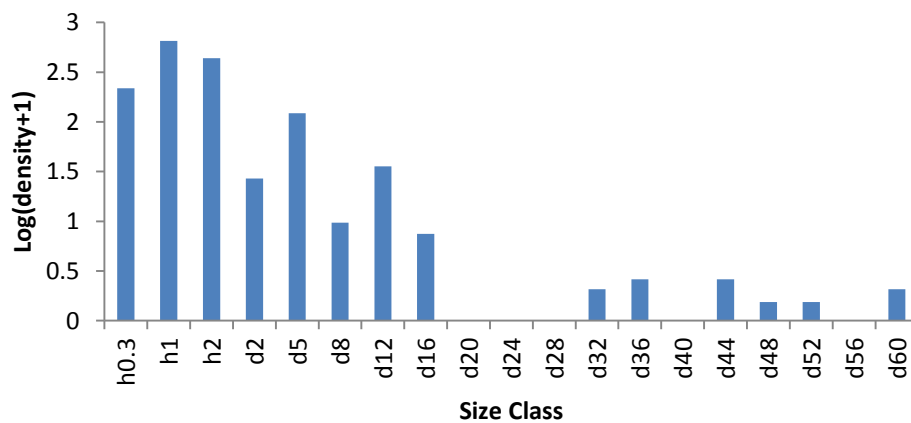
Mean (S.D.) density and frequency of live understory woody plants <2 m tall, in an old growth forest, Adirondacks, NY.

Species	Mean (S.D.) Density (stems/m²)	Frequency (proportion of CFI plots where present)
hobblebush	5.68 (7.26)	0.91
white ash	1.12 (3.86)	0.17
sugar maple	1.08 (2.85)	0.65
yellow birch	0.92 (2.39)	0.57
red maple	0.84 (2.71)	0.57
beechn	0.33 (0.92)	0.43
striped maple	0.17 (0.46)	0.48
red spruce	0.13 (0.42)	0.39
balsam fir	0.09 (0.74)	0.09
hemlock	0.07 (0.25)	0.26

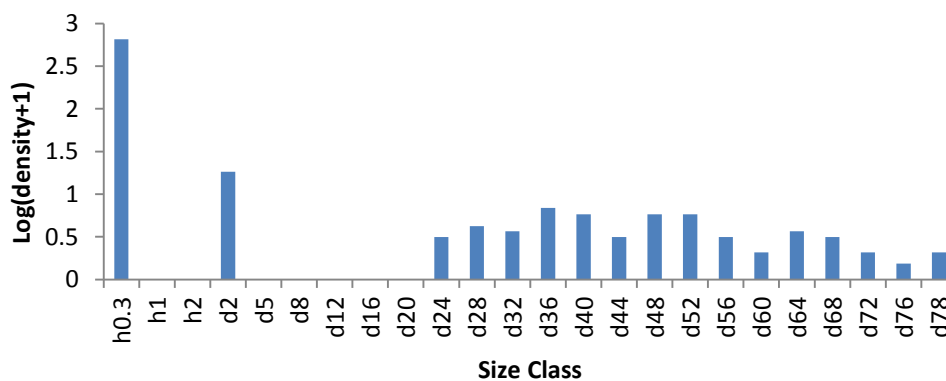
Appendix 2. Size class distributions by tree species found in an old growth forest at Huntington Wildlife Forest, Adirondacks, NY.



Log of beech density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

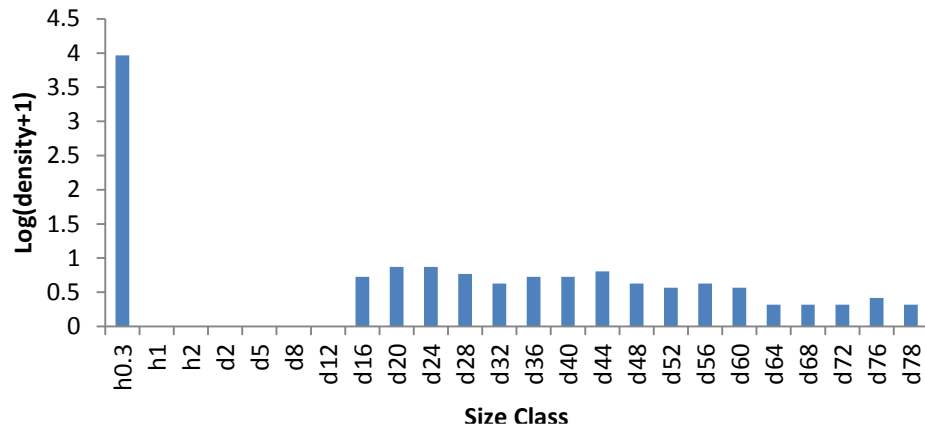


Log of red spruce density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

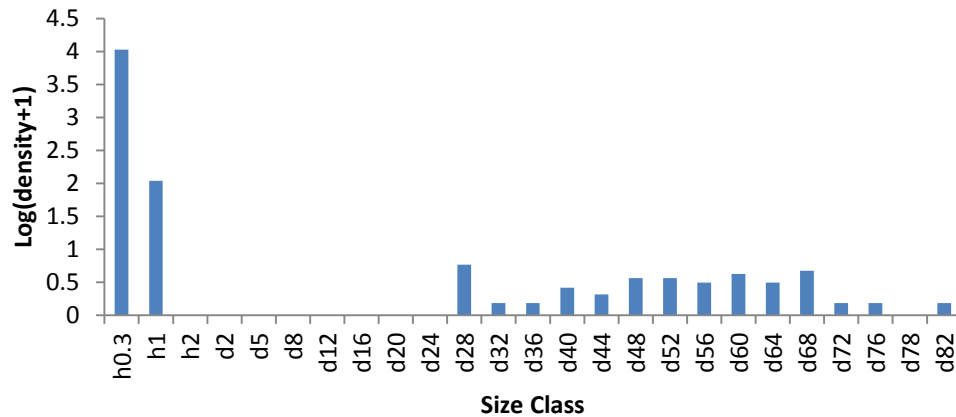


Log of hemlock density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

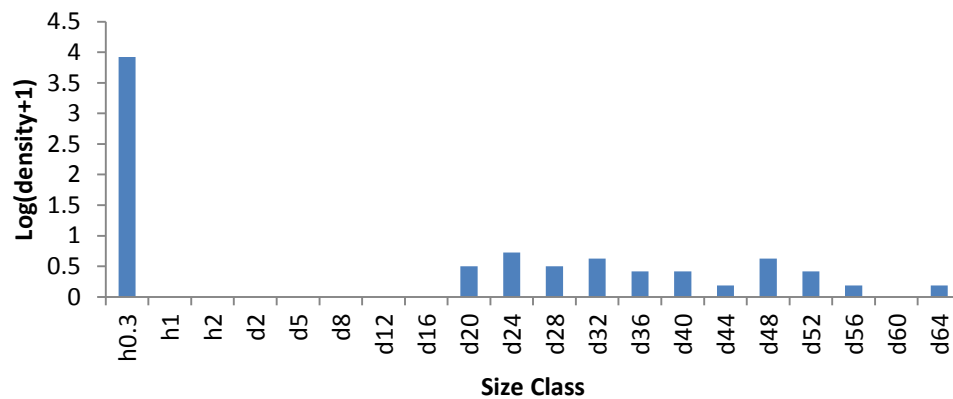
Appendix 2 continued.



Log of yellow birch density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

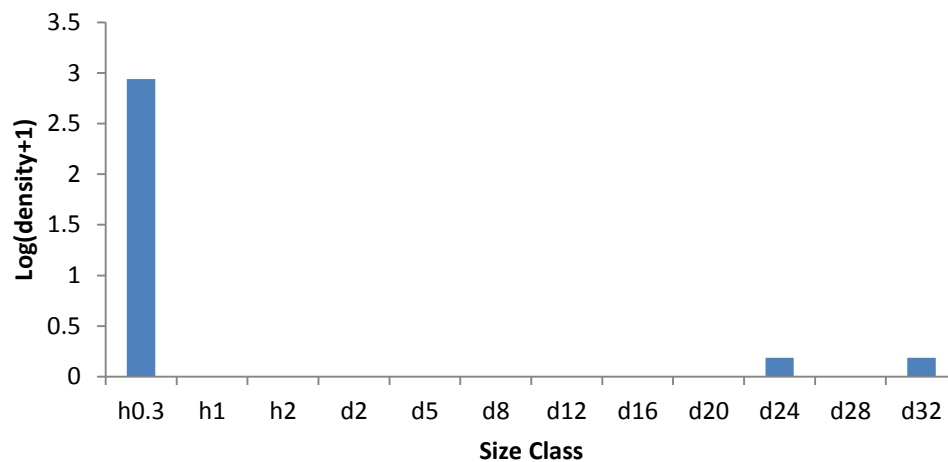


Log of sugar maple density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

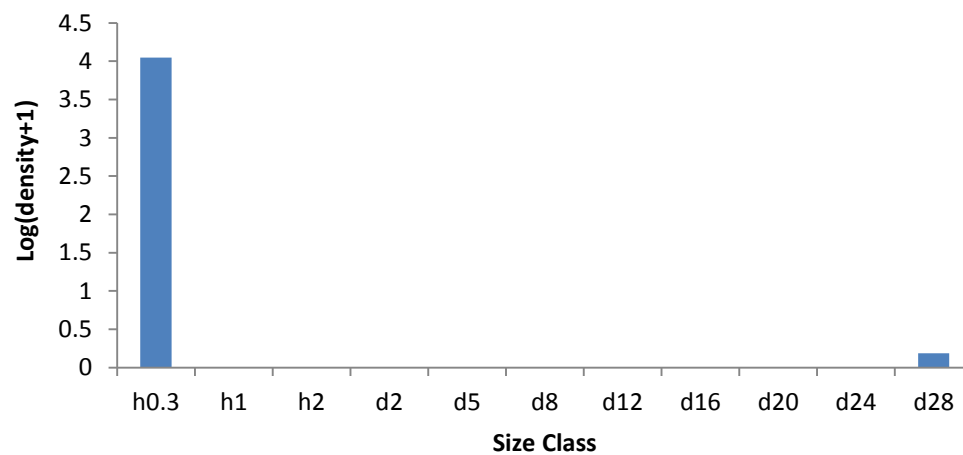


Log of red maple density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".

Appendix 2 continued.



Log of balsam fir density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".



Log of white ash density (trees/ha) by size class. Three height classes (m) with the upper bounds preceded by "h", and upper bound of dbh classes (cm) preceded by "d".