EFFECT OF FOREST STRUCTURE ON THE UNDERSTORY LIGHT ENVIRONMENT AND GROWTH POTENTIAL OF OAK SEEDLINGS IN A CLOSED CANOPY RIPARIAN FOREST

Except where reference is made to the work of others, the work described in this thesis is my own or was done in collaboration with my advisory committee. This thesis does not include proprietary or classified information.

Bradford J. Ostrom

Certificate of Approval:

Graeme Lockaby
Professor
Forestry and Wildlife Sciences

Edward F. Loewenstein, Chair
Assistant Professor
Forestry and Wildlife Sciences

Greg L. Somers
Associate Professor
Forestry and Wildlife Sciences

Stephen L. McFarland
Acting Dean
Graduate School

EFFECT OF FOREST STRUCTURE ON THE UNDERSTORY LIGHT ENVIRONMENT AND GROWTH POTENTIAL OF OAK SEEDLINGS IN A CLOSED CANOPY RIPARIAN FOREST

Bradford J. Ostrom

A Thesis

Submitted to

the Graduate Faculty

of Auburn University

in Partial Fulfillment of the

Requirements for the

Degree of

Masters of Science

Auburn, Alabama
December 16, 2005

EFFECT OF FOREST STRUCTURE ON THE UNDERSTORY LIGHT ENVIRONMENT AND GROWTH POTENTIAL OF OAK SEEDLINGS IN A CLOSED CANOPY RIPARIAN FOREST

Bradford J. Ostrom

Signature of Author

Date of Graduation

VITA

Bradford Jerome Ostrom, son of Mr. and Mrs. John Michael Ostrom, was born in Houston, TX on December 22, 1977. He graduated from St. Thomas Catholic High School, and from there attended the University of the South (Sewanee). At Sewanee he earned a Bachelor's of Science degree in Natural Resources, graduating *cum laude* from the University and with honors in the Department of Forestry and Geology in May 2000. Following graduation, he worked for two years as a Research Technician with the Department of Forestry and Geology at Sewanee before beginning his graduate degree. In January 2003 he entered the School of Forestry and Wildlife Sciences at Auburn University in pursuit of a Master's of Science Degree in Forestry. He was married to his wife, Anna Delores Truss of Birmingham, AL on July 17, 2004.

THESIS ABSTRACT

EFFECT OF FOREST STRUCTURE ON THE UNDERSTORY LIGHT ENVIRONMENT AND GROWTH POTENTIAL OF OAK SEEDLINGS IN A CLOSED CANOPY RIPARIAN FOREST

Bradford J. Ostrom

Master's of Science, August 8, 2005
(B.S., University of the South, 2000)

154 Typed Pages

Directed by Edward F. Loewenstein

This research was designed to examine the relationship between the residual structure following low intensity partial cutting regimes and the light characteristics found in a riparian hardwood forest. The relationships between these altered environments and oak seedling growth under the influence of a main canopy were also investigated. A better understanding of these relationships is needed to further the discussion of the feasibility of regeneration oak on mesic sites.

The model developed to describe the amount of photosynthetically active radiation (PAR) below the canopy indicated that a relationship exists between stem density, crown length, and crown closure. The presence of a midstory canopy significantly affects this relationship by increasing both stem density and overall canopy length. The models developed to describe light quality demonstrated that the R:FR ratio will depend on structure that impedes direct sunlight from reaching the forest floor. Thus, descriptions of vertical canopy density become important. The relative amount of blue light is dependent on diffuse light and is influenced most by the amount of visible blue sky below the canopy. Therefore, variables which describe canopy closure are significantly related to the blue light levels below the canopy.

The relationship between stand conditions and Nuttall oak (*Quercus nuttallii* Palmer) seedling growth indicate that, as individual variables, PAR transmittance and the presence of a midstory canopy accounted for roughly the same amount of variation (33-35%) in both diameter and height growth. Interestingly, the R:FR ratio also explained a considerable amount of variation in diameter and height growth in the low light levels examined (3-22% full sun). It is apparent that the only difference between the diameter and height growth models is the type of structure variable included. Canopy structure was more important for the diameter growth model, while basal area, a measure of stand density, accounted for more variation in the height growth model. The significance of this difference is difficult to determine. However, since minor changes in basal area may induce significant changes to the canopy, it is possible that seedling height growth is less sensitive to minor differences in canopy architecture than diameter growth.

Keywords: silviculture, riparian hardwood forest, partial cutting, midstory removal, Nuttall oak, PAR, R:FR ratio, light quality, light models, seedling growth model

ACKNOWLEDGEMENTS

The author would like to take this the opportunity to thank the Center for Forest Sustainability and the School of Forestry and Wildlife Sciences for the funding and support of this research. He would also like to acknowledge Dr. Edward Loewenstein, Dr. Greg Somers, Dr. Graeme Lockaby, Dr. Nancy Loewenstein, John Lhotka, Patrick Rawls and Troy Taylor for their guidance and assistance. Lastly, he would like to thank his wife, Anna, for her encouragement and understanding throughout the project.

STYLE MANUAL

The presentation of all information contained within this thesis, including all literature cited, is in keeping with the format used by the Canadian Journal of Forest Research. Any exceptions to this format result from directives given from committee members. All tables and figures are presented according to the wishes of the committee members. The computer software used in this thesis included Microsoft® Word and Microsoft® Excel, both of which are part of Microsoft Office Professional Edition 2003. Other software used included The SAS System for Windows, Version 8.02, and SigmaPlot 2002 for Windows, Version 8.0.

TABLE OF CONTENTS

CHAPTER 1 - INTRODUCTION

Single-tree selection, a form of uneven-aged silviculture, is arguably one of the least understood management tools foresters have at their disposal. In short, selection systems are based on the concept that there is a limited amount of growing space or resources that can be distributed among different age classes through partial cutting. The goal of the system is to establish and sustain growth of multiple age classes while maintaining continuous tree cover. To realize this goal, growing space must be allocated in such a way so that a dominant cohort does not have a disproportionate amount of resources to the detriment of a subordinate cohort; the process of resource allocation is typically achieved by removing trees from the upper and middle canopy tiers so that resources remain available to the youngest cohort (Smith and others 1997). Too often, however, unsustainable practices such as high-grading, the removal of only commercially valuable stems without regard for the residual stand, result from incorrect application of the selection system. Poor execution of the system often arises from the difficult process of developing and implementing target cutting guidelines that are tailored to the species and environment in which the user is working.

Although complex, single-tree selection is an inherently versatile system and has the potential to adapt to situations where current even-aged techniques are unable to satisfy landowner objectives, especially when those objectives require the maintenance of continuous tree cover. Single-tree selection may prove useful in situations such as in the extension of management into buffer strips between clear-cuts, or into streamside management zones, on steep slopes or on soils prone to erosion, or within view-sheds where maintaining tree cover may be of paramount importance. Aside from these examples, however, one other situation where even-aged techniques may prove unsuitable because of the inability to maintain continuous tree cover includes the management of increasingly fragmented stands within urban areas or the wildland-urban interface (WUI).

In the southeastern United States, urban expansion into rural areas near large population centers is leading to greater fragmentation of the forest landscape as development pressure increases (Wear and Greis 2002); former rural lands are being divided into small acreage properties in growing communities. In many cases the primary appeal of these properties to new landowners is that these areas are forested, or surrounded by a forested setting. While they may not own substantial acreage, many of these landowners are not opposed to forest management activities (Hull and others 2004, Edwards and Bliss 2003) although they have different objectives than traditional forest owners. Most strikingly, timber production is seldom an important consideration for this group; aesthetics, wildlife and forest health are often cited as more important goals (Hull and others 2004). Thus retaining a continuous canopy may be crucial to fulfilling the objectives of these stakeholders. A similar situation exists with publicly owned natural or semi-natural woodlands in urban or suburban settings. These forest remnants serve as parks, natural recreational areas, and community green-spaces, but may not be under an active management regime. Such forest stands may benefit from the application of varying intensities of single-tree selection.

The development of management options for these lands is important because forests change over time. The physical attributes that make forest lands appealing to those who live in their proximity are subject to change, especially when the disturbance regimes that initially created these woodlands are excluded from increasingly fragmented forests. An illustration of this point is seen in the example of fire being excluded from forests surrounding new communities located within a fire mediated ecosystem. Landowners want to protect their houses; however, the exclusion of fire from such a system will eventually alter the species composition in the forest. Furthermore, the change in species composition may be exacerbated by the introduction of non-native invasive plant species that escape from landscaping plantings. Such species often out-compete and replace native vegetation (Wear and Greis 2002). In short, new landowners should be aware that their property is unlikely to retain its present species composition or physical structure over time. If maintenance of the current, or similar, stand characteristics is desired, then some type of active management may be necessary.

Single-tree selection has traditionally been applied where the preferred species are tolerant of shade, such as in the northern hardwood region of the United States. Indeed, attempts at applying single-tree selection in stands dominated by shade intolerant hardwoods in the eastern U.S. have resulted in a shift in species composition to more shade tolerant species (Della-Bianca and Beck 1985, Schlesinger 1976, Trimble and Smith 1976). The problem seems to be that dense midstory canopy tiers composed of shade tolerant species found on productive sites alter the microclimatic environment on the forest floor to such a degree that few shade intolerant seedlings are able to become established. While many of the studies demonstrating a shift in species composition to shade tolerant species with single-tree selection have been in Appalachian and upland mixed hardwood forests, similar results are seen in southern riparian hardwood forests where the altered disturbance regime has encouraged the development of shade tolerant species such as hornbeam (*Carpinus caroliniana* Walt.), hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.), and American beech (*Fagus grandifolia* Ehrh.) (Meadows and Stanturf 1997). These species often form a midstory under canopies of oak (*Quercus sp.*), ash (*Fraxinus* sp.), sweetgum (*Liquidambar styraciflua* L.) and yellow-poplar (*Liriodendron tulipifera* L.). Research indicates that the presence of a dense midstory can limit seedling survival and growth of desirable oak reproduction (Janzen and Hodges 1987, Lockhart and others 1992). What is not known, however, is the extent of reduction in light levels given various midstory densities.

At first glance, it would not appear that single-tree selection can sustain establishment and growth of shade intolerant to moderately-tolerant species such as oaks, which have timber, aesthetic, and wildlife value. Yet, research has also shown that the method can be adapted to shade intolerant species such as ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in the southwest (Smith and others 1997), longleaf pine (*P. palustris* Mill.) along the Gulf Coastal Plain (Farrar 1996), shortleaf (*P. echinata* Mill.) and loblolly pine (*P. taeda* L.) in the southeastern United States (Baker and others 1996), and upland oak forests in the Missouri Ozarks (Larsen and others 1999 and Loewenstein and others 2000). The common thread among these distinct ecosystems that facilitates successful application of single-tree selection is the lack of significant amounts of shade tolerant competition. This situation is the result of either the xeric nature of the ecosystems or the active control of shade tolerant competition with herbicides.

Although competition is difficult to control on mesic sites in the southern U.S., the possibility of using single-tree selection in riparian forests cannot be dismissed as a silvicultural option for three reasons. First, conclusions drawn from research on single-tree selection in eastern hardwood forests were based on narrowly focused and rigidly defined prescriptions; a small selection among the many options available within a broad and flexible silvicultural system (Della-Bianca and Beck 1985, Schlesinger 1976, Trimble and Smith 1976, Johnson and Krinard 1989). It appears that these studies failed to tailor their prescriptions to the specific environmental constraints and silvics of the species with which they were dealing. Additionally, little effort was made initially to control the existing shade tolerant competition either mechanically or with herbicides (Della-Bianca and Beck 1985, Trimble and Smith 1976). With the adoption of a more intensive management regime, however, Della-Bianca and Beck (1985) demonstrated promising trends with regard to desirable reproduction.

Second, an effective prescription has been developed for promoting northern red oak (*Q. rubra* L.) seedling growth on good sites in the southern Appalachians using the shelterwood system (Loftis 1990). While the method described is not single-tree selection, the dynamics discussed are applicable nonetheless. Loftis (1990) demonstrated that it is possible to maintain oak reproduction under a continuous canopy for an extended period of time, more than a decade. The survival and growth described is a prerequisite for successful implementation of single-tree selection and suggests that when properly applied, the system may successfully sustain oak in a mesic ecosystem.

Finally the third point is the need to focus on the stakeholders along the wildland-urban interface. Those opposed to the use of single-tree selection on mesic sites would correctly argue that the intensity of competition control, the slow growth rates, and the potential need to underplant oak seedlings outlined in Loftis' (1990) prescription may not be cost effective for most landowners. Although single-tree selection may be a costly system to implement and maintain when compared to the alternative even-age prescriptions, it is important to remember that the objectives of the stakeholders in question are usually focused on maintaining forest health and aesthetics. Thus, for landowners who own small acreage tracts and whose primary objective is not to maximize profit from timber sales, the costs associated with implementing single-tree selection may be considered reasonable.

The dilemma which faces forest managers is whether single-tree selection can create the canopy disturbance intensity and frequency, and thus the light conditions, needed to regenerate oak without releasing other intolerant competitors while at the same time preventing a compositional shift toward shade tolerant species. Although not quantified specifically, Loftis (1990) indicated that this narrow range of light conditions does exist in the southern Appalachians. The question remains whether a similar threshold can be identified in the riparian hardwood forests of the southeast. Previous research has examined the growth response of several oak species to various light intensity levels (Gottschalk 1985, Gardiner and Hodges 1998, Crow 1992, Ziegenhagen and Kausch 1995) however the results of many of these studies raise additional questions. Another issue that requires further investigation is the effect of partial cutting on the spectral quality of light below the main canopy. Light quantity, measured as photosynthetically active radiation (PAR), and light quality are both important for seedling growth, but little is known as to how these characteristics of light are altered by partial cutting activities. Therefore the purpose of this research is to further the discussion of the feasibility of using partial cutting to establish competitive oak reproduction on mesic sites. This objective is addressed in two ways: first, by revealing how low intensity cutting alters the light environment below the main canopy, and secondly by examining the influence of the residual stand and light characteristics on desirable oak reproduction following these cutting treatments. Although not single-tree selection, the partial cutting used here creates conditions that resemble those that may appear during the conversion of an even-aged stand to single-tree selection, a critical step in the initiation of selection management. By identifying factors that are influential on seedling growth and by understanding how to create favorable light environments below the canopy, foresters can better evaluate the feasibility of the method in southern riparian forests.

CHAPTER 2 – LITERATURE REVIEW

A more thorough understanding of the light requirements of oak reproduction is needed before stand manipulations can be designed that provide the light conditions necessary for oak seedling establishment and growth. Previous research indicates that two distinct attributes of the light environment may impact seedling growth and vigor. Light quantity, often referred to as intensity, photosynthetically active radiation (PAR), photon flux density (PFD), or as a percent of full sunlight, is the most well recognized characteristic of light and is a measure of the amount of radiation occurring in the visible spectrum (approximately 380-710 nm) (Larcher 1980, Lieffers and others 1999). Radiation occurring in the range covered by PAR is known to drive the photosynthesis apparatus in plants, and therefore is crucial for plant growth and development (Lieffers and others 1999). The second measure, light quality, refers to the spectral composition of the light environment with wavelength groups often categorized by colors. Due to the difficulty in quantifying the spectral quality of a given light environment, light quality is most often reported as a ratio of red light (660nm) to far-red light (730nm). The red: far-red (R:FR) ratio is not without merit; evidence demonstrates the impact that the proportion of these wavelengths can have on the growth of many plant species (Holmes and Smith 1977b, Endler 1993, Smith 1982, Kwesiga and Grace 1986).

Effects of canopy structure on the vegetative light environment

Since leaves act as filters of light energy, the spectral composition of light is related to the structural arrangement of the canopies within a particular forest; structural characteristics of forest canopies have also been shown to influence light intensity levels as well (Brown and Parker 1994, Messier and Bellefleur 1988). Therefore, a discussion about the light requirements of oak reproduction in a natural setting cannot begin without first examining how canopy structure influences light characteristics on the forest floor. Leaf area density, total tree height, crown depth, height to the base of the live crown, leaf area index (LAI), and estimated aboveground biomass are a few of the parameters oftentimes examined when trying to associate light transmittance with canopy structure (Brown and Parker 1994, Messier and Bellefleur 1988, Canham and others 1994). Jenkins and Chambers (1989) modeled reductions in PAR based on several stand attributes of five bottomland hardwood stand-types in Louisiana, finding that percent basal area removed and percent crown closure were highly correlated with decreases in light intensity. However, all stems below 10 cm in diameter were removed prior to the implementation of the treatments and the measurement of the subsequent light levels (Jenkins and Chambers 1989). By eliminating these smaller stems Jenkins and Chambers (1989) present a relationship that overestimated the amount of light available to seedlings. Had these stems not been removed, the midstory would further reduce PAR levels via light interception of foliage. A few scattered stems will not likely have much influence on the light environment near the forest floor. However a dense sub-canopy may significantly alter vegetative light regimes.

Brown and Parker (1994) also explored the relationship between transmittance and canopy structure in mixed deciduous forests of Maryland. They found that the variables that described the vertical arrangement of leaves had the greatest correlations to PAR transmittance; the density of the leaves and their height above the ground in particular proved to be important (Brown and Parker 1994). In short, stands that consist of densely packed leaves with low canopy heights, as potentially would be the case in stands with several canopy layers, had the lowest PAR transmittance (Brown and Parker 1994). This finding suggests that modifications may be needed with regard to methodology for examining canopy structure. Leaf area index, the measure of leaf area over a particular ground area, is the most conventional method of describing leaf density and has been shown to be negatively associated with PAR levels below a vegetative canopy (Larcher 1980, Yirdaw and Luukkanen 2004). However, by itself, LAI may not be sufficient to describe canopy transmittance (Brown and Parker 1994). While LAI does provide an indication of the amount of leaf area in a canopy, by adding variables such as total canopy height and height to the base of live crown, a more accurate description of leaf density emerges. Theoretically, two stands with the same total leaf area and LAI values may differ in PAR transmittance due to differences in crown architecture; one stand with a relatively short crown and densely packed leaves close to the ground may transmit less light than one that consists of tall trees with elongated, sparse crowns.

The impact of crown structural characteristics is clearly seen when examining the differences between conifer and broadleaf deciduous species. Yirdaw and Luukkanen (2004) noted that of five forest plantation species found in Ethiopia, transmittance within the plantations varied based on canopy features. Two of the broadleaf species examined had more open crowns, higher crown bases, and lower LAI than two of the conifer species resulting in higher transmittance levels (Yirdaw and Luukkanen 2004). In addition to higher transmittance, the broadleaf deciduous plantations with the most open crowns had higher R:FR ratios than the conifer stands with dense crowns closer to the ground (Yirdaw and Luukkanen 2004).

Vezina and Pech (1964) indicate that there is a relationship between canopy depth and canopy closure, with a decrease in openness with an increase in crown depth or length. Although not indicated directly in Yirdaw and Luukkanen (2004), one may suspect that since the conifer plantation species measured had shorter clear boles, greater LAI, and more closed crowns, they may also have had greater crown length. It is possible that the longer crowns will carry more leaf biomass, which would translate into a greater LAI. This trend is most evident when examining species that are tolerant of shade. Shade tolerant species may exhibit greater crown length because they generally have lower light compensation points, allowing positive photosynthate production despite the low light conditions created by self-shading. Canham and others (1994) noted that for nine deciduous and coniferous species of southern New England, the shade tolerant species cast the deepest shade while the more shade intolerant species allowed greater light penetration through the canopy; these differences were closely related to crown depth. In a study of the light characteristics in pioneer and climax stage birch-beech and sugar maple stands, Messier and Bellefleur (1988) also found that the shade tolerant species cast the deepest shade while also producing the lowest R:FR ratio values. Overall the pioneer stage allowed significantly more transmittance and higher R:FR ratio values than the climax stage; the pioneer canopy allowed a greater proportion of diffuse light through gaps in the canopy, while the climax forest consisted of a midstory and a more irregular canopy structure (Messier and Bellefleur 1988).

Influence of light quantity and quality on seedling growth

Due to the physiological constraints of many plants, increased light quantity does not necessarily equate to higher yields of plant growth. For many plants an optimal level of light intensity exists well below 100% full sun, with reduced growth both above and below this value. Indeed, several studies suggest that such an optimum exists in some species of oaks. Gardiner and Hodges (1998) examined the effects of light availability on biomass distribution and growth of cherrybark oak (*Q. pagoda* Raf.) seedlings. The authors recorded the growth of seedlings planted under four light intensity levels (8%, 27%, 53%, 100%) produced with neutral density shade cloth. In this study height and root collar diameter increased as light intensity increased from 8% to 53% full sun. However, additional increases in light levels to 100% full sun produced second year growth outputs that were not statistically different from the 8% full sun treatment (Gardiner and Hodges 1998). Due to the parabolic response curve of seedling growth in relation to light quantity, we can surmise that an optimal light intensity level, defined as the light quantity which produces the greatest height and diameter growth of a seedling, exists somewhere above 27% full sun for cherrybark oak. In another study involving pedunculate oak (*Q. robur* L.) grown under shade cloth, Ziegenhagen and Kausch (1995) observed the same parabolic seedling growth pattern. Under 10%, 25%, 50%, and 100%

full sun, Ziegenhagen and Kausch (1995) noted that after two growing seasons the tallest seedlings were found under the 25% full sun treatment, followed by those grown under 50%, 100%, and 10% respectively. A similar trend has been found with northern red oak and black oak (*Q. velutina* Lam.) in an experiment that examined height, diameter, and root-shoot ratio development under a gradient of light intensity ranging from 8% to 94% full sun (Gottschalk 1985). Both northern red oak and black oak expressed the greatest height growth under 20% full sun and the smallest heights under the 8% treatment, with height growth generally decreasing with additional increases in light intensity above the 20% treatment (Gottschalk 1985).

The most significant result of these studies is the identification of a parabolic growth pattern over a range of light intensities. Therefore, if an optimal light level exists for Nuttall oak (*Q. nuttallii* Palmer), an important component of riparian and bottomland hardwood forests in the southern U.S., it may be detected using an experiment similar to those previously described. However, it should be noted that the studies mentioned above also raise additional questions. First and foremost, Gardiner and Hodges (1998), and Ziegenhagen and Kausch (1995) only relied on four light intensity levels to determine growth trends. Although Gottschalk (1985) did implement seven light treatments, clearly if we hope to model seedling growth more accurately in terms of PAR, light quantity should be examined at a finer scale. Without a closer assessment of growth trends, it is not possible to determine if the parabolic model suggested by previous research is actually the best description of oak seedling growth in response to various light quantity levels. Secondly, additional factors may have influenced the results from these studies. Most notably, Gottschalk (1985), Ziegenhagen and Kausch (1995), and Gardiner and Hodges (1998) conducted their respective studies on old field sites, rather than in a forested setting. While soil variability was minimized, Gottschalk (1985) and Gardiner and Hodges (1998) used neutral density shade cloth, which does not alter the color of the sunlight passing through it. This is not the case under a living forest canopy. Ziegenhagen and Kausch (1995) did use cloth that allowed for green light to pass to the seedlings, however, it is not certain if the spectral nature of this treatment was reflective of the light climate found under a forest canopy.

In a natural setting, light quantity on the forest floor decreases with increasing overstory canopy coverage and pigment content (Holmes and Smith 1977a). With increasing canopy coverage, light passing through the canopy will become more spectrally altered due to the differential absorption and reflectance of certain wavebands by leaves (Larcher 1980). Thus the 'color' of a 20% full sun light environment under a mature forest canopy may differ spectrally from the 'color' of 50% full sun light environment, and certainly differs from that of 50% full sun cast by neutral density shade cloth. Ecological research has shown that the color of vegetative light does have some direct implications for plant germination, growth, and development. Light that is rich in the red and blue wavebands have the most influence on plant growth (Morgan 1981). Hypocotyl elongation, growth and elongation of stems, expansion rate of leaves, photosynthetic rates, pigmentation, and physiological processes such as stomatal opening, are some of the plant growth characteristics that are influenced to some degree by light quality (Endler 1993, Holmes and Smith 1977b, Smith 1982). In short, as light passes through a canopy, solar energy is either absorbed by the leaves, reflected off the leaves, or is transmitted through a leaf (Larcher 1980). The leaf layer of a forest canopy will selectively absorb the blue and red wavelengths, but transmit green and far-red wavelengths. Therefore the light under the canopy tends to be rich in the green and far-red areas of the spectrum (Larcher 1980, Holmes 1981, Morgan 1981, Holmes and Smith 1977a).

Although research has shown that light quality is important for various physiological and morphological responses to the light environment in which a plant is growing, it is important to remember that the degree of influence is species specific (Lee and others 1996). Generally, plants considered to be shade intolerant are more responsive to light quality cues such as reduced R:FR ratios than those species which are normally considered to be tolerant of shade (Kwesiga and Grace 1986, Lee and others 1996, Lei and Lechowicz 1998). Furthermore Lee and others (1996) demonstrated in an experiment with six Asian tropical tree species that not only are some species more responsive than others, but that the relative importance of light quality as opposed to light quantity varies depending on the light quantity level. Similar findings have been seen with six Australian rainforest species (Turnbull 1991).

Overall, PAR appears more influential for plant development than light quality, especially in terms of affecting seedling root collar diameter, height growth, photosynthate allocation, and as found with paper birch (*Betula papyrifera* Marsh.), direction of seedling lean (Lee and others 1996, Muth and Bazzaz 2002). However, for the tropical species examined by Lee and others (1996), height growth is also highly dependent on the R:FR ratio, with the R:FR ratio expressing the greatest influence when

PAR levels were at 11% of full sun (PAR levels of 3% and 40% full sun were also tested). Turnbull (1991) likewise demonstrated that light quality can affect variables such as the maximum photosynthetic assimilation rate of several rainforest species, with the most influence being seen at light climates of 5% full sun; the influence of light quantity and quality was similar in deep shade (1% full sun). The lack of importance of the R:FR ratio at higher levels of PAR might be related to the fact that at approximately 40% full sun the R:FR ratio reaches a maximum; additionally, a decrease in the R:FR ratio has been shown to be strongly correlated with a drop in PAR (Lieffers and others 1999, Lee 1987).

If temperate species such as oaks native to the southeastern United States were to exhibit similar growth trends depending on both the PAR intensity and R:FR ratio, then experiments relying solely on neutral density shade cloth might underestimate potential height growth at middle and lower PAR levels by discounting the effects of light quality on plant physiology. Work conducted with jewelweed (*Impatiens capensis* Meerb.), an annual forb, showed that attributes such as internode length and mean shoot length may vary at the same light intensity depending on whether the reduction in PAR was due to the use of neutral shade cloth or leaves (Wulff 1989, Schmitt and Wulff 1993). Hoad and Leakey (1994) demonstrated a similar effect with eucalyptus (*Eucalyptus grandis* W. Hill ex Maiden). A constant photon flux density of 200 μmol m^{-2} s^{-1} over a range of R:FR ratios produced several developmental changes including significant differences in plant height, partitioning of dry weight between leaves and stems, and specific leaf area (Hoad and Leakey 1994). Consequentially, if neutral density shade cloth is used to alter the light environment reaching seedlings care should be taken to note that the resulting growth curve may not be supported in a natural setting since characteristics such as height and shoot length may be affected by the spectral composition of forest vegetative light.

Management implications

There are many aspects of vegetative light that need to be examined further to facilitate a better grasp of how light characteristics affect seedling growth. Additionally, an improved understanding of the factors which influence PAR and light quality beneath a forest canopy is also needed so that new research mimics the natural environment of interest as much as possible. Weather, time of day, reflectance of the ground, density and pigment content of vegetative canopies, and the physical structure of vegetative canopies are the primary factors that influence the amount and spectral characteristics of light in a given environment (Holmes 1981). Yet silvicultural prescriptions can only influence the light regime present below a forest canopy by manipulating the physical structure of that canopy. The implication of this knowledge for forest management can be described by the following example.

Gardiner and others (2001) demonstrated that under a three-year-old cottonwood (*Populus deltoides* Bartr. ex Marsh.) plantation light intensity levels may be roughly 43% of full sun; Nuttall oak seedlings planted in this environment did not differ from open grown seedlings in terms of gross photosynthesis (Ps), or net Ps, among other physiological characteristics. Applying this knowledge, forest managers could potentially reduce stand density to allow light intensity levels of 43% full sun and expect similar growth of under-planted seedlings as those found in a full sun environment. However, a three-year-old cottonwood plantation does not have the structural characteristics of a natural stand and cutting to this intensity may not be necessary or wise. As indicated previously, seedlings growing from seed origin in a full sun environment may not be expressing optimal growth. Furthermore, by creating environments with higher light intensity levels, there is a greater risk of promoting the establishment and growth of fast growing shade intolerant species with which oak cannot compete.

Gardiner (2002) demonstrated that, physiologically, Nuttall oak showed few differences between seedlings grown at 20% full sun as compared to those grown at 100% full sun. Although leaf morphology differed as expected with wider, less dense leaves under the shading treatment, there was no difference in net photosynthetic rates between the two treatments (Gardiner 2002). By creating the structural attributes needed to maintain 20% full sun environment, foresters theoretically could sustain growth of some oak species under a forest canopy while lessening the possibility of establishing severe competition. In certain circumstances it might be desirable to maintain seedling growth with even less disturbance to the main canopy resulting in still lower light conditions. However, as mentioned earlier, some studies indicate that at lower light levels, light quality becomes more important. Gardiner's (2002) study was conducted in a glasshouse, where the issue of light quality may not have been addressed. Recall that Gardiner and Hodges (1998) found second year growth at 8% full sun was not statistically different from 100% full sun. If light quality does indeed have a greater influence at lower light levels then perhaps greater height growth may be realized with the 8% treatment if light quality was addressed. This is further reason why we need to address the light quality characteristics found with partial cutting so that further research can be designed accordingly.

CHAPTER 3 – THE INFLUENCE OF FOREST STRUCTURE ON THE LIGHT ENVIRONMENT BELOW A RIPARIAN HARDWOOD FOREST CANOPY

Abstract

Research indicates that controlling shade-tolerant midstory competition on mesic and bottomland sites is critical for the successful development of desirable oak reproduction. However, the effects these treatments have on the light environment have not been explored. In this study, models were developed to describe the influence of forest structure on the amount of photosynthetically active radiation (PAR) transmitted through a riparian hardwood canopy, and the spectral quality of that light. The ratio of red to far-red light (R:FR ratio), and the proportion of PAR composed of blue light were used to describe the spectral quality of the light present below the main canopy. While the model developed to describe PAR transmittance illustrates a balanced relationship between stem density, crown length, and crown closure, the influence of this relationship on PAR is encapsulated by the presence of a midstory canopy tier. The presence of this lower canopy tier increases stem density and overall canopy length, which together likely increase crown closure. The models developed to describe the spectral quality of light below the main canopy illustrate that some characteristics of forest structure influence the light quality differently due to their source of origin. The R:FR ratio, originating from direct solar radiation, is affected by structure that blocks the sun and lessens the likelihood that light will pass directly through the canopy unaltered. Variables such as average crown ratio, height of the canopy, and the presence of a midstory canopy tier, therefore, become important since together they provide a description of vertical canopy density. On the other hand, stem density and height to the base of the canopy likely influence the relative amount of blue light by affecting the amount of visible blue sky through a canopy, and the amount of diffuse side light below the canopy. Regardless of the cause, it is apparent that the presence of a dense midstory canopy tier likely influences the both PAR and the quality of light below the main canopy. Since PAR is believed to be more critical for seedling development, however, understanding how forest structure affects PAR transmittance is likely more important for current management.

Keywords: riparian hardwood forest, partial cutting, midstory removal, PAR transmittance, R:FR ratio, blue light, light quality, light models

Introduction

The light environment below a forest canopy is known to affect the establishment, growth, and species composition of reproduction; low light levels have often been cited as a contributing cause of regeneration failure of valuable species such as oak (*Quercus spp.*) that are intolerant of deep shade (Hodges and Gardiner 1993, Lorimer 1993). Indeed, field trials have been established to determine the optimal light levels for regenerating species of interest (Mailly and Kimmins 1996, Atzet and Waring 1970, Gardiner and Hodges 1998). Understandably, much work has focused on defining and characterizing forest canopy structure and relating these structural attributes with the amount of light transmitted to the forest floor. Several complex models based on the Beer-Lambert equation have been developed that accurately predict PAR transmittance, however, these models do not have much practical use in forest management (Lieffers and others 1999). Rather, what is needed according to Lieffers and others (1999), are models that are based on variables from a standard timber cruise or simple plot sampling. If light transmittance can be effectively modeled from structural data, then foresters could manipulate stand and canopy structure to produce the light environment necessary for the establishment and growth of desirable reproduction.

Leaf area density, total tree height, crown depth, height to the base of the live crown, leaf area index (LAI), and estimated aboveground biomass are a few of the parameters often examined when trying to associate light transmittance with canopy structure (Brown and Parker 1994, Messier and Bellefleur 1988, Canham and others 1994). Jenkins and Chambers (1989) modeled reductions in photosynthetically active radiation (PAR) based on several stand attributes of five bottomland hardwood stand-types. They found that percent basal area removed and percent crown closure were highly correlated with decreases in light intensity. However, in their study, all stems below 10 cm in diameter were removed prior to the implementation of treatments and the measurement of light levels (Jenkins and Chambers 1989). While a useful model in its own right, by eliminating these smaller stems Jenkins and Chambers (1989) present a relationship that overestimates the amount of light available to seedlings in an unmanaged stand. Had these stems not been removed, the midstory would further reduce PAR levels via light interception by foliage. A few scattered stems will not likely bear much influence on the light environment; however a dense sub-canopy may potentially alter vegetative light regimes. Indeed, research in a deciduous forest in Maryland has shown that the variables that describe the vertical arrangement of leaves have the greatest correlations to PAR transmittance (Brown and Parker 1994). In short, stands that consist of densely packed leaves with low canopy heights, as potentially would be the case seen in stands with several canopy layers, had the lowest PAR transmittance (Brown and Parker 1994).

In addition to influencing the amount of light transmitted to the forest floor, forest canopy structure also influences the spectral character (quality) of that light. Since leaves act as filters of light energy, it would be reasonable to expect that the spectral composition of light in different forests would be related to the structural arrangement of the canopies within those forests (Brown and Parker 1994, Messier and Bellefleur 1988). With increasing canopy coverage, light passing through the canopy will become more spectrally altered due to the differential absorption and reflectance of certain wavebands by foliage (Larcher 1980). Since the spectral nature of light below a forest canopy depends on the relative strength of the various sources of the light energy present (Endler 1993), gaps will understandably influence the light environment. Under sunny conditions large gaps will be tend to exhibit a whitish spectrum due to the mixing effect of several light sources (vegetation, sunlight, blue sky), albeit the sources vary in strength with direct sunlight being the strongest (Endler 1993). In the same scenario, gaps receiving direct sunlight will have higher relative proportions of yellow and red light; blue sky, a brighter light source than vegetation, will mostly be excluded from small gaps due to the overall high percentage of canopy cover (Endler 1993). Furthermore, in woodlands and gaps that receive no direct sunlight but have blue sky visible, the blue portion of the spectrum predominates (Endler 1993). Because the leaf layer of a forest canopy selectively absorbs blue and red wavelengths, but transmits green and far-red wavelengths, the light under a contiguous forest canopy tends to be rich in the green and far-red portions of the spectrum (Larcher 1980, Holmes 1981, Morgan 1981, Holmes and Smith 1977a). Ecological research has shown that the color of vegetative light, in particular the ratio of red light to far-red light (R:FR ratio), does have some direct implications for plant germination, growth and development. Light that is rich in the red and blue wavebands have the most influence on plant growth (Morgan 1981, Endler 1993, Holmes and Smith 1977b, Smith 1982)

The influence of crown structural characteristics in shaping both the light quantity and quality present below a forest canopy is clearly seen when examining the differences between conifer and broadleaf deciduous species. Yirdaw and Luukkanen (2004) noted that of five forest plantation species found in Ethiopia, transmittance within the plantations varied based on canopy features. Two of the broadleaf species examined had more open crowns, higher crown bases, and lower LAI than two of the conifer species resulting in higher transmittance levels (Yirdaw and Luukkanen 2004). In addition to higher transmittance, the broadleaf deciduous plantations with the most open crowns had higher R:FR ratios than the conifer stands with dense crowns closer to the ground (Yirdaw and Luukkanen 2004).

Vezina and Pech (1964) indicate that there is a relationship between canopy depth and canopy closure, with a decrease in openness with an increase in crown depth. Although not indicated in Yirdaw and Luukkanen (2004), one may suspect that due to the shorter clear boles, greater LAI, and more closed crowns, that the conifer plantations measured also may have had greater crown depth. It is not difficult to imagine that deeper crowns may carry more leaf biomass, which would translate into a greater LAI. This trend is most evident when examining species that are tolerant of shade. Shade tolerant species will exhibit greater crown depth since they can hold onto their leaves despite self-shading. Canham and others (1994) noted that for nine deciduous and conifer species of southern New England, the shade tolerant species cast the deepest shade while the more shade intolerant species allowed greater light penetration through the canopy; these differences were closely related to crown depth. In a study of light characteristics in pioneer and climax stage birch-beech and sugar maple (*Betula alleghaniensis* Britton – *Fagus grandifolia* Ehrh. – *Acer saccharum* Marsh.) stands, Messier and Bellefleur (1988) also found that the shade tolerant species cast the deepest shade while also producing the lowest R:FR ratio values. Overall the pioneer stage allowed significantly more transmittance and higher R:FR ratio values than the climax stage; the pioneer canopy allowed a greater proportion of diffuse light through gaps in the canopy, while the climax forest consisted of a midstory and a more irregular canopy structure (Messier and Bellefleur 1988).

Given the relationships that have been shown to exist between PAR transmittance and various forest structure variables, we attempt to use these attributes to construct models that adequately describe the quantity and quality of light present below the canopy in a riparian hardwood forest. In general we suspected that with increasing crown length and crown closure and decreasing height to the base of the canopy, transmittance would also decrease. Successful construction of models explaining light characteristics in relation to forest structure will allow managers to better understand how partial cutting activities influence the light environment of the residual stand. This information will enable managers to plan partial cutting activities that generate the light conditions needed to promote desirable reproduction below the residual canopy.

Methods

Study site

The study site chosen was a riparian corridor within the Blanton Creek Wildlife Management Area located in west-central Georgia (32°44'N and 85°06'W). The trees are reproductively mature, and composed primarily of sweetgum (*Liquidambar styraciflua* L.), yellow-poplar (*Liriodendron tulipifera* L.) and dogwood (*Cornus florida* L.). Red maple (*Acer rubrum* L.), Florida maple (*Acer barbatum* Michx.), box-elder (*Acer negundo* L.), two-winged silverbell (*Halesia diptera* Ellis), mulberry (*Morus rubra* L.), ironwood (*Carpinus caroliniana* Walt.), winged elm (*Ulmus alata* Michx.), various hickories (*Carya spp.*), and various oaks (*Quercus spp.*) are also found on site. As a group, oaks comprise only a small portion of the stems present, with water oak (*Q. nigra* L.) being the most common. The age structure of these riparian forests is uncertain, although distinct even-aged stands of sweetgum are present.

Study design

In the early summer of 2003, fifty 0.05 hectare circular plots (12.62 m radius) were established along a transect that bisected the riparian corridor. The plots were laid out in a systematic fashion with 38 m separating each plot center. Plots were randomly assigned one of four cutting regimes: a control where no stems were removed, a 33% reduction in the number of midstory stems, a 50% reduction in the number of midstory stems, and a 100% midstory stem removal. Midstory stems were identified as trees with crowns that did not reach into the main canopy. In some plots designated for complete midstory removal some of the main canopy trees were also removed to slightly expand the gradient of light conditions being created. Yet, the sole purpose and focus of the cutting remained to generate forest structural conditions and light environments that might be typical of rather low intensity removals. Vegetation less than 1.37 m was not removed unless it posed a hazard to the cutting operation. Trees were felled with a chainsaw and left in place.

Measurements were taken at each plot to document the gradient of forest structure conditions resulting from the cutting regimes. Trees per hectare (TPH) and basal area per hectare (BA) were calculated for each plot. Additionally, several other variables were either measured directly or derived from plot data including, the number of midstory trees per hectare (MIDSTORY_TPH), the average height of all trees greater than 5 cm diameter at breast height (DBH: 1.37 m) (AVE_TREE_HT), the average height of the tallest 5 trees per plot (CANOPY_HT), the average height to the base of the canopy over the plot (BASE_CANOPY_HT), the average crown ratio of all trees over 5 cm DBH on each plot, the average height to the base of the crown of the 5 trees per plot with the lowest crowns (MIN_CANOPY_HT), and the length of the canopy (CANOPY_LENGTH), calculated by subtracting CANOPY_HT from

MIN_CANOPY_HT. Lastly, several variables formed by various interactions between TPH and CANOPY_LENGTH were also considered.

Light measurements

Light measurements were made during the summer of 2004 following full leaf expansion and concluded before leaf senescence. Light intensity was quantified with an AccuPar linear PAR/LAI ceptometer (Decagon Devices, Inc., Pullman, WA). Three measurement locations were established in every plot within 2 meters of plot center and approximately 1.2 m above the ground. For each measurement a total of 4 instantaneous readings were collected and averaged at each location. Each reading was an average of the 80 sensors equally spaced along the 80 cm long ceptometer array. This process was repeated at least three times throughout the growing season. The ceptometer was pointed in the direction of the brightest light source so that the operator's shadow was not cast on the measurement sensors. All PAR measurements were taken under overcast conditions, usually in the late morning hours. Measuring PAR under clear skies often will not translate into an accurate description of average daily PAR levels due to the wide variation caused by direct radiation reaching the forest floor in the form of sunflecks (Messier and Puttonen 1995). However, studies have shown that instantaneous measurement of PAR under overcast skies does provide a good representation of average daily light intensity levels (Messier and Puttonen 1995, Parent and Messier 1996).

In addition to the instantaneous PAR data collected with the ceptometer, 4 HOBO weather stations (Onset Computer Corp., Bourne, MA) were also placed near the center of plots systematically selected along the gradient of light environments created in this study. Each weather station was equipped with a LI-COR PAR sensor (LI-COR Inc., Lincoln, NE) that continuously recorded PAR levels over a period of approximately 3 weeks. Each weather station was moved three times over the course of the study. Thus, weather station data was collected on 12 plots for approximately 9 weeks during the growing season. A fifth weather station was placed in a clearcut adjacent to the study site and continuously recorded data throughout the study period. This station served as a control for the other weather stations and the ceptometer, enabling the calculation of PAR transmittance as a percentage of full sun ($\%T_{(PAR)}$).

Light quality was measured using a FieldSpec UV/VNIR handheld spectroradiometer (Analytical Spectral Devices, Inc., Boulder, CO) with a lambertian reflector panel. Each measurement was taken at the same location as the PAR measurements within each plot. The lambertian panel is calibrated to reflect 100% of the visible spectrum; all radiation emitting from the various sources composing the light environment below a forest canopy is reflected off the panel and collected by the spectroradiometer. Care was taken so that the handheld operator did not stand between a strong light source, such as a canopy gap, and the panel. Three replicates of spectral data were collected for 10 of the 50 plots that were systematically selected based on residual structural characteristics that were representative of the gradient of conditions created; an additional set of 33 one-time measurements supplemented this dataset. Unlike PAR measurements, light quality data can only be collected under clear skies when sampling under a forest canopy. The presence of clouds will cause a reduction in the spectral variation below the canopy, creating a whitening effect, since clouds represent a much brighter light source than the surrounding forest vegetation (Endler 1993).

Data analysis

Both light quantity and quality data was analyzed with linear regression using the SAS statistical software package (SAS 8.2, SAS Institute Inc., Cary, NC, USA). The goal was to develop models that could identify which forest structural attributes have the most influence on the light environment observed under the canopy of a riparian hardwood forest. Three models, average PAR transmittance ($\%T_{(PAR)}$), average R:FR ratio (RFR), and the average percentage of PAR composed of blue light (BLUE), were constructed using the Mallow's Cp procedure. A model was selected based on: *i*) whether each variable significantly contributed to the overall model (P-value < 0.05), *ii*) the amount of variation in the dependent variable explained by the model, and *iii*) the results of a series of residual diagnostics that included tests for serious outliers, and an examination of the residual graphs for non-constant variance. Collinearity diagnostics, specifically the variance inflation factor (VIF) and collinearity (COLLIN) procedures in SAS (SAS 8.2, SAS Institute Inc., Cary, NC, USA), were also conducted on each model to account for problems associated with multicollinearity. In the VIF procedure, variables which produce values greater than 10 are thought to be strongly related with other variables in the model to the degree that the reported R-square is an artifact of the multicollinearity in the model (Yu 2000). Likewise, when the COLLIN procedure reports values greater than 100 multicollinearity is thought to be a problem (Yu 2000). Therefore the models with the lowest VIF and COLLIN values were selected when possible.

Since light data was collected at specific measurement points within each plot while structure data was collected on the plot level, some may conclude that the worth of this study is compromised by the presence of pseudo-replication in the design of the project. The only way to ensure that this potentially serious error is eliminated would be to have taken forest structure data specifically for each light measurement location. However, it is likely that the collection of plot specific data for a collection of three measurement locations would not have significantly changed the results of this study. Since the three light measurement locations were positioned within 2 m of plot center, it is unlikely that forest structural features just outside the edge of the plot would be dramatically different from the plot itself. The largest difference would be in the number of trees present for those plots where all midstory stems were removed. However, even this variable is not expected to be dramatically different by shifting the plot over 2 meters.

Results

PAR transmittance model

The instantaneous measurements of diffuse light provided an accurate description of the average daily growing season PAR levels below the riparian hardwood forest canopy examined in this study. Of the 12 plots that had weather stations placed at plot center, 10 had average growing season PAR readings that were within 2.74% full sun of the average instantaneous measurements taken over the course of the growing season (Table 1). Moreover, the difference between the ceptometer and weather station PAR sensors was less than 40% of the instantaneous ceptometer measurement for all but one plot. The large discrepancy in both the absolute and relative differences between the two measuring devices on plot 9 can be attributed to the presence of a small dogwood near plot center. The weather station sensor was above this tree, but the ceptometer measurement locations were under its influence. With this discrepancy noted, it appears that using the methodology cited does produce accurate measurements of the average daily amount of PAR transmitted below the hardwood canopy over the course of a growing season.

The final data set used to construct the transmittance model excluded plots 9, 13, 21 and 22 because of structural features which should have disqualified these plots from being established; plots 9, 13, and 22 all had gaps in the overstory prior to cutting. Plot 21 was discarded due to the presence of kudzu in the main canopy, and to a lesser extent along the ground. With these plots discarded, there were 138 measurement locations used to develop the PAR transmittance model.

As an individual variable, CANOPY_LENGTH explained the most variability in PAR, accounting for approximately 43% of the variation witnessed. Other important single variable models included the terms BA, BASE_CANOPY_HT, and TPH, with R-square values of 0.2983, 0.2803, and 0.1853 respectively. Scatterplots of these variables against PAR, however, indicate that a linear relationship is ill-suited to describing the association between CANOPY_LENGTH, BA and TPH with PAR transmittance. Using a log transformation (lnCANOPY_LENGTH, lnBA, lnTPH), the new R-square values for these variables increase to 0.4698, 0.3832 and 0.2233 respectively. The interaction term (lnTPH*CANOPY_LENGTH), however, was the best overall predictor, accounting for 54% of the variation in PAR transmittance. With these variables included in the analysis, the following PAR transmittance model was developed:

[1]

$$\%T_{(PAR)} = b_0 - b_1 (\text{lnCANOPY\_LENGTH}) - b_2 (\text{lnBA}) - b_3 (\text{TPH/CANOPY\_LENGTH})$$

$$R^2 = .6635;\ \text{P-value} < .0001$$

The three-variable model above explains two-thirds of the variation seen in the average PAR transmittance below the canopy. The variables included, lnCANOPY_LENGTH (Figure 1), lnBA (Figure 2) and (TPH/CANOPY_LENGTH) (Figure 3), contribute 0.4698, 0.0611, and 0.1326 to the R-square respectively. The studentized residuals indicate that the three measurements taken on plot 32 are outliers, however, these did not appear to be too extreme. The cause of the outliers could not be determined beyond natural variation. The residual graphs do not indicate problems with normality or non-constant variance.

R:FR ratio model

The R:FR ratio was calculated by dividing the amount of light energy (µmols/m^2/sec) found in the red portion of the spectrum by the amount of light energy found in the far-red portion. Generally, 5 wavelengths (nm) on either side of the red and far-red peaks are grouped as the color band for R:FR ratio analysis. The literature typically reports that the red portion of the spectrum is centered at 660 nm while the far-red portion is centered on 730 nm (Holmes and Smith 1977a, Lieffers and others 1999). Both the red and far-red peaks were identified when analyzing the spectral graphs collected, however, the far-red peak appeared to be shifted to higher wavelengths of the spectrum (Figure 4). For this study, therefore, the far-red band was centered on 751 nm; thus the actual far-red peak was included in the analysis. Table 2 shows the reductions in the standard error, standard deviation and the increase in the mean of the amount of far-red radiation associated with the shift in the analysis to higher wavelengths from where it is typically calculated. Using the actual far-red peak as indicated by the spectroradiometer rather than that reported in the literature results in a more accurate and precise measure of far-red radiation, and thusly the R:FR ratio.

The R:FR ratios calculated for this study appear reasonable based on other research (Endler 1993, Smith 1982). Over 70% of the measurement locations in this study had R:FR ratios of less than 0.30; the minimum and maximum were 0.10 and 0.59 respectively. Messier and Bellefleur (1988) noted that R:FR ratio values of 0.1 to 0.7 can be typical in birch-beech-sugar maple stands. Endler (1993) reported R:FR values greater than 1.4 in large gaps under sunny conditions in tropical and temperate regions. The maximum R:FR ratio value of 1.20 in this study was recorded in a clearcut adjacent to the study site.

The data set used to construct the explanatory models for the R:FR ratio consisted of 56 measurements. Thirty of these readings were the averaged value at a location that was measured at least 3 times over the course of the growing season. As with the PAR measurements taken at the same locations, the instantaneous measurements were averaged over the course of the growing season in an attempt to obtain measurements that reflect the overall growing season environment. The remaining 26 measurements were one-time readings. Overall, 7 observations were eliminated from the data set, all from the non-replicated locations. Four of the deletions were due to the presence of sunflecks directly on the reflectance panel which artificially increased the R:FR ratio despite the influence of the forest canopy. The other 3 measurements were discarded because the presence of a large gap in the overstory of plot 22. The structural variables analyzed in the development of the R:FR ratio models were the same ones described in the PAR transmittance section previously.

Few of the variables used to describe the canopy structure explained much of the variation in the recorded R:FR values. The variable CROWN_RATIO explained the greatest amount of variation in the R:FR ratio, approximately 36%, while CANOPY_LENGTH accounted for approximately 23%. Variables describing density such as BA and TPH only explained 15% and 7% respectively. Of these variables only CROWN_RATIO was included in the final model.

[2]

Ave. RFR = $b_0 - b_1$ **(CROWN_RATIO) –** b_2 **(TPH/CANOPY_LENGTH) –** b_3 **(Canopy_HT)**

$R^2 = .6006$; P-value < .0001

Like the PAR transmittance model, the interaction term (TPH/CANOPY_LENGTH) contributed significantly to model 2. Two other variables that were included, CROWN_RATIO (Figure 5) and Canopy_HT (Figure 6), adding 0.3594 and 0.1468 to the R-square value of 0.6006; the interaction term (TPH/CANOPY_LENGTH) accounted for the remaining 0.0943 (Figure 7). There was no serious multicollinearity in this model; in addition, there were no outliers in this model, or indication of non-constant variance.

Besides forest structure alone, PAR transmittance was also examined as an independent variable and included in the model building process along with structure variables. However, as a single variable model PAR transmittance only explained approximately 15% of the variation in the R:FR ratio, roughly the same amount explained by BA. The inclusion of $\%T_{(PAR)}$ in the model building process failed to yield a better model than model 2.

Blue light model

Unlike the R:FR ratio, the research covering blue light in natural settings failed to adequately define a range of wavelengths that comprise the blue portion of the spectrum. Based on the spectral scans from this study, blue light was defined as 440 nm to 490 nm. Since the proportion of blue light to overall PAR was calculated from the same spectral graphs that were analyzed for the R:FR ratio, the measurements that were eliminated from the R:FR ratio model due to sunflecks or gaps in the main canopy, were also discarded for this analysis. Thus, a total of 56 measurements were used in the construction of the blue light models. Interestingly, blue light contribution appears to reach a maximum level of about 20% of PAR, when PAR transmittance is approximate 10% of full sun conditions. Measurements taken in a nearby clearcut indicate that, while the overall amount of energy in the blue light wavelengths is much greater, the proportion of blue light in full sun conditions is approximately 17%, a decline from that found in 10% full sun conditions.

Unlike the models developed in the R:FR analysis, the first blue light model developed did not include an interaction term; rather model 3 consists of just two variables, lnBASE_CANOPY_HT and MIDSTORY_TPH. The scatterplot of blue light and BASE_CANOPY_HT indicated that a log transformation was needed for BASE_CANOPY_HT. As individual variables, lnBASE_CANOPY_HT and MIDSTORY_TPH explained the greatest amount of variation seen in the amount of blue light present below the canopy, accounting for 56% and 46% respectively.

[3]

Ave. Blue = $b_0 + b_1$ **(lnBASE_CANOPY_HT) –** b_2 **(MIDSTORY_TPH)**

$R^2 = .6104$; **P-value < .0001**

Both lnBASE_CANOPY_HT (Figure 8) and MIDSTORY_TPH (Figure 9) significantly contribute to the final model, which explains approximately 61% of the variation in blue light readings under the hardwood canopy; the variable lnBASE_CANOPY_HT is responsible for 0.5603 of the R-square value of model 3. There did not appear to be any problems with multicollinearity, non-constant variance, or violations of the normality assumption. Additionally, no measurements appeared to be serious outliers.

When the variable $\%T_{(PAR)}$ was included in the analysis, it became evident that blue light and $\%T_{(PAR)}$ were not related in a linear fashion. The log transformation of $\%T_{(PAR)}$ ($\ln\%T_{(PAR)}$) in turn became the second best predictor of blue light, explaining 54% of the variation. With $\ln\%T_{(PAR)}$ in the model, lnBASE_CANOPY_HT and the interaction term (CANOPY_LENGTH/lnTPH) also entered the model. This 3-variable model accounted for approximately 71% of the variation in blue light levels below a hardwood canopy.

[4]

Ave. Blue = $b_0 + b_1$ **(lnBASE_CANOPY_HT) +** b_2 **(ln%**$T_{(PAR)}$**) +** b_3 **(CANOPY_LENGTH/lnTPH)**

$R^2 = .7100$; P-value < .0001

There did not appear to be any significant outliers or problems with multicollinearity. The variable ln%$T_{(PAR)}$ accounted for 0.5356 of the overall R-square value for the model (Figure 10); lnBASE_CANOPY_HT and (CANOPY_LENGTH/lnTPH) (Figure 11) contributed an additional 0.1133 and 0.0612 to the final R-square value respectively. Again, it appeared that the error terms are normally distributed and that there are no indications of non-constant variance among the residuals.

As indicated earlier, the presence of pseudo-replication in the design of this study could potential raise questions regarding the validity of the resulted presented above. Although pseudo-replication is not believed to be an issue in this study, the fact remains that the forest structure measurements corresponding to the light measurement locations are not truly independent of one another. Therefore a second round of analysis was conducted with plot average light data. All the models constructed in this second analysis contained the same variables as the original models with one exception. The model of blue light that included PAR transmittance in the model building process did not contain the interaction term (CANOPY_LENGTH/lnTPH) as seen in model 4 above; the term did not significantly contribute to the model at the .05 level (p-value = 0.0926). Overall, given the similarity of these models, it is not likely that pseudo-replication is adversely impacting the results presented above.

Discussion

Light quantity

The partial cutting treatments implemented in this study did not create open light conditions. The maximum PAR levels produced were approximately 22% of full sun. Therefore model 1 is restricted to describing the relationship between forest structure and the low light quantity levels that exist below a continuous hardwood canopy with similar species composition and structural features. Although the narrow range of low light environments modeled may appear to be of limited value (3-22% full sun), the conditions examined are of particular interest to silviculturists working on mesic sites. Research has shown that controlling the midstory canopy tier is a crucial aspect of establishing and maintaining moderately shade tolerant species such as oak on these sites (Loftis 1990, Janzen and Hodges 1987, Lockhart and others 1992). The presence of a midstory canopy is believed to reduce light levels to a point that only shade tolerant species are able to maintain growth. Yet, the actual influence the presence of a midstory has on the light environment has not been quantified.

It was hypothesized that PAR transmittance would decrease with increasing canopy length and decreasing height to the base of the canopy. It was originally believed that the presence of a midstory canopy tier would negatively impact PAR transmittance by further increasing overall canopy length and decreasing the height to the base of the canopy. Based on the variables included in model 1, it appeared that the presence of a midstory canopy tier was indeed influential in affecting the light environment. There are two types of variables represented in model 1, density variables and variables that describe canopy structure. Although the influence of stand density was not initially considered to be as strongly related to PAR transmittance as canopy structure, both of these types of variables are impacted by the presence of a midstory canopy tier.

The variables lnBA and the interaction term (TPH/CANOPY_LENGTH) in model 1 describe stand density. It is not the actual amount of basal area that is impacting PAR levels, but rather basal area is a surrogate measure of crown architecture. A strong relationship is difficult to establish between BA and PAR since crown characteristics may be dramatically different in two stands of equal basal area depending on the age of the stand and average tree size. However, if other variables are held constant, as basal area increases the light levels below the main canopy will decrease.

A midstory canopy tier adds to the overall basal area of a stand, yet the increase may be slight given the typically small diameter of these stems. The presence of a midstory canopy has a larger impact on the second measure of stand density in model 1, the interaction term (TPH/CANOPY_LENGTH). This variable may be considered another measure of density because of the influence of TPH in the interaction. Like BA, TPH will increase when a midstory canopy is present, however, the influence will be proportionately greater. For instance, if a stand has 1 $m^2 ha^{-1}$ of basal area in 1000 midstory stems, the contribution of this canopy tier to overall forest structure will be more significant for number of stems rather than stand basal area. The interaction term (TPH/CANOPY_LENGTH) reflects this reality given that TPH ranged from 120 to 1860 trees ha^{-1} in this study. Although it is not included in model 1, the interaction (lnTPH*CANOPY_LENGTH) which was the single best predictor of PAR transmittance, is influenced by the presence of the midstory canopy in a similar way.

Thus as TPH becomes extreme due to a large number of trees in lower canopy positions, PAR levels will decrease. Yet, the variable TPH did not completely capture the influence of a midstory canopy tier; this sub-canopy tier also impacts canopy structure. The variable in model 1 that describes canopy structure is lnCANOPY_LENGTH, which accounts for 47% of the variation in PAR as a single variable. The relationship between canopy length and the presence of a midstory is clear. A midstory existing below the main canopy will increase overall stand level canopy length.

Research indicates that crown closure, a measure of the percent of open sky visible under a forest canopy, is highly correlated to PAR transmittance (Jenkins and Chambers 1989, Yirdaw and Luukkanen 2004). In one study involving bottomland hardwoods, Jenkins and Chambers (1989) illustrated the relationship between crown closure and PAR transmittance following partial overstory removals in a mature stand. As a single predictor, crown closure (labeled crown cover in their study) explained 71% of the variation in PAR. Vezina and Pech (1964) suggest that an increase in crown closure would be expected as canopy length increases since a greater portion of the sky would be obscured. Although crown closure was not measured directly in the current study, it is likely that the combination of canopy length and stem density variables served as a surrogate measure of closure.

Clearly there are some limits to the crown length-closure-density relationship. Individual crown lengths will lessen in very dense stands and open grown trees may have long crowns but low crown closure if stem density is low. However, the emphasis in this study is not on individual stem crown lengths but on the overall canopy length. The importance of crown closure is best understood when considered with the impact that canopy length has on PAR transmittance. In short, crown closure explains the decrease in sunlight because of foliage obscuring the visible sky, while canopy length illustrates that the longer the pathway that solar radiation has to pass through a crown, the more chance it has of being deflected or absorbed and not making it to the forest floor. Canopy length is just one characteristic which helps to explain why crown closure is strongly related to PAR transmittance.

Light quality

Like the PAR transmittance model, the hypothesis for this analysis was that the presence of a midstory canopy tier would decrease the R:FR ratio below the main canopy. Since vegetation will alter the R:FR ratio due to the propensity of leaves to absorb red, but not far-red radiation, it follows that the presence of a midstory canopy tier below the main canopy will decrease the R:FR ratio further by increasing the amount of leaves in the canopy. Model 2 seems to indicate that the presence of a midstory canopy tier was important in explaining the variation in the R:FR ratios below a riparian hardwood canopy. Additionally the average crown ratio, while not an all encompassing measure of vertical canopy density, does provide at least an indication of vertical density. An increase in average crown ratio indicates that a larger proportion of total stand height is composed of light absorbing leaves. Therefore, there is a decreased chance that direct radiation will reach the forest floor unaltered. Interestingly, there is not a significant relationship between the R:FR ratio and the variables (TPH/CANOPY), and CANOPY_HT when considered individually. When placed in the model with CROWN_RATIO, however, these variables do contribute significantly to the overall model. While the relationship between the variables in model 2 and the R:FR ratio is not clear, the addition of (TPH/CANOPY) and CANOPY_HT to CROWN_RATIO likely strengthens the overall portrayal of vertical canopy structure.

A second possible way that the average crown ratio is related to canopy density, and thus reduced R:FR ratios, is associated to species composition. In riparian areas it is common to find a midstory composed of primarily shade tolerant species. Species such as dogwood, boxelder, red maple, silverbell, and ironwood are common in our study site may be able to persist with high crown ratios in low light conditions due to their shade tolerance. Stands that contain large numbers of these shade tolerant midstory stems may have a high average crown ratio as well as an elevated leaf density because of the extra biomass carried by these shade tolerant species. Decreases in the R:FR ratio would be expected in these stands given the increases in leaf density created by the presence of the midstory. As was the case in the final PAR transmittance model, the interaction term (TPH/CANOPY_LENGTH) may further quantify the presence of this sub-canopy tier. By decreasing the possibility that direct solar radiation would pass unaltered to the forest floor, it would seem that the R:FR ratio would also decrease by necessity.

What may be of most interest, however, is what was not included in model 2. Although PAR transmittance explained only 15% of the variation in the R:FR ratios, it was surprising that PAR transmittance did not contribute to the final model. Lee (1987) found a strong relationship between PAR and the R:FR ratio in a study in Costa Rica and Panama; using the R:FR ratio as a predictor of the log transformation of percent PAR transmittance, regression equations developed were able to explain upwards of 97% of the variation in PAR. Since Lee (1987) measured PAR and the R:FR ratio simultaneously across a range of conditions from diffuse light to sunflecks, a strong correlation between PAR and the R:FR ratio is expected; progressively more open conditions will increase both PAR levels and the R:FR ratio. Additionally, the relatively small range of low light conditions sampled and the exclusion of sunflecks from PAR measurements contribute to the weak relationship between PAR transmittance and the R:FR ratio in the current study. A stronger relationship might become more evident if a larger sample of PAR levels were included in the analysis.

As with the R:FR ratio, it was believed that the presence of a midstory canopy tier would decrease the proportion of PAR composed of blue light below the forest canopy. Since blue and red light levels are both highly absorbed by leaves and react in the same manner when being transmitted through a forest canopy (Holmes 1981), it was believed that the same variables that were important in determining the R:FR ratio would also be important for blue light levels. Yet, there are substantial differences between the R:FR ratio and blue light models. One major difference between the two measures of light quality is that while no single structural variable describing stem density accounted for more than 15% of the variation in the R:FR ratio, stem density variables had a stronger relationship with blue light levels. Single variable models with the variables MIDSTORY_TPH and TPH accounted for 46% and 35% of the variation in blue light, respectively. Additionally, many of the individual variables that best predict the R:FR ratio had weak relationships with blue light. For example, CROWN_RATIO accounted for 36% of the variation in the R:FR ratio, but demonstrated no influence on blue light. The disparity in importance of various structural variables seems to indicate that, while red and blue wavelengths are both absorbed by leaves, there are distinct differences in how they are influenced by forest structure.

When the sources of these measures of light quality are considered, the differences in how forest structure influences the R:FR ratio and blue light is understandable. Since little far-red radiation is absorbed by a vegetative canopy, the R:FR ratio is largely determined by the amount of direct solar radiation that passes through the canopy unaltered. Blue light, on the other hand, originates from diffuse radiation rather than direct solar radiation. Any source of light other than the sun is considered to be diffuse in nature (Endler 1993). Endler (1993) demonstrated that the spectral signature of a forest environment is a collection of several light sources, with the brightest source having the most influence. On clear days the sun is the brightest source. If the forest floor is receiving direct solar radiation, notably from gaps in the overstory with the sun visible, there will likely be a significant amount of red light present below the canopy. However, if the sun is obscured by the main canopy but the sky is free of clouds, then blue sky is the next brightest light source influencing the spectral signature of the light environment below the main canopy. Vegetation is generally a weaker light source, however the spectral signature is dominated by green light because of the sheer quantity of green light compared to blue or red light; green light is weakly absorbed by other vegetation (Endler 1993, Holmes 1981).

Since red light is influenced by the ability of direct solar radiation to pass through the canopy unaltered, it is logical that several canopy attributes will influence the R:FR ratio. The percentage of visible sky, characterized by crown closure, will obviously affect the likelihood of direct solar radiation reaching the forest floor unaltered by simply obscuring the sun. Besides the simple presence of an overstory canopy, however, it stands to reason that red light has a greater chance of reaching the forest floor when the canopy is thin or sparsely vegetated due to its high energy level. It becomes evident, therefore, that attributes that describe the density of the canopy and the length of the pathway that direct sunlight must travel through the canopy will exhibit greater influence on the amount of red light reaching the forest floor, and consequently, the R:FR ratio. The fact that the variables in model 2 account for canopy closure, given the contribution of stand density in the form of the interaction term (TPH/CANOPY_LENGTH), and measures of vertical density, seems to support this reasoning.

When considering blue light, on the other hand, it is necessary to understand how diffuse radiation is affected by forest structure. As with red light, the presence of a continuous overstory canopy will decrease the amount of blue light below the main canopy on clear days due to the selective absorption of blue light by leaves (Larcher 1980, Holmes 1981, Morgan 1981, Holmes and Smith 1977a). Since blue light is a product of diffuse radiation and has less energy than red light, attributes such as the length of the pathway light must travel through the canopy become less important. Instead, more influence is attributed to variables that describe the proportion of clear blue sky visible from below the main canopy since blue light does not originate from only one point, such as the sun. Additionally, forest structural characteristics that negatively affect the ability of side light, diffuse radiation emitting from nearby openings or gaps, to travel through a forest would also impact the proportion of blue light below the main canopy. If a stand is composed of densely packed trees with crowns that extend near to the ground, it is reasonable to suspect that side light resulting from a small gap in such a stand will not penetrate greatly into the surrounding forest.

While the variables in model 3 do not describe crown closure directly, it makes sense that a description of the midstory would be in the model; as canopy length is extended it is likely that crown closure will increase (Vezina and Pech 1964). The positive relationship seen between blue light and the variable lnBASE_CANOPY_HT is also reasonable. As the height to the base of the canopy increases, more diffuse light is present below the canopy. As previously noted, by raising the height to the base of the main canopy it is also likely that diffuse radiation in the form of side light may extend further into the forest matrix surrounding a gap from which blue sky is visible. If a midstory component is not present, then it is likely that crown closure will be lessened and that the height to the base of the canopy will increase, thereby increasing the proportion of blue light under the canopy.

Since blue light is a product of diffuse radiation, and that PAR transmittance below a continuous canopy is influenced most by diffuse radiation when there is no direct sunlight, it is understandable that the blue light model has more in common with the PAR transmittance model than the R:FR ratio model. Forest structure which diminishes the flow of diffuse light will impact blue light and PAR transmittance more so that the R:FR ratio. It is even less surprising that a fairly strong relationship exists between the proportion of PAR composed of blue light and $\%T_{(PAR)}$ as seen in model 4 when recalling that all measurements of PAR were measurements of diffuse radiation under overcast conditions. The correlation coefficient between blue light and $\%T_{(PAR)}$ was 0.77482. In addition to PAR transmittance, the other variables in model 4 are basically the same as those found in model 3. The only difference between the two models is the replacement of MIDSTORY_TPH with the interaction term is (CANOPY_LENGTH/lnTPH). In reality, however, these two variables are likely representing similar aspects of forest structure, namely the presence of a midstory canopy tier and the contribution that this canopy layer has on stem density.

Conclusions

The models generated in this study serve to illustrate how forest structure influences the light environment on the forest floor at low light levels. Whereas previous research has yielded important predictive models and has brought attention to the relationship between variables such as crown closure and PAR transmittance (Jenkins and Chambers 1989), this work helps explain how these relationships are expressed in stands where the main canopy is kept intact. This critical look at the influence of forest structure on the light environment near the forest floor also provides a way to characterize the effect that particular silvicultural prescriptions may have on the light regimes within a stand.

Low intensity treatments are likely to have subtle effects on light regimes. For example, partial cutting in a riparian forest type, such as the midstory competition control examined in this study, will likely have the greatest influence by increasing the proportion of PAR composed of blue light. Yet the implications of this are not known. It could be speculated that by increasing PAR to at least 10% full sun, the relative amount of blue light is maximized. Since blue light is composing a larger amount of the spectra, and overall PAR levels are increasing, actual blue light radiance could be substantially improved. However, further work needs to be conducted to see what radiance levels of blue light are needed to affect seedling characteristics such as germination rates and hypocotyl extension before deciding whether the increase in the relative amount of blue light is of consequence to desired reproduction. Research has shown that the importance of light quality, namely the R:FR ratio, is overwhelmed by the influence that overall PAR levels have over seedling growth (Lee and others 1996, Muth and Bazzaz 2002, Turnbull 1991). Yet, some evidence suggests that the R:FR ratio is more influential at low levels of PAR (Turnbull 1991, Lee and others 1996); blue light may have a similar limited contribution to seedling growth and development.

It is apparent that treatments such as a complete midstory removal will influence the R:FR ratio by reducing stem density and reducing the total length of the canopy. However, the significance of a slight increase in the R:FR ratio for desired temperate species is unknown at this time. More substantial increases in the R:FR ratio would occur in operations that remove all stems from the midstory in addition to some stems from the co-dominant and dominant crown positions. Yet the increase in PAR availability in these situations is likely to be more significant for seedling growth than the changes in the R:FR ratio. If a cutting treatment leaves the main canopy intact and PAR transmittance is kept below 20% full sun, then the impact of the R:FR ratio on vegetation following the treatment will likely be minor compared to the expected increase in PAR transmittance. Therefore, given the importance of PAR on the growth and survival of desired reproduction, the implications of the PAR transmittance model for silvicultural prescriptions should be considered.

One example of the usefulness of the PAR transmittance model developed in this study relates to the management problem of regenerating oak on mesic sites. Partial cutting similar to the complete midstory removal used in this study has been suggested as a step to facilitate the establishment and growth of desirable oak reproduction on these sites; Loftis (1990) used midstory competition control as the initial cut in a shelterwood prescription. Research has shown that there is a narrow range of light conditions that promote the successful growth of advanced oak reproduction relative to shade-intolerant competition on these sites (Loftis 1990, Hodges and Gardiner 1993). Loftis' (1990) shelterwood prescription demonstrates that midstory competition control apparently creates light conditions within this window of opportunity. However, the actual effect of these treatments on the light environment below the main canopy has not been described or quantified. By examining the relationship between PAR levels and forest structure in this study, some inferences can be made regarding the complex structure present on many of these productive sites.

The PAR transmittance model indicates that in a stand with similar structure as the one in this study, the PAR levels below the canopy are strongly related to the length of the canopy. Because of the productivity of these sites it is reasonable to expect that unmanaged stands characteristic of mesic forest types will naturally have long canopy lengths for two reasons: i) total tree height will likely be high as reflected by site index, and ii) these productive sites usually have a shade tolerant sub-canopy tier which adds to the length of the total canopy. In addition to increasing canopy length, a dense midstory of shade tolerant competitors may also further reduce light levels because of the increased amount of leaf biomass and by increasing crown closure. Given these characteristics, it is understandable that partial cutting that leaves the main canopy intact may improve light conditions because the tolerant midstory is removed, which shortens canopy length and reduces canopy closure. The reduced canopy length in combination with the tall trees on productive sites allows ample diffuse side light which increases both overall PAR levels, and the proportion of blue light in the visible spectrum.

Literature Cited

Atzet, T., and Waring, R.H. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Canadian Journal of Botany 48: 2163-2167.

Brown, M.J., and Parker, G.G. 1994. Canopy light transmittance in a chronosequence of mixed species deciduous forests. Canadian Journal of Forest Research 24: 1694-1703.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 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.

Endler, J.A. 1993. The color of light in forests and its implications. Ecological Monographs. 63: 1-27.

Gardiner, E.S., and Hodges, J.D. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. Forest Ecology and Management 108: 127-134.

Hodges, J.D., and Gradiner, E.S. 1993. Ecology and physiology of oak regeneration. Pgs. 54-65. In: Loftis, D.L., and McGee, C.R. (eds.) Proc., Oak Regeneration: Serious Problems, Practical Recommendations, USDA Forest Service GTR SE-84.

Holmes, M.G. 1981. Shadelight quality effects on plant growth. In: H. Smith (editor), Plants and the Daylight Spectrum. Academic Press, London, pp. 147-158.

Holmes, M.G., and Smith, H. 1977a. The function of phytochrome in the natural environment II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. Photochemistry and Photobiology 25: 539-545.

Holmes, M.G., and Smith, H. 1977b. The function of phytochrome in the natural environment IV. Light quality and plant development. Photochemistry and Photobiology 25: 551-557.

Janzen, G.C., and Hodges, J.D. 1987. Development of advanced oak regeneration as influenced by removal of midstory and understory vegetation. Pgs. 455-461. In: Douglas, P.R. (editor) Proceedings of the forth biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SE-042.

Jenkins, M.W., and Chambers, J.L. 1989. Understory light levels in mature hardwood stands after partial overstory removal. Forest Ecology and Management 26: 247-256.

Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, New York, pp. 5-18.

Lee, D.W. 1987. The spectral distribution of radiation in two neotropical rainforests. Biotropica 19(2): 161-166.

Lee, D.W., Baskaran, K., Mansor, M., Mohamad, H., and Kheong, S. 1996. Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. Ecology 77(2): 568-580.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29: 796-811.

Lockhart, B.R., Hodges, J.D., and Guldin, J.M. 1992. Development of advanced cherrybark oak reproduction following midstory and understory competition control and seedling clipping: 4-year results. Pgs. 109-115. In: J.C. Brissette. ed. Proceedings of the seventh biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SO-93.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the Southern Appalachians. Forest Science 36(4): 917-929.

Lorimer, C.G. 1993. Causes of the oak regeneration problem. Pgs. 14-65. In: Loftis, D.L., and McGee, C.R. (eds.) Proc., Oak Regeneration: Serious Problems, Practical Recommendations, USDA Forest Service GTR SE-84.

Mailly, D., and Kimmins, J.P. 1996. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. Canadian Journal of Botany 75: 1424-1435.

Messier, C., and Bellefleur, P. 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch-beech-sugar maple stand. Canadian Journal of Forest Research 18: 615-622.

Messier, C., and Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Canadian Journal of Forest Research 25: 343-354.

Morgan, D.C. 1981. Shadelight quality effects on plant growth. In: H. Smith (editor), Plants and the Daylight Spectrum. Academic Press, London, pp. 205-221.

Muth, C.C., and Bazzaz, F.A. 2002. Tree seedling canopy responses to conflicting photosensory cues. Oecologia 132: 197-204.

Parent, S., and Messier, C. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. Canadian Journal of Forest Research 26: 151-154.

Smith, H. 1982. Light quality, photoperception, and plant strategy. Annual Review of Plant Physiology 33: 481-518.

Turnbull, M.H. 1991. The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87: 110-117.

Vezina, P.E., and Pech, G.Y. 1964. Solar radiation beneath conifer canopies in relation to crown closure. Forest Science 10(4): 443-451.

Yirdaw, E., and Luukkanen, O. 2004. Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecology and Management 188: 17-24.

Yu, C.H. 2000. An overview of remedial tools for collinearity in SAS. Proceedings of 2000 Western Users of SAS Software Conference, pp. 196-201.

Table 1: PAR transmittance by plot as measured by the weather station and ceptometer

Plot	Ceptometer[1]	Weather Station PAR[2]	Absolute Difference	Relative Difference (%)
	Percent Transmittance			
40	3.60	3.10	0.50	13.90
10	3.84	2.32	1.52	39.49
36	4.13	3.52	0.61	14.76
9	5.80	11.91	6.11	105.49
43	6.98	6.03	0.95	13.60
20	7.36	9.76	2.40	32.65
15	7.71	7.39	0.32	4.18
12	8.38	9.04	0.67	7.97
17	9.69	6.95	2.74	28.28
16	13.16	11.77	1.39	10.56
28	14.14	15.19	1.06	7.47
32	21.11	26.28	5.17	24.48

[1] AccuPAR linear PAR/LAI ceptometer
[2] LI-COR quantum sensor (LI-COR Inc., Lincoln, NE)

Table 2: A comparison of descriptive statistics from a typical light quality measurement illustrating how a shift in the far-red color band from 730 nm to 751 nm improves the estimate of the far-red peak

	725 nm - 735 nm[1]	746 nm - 756 nm[2]
Mean	28800.9	41319.6
Standard Error	1197.1	107.8
Standard Deviation	3970.4	357.5

[1] Far-red peak typically cited in light quality literature (Holmes and Smith 1977a, Lieffers and others 1999)
[2] Far-red peak based on field measurements (Figure 2)

Figure Index

Figure 8: Relationship between the relative amount of blue light and lnBASE_CANOPY_HT (R^2 contribution to final model = 0.5603)

Figure 9: Relationship between the relative amount of blue light and the number of midstory stems per hectare (R^2 contribution to final model = 0.0501)

Figure 10: Relationship between the relative amount of blue light and the log transformation of PAR transmittance (R^2 contribution to final model = 0.5356)

Figure 11: Relationship between the relative amount of blue light and the interaction term (CANOPY_LENGTH/lnTPH) (R^2 contribution to final model = 0.0612)

Figure 1

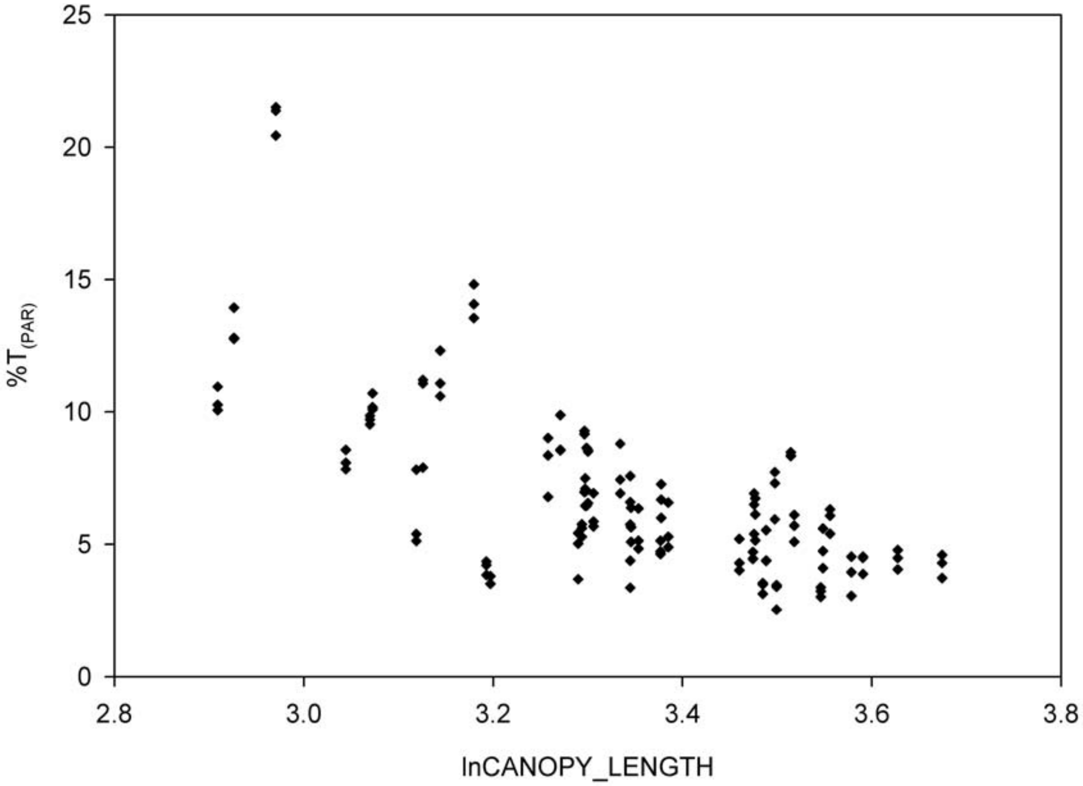


Figure 2

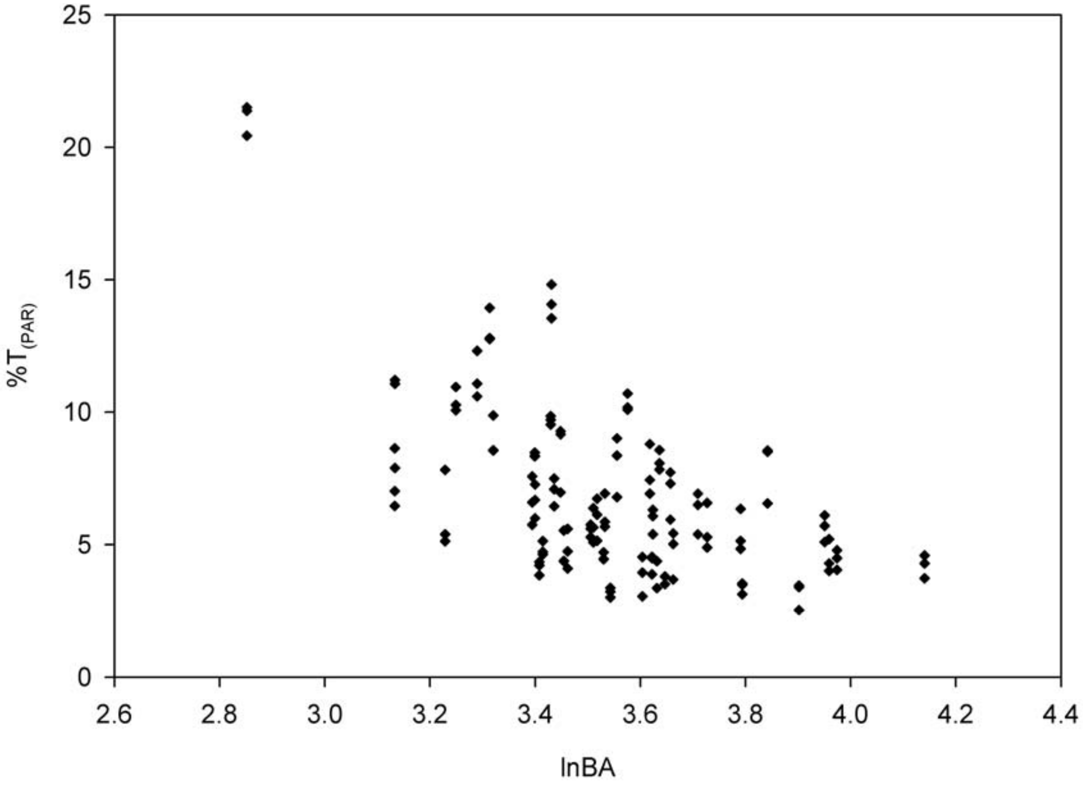


Figure 3

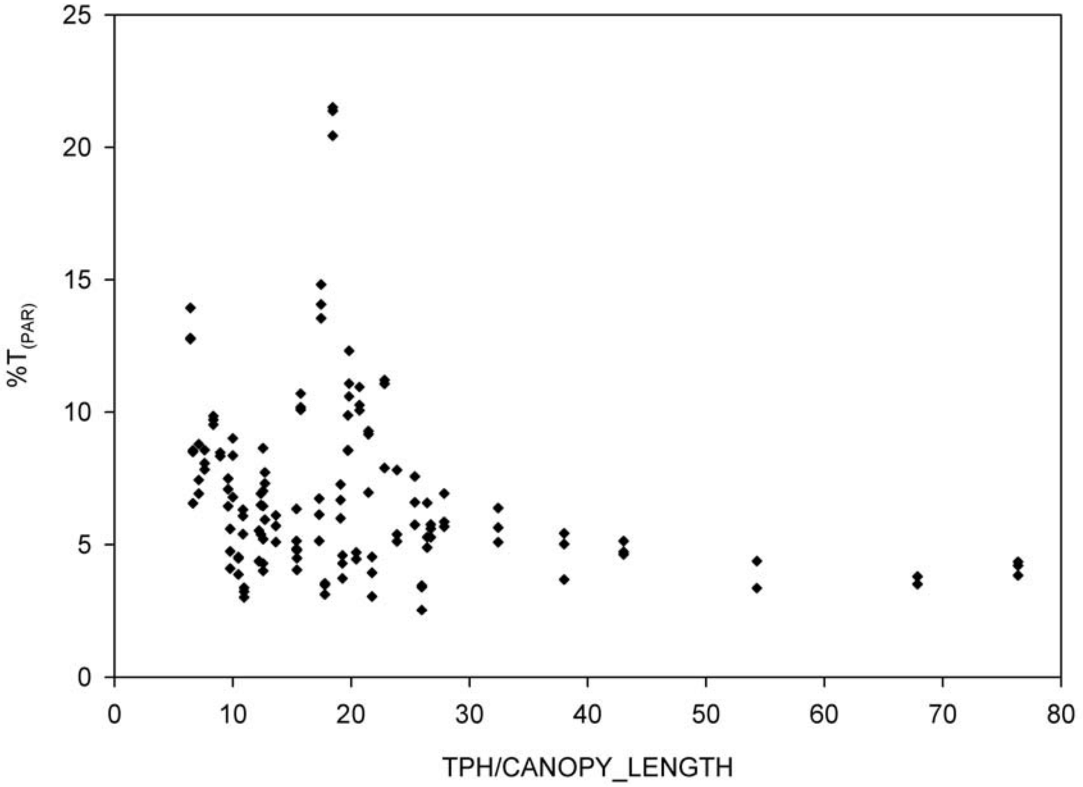


Figure 4

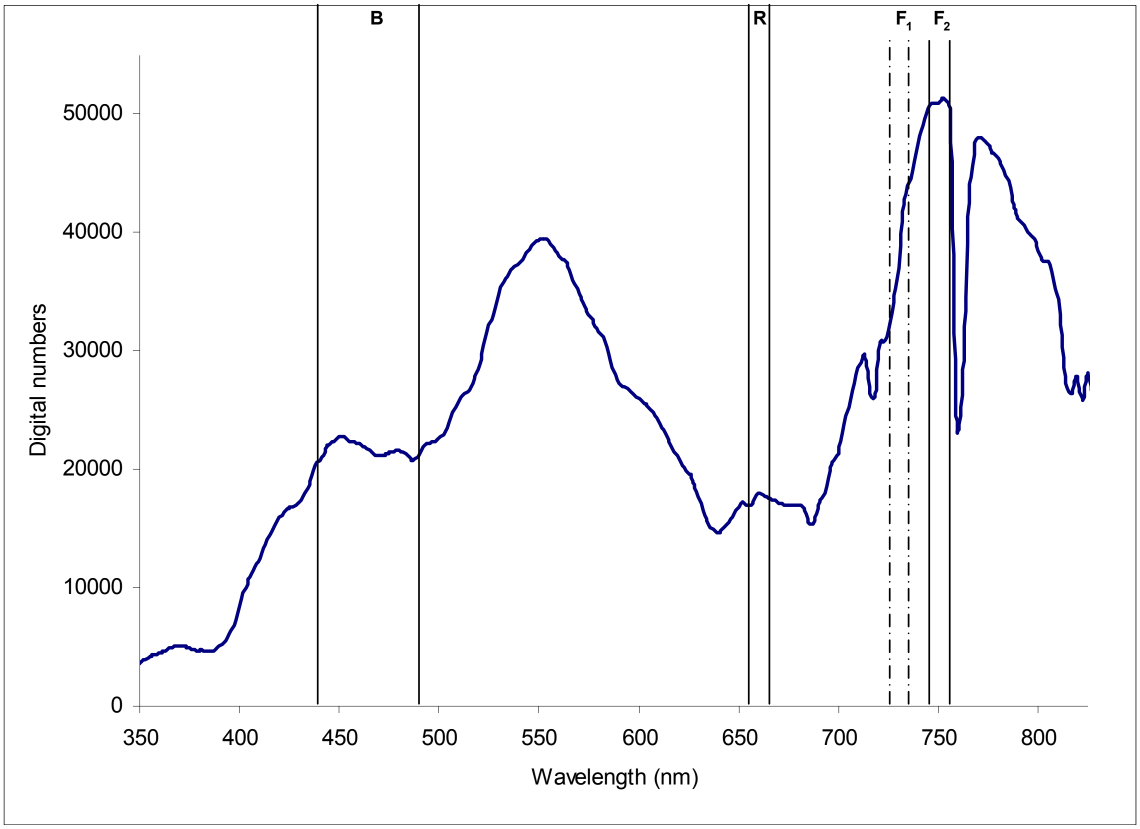

B
R
F$_1$
F$_2$
Digital numbers
0
10000
20000
30000
40000
50000
350
400
450
500
550
600
650
700
750
800
Wavelength (nm)

Figure 5

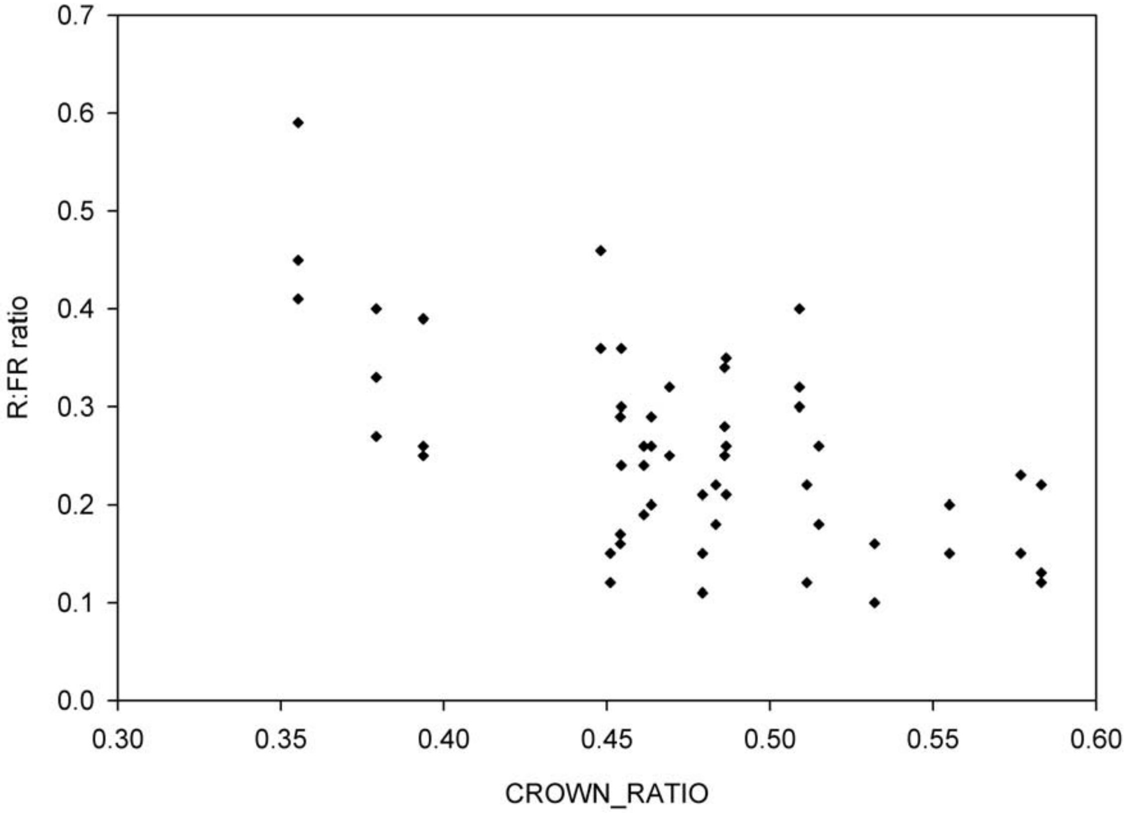
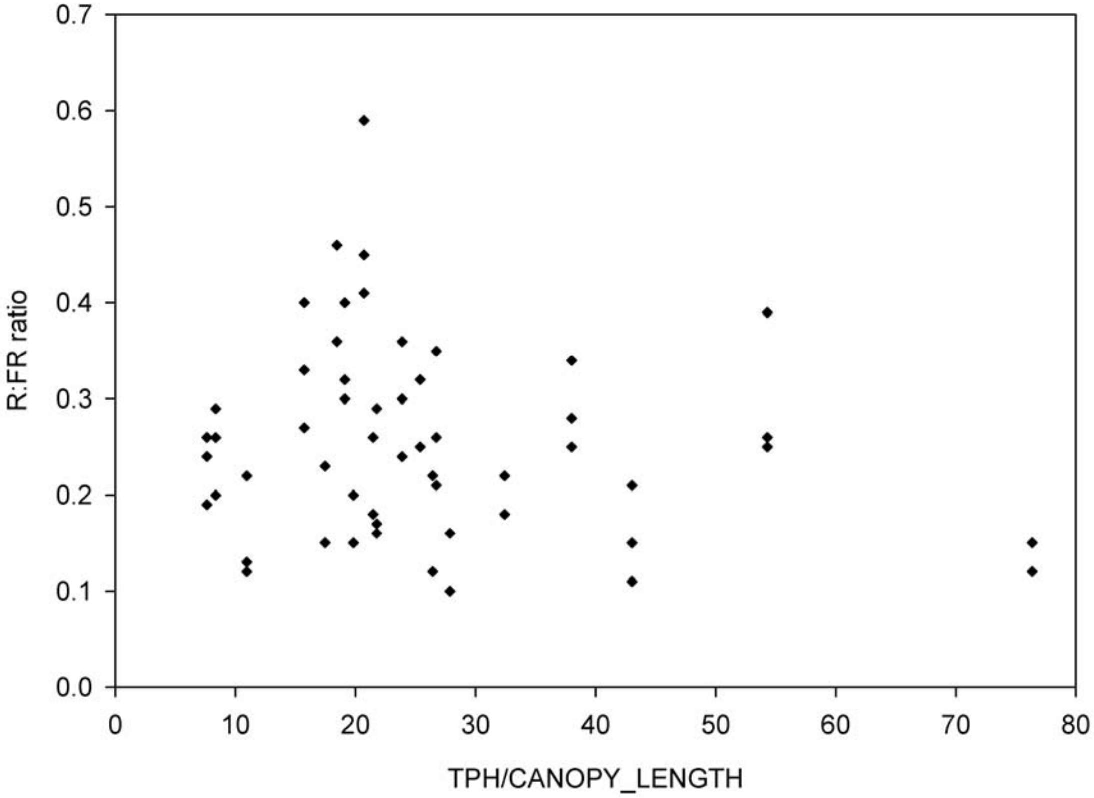

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
R:FR ratio
0.30
0.35
0.40
0.45
0.50
0.55
0.60
CROWN_RATIO

Figure 6



R:FR ratio
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
10
20
30
40
50
60
70
80
TPH/CANOPY_LENGTH

Figure 7

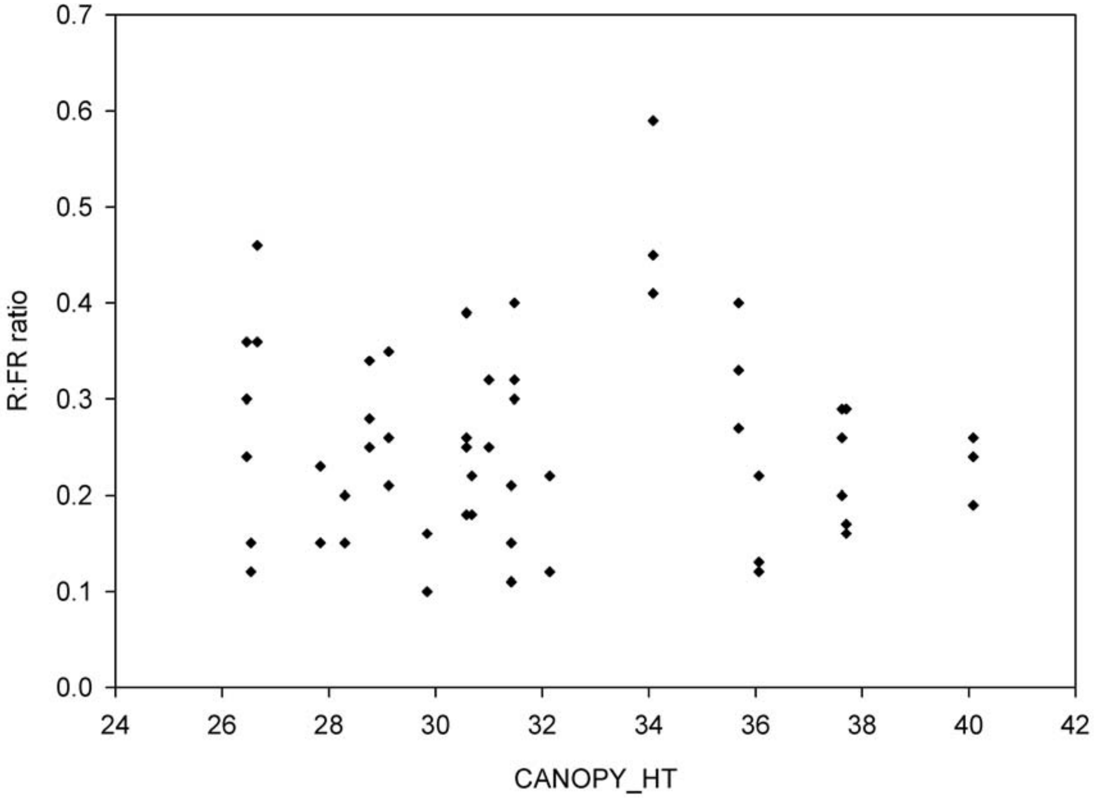
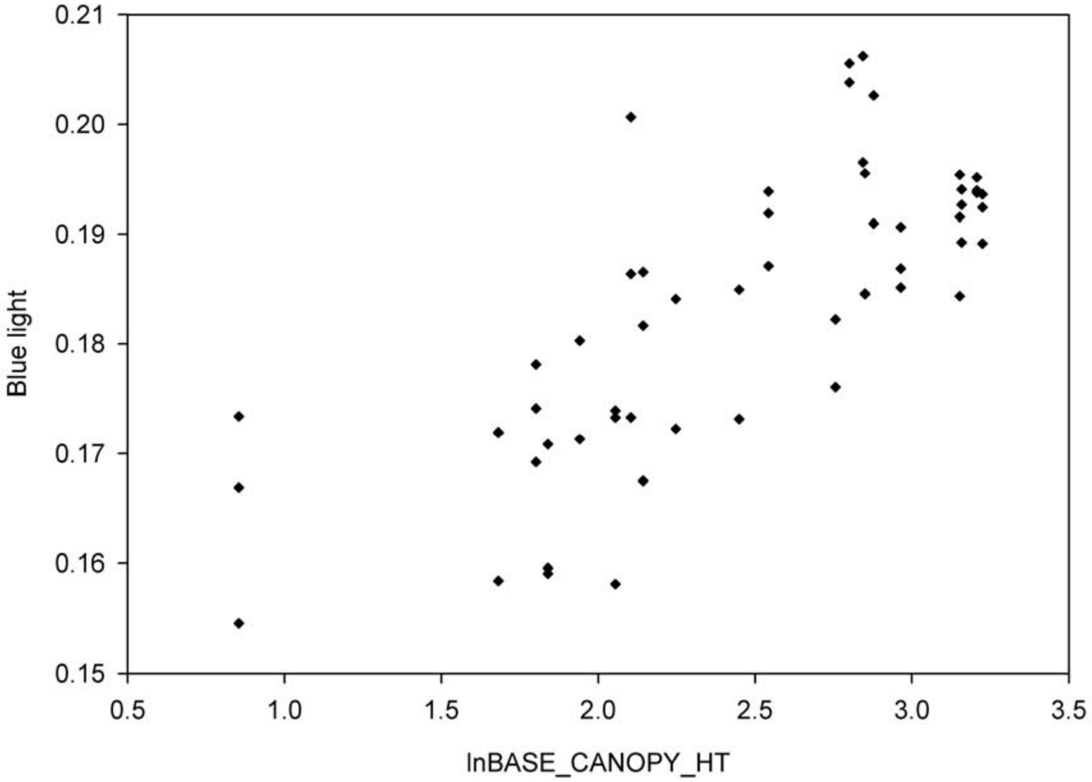

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
R:FR ratio
24
26
28
30
32
34
36
38
40
42
CANOPY_HT

Figure 8



0.21
0.20
0.19
0.18
0.17
0.16
0.15
Blue light
0.5
1.0
1.5
2.0
2.5
3.0
3.5
lnBASE_CANOPY_HT

Figure 9

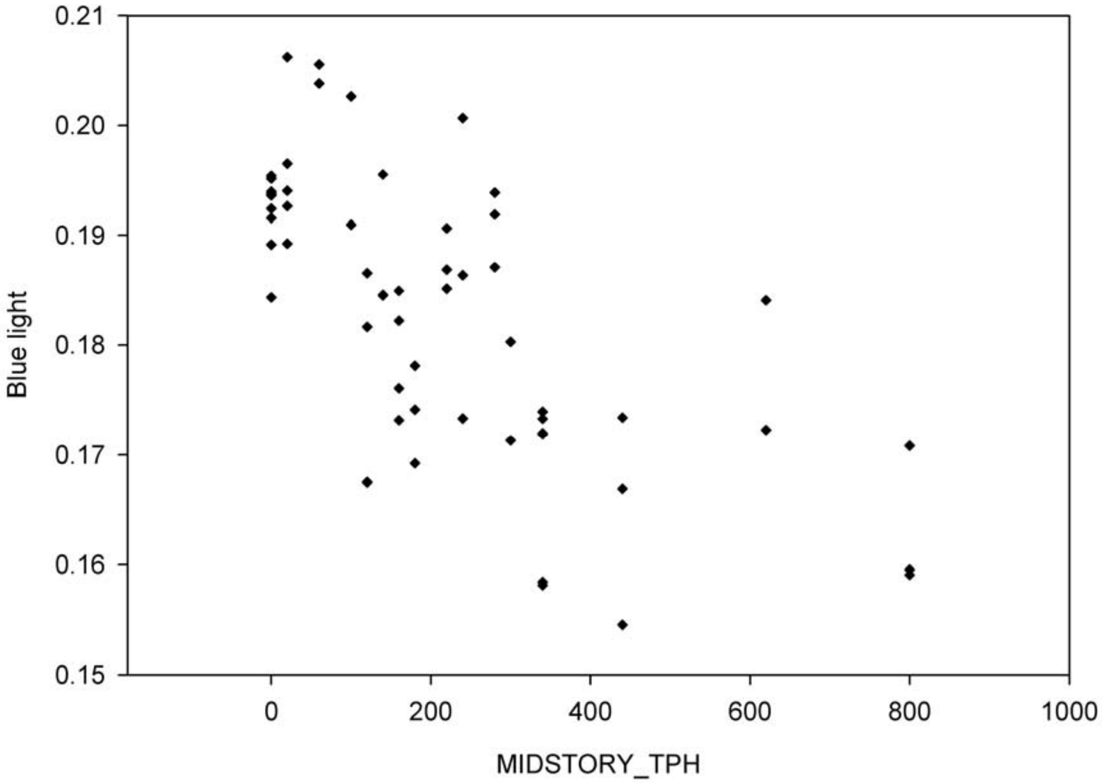

0.21
0.20
0.19
0.18
0.17
0.16
0.15
Blue light
0
200
400
600
800
1000
MIDSTORY_TPH

Figure 10

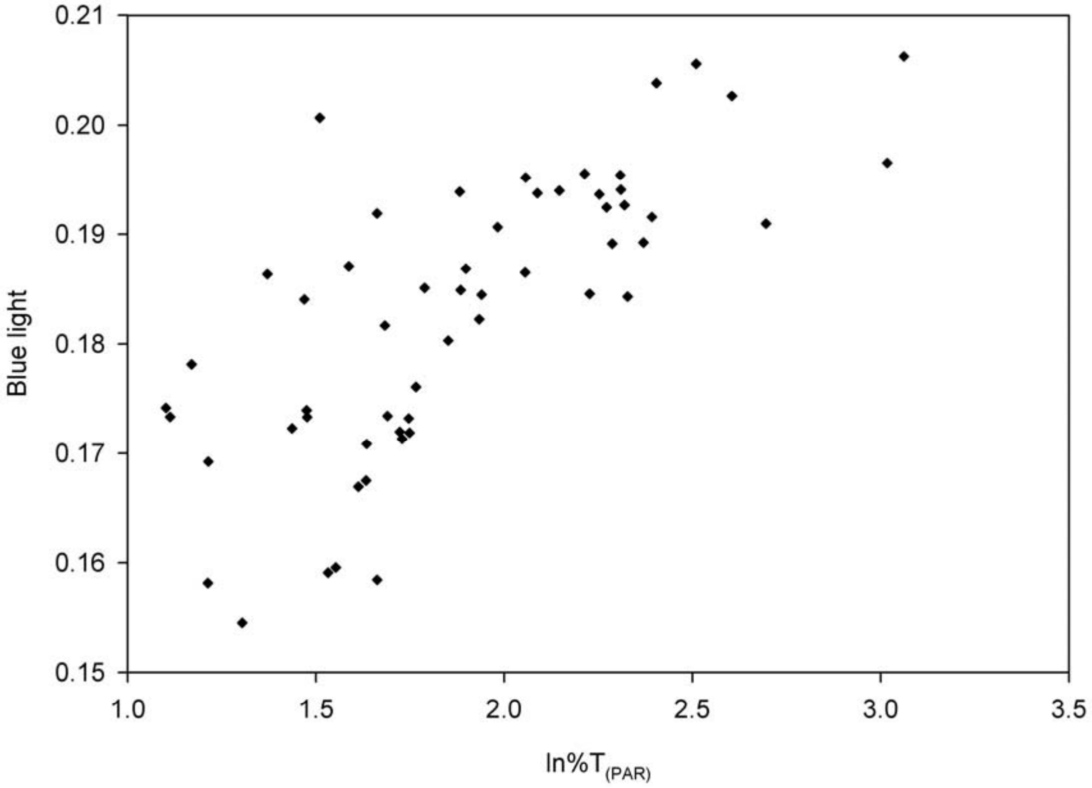
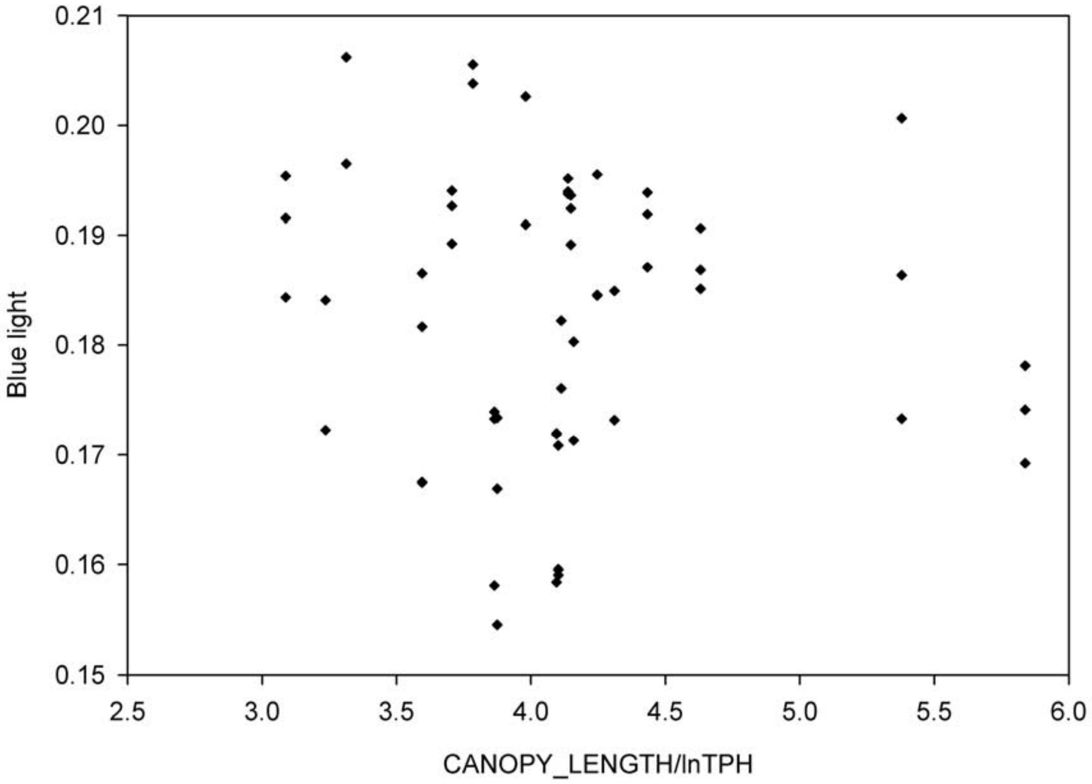


Figure 11


Blue light
0.21
0.20
0.19
0.18
0.17
0.16
0.15
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
CANOPY_LENGTH/lnTPH

CHAPTER 4 – THE INFLUENCE OF LIGHT CHARACTERISTICS AND FOREST STRUCTURE ON SEEDLING GROWTH BENEATH A RIPARIAN HARDWOOD FOREST CANOPY

Abstract

The relationship between environmental and stand conditions and the growth of Nuttall oak (*Quercus nuttallii* Palmer) seedlings was examined following midstory competition control in a riparian hardwood forest in the southeastern United States. Seedling height and ground-line diameter growth models were developed based on the influence of photosynthetically active radiation (PAR), light quantity, light quality, and the surrounding forest structure. The amount of PAR explained the most variation in diameter and height growth as a single variable, accounting for 35% and 34% respectively. Interestingly, the presence of a midstory canopy accounted for roughly 33% of variation for both diameter and height growth. The seedling diameter growth model included the height to the base of the canopy in addition to PAR transmittance, and accounted for 42% of the variation witnessed. Likewise, the height growth model included PAR transmittance, initial seedling diameter, basal area, and the height to the base of the canopy, accounting for 44% of the variation in height growth increment.

Unexpectedly, when light quality was examined, the R:FR ratio accounted for a substantial amount of variation in diameter and height growth in the low light conditions examined (3-22% full sun). The diameter and height growth models developed are similar in that measures of light and initial seedling diameter were of some importance in both models. The only difference witnessed was in the types of forest structure variables included. For seedling diameter growth, variables describing canopy structure were apparently important, while the height growth model included a measure of stand density. This difference may indicate that more drastic changes in forest structure are needed to get a response in seedling height growth compared to diameter growth.

Keywords: riparian hardwood forest, partial cutting, midstory removal, PAR transmittance, R:FR ratio, blue light, light quality, seedling growth models, Nuttall oak

Introduction

Oak (*Quercus* spp.) regeneration on mesic sites has been the focus of much research, because of the value of oak as a timber product and as a food source for wildlife. For this reason silviculturists have attempted to develop management regimes that will maintain oak in these stands. While many variables contribute to recurrent regeneration failure, a primary abiotic factor is the low light levels present in unmanaged mesic forests (Lorimer 1993). The low light conditions in these stands are problematic specifically because of the conservative growth strategy of oak reproduction. Oak seedlings will often exhibit slow initial height growth as true seedlings, instead allocating resources to the development of a large root system. Whereas the strategy is well adapted to dry sites or sites with frequent disturbance, this pattern of growth can be detrimental in mesic forests.

Once released by overstory removal these seedlings are unable to compete with faster growing, shade intolerant species such as yellow-poplar (*Liriodendron tulipifera* L.) that are common on these sites. Complicating matters, oak seedlings cannot survive for an extended period of time without increases in the light levels on these productive sites (Lorimer 1993, Hodges and Gardiner 1993).

Because oak cannot compete with faster growing shade-intolerant species in open conditions on high quality sites, clearcutting is rarely a viable regeneration strategy. Logically, some form of partial cutting is likely required. The only silvicultural method that has yielded any real promise in terms of maintaining oak seedlings on mesic sites has been the shelterwood method, although results vary and often a crop of desired reproduction fails to emerge (Loftis 1990, Schuler and Miller 1995). When successful, the partial cutting associated with the preparatory and/or seed cuts in this method creates light conditions that are not sufficient for the establishment of shade intolerant species, but high enough for oak seedlings present to remain competitive compared to other seedlings in the understory (Loftis 1990).

The conditions created by some partial cutting activities not only allow oak to remain competitive, but several studies suggest that maximum growth is achieved in partial sun environments (Gardiner and Hodges 1998, Ziegenhagen and Kausch 1995, Gottschalk 1985, Crow 1992). For example, Gardiner and Hodges (1998) examined the effects of light availability on biomass distribution and growth of cherrybark oak (*Quercus pagoda* Raf.) seedlings. Testing growth under four light regimes, they found that height and root collar diameter increased as light intensity increased from 8% to 53% full sun. However, additional increases in light levels to 100% full sun produced second year growth that was not statistically different from the 8% full sun treatment (Gardiner and Hodges 1998). Ziegenhagen and Kausch (1995) reported a similar trend for pedunculate oak (*Q. robur* L.); after two growing seasons the 25% full sun treatment produced the best height growth, followed by the 50%, 100%, and 10% full sun treatments, respectively. Likewise, Gottschalk (1985) observed that both northern red (*Q. rubra* L.) and black oak (*Q. velutina* Lam.) expressed their greatest height growth under 20% full sun and the least under an 8% treatment; height growth generally decreased with additional increases in light intensity above the 20% treatment.

The most significant result of these studies is the identification of a parabolic growth pattern over a range of light intensity levels. However, the studies mentioned above also raise additional questions. First, Gardiner and Hodges (1998), and Ziegenhagen and Kausch (1995) relied on only four light intensity levels across a range from 8% and 10% respectively, to 100% full sunlight to determine growth trends. Although Gottschalk (1985) did implement seven light treatments across a similar range, clearly if we hope to model seedling growth more accurately in terms of PAR, light quantity should be examined at a finer scale. Secondly, additional factors may have influenced the results from these studies. Most notably, Gottschalk (1985), Ziegenhagen and Kausch (1995), and Gardiner and Hodges (1998) conducted their respective studies on old field sites, rather than in a forested setting. While soil variability was minimized, Gottschalk (1985) and Gardiner and Hodges (1998) used neutral density shade cloth, which does not alter the color of the sunlight passing through it. This is not the case under a living forest canopy. Ziegenhagen and Kausch (1995) did use cloth that allowed for green light to pass to the seedlings, however, it is not certain if the spectral nature of this treatment was reflective of the light climate found under a forest canopy.

With increasing canopy coverage, light is filtered through the canopy and becomes spectrally altered due to the differential absorption and reflectance of certain wavebands by leaves (Larcher 1980). Thus the 'color' of a 20% full sun light environment under a mature forest canopy may differ spectrally from the 'color' of 50% full sun light environment, and certainly differs from 50% full sun cast by neutral density shade cloth. Indeed, work conducted with jewelweed (*Impatiens capensis* Meerb.), an annual forb, showed that attributes such as internode length and mean shoot length may vary at the same light intensity depending on whether the reduction in PAR was due to the use of neutral shade cloth or leaves (Wulff 1989, Schmitt and Wulff 1993).

Research has shown that the color of light has implications for plant germination, growth, and development; light that is rich in the red and blue wavebands has the most influence on plant growth (Morgan 1981). Hypocotyl elongation, growth and elongation of stems, expansion rate of leaves, photosynthetic rates, pigmentation, and physiological processes such as stomatal opening, are some of the plant growth characteristics that are influenced by light quality (Endler 1993, Holmes and Smith 1977, Hoad and Leakey 1994, Smith 1982). Overall, PAR appears more influential for plant development than light quality, especially in terms of affecting seedling root collar diameter, height growth, photosynthate allocation, and as found with paper birch (*Betula papyrifera* Marsh.), direction of seedling lean (Lee and others 1996, Muth and Bazzaz 2002). However, Lee and others (1996) demonstrated that height growth is also highly dependent on the R:FR level in some tropical species. In their study, the R:FR ratio expressed the most influence when PAR levels were at 11% of full sun. Likewise, Turnbull (1991) demonstrated that light quality can affect variables such as the maximum photosynthetic assimilation rate of several rainforest species, with the most influence being seen at light climates of 5% full sun.

Clearly, partial cutting activities will alter many abiotic characteristics of a particular microsite; the degree of change dependent on the intensity of treatment. However, the resulting alterations to the light environment will likely be a major factor in determining whether seedlings persist on mesic sites. The purpose of this study was to examine the relationship between light characteristics and seedling growth under a riparian hardwood canopy, and to identify the forest structural features that are associated with seedling growth. From these data, seedling growth models were developed. Forest managers can only influence the environment below the canopy through the manipulation of forest structure. By defining the light and forest structure characteristics influential for sustain growth, managers may be able to better tailor partial cutting activities to create favorable conditions in southern riparian hardwood forests.

Methods

Study site

The study site chosen was a riparian corridor within the Blanton Creek Wildlife Management Area located west-central Georgia. The riparian forests are reproductively mature, and composed primarily of sweetgum (*Liquidambar styraciflua* L.), yellow-poplar, and dogwood (*Cornus florida* L.). Red maple (*Acer rubrum* L.), Florida maple (*Acer barbatum* Michx.), box-elder (*Acer negundo* L.), two-winged silverbell (*Halesia diptera* Ellis), mulberry (*Morus rubra* L.), ironwood (*Carpinus caroliniana* Walt.), winged elm (*Ulmus alata* Michx.), various hickories (*Carya* spp.), and various oaks (*Quercus* spp.) are also found on site. As a group, oaks comprise only a small portion of the stems present, with water oak (*Q. nigra* L.) being the most common. The age structure of these riparian forests is uncertain, although distinct even-aged stands of sweetgum are present.

Study design

In the early summer of 2003, fifty 0.05 hectare circular plots (12.62 m radius) were established along a transect that bisected the riparian corridor. The plots were laid out in a systematic manner with at least 38 m separating each plot center. Plots were randomly assigned one of four cutting regimes: a control where no stems were removed, a 33% reduction in the number of midstory stems, a 50% reduction in the number of midstory stems, and a 100% midstory stem removal. Midstory stems were identified as trees with crowns that did not reach into the main canopy. In some plots designated for complete midstory removal some of the main canopy trees were also removed to slightly expand the gradient of light conditions being created. Yet, the sole purpose and focus of the cutting remained to generate forest structural conditions and light environments that might be typical of rather low intensity removals. Vegetation less than 1.37 m was not cut unless it posed a hazard to the operation. The cutting was completed exclusively by chainsaw and all trees were left in place.

Measurements were taken at each plot to document the gradient of forest structure conditions resulting from the cutting regimes. Trees per hectare (TPH) and basal area per hectare (BA) were calculated for each plot. Additionally, several other variables were either measured directly or derived from plot data including, the number of midstory trees per hectare (MIDSTORY_TPH), the average height of all trees greater than 5 cm diameter at breast height (DBH: 1.37 m) (AVE_TREE_HT), the average height of the tallest 5 trees per plot (CANOPY_HT), the average height to the base of the canopy over the plot (BASE_CANOPY_HT), the average crown ratio of all trees over 5 cm DBH on each plot, the average height to the base of the crown of the 5 trees per plot with the lowest crowns (MIN_CANOPY_HT), and the length of the canopy (CANOPY_LENGTH), calculated by subtracting CANOPY_HT from MIN_CANOPY_HT. Lastly, several variables formed by various interactions between TPH and CANOPY_LENGTH were also considered.

In January 2004, 125 containerized, one-year-old Nuttall oak seedlings were transplanted into 47.6 liter pots and placed in the study area. Two potted seedlings were placed in each plot initially, while the remaining 25 potted seedlings were distributed within each cutting treatment with seven pots in the complete midstory removal treatment. The potting mix, Faford No. 2 (Conrad Fafard, Inc., Agawan, MA), is a sphagnum peat moss (70%) – perlite – vermiculite mixture. A slow release fertilizer (13-13-13) was added to each pot after transplanting the seedlings. The seedlings were potted rather than planted in order to control the influence of hydrology and soil variation on seedling growth. The pots were watered throughout the study, ensuring that the seedlings had adequate moisture and that the potting medium did not to dry out. To control deer browse, a circular wire cage was placed around each pot. The wire cages were approximately 61 cm in diameter and 122 cm tall, constructed out of 14 gauge wire fencing; the mesh size of the fencing material was 5.08 cm by 10.16 cm. Initial height (HT_I) and ground-line diameter (GLD) were recorded for each seedling prior to budbreak early in 2004. In late September 2004, once the seedlings had set bud, the seedlings were re-measured and any mortality was noted.

Light measurements

Beginning after full leaf expansion, light quantity measurements were taken at each seedling location on overcast days following the methodology outlined in Messier and Puttonen (1995). It was confirmed that on overcast days when the sun is completely obscured, instantaneous measurements of PAR closely approximate average daily rates (data not shown). Light intensity was measured using a linear PAR/LAI ceptometer (Decagon Devices, Inc., Pullman, WA); four instantaneous measurements were taken with the instrument above each potted seedling. Care was taken to ensure that the ceptometer was pointed in the direction of the brightest light source so that the operator's shadow was not cast on the measurement sensors. A weather station equipped with a LI-COR PAR sensor was placed in a clearcut adjacent to the study area and served as a control for the ceptometer measurements.

Light quality was measured using a FieldSpec UV/VNIR handheld spectroradiometer (Analytical Spectral Devices, Inc., Boulder, CO) with a lambertian reflector panel. The lambertian panel is calibrated to reflect 100% of the visible spectrum. All radiation emitting from the various sources composing the light environment below a forest canopy is reflected off the panel and collected by the spectroradiometer; care was taken that the operator did not stand between a strong light source, such as a canopy gap, and the panel. Three replicates of spectral data were collected for seedlings on 10 of the 50 plots that were systematically selected to be representative of the gradient of forest structural conditions present in the study area; an additional set of 33 one-time measurements supplemented this dataset. Unlike PAR measurements, light quality data can only be collected under clear skies when sampling under a forest canopy (Endler 1993). From the spectral data collected, the R:FR ratio and the percent of PAR composed of blue light was calculated for each seedling (see chapter 3).

Data analysis

Using the light characteristics, forest structure, and seedling data collected, regression analysis was used to determine the relationship between seedling growth and the forest structure and light conditions that exist below a riparian hardwood canopy. Since the seedlings were not equal in their initial heights, only the amount of new growth added during the growing season, the height growth increment (HGI), was used to determine the seedling height growth response to its environment. Likewise, the diameter growth increment (DGI), rather than the total GLD, was of primary interest.

For both seedling height and diameter growth, two different datasets were used to construct models using the Mallow's Cp procedure in the SAS statistical software package (SAS 8.2, SAS Institute Inc., Cary, NC, USA). The first contained forest structure, seedling growth, and PAR data for all surviving seedlings. The second dataset included the same variables as the first, but also incorporated variables describing the average R:FR ratio (655-665 nm / 746 – 756 nm) and proportion of PAR composed of blue light (440 - 490 nm / 400 – 700 nm) at each seedling location. The second dataset was smaller because of the greater difficulty in collecting the light quality data.

The favored growth models for both datasets were selected based on: *i*) whether each variable significantly contributed to each overall model (P-value < 0.05), *ii*) the amount of variation explained (R^2), and *iii*) the results of a series of residual diagnostics that included tests for outliers and an examination of the residual graphs for non-constant variance. Collinearity diagnostics were also conducted on each model to identify problems associated with multicollinearity; most notably, the variance inflation factor (VIF) and collinearity (COLLIN) procedures in SAS (SAS 8.2, SAS Institute Inc., Cary, NC, USA). In the VIF procedure, variables which produce values greater than 10 are thought to be strongly related with other variables in the model to the degree that the reported R-square is an artifact of the multicollinearity in the model (Yu 2000). Likewise, when the COLLIN procedure reports values greater than 100 multicollinearity is thought to be a problem (Yu 2000). Therefore the models with the lowest VIF and COLLIN values were selected when possible.

Results

Of the 125 seedlings initially planted in this study, 13 apparently died from transplant shock; the majority of these failed to break bud. Five additional seedlings were discarded from the data set because these pots were not watered properly during the growing season and experienced an unknown amount of time potentially under moisture stress.

Therefore, 107 seedlings were used to construct diameter and height growth models based on stand structure and light quantity in the first dataset. The second dataset, on the other hand, consisted of 42 seedlings that had light quality data collected in addition to structure and PAR data.

Ground-line diameter growth

Of the variables examined in the first dataset, PAR transmittance ($\%T_{(PAR)}$) proved to be the best single variable model, explaining 35% of the variation observed in seedling diameter growth. Other important variables included BASE_CANOPY_HT, and the log transformation of TPH (lnTPH), which explained 31% and 27% of the variation in diameter growth as single variable models, respectively. The interaction term (lnTPH*lnCANOPY_LENGTH) also accounted for 33% of the variation in diameter growth. Somewhat surprisingly, the initial ground-line diameter (GLD) was not significantly correlated to the diameter growth increment (correlation coefficient 0.13573; p-value = 0.1633). However, the favored model for the first dataset included both $\%T_{(PAR)}$ and BASE_CANOPY_HT.

[1]

$$\mathbf{DGI} = b_0 + b_1 (\%T_{(PAR)}) + b_2 (\mathrm{BASE\_CANOPY\_HT})$$

$$R^2 = .4213; \text{P-value} < .0001$$

Both variables contribute significantly to the final model, with $\%T_{(PAR)}$ explaining approximately 35% of the variation (Figure 1); the variable BASE_CANOPY_HT contributed an additional 0.0695 to the final R-square (Figure 2). Multicollinearity did not appear to be a problem. There were no serious outliers nor were there signs of non-constant variance or violations of the normality assumption.

When the data from the second dataset (light quality included) was analyzed, %$T_{(PAR)}$ again proved to be the best single variable model, accounting for 57% of the variation in DGI. Likewise, the variable BASE_CANOPY_HT remained the second best single variable model, explained 43% of the recorded variation in DGI. As for the light quality variables, RFR and BLUE account for 25% and 28% of the variation in DGI respectively. Overall eight variables had R-square values equal to or greater than 0.2500. Of these, the final model only includes %$T_{(PAR)}$.

[2]

DGI = $b_0 + b_1$ **(%$T_{(PAR)}$) +** b_2 **(RFR) +** b_3 **(CANOPY_HT)**

R^2 = .6615; P-value < .0001

All three variables, %$T_{(PAR)}$, RFR, and CANOPY_HT, significantly contribute to the model (Figures 3, 4, and 5). When %T(PAR) and CANOPY_HT are already present in the model, however, the variable RFR is slightly above the 0.05 threshold, with a P-value of 0.0620. Yet, given the amount of variability that remains unaccounted for, this P-value was deemed acceptable. There were no signs of serious multicollinearity, nor were there significant outliers or patterns in the residual plots such as non-constant variance.

Height growth

Thirty-eight of the seedlings planted experienced some degree of top dieback on the terminal stem prior to initial growth. However, a lateral branch usually surpassed the original height before the end of the growing season. Only 9 of the surviving 107 seedlings failed to reach their original height, and therefore had a negative height growth increment (HGI). The individual variables which served as the best predictors of HGI in the first dataset, when light quality was not considered, included $\%T_{(PAR)}$ and the interaction term (lnTPH*CANOPY_LENGTH), explaining 34% and 33% of the variation in HGI respectively. The final model consisted of four variables, $\%T_{(PAR)}$, BA, BASE_CANOPY_HT, and GLD, which accounted for roughly 44% of the variation in HGI.

[3]

$$\mathbf{HGI} = b_0 + b_1\,(\%T_{(PAR)}) - b_2\,(\mathrm{BA}) + b_3\,(\mathrm{BASE\_CANOPY\_HT}) + b_4\,(\mathrm{GLD})$$

$$R^2 = .4390;\ \text{P-value} < .0001$$

All the variables significantly contribute to the model, with $\%T_{(PAR)}$ accounting for 34% of the explained variation (Figure 6); the variables BA, BASE_CANOPY_HT and GLD contribute an additional 3%, 4%, and 2% respectively (Figures 7, 8, and 9). There were no indications of multicollinearity, or signs of non-constant variance. Two seedlings, however, may be considered outliers. One, exhibiting a HGI of -13 cm, failed to growth much throughout the season even though a small lateral branch near the base of the seedling remained living following top dieback. The second outlier was a seedling with a HGI of approximately 8 cm. This seedling failed to grow as vigorously as the other seedling present in its plot; this other seedling had a HGI of roughly 40 cm.

When the light quality data was analyzed in the second dataset, the single variable model with $\%T_{(PAR)}$ was the most effective model, explaining roughly 53% of the variation in

HGI. Variables describing basal area, the R:FR ratio and the total length of the crown accounted for 42%, 31% and 32% of the variation in HGI, respectively. The final multiple variable model contained three variables, $\%T_{(PAR)}$, RFR, and BA, explaining roughly 66% of the variation in HGI.

[4]

$$\mathbf{HGI} = b_0 + b_1 (\%T_{(PAR)}) + b_2 (RFR) - b_3 (BA)$$

$$R^2 = .6590; \text{P-value} < .0001$$

All three variables were deemed to significantly contribute to the final model (Figures 10, 11, and 12). However, as was the case in the DGI model constructed from this second dataset, the P-value for the variable RFR in model 4 was boarding on the .05 significance level (P-value = 0.0552). Multicollinearity was not apparent among the variables included in model 4. For this model only the seedling with the HGI of -13 cm was determined to be an outlier although this measurement was not discarded. The seedling with the HGI of 8 cm that was an outlier in the first dataset was randomly excluded from the secondly dataset. There did not appear to be any patterns in the residual plots.

Discussion

The objective of this study was to model the growth response of oak seedlings exposed to a gradient of low light environments and forest structure conditions. It was of interest to identify the structural attributes and light characteristics that are significantly related to the ground-line diameter and height growth of seedlings placed under a closed canopy riparian hardwood forest. A particular concern was to determine what measurable influence, if any, light quality variables have on growth trends. By design, the treatments in this study produced a narrow range of light conditions, approximately 3% to 22% of full sun. Such conditions are needed to present an informed discussion of the appropriateness of using low intensity partial cutting regimes to regenerate oak on riparian sites. Substantial disturbance of the main canopy results in excessive increases in light intensity. This in turn leads to the establishment of fast growing shade intolerant species such as yellow-poplar with which oak seedlings cannot compete. Previous work indicates that the control of the sub-canopy tier under an intact main canopy allows northern red oak reproduction to maintain growth while maintaining suppression of shade intolerant competitors (Loftis 1990). However, it is not known how the conditions created by similar treatments will influence other oak species growing in riparian areas.

Ground-line diameter growth

Forest structure influences seedling growth by altering abiotic variables such as light, temperature, and moisture availability, each of which may impact growth rates. However, in this study, soil and moisture variability were controlled to the extent possible in an attempt to isolate the effect of light and forest structure on seedling growth. Model 1 explained approximately 42% of the variation in the diameter growth increment of the seedlings. Model 2 was constructed from a second dataset and included light quality variables. This second model explained approximately 66% of the variation in DGI. While a tendency to suggest that model 2 has significantly greater explanatory power than model 1 may exist, this would be a false comparison. Due to the differences in sample size between the two dataset, it is impossible to directly compare the two models. Rather, the significance of each model must be considered individually.

For model 1, as expected, the amount of PAR transmittance had the strongest correlation with seedling diameter growth (correlation coefficient = 0.59313). There is a positive relationship between diameter growth and PAR availability under low light conditions (Figure 1). The contribution that the variable BASE_CANOPY_HT makes to model 1 may be characterized as one of "high" versus "low" shade. Seedling diameter growth increment increased as the height to the base of the canopy increased (Figure 2). While it was not possible to determine what, if any, influence the height to the canopy had on microclimatic attributes such as temperature or relative humidity in this study, it has been demonstrated that the amount of diffuse light below a forest canopy is increased by raising the height to the canopy (see Chapter 3). Because of this relationship, it is possible that the amount of blue light also increases with increasing height to the canopy because blue light originates from diffuse radiation (Ender 1993). Indeed, the correlation coefficient between PAR, measured as diffuse radiation in this study, and the relative amount of blue light present was 0.68443, while the correlation coefficient between the relative amount of blue light and the height to the canopy was 0.71655. Thus the variable describing the height to the base of the canopy potentially may be incorporating the affects caused by the amount of blue light present below the main canopy. Lastly, it should be noted that the term GLD was nearly a significant addition to model 1 (P-value = .0626). It would appear logical that seedlings with the largest initial diameters are more likely to improve in diameter over the course of the growing season. If GLD is considered as part of the final model, the amount of variation in diameter growth explain increases from 42% to 44%.

In model 2, PAR transmittance again appears to be the single best predictor of seedling diameter growth. However, it is likely that the overall strength of the relationship between $\%T_{(PAR)}$ and DGI is somewhat inflated due to the increased variability and decreased sample size. However, given the weight that PAR transmittance held in model 1, the relative importance of this variable in model 2 is not called into question. While the importance of PAR transmittance was expected in the model, what was not expected was the inclusion of the R:FR ratio in model 2. Potentially, the combination of variables describing the overall canopy height and the R:FR ratio act as a surrogate measure of canopy structure that is influencing seedling growth in some other than light intensity. While it cannot be implied from this analysis that the R:FR ratio is directly influencing seedling diameter growth, the fact remains that the variable RFR does add to the ability of the model to explain variation in seedling diameter growth. It would be of great interest to see if the variable RFR remains in the model with a larger dataset.

Height growth

The first model developed to describe the seedling height growth increment accounted for roughly 44% of the variation measured. The analysis of the single variable models demonstrated that, as expected, the level of PAR availability was strongly related to seedling height growth. However, it should be noted that the interaction term (lnTPH*CANOPY_LENGTH) explained roughly the same amount of variation in height growth, indicating that these variables may be interchangeable with regards to HGI. Indeed, the correlation coefficients between HGI and the variables $\%T_{(PAR)}$ and (lnTPH*CANOPY_LENGTH) are identical for all intensive purposes (0.57994 and

0.57245 respectively). Therefore, the influence that the interaction term has on seedling growth is likely due to reductions in PAR transmittance. This fact supports the belief that the presence of a midstory canopy tier will impede oak seedling growth on mesic sites due to reductions in light levels (Janzen and Hodges 1987, Lockhart and others 1992). As the influence of the midstory canopy tier becomes more prevalent in the stand, there is a decrease in the height growth increment of the seedlings.

The variables that were in model 3 besides $\%T_{(PAR)}$, included the plot basal area, the average height to the base of the canopy, and the initial ground-line diameter of the seedlings. The inclusion of initial seedling diameter in the model is not surprising; a larger root collar might indicate increased carbohydrate storage in the root system, which would equate to greater growth potential. Interpreting the biological influence that plot basal area and the height to the base of the canopy have on seedling height growth is less straightforward. While these measures of forest structure do not directly influence seedling height growth, they likely determine abiotic factors such as light, temperature and moisture which do affect seedling growth. However, the purpose of this research was not to necessarily identify the mechanism by which forest structure influences growth. Rather, the value of identifying the variables BA and BASE_CANOPY_HT as important is in the recognition that both stem density and canopy structure are related to seedling height growth. Moreover, the majority of variation in model 3, 37% of the total 44%, was explained by PAR transmittance and basal area.

When examining the second dataset, the ability of PAR transmittance and basal area to explain variation in seedling height growth is again shown. Recall, that as single variable models, these two predictors explained 53% and 42% of the variation in HGI, respectively. As indicated with the diameter growth model previously, the overall importance of PAR transmittance may again be high due to smaller sample size and an effort to ensure that the second dataset was representative of the entire gradient of conditions created. Yet, given the importance of PAR in model 3, it is likely that $\%T_{(PAR)}$ would remain strongly related to HGI even if more observations were included. As with the analysis of the diameter growth model derived from the second dataset, the most interesting aspect of model 4 is the inclusion of the variable RFR. Interestingly, with $\%T_{(PAR)}$ already in the model, the R:FR ratio actually contributes more to the overall explanatory power of the model than basal area. While the exact nature of the relationship between the R:FR ratio and seedling height growth cannot be determined from this analysis, the fact that the variable RFR does significantly add to the model given the amount of unexplained variation present indicates that it should be explored further in an expanded dataset.

Conclusions

From the models constructed, it is evident that the quantity of PAR available to seedlings is strongly related to the growth trends witnessed in the low light conditions (3% to 22% full sun) created in this study. It has been also been demonstrated that aspects of forest structure, in particular the presence of a midstory canopy tier, are related to PAR transmittance (see Chapter 3). While the current study is unable to ascribe decreases in seedling growth trends to decreases in PAR transmittance, the relationship between light quantity levels and midstory canopy structure supports the results other work that attribute seedling decline to the presence of a midstory canopy tier (Janzen and Hodges 1987, Lockhart and others 1992). While it is clear that PAR transmittance is related to the successful growth of seedlings under a closed canopy, the most surprising result of this study was recognizing the contribution that the R:FR ratio had in explaining the variability of seedling height and diameter growth. Although the influence of PAR has been shown to be more important for seedling growth than the R:FR ratio overall, it is noteworthy that research has indicated that the R:FR ratio may be important for seedling growth in low light conditions (Lee and others 1996, Turnbull 1991). While it should not be insinuated that the R:FR ratio is producing a growth response in the seedlings based on the current work, this study does suggest both light quantity and quality are related to seedling growth. Furthermore, when examining the influence of the light environment on oak seedling growth, both aspects of the light environment need to be accounted for in low light conditions.

When examining the diameter and height growth models developed it becomes apparent that the models contain interesting similarities and differences. The DGI and HGI models developed from the first dataset, for example, both include the variables $\%T_{(PAR)}$ and BASE_CANOPY_HT. The only difference between the models is that the HGI model also contained the variables BA and GLD. However, given the fact that GLD was nearly significant in the DGI model, the most interesting aspect of the two models is the difference in the forest structure variables reported. Since the amount of unexplained variation in seedling diameter and height growth remains considerable, it is difficult to discern the exact nature of the relationship between structural variables and seedling growth. Yet it is interesting to note that a variable describing canopy structure, BASE_CANOPY_HT, is included in the DGI model while BA, a measure of stand density, is included in the HGI model. Similar to the models developed from the first dataset, the second set of models, which included light quality data, were more similar than different. Notably, PAR transmittance and the R:FR ratio were included in both seedling diameter and height growth models. Likewise, the only differences between the models were in the variables describing forest structure. As was the case in the first set of models, due to the amount of unexplained variation remaining in the seedling growth trends, it is difficult to suggest that the structural variables included are the attributes driving the relationship between structure and growth. Interestingly, when looking at the types of forest structural variables included in each model, the variable included in the DGI model is a description of canopy structure, CANOPY_HT, while its counterpart in the HGI model is again BA, a measure of stand density. Although the cause of this discrepancy between the types of forest structural variables included in both sets of growth models is unknown at this time, it should be mentioned that one aspect of forest structure was related to both diameter and height growth in a similar fashion. The interaction terms describing the midstory canopy tier accounted of approximately 33% of the variation in both diameter and height growth in the first dataset.

Although the mechanisms driving the relationships between light and structure with seedling growth cannot be determined from this study, some basic observations can be made regarding how seedlings might respond to management activities. For example, the results indicate that the presence of a midstory canopy, basal area, and the height to the base of the canopy are significantly related to both seedling diameter and height growth. By implementing a midstory competition control treatment these variables would be affected in a way that may result in a corresponding positive response in seedling growth. However, it is difficult to predict exactly how seedlings in a natural setting would respond to light alterations in forest structure since soil and moisture variability, which were controlled in this study, may confound the trends witnessed here.

The question that should be addressed in the future is whether or not the growth trends seen in this study are enough to keep oak seedlings in a competitive position. Although seedling growth may be slow in the low light environments found under a closed canopy, as long as conditions allow desirable oak seedlings to remain viable relative to the competition then these growth rates may be considered acceptable. What is not known is how midstory removal treatments affect competitor species on riparian sites that are able to become established and grow in low light environments. Chambers and Henkel (1989) attempted to address this problem although a definitive conclusion to this question has not been reached.

Literature Cited

Chambers, J.L., and Henkel, M.W. 1989. Survival and growth of natural and artificial regeneration in bottomland hardwood stands after partial overstory removal. Pgs. 277-283. In: J.H. Miller. compiler. Proceedings of the fifth biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SO-74.

Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91: 192-200.

Endler, J.A. 1993. The color of light in forests and its implications. Ecological Monographs. 63: 1-27.

Gardiner, E.S., and Hodges, J.D. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. Forest Ecology and Management 108: 127-134.

Gottschalk, K. 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. I. Height, diameter, and root/shoot ratio. Pgs. 189-195. In: Dawson, J.O., and Majerus, K.A. (eds.) Proceedings of the fifth central hardwood forest conference. SAF Pub. 85-05.

Hoad, S.P., and Leakey, R.R.B. 1994. Effects of light quality on gas exchange and dry matter partitioning in *Eucalyptus grandis* W. Hill ex Maiden. Forest Ecology and Management 70: 265-273.

Hodges, J.D., Gradiner, E.S. 1993. Ecology and physiology of oak regeneration. Pgs. 54-65. In: Loftis, D.L., and McGee, C.R. (eds.) Proc., Oak Regeneration: Serious Problems, Practical Recommendations, USDA Forest Service GTR SE-84.

Holmes, M.G., and Smith, H. 1977. The function of phytochrome in the natural environment IV. Light quality and plant development. Photochemistry and Photobiology 25: 551-557.

Janzen, G.C., and Hodges, J.D. 1987. Development of advanced oak regeneration as influenced by removal of midstory and understory vegetation. Pgs. 455-461. In: Douglas, P.R. (editor) Proceedings of the forth biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SE-042.

Kwesiga, F., and Grace, J. 1986. The role of the red/far-red ratio in the response of tropical tree seedlings to shade. Annals of Botany 57: 283-290.

Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, New York, pp. 5-18.

Lee, D.W., Baskaran, K., Mansor, M., Mohamad, H., and Kheong, S. 1996. Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. Ecology 77(2): 568-580.

Lei, T.T., and Lechowicz, M.J. 1998. Diverse responses of maple saplings to forest light regimes. Annals of Botany 82: 9-19.

Lockhart, B.R., Hodges, J.D., and Guldin, J.M. 1992. Development of advanced cherrybark oak reproduction following midstory and understory competition control and seedling clipping: 4-year results. Pgs. 109-115. In: J.C. Brissette. ed. Proceedings of the seventh biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SO-93.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the Southern Appalachians. Forest Science 36(4): 917-929.

Lorimer, C.G. 1993. Causes of the oak regeneration problem. Pgs. 14-65. In: Loftis, D.L., and McGee, C.R. (eds.) Proc., Oak Regeneration: Serious Problems, Practical Recommendations, USDA Forest Service GTR SE-84.

Messier, C., and Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for a quick and efficient method of characterizing light. Canadian Journal of Forest Research 25: 343-354.

Morgan, D.C. 1981. Shadelight quality effects on plant growth. In: Smith, H. (editor), Plants and the Daylight Spectrum. Academic Press, London, pp. 205-221.

Muth, C.C., and Bazzaz, F.A. 2002. Tree seedling canopy responses to conflicting photosensory cues. Oecologia 132: 197-204.

Schmitt, J., and Wulff, R.D. 1993. Light spectral quality, phytochrome and plant competition. TREE 8(2): 47-51.

Schuler, T.M., and Miller, G.W. 1995. Shelterwood treatments fail to establish oak reproduction on mesic forest sites in West Virginia – 10-year results. Pgs. 375-387. In: Gottschalk, K.W., and Fosbroke, S.L.C. (eds.) Proceedings of the tenth central hardwood forest conference. USDA Forest Service Gen. Tech. Rep. NE-197.

Smith, H. 1982. Light quality, photoperception, and plant strategy. Annual Review of Plant Physiology 33: 481-518.

Turnbull, M.H. 1991. The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87: 110-117.

Wulff, R.D. 1989. The effects of reduced irradiance and low red to far-red ratios on the growth and photosynthetic capacity in *Impatiens capensis*. Supplement to American Journal of Botany 76 (6): 131-132.

Yu, C.H. 2000. An overview of remedial tools for collinearity in SAS. Proceedings of 2000 Western Users of SAS Software Conference, pp. 196-201.

Ziegenhagen, B., and Kausch, W. 1995. Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. Forest Ecology and Management 72: 97-108.

Figure Index

Figure 7: Relationship between seedling height growth increment (HGI) and stand basal area in the first dataset (R^2 contribution to final model = 0.0315)

Figure 8: Relationship between seedling height growth increment (HGI) and the average height to the base of the canopy (BASE_CANOPY_HT) in the first dataset (R^2 contribution to final model = 0.0432)

Figure 9: Relationship between seedling height growth increment (HGI) and initial seedling diameter (GLD) in the first dataset (R^2 contribution to final model = 0.0279)

Figure 10: Relationship between seedling height growth increment (HGI) and the amount of photosynthetically active radiation (PAR) beneath the canopy in the second dataset (R^2 contribution to final model = 0.5321)

Figure 11: Relationship between seedling height growth increment (HGI) and the R:FR ratio beneath the canopy in the second dataset (R^2 contribution to final model = 0.0760)

Figure 12: Relationship between seedling height growth increment (HGI) and stand basal area for the second dataset (R^2 contribution to final model = 0.0509)

Figure 1

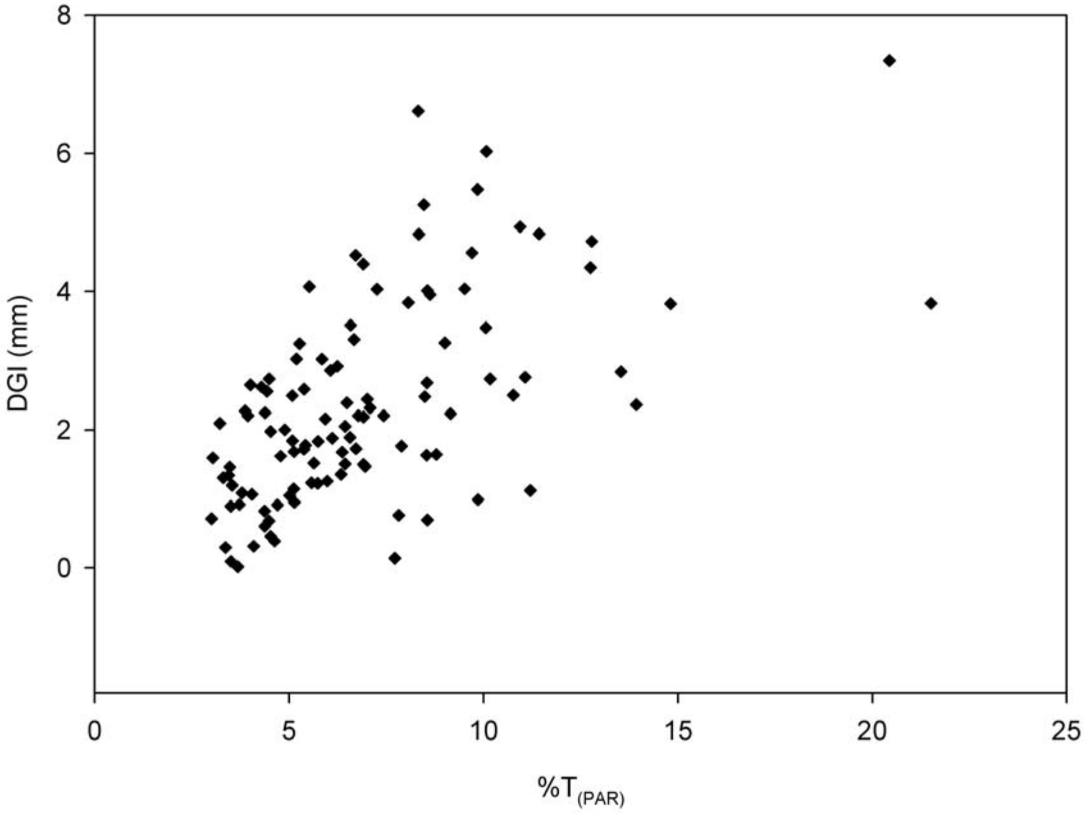


Figure 2

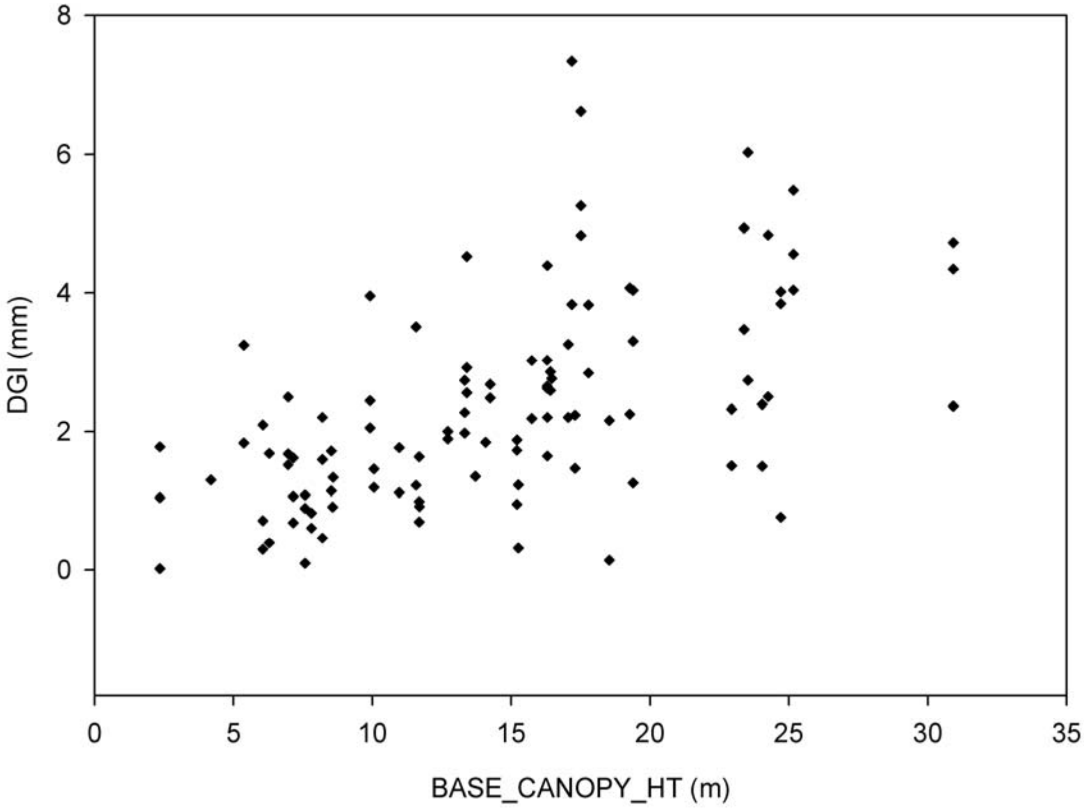


Figure 3

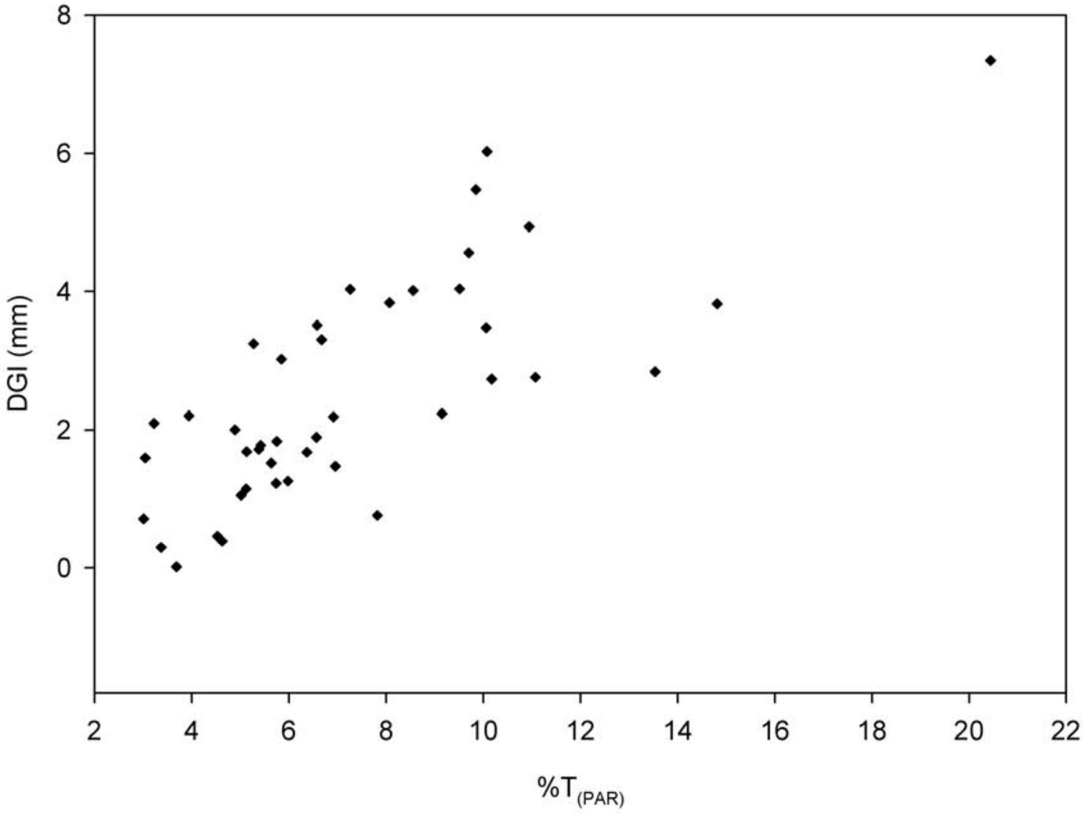


Figure 4

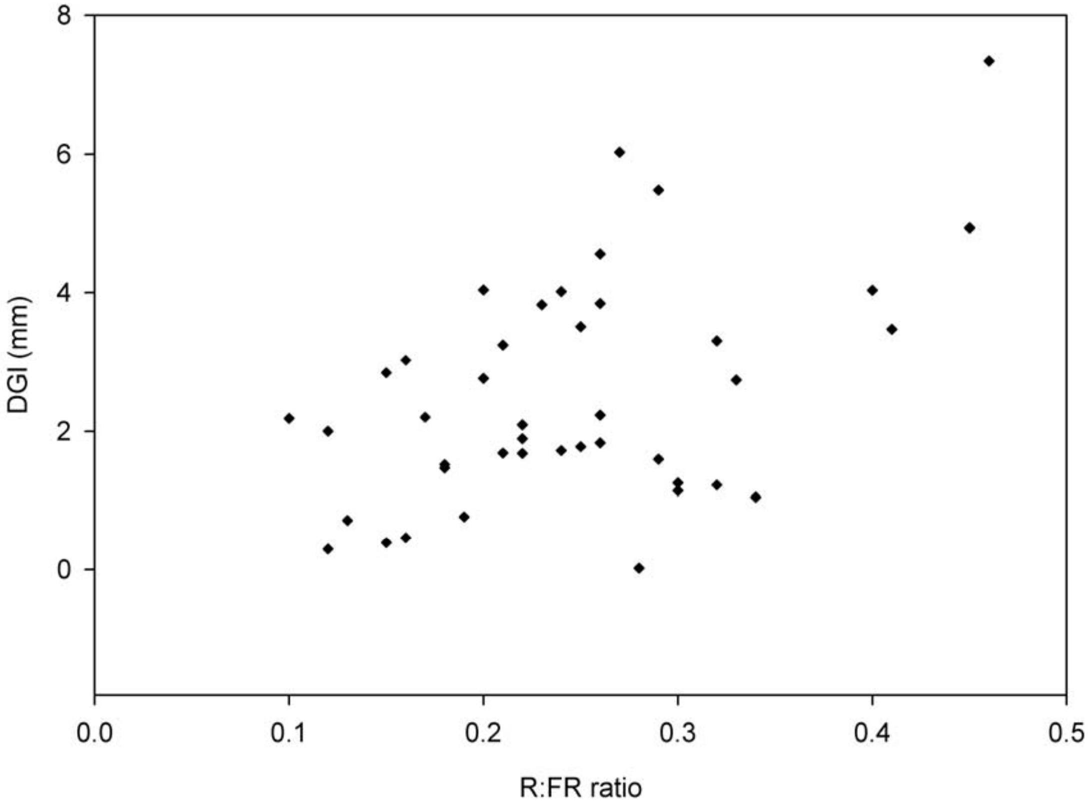


Figure 5

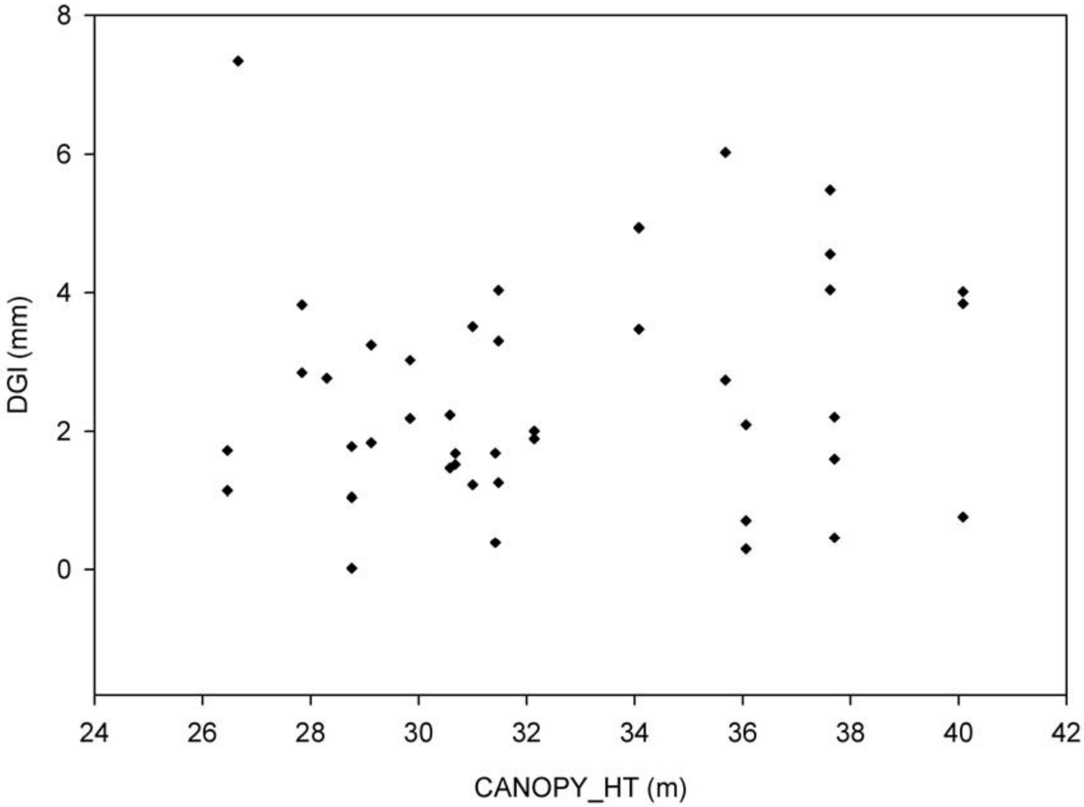


Figure 6

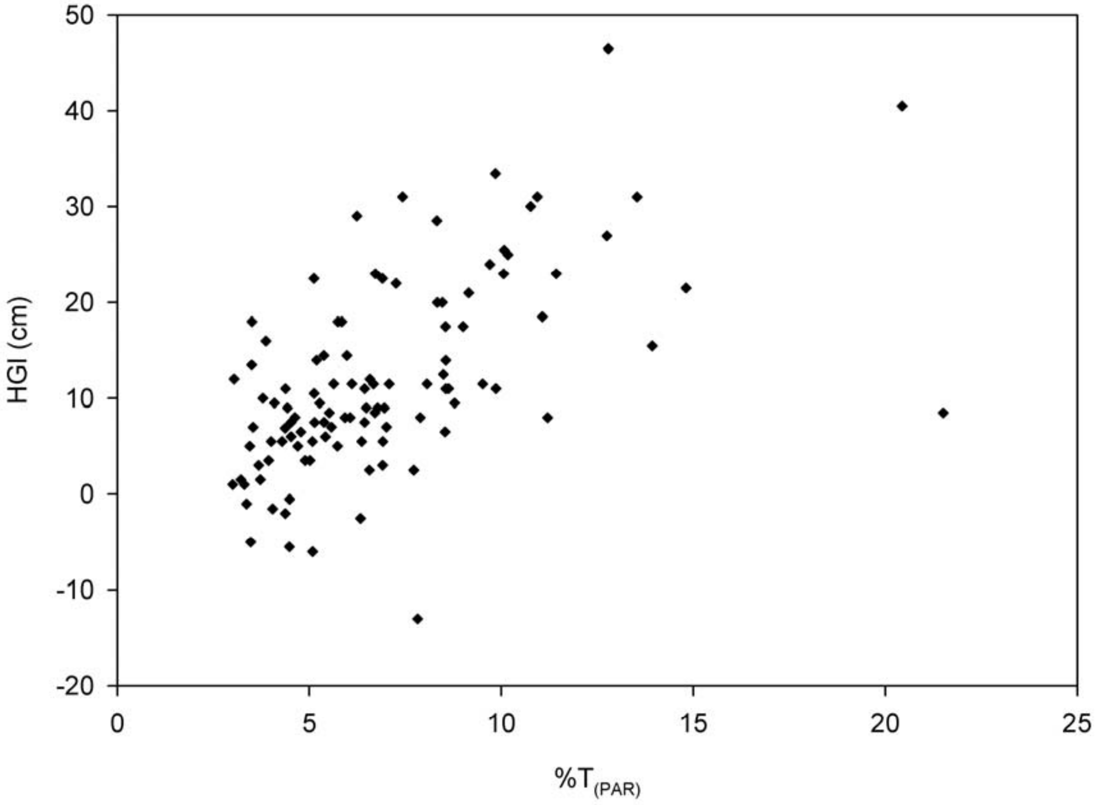


Figure 7

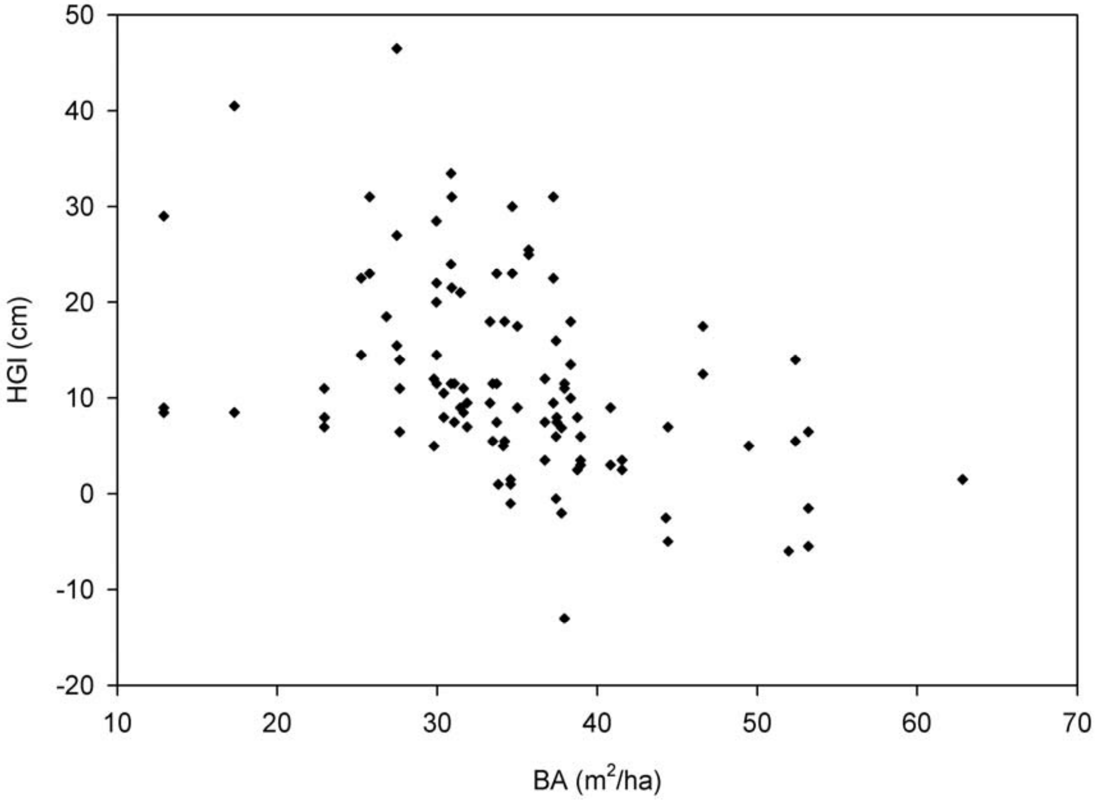


Figure 8

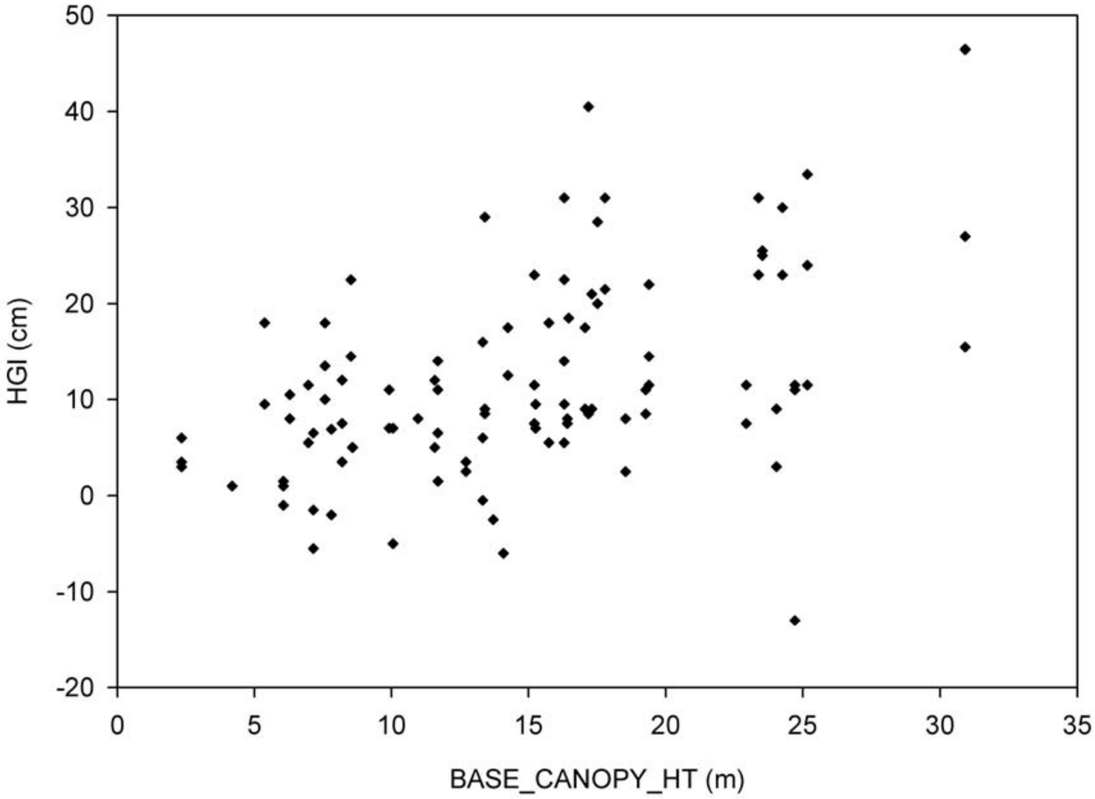


Figure 9

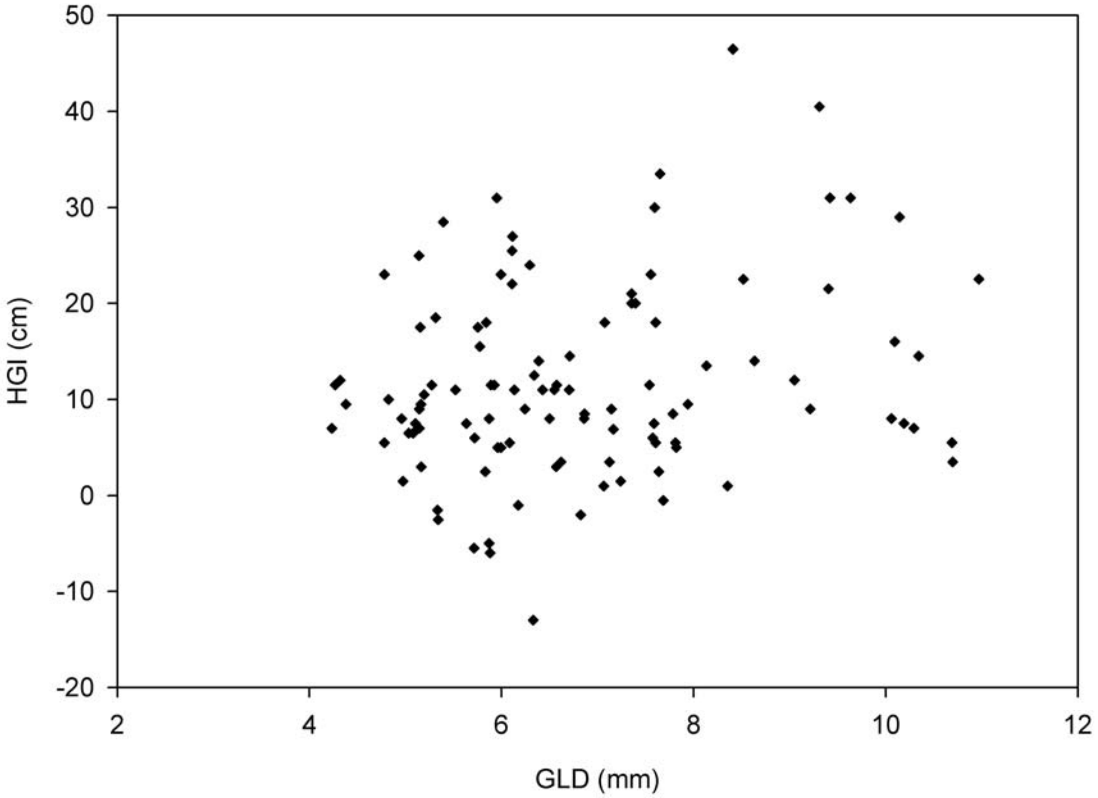


Figure 10

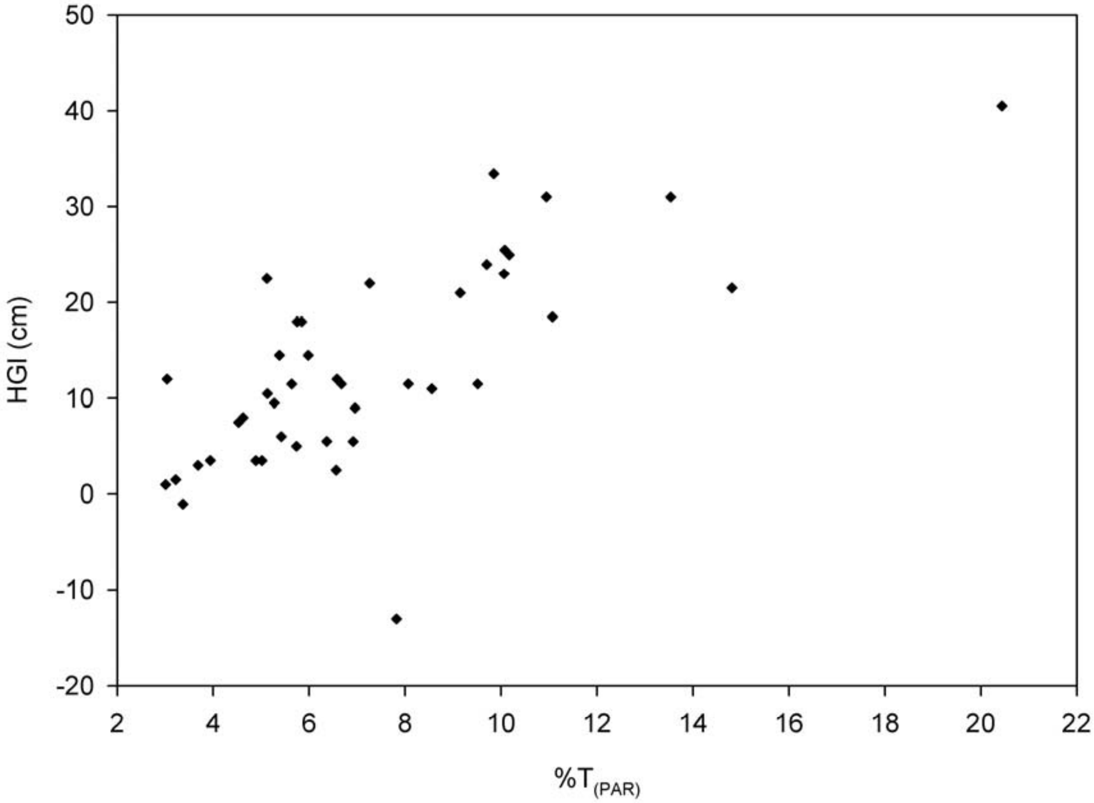


Figure 11

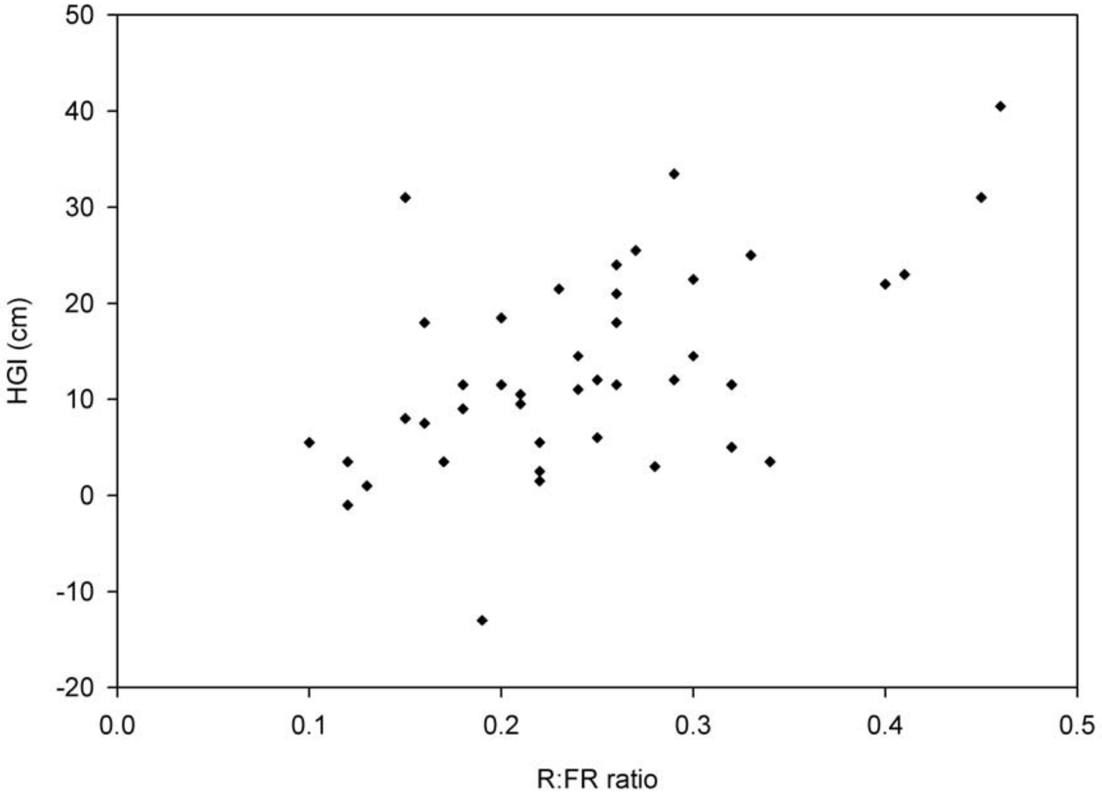
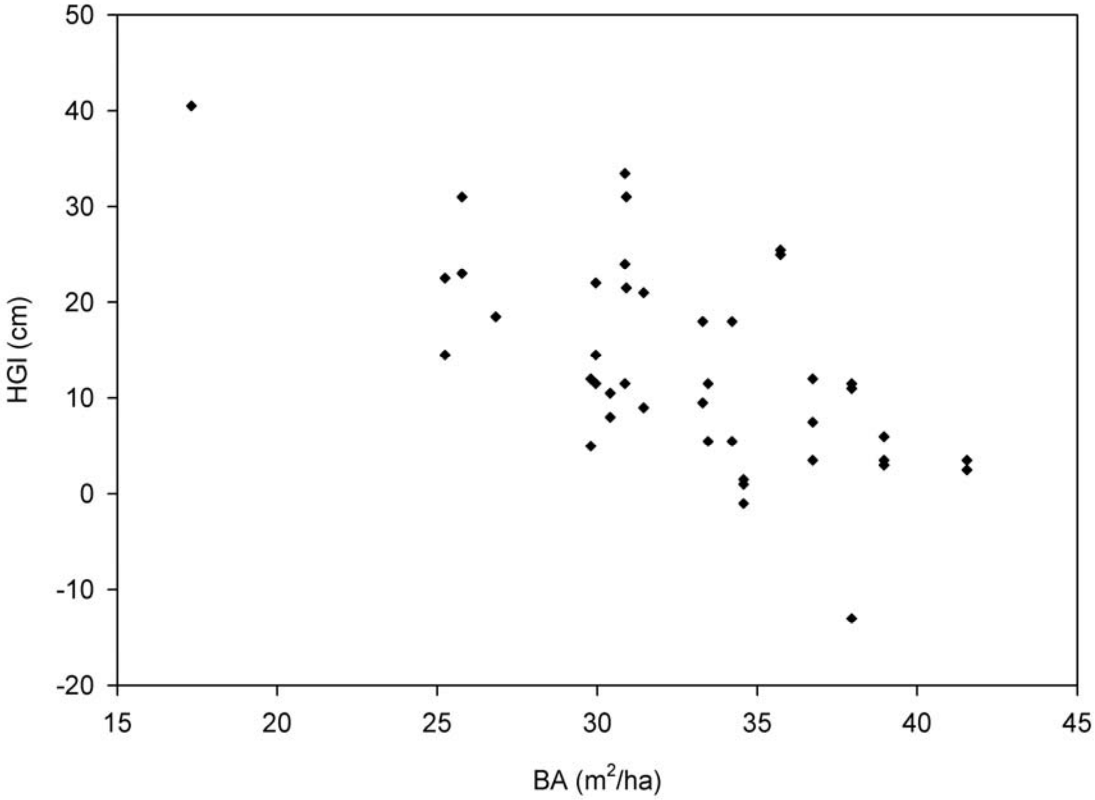


Figure 12



CHAPTER 5 – SUMMARY CONCLUSION

Changes in forest ownership indicate that managers may need to rely on complex silvicultural systems that employ intermittent stand entries or a series of regulated partial cutting activities to meet the needs of forestland owners along the wildland-urban interface. The retention of continuous canopy cover is a common objective for many of these new landowners (Hull and others 2004, Edwards and Bliss 2003). Where the perpetuation of oak is also a goal, research suggests that the most practical way to develop competitive oak reproduction on mesic sites is through the use of planned partial cutting activities, typically in the form of midstory competition control (Loftis 1990, Janzen and Hodges 1987, Lockhart and others 1992). This finding serves as the basis from which alternative two-aged, and shelterwood prescriptions can be developed; the initial cut in the shelterwood system or two-age system on mesic sites requires the successful development of desirable reproduction in partial shade. Additionally, while the use of single-tree selection has rarely been considered to be an appropriate management tool to promote oak on high quality sites, the ability to regenerate oak under a continuous canopy suggests that this uneven-aged system also warrants further consideration. Before single-tree selection can be implemented, a stand usually must go through a conversion process to develop at least three age classes under shaded conditions. Yet, even with the apparent success of using partial cutting to target a specific canopy tier, it is not known how the residual structure following the activity influences the light environment on riparian sites in the southern United States. Furthermore, it is unknown how oak reproduction in this region will respond to these changes in microsite conditions and site characteristics. Therefore, the objective of this thesis research was to further the discussion of the biological feasibility of maintaining and/or promoting oak in riparian forests with partial cutting activities by examining the relationship between forest structure, light characteristics, and seedling growth.

To accomplish this goal, I first described the influence that forest structure has on the light environment following the implementation of a gradient of partial cutting regimes. By identifying the attributes of forest structure that are strongly related to light characteristics, the models developed in this project allow us to forecast the light environment of a similar stand based on the residual characteristics following partial cutting activities. Conversely, by exploring the relationships between the light environment and stand structure characteristics, partial cutting activities may be able to be tailored to create conditions most favorable to seedling growth. The exploration of the relationship between the light environment and residual structure with the growth of Nuttall oak seedlings was the purpose of the second study. Combining the information in these two studies allows us to assess the potential for maintaining oak reproduction based on the residual features of a riparian forest following low intensity partial cutting regimes. The overall low intensity nature of the cutting treatments used in this study reflects those that might be used during the initial conversion process to single-tree selection, or in the establishment cut of a shelterwood or two-aged system.

The models developed in the first study of this thesis characterized the light environment based on the structural features present following the implementation of the cutting regimes. While the importance of the relationship between light quantity and a midstory canopy tier was evident, the key point to emerge from this process was the realization of why the sub-canopy was influential for PAR transmittance. In short, the decrease in PAR is strongly affected by a decrease in canopy openness, which is brought about by the extension of canopy length and density of stems by the presence of a midstory. Thus, by removing the midstory stems, the amount of PAR available to seedlings will increase because stem density and stand basal area has been reduced and canopy length shortened.

The second aspect of this transmittance study was to extend the characterization of the light environment below the main canopy to include the spectral quality of the light available to seedlings. Like PAR transmittance, both measures of light quality are affected by the presence of a midstory canopy tier. From the models developed, it becomes clear that the relative amount of blue light is influenced by forest structure in a similar way to PAR transmittance since both characteristics are affected by low energy diffuse light. By decreasing the canopy length and increasing canopy openness by reducing stem density a greater portion of blue light is present below the main canopy. Although the R:FR ratio is influenced by direct radiation rather than diffuse light, it is apparent that a complete midstory removal would have some implications for this measure of light quality. Decreasing the density of the canopy and canopy length increases the probability of direct sunlight to pass through the canopy unaltered.

The second study included in this thesis examined the growth of Nuttall oak seedlings in the partial cuts used to model light transmittance. By examining growth trends in a gradient of low light conditions, we identified those factors that influenced seedling growth following partial cutting activities. Although measurements should be extended for several more growing seasons to ensure accurate growth trends and to monitor survival, it is apparent that a more complete description of the light environment, including both PAR and light quality, accounts for a considerable amount of the variation in the growth trends observed at these low light levels. As for structural features, it was interesting that the presence of a midstory canopy tier explained roughly the same amount of variation in seedling diameter and height growth. However, the models used to describe seedling growth illustrate another interesting point. Diameter growth appears to be more strongly related to canopy structure while stand density, particularly basal area, was more strongly related to height growth. Because it is difficult to determine the exact nature of the relationship between specific measures of forest structure and seedling growth, another explanation of the difference noted above is possible. The fact that seedling height growth had a stronger relationship with basal area may indicate that diameter growth is more sensitive to minor changes in structure since considerable changes in basal area will likely be accompanied by significant changes in density and canopy structure.

The observations made in this thesis project expand our current understanding of how forest structure influences the light environment following low intensity partial cutting activities. Likewise, the models developed to explain the influence of light characteristics and forest structure on seedling growth raise some interesting points regarding the relative importance of structural features for seedling diameter versus height growth. However, the contribution that this research offers to management is to affirm the current practice of complete midstory removal when designing partial cutting treatments on productive sites. The main benefit of these treatments is to increase the average daily growing season PAR levels below the canopy. However, increases in the proportion of blue light and the R:FR ratio are also likely.

Although complete midstory competition control will increase the PAR levels below the main canopy and may alter forest structure to the benefit of oak seedlings present below the canopy, we are unable to answer the question of whether these treatments alone are enough to maintain oak reproduction on riparian sites. Further alterations to the main canopy in addition to complete midstory removal would increase PAR levels and the potential for desirable seedling growth. However, increasing PAR beyond a certain level will lead to the establishment and growth of shade intolerant species that will out-compete desirable oak reproduction. Therefore, further alterations to stand structure beyond midstory removal may not be advisable. What is not known is whether the light environment created by these treatments allows the desirable reproduction to remain in a competitive position relative to shade tolerant species common on riparian sites. The success seen in Loftis (1990) is an indication that the improvement in conditions are enough for oak to remain competitive below a canopy, yet work specific to the species in this forest type needs to be conducted.

Literature Cited

Baker, J.B., Cain, M.D., Guldin, J.M., Murphy, P.A., and Shelton, M.G. 1996. Uneven aged silviculture for the loblolly and shortleaf pine forest cover types. USDA Forest Service Gen. Tech. Rep. SO-118.

Brown, M.J., and Parker, G.G. 1994. Canopy light transmittance in a chronosequence of mixed species deciduous forests. Canadian Journal of Forest Research 24: 1694-1703.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 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.

Crow, T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia 91: 192-200.

Della-Bianca, L., and Beck, D.E. 1985. Selection management in Southern Appalachian hardwoods. Southern Journal of Applied Forestry 9(3): 191-196.

Edwards, K.K., and Bliss, J.C. 2003. It's a neighborhood now: Practicing forestry at the urban fringe. Journal of Forestry 101(3): 6-11.

Endler, J.A. 1993. The color of light in forests and its implications. Ecological Monographs. 63: 1-27.

Farrar, R.M. 1996. Fundamentals of uneven-aged management in southern pine. Moser, W.K., and Brennan, L.A., editors. Tall Timbers Research Station Miscellaneous Publication No. 9. Tallahassee, FL. 68 p.

Gardiner, E.S., and Hodges, J.D. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. Forest Ecology and Management 108: 127-134.

Gardiner, E.S., Schweitzer, C.J., and Stanturf, J.A. 2001. Photosynthesis of Nuttall Oak (*Quercus nuttallii* Palm.) seedlings interplanted beneath an eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.) nurse crop. Forest Ecology and Management 149: 283-294.

Gardiner, E.S. 2002. Photosynthetic light response of bottomland oak seedlings raised under partial sunlight. Pgs. 86-91. In: Outcalt, K.W. (editor) Proceedings of the eleventh biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SRS-48.

Gottschalk, K. 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry, and red maple seedlings. I. Height, diameter, and root/shoot ratio. Pgs. 189-195. In: Dawson, J.O., and Majerus, K.A. (editors) Proceedings of the fifth central hardwood forest conference. SAF Pub. 85-05.

Hoad, S.P., and Leakey, R.R.B. 1994. Effects of light quality on gas exchange and dry matter partitioning in *Eucalyptus grandis* W. Hill ex Maiden. Forest Ecology and Management 70: 265-273.

Holmes, M.G. 1981. Shadelight quality effects on plant growth. In: H. Smith (editor), Plants and the Daylight Spectrum. Academic Press, London, pp. 147-158.

Holmes, M.G., and Smith, H. 1977a. The function of phytochrome in the natural environment II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. Photochemistry and Photobiology 25: 539-545.

Holmes, M.G., and Smith, H. 1977b. The function of phytochrome in the natural environment IV. Light quality and plant development. Photochemistry and Photobiology 25: 551-557.

Hull, R.B., Robertson, D.P., and Buhyoff, G.J. 2004. “Boutique” forestry: New forest practices in urbanizing landscapes. Journal of Forestry 102(1): 14-19.

Janzen, G.C., and Hodges, J.D. 1987. Development of advanced oak regeneration as influenced by removal of midstory and understory vegetation. Pgs. 455-461. In: Douglas, P.R. (editor) Proceedings of the forth biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SE-042.

Jenkins, M.W., and Chambers, J.L. 1989. Understory light levels in mature hardwood stands after partial overstory removal. Forest Ecology and Management 26: 247-256.

Johnson, R.L., and Krinard, R.M. 1989. Survival and growth of Nuttall oak seedlings following selection cutting – 28-year remeasurement. Southern Journal of Applied Forestry 13(1): 43-46.

Kwesiga, F., and Grace, J. 1986. The role of the red/far-red ratio in the response of tropical tree seedlings to shade. Annals of Botany 57: 283-290.

Larcher, W. 1980. Physiological plant ecology. Springer-Verlag, New York, pp. 5-18.

Larsen, D.R., Loewenstein, E.F., and Johnson, P.S. 1999. Sustaining recruitment of oak reproduction in uneven-aged stands in the Ozark Highlands. USDA Forest Service Gen. Tech. Rep. NC-203.

Lee, D.W. 1987. The spectral distribution of radiation in two neotropical rainforests. Biotropica 19(2): 161-166.

Lee, D.W., Baskaran, K., Mansor, M., Mohamad, H., and Kheong, S. 1996. Irradiance and spectral quality affect Asian tropical rain forest tree seedling development. Ecology 77(2): 568-580.

Lei, T.T., and Lechowicz, M.J. 1998. Diverse responses of maple saplings to forest light regimes. Annals of Botany 82: 9-19.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research 29: 796-811.

Lockhart, B.R., Hodges, J.D., and Guldin, J.M. 1992. Development of advanced cherrybark oak reproduction following midstory and understory competition control and seedling clipping: 4-year results. Pgs. 109-115. In: Brissette, J.C. (editor) Proceedings of the seventh biennial southern silvicultural research conference. USDA Forest Service Gen. Tech. Rep. SO-93.

Loewenstein, E.F., Johnson, P.S., and Garrett, H.E. 2000. Age and diameter structure of a managed uneven-aged oak forest. Canadian Journal of Forest Research 30: 1060-1070.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the Southern Appalachians. Forest Science 36(4): 917-929.

Meadows, J.S., and Stanturf, J.A. 1997. Silvicultural systems for southern bottomland hardwood forests. Forest Ecology and Management 90: 127-140.

Messier, C., and Bellefleur, P. 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch-beech-sugar maple stand. Canadian Journal of Forest Research 18: 615-622.

Morgan, D.C. 1981. Shadelight quality effects on plant growth. In: H. Smith (editor), Plants and the Daylight Spectrum. Academic Press, London, pp. 205-221.

Muth, C.C., and Bazzaz, F.A. 2002. Tree seedling canopy responses to conflicting photosensory cues. Oecologia 132: 197-204.

Schlesinger, R.C. 1976. Sixteen years of selection silviculture in upland hardwood stands. USDA Forest Service Res. Pap. NC-125.

Schmitt, J., and Wulff, R.D. 1993. Light spectral quality, phytochrome and plant competition. TREE 8(2): 47-51.

Smith, H. 1982. Light quality, photoperception, and plant strategy. Annual Review of Plant Physiology 33: 481-518.

Smith, D.M., Larson, B.C., Kelty, M.J. and Ashton, P.M.S. 1997. The Practice of Silviculture: Applied Forest Ecology. 9th edition. John Wiley & Sons, New York, 537 p.

Trimble, G.R., Jr., and Smith, H.C. 1976. Stand structure and stocking control in Appalachian mixed hardwoods. USDA Forest Service Res. Pap. NE-340.

Turnbull, M.H. 1991. The effect of light quantity and quality during development on the photosynthetic characteristics of six Australian rainforest tree species. Oecologia 87: 110-117.

Vezina, P.E., and Pech, G.Y. 1964. Solar radiation beneath conifer canopies in relation to crown closure. Forest Science 10(4): 443-451.

Wear, D. N., and Greis, J.G. 2002. Southern forest resource assessment: Summary of findings. Journal of Forestry 100(7): 6-14.

Wulff, R.D. 1989. The effects of reduced irradiance and low red to far-red ratios on the growth and photosynthetic capacity in *Impatiens capensis*. Supplement to American Journal of Botany 76 (6): 131-132.

Yirdaw, E., and Luukkanen, O. 2004. Photosynthetically active radiation transmittance of forest plantation canopies in the Ethiopian highlands. Forest Ecology and Management 188: 17-24.

Ziegenhagen, B., and Kausch, W. 1995. Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. Forest Ecology and Management 72: 97-108.

APPENDIX

Variable names and descriptions used in the construction of the models

Variable_ID	Description
AVE_TREE_HT	Average height (m) of all trees > 5cm DBH on each plot
BA	Basal area per hectare by plot (m^3)
BASE_CANOPY_HT	Average basal canopy height (m) above plot (includes trees < 5cm DBH)
CANOPY_HT	Average height (m) of the tallest 5 trees per plot (100 trees per hectare)
BLUE	Average amount of PAR composed of blue light level
CANOPY_LENGTH	Crown length per plot (m), calculated by CANOPY_HT - MIN_CANOPY_HT
CROWN_RATIO	Average crown ratio of all trees > 5cm DBH on each plot
DGI	Seedling ground-line diameter growth increment (mm)
GLD	Initial ground-line diameter (mm)
HGI	Seedling height growth increment (cm)
HT_I	Initial seedling hieght (cm)
MIDSTORY_TPH	The number of midstory trees per hectare (trees with HBLC $\leq$ 5 m) by plot
MIN_CANOPY_HT	Average height (m) of the base of live crown for the trees with the 5 lowest crowns per plot (100 trees per hectare)
RFR	Average R:FR ratio
$\%T_{(PAR)}$	Average growing season PAR transmittance (% of full sun)
TPH	The number of trees per hectare by plot
TPH*CANOPY_LENGTH	interaction term
TPH/CANOPY_LENGTH	interaction term
* note that when the variable ID is preceded by 'ln' a log transformation has been preformed on the variable	

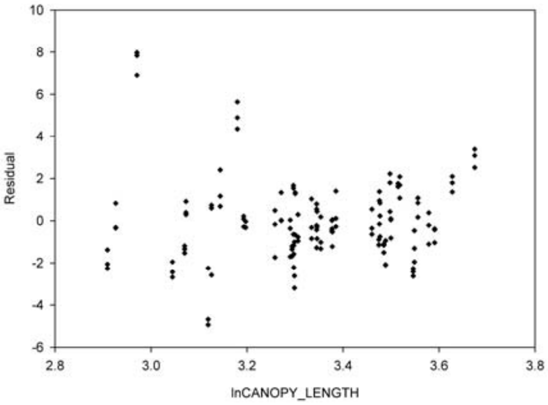
List of full models described in the thesis with residual graphs included

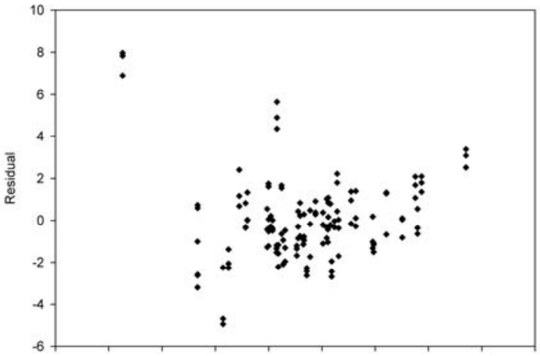
PAR transmittance model

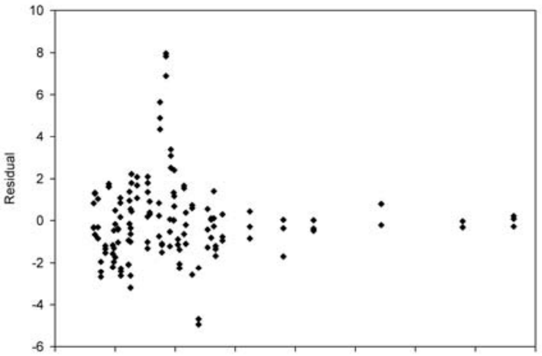
[1]

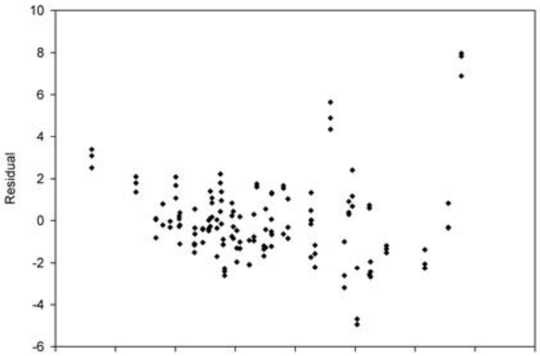
%T$_{(PAR)}$ = 56.236 – 9.902 (lnCANOPY_LENGTH) – 4.106 (lnBA) – 0.0851 (TPH/CANOPY_LENGTH)

R^2 = .6635; P-value = < .0001







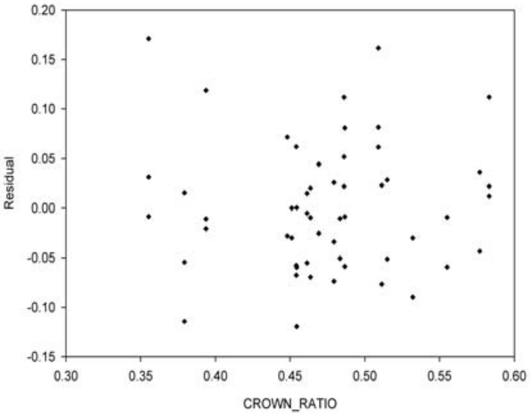


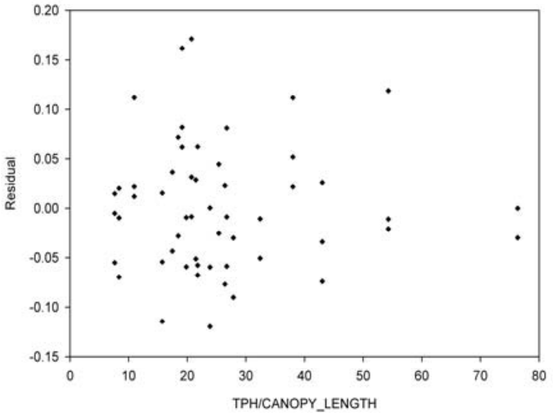
R:FR ratio model

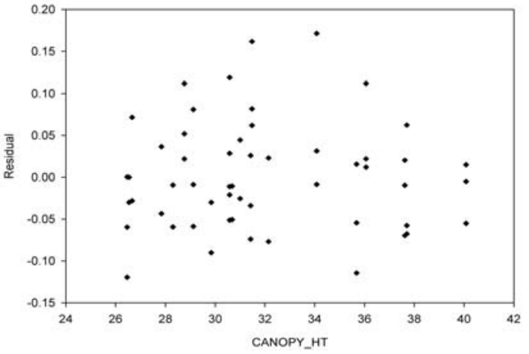
[2]

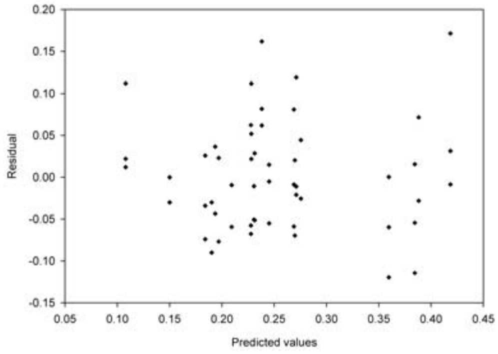
Ave. RFR = 1.438 – 1.428 (CROWN_RATIO) – 0.0041 (TPH/CANOPY_LENGTH) – 0.0125 (Canopy_HT)

R^2 = .6006; P-value = < .0001







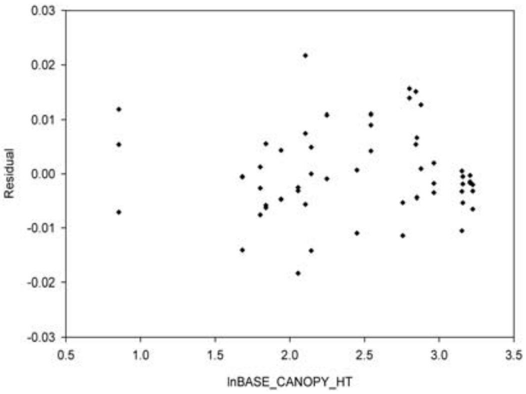


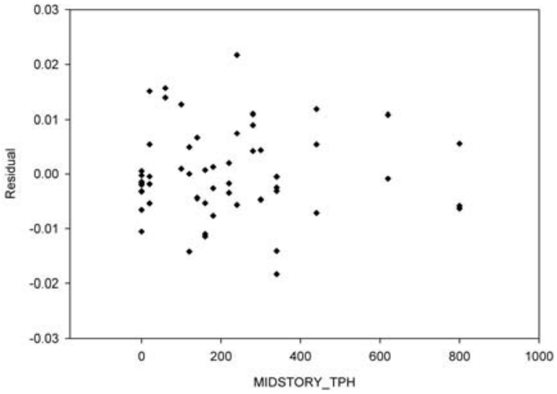
Blue light model

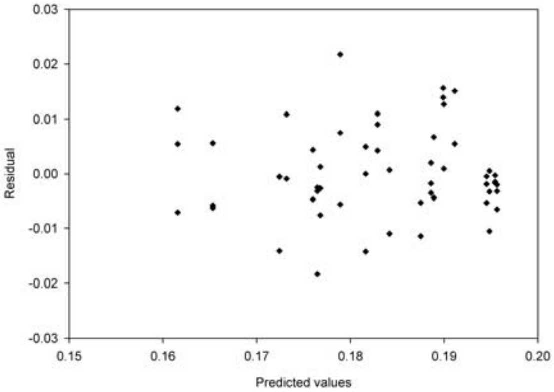
[3]

Ave. Blue = 0.1608 + 0.0108 (lnBASE_CANOPY_HT) - 0.00002 (MIDSTORY_TPH)

R^2 = .6104; P-value = < .0001



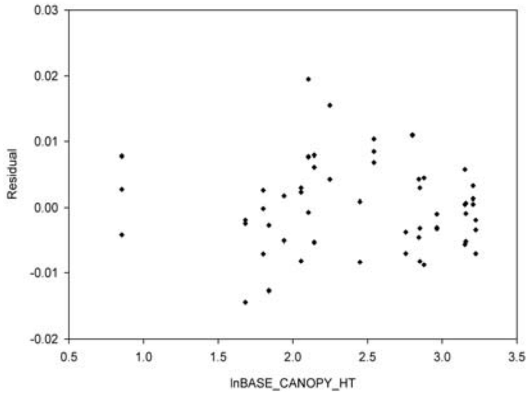


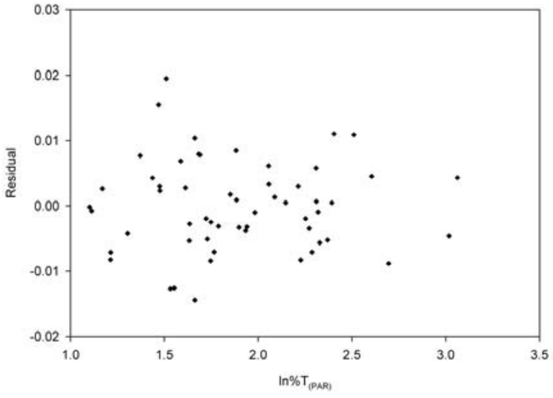


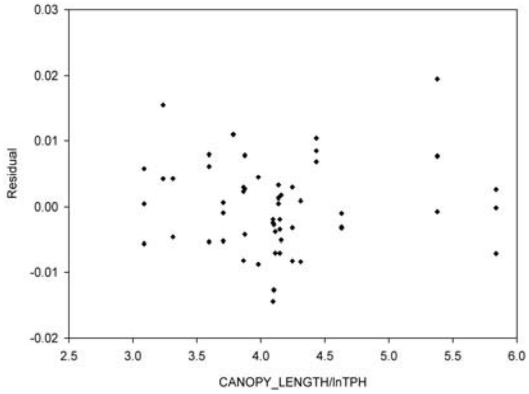
[4]

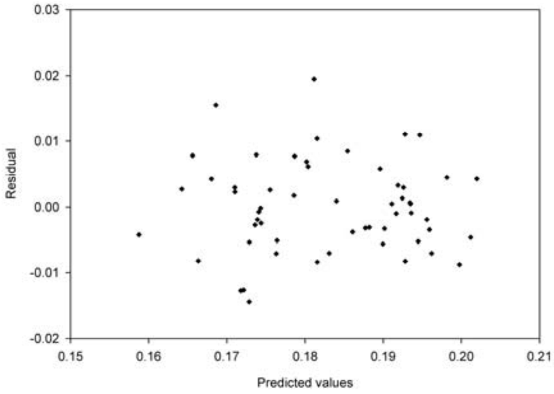
Ave. Blue = 0.1056 + 0.0077 (lnBASE_CANOPY_HT) + 0.0178 (ln%$T_{(PAR)}$) + 0.0060 (CANOPY_LENGTH/lnTPH)

R^2 = .7100; P-value = < .0001







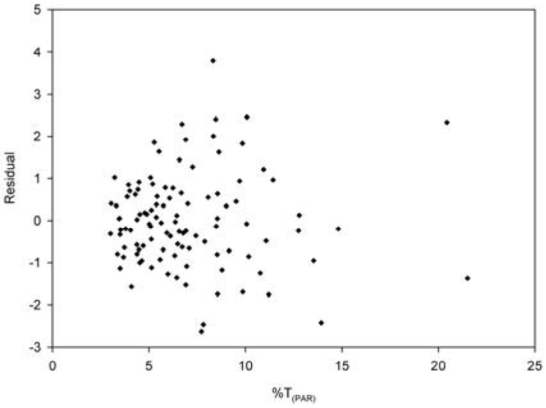


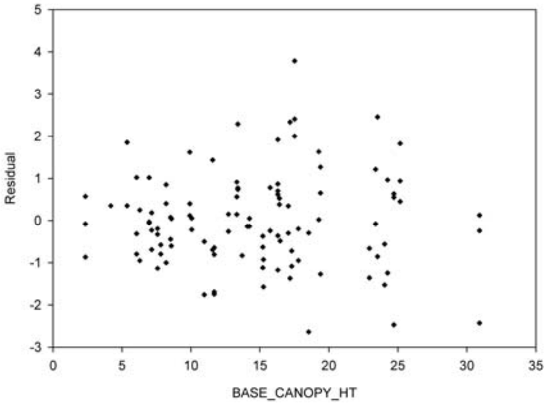
Diameter growth model

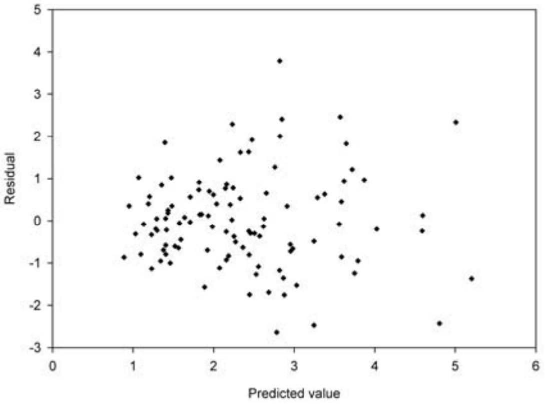
[1]

DGI = 0.0475 + 0.1824 (%$T_{(PAR)}$) + 0.0717 (BASE_CANOPY_HT)

R^2 = .4213; P-value = <.0001



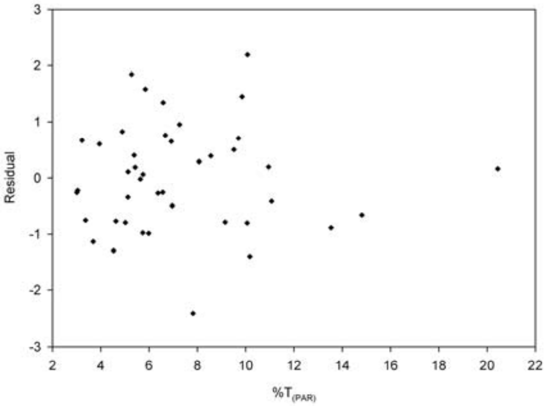


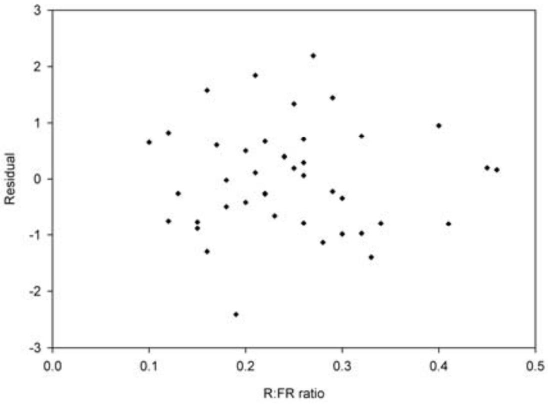


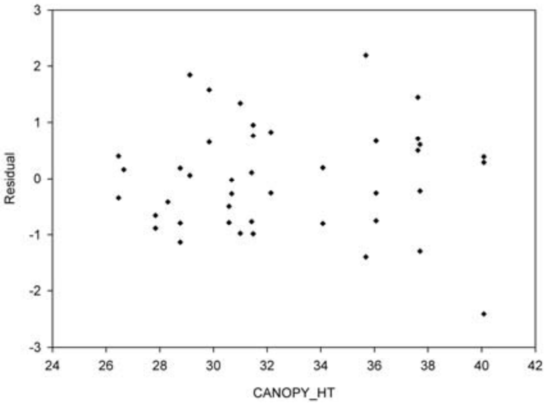
[2]

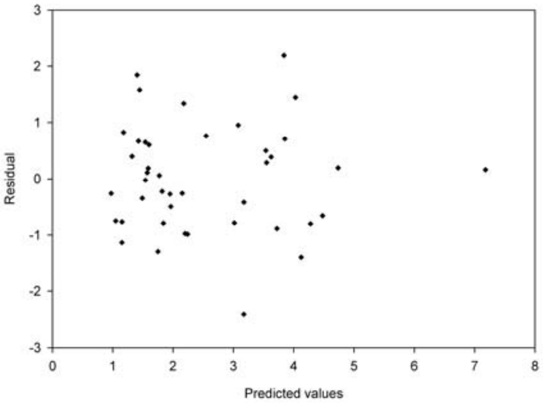
DGI = -3.9265 + 0.3259 (%$T_{(PAR)}$) + 4.2518 (RFR) + 0.0934 (CANOPY_HT)

R^2 = .6601; P-value = <.0001







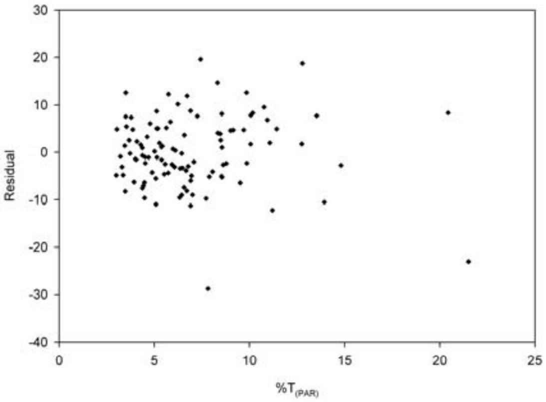


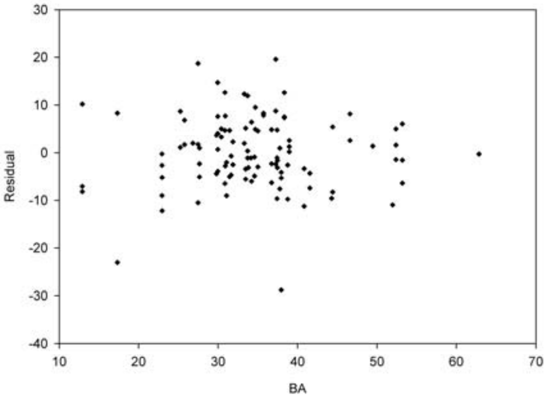
Height growth model

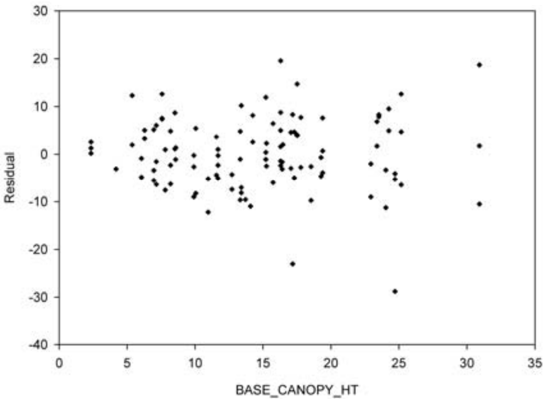
[1]

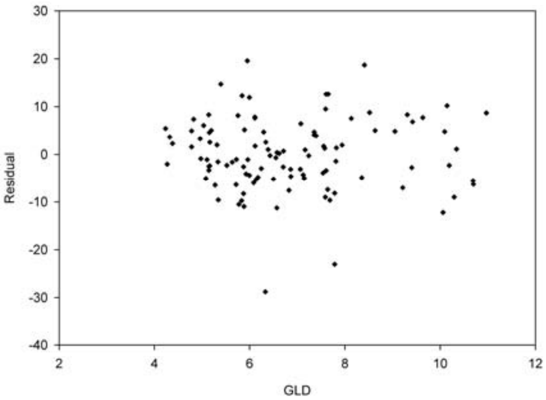
HGI = $-1.3586 + 0.9535\,(\%T_{(PAR)}) - 0.2147\,(BA) + 0.4431\,(BASE\_CANOPY\_HT) + 1.0881\,(GLD)$

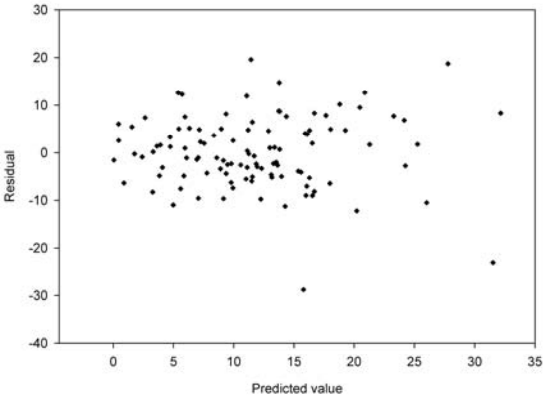
$R^2 = .4390$; P-value <.0001







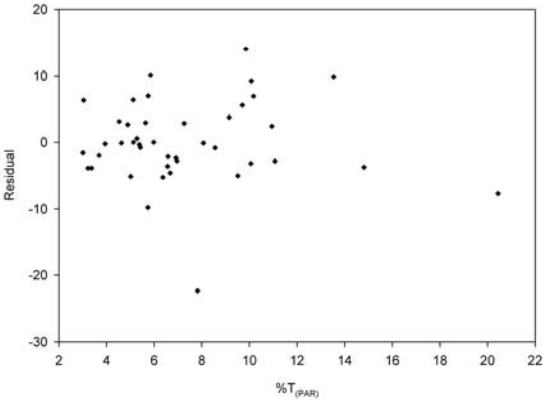


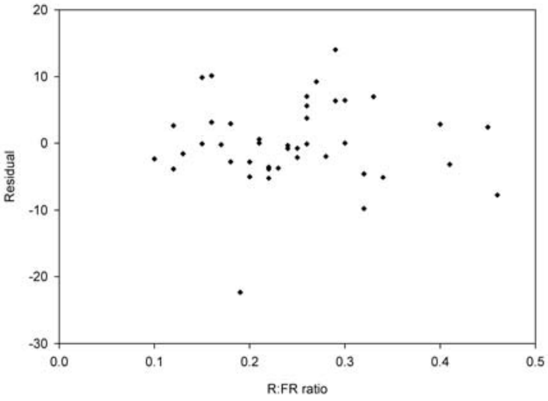


[2]

HGI = $15.7657 + 1.4964\ (\%T_{(PAR)}) + 27.2335\ (RFR) - 0.6140\ (BA)$

$R^2 = .6590$; P-value <.0001





Correlation matrix for variables used in the development of light transmittance models – page 1 of 6

	$\%T_{(PAR)}$	$\ln\%T_{(PAR)}$	RFR	BLUE	BA	TPH	lnBA	lnTPH
$\%T_{(PAR)}$	1	NA	0.45083	NA	NA	NA	-0.6295	-0.48052
		NA	0.0403	NA	NA	NA	<.0001	0.0007
	46	NA	21	NA	NA	NA	46	46
$\ln\%T_{(PAR)}$	NA	1	NA	0.77482	-0.56644	-0.51727	-0.61549	-0.55864
	NA		NA	<.0001	<.0001	0.0002	<.0001	<.0001
	NA	46	NA	21	46	46	46	46
RFR	0.45083	NA	1	0.18333	-0.44129	-0.32564	NA	NA
NA	0.0403	NA		0.4263	0.0452	0.1497	NA	NA
	21	NA	21	21	21	21	NA	NA
BLUE	NA	0.77482	0.18333	1	-0.35488	NA	NA	-0.65345
	NA	<.0001	0.4263		0.1144	NA	NA	0.0013
	NA	21	21	21	21	NA	NA	21
BA	NA	-0.56644	-0.44129	-0.35488	1	0.08538	0.98275	0.12532
	NA	<.0001	0.0452	0.1144		0.5726	<.0001	0.4066
	NA	46	21	21	46	46	46	46
TPH	NA	-0.51727	-0.32564	NA	0.08538	1	0.10549	0.92436
	NA	0.0002	0.1497	NA	0.5726		0.4853	<.0001
	NA	46	21	NA	46	46	46	46
lnBA	-0.6295	-0.61549	NA	NA	0.98275	0.10549	1	0.13277
	<.0001	<.0001	NA	NA	<.0001	0.4853		0.3791
	46	46	NA	NA	46	46	46	46
lnTPH	-0.48052	-0.55864	NA	-0.65345	0.12532	0.92436	0.13277	1
	0.0007	<.0001	NA	0.0013	0.4066	<.0001	0.3791	
	46	46	NA	21	46	46	46	46
BASE_CANOPY_HT	0.53837	0.62114	0.33944	NA	-0.18442	-0.62114	-0.17736	-0.72969
	0.0001	<.0001	0.1322	NA	0.2198	<.0001	0.2383	<.0001
	46	46	21	NA	46	46	46	46
lnBASE_CANOPY_HT	NA	0.58626	NA	0.81407	-0.15275	-0.61363	-0.15735	-0.68498
	NA	<.0001	NA	<.0001	0.3108	<.0001	0.2963	<.0001
	NA	46	NA	21	46	46	46	46

Correlation matrix for variables used in the development of light transmittance models – page 2 of 6

	$\%T_{(PAR)}$	$\ln\%T_{(PAR)}$	**RFR**	**BLUE**	**BA**	**TPH**	**lnBA**	**lnTPH**
CANOPY_LENGTH	NA	-0.69069	-0.51466	-0.48855	0.61556	0.05269	0.62372	0.22163
	NA	<.0001	0.017	0.0246	<.0001	0.728	<.0001	0.1388
	NA	46	21	21	46	46	46	46
lnCANOPY_LENGTH	-0.69699	-0.70642	NA	NA	0.60257	0.08195	0.62032	0.25254
	<.0001	<.0001	NA	NA	<.0001	0.5882	<.0001	0.0904
	46	46	NA	NA	46	46	46	46
CANOPY_HT	-0.26549	-0.22522	0.00817	0.15049	0.57678	-0.46443	0.59182	-0.48677
	0.0746	0.1323	0.9719	0.515	<.0001	0.0011	<.0001	0.0006
	46	46	21	21	46	46	46	46
CROWN_RATIO	-0.21492	-0.21821	-0.66118	0.06115	0.37703	-0.35949	0.37286	-0.25046
	0.1515	0.1452	0.0011	0.7923	0.0098	0.0141	0.0107	0.0932
	46	46	21	21	46	46	46	46
MIDSTORY_TPH	-0.52449	-0.58964	-0.42412	-0.73814	0.13374	0.8044	0.15653	0.80185
	0.0002	<.0001	0.0554	0.0001	0.3755	<.0001	0.2989	<.0001
	46	46	21	21	46	46	46	46
var8[1]	-0.28561	-0.3593	-0.23949	-0.54741	-0.06543	0.97115	-0.04713	0.85798
	0.0543	0.0142	0.2957	0.0102	0.6657	<.0001	0.7558	<.0001
	46	46	21	21	46	46	46	46
var10[2]	-0.74701	-0.79922	-0.49488	-0.62669	0.57732	0.41934	0.58425	0.58726
	<.0001	<.0001	0.0226	0.0024	<.0001	0.0037	<.0001	<.0001
	46	46	21	21	46	46	46	46
var12[3]	-0.45105	-0.43023	-0.43373	-0.16977	0.54175	-0.37001	0.55186	-0.25439
	0.0017	0.0028	0.0495	0.4619	0.0001	0.0114	<.0001	0.088
	46	46	21	21	46	46	46	46

[1] Var 8 = TPH/CANOPY_LENGTH

[2] Var 10 = lnTPH*CANOPY_LENGTH

[3] Var 12 = CANOPY_LENGTH/lnTPH

Correlation matrix for variables used in the development of light transmittance models – page 3 of 6

	BASE_CANOPY_HT	lnBASE_CANOPY_HT	CANOPY_LENGTH	lnCANOPY_LENGTH
$\%T_{(PAR)}$	0.53837	NA	NA	-0.69699
	0.0001	NA	NA	<.0001
	46	NA	NA	46
ln$\%T_{(PAR)}$	0.62114	0.58626	-0.69069	-0.70642
	<.0001	<.0001	<.0001	<.0001
	46	46	46	46
RFR	0.33944	NA	-0.51466	NA
	0.1322	NA	0.017	NA
	21	NA	21	NA
BLUE	NA	0.81407	-0.48855	NA
	NA	<.0001	0.0246	NA
	NA	21	21	NA
BA	-0.18442	-0.15275	0.61556	0.60257
	0.2198	0.3108	<.0001	<.0001
	46	46	46	46
TPH	-0.62114	-0.61363	0.05269	0.08195
	<.0001	<.0001	0.728	0.5882
	46	46	46	46
lnBA	-0.17736	-0.15735	0.62372	0.62032
	0.2383	0.2963	<.0001	<.0001
	46	46	46	46
lnTPH	-0.72969	-0.68498	0.22163	0.25254
	<.0001	<.0001	0.1388	0.0904
	46	46	46	46
BASE_CANOPY_HT	1	0.94904	-0.3728	-0.40583
		<.0001	0.0107	0.0051
	46	46	46	46
lnBASE_CANOPY_HT	0.94904	1	-0.2662	-0.29414
	<.0001		0.0737	0.0472
	46	46	46	46

Correlation matrix for variables used in the development of light transmittance models – page 4 of 6

	BASE_CANOPY_HT	lnBASE_CANOPY_HT	CANOPY_LENGTH	lnCANOPY_LENGTH
CANOPY_LENGTH	-0.3728	-0.2662	1	0.99438
	0.0107	0.0737		<.0001
	46	46	46	46
lnCANOPY_LENGTH	-0.40583	-0.29414	0.99438	1
	0.0051	0.0472	<.0001	
	46	46	46	46
CANOPY_HT	0.35423	0.34102	0.51578	0.46367
	0.0157	0.0204	0.0002	0.0012
	46	46	46	46
CROWN_RATIO	-0.046	0.02838	0.5216	0.54114
	0.7615	0.8515	0.0002	0.0001
	46	46	46	46
MIDSTORY_TPH	-0.68169	-0.70385	0.30013	0.32567
	<.0001	<.0001	0.0427	0.0272
	46	46	46	46
var8[1]	-0.52843	-0.53611	-0.1623	-0.13238
	0.0002	0.0001	0.2812	0.3805
	46	46	46	46
var10[2]	-0.59694	-0.497	0.91676	0.92131
	<.0001	0.0004	<.0001	<.0001
	46	46	46	46
var12[3]	-0.03015	0.057	0.88341	0.86692
	0.8423	0.7067	<.0001	<.0001
	46	46	46	46

[1] Var 8 = TPH/CANOPY_LENGTH
[2] Var 10 = lnTPH*CANOPY_LENGTH
[3] Var 12 = CANOPY_LENGTH/lnTPH

Correlation matrix for variables used in the development of light transmittance models – page 5 of 6

	CANOPY_HT	**CROWN_RATIO**	**MIDSTORY_TPH**	**var8**[1]	**var10**[2]	**var12**[3]
$\%T_{(PAR)}$	-0.26549	-0.21492	-0.52449	-0.28561	-0.74701	-0.45105
	0.0746	0.1515	0.0002	0.0543	<.0001	0.0017
	46	46	46	46	46	46
$\ln\%T_{(PAR)}$	-0.22522	-0.21821	-0.58964	-0.3593	-0.79922	-0.43023
	0.1323	0.1452	<.0001	0.0142	<.0001	0.0028
	46	46	46	46	46	46
RFR	0.00817	-0.66118	-0.42412	-0.23949	-0.49488	-0.43373
	0.9719	0.0011	0.0554	0.2957	0.0226	0.0495
	21	21	21	21	21	21
BLUE	0.15049	0.06115	-0.73814	-0.54741	-0.62669	-0.16977
	0.515	0.7923	0.0001	0.0102	0.0024	0.4619
	21	21	21	21	21	21
BA	0.57678	0.37703	0.13374	-0.06543	0.57732	0.54175
	<.0001	0.0098	0.3755	0.6657	<.0001	0.0001
	46	46	46	46	46	46
TPH	-0.46443	-0.35949	0.8044	0.97115	0.41934	-0.37001
	0.0011	0.0141	<.0001	<.0001	0.0037	0.0114
	46	46	46	46	46	46
lnBA	0.59182	0.37286	0.15653	-0.04713	0.58425	0.55186
	<.0001	0.0107	0.2989	0.7558	<.0001	<.0001
	46	46	46	46	46	46
lnTPH	-0.48677	-0.25046	0.80185	0.85798	0.58726	-0.25439
	0.0006	0.0932	<.0001	<.0001	<.0001	0.088
	46	46	46	46	46	46
BASE_CANOPY_HT	0.35423	-0.046	-0.68169	-0.52843	-0.59694	-0.03015
	0.0157	0.7615	<.0001	0.0002	<.0001	0.8423
	46	46	46	46	46	46
lnBASE_CANOPY_HT	0.34102	0.02838	-0.70385	-0.53611	-0.497	0.057
	0.0204	0.8515	<.0001	0.0001	0.0004	0.7067
	46	46	46	46	46	46

[1] Var 8 = TPH/CANOPY_LENGTH
[2] Var 10 = lnTPH*CANOPY_LENGTH
[3] Var 12 = CANOPY_LENGTH/lnTPH

Correlation matrix for variables used in the development of light transmittance models – page 6 of 6

	CANOPY_HT	**CROWN_RATIO**	**MIDSTORY_TPH**	**var8[1]**	**var10[2]**	**var12[3]**
CANOPY_LENGTH	0.51578	0.5216	0.30013	-0.1623	0.91676	0.88341
	0.0002	0.0002	0.0427	0.2812	<.0001	<.0001
	46	46	46	46	46	46
lnCANOPY_LENGTH	0.46367	0.54114	0.32567	-0.13238	0.92131	0.86692
	0.0012	0.0001	0.0272	0.3805	<.0001	<.0001
	46	46	46	46	46	46
CANOPY_HT	1	0.27603	-0.27077	-0.58475	0.25233	0.72948
		0.0633	0.0687	<.0001	0.0907	<.0001
	46	46	46	46	46	46
CROWN_RATIO	0.27603	1	-0.04179	-0.46488	0.32152	0.64022
	0.0633		0.7827	0.0011	0.0293	<.0001
	46	46	46	46	46	46
MIDSTORY_TPH	-0.27077	-0.04179	1	0.7088	0.58096	-0.07798
	0.0687	0.7827		<.0001	<.0001	0.6065
	46	46	46	46	46	46
var8[1]	-0.58475	-0.46488	0.7088	1	0.20891	-0.54579
	<.0001	0.0011	<.0001		0.1635	<.0001
	46	46	46	46	46	46
var10[2]	0.25233	0.32152	0.58096	0.20891	1	0.62402
	0.0907	0.0293	<.0001	0.1635		<.0001
	46	46	46	46	46	46
var12[3]	0.72948	0.64022	-0.07798	-0.54579	0.62402	1
	<.0001	<.0001	0.6065	<.0001	<.0001	
	46	46	46	46	46	46

[1] Var 8 = TPH/CANOPY_LENGTH
[2] Var 10 = lnTPH*CANOPY_LENGTH
[3] Var 12 = CANOPY_LENGTH/lnTPH

Correlation matrix for variables used in the development of seedling growth models – page 1 of 4

	GLD	DGI	HT_I	HGI	$\%T_{(PAR)}$	BA	TPH	lnTPH	CANOPY_LENGTH
GLD	1	0.13573	0.65967	0.22591	0.09301	-0.28632	0.0599	0.10771	-0.13286
	0.1633		<.0001	0.0193	0.3407	0.0028	0.54	0.2695	0.1746
	107	107	107	107	107	107	107	107	106
DGI	0.13573	1	0.04182	0.64457	0.59313	-0.33007	-0.48744	-0.5163	-0.37972
	0.1633		0.6689	<.0001	<.0001	0.0005	<.0001	<.0001	<.0001
	107	107	107	107	107	107	107	107	106
HT_I	0.65967	0.04182	1	0.0687	0.04654	-0.20135	0.11364	0.19328	-0.01805
	<.0001	0.6689		0.482	0.6341	0.0376	0.2438	0.0461	0.8543
	107	107	107	107	107	107	107	107	106
HGI	0.22591	0.64457	0.0687	1	0.57995	-0.42439	-0.27861	-0.3748	-0.52391
	0.0193	<.0001	0.482		<.0001	<.0001	0.0037	<.0001	<.0001
	107	107	107	107	107	107	107	107	106
$\%T_{(PAR)}$	0.09301	0.59313	0.04654	0.57995	1	-0.4548	-0.44763	-0.50799	-0.67298
	0.3407	<.0001	0.6341	<.0001		<.0001	<.0001	<.0001	<.0001
	107	107	107	107	107	107	107	107	106
BA	-0.28632	-0.33007	-0.20135	-0.42439	-0.4548	1	0.14902	0.13203	0.51753
	0.0028	0.0005	0.0376	<.0001	<.0001		0.1255	0.1752	<.0001
	107	107	107	107	107	107	107	107	106
TPH	0.0599	-0.48744	0.11364	-0.27861	-0.44763	0.14902	1	0.92065	0.13669
	0.54	<.0001	0.2438	0.0037	<.0001	0.1255		<.0001	0.1623
	107	107	107	107	107	107	107	107	106
lnTPH	0.10771	-0.5163	0.19328	-0.3748	-0.50799	0.13203	0.92065	1	0.31738
	0.2695	<.0001	0.0461	<.0001	<.0001	0.1752	<.0001		0.0009
	107	107	107	107	107	107	107	107	106
CANOPY_LENGTH	-0.13286	-0.37972	-0.01805	-0.52391	-0.67298	0.51753	0.13669	0.31738	1
	0.1746	<.0001	0.8543	<.0001	<.0001	<.0001	0.1623	0.0009	
	106	106	106	106	106	106	106	106	106
CROWN_RATIO	-0.11321	-0.07147	-0.11175	-0.23727	-0.21486	0.2636	-0.38564	-0.22806	0.5144
	0.2456	0.4644	0.2518	0.0139	0.0263	0.0061	<.0001	0.0181	<.0001
	107	107	107	107	107	107	107	107	106

Correlation matrix for variables used in the development of seedling growth models – page 2 of 4

	GLD	**DGI**	**HT_I**	**HGI**	**$\%T_{(PAR)}$**	**BA**	**TPH**	**lnTPH**	**CANOPY_LENGTH**
BASE_CANOPY_HT	-0.11485	0.55843	-0.09312	0.4807	0.57928	-0.15975	-0.65099	-0.75093	-0.43707
	0.2388	<.0001	0.3401	<.0001	<.0001	0.1003	<.0001	<.0001	<.0001
	107	107	107	107	107	107	107	107	106
CANOPY_HT	-0.27926	0.0934	-0.24655	-0.10962	-0.15541	0.5385	-0.4681	-0.52118	0.3856
	0.0037	0.341	0.0108	0.2633	0.1117	<.0001	<.0001	<.0001	<.0001
	106	106	106	106	106	106	106	106	106
RFR	0.09952	0.49618	-0.02815	0.56008	0.42586	-0.47544	-0.2054	-0.15912	-0.46957
	0.5306	0.0008	0.8595	0.0001	0.0049	0.0015	0.1919	0.3142	0.0017
	42	42	42	42	42	42	42	42	42
BLUE	0.16085	0.53104	0.23101	0.39567	0.64456	-0.16495	-0.6264	-0.57085	-0.38767
	0.3088	0.0003	0.141	0.0095	<.0001	0.2965	<.0001	<.0001	0.0112
	42	42	42	42	42	42	42	42	42
MIDSTORY_TPH	-0.02883	-0.47326	0.01457	-0.36231	-0.53574	0.11208	0.74988	0.78043	0.38606
	0.7693	<.0001	0.8821	0.0001	<.0001	0.2527	<.0001	<.0001	<.0001
	106	106	106	106	106	106	106	106	106
var 10[1]	-0.06191	-0.51491	0.07152	-0.57245	-0.74016	0.48033	0.48433	0.65334	0.92264
	0.5284	<.0001	0.4663	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
	106	106	106	106	106	106	106	106	106
var 16[2]	0.02005	-0.57133	0.13832	-0.52249	-0.69214	0.32722	0.77827	0.9137	0.67343
	0.8384	<.0001	0.1573	<.0001	<.0001	0.0006	<.0001	<.0001	<.0001
	106	106	106	106	106	106	106	106	106
var 17[3]	0.20039	-0.30183	0.22041	-0.07884	-0.12598	-0.15895	0.8582	0.84105	-0.24023
	0.0394	0.0017	0.0232	0.4218	0.1981	0.1037	<.0001	<.0001	0.0131
	106	106	106	106	106	106	106	106	106

[1] Var 10 = lnTPH*CANOPY_LENGTH
[2] Var 16 = lnTPH*lnCANOPY_LENGTH
[3] Var 17 = lnTPH/lnCANOPY_LENGTH

Correlation matrix for variables used in the development of seedling growth models – page 3 of 4

	CROWN_RATIO	**BASE_CANOPY_HT**	**CANOPY_HT**	**RFR**	**BLUE**	**MIDSTORY_TPH**	**var 10**[1]	**var 16**[2]	**var 17**[3]
GLD	-0.11321	-0.11485	-0.27926	0.09952	0.16085	-0.02883	-0.06191	0.02005	0.20039
	0.2456	0.2388	0.0037	0.5306	0.3088	0.7693	0.5284	0.8384	0.0394
	107	107	106	42	42	106	106	106	106
DGI	-0.07147	0.55843	0.0934	0.49618	0.53104	-0.47326	-0.51491	-0.57133	-0.30183
	0.4644	<.0001	0.341	0.0008	0.0003	<.0001	<.0001	<.0001	0.0017
	107	107	106	42	42	106	106	106	106
HT_I	-0.11175	-0.09312	-0.24655	-0.02815	0.23101	0.01457	0.07152	0.13832	0.22041
	0.2518	0.3401	0.0108	0.8595	0.141	0.8821	0.4663	0.1573	0.0232
	107	107	106	42	42	106	106	106	106
HGI	-0.23727	0.4807	-0.10962	0.56008	0.39567	-0.36231	-0.57245	-0.52249	-0.07884
	0.0139	<.0001	0.2633	0.0001	0.0095	0.0001	<.0001	<.0001	0.4218
	107	107	106	42	42	106	106	106	106
%$T_{(PAR)}$	-0.21486	0.57928	-0.15541	0.42586	0.64456	-0.53574	-0.74016	-0.69214	-0.12598
	0.0263	<.0001	0.1117	0.0049	<.0001	<.0001	<.0001	<.0001	0.1981
	107	107	106	42	42	106	106	106	106
BA	0.2636	-0.15975	0.5385	-0.47544	-0.16495	0.11208	0.48033	0.32722	-0.15895
	0.0061	0.1003	<.0001	0.0015	0.2965	0.2527	<.0001	0.0006	0.1037
	107	107	106	42	42	106	106	106	106
TPH	-0.38564	-0.65099	-0.4681	-0.2054	-0.6264	0.74988	0.48433	0.77827	0.8582
	<.0001	<.0001	<.0001	0.1919	<.0001	<.0001	<.0001	<.0001	<.0001
	107	107	106	42	42	106	106	106	106
lnTPH	-0.22806	-0.75093	-0.52118	-0.15912	-0.57085	0.78043	0.65334	0.9137	0.84105
	0.0181	<.0001	<.0001	0.3142	<.0001	<.0001	<.0001	<.0001	<.0001
	107	107	106	42	42	106	106	106	106
CANOPY_LENGTH	0.5144	-0.43707	0.3856	-0.46957	-0.38767	0.38606	0.92264	0.67343	-0.24023
	<.0001	<.0001	<.0001	0.0017	0.0112	<.0001	<.0001	<.0001	0.0131
	106	106	106	42	42	106	106	106	106
CROWN_RATIO	1	-0.07964	0.20946	-0.58207	-0.15214	-0.01157	0.30421	0.0484	-0.54993
		0.4148	0.0312	<.0001	0.3361	0.9063	0.0015	0.6222	<.0001
	107	107	106	42	42	106	106	106	106

[1]Var 10 = lnTPH*CANOPY_LENGTH; [2]Var 16 = lnTPH*lnCANOPY_LENGTH; [3]Var 17 = lnTPH/lnCANOPY_LENGTH

Correlation matrix for variables used in the development of seedling growth models – page 4 of 4

	CROWN_RATIO	BASE_CANOPY_HT	CANOPY_HT	RFR	BLUE	MIDSTORY_TPH	var 10[1]	var 16[2]	var 17[3]
BASE_CANOPY_HT	-0.07964	1	0.40372	0.30031	0.75124	-0.71823	-0.64561	-0.77861	-0.52371
	0.4148		<.0001	0.0533	<.0001	<.0001	<.0001	<.0001	<.0001
	107	107	106	42	42	106	106	106	106
CANOPY_HT	0.20946	0.40372	1	-0.10614	0.30663	-0.30587	0.12163	-0.24092	-0.73899
	0.0312	<.0001		0.5035	0.0483	0.0014	0.2142	0.0129	<.0001
	106	106	106	42	42	106	106	106	106
RFR	-0.58207	0.30031	-0.10614	1	0.15061	-0.25156	-0.41184	-0.31844	0.18174
	<.0001	0.0533	0.5035		0.3411	0.108	0.0067	0.0399	0.2494
	42	42	42	42	42	42	42	42	42
BLUE	-0.15214	0.75124	0.30663	0.15061	1	-0.68112	-0.49097	-0.56682	-0.40193
	0.3361	<.0001	0.0483	0.3411		<.0001	0.001	<.0001	0.0083
	42	42	42	42	42	42	42	42	42
MIDSTORY_TPH	-0.01157	-0.71823	-0.30587	-0.25156	-0.68112	1	0.63269	0.78158	0.56373
	0.9063	<.0001	0.0014	0.108	<.0001		<.0001	<.0001	<.0001
	106	106	106	42	42	106	106	106	106
var 10[1]	0.30421	-0.64561	0.12163	-0.41184	-0.49097	0.63269	1	0.903	0.14572
	0.0015	<.0001	0.2142	0.0067	0.001	<.0001		<.0001	0.1361
	106	106	106	42	42	106	106	106	106
var 16[2]	0.0484	-0.77861	-0.24092	-0.31844	-0.56682	0.78158	0.903	1	0.5491
	0.6222	<.0001	0.0129	0.0399	<.0001	<.0001	<.0001		<.0001
	106	106	106	42	42	106	106	106	106
var 17[3]	-0.54993	-0.52371	-0.73899	0.18174	-0.40193	0.56373	0.14572	0.5491	1
	<.0001	<.0001	<.0001	0.2494	0.0083	<.0001	0.1361	<.0001	
	106	106	106	42	42	106	106	106	106

[1] Var 10 = lnTPH*CANOPY_LENGTH
[2] Var 16 = lnTPH*lnCANOPY_LENGTH
[3] Var 17 = lnTPH/lnCANOPY_LENGTH