PREDICTING LIGHT TRANSMITTANCE AND SEEDLING GROWTH ACROSS A GRADIENT OF RIPARIAN FOREST CANOPY STRUCTURES

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DISSERTATION ABSTRACT

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In response to shifts in forest management that have favored continued retention of forest cover, the objective of this study was to explore how forest structure influences the understory light environment and seedling growth. The study was conducted within western Georgia along a created gradient of mixed-hardwood riparian forest structures ranging from 50 to 100 percent cover. This gradient was created by random assignment of four levels of midstory removal to fifty 0.05 ha plots. Forest structure, light transmittance, and development of planted seedlings were quantified within each plot. A modeling approach was then used to construct equations predicting understory light levels using metrics describing the forest canopy. Mortality and growth models were also fit to explore the relationship between seedling development and forest structure over two growing seasons (2004, 2005). Results suggest that the vertical sighting method of estimating canopy cover was the best evaluated measure for predicting light transmittance. Addition of stand density and top height to this model increased the variance explained to nearly eighty percent. Analysis of seedling growth data resulted in models with limited predictive power. However, models do provide some general inferences about the relation between structure and seedling growth. Logistic regression showed that the probability of seedling mortality was related to the interaction between basal area (m^2 ha^{-1}) and canopy depth as well as percent canopy closure estimated using hemispherical photography. Growth models found that seedling diameter and height increments were most strongly related to canopy height, canopy closure, and seedling basal diameter. Above all, this research highlights the potential importance of quantifying vertical and horizontal canopy characteristics when evaluating effects of forest structure on seedling growth and the understory environment. Moreover, structural relationships provided by this research may assist in the formulation of riparian forest management strategies that promote the development of seedling reproduction under an existing forest canopy.

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CHAPTER I – INTRODUCTION

Recent shifts in forest management have begun to focus silvicultural activities away from more traditional even-aged management. The shifting nature of management has been a result of a variety of influences from the natural resources community as well as the public. One driving force is the impacts of the urbanizing landscape and the change in stakeholder values and preferences. While traditional management focused on production, today's stakeholders value multiple-use objectives such as sustainability of ecosystem function and dynamics (Coates and Burton 1997), forest aesthetics, restoration, wildlife management, water quality, and recreation (Shelby et al. 2004). In response, silviculturists have explored the use of uneven-aged management (Guldin 1996) and continuous cover forestry (Hale 2003, Pommerening and Murphy 2004) in meeting diverse objectives.

While uneven-aged and continuous cover management approaches have benefits, the development and perpetuation of such systems have increased regeneration and recruitment complexity when compared to even-aged systems. The factor that makes these alternative approaches different from even-aged management is the continued presence of a dominant canopy layer and its effect on the long-term development of lower tree strata and forest reproduction (Daniel et al. 1979, Nyland 2002). This notion is supported by past research which has shown that forest canopy structure can influence environmental factors known to control the development of forest reproduction (Parker 1995, Carlson and Groot 1997, Morecroft 1998, Assenac 2000).

Of the variables influenced by structure, transmittance of light into the understory has been studied in great detail. This work has shown an inverse relationship between canopy closure and the amount of light reaching the forest understory (Vales and Bunnell 1988, Comeau and Heineman 2003, Drever and Lertzman 2003). With regard to general trends of the belowground environment, as canopy cover decreases soil moisture (Minkler et al. 1971, Gray et al. 2002, Clinton 2003) and soil temperature (Carlson and Groot 1997, Potter et al. 2001, Gray et al. 2002) increase. It should be noted that increases in soil moisture are usually attributed to lower transpiration rates and enhanced water availability resulting from the removal of forest vegetation (Spurr and Barnes 1992). Unlike soil temperature, air temperature has been shown to be similar between forest and open conditions (Carlson and Groot 1997, Morecroft et al. 1998, Meyer et al. 2001, Porté et al. 2004). The similarity in air temperatures between these two environments is likely related to the mixing effect of wind in forest openings (Gray et al. 2002). However, air temperatures in open conditions can be higher when driven by high solar intensities (Morecroft et al. 1998).

The response of forest reproduction to the environmental variables modified by forest structure is also important in the context of silviculture. Generally higher light, moisture, and fertility environments result in increased survival and growth rates. However, studies exploring multiple resource limitations have highlighted that no one pattern can describe all species responses to these environmental gradients (Kolb et al. 1990, Canham et al. 1996). Likewise, the responses of a given species to a resource environment are influenced by shade tolerance and its morphological and physiological plasticity (Canham 1989). The influence of shade tolerance is further supported by additional research that found that survival and growth was higher for shade tolerant species than intolerants in low light conditions (Mailly and Kimmins 1997, Mason et al. 2004).

Upon consideration of research pertaining to relationships between structure, environment, and growth, it becomes clear that one must apply these underlying relationships when developing management systems that retain forest cover in perpetuity. Without considering the structural characteristics and environmental conditions needed to promote the growth of forest reproduction and other sub-canopy trees, establishment and long-term recruitment of trees into the upper canopy stratums may be limited. Species-specific differences in physiologic characteristics and ecological growth strategies also require that these created structural conditions be tailored for one's target species. Hence, species-specific models and quantitative tools that allow silviculturists to evaluate and apply these relationships to the development of continuous cover and uneven-aged management systems may have great utility.

One type of model framework that could benefit the development of silvicultural systems is one that relates the understory environment to stand structure. While no one microclimatic variable controls the growth of forest vegetation (Kozlowski and Pallardy 1997), development of models exploring the relation between forest structure and environment have focused on transmittance of photosynthetically active radiation (PAR). PAR transmittance is important to growth because it represents the portion of the light spectrum (400 to 700 nm) reaching the understory that is used by plants during photosynthesis (Gendron et al. 1998). The ability to understand and predict the relationship between forest structure and PAR is critical because it enhances the ability of silviculturists to manage the light environment and development of forest reproduction through canopy manipulations (Lieffers et al. 1999). Levels of light transmittance are commonly measured using either quantum sensors (Brown and Parker 1994, Hale 2003, Yirdaw and Luukkanen 2004) or photosensitive ozalid paper (Buckley et al. 1999, Lieffers et al. 1999). The benefit of quantum sensors is that they allow one to calculate percent transmittance of PAR, while ozalid paper can only estimate total (plant available and unavailable) light transmittance (Lieffers et al. 1999). Most light models have used these direct measures as a response variable and structural metrics as predictors. Common stand inventory parameters such as basal area, density, and mean diameter have been used (Vales and Bunnell 1988, Brown and Parker 1994, Buckley et al. 1999, Comeau and Heineman 2003). Similarly, canopy cover (Johansson 1996) and canopy closure (Jenkins and Chambers 1989, Engelbrecht and Hertz 2001) estimates as well as the analysis of hemispherical photography (Anderson 1964, Frazier et al. 2001, Beaudet and Messier 2002, Yirdaw and Luukkanen 2004) have been employed to indirectly assess understory light levels. Other important structural characteristics that have been shown to influence understory light transmittance include canopy heights and the overall vertical profile of the forest canopy (Brown and Parker 1994, Parker et al. 2002, Bellow and Nair 2003). This body of light transmittance work suggests predictive models may need to include both horizontal and vertical components of the forest canopy.

In addition to work with light transmittance, models predicting seedling growth from stand structure have also been developed and have potential application in silviculture. Unlike process models that relate growth directly to environmental variables (Vanclay 1994), structure-based models relate seedling growth to variables describing the forest canopy. Such a linkage can be beneficial because it may allow model predictions to be more seamlessly integrated into stand marking prescriptions (Buckley et al. 1999). This improved linkage stems from the idea that silvicultural treatments directly modify structure and only indirectly affect the understory environment (Daniel et al. 1979). Research relating to stand structure resulting from specific silvicultural treatments has generally shown that seedling survival and growth is inversely related to the amount of forest cover. Specific modeling work has incorporated structural variables such as canopy closure (Brandeis et al. 2001) and percent visible sky (Jain et al. 2004) to predict seedling growth. While the level of forest cover is undoubtedly related to seedling growth, other interacting variables such as seedling size and intensity of understory competition can influence the response of a given species. Specifically, descriptive seedling size variables such as basal diameter have been shown to be significant predictors of growth (Loftis 1990, Dey and Parker 1997, Mason 2001, Spetich et al. 2002). Additionally, woody and herbaceous vegetation are known to influence seedling growth and appropriate control of that vegetation has been associated with increased growth rates (Cain 1991, Wetzel and Burgess 2001, McGill and Brenneman 2002, Spetich et al. 2002). Work relating overstory and understory structure along with seedling biomass characteristics seem to indicate that no one measure can explain species-specific seedling growth patterns. In turn, it is suggested that in order to more appropriately develop structural based seedling growth models the incorporation of additional metrics describing understory competition and seedling size may be required.

Building upon past research, this study works to extend our understanding of the structure-light and structure-seedling growth relationships within mixed-hardwood riparian forests of the Southeastern US. The study employs a modeling approach and will explore these relationships across a gradient of canopy conditions similar to those present within uneven-aged and continuous cover silvicultural systems as well as in other low-intensity partial harvests such as midstory removals. The project will be conducted in two general parts and the first will assess the relationship between canopy structure and understory PAR transmittance across a 50 to 100 % canopy cover gradient. While much past research has focused on the relationship between light and horizontal components of stand structure such as basal area, density, canopy cover/closure, this research incorporates a combination of horizontal and vertical metrics. Results will highlight the importance of a given structural measure on predicting understory light within the forest type and structural gradient presented within the study.

The second portion of the study will focus on the relationship between seedling growth and canopy structure. Because vertical structure has the potential to influence the understory environment (Brown and Parker 1994, Parker et al. 2002, Bellow and Nair 2003), seedling growth models will also account for the potential influence of vertical components such as canopy heights. Additionally, based upon inferences drawn from existing research, the interacting influence of seedling size characteristics (Loftis 1990, Dey and Parker 1997, Mason 2001, Spetich et al. 2002) along with the presence and absence of understory composition (Cain 1991, Wetzel and Burgess 2001, McGill and Brenneman 2002, Spetich et al. 2002) will be incorporated into study methodology. Relationships between structural metrics and seedling mortality, diameter and height growth patterns will be presented for data collected over two growing seasons (2004, 2005). In response to research highlighting the potential impact that shade tolerance and physiological and morphological differences between species can have on growth relationships (Canham 1989), mortality and growth models will be developed separately for each of the study's species.

The overall goal of this study is to further the understanding of the ecological principles underlying the development of management systems that establish and recruit tree reproduction under the presence of a dominant overstory canopy. Because the models in this study evaluate the relationships between structure, environment, and growth, they have potential application in general silvicultural approaches such as continuous cover forestry, uneven-aged management, and even-aged regeneration systems that require advanced reproduction prior to final overstory removal. However, the specific applications of the two types of structural models (light and seedling growth) are slightly different. The utility of the constructed light models is geared toward estimating a stand's light environment based upon its current structure as well as predicting potential changes in transmittance following a proposed canopy manipulation. Linking the study's estimates with existing research pertaining to a species' growth potential under a given light environment could be used to evaluate whether or not a structure is favorable for the development of that species or its competitors. Thus, model outputs could be used to direct structural treatments that enhance the development of a target species (Lieffers et al. 1999). It should be noted that models relating light transmittance and growth responses are available for a variety of species common to the Southeastern US (Kolb et al. 1990, Groninger et al. 1996, Gardner and Hodges 1998, Gardiner et al. 2001). The structure-based seedling growth models could also be used to aid in development of silvicultural treatments designed to favor the growth of seedling reproduction under a forest canopy. However, because these models may predict growth based upon specific structural components that can be modified by a management treatment, direct application of the model outputs could more easily be integrated into formulation and implementation of stand prescriptions (Buckley et al. 1999). Finally, the project will work to extend the understanding of structure – light – growth relationships of partial harvests (50 to 100 % cover) within mixed-hardwood riparian forests. Moreover, the research attempts to design quantitative tools that may assist in the formulation of sound, objective-driven management strategies for these forest systems.

CHAPTER 2 – LITERATURE REVIEW

An ecological factor critical to understanding the development and implementation of silvicultural systems is the relationship between canopy structure and the forest environment (Aussenac 2000). Because changes in structural characteristics resulting from disturbance alter the forest environment, they also impact the establishment, growth, and mortality of the residual stand (Daniel et al. 1979). Therefore, understanding how a stand will respond to a change in structure and environment is essential in the practice of silviculture. Such knowledge is especially valuable because it can be used to formulate structural manipulations designed to address diverse forest management objectives.

Relationship between forest structure and understory environment

Vertical and horizontal canopy structure has been shown to have a direct influence on environmental variables such as light, air temperature, relative humidity, wind, and soil temperature and moisture (Aussenac 2000). Several general aspects of structure have been linked to changes in the forest environment. The first is the horizontal component that is commonly quantified using metrics such as density (trees ha^{-1}), basal area ($m^2\ ha^{-1}$) (Buckley et al. 1999, Meyer et al. 2001, Clinton 2003), and percent cover (Johansson 1996). In addition to the horizontal arrangement of the forest canopy, the vertical aspects including canopy height, depth, and complexity are known to influence below-canopy microclimatic conditions (Parker et al. 2002, Parker et al. 2004). The relationship between the presence and properties of canopy gaps and forest environmental conditions has also been evaluated. One metric that has been used in gap research is view factor. This variable takes into account gap size, gap geometry, and canopy height (Carlson and Groot 1997). Hence, view angle attempts to capture how the horizontal and vertical nature of a gap relates to its associated environmental conditions. Distance from forest edge (Meyer et al. 2001) as well as edge height and fullness are also thought to affect the forest environment (Carlson and Groot 1997). Undoubtedly, no single measure can wholly quantify the relationship between forest structure and understory environment. Therefore, in order to understand and apply the structure-environment relationship, one must consider a complex interaction between structural and environmental variables.

Of the many environmental factors, the relationship between understory light transmittance and canopy structure has been evaluated in considerable detail. This research has highlighted an inverse relationship between understory light transmittance and present forest cover. Research within various forest types has highlighted that light availability increases as canopy gap sizes increase (Minkler et al. 1973, Carlson and Groot 1997, Morecroft et al. 1998, Gray et al. 2002). Within natural or artificially created forest gaps, light levels are influenced by gap position and generally the highest light levels can be found within the gap's center (Minkler et al. 1973 and Gray et al. 2002).

Metrics derived from tree inventory data have also been used to model the relationship between structure and light. Of these, models incorporating stand basal area and density have identified strong relationships between canopy openness and light transmittance, thus supporting the inverse trend between light and structure (Vales and Bunnell 1988, Comeau and Heineman 2003, Drever and Lertzman 2003). Other work has emphasized the importance of vertical structure and has highlighted that canopy height and profile likely impact understory light transmittance (Brown and Parker 1994, Comeau and Heineman 2003, Drever and Lerzman 2003, Parker et al. 2004).

In many cases, it is possible to model light transmittance using variables such as canopy cover and closure. Johansson (1996) found that 86% of the variance in light transmittance was explained by canopy cover measured using a densitometer (i.e. vertical sighting tube method). Similarly, the study of Jenkins and Chambers (1989), study conducted within southern bottomland hardwood forests found that spherical densiometer measures of canopy closure explained 71% of the variance in transmittance. Other studies using densiometer measures have shown stronger relationships and presented coefficients of determination (R^2) ranging between 0.89 and 0.99 (Comeau et al. 1998, Buckley et al. 1999, Bellow and Nair 2003). Another method used to estimate the interactions between canopy structure and light environment has been hemispherical photography (Anderson 1964, Frazier et al. 2001, Beaudet and Messier 2002, Bellow and Nair 2003, Yirdaw and Luukkanen 2004). Models developed using photography have also shown a strong relationship between canopy structure and light, with many models explaining greater than 60% of the variance in understory transmittance (Machado and Reich 1999, Bellow and Nair 2003, Yirdaw and Luukkane 2004).

Two additional and related environmental factors impacted by structural characteristics are wind speed and air temperature. Morecroft et al. (1998) found that wind speed is influenced by canopy openness and that wind speeds are generally lower in woodlands when compared to open areas. On the other hand, many studies suggest that air temperatures in forest and forest openings do not differ significantly (Carlson and Groot 1997, Morecroft et al. 1998, Meyer et al. 2001, Porté et al. 2004). This similarity has been attributed to the mixing effect of wind within forest openings (Gray et al. 2002). An exception to these air temperature similarities is when open field temperatures are driven by high solar intensities within the summer months (Morecroft et al. 1998). Morecroft et al. (1998) also suggested that air temperature extremes can increase with increasing gap size. Finally, Potter et al. (2001) highlighted that temperature differences between forest and open conditions are dependent upon magnitudes of minimum and maximum daily temperatures and can be altered by year-to-year variation in climatic conditions.

Additionally, soil temperature and moisture can have a large impact on the response of forest growth and thus understanding their relationship with canopy structure is important. In contrast to air temperatures, soil temperatures are generally higher in forest openings than under forest canopies (Carlson and Groot 1997, Potter et al. 2001, Gray et al. 2002). Similar to light levels, canopy heights and vertical structure can influence soil temperatures. For example, the presence of low herbaceous or woody vegetation has been shown to moderate daily minimum and maximum soil temperatures (Clinton 2003). In contrast to the soil temperature conditions, soil moisture tends to increase with increasing canopy openness. The specific soil moisture conditions across a canopy opening can vary depending on location and are commonly highest in the area's center (Minkler et al. 1971, Gray et al. 2002, Clinton 2003). This relationship with soil moisture can be attributed to lowered transpiration rates and enhanced water availability that accompany the removal of forest vegetation (Spurr and Barnes 1992).

Relationship between seedling growth and the forest environment

Light, air temperature, relative humidity, and wind speed, as well as soil temperature, moisture, and fertility, commonly influence plant development (Kozlowski and Pallardy 1997). Hence, the environment resulting from a forest's canopy characteristics is often the primary factor driving resource availability and associated seedling growth (Aussenac 2000). Quantifying how these environmental factors impact species-specific establishment, growth, and mortality trends is essential to understanding stand dynamics and the development of silvicultural strategies (Oliver and Larson 1996). By understanding the relationship between resource availability and species-specific seedling growth patterns, one could enhance the development of a given species by altering the forest environment to match its physiological requirements (Daniel et al. 1979). Conversely, structural treatments could also be used to create environmental conditions that hinder a species' competitive ability (Loftis 1990). In this manner, inter-specific competition dynamics could be influenced by altering environmental conditions through canopy manipulations. These principles are especially critical within silvicultural systems that are designed to promote the development of forest reproduction under existing forest canopies (Hale 2003).

Much work has been completed to evaluate how specific microclimatic factors influence the survival and development of forest reproduction. Of the many important variables, transmittance of photosynthetically active radiation (PAR) has received considerable interest. PAR represents the portion of the light spectrum (400 – 700 nm) captured by plants during photosynthesis and thus is important in relating light transmittance to plant growth and survival (Gendron et al. 1998). The ability of a species to respond to varying levels of PAR is controlled, in part, by its shade tolerance and its morphological and physiological plasticity (Canham 1989). For example, the morphological plasticity common among shade tolerant species may assist them in sustaining growth under low light environments, but their lower physiological plasticity may limit their response to large canopy gaps (Canham 1989). Mailly and Kimmins (1997), along with Mason et al. (2004), found a similar relationship between light transmittance and survival and suggest that survival in low light environments was higher for shade tolerant than intolerant species.

Another important interaction between environment and physiology is the influence of light on species-specific height growth patterns and competition dynamics among forest reproduction (Coates and Burton 1999, Messier et al. 1999). One such aspect is how seedling physiology affects the point on the light intensity gradient where a particular species reaches its maximum height growth. Gardiner and Hodges (1998) evaluated the two-year height growth of cherrybark oak (*Quercus pagoda* Raf.) at 8, 27, 53, and 100% full-sun conditions. The study's data highlighted a parabolic growth pattern for cherrybark oak and found seedlings were significantly taller within the 53 and 27% full-sun treatments than in the 100 or 8% full sun treatments. Moreover, Gardiner and Hodges (1998) found that root-collar diameter was significantly larger at 53% full sun than the other three light environments. A study conducted by Logan (1965) found a similar pattern of height growth vs. light intensity for birch (*Betula* spp.) and maple (*Acer* spp.). Specifically, Logan (1965) found that five-year height growth was generally greater at 45% of full sun than at the 13, 25, or 100% light levels. An additional light transmittance-growth study completed by Groninger et al. (1996) found that loblolly pine (*Pinus taeda* L.) was significantly taller under full-sun conditions than in shaded treatments (79% and 89% shade), while yellow poplar (*Lirodendron tulipfera* L.) was significantly taller under 89% shade. Unlike the height growth patterns presented, stem diameter was significantly greater under full sun for all species (Groninger et al. 1996). Therefore, it would appear that seedling growth and biomass allocation may differ by species along a gradient of light intensities. Shading treatments implemented by Kolb et al. (1990), Gottschalk (1994), and Bartlett and Remphrey (1998) further support the notion of species-specific growth and biomass allocations patterns.

While light undoubtedly plays a large role in species growth and resource allocation patterns, other interacting factors also influence these relationships. Several studies have attempted to quantify these relationships by exploring seedling growth patterns from a multiple resource limitation approach. Canham et al. (1996) evaluated red maple (*Acer rubra* L.), sugar maple (*Acer saccharum* Marsh.), eastern white pine (*Pinus strobus* L.), and northern red oak (*Quercus rubra* L.) at five light intensities as well as under low and high moisture and nitrogen levels. Results support the idea that fertility, moisture, and light influence root and shoot biomass allocation differently between species. Likewise, the study highlighted that soil resources have a larger influence on seedling growth as light intensities increase. Data presented by Kolb et al. (1990) also support this notion. Within their study, Kolb et al. (1990) found that reductions in northern red oak and yellow poplar seedling growth, as a result of decreased levels of fertility and moisture, were greater under 100% full sun conditions than in shaded conditions (20% full sun). However, the overall growth reduction in lower resource environments was of a higher magnitude for yellow-poplar when compared to northern red oak. Similarly, relative heights between each species were not significantly different in the low moisture or low fertility treatments. In contrast, under high resource availability, yellow-poplar had the ability to significantly outgrow northern red oak. In turn, Kolb et al. (1990) suggest shade tolerance and morphological adaptations may influence a species' ecological growth strategies and thus its ability to gain a competitive advantage under a given resource environment.

From the reviewed literature, it is apparent that no single environmental factor entirely controls seedling biomass allocation and growth patterns. Likewise, developmental responses along an interacting gradient of environmental conditions are species-specific. Therefore, in order to predict the response of seedling reproduction, one must consider both the forest environment and the ecological growth strategy of each species. By applying the structure-environment-growth relationship to silviculture, one could create forest conditions that influence seedling dynamics by favoring or hindering a species based upon its growth strategy and resource requirements.

Relationship between forest canopy structure and seedling growth

While models incorporating microclimatic variables can be used to predict seedling development, the utility of such models in management can be limited by problematic integration with traditional stand prescriptions and increased data collection costs (Buckley et al. 1999). Integrating microclimatic variables into silvicultural prescriptions is difficult because such operations directly modify the forest canopy and only indirectly influence specific understory environmental factors (Daniel et al. 1979). Thus, in order to use seedling growth models in the formulation of management strategies, models must integrate variables which describe specific structural characteristics that can be directly controlled by a stand treatment. In response, additional research has focused on methods that relate seedling growth directly to measures of forest canopy structure (Brandeis et al. 2001, Mitchell 2001, Jain et al. 2004). Within this approach, changes in the understory environment and influence of microclimatic conditions on seedling growth are not directly measured, but are indirectly accounted for in the quantification of a forest's structural characteristics. These models allow patterns of seedling development to be directly linked with metrics common to silvicultural prescriptions (e.g. basal area, density, canopy cover) (Brandeis et al. 2001), thus giving structure based growth models an advantage over models incorporating detailed environmental data.

While seedling growth models based on structural measures have great utility to the application of silvicultural treatments, their development has been problematic (Brandeis et al. 2001). However, several studies have attempted to quantify the relationship between structure and growth within a variety of general silvicultural treatments. These studies suggest that seedling survival and growth increase with decreasing residual canopy cover (Crow 1992, Gray and Spies 1996, Larsen et al. 1997, Dey and Parker 1997). Research also suggests that growth response across a gradient of canopy densities differs among species (Gray and Spies 1996, Brandeis et al. 2001, Mitchell 2001). Thus, these studies highlight that the relationship between structure and seedling growth follows a similar pattern as the light transmittance-seedling growth relationship. This notion is not unreasonable due to the strong relationship present between forest canopy structure and light transmittance (Jenkins and Chambers 1989, Johansson 1996, Comeau et al. 1998, Buckley et al. 1999).

In contrast to research that outlines seedling growth patterns resulting from general silvicultural treatment types, other studies have attempted to use continuous (i.e. ratio scale) structural variables to predict seedling growth. One such study conducted by Brandeis et al. (2001) used basal area, hemispherical photography derived canopy closure, and visual coverage estimates to predict seedling volume. Data from their study suggest that visual coverage estimates taken over each seedling was a better predictor of volume than either basal area or canopy closure derived from photos taken over seedling groups. Furthermore, the authors suggest hemispherical photography taken over seedling groups (approximately a 21 by 6 m area) may not accurately depict canopy closure above an individual seedling due to small scale structural variation (Brandeis et al. 2001). This suggests that the scale of structural sampling must be considered when developing similar growth models in order to minimize variance due to canopy heterogeneity.

In contrast to the seedling volume prediction of Brandeis et al. (2001), Jain et al. (2004) used percent visible sky (100 % - % canopy closure) derived from hemispherical photography to predict diameter and height of naturally established forest reproduction. Within 0.6-m-radius plots, each seedling was inventoried and a photo was used to quantify the structural conditions present within the plot. For their species of interest, western white pine (*Pinus monticola* Dougl. Ex D. Don), percent visible sky explained 56% of the variation in seedling basal diameter and 53% of the variation in height.

Seedling and structural data were then used to construct dominance probabilities for white pine and its common competitors along a gradient of canopy conditions. Dominance probabilities between species were used to establish thresholds in percent visible sky in which white pine was at a competitive advantage and at free-to-grow status (Jain et al. 2004). Constructing similar models and identifying competition thresholds between species could be especially important to silviculturists designing treatment strategies that must retain forest cover, but also influence interspecies seedling competition dynamics. However, because Jain et al. (2004) presents dominance probabilities of species possessing large differences in shade tolerance, it is unclear if this technique will work for competition thresholds between species of similar shade tolerance and growth strategies.

Overall, the reviewed literature has provided examples of how researchers have approached modeling the relationship between canopy structure and seedling growth. While none of these studies presents a definitive framework, they do suggest that growth models based upon structural variables can be developed. The advantage of models incorporating structural variables is that they can be more easily linked with stand prescriptions and thus may have utility in applied forestry. By linking seedling growth directly to forest structure, predictions can be made on how reproduction may respond to structural manipulation. This can give silviculturists a coarse decision-making tool to evaluate how different stand prescriptions will impact post-treatment seedling growth rates and interspecific competition.

Management implications within mixed hardwood riparian forests

One goal of continuous cover management systems is to promote the continued development of forest reproduction, while retaining a sufficient overwood canopy to meet diverse objectives such as forest aesthetics (Hale 2003). However, in order to develop and implement such management systems, it is essential to understand the interactions between forest structure, understory microenvironment, and seedling growth. By managing variables such as PAR transmittance through the manipulation of the forest canopy, one can influence the response and competitive dynamics of forest reproduction (Messier et al. 1999).

One linkage to the management of Southern riparian forests is understanding the relationship between structural conditions and light transmittance. Research completed in the Southern Bottomland Region supports light work conducted across many forest types and highlights the inverse relationship between forest canopy density and light transmittance. Jenkins and Chambers (1998) found that canopy closure explained approximately 86 % of the variation in light transmittance. In additional to the horizontal aspects of forest structure highlighted in Jenkins and Chambers (1998), other work has highlighted that vertical characteristics such as canopy height and profile can influence light relationships within structurally diverse forest types (Brown and Parker 1994, Comeau and Heineman 2003) such as many riparian forest communities found in the southern United States (Janzen and Hodges 1985, Heitzman et al. 2004). Because horizontal and vertical structural components can influence understory environment, both should be considered when developing strategies to alter the light environment through stand manipulations. Without considering the appropriate structural components, the evaluation and prediction of post-treatment light environments may have diminished accuracy.

Understanding light relationships is especially useful in management because of the information available relating seedling growth and light for species of the southern United States (Kolb et al. 1990, Groninger et al. 1996, Bartlett and Remphrey 1998, Gardiner and Hodges 1998). By understanding how structure influences light and how light relates to growth, a silviculturist can estimate the potential seedling development of a given species. Two commercially important hardwood species in the southern United States are yellow-poplar and cherrybark oak. Their respective physiological characteristics and ecological growth strategies differ and thus, each may respond differently to a given set of silvicultural treatments, structural conditions, or understory environmental factors. Gardiner and Hodges (1998) suggest that cherrybark oak may reach optimum height and diameter growth under moderate levels of shade. In contrast, Kolb et al. (1990) suggest that yellow-poplar may have greater height growth rates in full sun than in shaded conditions. However, within their study, when grown under low moisture and fertility, yellow-poplar's growth was not significantly different than that of northern red oak. Similarly, the growth reductions resulting from below-ground resource limitation were much more pronounced for yellow-poplar than northern red oak (Kolb et al. 1990). This suggested that yellow-poplar and oak possess different growth strategies and responses to resource gradients and reaffirms that seedling growth is influenced by complex interactions between plant physiology, forest structure, and resource availability.

Groninger et al. (1996) evaluated the growth of yellow-poplar in similar light regimes as Kolb et al. (1990). They found that it had greater height growth under shaded conditions (89% shade) than in full-sun. The different results from these two growth studies suggest that yellow-poplar exhibits a plastic growth response depending on its specific resource environment. It should be noted that each of these seedling growth studies was completed under artificially created shade and thus there is potential for these species to react differently in natural conditions. Nonetheless, these studies comparing the growth response of oak and yellow-poplar highlight the developmental differences that can occur between species in reaction to their environment. As a result, managers must consider species composition, canopy characteristics, light environment, and site quality when evaluating or predicting post-treatment seedling development. It is therefore essential for silviculturists to understand these complex ecological interactions when developing continuous cover systems designed to promote the development of desired forest reproduction while maintaining sufficient high forest cover.

CHAPTER III – INDIRECT MEASURES FOR CHARACTERIZING LIGHT ALONG A GRADIENT OF MIXED-HARDWOOD RIPARIAN FOREST CANOPY STRUCTURES

Abstract

Understanding the effect of canopy structure on the understory light environment is useful in the design of silvicultural strategies that facilitate sustainable tree recruitment. To address this need, a study was designed to quantify the relationship between forest structure and light along a gradient of fifty to one-hundred percent canopy cover. The gradient was created by applying one of four midstory removal treatments to each of fifty 0.05 ha plots located within a mixed-hardwood riparian forest corridor. The light environment was directly quantified with a linear ceptometer and regression analysis was used to examine the relationship between photosynthetically active radiation (PAR) and various metrics of vertical and horizontal structure. Vertical sighting tube estimates of canopy cover ($R^2 = 0.73$), light estimates derived from hemispherical photography ($R^2 = 0.70$), and spherical densiometer estimates of canopy closure ($R^2 = 0.68$) were the best single predictors of understory light transmittance. Including top height and tree density improved the fit of canopy cover based models ($R^2 = 0.80$). Canopy closure estimates derived from hemispherical photography generally showed a weaker relationship with PAR than other measures of stand structure. Further, the strength of this relationship depended upon photo the analysis angle. In general, the vertical component of stand structure influences light transmittance through the forest canopy. This vertical complexity must be addressed when evaluating structure-light relations.

Keywords: Light Transmittance, Canopy Cover, Canopy Closure, Crown Width Models, Uneven-aged Silviculture

Introduction

An important impact of forest structure is its resulting influence on the properties of the understory environment. A large body of literature supports this notion and has shown a strong positive relationship between forest canopy structure and understory light transmittance (Akulova et al. 1964, Anderson 1966, Vales and Bunnell 1988b, Jenkins and Chambers 1989, Comeau and Heineman 2003). Complex interactions of environmental variables also impact survival and growth of tree seedling reproduction. Of these variables, past research has specifically highlighted light's role in species-specific growth rates and biomass allocation (Kolb et al. 1990, Gottschalk 1994, Groninger et al. 1996, Mason et al. 2004). Furthermore, it has been suggested that a species' shade tolerance and growth response to a given light environment are important to growth strategies, competition dynamics, and long-term stand development (Canham 1989, Mason et al. 2004). Therefore, understanding how structural characteristics influence the understory light environment is critical to understanding the growth and mortality patterns of forest reproduction.

Levels of understory light transmittance have been quantified in many forest ecosystems. Quantum sensors (Brown and Parker 1994, Hale 2003, Yirdaw and Luukkanen 2004) and photosensitive paper (ozalid paper) (Buckley et al. 1999, Lieffers et al. 1999) are two common direct measures of light and usually include a comparison of below canopy readings to reference readings recorded for full sun to calculate percent transmittance. One major difference between these two techniques is that the quantum sensors allow for determination of percent transmittance of photosynthetically active radiation (PAR), while ozalid paper only provides an estimate of overall percent light transmittance (Lieffers et al. 1999). The importance of this difference is that PAR represents that portion of the light spectrum (400 – 700 nm) which can be captured by plants during photosynthesis and thus is important in relating light transmittance to plant growth (Gendron et al. 1998).

Basic metrics of forest structure such as stem density, basal area, and quadratic mean diameter have been used to assess understory light transmittance indirectly (Vales and Bunnell 1988b, Brown and Parker 1994, Buckley et al. 1999, Comeau and Heineman 2003) as has canopy cover (Johansson 1996), canopy closure (Jenkins and Chambers 1989, Buckley et al. 1999, Engelbrecht and Herz 2001), and hemispherical photography (Anderson 1964, Frazer et al. 2001, Beaudet and Messier 2002, Bellow and Nair 2003, Yirdaw and Luukkanen 2004). In addition, stand parameters quantifying vertical aspects of forest structure and the overall vertical profile of a forest have also been shown to influence understory light transmittance (Brown and Parker 1994, Parker et al. 2002, Bellow and Nair 2003). Thus, current research suggests that both horizontal and vertical structural components must be considered when developing predictive models of understory light transmittance.

These direct and indirect measures can be used to manage the light environment through structural manipulation in order to provide conditions for development of forest reproduction (Lieffers et al. 1999). Understanding the relationship between structure, light, and growth is especially important in continuous cover forestry systems that work to retain sufficient overstory cover while simultaneously promoting the continued development of seedling reproduction (Hale 2003). However, these relationships are also of concern in even-aged systems if the regeneration of desired species relies upon advanced reproduction. With knowledge of species-specific ecological growth strategies and resources requirements (i.e. silvics), managers could use light transmittance models to aid in the formulation of silvicultural prescriptions to enhance the development of advance reproduction or to create conditions favoring the competitive ability of one species over another (Messier et al. 1999).

While instruments that measure light directly may provide the best understory transmittance estimates, linking these direct measurements to stand prescriptions and marking guidelines of silvicultural operations is difficult (Buckley et al. 1999). The use of direct measures by field practitioners may also be limited by cost or conditions needed for measurement (Buckley et al. 1999, Engelbrecht and Herz 2001). Therefore, with regard to applied forestry, light transmittance models based upon readily measured forest structural metrics may have a greater utility than direct measures. However, the application of structure-based models may be influenced by the forest structure from which it was developed and the predictor variables included.

Much of the past research regarding structure based light transmittance models has focused on even-aged forest structures. While it has been suggested that the complexity of a stand's vertical structure can influence light transmittance (Vales and Bunnell 1988b, Buckley et al. 1999, Bellow and Nair 2003), research addressing structure based light models in vertically complex forests such as natural multistoried stands or stands managed using selection silviculture has been more limited. In response, this study was designed to quantify the understory light environment across a gradient of canopy structure common to uneven-aged management and continuous cover forestry. Specifically, this paper compares common indirect measures of light along a series of canopy structures created in a mixed-hardwood riparian forest. It presents best-fit light transmittance models developed using various metrics of forest structure as well as models incorporating only variables derived from common tree inventory data.

Methodology

Site Description

The study site was located in the Lower Piedmont physiographic region and the surrounding landscape consisted of rolling terrain. Specifically, the study was conducted within the riparian forest corridor of a 450 ha watershed in Harris County, Georgia, U.S.A. (approximately 32° N, 85° W) (Appendix A). While the historical land-use of this riparian corridor is not well understood, the local area was subjected to extensive cotton farming and periodic timber harvests of variable intensities. At the time of the study, the selected watershed was greater than 90% forested and the dominate land cover included pine plantations and natural mixed hardwood forests. The portion of the riparian corridor used for the study was approximately 2.05 km in length and was oriented in north-south direction between the surrounding upland forests. The soils of these bordering uplands were fine, kaolinitic, thermic Typic Kanhapludults (Pacolet sandy loam). Slopes found on this upland soil type are commonly 15 to 25 percent, but can range from 2 to 60 percent. Soils within the riparian corridor study area were generally considered fine-loamy, mixed, active, thermic Oxyaquic Udifluvents (Congaree series). It should be noted that no flooding occurred during the time period of the study.

Within the study area, the overstory was primarily composed of yellow-poplar (*Liriodendron tulipifera* L.) and sweetgum (*Liquidambar styraciflua* L.) and averaged 32.2 m in height. Water oak (*Quercus nigra* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and boxelder (*Acer negundo* L.) are minor components of the stand. A dense midstory was present across much of the area, dominated by flowering dogwood (*Cornus florida* L.), two-winged silverbell (*Halesia diptera* Ellis.), musclewood (*Carpinus caroliniana* Walt.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch). The understory was primarily composed of Japanese honeysuckle (*Lonicera japonica* Thunb.), Nepalese browntop (*Microstegium vimineum* (Trin.) A. Camus), and blackberry (*Rubus* spp.).

Study Design

In the summer of 2003, fifty 0.05 ha (12.62-m-radius) circular plots were systematically established along a transect bisecting the study area's riparian forest corridor parallel to the stream channel (Appendix B). Plots were located only in portions of the corridor that were at least 38 m wide and a minimum of 38 m separated each plot center. All plots were located under closed canopy forest and establishment criteria ensured that all plot centers were not less than 19 m from the edge of the riparian corridor and not less than 12.6 m from a forest gap (> 0.025 ha).

To create a gradient of canopy cover along this transect, each plot was randomly assigned one of four treatments: Uncut - No trees were removed; Light - removed 1/3 of all midstory trees; Moderate - removed 1/2 of all midstory trees; Complete - removed all midstory trees. Midstory trees were defined as those stems not present in the dominant/co-dominant canopy layer. Treatments were applied during the summer/fall of 2003 using directional chainsaw felling. Vegetation < 1.4 m tall was not removed unless it created a safety hazard during felling operations. No trees were removed from the site, but they were cut up to speed decomposition and to ease future plot measurements.

Data Collection and Analysis

Following treatment, overstory tree inventories were completed for each 0.05 ha plot. All trees > 5 cm DBH were measured and total height (m), height (m) to the base of the live crown (HBLC), DBH (cm), and species were recorded. Live crown height (HBLC) was measured at the lowest live branch that was not considered an epicormic sprout. Tree inventory data were summarized and density (trees ha^{-1}), basal area (m^2 ha^{-1}), quadratic mean diameter (cm), mean HBLC, and top height were calculated for each plot. Top height was defined as the average height (m) of the tallest 100 trees ha^{-1} on each plot (Rennolls 1978).

In the summer of 2004, canopy cover and canopy closure were quantified for each plot. Jennings et al. (1999) defined canopy cover as “the proportion of the forest floor covered by the vertical projection of the tree crowns” and canopy closure as “the proportion of the sky hemisphere obscured by vegetation when viewed from a single point”. Following leaf expansion, the vertical sighting tube method using a GRS Densitometer (Geographic Resource Solutions, Arcata, CA) was employed to estimate canopy cover (Johansson 1985, Johansson 1996). Observations were taken on a 2x2 m grid with a total of 113 points located on each plot. The instrument was leveled at every sample point and the presence or absence of canopy was tallied. Point sample measurements did not distinguish between within-tree or between-tree crown gaps and crown cover from all trees on the plot was included in the presence/absence tallies. Percent cover was calculated by dividing the number of points for which canopy was present by the total number of sample points in each plot.

In addition to direct field measurement, canopy cover was estimated using tree inventory data and species-specific crown width models. Canopy cover calculation involved three computational steps. Allometric crown width models were used to estimate each tree’s horizontally projected crown area (Bechtold 2003). These estimated crown areas were then summed to determine a plot’s total projected crown area (CA_{tot}). Finally, canopy cover was determined by inputting CA_{tot} into the crown overlap correction function (Equation 1) presented by Crookston and Stage (1999).

$$(3.1)\ \%\ \text{canopy cover} = 100\ [1 - \text{Exp}\ (-0.01*(100*(CA_{tot}/10000)))].$$

Canopy closure was estimated using a convex spherical densiometer (Lemon 1956). Readings were taken directly over plot center in each of the four directions and average closure was recorded (Buckley et al. 1999). Because research has suggested that observer effect can introduce bias into densiometer readings (Vales and Bunnell 1988a), a single individual collected the data. For comparison with other measures of canopy closure, it should be noted that a convex spherical densiometer has a view angle of approximately 60 degrees (Cook et al. 1995, Englund et al. 2000).

Hemispherical photography was also used to quantify canopy closure (Beaudet and Messier 2002, Bellow and Nair 2003, Jain et al. 2004). One photograph was taken 1.25 meters above each plot center using a Nikon Coolpix 5700 (5 megapixel) digital camera and fisheye converter (183° view angle). Although research suggests that digital and film hemispherical photography can yield comparable results (Englund et al. 2000, Hale and Edwards 2002), factors such as digital image size, compression, quality, and saturation can influence the analysis of digital fisheye photos (Englund et al. 2000, Frazer et al. 2001, Inoue et al. 2004). To minimize these issues, the following camera settings were used: image quality - 1:4 compression JPEG format; saturation - black and white; and image size - full (2560x1920 pixels) (Frazer et al. 2001). Additionally, all photos were taken during uniformly overcast conditions when the solar disk was completely obscured. The camera was leveled and the fisheye lens oriented toward magnetic north using a compass prior to each shot.

Percent visible sky was obtained from the hemispherical photographs by using Hemiview software (Delta-T Devices, Cambridge, UK) and canopy closure (100% - % visible sky) was calculated. Hemiview was also used to provide an indirect estimate light transmittance from the photos. Following the rationale presented by Hale (2003), indirect site factor (ISF) was calculated in Hemiview and used as an estimate of each plot's light transmittance. For both analyses, the threshold pixel classification of 'sky' vs. 'canopy' was set manually for every photo following guidelines outlined in Hemiview’s user manual (Delta-T Devices Ltd 1999). To minimize variance with threshold selection, one operator completed all analyses. Research suggests that the relationship between hemispherical photography and light may be influenced by photo analysis angle (Bellow and Nair 2003). To determine the influence angle may have on the prediction of light transmittance, each photo was analyzed at a 180, 120, 90, and 60 degree angle by constraining the proportion of the photo processed by Hemiview. For each constrained view angle, photo analysis width was determined using trigonometry and by setting a leveled height pole at a calibrated distance and height from the camera. The analysis radius was set at the point of intersection with the top of the height pole in the photo. The approximate width of the analysis area for the 120, 90, and 60 degree angles are 569 Rad. (Hemiview's measure of analysis circle width), 392, and 261, respectively.

Light measurements were taken during in the summer of 2004 following full leaf expansion and concluding before leaf senescence. Light intensity was directly quantified with an AccuPar linear PAR/LAI ceptometer (Decagon Devices, Inc., Pullman, WA). A total of 12 readings were taken on each plot (4 readings at each of 3 locations), within 2 meters of plot center, and approximately 1.25 m above the ground. Every reading was an average of 80 individual sensors along the 0.8 m long ceptometer array. Care was taken to ensure that the ceptometer was leveled and pointed in the direction of the brightest light source, so that the operator’s shadow was not cast on the sensors. Messier and Puttonen (1995) have suggested that measurement of PAR under clear skies may not accurately reflect average daily PAR levels due to the high variation caused by direct radiation reaching the forest floor in the form of sunflecks (Messier and Puttonen 1995). Conversely, 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). Therefore, all PAR measurements were made under overcast conditions, usually in the late morning hours.

To provide a reference for understory transmittance calculations, a HOBO (Onset Computer Corporation, Pocasset, MA) weather station PAR sensor was located within a nearby clearcut. Sensor calibration between the HOBO sensor and ceptometer were based on readings taken over an entire day under clear skies. A constant was calculated to standardize readings between the two instruments. Light transmittance was determined by dividing the calibrated understory PAR (ceptometer) by open-field PAR (HOBO sensor). Direct comparisons between the HOBO sensor and ceptometer were possible because of the time stamp output with each sensor's readings.

Simple linear regression was used to evaluate the relationship between mean PAR transmittance and common indirect measures for estimating understory light levels (Table 3.1). It should be noted that the PAR data were directly quantified using an accepted method of light measurement under overcast sky conditions (Messier and Puttonen 1995, Parent and Messier 1996). Analysis included observed structural variables as well as calculated variables in an attempt to further quantify vertical characteristics of forest structure. Variables of vertical structure evaluated included top height (Topht), mean height to base of live crown (HBLC), crown depth (CD = Topht - HBLC), and the interaction of density and height to base of live crown (TPH*HBLC) (Table 3.1). Because past research has shown non-linear relationships between light transmittance and measures such as basal area, density (Vales and Bunnell 1988b, Johansson 1996, Comeau and Heineman 2003), and Hemiview's indirect site factor (Hale 2003), non-linear models were also evaluated for the indirect measures evaluated by the study. Next, multiple regression was used to construct best-fit models from two groups of variables. The first set of models evaluated each of the forest structural metrics and the second incorporated only variables derived from tree inventory data. Goodness of fit was evaluated using the coefficient of determination, commonly referred to as R^2 (Neter et al. 1996). Residual analysis was used to assess homogeneity of variance and normality of residuals (Appendix C). Also, for models with two or more independent variables, variance inflation factor (VIF) was used to evaluate multicollinearity. Any variable with a VIF greater than ten was removed from the model (Neter et al. 1996). Finally, to further understand the relationships among measures of forest structure, a Pearson's correlation coefficient matrix was constructed.

Results

Structural manipulations applied to the fifty sample plots resulted in an understory light transmittance gradient of approximately 3 to 21 % full sun (ceptometer), 51 to 96 percent canopy cover (vertical sighting tube method), and 75 to 96 % canopy closure (spherical densiometer). In comparison, the canopy closure range found by hemispherical photography only roughly approached the range of the spherical densiometer and the resulting range differed by photo analysis angle. The resulting range for the 60°, 90°, 120°, and 180° degree analysis angles were 60 to 90 %, 71 to 89 %, 80 to 92 %, and 90 to 95 % respectively. Basal area along this gradient ranged from 13 to

63 m^2 ha^{-1}. The correlation matrix of the structural metrics is presented in Table 3.2.

Results from simple linear regression analysis suggest that the vertical sighting method of estimating canopy cover ($R^2 = 0.7271$), light transmittance estimated by Hemiview's indirect site factor ($R^2 = 0.6994$), spherical densiometer estimates of canopy closure ($R^2 = 0.6804$), and canopy closure estimated using a 90° hemispherical photograph ($R^2 = 0.5495$) were the four variables that explained the largest proportion of variance in light transmittance (Figure 3.1, Table 3.3). With regard to the four photo angles analyzed, a 90° angle was a better predictor of light transmittance than either the 60° ($R^2 = 0.4567$), 120° ($R^2 = 0.3599$), 180° ($R^2 = 0.3222$) angle. Of variables incorporating tree inventory data, canopy cover predictions based on crown width models explained 44.4 percent of the variation in transmittance. Of the remaining tree inventory variables, only crown depth ($R^2 = 0.3267$), basal area ($R^2 = 0.2770$), and density ($R^2 = 0.2177$) had a coefficient of determination greater than 0.20 (Table 3.3). It must be noted that relationships between light transmittance and indirect site factor, basal area, and density all were found to be non-linear.

A multiple regression approach was used to develop models for estimating light transmittance as a function of the structural attributes of stands. After evaluating each of the structural variables, the best-fit light transmittance model included the variables vertical sighting tube estimated cover, tree density, and top height and possessed a coefficient of determination equal to 0.7858.

(3.2) Light Transmittance = $b_o + b_1$Cover+ b_2Density + b_3Topht

where,

Light Transmittance = Percent understory light transmittance 1.25 m above ground

Cover = Vertical sighting tube estimated canopy cover

Density = Stand density (trees ha^{-1})

TopHt = Top Height (m)

An additional model was fit (Equation 3.3) that incorporated the spherical densiometer measure of canopy closure rather than canopy cover. Once again, all vertical structure variables were examined and the best three variable model included stand density and top height.

(3.3) Light Transmittance = $b_o + b_1$Closure + b_2Density+ b_3Topht

where,

Light Transmittance = Percent understory light transmittance 1.25 m above ground

Closure = Convex spherical densiometer estimated canopy closure

Density = Stand density (trees ha^{-1})

TopHt = Top Height (m)

This model yielded similar predictive power and fit as did model 3.2 ($R^2 = 0.7827$) (Figure 3.2).

A final series of models were also evaluated incorporating only variables derived from commonly collected tree inventory data (i.e. species, diameter, height, and crown ratio). This analysis highlighted a model of best fit that incorporated canopy cover estimated from crown width models and the vertical metric, canopy depth (CD).

(3.4) $\log(\text{Light Transmittance}) = b_o + b_1\text{CoverCW} + b_3\text{CD}$

where,

Light Transmittance = Percent understory light transmittance 1.25 m above ground

log = Natural logarithm

CoverCW = Canopy cover estimated using crown width models

CD = Crown Depth (m) (top height – average height to base of live crown)

Note that light transmittance was natural logarithmic (Log) transformed to improve linearity; the R^2 for this model is 0.5845. Model coefficients and additional fit statistics, for the models outlined above, are also presented in Table 3.3.

Discussion

One foundation of forest ecological understanding is that canopy structure can influence the understory environment. While many microclimatic variables are influenced by forest structure, the role of forest canopies on the understory light environment has received considerable interest (Anderson 1966, Jenkins and Chambers 1989, Brown and Parker 1994, Engelbrecht and Herz 2001, Hale 2003, Yirdaw and Luukkanen 2004). Past research has highlighted the effect of horizontal distribution and vertical complexity on light transmittance. By applying this relationship between light and structure to silviculture, one is able to manage understory light availability and growth of forest reproduction through canopy manipulation (Lieffers et al. 1999).

Of the single predictive measures used within this study, canopy cover (vertical sighting tube), indirect site factor (photo estimated light), and canopy closure (spherical densiometer) showed the highest correlations with light transmittance and had an R^2 values of 0.73, 0.70, and 0.68, respectively. Working in a bottomland hardwood forest, Jenkins and Chambers (1989) found a similar fit ($R^2 = 0.71$) between light and spherical densiometer estimates of canopy closure. Additional research incorporating spherical densiometer measurements (Comeau et al. 1998, Buckley et al. 1999, Bellow and Nair 2003) found better fit than our study as well as the Jenkins and Chambers (1989) study. Published work has also reported stronger relationships between light transmittance and other common indirect measures such as the vertical sighting tube (Johansson 1996), indirect site factor (Hale 2003), basal area (Vales and Bunnell 1988b, Johansson 1996, Comeau and Heineman 2003, Buckley et al. 1999), and hemispherical photo derived canopy closure (Machado and Reich 1999, Bellow and Nair 2003, Yirdaw and Luukkane 2004).

So why do our single variable relationships diverge from published data? Buckley et al. (1999) have suggested that relationships between structure and light transmittance may be stronger in stands lacking complex vertical structure. Because much of the light-structure literature reviewed was developed from stands with limited structural diversity (i.e. plantations or young even-aged stands), it is likely that vertical complexity, created by the treatments along this study's gradient, may be influencing the strength of the relationships. This notion is supported by Vales and Bunnell (1988b) who suggest that a stand’s height to base of live crown may influence the fit of structural based light transmittance models. Models developed within this study are also limited to a more restricted range of structural conditions and lower levels of light transmittance than the reviewed literature. Our current study explores a range of canopy closure of 75 to 96 percent, while the majority of reviewed work quantified light across a greater range of canopy closure conditions. It is suggested that these differences between the evaluated structural gradients may have an influence on the fit of our models when compared to other published work.

Another possible effect of the structural gradient is its influence on instrument variation. Bunnell and Vales (1990) highlighted that live crown height can influence the measured range resulting from spherical densiometer observations. Similarly, Johansson (1985) suggested that the coefficient of variation with the vertical sighting tube method increases with increasing stand density. Authors have also suggested that descriptive measures created using hemispherical photography may have limited power in stands exceeding ninety percent cover (Machado and Reich 1999, Frazer et al. 2001). Another potential influence is interactions between instrument view angle, plot size, and tree height (Bunnell and Vales 1990, Puettmann and D'Amato 2002). Combination of plot size and tree height may have caused wider angle measures to quantify structure that fell outside of the treated area, thus influencing the resulting light relationships (Bunnell and Vales 1990). Finally, species composition and sample design could influence the comparison of light-structural relationships.

While a complex combination of stand and instrument characteristics may affect the indirect assessment of the light environment under a continuous canopy cover, we were still able to develop two multiple regression models (3.2, 3.3) that explained nearly

80 percent of the variance in light transmittance. The ability of these models to explain variance in light over-and-above what is captured by canopy cover or closure is due to the incorporation of variables accounting for density and vertical profile. The inclusion of density and top height in Model 3.2 and 3.3 is supported by existing work. Comeau and Heineman (2003) developed a transmittance model based on the density and height of the tallest broadleaf tree. Similarly, Brown and Parker (1994) found mean leaf height had the highest correlation (-0.73) with understory light. Likewise, the study's best-fit model based upon tree inventory data includes not only a measure of horizontal structure, but also the vertical component, canopy depth. The presence of such variables in our models would seem to further emphasize importance of vertical structure on light transmittance.

Because of the difficulty with incorporating direct light readings into stand prescriptions, it has been suggested that structure based light transmittance models may have application in forest management (Buckley et al. 1999). Such models may allow silviculturists to quantify a stand's current light environment or to predict the potential environment resulting from a proposed treatment. Models 3.2 and 3.3 have the highest predictive power and provide the best alternative for estimating current light environment in a stand. Because the fits of these models are similar, they allow a forester to choose a model based upon instrument familiarity and the inventory variables collected. It should be noted that the vertical sighting tube method used in model 3.2 is subject to less observer bias than the spherical densiometer measures employed within model 3.3 (Johansson 1996, Vales and Bunnell 1988a). One potential drawback of Models 3.2 and 3.3 is difficult in predicting how a light environment would be altered by a proposed structural treatment. This is due to the complexity of predicting how vertical sighting tube or densiometer measurements might change in response to a given treatment.

While Model 3.4 has less predictive power ($R^2 = 0.5845$) than either Model 3.2 or 3.3, it does possess an advantage because it can provide a general estimate of understory light conditions from the collection of standard tree inventory data. Another advantage of such crown projection based transmittance models is their potential linkage to forest development models such as Forest Vegetation Simulator (FVS) (USDA Forest Service, Fort Collins, CO). Connecting such models may allow silviculturists to evaluate how a proposed treatment will affect a stand's post-harvest understory light environment.

It should be noted that the light transmittance models presented by this paper are not intended for broad application across a diversity of forest types. The paper does present structure-light relationships that are potentially applicable to mixed yellow-poplar and sweetgum stands in the southeastern United States under closed canopy conditions (50 to 100% canopy cover). However, it is strongly suggested that the direct use of the light transmittance models presented should be restricted to only those stands in the western Georgia Piedmont region that possess similar species composition, horizontal and vertical structures, site conditions, landform characteristics, and hydrologic regimes. These models help describe the relationship between forest structure and light transmittance and emphasize the important role of vertical structure. Implementation of these models may assist in estimating a stand's current light environment as well as in formulating continuous cover riparian forest management strategies that retain high forest cover, while promoting the continued development of tree reproduction. Most importantly, the paper highlights the potential importance of including both vertical and horizontal metrics into structure based light models designed for use in stands that possess heterogeneous vertical structures.

Conclusions

This study highlights the variability resulting from the use of structural measures to predict light transmittance. Of the metrics evaluated, data suggest the vertical sighting tube method of estimating canopy cover, hemispherical photo derived light estimates, and spherical density measure of canopy closure were best single predictors of light transmittance. Crown projection based approaches may also have utility by providing general light transmittance estimates using only tree inventory data and available crown width models. Potential application of the reviewed indirect methods may be limited due to low model R^2. A final relationship highlighted was that the models with the best predictive power included a vertical canopy component. Thus, our data seem to support the notion that the horizontal structure as well as the vertical canopy profile and complexity can affect the prediction of understory light transmittance.

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Table 3.1. Descriptive Statistics (n = 50) for Evaluated Forest Structural Variables

Variable	Label	Mean	Minimum	Maximum	Std Dev
Light Transmittance	Trans	7.00	3.13	21.11	3.37
Quadratic Mean Diameter	QMD	31.60	14.38	60.67	10.58
Density (trees ha^{-1})	TPH	569.20	120.00	1860.00	371.30
Basal Area (m^{2} ha^{-1})	BA	34.85	12.91	62.85	9.20
Top Height	TopHt	32.24	25.94	39.57	3.89
Height to the Base of Live Crown	HBLC	10.53	4.76	20.94	3.90
Crown Depth[1]	CD	21.72	13.12	31.27	3.93
Cover - Vertical Sight Tube	Cover	0.84	0.51	0.96	0.09
Cover - Crown Width Models[2]	CoverCW	77.24	56.20	92.72	9.55
Closure - Spherical Densiometer	Closure	0.91	0.75	0.96	0.05
Closure - Photo Angle 180	ClosurePA180	0.92	0.90	0.95	0.01
Closure - Photo Angle 120	ClosurePA120	0.87	0.80	0.92	0.03
Closure - Photo Angle 90	ClosurePA90	0.82	0.71	0.89	0.05
Closure - Photo Angle 60	ClosurePA60	0.79	0.60	0.91	0.07
Indirect Site Factor	ISF	0.13	0.08	0.17	0.02
Log(TPH * HBLC)	TPH * HBLC	8.46	7.66	9.77	0.49

[1] Crown Depth = (Top Height - Height to Base of Live Crown)

[2] Crown width model form: $b_0 + b_1$(dbh)

Table 3.2. Pearson's Correlation Coefficient Matrix for Overstory Density, Canopy Cover, and Canopy Closure Measures

Variable	TPH	BA	Cover	CoverCW	Closure	ClosurePA180	ClosurePA120	ClosurePA90
TPA	1							
BA	0.0842	1						
Cover	0.3452	0.4749	1					
CoverCW	0.7148	0.6248	0.6767	1				
Closure	0.3858	0.4536	0.8240	0.6620	1			
ClosurePA180	0.6118	0.1067	0.3974	0.4997	0.4648	1		
ClosurePA120	0.2429	0.2843	0.5614	0.4014	0.6471	0.5974	1	
ClosurePA90	0.2680	0.4252	0.6952	0.5182	0.7818	0.5168	0.9038	1
ClosurePA60	0.2653	0.4260	0.6482	0.5146	0.7199	0.3858	0.7002	0.8991

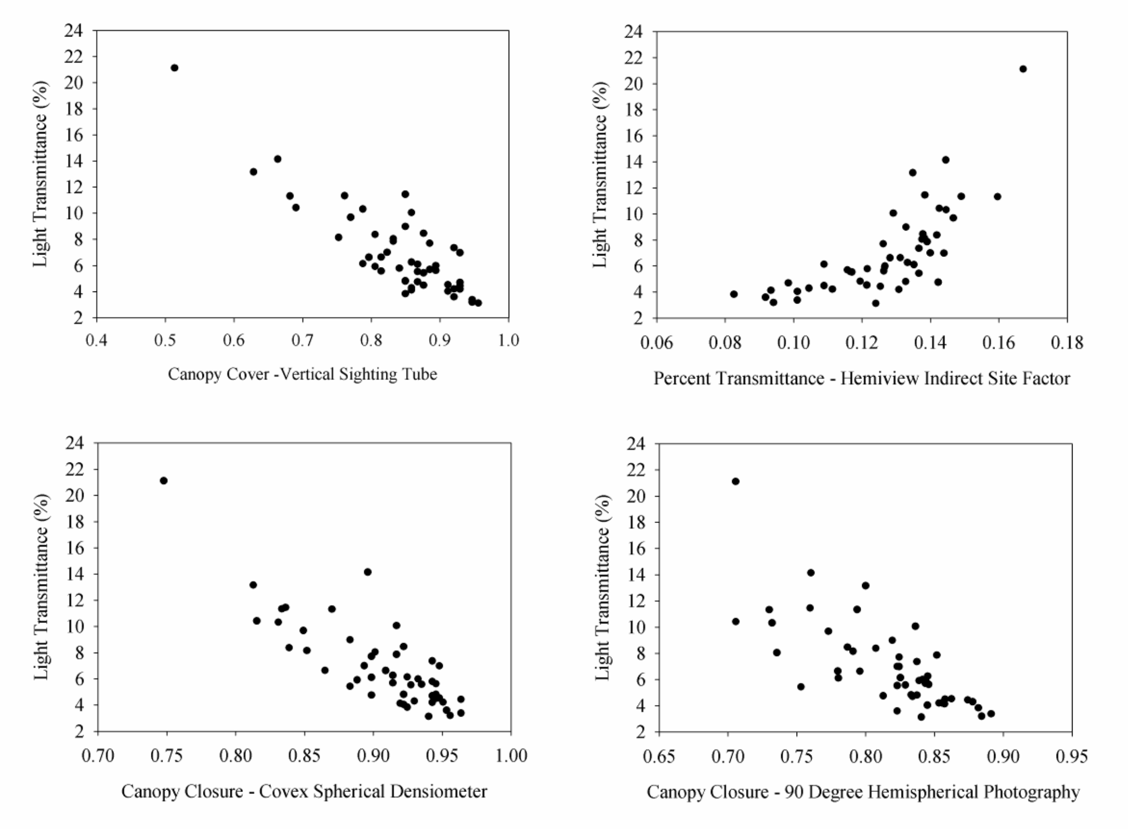
Table 3.3. Fit Statistics and Coefficients for Light Transmittance Models

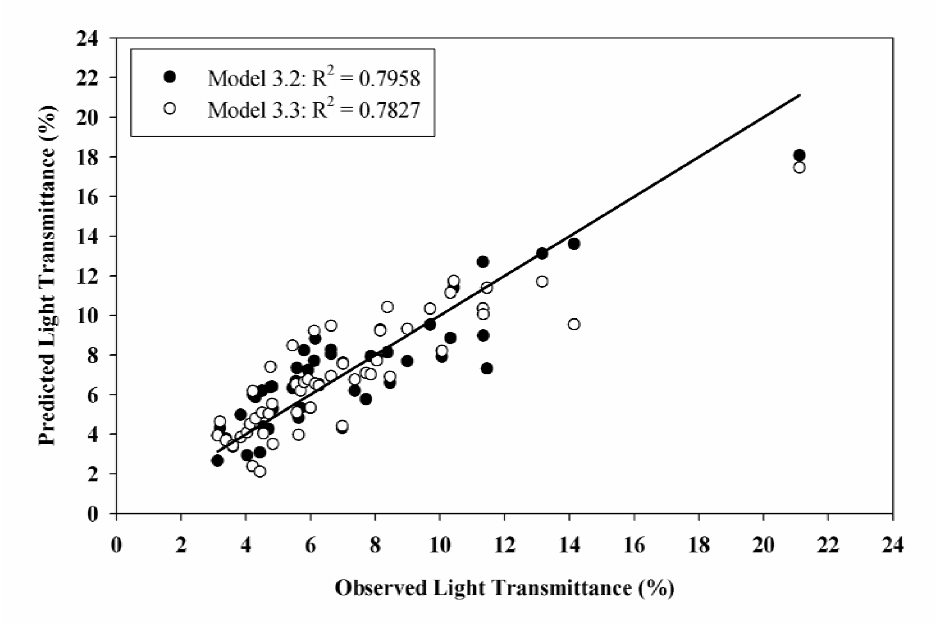
Model	R-Square	B_0	B_1	B_2	B_3
$b_o + b_1$QMD	0.0557	4.6267	0.0750	.	.
$b_o + b_1$EXP(b_2BA)	0.2770	0.8528	18.3854	-0.0327	.
$b_o + b_1$EXP(b_2Density)	0.2177	3.7909	8.2455	-0.00196	.
$b_o + b_1$TopHt	0.0449	12.9068	-0.1832	.	.
$b_o + b_1$HBLC	0.1323	3.6978	0.3135	.	.
$b_o + b_1$CD*\	0.3267	17.6316	-0.48964	.	.
$b_o + b_1$Cover	0.7271	34.5317	-32.7645	.	.
$b_o + b_1$Cover + b_2Density + b_3TopHt	0.7958	39.2201	-27.8988	-0.0026	-0.2263
$b_o + b_1$CoverCW	0.4437	25.1315	-0.23476	.	.
$b_o + b_1$CoverCW + b_2CD	0.5845	4.5541	-0.0241	-0.0385	.
$b_o + b_1$Closure	0.6804	61.0808	-59.757	.	.
$b_o + b_1$Closure + b_2Density + b_3TopHt	0.7827	64.4710	-51.2954	-0.0027	-0.2948
$b_o + b_1$ClosurePA60	0.4567	32.1480	-31.8429	.	.
$b_o + b_1$ClosurePA90	0.5495	51.5422	-54.5065	.	.
$b_o + b_1$ClosurePA120	0.3599	72.1610	-75.0082	.	.
$b_o + b_1$ClosurePA180	0.3322	165.9057	-173.4482		
$b_o + b_1$EXP(b_2ISF)	0.6994	3.2121	0.01371	42.3349	
$b_o + b_1$Log(TPH*HBLC)	0.1274	27.6345	-2.4396	.	.

Figure Captions

Figure 3.1. Relationship between understory light transmittance (%) and the vertical sighting tube (Cover), Hemiview's indirect site factor (ISF), the spherical densiometer (Closure), and 90° hemispherical photography (ClosurePA90).

Figure 3.2. Comparing the prediction of understory light transmittance (%) by Model 3.2: $b_o + b_1$Cover + b_2Density + b_3TopHt and Model 3.3: $b_o + b_1$Closure + b_2Density + b_3TopHt. The solid line represents a 1:1 reference where predicted understory light transmittance (%) equals observed transmittance.


Light Transmittance (%)
24
22
20
18
16
14
12
10
8
6
4
2
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Canopy Cover -Vertical Sighting Tube
Light Transmittance (%)
0.06
0.08
0.10
0.12
0.14
0.16
0.18
Percent Transmittance - Hemiview Indirect Site Factor
Light Transmittance (%)
0.70
0.75
0.80
0.85
0.90
0.95
1.00
Canopy Closure - Covex Spherical Densiometer
Light Transmittance (%)
0.65
0.70
0.75
0.80
0.85
0.90
0.95
Canopy Closure - 90 Degree Hemispherical Photography


Model 3.2: $R^2 = 0.7958$
Model 3.3: $R^2 = 0.7827$
Predicted Light Transmittance (%)
Observed Light Transmittance (%)
0
2
4
6
8
10
12
14
16
18
20
22
24

CHAPTER IV – RELATIONSHIP BETWEEN CANOPY STRUCTURE AND INITIAL GROWTH OF TREE REPRODUCTION ALONG A RANGE OF PARTIAL HARVEST CONDITIONS PRESENT WITHIN A SOUTHEASTERN RIPARIAN FOREST

Abstract

In order to develop structure-based silvicultural strategies that promote the development of seedling reproduction under the presence of high forest cover, one must understand the species-specific relationships between the forest canopy and seedling growth. This study explores the linkage between canopy structure and initial development of forest reproduction along a gradient of partial harvest conditions (50 to 100 % canopy cover). The structural range was created by applying one of four midstory removal treatments to each of fifty 0.05 ha plots located within a mixed-hardwood riparian forest corridor. Following midstory removals in fall 2003, twelve planting groups were established within each plot and included yellow-poplar (*Liriodendron tulipifera* L.), cherrybark oak (*Quercus pagoda* Raf.), and water oak (*Quercus nigra* L.) seedlings. Seedling survival, basal diameter, and height were monitored through two growing seasons (2004, 2005). Canopy closure estimated using hemispherical photography, canopy height, and basal area were quantified for each seedling planting group. Based upon these data, species-specific regression models were developed for predicting mortality probability as well as height and basal diameter growth. Our analysis generally suggests that no single metric can be used to describe the relationship between seedling growth and forest structure under the conditions present in the study. Of the variables evaluated, canopy height and seedling size were most strongly related to height and diameter growth. While the presented models possessed limited predictive power, they highlight the potential importance of quantifying canopy height and density as well as seeding size when evaluating and modeling the relationship between structure and seedling development.

Keywords: Canopy Structure, Forest Reproduction, Silviculture, Continuous Cover Forestry

Introduction

The growth and survival of tree reproduction is influenced by a complex interaction of environmental variables. Of these variables, considerable attention has been given to the level of photosynthetically active radiation (PAR) available in the forest understory (Vales and Bunnell 1988, Brown and Parker 1994, Comeau and Heineman 2003, Drever and Lerzman 2003) and its influence on seedling development (Smith 1940, Wang et al. 1994, Mailly and Kimmins 1997, Coates and Burton 1999, Messier et al. 1999, Mason et al. 2004). PAR is important to seedling development because it is the portion of the light spectrum (400 – 700 nm) which can be captured by plants during photosynthesis (Gendron et al. 1998). Research relating light and plant growth generally suggests that PAR availability is directly related to seedling growth. However, the specific response of a species to a given light environment is affected by its shade tolerance and its morphological and physiological plasticity (Canham 1989). Forest reproduction growth can be further altered by variables such as soil moisture and fertility (Kolb et al. 1990, Aussenac 2000, McKinley and Van Auken 2005). In response, the interacting influence between light, moisture, and fertility has been explored from a multiple resources limitation prospective. The resulting body of research has highlighted that overall growth responses and biomass allocation patterns across a gradient of resource conditions are species-specific (Kolb et al. 1900, Canham et al. 1996, Coates and Burton 1999, Mason et al. 2004). Therefore, to characterize the growth responses of forest reproduction, one must not only understand the understory environment, but also how species-specific physiology and morphological adaptations interact with a given environment.

The relationship between the understory environment and species-specific seedling development is critical to the ecological principles behind silvicultural prescriptions. This relationship has utility in traditional even-aged regeneration systems, as well as in uneven-aged and continuous cover systems that are designed to retain sufficient overwood to meet diverse objectives, while still promoting the establishment and growth of forest reproduction (Hale 2003). Modeling approaches, such as process modeling, can directly incorporate the interacting influence of specific environment factors and plant growth (Vanclay 1994). However, while process models based upon environmental variables can provide insight into the interactions between environment and growth, they can be difficult to integrate into stand prescriptions (Buckley et al. 1999). This is because silvicultural operations directly modify the forest canopy and only indirectly influence specific understory environmental variables such as light, temperature, and moisture (Daniel et al. 1979). Hence, it is suggested that in order to use seedling growth models in the direct formulation of management strategies, models must integrate variables that can describe the structural characteristics of a stand.

In contrast to models predicting seedling growth from environmental variables such as light transmittance, other models have been constructed to evaluate the relationship between forest structure and the development of forest reproduction. While these models do not directly quantify variation in specific environmental variables, structural based models consider trends in the growth environment because of the implied relationship present between forest canopy structure and the understory microclimate (Parker 1995, Aussenac 2000). Research has described seedling development within a variety of silvicultural treatments and suggests that seedling survival and growth increases with decreasing residual cover (Crow et al. 1992, Gray and Spies 1996, Larsen et al. 1997, Mitchell 2001). Other work has used specific measures such as percent canopy closure (Brandeis et al. 2001) or percent visible sky (Jain et al. 2004) to predict seedling growth, but has generally found a weaker relationship between these individual variables.

While a likely connection exists between structure and growth, other important interacting variables, such as seedling size, biomass allocation, and understory competition intensity, are not accounted for by models based solely on canopy structure. Past research has documented that initial seedling basal diameter is an important variable in predicting survival and growth of forest reproduction (Loftis 1990, Dey and Parker 1997, Mason 2001, Spetich et al. 2002). This linkage between basal diameter and growth is supported by other work which has suggested that basal diameter is highly correlated with root characteristics known to influence potential seedling growth (Johnson 1984, Johnson et al. 1984). In addition to work regarding seedling biomass characteristics, other research has highlighted the potential for understory herbaceous and woody competition to influence seedling growth and has suggested that seedling growth can be increased with the control of competing vegetation (Cain 1991, Wetzel and Burgess 2001, McGill and Brenneman 2002, Spetich et al. 2002). The existing literature regarding the development of forest reproduction shows that no one metric can explain seedling growth patterns. Therefore, it is suggested that structural based models must consider not only the properties of the forest canopy, but also seedling characteristics and the potential influence of understory competition.

Structural based seedling growth models are applicable to silviculture by managing the development of forest reproduction through structural manipulation. Understanding the relationship between structural properties of the forest canopy and corresponding growth is especially important in management systems which retain overstory canopy in perpetuity (i.e., uneven-aged and continuous cover systems), but also is of concern in even-aged systems if the regeneration of desired species relies upon advanced reproduction (Nyland 2002). In response to the potential application of structural based seedling growth models, this study will explore the relationship between forest canopy structure and the initial development of forest reproduction along a gradient of created canopy structures (50 to 100 % canopy cover) within a mixed hardwood riparian forest. Because vertical and horizontal components of the forest canopy are known to influence the understory environment (Vales and Bunnell 1988, Drever and

Lertzman 2002, Comeau and Heineman 2003), structural metrics representing both of these components will be quantified. Furthermore, the developed models will incorporate seedling biomass allocation characteristics as well as the influence of the presence and absence of herbaceous and woody understory competition. Finally, for each species evaluated by the study, the influence of structure on seedling mortality, diameter increment, and height increment over two growing seasons will be presented.

Methodology

Site Description

The study area was located in the Lower Piedmont physiographic region and the surrounding landscape consisted of rolling terrain. The research site was installed within the riparian forest corridor of a 450 ha watershed in Harris County, Georgia, U.S.A. (approximately 32° N, 85° W) (Appendix A). While the historical land-use of this riparian forest is not well understood, the local area was subjected to extensive cotton farming and periodic timber harvests of variable intensities. At the time of the study, the selected watershed was greater than 90% forested and the dominate land cover included pine plantations and natural mixed hardwood forests. The portion of the riparian corridor used for the study was approximately 2.05 km in length and was oriented in north-south direction between the adjacent upland forests. The soils of these bordering uplands were fine, kaolinitic, thermic Typic Kanhapludults (Pacolet sandy loam). Slopes found on this soil type are commonly 15 to 25 percent, but can range from 2 to 60 percent. Finally, soils within the riparian corridor study area were generally considered fine-loamy, mixed, active, thermic Oxyaquic Udifluvents (Congaree series).

The thirty-year average yearly precipitation for the region surrounding the study site was approximately 124.5 cm. Precipitation totals in the first year of the study (2004) were below average (118.8 cm), while second-year totals (2005) were above average (148.9 cm) (Figure 4.1). When considering growing season (April through September) precipitation totals, both 2004 (70.5 cm) and 2005 (86.8 cm) had greater totals than the thirty year average (59.5 cm). Additionally, a comparison of monthly precipitation patterns for the study period and thirty-year averages are presented in Figure 4.1.

The riparian corridor overstory was primarily composed of yellow-poplar (*Liriodendron tulipifera* L.) and sweetgum (*Liquidambar styraciflua* L.). Water oak (*Quercus nigra* L.), green ash (*Fraxinus pennsylvanica* Marsh.), and boxelder (*Acer negundo* L.) are minor components of the stand. A dense midstory was present across much of the area, dominated by flowering dogwood (*Cornus florida* L.), two-winged silverbell (*Halesia diptera* Ellis), musclewood (*Carpinus caroliniana* Walt.), and ironwood (*Ostrya virginiana* (Mill.) K. Koch). The understory was primarily composed of Japanese honeysuckle (*Lonicera japonica* Thunb.), Nepalese browntop (*Microstegium vimineum* (Trin.) A. Camus), and blackberry (*Rubus* spp.). Little or no advanced seedling reproduction was present within the understory. The study area was subjected to no flooding during the duration of the project.

Study Design

In August 2003, fifty 0.05 ha circular plots (12.62-m-radius) were established within portions of the riparian forest corridor that were at least 38 m wide. Plots were systematically located along a transect bisecting this corridor and a minimum of 38 m separated each plot center. To ensure that all plots were located under closed canopy conditions, establishment criteria ensured that all plot centers were not less than 19 m from the edge of the riparian corridor and not less than 12.6 m from a forest gap (> 0.025 ha).

A canopy cover gradient was then created across the 50 plots by randomly assigning one of four midstory removal treatments: Uncut - No trees were removed; Light - removed 1/3 of all midstory trees; Moderate - removed 1/2 of all midstory trees; Complete - removed all midstory trees. Midstory trees were defined as those stems not present in the dominant/co-dominant canopy layer. Structural manipulations were completed using directional chainsaw felling between August and October of 2003. Vegetation < 1.4 m tall was not removed unless it created a safety hazard during felling operations. No trees were removed from the site, but they were cut up to speed decomposition.

Following the structural manipulations, a seedling planting area was located within 6.31 m of each plot center (Appendix B). The outer portion of the 0.05 ha plot surrounding the seedling planting area served as a buffer. Within each plot's planting area, 12 seedling planting groups were established on a systematic grid. A randomly selected compass azimuth determined the directional orientation of the planting grid within each plot. In 8 of 12 planting groups within each plot, one 1-0 cherrybark oak (*Quercus pagoda* Raf.), yellow-poplar, and water oak containerized seedling were planted in a triangle pattern. Within the remaining four planting groups, one 1-0 cherrybark oak and yellow-poplar were planted. Thus, the initial planting design included a total of 400 water oak, 600 cherrybark oak, and 600 yellow-poplar. The unbalanced nature of the water oak plantings resulted from unforeseen inventory problems at the nursery. Similarly, the final planting numbers differed slightly from the planned numbers due to mislabeled species being shipped with the cherrybark oak seedlings. This phenomenon resulted in total planting numbers that included 407 water oak, 589 cherrybark oak, and 600 yellow-poplar. It should be noted that the yellow-poplar seedlings were top-clipped by the nursery. All seedlings were planted 35.6 cm apart using a gas-powered auger and were watered following planting. Because of known problems with deer browse in Piedmont forests (Romagosa and Robison 2003), each planting group was enclosed with a 71 x 122 cm circular wire mesh cage that was secured using bamboo stakes. All planting occurred within October and November of 2003.

In order to evaluate how seedling growth is influenced by the presence of understory competition, vegetation control was completed around six planting groups with each plot. To assign this treatment, each plot's planting area was divided into two sections of six planting groups each. One section was then randomly assigned the competition control treatment. The remaining six planting groups received no competition control. Herbaceous and woody understory vegetation was controlled by hand weeding within the seedling group's cage and application of Roundup Pro (3% solution by volume) around each cage. This vegetation control was completed during the 1st (June 2004) and 2nd (July 2005) growing seasons following planting.

Data Collection and Analysis

Seedling growth was monitored during two growing seasons (2004, 2005) and seedling inventories were completed prior to budbreak in the spring of 2004 and after final terminal bud formation in the fall of 2004 and 2005. At each inventory, basal diameter (mm), height (cm), and survival were recorded for the planted seedlings. Descriptive statistics for seedling planting size by inventory date are provided in Table 4.1. The number of growth flushes and height-to-dieback (cm) were also recorded for each seedling in the fall 2004 and fall 2005 inventories.

In order to link seedling growth patterns to forest structural conditions, canopy closure, basal area, and canopy height (m) were quantified over each of the 600 planting groups between April and September of 2004. Basal area was measured using a 10 basal area factor (BAF) sighting gauge and height to the forest canopy above each seedling group (i.e. canopy height) was estimated using a hypsometer. To quantify canopy closure over each seedling group, hemispherical photography was used (Beaudet and Messier 2002, Bellow and Nair 2003, Jain et al. 2004). Photos were taken 1.25 m above the center of each planting group using a Nikon Coolpix 5700 (5 megapixel) digital camera and fisheye converter (183° view angle) and were completed during overcast conditions when the solar disk was completely obscured. In addition, the camera was leveled and the fisheye lens oriented toward magnetic north using a compass prior to each photo. While research suggests digital and film hemispherical photography can produce comparable results (Englund et al. 2000, Hale and Edwards 2002), digital image size, compression, quality, and saturation can influence the analysis of digital fisheye photos (Englund et al. 2000, Frazer et al. 2001, Inoue et al. 2004). To minimize potential error associated with factors, the following camera settings were used: image quality - 1:4 compression JPEG format; saturation - black and white; and image size - full (2560x1920 pixels) (Frazier et al. 2001).

To determine percent canopy closure from each hemispherical photograph, Hemiview (Delta-T Devices, Cambridge, UK) photo analysis software was used to compute percent visible sky and canopy closure (100 % - % visible sky) was then calculated. Pixel classification threshold for 'sky' vs. 'canopy' was set individually for every photo and one analyst completed all photos. Because research suggests that the relationship between hemispherical photography and light may be influenced by the angle at which the photo is analyzed (Bellow and Nair 2003), we hypothesized that the relationship between seedling growth and photo derived canopy closure may also be influenced by view angle. In response, each photo was analyzed by constraining Hemiview's analysis circle tool to the appropriate width for a 120, 90, and 60 degree view angle. The analysis widths were determined by using trigonometry to set a leveled height pole at the appropriate distance and height from the camera. Sample photos for each view angle were taken and then imported into Hemiview. The analysis radius was set at the point of intersection with the top of the height pole in the photo. The approximate width of the analysis area for the 120, 90, and 60 degree angles are 569 Rad. (Hemiview's measure of analysis width), 392 Rad., and 261 Rad., respectively.

Analysis for this study was completed in three sections and models were developed for mortality, height increment, and diameter increment. Mortality models were fit for each species using logistic regression methods. To limit the impact of seedling damage by herbicide overspray, mortality models were constructed using only data from seedling groups that did not receive the competition control treatment. A multiple regression approach was used to fit the logistic models and seedling characteristics and seedling group specific structural data were used as predictor variables. Since the evaluated independent variables are continuous, chi-square statistics (i.e. likelihood ratio chi-square and score statistic) for assessing overall model fit could not be used because for data at the individual level the deviance did not follow a chi-square distribution (Hosmer and Lemeshow 2000). In response, model fit was assessed using the Hosmer-Lemeshow statistic and a model's predictive ability was evaluated using the area under a receiver operating characteristic (ROC) curve commonly referred to as the c statistic (Allison 1999, Hosmer and Lemeshow 2000). The c statistic ranges between a value of 0 and 1 with the predictive power of a model increasing as the c statistic approaches a value of 1. Species-specific models were constructed for first year (2004) and two-year (2004 and 2005) seedling mortality.

Species-specific height and diameter increment models were constructed using linear regression and were completed for Year 1 (2004), Year 2 (2005), and two-year (2004-2005) height increments as well as for two-year (2004-2005) diameter increment. Similar to the analysis completed for mortality models, height and diameter growth models incorporated seedling group specific canopy structure and seedling data. For height increment analysis, it should be noted that the Year 1 and Year 2 increments were adjusted for dieback that occurred within each given year and were calculated using equation 4.1.

(4.1) Height Increment Year_i = (Total Height Year_i) – (Dieback Corrected Initial Height Year_i)

In contrast, two-year height increment represents the change in overall height between planting and the end of the second growing season (Equation 4.2).

(4.2) Two-Year Height Increment = (Year-Two Height) – (Initial Planting Height)

An additional set of height increment models was also fitted for a subset of data that excluded seedlings which experienced dieback. However, this analysis produced equivalent models to those fit for the overall dataset and thus are not presented (Appendix D). To account for negative diameter increments resulting from measurement error, diameter increment data were trimmed to remove the negative values as well as the same number of positive values for each species (Appendix E). For each height and diameter model, fit was evaluated using the coefficient of determination (R^2) and residual analysis was completed to assess homogeneity of variance and normality of residuals (Appendices F, G, H, I). If problems with normality or heterogeneity of variance were present, a Box-Cox power transformation (equation 4.3) was employed (SAS Institute Inc. 2004, Ott 2005).

(4.3) $Y_t = (Y_i^{\lambda} - 1)/\lambda$, when $\lambda \neq 0$

$Y_t = \log(Y_i)$, when $\lambda = 0$

where,

Y_i = Observed Y_i

Y_t = Transformed Y_i

λ = Box-Cox Transformation Power (Lambda)

Log = Natural logarithm

Appropriate transformation powers were determined by using maximum likelihood estimates output by SAS® Transreg procedure (SAS Institute Inc. 2004). Also, for models with two or more independent variables, variance inflation factor (VIF) was used to evaluate multicollinearity. Any variable with a VIF greater than ten was removed from the model to limit potential multicollinearity problems (Neter et al. 1996). Finally, the number of independent variables to include in the final best-fit model was evaluated by assessing the p-values (alpha = 0.05) for a given parameter's significance test as well as a cumulative R^2 change test (SAS Institute Inc. 2004). Within these multiple regression models, variance uniquely explained by a given independent variable was evaluated by using squared semi-partial correlation coefficients (Cohen and Cohen 1983, SAS Institute Inc. 2004).

Results

The purpose of the randomly assigned cutting treatments imposed within the study's plots was to create a gradient of vertical and horizontal structural conditions across the 600 seedling planting groups. These structural manipulations resulted in a canopy closure gradient that range between 53 and 96 %. However, it should be noted that the canopy closure range due to the analysis angles evaluated for the hemispherical photography. The resulting closure measurements included the following ranges: 0.75 to 0.93 (120 degree photo angle), 0.64 to 0.92 (90 degree photo angle), and 0.53 to 0.96 (60 degree photo angle). With regard to basal area (m^2 ha^{-1}) and canopy height (m), the values ranged between 14.0 to 53.0 m^2 ha^{-1} and 1.1 to 36.5 m, respectively. Seedling planting group structural conditions are summarized in Table 4.2.

Mortality

Mortality over the two growing seasons presented in the study differed by species and competition control treatment. Of the seedlings planted, 2.8 % of yellow-poplar, 8.3 % of cherrybark oak, and 16.7% of water oak were dead at the start of the 2004 growing season. By the end of the first growing season, yellow-poplar experienced an additional 17.2 % mortality, while cherrybark oak and water oak each had approximately 7% additional mortality (Table 4.3). With regard to yellow-poplar, it should be noted that 71.8 % of total mortality during the 2004 growing season occurred within the competition control treatment. The logistic regression mortality models fit in the study are based upon on the subset of species groups that did not receive the competition control treatment. The analysis was completed in this manner in order to limit the impact of herbicide overspray induced mortality on the constructed probability models. For 2004 mortality, the species-specific model fitting process resulted in a model based upon the interaction of basal area and canopy height as well as canopy closure (photo angle 90).

(4.3) $\text{Prob}_{2004} = (1+\exp(-B_0 - B_1\text{BA*CH} - B_2\text{Closure90})^{-1}$

where,

Prob_{2004} = Probability of mortality 2004 growing season

BA = Basal Area (m^2 ha^{-1})

CH = Height to canopy above seedling group

Closure90 = Percent canopy closure 90 degree photo analysis angle

exp = Exponential function

B_0, B_1, B_2 = Species-specific coefficients

The predictive power of each model was assessed with the c statistic and was near 0.70 for yellow-poplar (0.735), cherrybark oak (0.699), and water oak (0.737). Mortality model coefficients and fit statistics are summarized in Table 4.4.

With regard to the second growing season, species-specific mortality percentages for yellow-poplar, cherrybark oak, and water oak equaled 3.5 %, 3.9 %, and 5.4 %, respectively. The general form of the logistic mortality models fitted for the 2005 growing season was similar to the one developed for the 2004 data. The model for water oak included the interaction of basal area and canopy height along with canopy closure (photo angle 90), while the equations for yellow-poplar and cherrybark included only the interaction of canopy height and basal area (Table 4.4). Predictive power (as measured by the c statistic) for the second growing season was equal to 0.713, 0.627, and 0.723 for yellow-poplar, cherrybark oak, and water oak, respectively.

Diameter Growth

Species-specific diameter increments (mm) were assessed using the change in basal diameter between initial planting and the end of the second growing season. The resulting two-year average diameter increments for yellow-poplar, cherrybark oak, and were equal to 3.16, 1.07, and 1.20 mm, respectively. The range of the resulting diameter increments were narrower for cherrybark oak (0 to 2.70 mm) or water oak (0 to 2.69 mm) than for yellow-poplar (0 to 10.48 mm). In the model fitting process, structural variables (Table 4.2) and seedling characteristic variables such as initial basal diameter ($\text{diam}_{\text{initial}}$), total height ($\text{ht}_{\text{initial}}$), and diam-to-height ratio ($\text{diam:ht}_{\text{initial}}$) were evaluated. The resulting best-fit models for yellow-poplar (model 4.4) and cherrybark oak (model 4.5) were Box-Cox transformed (model 4.3) to improve residual homogeneity and normality included significant predictor variables that quantified both canopy structure and seedling size. It should be noted that the Box-Cox transformation lambda coefficient was equal to 0.39 for yellow-poplar and 0.54 for cherrybark oak.

(4.4) $\boldsymbol{\Delta}$ $\text{Diam}_{\text{Box-Cox}} = B_0 + B_1\text{CH} + B_2\text{BA} + B_3\text{Diam:Ht}_{\text{initial}}$

(4.5) $\boldsymbol{\Delta}$ $\text{Diam}_{\text{Box-Cox}} = B_0 + B_1\text{CH} + B_2\text{Diam}_{\text{initial}}$

where,

$\boldsymbol{\Delta}$ $\text{Diam}_{\text{Box-Cox}}$ = Two-Year Box-Cox transformed diameter increment

CH = Height to canopy above seedling group

BA = Basal Area (m^2 ha^{-1})

$\text{Diam:ht}_{\text{initial}}$ = initial seedling diameter-to-height ratio

$\text{Diam}_{\text{initial}}$ = initial seedling basal diameter (mm)

B_0, B_1, $B_{2,}$ B_3= Species-specific coefficients

In contrast, to yellow-poplar and cherrybark oak, the water oak's best-fit model (model 4.6) included only one predictive variable, canopy closure (photo angle 60).

(4.6) $\boldsymbol{\Delta}$ $\text{Diam} = B_0 + B_1\text{Closure60}$

where,

$\boldsymbol{\Delta}$ Diam = Two-year diameter increment

Closure60 = Percent canopy closure 60 degree photo analysis angle

B_0, B_1 = Species-specific coefficients

While the resulting diameter increment models do include significant predictor variables (alpha = 0.05), the models for each species account for only a small proportion of the total variance in diameter growth and thus limited predictive power. Table 4.5 outlines the parameter coefficients and overall fit for these species-specific diameter increment models.

Height Growth

Average height increments (cm) within the first growing season (2004) equaled 32.9 cm for yellow-poplar. In comparison, first-year increment for cherrybark was 8.2 cm and 7.2 cm for water oak. The total increment range across all species followed the same pattern with yellow-poplar (3.5 to 137.5 cm) having a wider range in first-year growth than cherrybark oak (0 to 64 cm) and water oak (0 to 33.5 cm). Similar to the diameter increment, the 2004 height increments ($\mathbf{\Delta}$ Ht_{2004}) were Box-Cox transformed (model 4.3) to improve residual normality and homogeneity in the best-fit multiple regression models. For each species, the fit procedures produced models with different variable combinations. Each model included metrics of forest structure as well as initial basal diameter as a measure of seedling size as significant predictors (alpha = 0.05). The model for yellow-poplar (model 4.7) incorporated canopy height, initial seedling basal diameter, and a dummy variable (Control) representing the competition control treatment (0 = no control and 1 = understory competition controlled) and explained 23.35 % of the variance in 2004 yellow-poplar height increment.

(4.7) $\mathbf{\Delta}\ Ht_{2004\ \text{Box-Cox}} = B_0 + B_1CH + B_2Diam_{initial} + B_3Control$

where,

$\mathbf{\Delta}\ Ht_{2004\ \text{Box-Cox}}$ = 2004 Box-Cox transformed (Lamba = 0.38) height increment

CH = Height to canopy above seedling group

$Diam_{initial}$ = initial seedling basal diameter (mm)

Control = Dummy variable representing competition control treatment (0 = no control and 1 = understory competition controlled

B_0, B_1, B_2, B_3 = Species-specific coefficients

Of the parameters for yellow-poplar, canopy height uniquely explained approximately 20 % of the total variance in height increment, while each additional variable accounted for less than 2 %.

The fit height increment equation for cherrybark oak also utilized the variables, canopy height and initial basal diameter (model 4.8). This combination yielded a $R^2 = 0.2219$, but unlike yellow-poplar initial basal diameter explained the greatest amount of variance (20.5%) instead of canopy height.

(4.8) $\mathbf{\Delta}\ Ht_{2004\ Box\text{-}Cox} = B_0 + B_1 Diam_{initial} + B_2 CH$

where,

$\mathbf{\Delta}\ Ht_{2004\ Box\text{-}Cox}$ = 2004 Box-Cox transformed (Lambda = 0.32) height increment

$Diam_{initial}$ = initial seedling basal diameter (mm)

CH = Height to canopy above seedling group

B_0, B_1, B_2= Species-specific coefficients

The fit procedure for water oak resulted in a height increment model that included initial seedling basal diameter and percent canopy closure assessed using a photo analysis angle of 60 degrees.

(4.9) $\boldsymbol{\Delta}\ \mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}} = B_0 + B_1\mathrm{Closure60} + B_2\mathrm{Diam}_{\mathrm{initial}}$

where,

$\boldsymbol{\Delta}\ \mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}}$ = 2004 Box-Cox transformed (Lambda = 0.38) height increment

Closure60 = Percent canopy closure estimated with 60 degree photo analysis angle

$\mathrm{Diam}_{\mathrm{initial}}$ = initial seedling basal diameter (mm)

B_0, B_1, B_2= Species-specific coefficients

While each variable was a significant predictor at alpha = 0.05, the best-fit variable combination only managed to account for 8.2 percent of the variance in water oak's height growth.

With regard to the 2005 growing season, yellow-poplar possessed an average increment of 40.0 cm and its growth ranged from 0 to 158 cm. The height increment for cherrybark oak was 15.4 cm and ranged between 0 to 96.5 cm, while water oak's height increment and growth range were 12.3 cm and 0 to 89 cm, respectively. The growth models developed for the 2005 height increment data resulted in higher coefficients of determination than those fit from the 2004 data (Table 4.6). However, the general framework of these models was similar and included variables that quantified canopy height, canopy closure, and seedling size. Fitting procedures resulting in a predictive equation for yellow-poplar that explained 48 % of the variance in 2005 height increment and was developed using the variables canopy height, fall 2004 seedling height (Ht_{2004}), canopy closure estimated from 120 degree analysis angle (closure120), and fall 2004 seedling basal diameter (diam_{2004}).

(4.10) $\Delta\ Ht_{2005\ Box\text{-}Cox} = B_0 + B_1CH + B_2Ht_{2004} + B_3Closure120 + B_4Diam_{2004}$

where,

$\Delta\ Ht_{2005\ Box\text{-}Cox}$ = 2005 Box-Cox transformed (Lambda = 0.43) height increment

CH = Height to canopy above seedling group

Ht_{2004} = Seedling height (cm) fall 2004

Closure120 = Percent canopy closure estimated with 60 degree photo analysis angle

$Diam_{2004}$ = Seedling basal diameter (mm) fall 2004

B_0, B_1, B_2, B_3, B_4 = Species-specific coefficients

With regard to the selected variables, canopy height uniquely explained 15 % of the variance in 2005 height increment, while each remaining variable explained less than 4 %. Next, the 2005 best-fit model for cherrybark (model 4.11) included the same variables as model 4.10, but possessed an R^2 of 0.3461.

(4.11) $\Delta\ Ht_{2005\ Box\text{-}Cox} = B_0 + B_1Diam_{2004} + B_2CH + B_3Closure120$

where,

$\Delta\ Ht_{2005\ Box\text{-}Cox}$ = 2005 Box-Cox transformed (Lambda = 0.11) height increment

$Diam_{2004}$ = Seedling basal diameter (mm) fall 2004

CH = Height to canopy above seedling group

Closure120 = Percent canopy closure estimated with 120 degree photo analysis angle

B_0, B_1, B_2, B_3 = Species-specific coefficients

Specifically, the variables diam_{2004}, canopy height, and closure120 each uniquely explained 19.1%, 13.1%, and 1.3% of the variance in height increment, respectively. Thus, of the variables quantified by the study, the analysis suggests that 2005 height growth of cherrybark oak was most strongly related to seedling diameter and height to forest canopy above a given seedling. Similar to the equation developed for cherrybark oak, the one fit for water oak included previous seedling diameter, canopy height, and canopy closure (model 4.12). However, water oak's equation utilizes canopy closure estimated at a 60 degree photo angle instead of a 120 degree analysis angle.

(4.12) $\boldsymbol{\Delta}\ \text{Ht}_{2005\ \text{Box-Cox}} = B_0 + B_1\text{Diam}_{2004} + B_2\text{CH} + B_3\text{Closure120}$

where,

$\boldsymbol{\Delta}\ \text{Ht}_{2005\ \text{Box-Cox}}$ = 2005 Box-Cox transformed (Lambda = 0.21) height increment

Diam_{2004} = Seedling basal diameter (mm) fall 2004

CH = Height to canopy above seedling group

Closure120 = Percent canopy closure estimated with 120 degree photo analysis angle

B_0, B_1, B_2, B_3 = Species-specific coefficients

With regard to model 4.12, no variable present uniquely explained greater than 7 % of the variance in height increment and their combination only yielded an $R^2 = 0.1884$. While this model has decreased fit when compared to the 2005 yellow-poplar or cherrybark oak models, it possesses a higher coefficient of determination than does the 2004 water oak height increment model.

Two-year growth analysis was completed to assess height growth between initial planting and the end of the 2005 growing season. Over this two-year period yellow-poplar possessed an average increment equal to 72.3 cm. During the same time, average height growth equaled 23.2 cm for cherrybark oak and 19.4 cm for water oak. Yellow-poplar's growth across the created structural gradient was variable and ranged from essentially no net growth (0.5 cm) to nearly 2.5 meters. In comparison, two-year height growth for cherrybark oak ranged between 0.5 cm and 134 cm, while water oak's growth ranged between 0 and 99.5 cm. Looking at these 2004 to 2005 patterns from a more probabilistic perspective, yellow-poplar was the tallest species in 54.9 % of the seedling groups and possessed the largest height increment in 75.9 % of these groups. Cherrybark oak was second to yellow-poplar and was tallest in 32 % of the groups and had the greatest increment at a rate of 16.0 %. Finally, the dominance of water oak in both total height and growth increment was limited to 13.4 % and 8.1 %, respectively.

To aid in understanding how forest structure and seedling characteristics may have influenced two-year height growth patterns, species-specific multiple regression models were fit. These two-year models resulted in coefficients of determination larger than the year-one data, but less than year-two. Yellow-poplar's equation had a higher R^2 (0.3550) than did either cherrybark oak ($R^2 = 0.2582$) or water oak ($R^2 = 0.1238$) and incorporated canopy height, canopy closure (120 degree angle), and basal area.

(4.13) $\Delta Ht_{2yr\ Box\text{-}Cox} = B_0 + B_1 CH+ + B_2 Closure120 + B_3 BA$

where,

$\Delta Ht_{2yr\ Box\text{-}Cox}$ = Two-year Box-Cox transformed (Lambda = 0.38) height increment

CH = Height to canopy above seedling group

Closure120 = Percent canopy closure estimated with 120 degree photo analysis angle

BA = Basal Area ($m^2\ ha^{-1}$)

$B_0, B_1, B_{2,} B_3$ = Species-specific coefficients

While each variable in model 4.13 was a significant predictor, canopy closure (120 degree angle) and basal area each explained only about 1 % of the variance in two-year height increment. On the other hand, canopy height explained greater than 30 % of the variance. The two-year height growth models developed for cherrybark oak and water oak followed similar frameworks for models previously fit for those species. The variables used for cherrybark oak included initial seedling basal diameter and canopy height (model 4.14), while water oak's equation utilized initial seedling diameter, canopy height, and canopy closure (model 4.15).

(4.14) $\Delta Ht_{2yr\ Box\text{-}Cox} = B_0 + B_1 Diam_{initial} + B_2 CH$

where,

$\Delta Ht_{2yr\ Box\text{-}Cox}$ = Two-year Box-Cox transformed (Lambda = 0.22) height increment

$Diam_{initial}$ = Initial seedling basal diameter (mm)

CH = Height to canopy above seedling group

B_0, B_1, B_2 = Species-specific coefficients

(4.15) $\Delta\ Ht_{2yr\ Box\text{-}Cox} = B_0 + B_1 Closure60 + B_2 CH + B_3 Diam_{initial}$

where,

$\Delta\ Ht_{2yr\ Box\text{-}Cox}$ = Two-year Box-Cox transformed (Lambda = 0.29) height increment

$Diam_{initial}$ = Initial seedling basal diameter (mm)

CH = Height to canopy above seedling group

Closure60 = Percent canopy closure estimated with 60 degree photo analysis angle

B_0, B_1, B_2, B_3 = Species-specific coefficients

Unlike canopy height in equation 4.13, parameters used for models 4.14 and 4.15 explained approximately equal proportions of the variance in height growth within each of their respective models. A summary of the model coefficients, fit statistics, and Box-Cox transformation coefficients for all preceding species-specific height increment models are provided in Table 4.6.

Discussion

One critical concept underlying silvicultural strategies that promote the development of forest reproduction under presence of overstory cover is the linkage between canopy structure, above- and below-ground microenvironment, and seedling growth. It has been well documented that a forest's structural characteristics can influence the environmental factors known to control the development of forest reproduction (Parker 1995, Carlson and Groot 1997, Morecroft 1998, Assenac 2000). In turn, it has been stressed that manipulation of the forest canopy can be used to manage the forest microclimate in order to influence the development of tree seedlings and other understory vegetation as well as the growth of sub-canopy trees in mixed-species and uneven-aged systems (Lieffers et al. 1999). Moreover, because response to a given understory environment may be species-specific (Kolb et al. 1900, Canham et al. 1996, Coates and Burton 1999, Mason et al. 2004), structural-based prescriptions can be tailored based upon site conditions to favor the growth of target species over competitors that differ in ecological growth strategy (Loftis 1990b). The application of forest structure based seedling growth may therefore allow managers develop specific residual structure prescriptions that promote growth of forest reproduction as well as maintain high forest cover (Brandeis et al. 2001).

The structural models in this study suggest that no one variable can describe the species-specific relationship between structure and seedling development. Across the mortality, diameter, and height growth models, variables such as canopy height, canopy closure, basal area and seedling basal diameter were shown to be significant predictors. The importance of such variables in the development and mortality of seedlings has also been highlighted through previous research. Horizontal measures of overstory density such as basal area have been shown to be inversely related to the mortality and growth of hardwood forest reproduction (Crow 1992, Larsen et al. 1997, Mitchell 2001). Other work also supports the notion that canopy openness or closure can be related to seedling diameter and height growth (Brandeis et al. 2001, Collet et al. 2001, Kruegar and Puettmann 2004, Jain et al. 2005). The height of canopy above a seedling (canopyht) was quantified in this study in an attempt to quantify the vertical characteristics of the canopy. The developed models suggest that canopy height may be important in predicting the mortality and growth of tree seedlings. Other work, within a variety of forest types, has suggested that canopy heights and vertical complexity can influence understory microclimatic variables (Vales and Bunnell 1988, Drever and Lertzman 2002, Comeau and Heineman 2003) known to effect the development and mortality of tree seedlings (Assenac 2000). In turn, it is logical that the height to the forest canopy may influence the developmental response of understory vegetation.

In addition to variables describing the forest canopy, seedling size (basal diameter, height, or diameter:height ratio) was also included in several of the diameter and height increment models. The idea that a seedling's initial size influences its growth response is supported by other work that found that seedling basal diameter and height were significantly related to seedling development for both hardwood (Loftis 1990a, Dey and Parker 1997, Spetich et al. 2002) and conifer species (Mason 2001, Krueger and Puettmann 2004). Besides the interacting effect of forest structure and seedling size, understory competition intensity has also been suggested as a potential influence on seedling growth (Cain 1991, Wetzel and Burgess 2001, McGill and Brenneman 2002, Spetich et al. 2002). In contrast, the constructed models suggest that the presence or absence of competition was not a significant predictor of diameter or height increment. The only exception to this trend was the first-year (2004) yellow-poplar height increment model, which included the competition control dummy variable as a significant predictor. The coefficient for this parameter was negative (-0.53064) and suggests that the competition control treatment decreased height increment for yellow-poplar. Field observations suggest that the presence of this variable in the model and its negative influence on height growth may be related to the herbicide overspray damage inflicted on the yellow-poplar within the first growing season. It should be noted that improved caution was taken during the 2005 application of herbicide and minimal herbicide damage occurred during the second year.

While the height increment models constructed for Year 1 (2004), Year 2 (2005), and for two years (2004-2005) incorporated similar combinations of parameters, the fit between the three model groups was variable (Table 4.6). Each 2005 model had an improved fit when compared to 2004 or two-year models. Some potential factors that may have influenced the initial response of these seedlings to the structural gradient include planting stock quality and transplant shock. The average initial height and basal diameter for the seedlings planted were below the minimum thresholds suggested for acceptable planting stock. For comparison, Allen et al. (2001) suggests a minimum of 0.6 cm basal diameter for planting of hardwoods in Southern bottomland forests. In this study, the average basal diameter (cm) for yellow-poplar, cherrybark oak, and water oak were equal to 0.81, 0.44, and 0.42, respectively. Layered with the small planting stock is the potential for transplant shock to limit the initial growth of planted seedlings (McKay 1996, South and Zwolinski 1996). Factors such as root damage, desiccation, rough handling, and storage environment are known to degrade a seedling's post-planting performance (McKay 1996). Due to the likelihood of a carryover affect from the nursery and post-planting shock within the 2004 height growth data, only 2005 data and models will be used to discuss differences between the structure-growth relationship for yellow-poplar, cherrybark oak, and water oak. However, it must be stated that potential impact of transplant shock is not limited to only the first growing season after outplanting (South and Zwolinski 1996).

Species-specific growth patterns for the 2005 data showed that average increment and total heights were larger for yellow-poplar than the oaks. Specifically, yellow-poplar was the tallest seedling within 54.7 % of the seedling planting groups and possessed the largest two-year increment in 75.9 % of groups. Generally, yellow-poplar is considered intolerant to shade (Beck 1990) and is a fast growing, strong competitor in open conditions (Beck and Della-Bianca 1981, Beck and Hooper 1986). Our data suggest it was able to maintain positive height growth through two growing seasons below a forest canopy ranging between approximately 50 to 100 % cover. This notion is supported by Groninger et al. (1996) who found that yellow-poplar had greater two-year heights under shaded conditions (79 and 89 % shade) than in full sun. Kozlowski (1949) also states that yellow-poplar may reach near maximum photosynthetic rates at relatively low light intensities. Based upon the growth data of this study and upon other published work, it is suggested that yellow-poplar may have the ability to sustain growth when planted within partial harvests. Moreover, the different mean height increments among species indicate that underplanted yellow-poplar could represent a competitive problem for oaks within stand conditions similar to the midstory removals completed in this study. Further growth and physiological data are needed to assess the long-term dynamics between yellow-poplar, cherrybark oak, and water oak under the continued presence of an overstory canopy as well as to address potential growth response differences between naturally established and planted seedlings in these conditions.

With regard to the 2005 height increment models, each contained the variables canopy closure, canopy height, and basal diameter. The difference between the models was the overall fit and the unique contributions of the individual variables. Yellow-poplar differed from the oaks in that canopy height accounted for the majority of the total variance explained by the model. Height and basal diameter prior to the growing season were also included in yellow-poplars, while the oaks only included basal diameter. Due to poor variance explanation and predictability, direct utility of these models to the development of management systems is severely limited. Therefore, these equations should not be used to predict the specific response of cherrybark oak, water oak, and yellow-poplar.

In terms of growth trends of these species to the created gradient, the significant predictor variables do suggest that height increment may be inversely related to canopy height and closure and may be larger with increasing initial seedling size. This relationship between basal diameter and seedling development under the presence of forest cover is supported by research assessing underplanting within upland hardwood shelterwoods (Dey and Parker 1997, Spetich et al. 2000). Likewise, prescriptions presented by Loftis (1990b) implicitly suggest that seedling development can be enhanced by increasing the canopy height above a seedling cohort. Within Loftis's recommendations, he proposes the removal of a stand's midstory layers without creating large overstory gaps to enhance the development of northern red oak in the Southern Appalachian region. This midstory treatment essentially lengthens the distance between the canopy and seedlings and thus lengthens the stand's canopy height. In summary, while the models presented undoubtedly have weak predictive power, they do highlight the potential importance of quantifying canopy height and density as well as seedling size when evaluating and modeling the relationship between structure and seedling development for yellow-poplar, cherrybark oak, and water oak. In turn, to develop structural based seedling growth models that aid in the formulation of silvicultural prescriptions, one may need to incorporate seedling size characteristics as well as a combination of metrics describing the horizontal and vertical components of a forest canopy.

Conclusions

Two-year data suggest that yellow-poplar, cherrybark oak, water oak are able to maintain positive height increments in the presence of an overstory canopy between approximately 50 to 100 % cover. Moreover, during two growing seasons yellow-poplar's height increment was largest within 76 % of the planting groups. From these trends, it is suggested that underplanted yellow-poplar may potentially compete with oak seedlings growing under partial harvests conditions similar to those created in this study. However, because the data only represent initial responses, long-term competition outcome between species remain uncertain.

The models developed in the study have limited predictive power and should not be used to predict specific mortality or growth responses of yellow-poplar, cherrybark oak, or water oak seedlings. They do, however, suggest that mortality and growth of these seedlings is related to the structural and seedling variables quantified in the study. Mortality was shown to be related to the interaction between basal area and canopy height. Species-specific diameter and height increment models suggest that these growth parameters are related to stand structure as well as the size and biomass characteristics of the species. Finally, data indicate that both vertical and horizontal canopy components may be important in describing the relationship between seedling growth and forest structure.

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Table 4.1. Descriptive Statistics for Seedling Height (cm) and Basal Diameters (mm) by Inventory Date and Species

Species	Inventory Date	Seedling Height (cm)				Seedling Basal Diameter (mm)			
		Mean	Standard Deviation	Min	Max	Mean	Standard Deviation	Min	Max
Yellow-Poplar	Winter 2004	21.47	8.09	2.0	71.0	8.05	1.99	2.1	14.1
	Fall 2004	53.22	20.84	1.0	170.0	9.30	2.28	3.2	19.7
	Fall 2005	93.58	45.80	1.0	278.0	11.62	4.08	4.3	27.3
Cherrybark Oak	Winter 2004	45.77	15.54	1.0	104.0	4.44	1.44	2.0	12.5
	Fall 2004	54.41	19.19	15.5	129.0	4.90	1.67	1.5	11.5
	Fall 2005	69.54	29.81	17.0	204.0	5.71	2.04	1.9	14.5
Water Oak	Winter 2004	39.73	13.15	1.0	82.0	4.24	1.18	1.0	8.9
	Fall 2004	47.65	14.51	1.0	91.5	4.92	1.45	2.3	10.2
	Fall 2005	60.49	21.03	10.0	148.5	5.70	1.65	2.7	11.8

Table 4.2. Descriptive Structural Statistics for Seedling Planting Groups (n = 600)

Variable Description	Label	Mean	Standard Deviation	Minimum	Maximum
Basal Area (m^2 ha^{-1})	BA	28.59	6.52	14.0	53.0
Canopy Height (m) above Seedling Group	CH	14.23	8.21	1.1	36.5
% Canopy Closure - Photo Angle 120	Closure120	0.83	0.03	0.75	0.93
% Canopy Closure - Photo Angle 90	Closure90	0.77	0.05	0.64	0.92
% Canopy Closure - Photo Angle 60	Closure60	0.74	0.08	0.53	0.96

Table 4.3. Mortality by Species, Growing Season, and Competition Control Treatment

Species	Mortality Status	Number of Seedlings	
		No Competition Control	Competition Control
Yellow-Poplar	Died Post-Planting	7	10
	Died 2004	29	74
	Died 2005	9	12
	Alive Fall 2005	252	205
Cherrybark Oak	Died Post-Planting	26	23
	Died 2004	15	23
	Died 2005	15	8
	Alive Fall 2005	236	241
Water Oak	Died Post-Planting	31	37
	Died 2004	19	9
	Died 2005	12	10
	Alive Fall 2005	142	147

Table 4.4. 2004 and 2005 Growing Season Mortality Model Coefficients and Fit Statistics by Species

Mortality Models	B_0	B_1	B_2	C-Statistic	Hosmer and Lemeshow	
					Chi-Square	P-Value
Yellow Poplar:						
$\text{Prob}_{2004} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt} - B_2\text{Closure90})^{-1}$	-2.5971	-0.00385	2.0571	0.735	6.8965	0.5478
$\text{Prob}_{2005} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt})^{-1}$	-0.727	-0.00358	.	0.713	4.9938	0.7582
Cherrybark Oak:						
$\text{Prob}_{2004} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt} - B_2\text{Closure90})^{-1}$	-7.9437	-0.00199	7.3483	0.699	3.4221	0.9051
$\text{Prob}_{2005} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt})^{-1}$	-1.3985	-0.00191	.	0.627	3.3805	0.9038
Water Oak:						
$\text{Prob}_{2004} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt} - B_2\text{Closure90})^{-1}$	-9.3051	-0.00258	10.1556	0.737	5.4031	0.7138
$\text{Prob}_{2005} = (1+\exp(-B_0 - B_1\text{BA*CanopyHt} - B_2\text{Closure90})^{-1}$	-7.8618	-0.0024	9.08	0.723	6.7463	0.5642

Table 4.5. Two-Year (2004-2005) Diameter Increment Model Coefficients, Fit Statistics, and Box-Cox Transformation Lambda by Species

	B_0	B_1	B_2	B_3	Box-Cox Lambda	R^2
Yellow Poplar:						
Δ Diameter* = $B_0 + B_1$CanopyHt + B_2BA + B_3Diam:Ht$_{\text{initial}}$	1.09459	0.07848	-0.02401	-1.03851	0.39	0.2605
Cherrybark Oak:						
Δ Diameter*= $B_0 + B_1$CanopyHt + B_2Diameter$_{\text{initial}}$	-0.09533	0.02950	0.09904	.	0.54	0.1255
Water Oak:						
Δ Diameter = $B_0 + B_1$Closure60	2.36498	-1.57125	.	.	.	0.0357

* Box-Cox Transformed: $Y_t = (Y_i^{\lambda} - 1)/\lambda$, when $\lambda \neq 0$

Table 4.6. 1st Year (2004), 2nd Year (2005), and Two-Year (2004-2005) Height Increment Model Coefficients, Fit Statistics, and Box-Cox Transformation Lambda by Species

Height Increment Models*	B_0	B_1	B_2	B_3	B_4	Box-Cox Lambda	R-Square
Yellow Poplar:							
$\Delta \mathrm{Ht}_{2004} = B_0 + B_1\mathrm{CH} + B_2\mathrm{Diam}_{\mathrm{initial}} + B_3\mathrm{Control}$	4.50738	0.11132	0.12000	-0.53638	.	0.38	0.2335
$\Delta \mathrm{Ht}_{2005} = B_0 + B_1\mathrm{CH} + B_2\mathrm{Ht}_{2004} + B_3\mathrm{Closure120} + B_4\mathrm{Diam}_{2004}$	-12.35582	0.19885	0.05182	14.91452	0.26119	0.43	0.4817
$\Delta \mathrm{Ht}_{2yr} = B_0 + B_1\mathrm{CH} + B_2\mathrm{Closure120} + B_3\mathrm{BA}$	-1.01285	0.22981	11.20733	-0.05193	.	0.38	0.3550
Cherrybark Oak:							
$\Delta \mathrm{Ht}_{2004} = B_0 + B_1\mathrm{Diam}_{\mathrm{initial}} + B_2\mathrm{CH}$	-0.83747	0.58129	0.03707	.	.	0.32	0.2219
$\Delta \mathrm{Ht}_{2005} = B_0 + B_1\mathrm{Diam}_{2004} + B_2\mathrm{CH} + B_3\mathrm{Closure120}$	-4.24617	0.36859	0.06351	4.91027	.	0.11	0.3461
$\Delta \mathrm{Ht}_{2yr} = B_0 + B_1\mathrm{Diam}_{\mathrm{initial}} + B_2\mathrm{CH}$	0.57890	0.48681	0.07672	.	.	0.22	0.2582

* Height Increment ($\Delta \mathrm{Ht}_{\mathrm{year}}$) in all models are Box-Cox transformed: $Y_t = (Y_i^{\lambda} -1)/\lambda$, when $\lambda \neq 0$

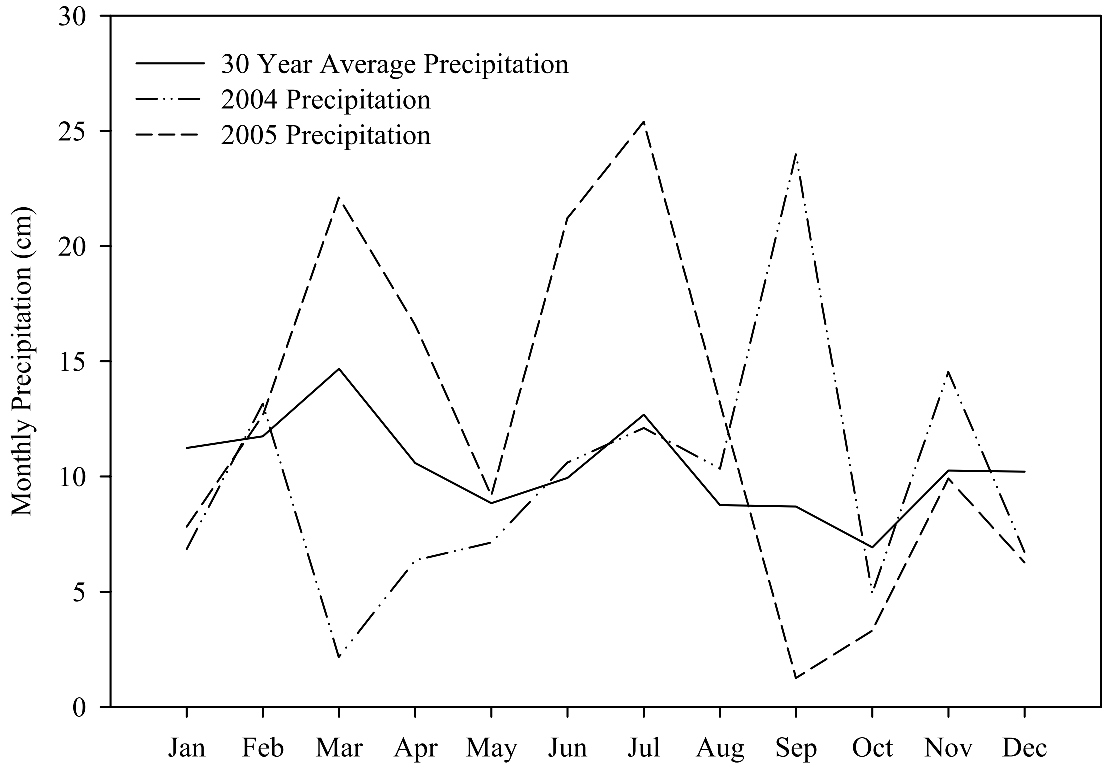
Table 4.6 (Continued). 1st Year (2004), 2nd Year (2005), and Two-Year (2004-2005) Height Increment Model Coefficients, Fit Statistics, and Box-Cox Transformation Lambda by Species

Height Increment Models*	B_0	B_1	B_2	B_3	B_4	Box-Cox Lambda	R-Square
Water Oak:							
$\Delta\ \mathrm{Ht}_{2004} = B_0 + B_1\mathrm{Closure60} + B_2\mathrm{Diam}_{\mathrm{initial}}$	4.52912	-4.48399	0.27920	.	.	0.38	0.0815
$\Delta\ \mathrm{Ht}_{2005} = B_0 + B_1\mathrm{Diam}_{2004} + B_2\mathrm{CH} + B_3\mathrm{Closure60}$	2.59343	0.31825	0.04601	-2.79805	.	0.21	0.1884
$\Delta\ \mathrm{Ht}_{2\mathrm{yr}} = B_0 + B_1\mathrm{Closure60} + B_2\mathrm{CH} + B_3\mathrm{Diam}_{\mathrm{initial}}$	5.44086	-4.02054	0.04393	0.23629	.	0.29	0.1238

* Height Increment ($\Delta\ \mathrm{Ht}_{\mathrm{year}}$) in all models are Box-Cox transformed: $Y_t = (Y_i^{\lambda} - 1)/\lambda$, when $\lambda \neq 0$

Figure Captions

Figure 4.1. 2004, 2005, and 30 year average precipitation (cm) for the portion of the western Georgia Piedmont region near Blanton Creek Wildlife Management Area


30 Year Average Precipitation
2004 Precipitation
2005 Precipitation
Monthly Precipitation (cm)
0
5
10
15
20
25
30
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

CHAPTER V – CONCLUSION

Project Summary

Uneven-aged and continuous cover forest management strategies have been proposed as alternative approaches to meet changing multiple-use forest management objectives. Each system works to retain a continued presence of forest canopy cover and both require periodic recruitment of new tree cohorts to maintain desired stand structure. Thus, successful development and implementation of such systems involves understanding the linkage between structure of the overstory canopy and its influence on the response of forest reproduction. By applying such underlying principles, silviculturists could design manipulation treatments that alter the canopy and create an understory resource environment that enhances growth within subordinate tree strata. However, complexity of the structure – environment – growth relationships can make the formulation of such management approaches difficult. Incorporation of quantitative tools that help describe these relationships may therefore aid the creation of silvicultural approaches designed to address society's diverse objectives.

The goal of this project was to expand the current understanding of the relationship between forest structure, light transmittance, and seedling growth across a gradient of riparian forest canopies ranging between 50 to 100 % cover. The project's two overall objectives were to model: 1) the relationships between canopy structure and understory PAR transmittance, and 2) the species-specific relationships between structural metrics and seedling mortality, diameter and height growth patterns over two growing seasons (2004, 2005).

The research was initiated within a mixed-hardwood riparian forest located in the lower Piedmont portion of western Georgia. The gradient required to meet the project's objectives was creating by randomly assigning one of four midstory treatments to fifty 0.05 hectare circular plots. Modeling the relationship between light and structure along the created gradient was accomplished by direct measurement of light transmittance and forest canopy characteristics. These metrics included traditional stand variables such as basal area, top height, density, and quadratic mean diameter, but also canopy cover (spherical densiometer and hemispherical photography), canopy closure, height to base of live crown measurements, and light transmittance estimated through hemispherical photography. Linear regression analysis was used to construct transmittance models based upon these data. Analysis included a comparison of individual predictors as well as models of best fit.

The seedling growth portion of the project was established within the same plots as the light transmittance work. After the midstory manipulations were complete, twelve planting groups of 1-0 containerized yellow-poplar, cherrybark oak, and water oak seedlings were established within each plot. Seedlings were planted in fall 2003 using a gas-powered auger and caged to limit animal browse. To evaluate the role of understory competition on growth of the planted seedling, half of each plot's seedling groups were randomly selected to receive an understory control treatment. Selected groups received understory competition control in 2004 and 2005 growing seasons. Assessment of canopy structure above each seedling group was completed by quantifying canopy closure (hemispherical photo estimates), basal area, and canopy heights. Species-specific mortality and growth patterns were monitored by inventorying seedling survival, basal diameter (mm), and total height (cm) in spring 2004, fall 2004, and fall 2005. Logistic regression and collected forest structure data were employed to construct mortality probability models for each species. Least-squares regression was then used to predict diameter and height increment patterns over two growing seasons for the yellow-poplar, cherrybark oak, and water oak seedlings.

Analysis of light transmittance found that the vertical sighting method of estimating canopy cover ($R^2 = 0.7271$), light transmittance estimated by Hemiview's indirect site factor ($R^2 = 0.6994$) and spherical densiometer estimates of canopy closure ($R^2 = 0.6804$) were the best single predictors of understory PAR levels. The development of multiple variable best-fit models resulted in two predictive equations with essentially the same fit ($\sim 0.79\ R^2$) and incorporated stand density and top height with either canopy cover (vertical sighting tube) or canopy closure (spherical densiometer). A best fit model incorporating only variables derived from common tree inventory data (i.e. species, diameter, height, and crown ratio) was also fitted. This process resulted in an equation with a coefficient of determination equal to 0.58 and included the variables canopy cover (crown width model estimated) and canopy depth (top height – height to base of live crown). While the hemispherical photographic did not yield superior fit to other measures, it did suggest that the angle in which a photograph is analyzed can influence the relationships between Hemiview's output and light transmittance. Regression analysis found that canopy closure estimates using a ninety degree photo angle had better fit than 60, 120, or 180 degree angles. Finally, results suggest that a combination of horizontal and vertical metrics may be necessary to assess the relationship between structure and light transmittance within vertically heterogeneous forests.

Similar to the models predicting light transmittance, seedling development analysis suggests that mortality and growth are influenced by both horizontal and vertical structure. First, species-specific equations developed using logistic methods found that the interaction between basal area and canopy height along with canopy closure estimated using hemispherical photographs (90 degree analysis angle) were the best predictors of year-one and two-year mortality. The ability of these equations to predict morality was evaluated using the c statistic (Allison 1999, Hosmer and Lemeshow 2000) and showed the presented models were able to appropriately predict mortality on approximately 65 and 75 percent of seedlings. Further analysis of model predictions showed that, at a given basal area and canopy closure, the probability of mortality increases as canopy height decreases. Hence, it is suggested that the mortality of yellow-poplar, cherrybark oak, and water oak are influenced by both horizontal and vertical components of the forest canopy.

Analysis of diameter growth over two growing seasons revealed that the variables measured in the study did not sufficiently explain species-specific patterns. Regression procedures resulted in models that accounted for only a small portion of the variance in diameter growth for yellow-poplar ($R^2 = 0.26$), cherrybark oak ($R^2 = 0.13$), and water oak ($R^2 = 0.04$). Poor fit of these models inhibits them from being used as predictor equations, but their inclusion of significant predictors suggests variables that may influence diameter growth of these species. General frameworks of resulting models suggest that horizontal structure (canopy closure and basal area), canopy heights, and seedling size may affect diameter growth.

Height growth patterns within two growing seasons suggest the resource environment present along the gradient favored the development of yellow-poplar over the oaks. This is supported by the fact that yellow-poplar was the tallest seedling within 54.7 percent of the planting groups and possessed the largest two-year increment in 75.9 percent of groups. Species-specific height increment models were developed for year-one (2004), year-two (2005), and two-year (2004 to 2005) seedling data. All species height increment coefficients of determination were highest in year-two and lowest for year-one. Similarly, time period specific R^2 coefficients were arranged in the following species order: yellow-poplar > cherrybark oak > water oak. General model parameter trends suggest that height increments were related to the latent variables forest structure and seedling size. Structural variables related to height growth included canopy height, canopy closure, and basal area. Models also incorporated descriptors of seedling size such as basal diameter and total height prior to a given growing season. In contrast to some other studies, understory competition control was a significant predictor only in year-one yellow-poplar growth and its negative influence on height was likely due to herbicide damage that occurred during initial competition control treatments. Overall relationships in the presented models demonstrate that seedling develop may be influenced by a combination of stand structure parameters as well as the specific size characteristics of a given seedling.

The objectives of this research project were to explore the relationship between structure and light along with structure and seedling growth. Models that indirectly estimate understory light transmittance using metrics of forest structure were developed. In addition, equations for predicting mortality probability, diameter growth, and height increment were provided. Insight provided by the models suggests that no single metric of forest structure can describe patterns in light transmittance or seedling development. Most importantly, results emphasize the potential importance of quantifying the vertical characteristics of the canopy when evaluating the influence of stand structure on the understory environment or seedling growth within structurally complex forest systems.

Implications in Management and Research

Potential application avenues for light transmittance models presented by this research are twofold. First, best-fit equations might potentially be useful for indirectly estimating understory light environments within mixed yellow-poplar/sweetgum stands that range from 50 to 100 percent cover. Such estimates may allow foresters to evaluate a stand's understory light availability without needing costly light measurement equipment. Combining light estimates with existing models predicting seedling growth using light levels might also allow managers to evaluate whether or not a stand's understory was conducive to the development of a given species. Secondly, presented tree inventory based equations could be employed to evaluate how a change in canopy structure might alter the understory light environment. This process would be completed by using these light models in conjunction with forest development software such as Forest Vegetation Simulator (FVS). Forest development software would first be used to predict how a stand's current structure would change from proposed treatments. Next, software structural outputs could be input into the light model to estimate understory

PAR transmittance. The outlined process might serve as a quantitative aid for use in the development of silvicultural strategies geared toward development of seedling reproduction under existing forest canopy. However, it is strongly cautioned that the direct use of the untested light transmittance models presented should be restricted to only those stands in the western Georgia Piedmont region that possess similar species compositions, horizontal and vertical structures, site characteristics, and hydrologic regimes.

Because the study's structure based seedling development models had low predictive power and were developed from data collected on a single site, presented equations should not be used in the direct estimate of mortality or growth. The models do, however, provide useful insight into potential structural variable combinations that may be related to the successful development of seedlings within stands possessing at least 50 percent cover. Of these variables, canopy height and seedling basal diameter were shown to be important in predicting height growth. Results showed that as basal diameter or canopy height increased height increments increased. Such trends suggest that planting larger seedling stock may increase their potential for positive height increment. Likewise, models suggest that as the height from a seedling to the forest canopy increases its height growth may increase and mortality may decrease. Consequently, it is suggested that partial harvest strategies which increase canopy heights have the potential to enhance yellow-poplar, cherrybark oak, and water oak seedling development. Above all, results highlight the importance of considering the potential effects of canopy structure and plant size on the development of forest reproduction.

Future Research

Many potential avenues of research stem from the research presented here. These avenues include understory environment modeling, long-term seedling competition dynamics, methodologies for quantifying forest structure, and prediction of crown dynamics. However, with regard to management and restoration of riparian forest systems of the southeastern United States, I feel future research applying the inferences gained from the study's models to management warrants further discussion. Essentially, this research links the ecological relationships between forest structure, understory environment, and seedling growth to the formulation of silvicultural strategies for developing forest reproduction under existing canopy cover. A series of management strategies designed using computer simulations could be applied directly in the field. The ability of the selected management approaches to successfully establish and grow desired forest reproduction within partial harvests would then be evaluated. Such work may result in the development of alternative silvicultural strategies for addressing society's diverse objectives. Likewise, it would suggest whether or not the ecological relationships identified by the models designed in this study are applicable to a broader array of species compositions and stand structures.

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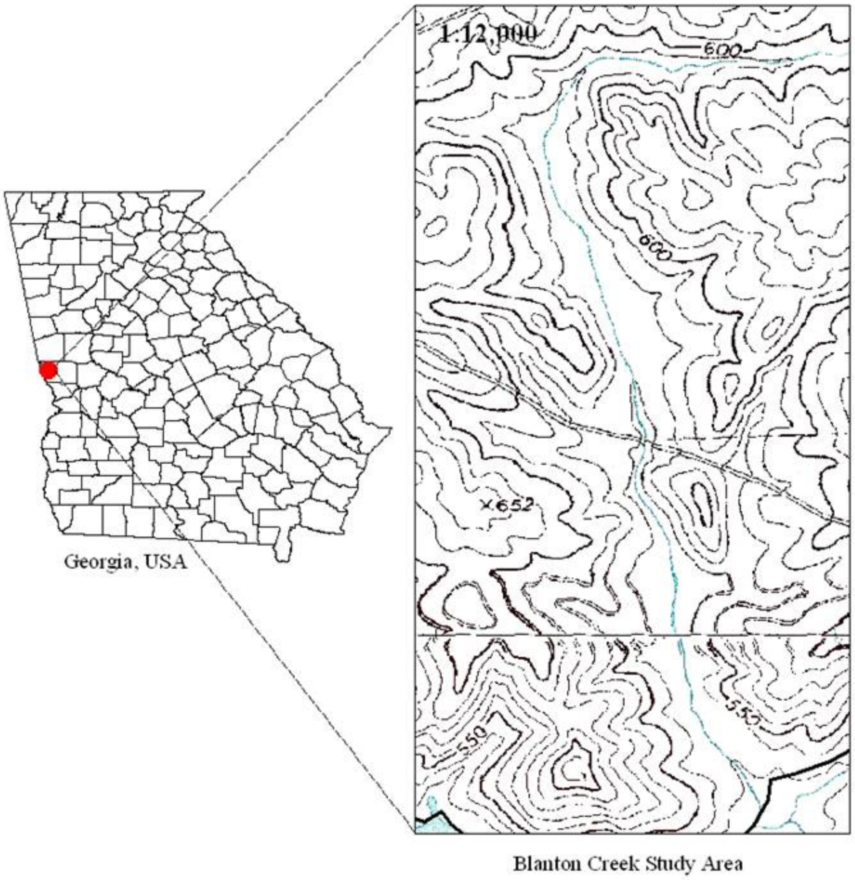
APPENDICES

APPENDIX A

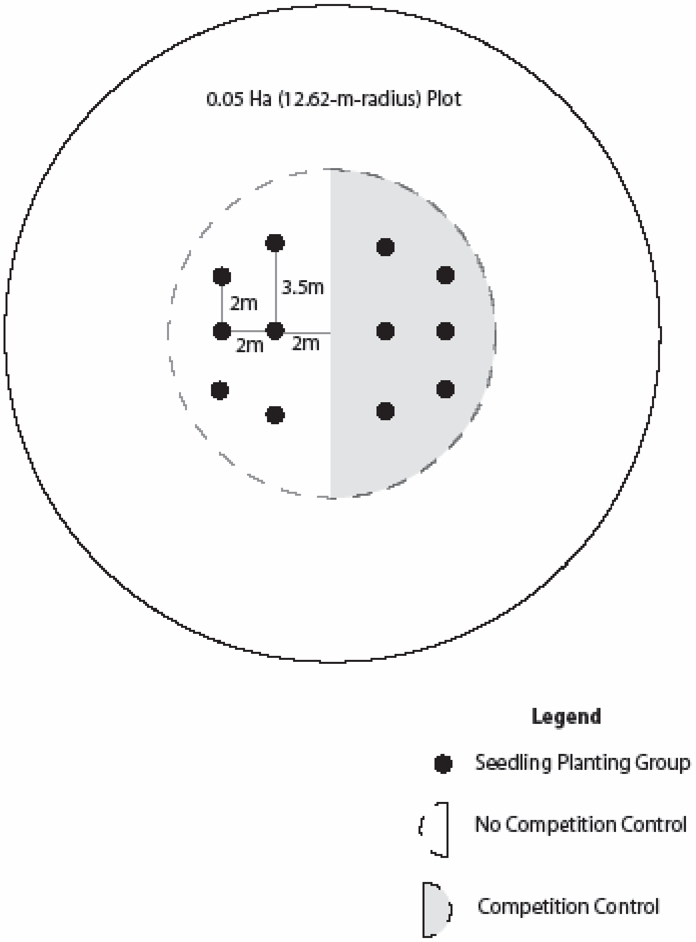
STUDY LOCATION MAP



Appendix A.1. Blanton Creek study site geographic location and topographical map

APPENDIX B

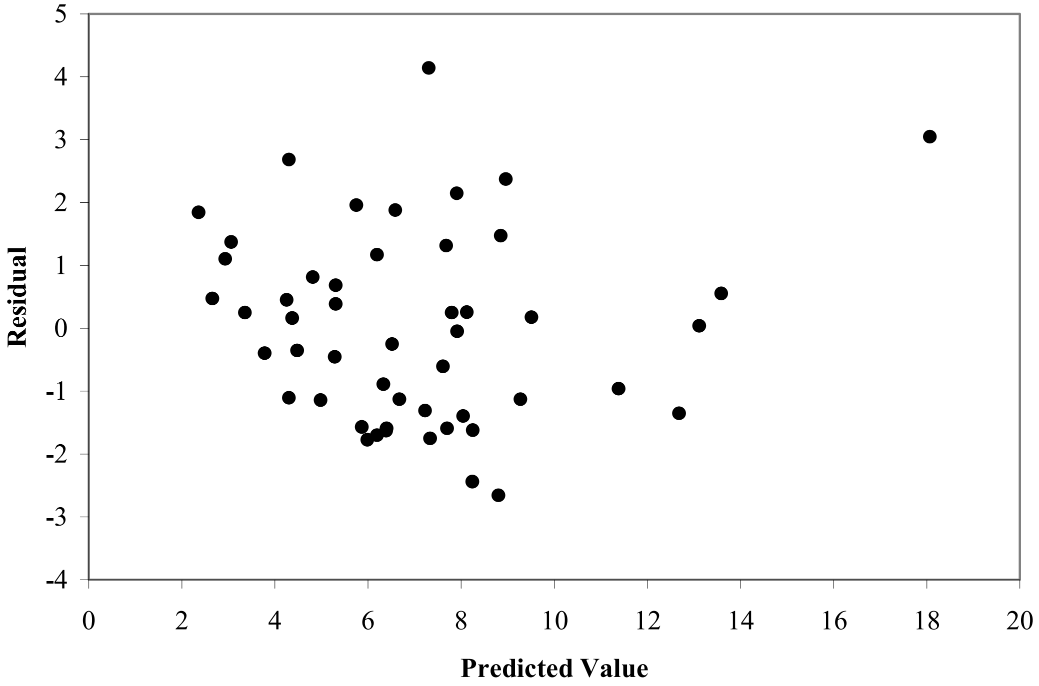
0.05 HECTARE SAMPLE PLOT DESIGN



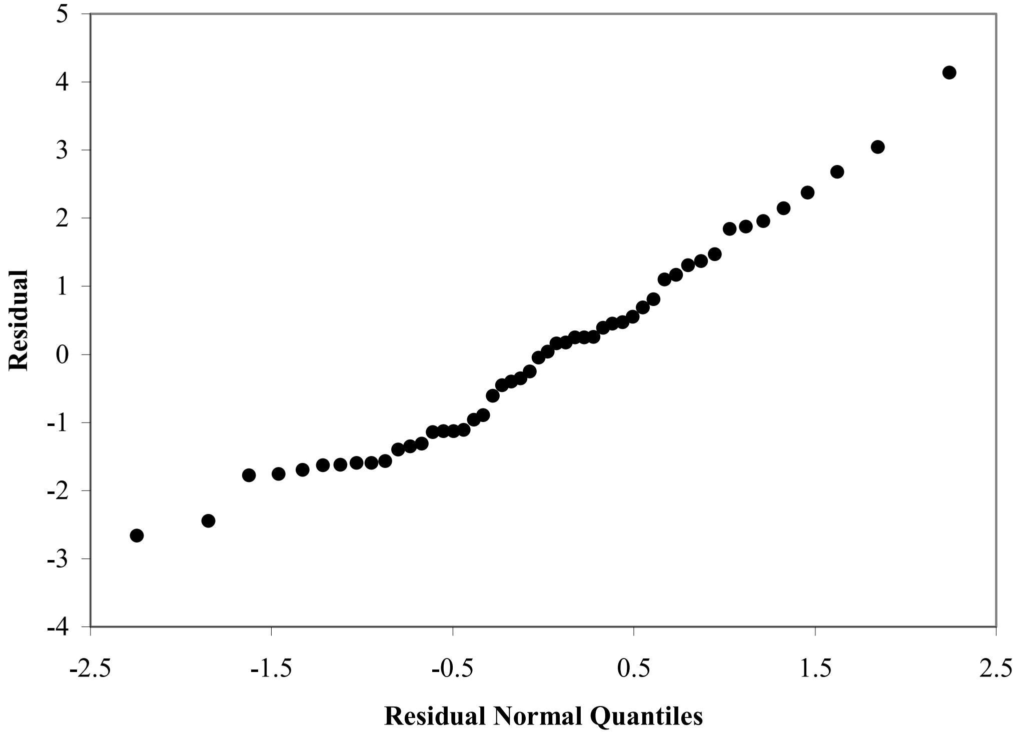
Appendix B.1. Blanton Creek study plot seedling planting group and competition control treatment design

APPENDIX C

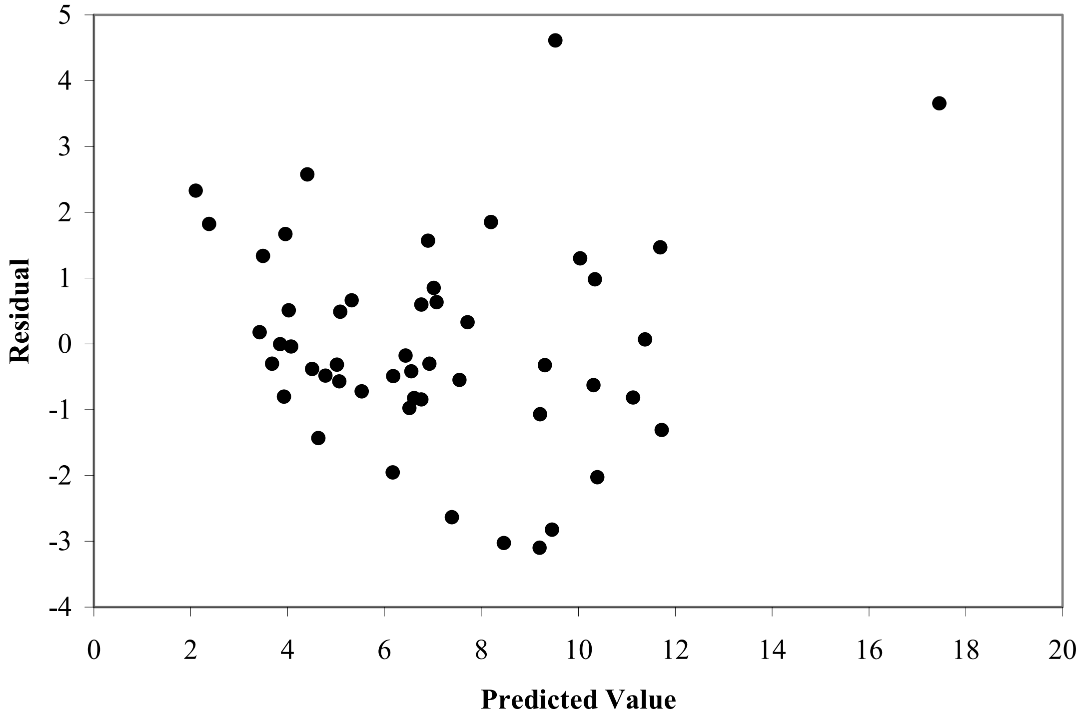
RESIDUAL PLOTS - LIGHT TRANSMITTANCE MODELS



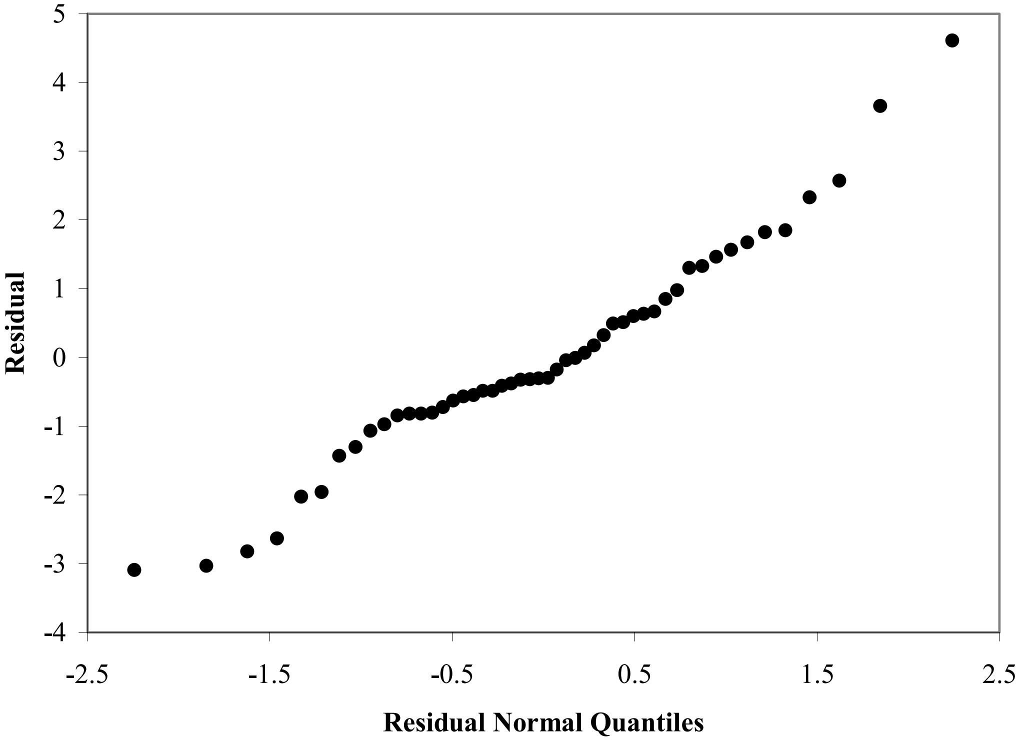
Appendix C.1. Residual vs. predicted plot for model 3.2 -- Light Transmittance % = b_o + b_1CoverD + b_2TPH + b_3TopHt ($R^2 = 0.7958$)



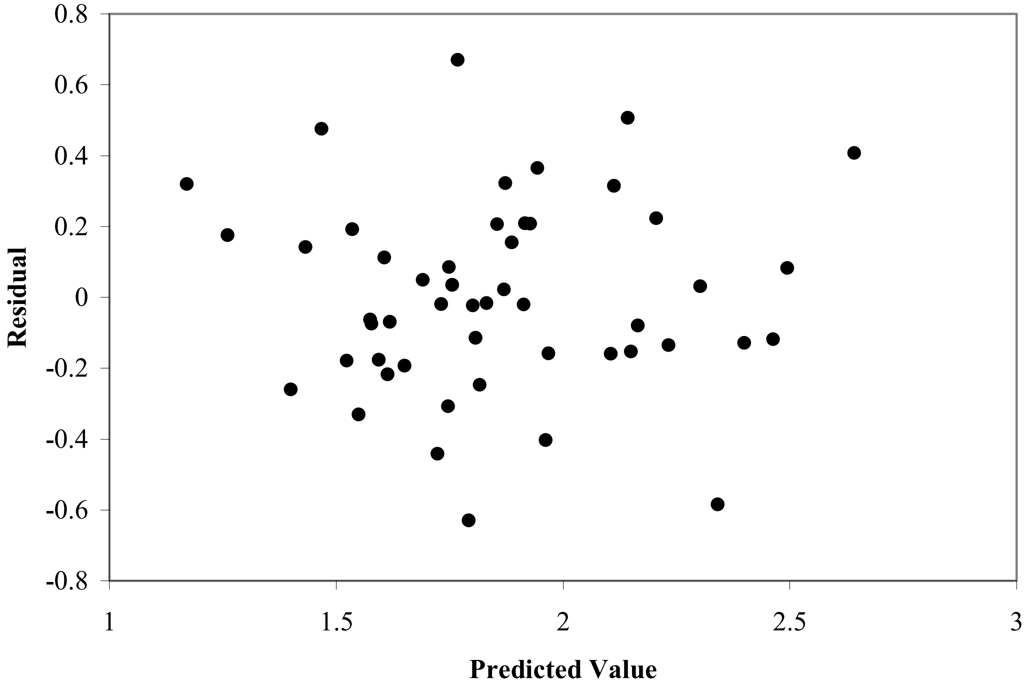
Appendix C.2. QQ-plot for Model 3.2 -- Light Transmittance % = b_o + b_1CoverD + b_2TPH + b_3TopHt ($R^2 = 0.7958$)



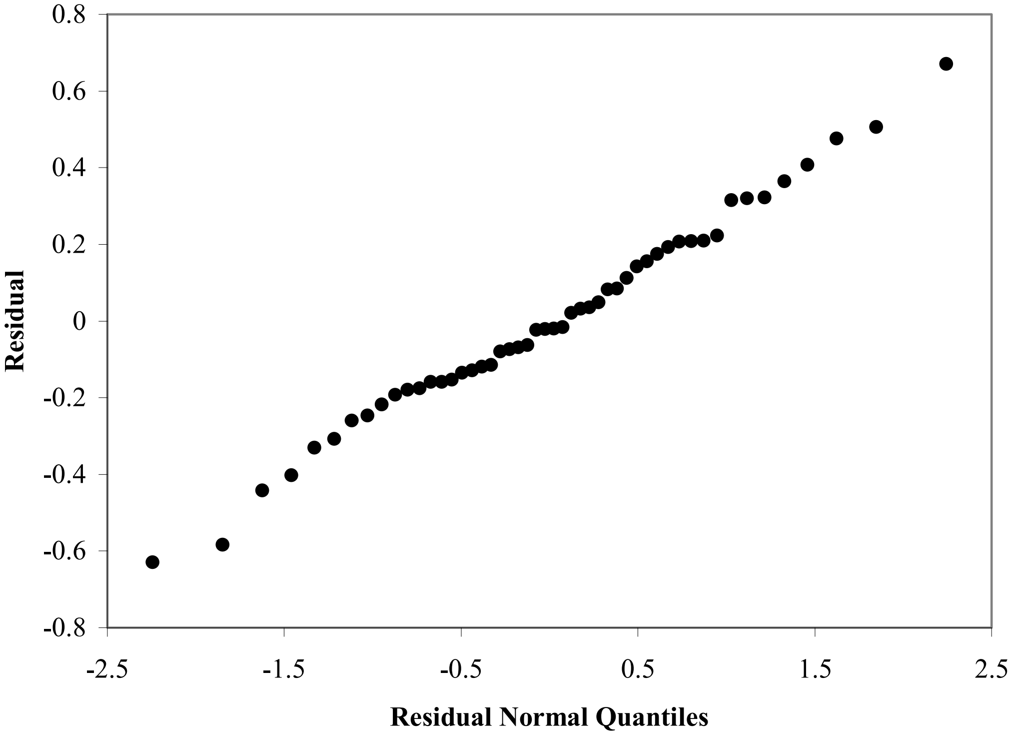
Appendix C.3. Residual vs. predicted plot for Model 3.3 -- Light Transmittance % = b_o + b_1Closure + b_2 + b_3TopHt (R^2 = 0.7827)



Appendix C.4. QQ-plot for Model 3.3 -- Light Transmittance % = b_o + b_1Closure + b_2 + b_3TopHt ($R^2 = 0.7827$)



Appendix C.5. Residual vs. predicted plot for Model 3.4 – log(Light Transmittance %) = $b_o + b_1$CoverCW+ b_2 CD ($R^2 = 0.5845$)



Appendix C.6. QQ-plot for Model 3.4 -- Light Transmittance (%) = b_o + b_1CoverCW+ b_2 CD ($R^2 = 0.5845$)

APPENDIX D

HEIGHT INCREMENT MODELS FOR DATA SUBSET REMOVING DIEBACK SEEDLINGS

Appendix D.1. 2005 yellow-poplar Box-Cox transformed (Lambda = 0.42) height increment model for data subset removing dieback seedling

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	2667.075	666.769	103.98	<.0001
Error	424	2718.854	6.41239		
Corrected Total	428	5385.929			

Root MSE	2.5323	R-Square	0.4952
Dependent Mean	8.1898	Adj R-Sq	0.4904
Coeff Var	30.92		

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	-9.7658	3.0678	-3.18	0.0016	0
CH	1	0.18652	0.0167	11.17	<.0001	1.2175
Ht_{2004}	1	0.0496	0.00854	5.81	<.0001	1.98228
Closure120	1	12.08306	3.67805	3.29	0.0011	1.02437
$Diam_{2004}$	1	0.25865	0.07247	3.57	0.0004	1.85714

Appendix D.2. 2005 cherrybark oak Box-Cox transformed (Lambda = 0.11) height increment model for data subset removing dieback seedling

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	288.37045	144.1852	107.93	<.0001
Error	421	562.41066	1.33589		
Corrected Total	423	850.78112			

Root MSE	1.15581	R-Square	0.3389
Dependent Mean	2.56184	Adj R-Sq	0.3358
Coeff Var	45.1164		

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	-0.18571	0.19822	-0.94	0.3494	0
Diam_{2004}	1	0.37249	0.0345	10.8	<.0001	1.00725
CH	1	0.06268	0.00695	9.01	<.0001	1.00725

Appendix D.3. 2005 water oak Box-Cox transformed (Lambda = 0.21) height increment model for data subset removing dieback seedling

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	130.72481	43.57494	18.45	<.0001
Error	224	528.93045	2.3613		
Corrected Total	227	659.65526			

Root MSE	1.53665	R-Square	0.1982
Dependent Mean	2.8567	Adj R-Sq	0.1874
Coeff Var	53.7911		

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	4.08476	1.8315	2.23	0.027	0
Diam_{2004}	1	0.31965	0.07423	4.31	<.0001	1.07284
CH	1	0.05346	0.01466	3.65	3E-04	1.16916
Closure90	1	-4.68956	2.0821	-2.25	0.025	1.24537

Appendix D.4. Two-year (2004 to 2005) yellow-poplar Box-Cox transformed (Lambda = 0.32) height increment model for data subset removing dieback seedling

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	837.98696	279.32899	80.42	<.0001
Error	425	1476.11109	3.4732		
Corrected Total	428	2314.09806			

Root MSE	1.8637	R-Square	0.3621
Dependent Mean	8.8431	Adj R-Sq	0.3576
Coeff Var	21.075		

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	1.34976	2.2518	0.6	0.5492	0
CH	1	0.17477	0.01129	15.48	<.0001	1.02616
Closure120	1	7.25067	2.75044	2.64	0.0087	1.05973
BA	1	-0.04073	0.01411	-2.89	0.0041	1.05084

Appendix D.5. Two-year (2004 to 2005) cherrybark oak Box-Cox transformed (Lambda = 0.22) height increment model for data subset removing dieback seedling

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	369.34383	184.67191	77.94	<.0001
Error	413	978.56395	2.3694		
Corrected Total	415	1347.90778			

Root MSE	1.53929	R-Square	0.274
Dependent Mean	3.95723	Adj R-Sq	0.2705
Coeff Var	38.89814		

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	0.52805	0.29084	1.82	0.0702	0
$Diam_{initial}$	1	0.49598	0.05296	9.37	<.0001	1.00166
CH	1	0.08014	0.00929	8.63	<.0001	1.00166

Appendix D.6. Two-year (2004 to 2005) water oak Box-Cox transformed (Lambda = 0.30) height increment model for data subset removing dieback seedling

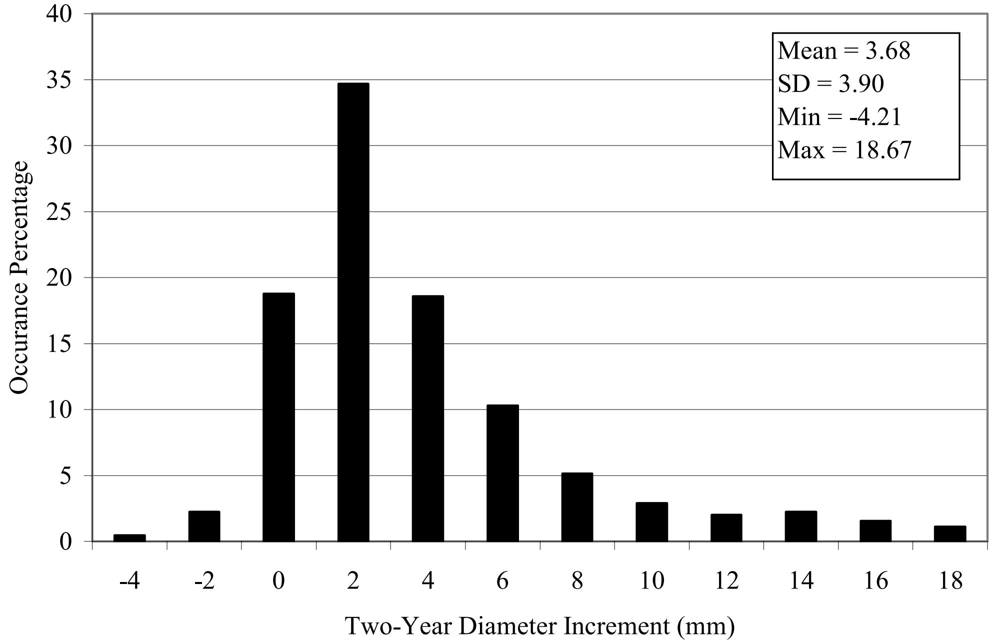
Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	107.47891	35.8263	10.98	<.0001
Error	221	720.91309	3.26205		
Corrected Total	224	828.39199			

Root MSE	1.8061	R-Square	0.1297
Dependent Mean	4.3994	Adj R-Sq	0.1179
Coeff Var	41.054		

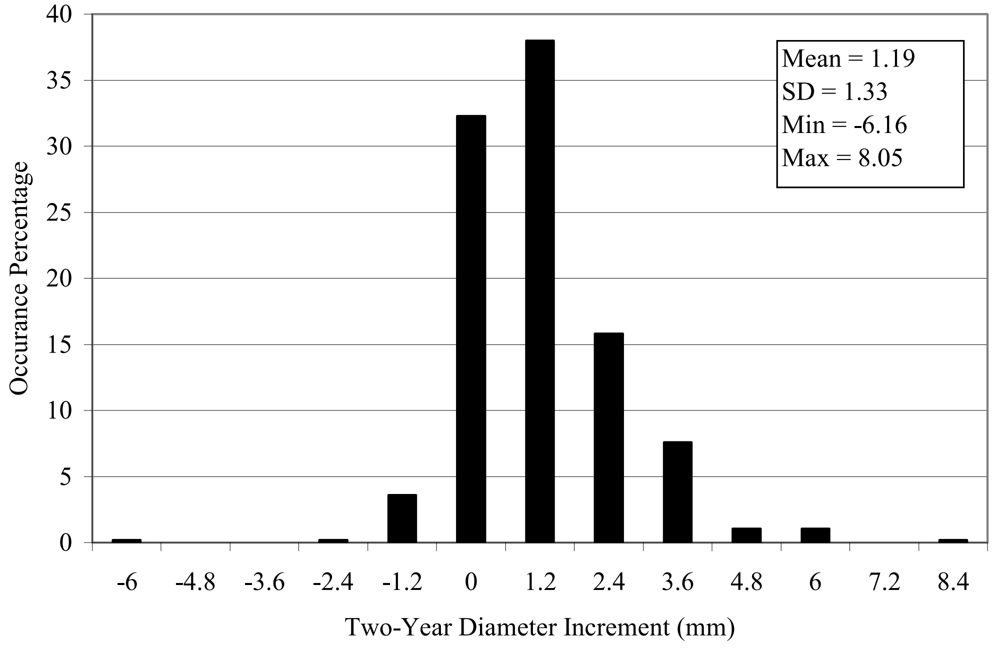
Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|	Variance Inflation
Intercept	1	7.40535	1.34802	5.49	<.0001	0
Closure60	1	-5.75985	1.55767	-3.7	0.0003	1.28709
Diam:$Ht_{initial}$	1	7.30444	3.82829	1.91	0.0577	1.00469
CH	1	0.03194	0.01821	1.75	0.0808	1.2884

APPENDIX E

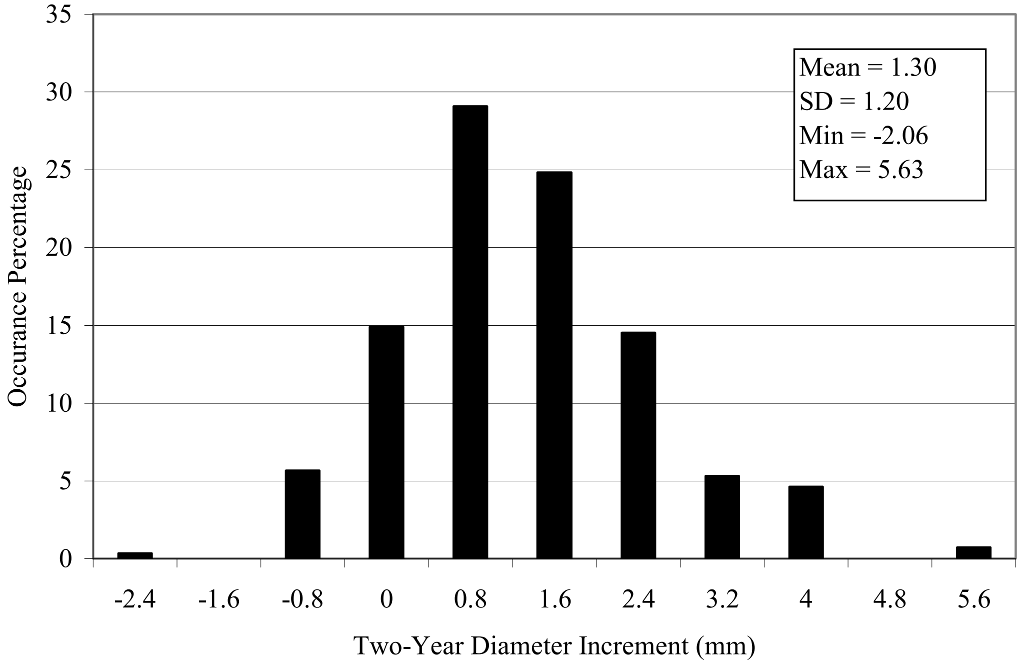
DATA DISTRIBUTIONS FOR UNTRIMMED AND TRIMMED SEEDLING DIAMETER INCREMENT DATASETS BY SPECIES



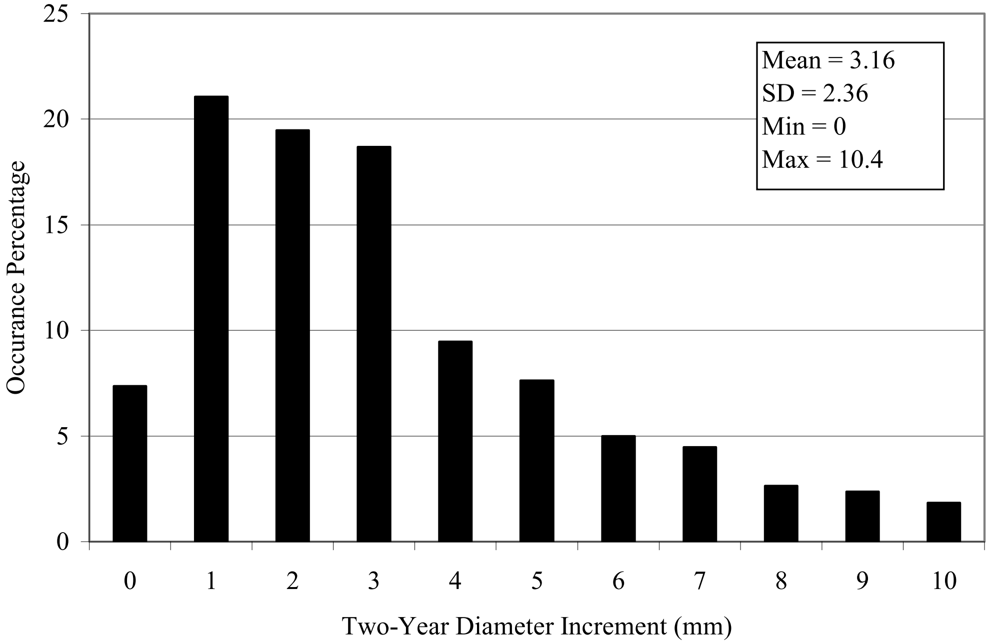
Appendix E.1. Data distribution for untrimmed seedling diameter increments: yellow-poplar



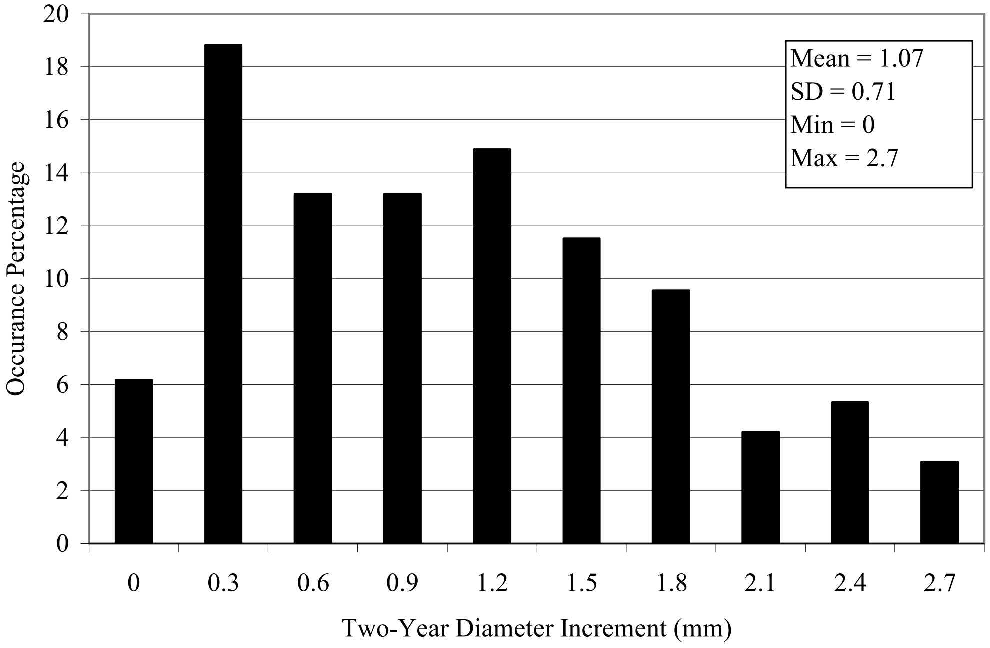
Appendix E.2. Data distribution for untrimmed seedling diameter increments: cherrybark oak



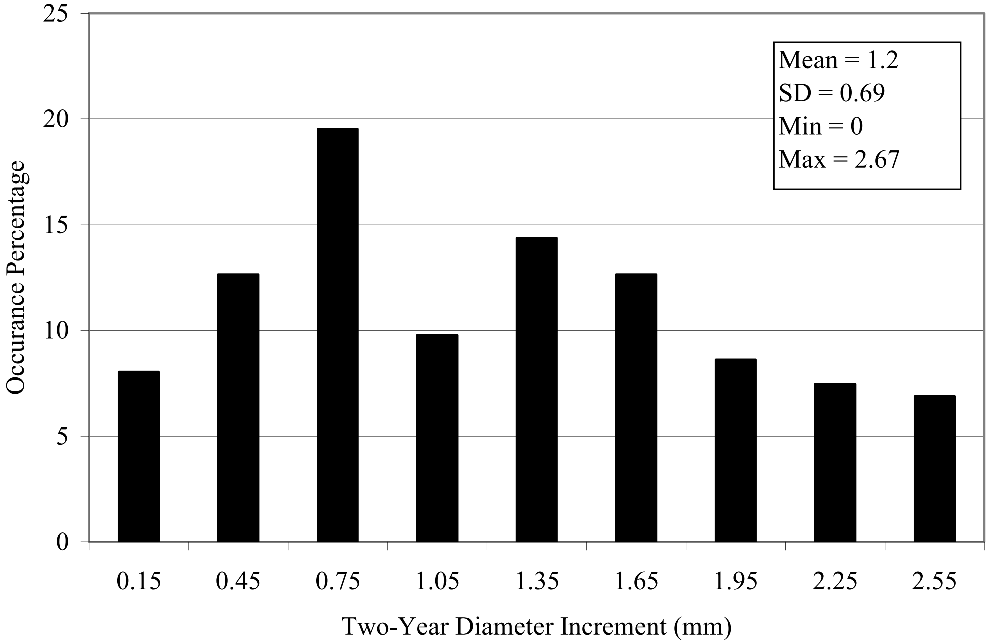
Appendix E.3. Data distribution for untrimmed seedling diameter increments: water oak



Appendix E.4. Data distribution for trimmed seedling diameter increments: yellow-poplar



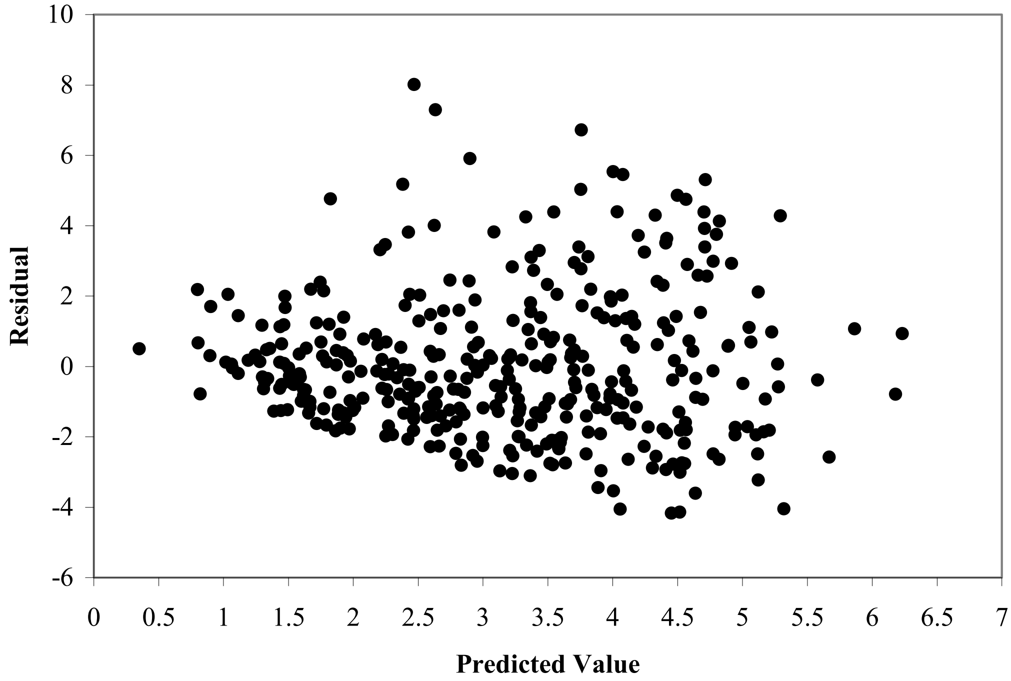
Appendix E.5. Data distribution for trimmed seedling diameter increments: cherrybark oak



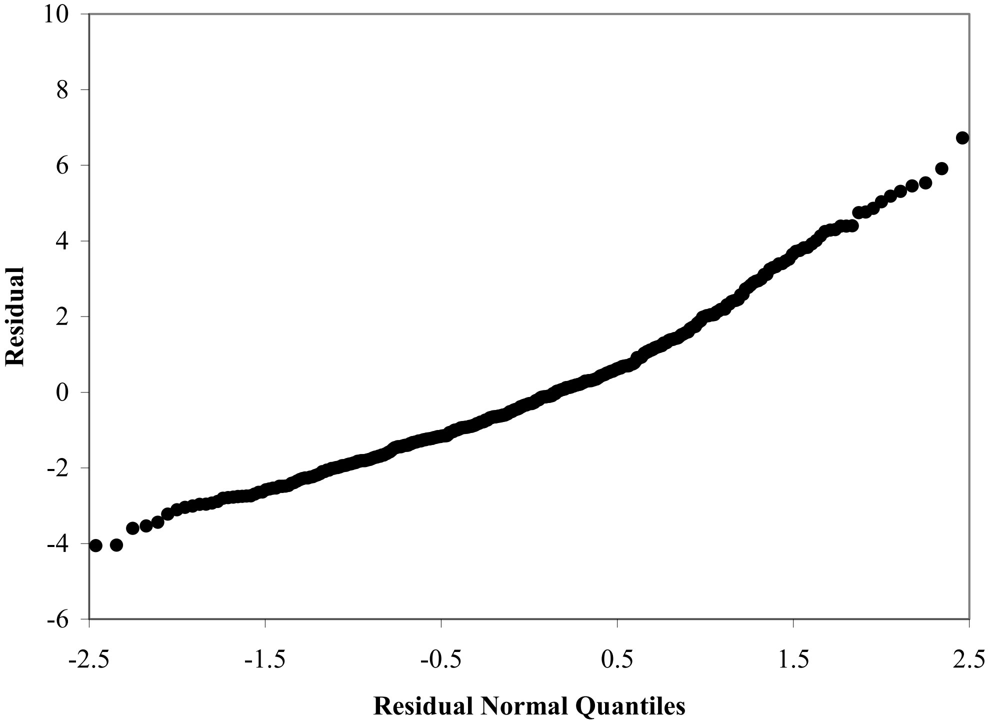
Appendix E.6. Data distribution for trimmed seedling diameter increments: water oak

APPENDIX F

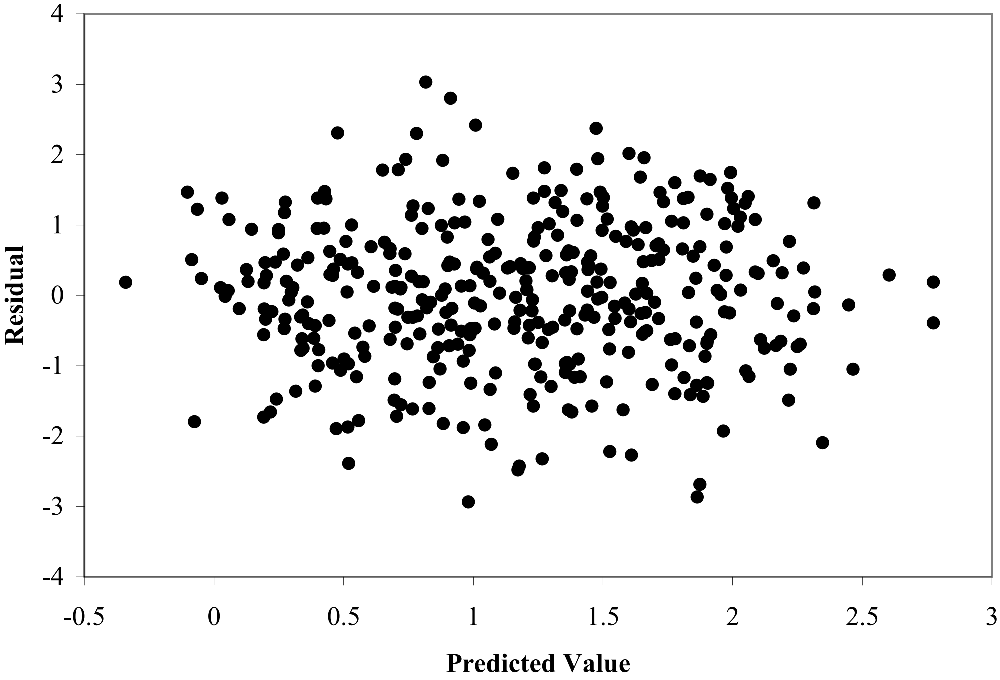
RESIDUAL ANALYSIS PLOTS FOR SPECIES SPECIFIC TWO-YEAR (2004 TO 2005) UNTRANSFORMED AND BOX-COX TRANSFORMED DIAMETER INCREMENT MODELS



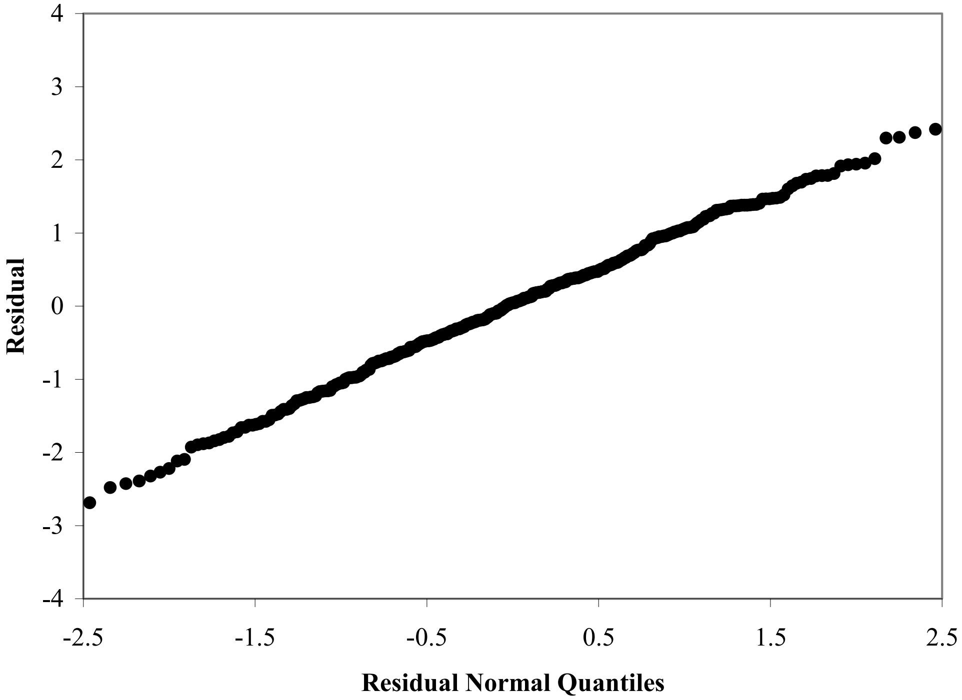
Appendix F.1. Residual vs. predicted plot for yellow-poplar two-year (2004 to 2005) untransformed diameter increment model: Δ Diam = $b_0 + b_1$CH + b_2BA + b_3Diam:Ht$_{\text{initial}}$



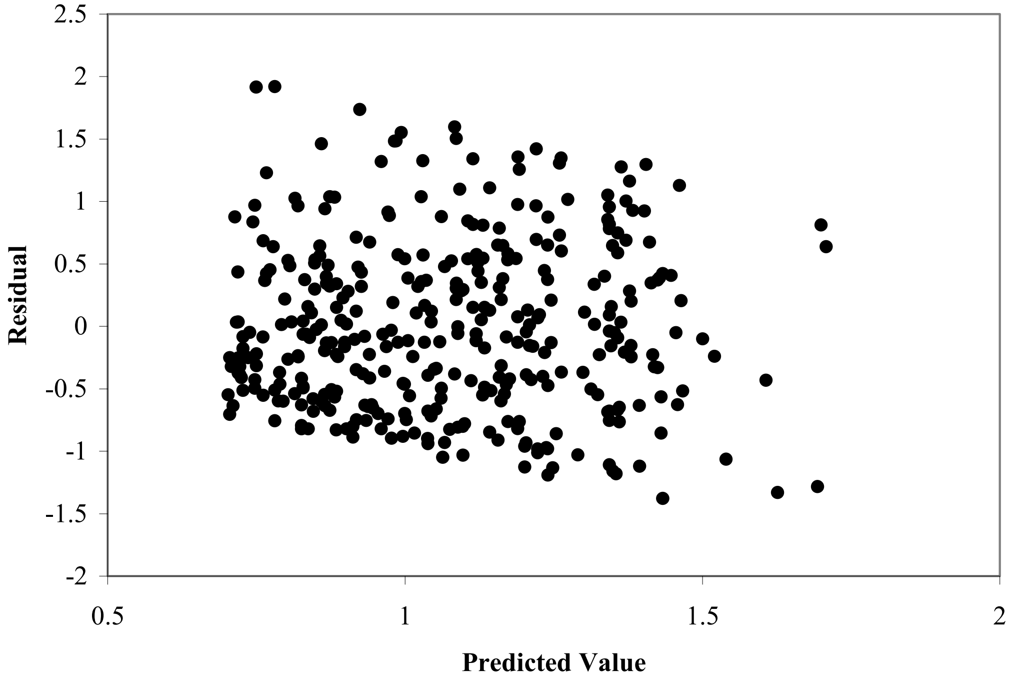
Appendix F.2. QQ-plot for yellow-poplar two-year (2004 to 2005) untransformed diameter increment model: $\mathbf{\Delta}$ Diam = b_0 + b_1CH + b_2BA + b_3Diam:Ht$_{\text{initial}}$



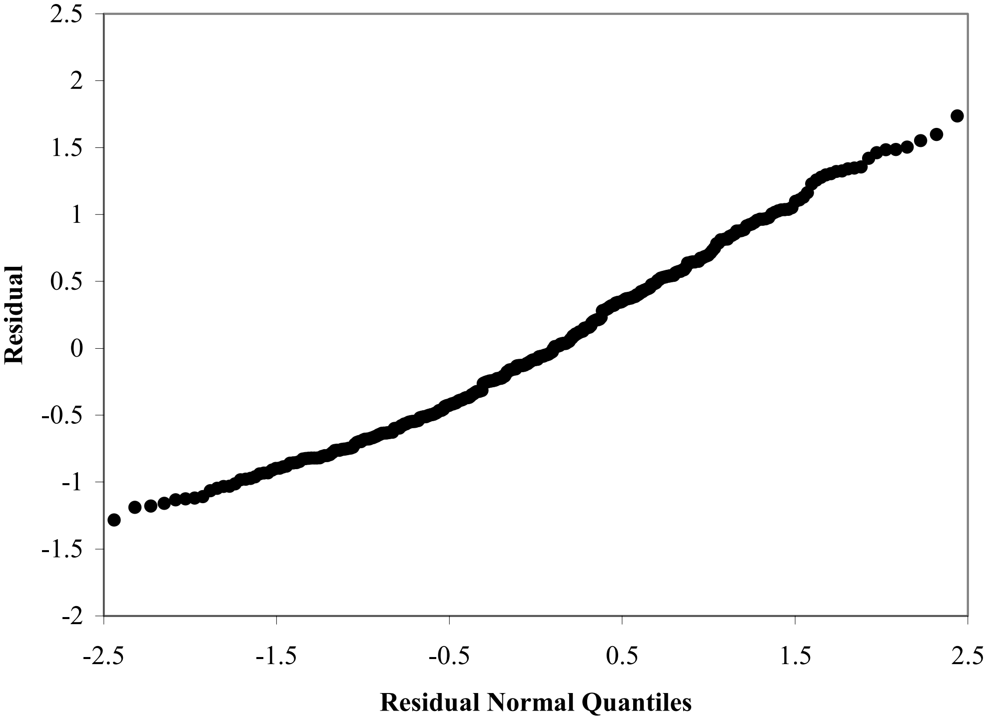
Appendix F.3. Residual vs. predicted plot for yellow-poplar two-year (2004 to 2005) Box-Cox transformed diameter increment model (3.4): **Δ** $\text{Diam}_{\text{Box-Cox}} = b_0 + b_1\text{CH} + b_2\text{BA} + b_3\text{Diam:Ht}_{\text{initial}}$



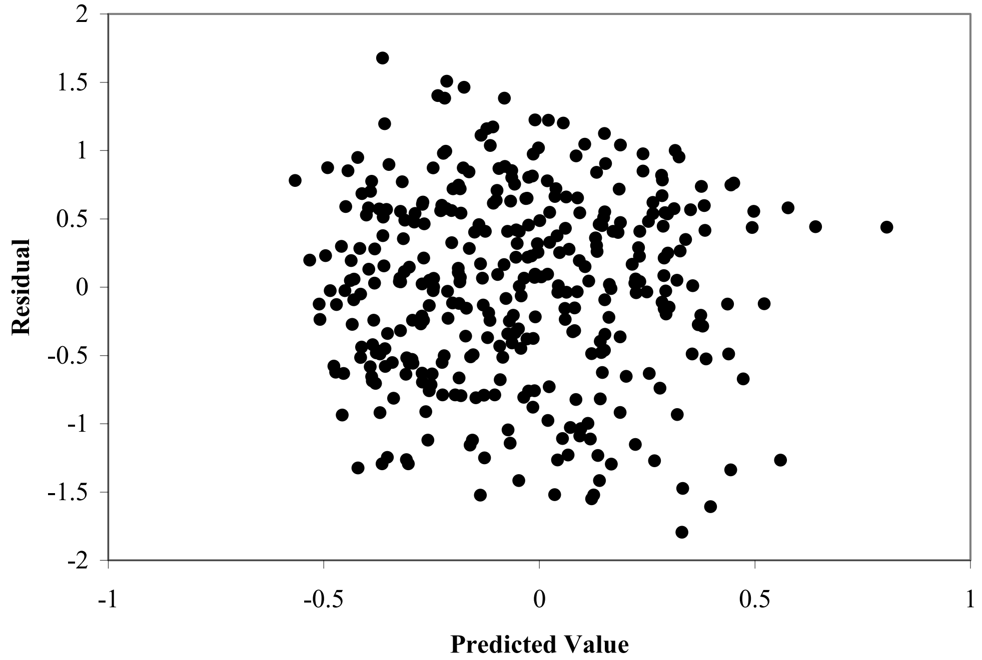
Appendix F.4. QQ-plot for yellow-poplar two-year (2004 to 2005) Box-Cox transformed diameter increment model (3.4): $\mathbf{\Delta}\ \mathrm{Diam}_{\mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{CH} + b_2\mathrm{BA} + b_3\mathrm{Diam{:}Ht}_{\mathrm{initial}}$



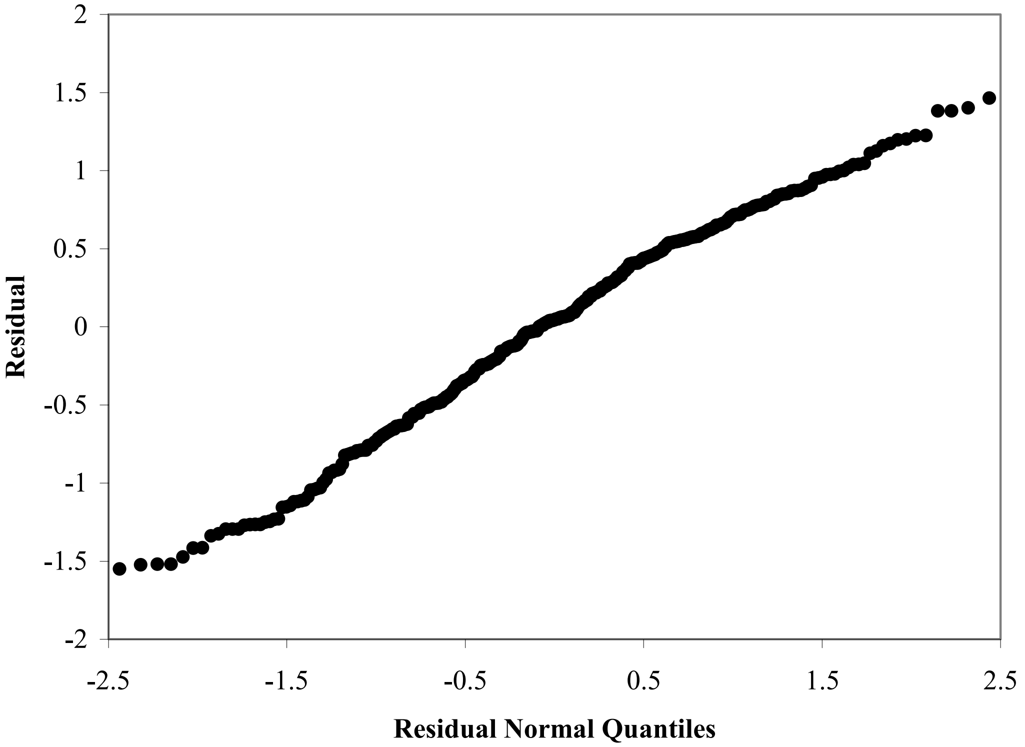
Appendix F.5. Residual vs. predicted plot for cherrybark oak two-year (2004 to 2005) untransformed diameter increment model: $\mathbf{\Delta}$ Diam = b_0 + b_1CH + b_2Diam$_{\text{initial}}$



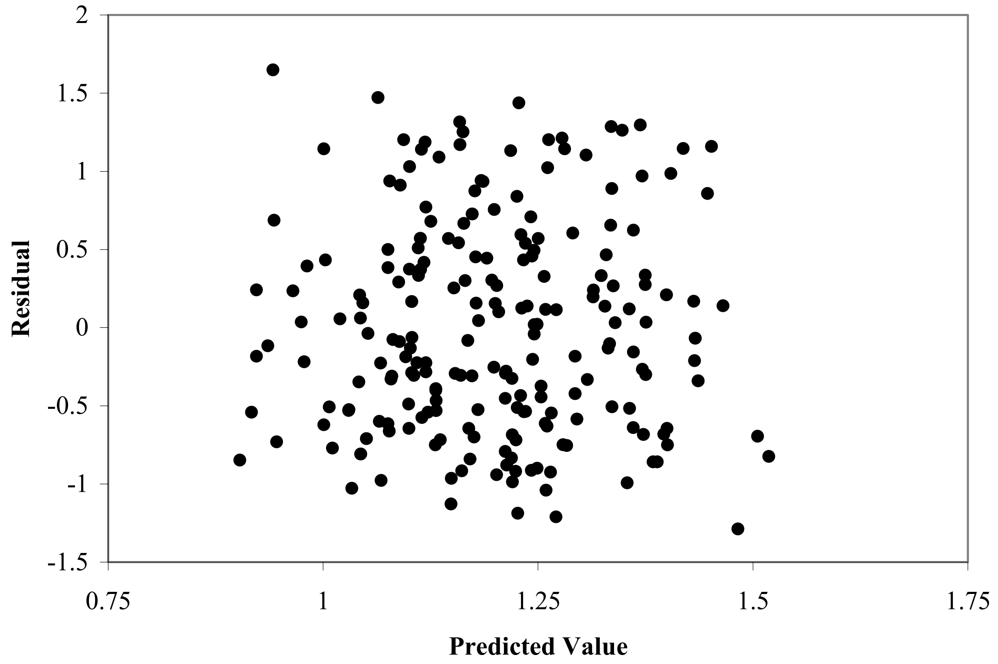
Appendix F.6. QQ-plot for cherrybark oak two-year (2004 to 2005) untransformed diameter increment model: Δ Diam = b_0 + b_1CH + b_2Diam$_{initial}$



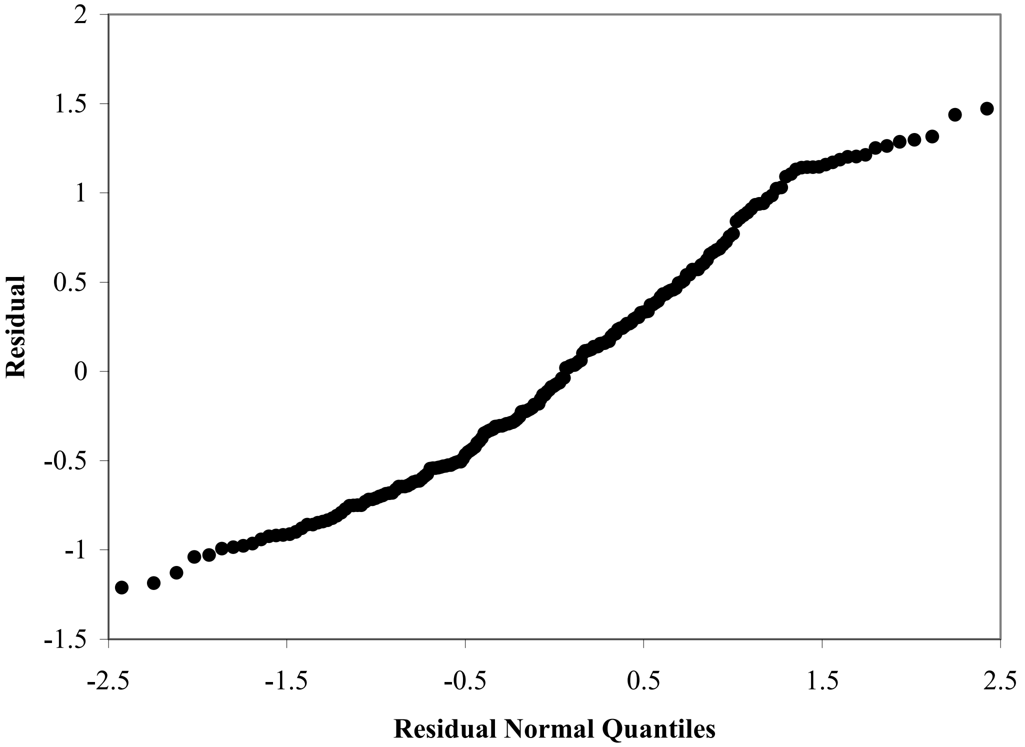
Appendix F.7. Residual vs. predicted plot for cherrybark oak two-year (2004 to 2005) Box-Cox transformed diameter increment model (3.5): $\mathbf{\Delta}$ Diam$_{\text{Box-Cox}}$ = b_0 + b_1CH + b_2Diam$_{\text{initial}}$



Appendix F.8. QQ-plot for cherrybark oak two-year (2004 to 2005) Box-Cox transformed diameter increment model (3.5): $\mathbf{\Delta}\ \mathrm{Diam}_{\mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Diam}_{\mathrm{initial}}$



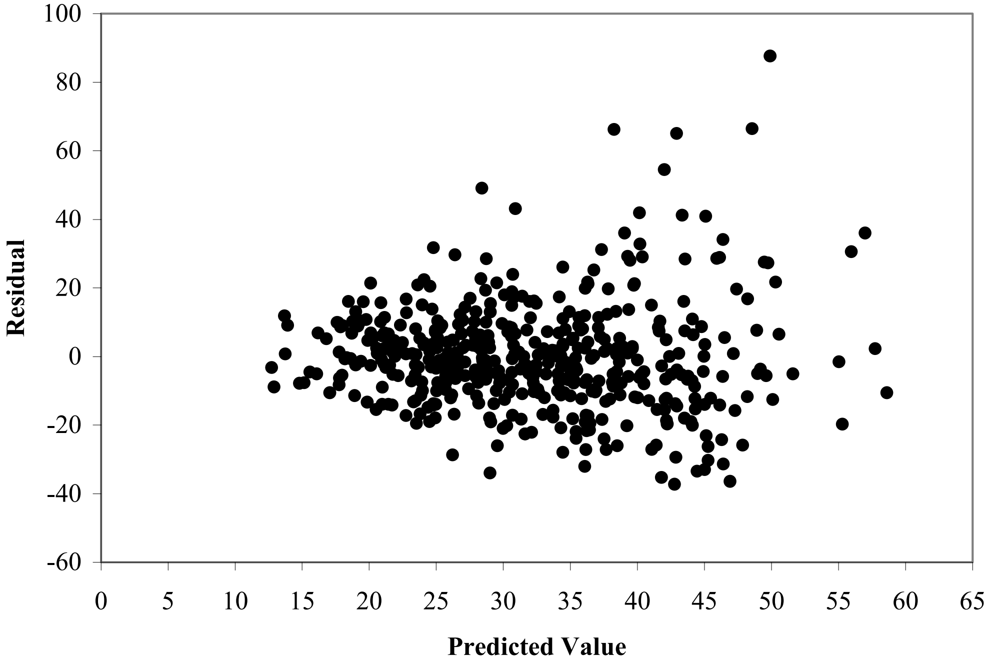
Appendix F.9. Residual vs. predicted plot for water oak two-year (2004 to 2005) untransformed diameter increment model (3.6): Δ Diam = b_0 + b_1Closure60



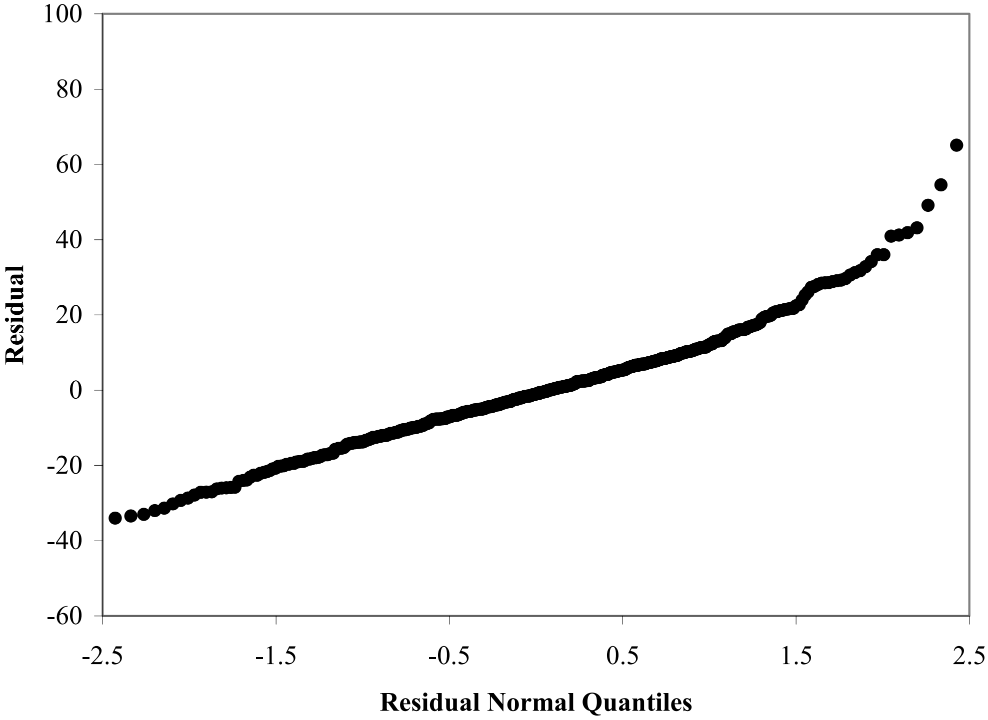
Appendix F.10. QQ-plot for water oak two-year (2004 to 2005) untransformed diameter increment model (3.6): $\mathbf{\Delta}$ Diam = b_0 + b_1Closure60

APPENDIX G

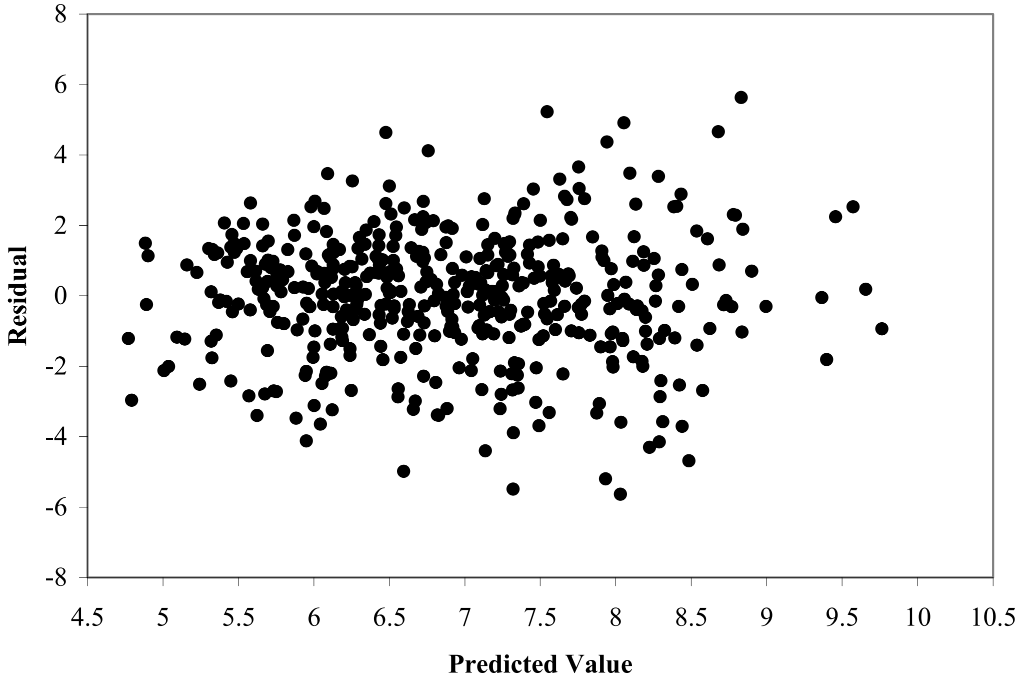
RESIDUAL ANALYSIS PLOTS FOR SPECIES-SPECIFIC 2004 UNTRANSFORMED AND BOX-COX TRANSFORMED HEIGHT INCREMENT MODELS



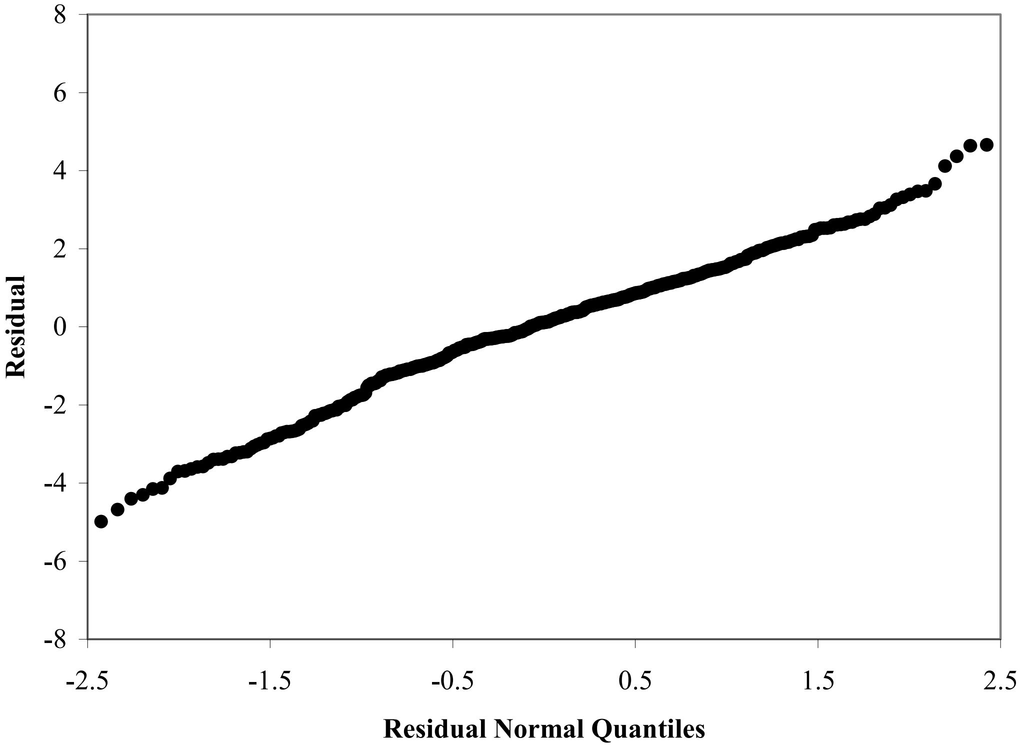
Appendix G.1. Residual vs. predicted plot for yellow-poplar 2004 untransformed height increment model: $\boldsymbol{\Delta}$ $\mathrm{Ht}_{2004} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Diam}_{\mathrm{initial}} + b_3\mathrm{Control}$



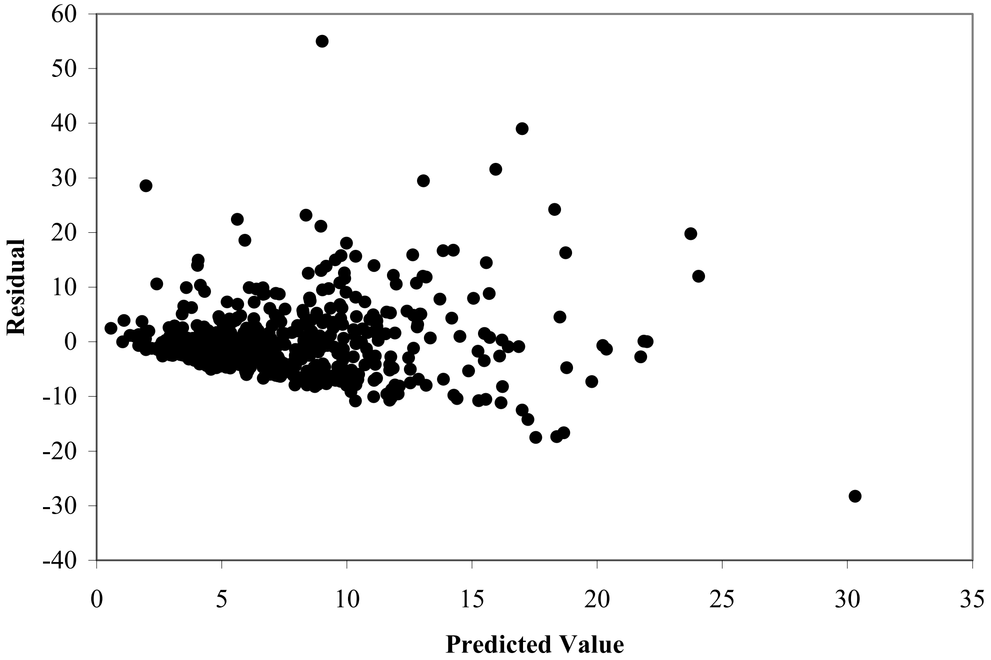
Appendix G.2. QQ-plot for yellow-poplar 2004 untransformed height increment model: $\mathbf{\Delta}$ $\mathrm{Ht}_{2004} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Diam}_{\mathrm{initial}} + b_3\mathrm{Control}$



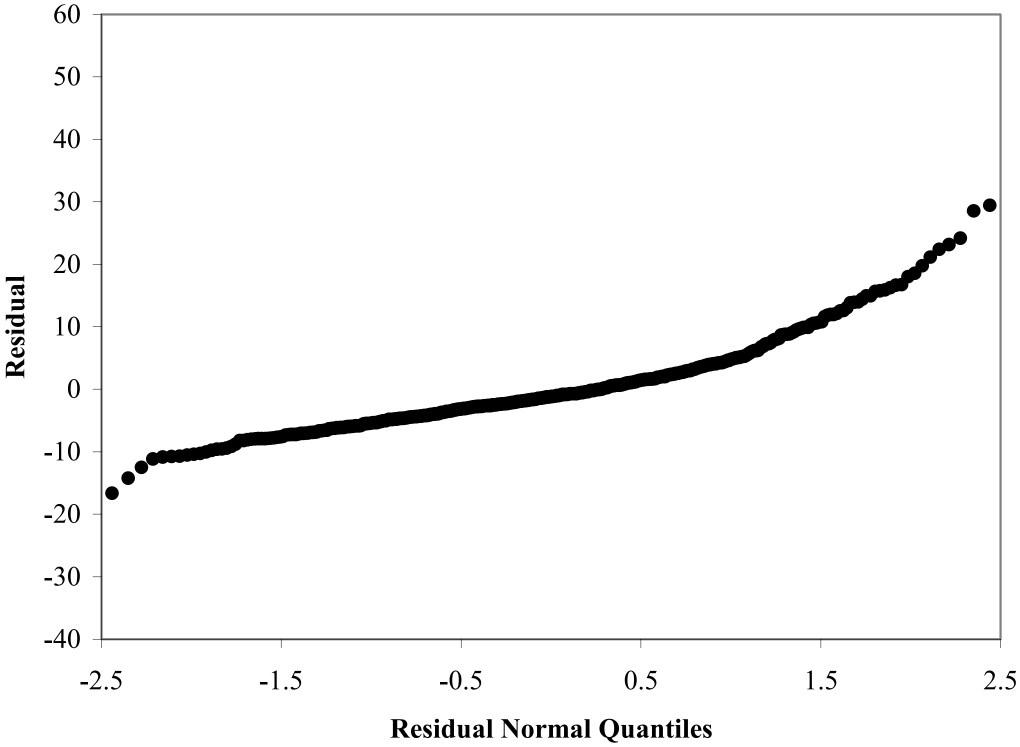
Appendix G.3. Residual vs. predicted plot for yellow-poplar 2004 Box-Cox transformed height increment model (3.7): Δ $Ht_{2004\ \text{Box-Cox}} = b_0 + b_1CH + b_2Diam_{initial} + b_3Control$



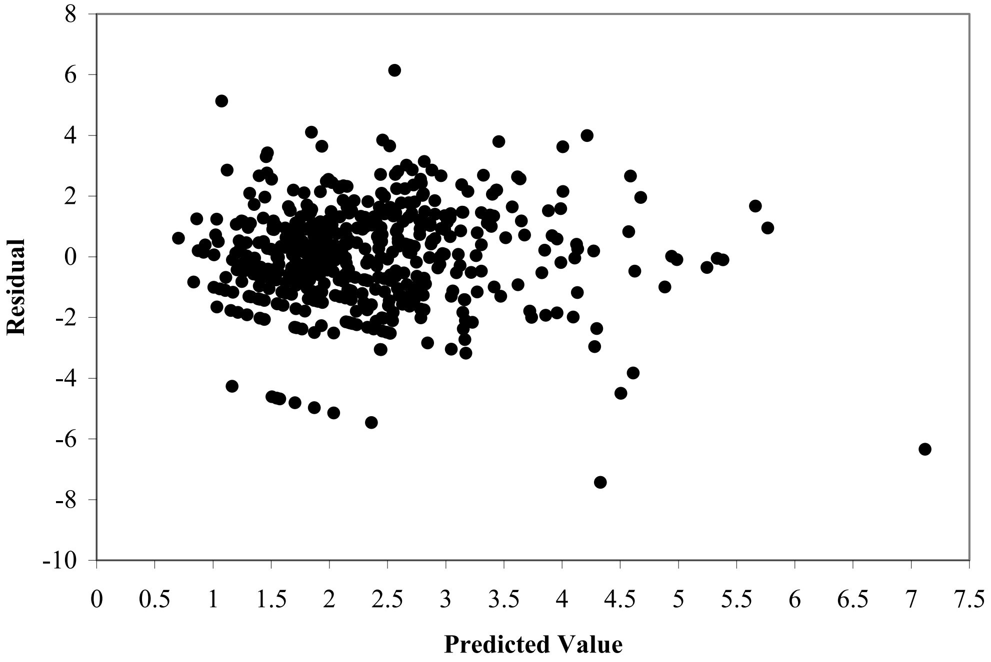
Appendix G.4. QQ-plot for plot for yellow-poplar 2004 Box-Cox transformed height increment model (3.7): $\mathbf{\Delta}$ $\mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Diam}_{\mathrm{initial}} + b_3\mathrm{Control}$



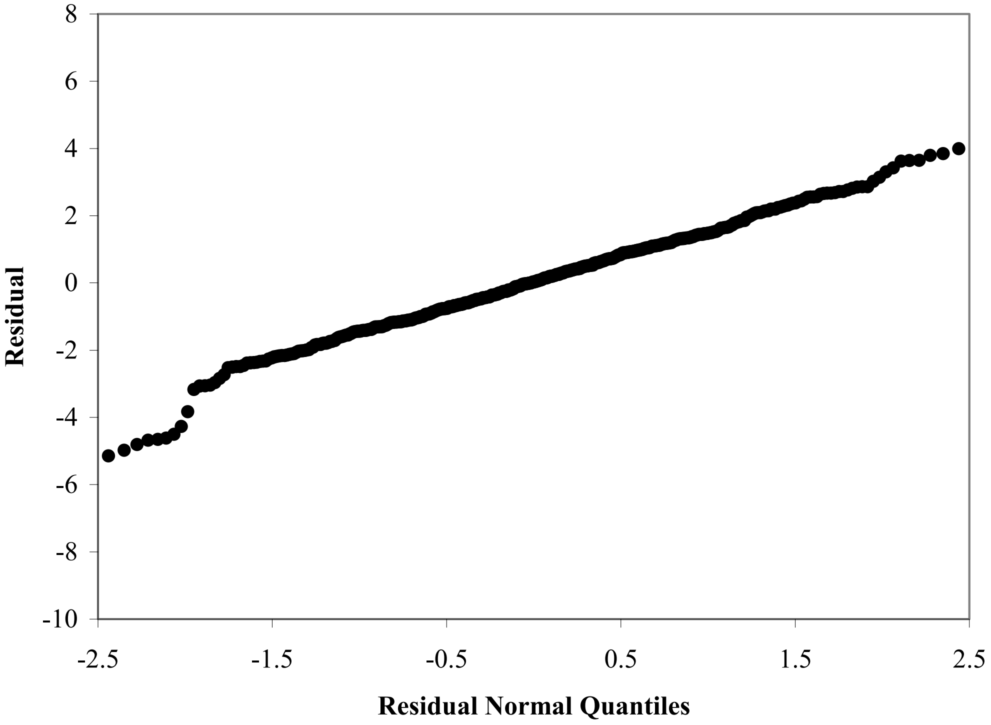
Appendix G.5. Residual vs. predicted plot for cherrybark oak 2004 untransformed height increment model: $\mathbf{\Delta}\ \mathrm{Ht}_{2004} = b_0 + b_1\mathrm{Diam}_{\mathrm{initial}} + b_2\mathrm{CH}$



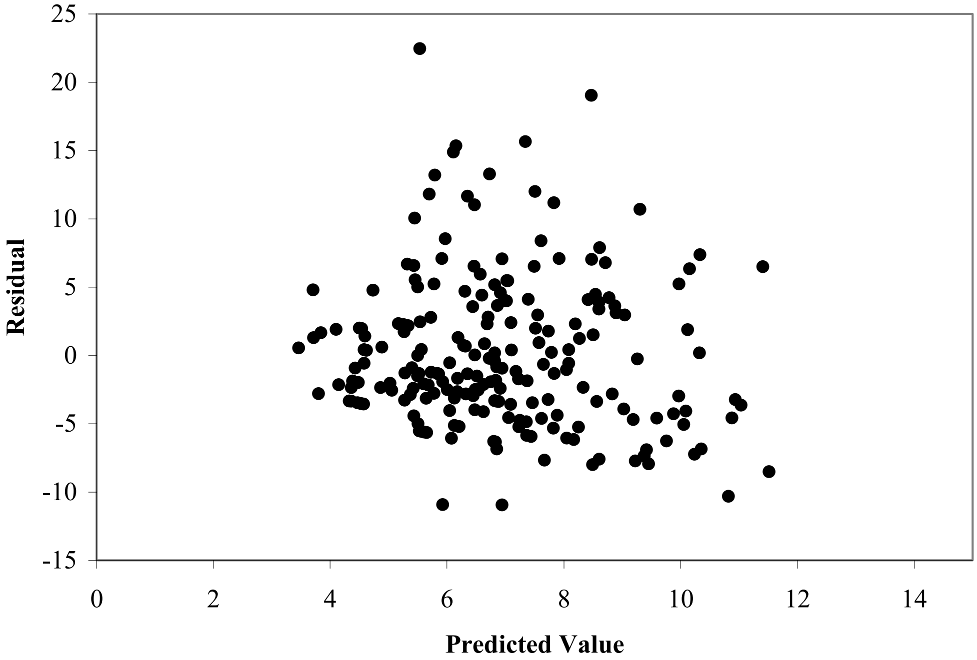
Appendix G.6. QQ-plot for cherrybark oak 2004 untransformed height increment model:
$\mathbf{\Delta}$ $\mathrm{Ht}_{2004} = b_0 + b_1\mathrm{Diam}_{\mathrm{initial}} + b_2\mathrm{CH}$



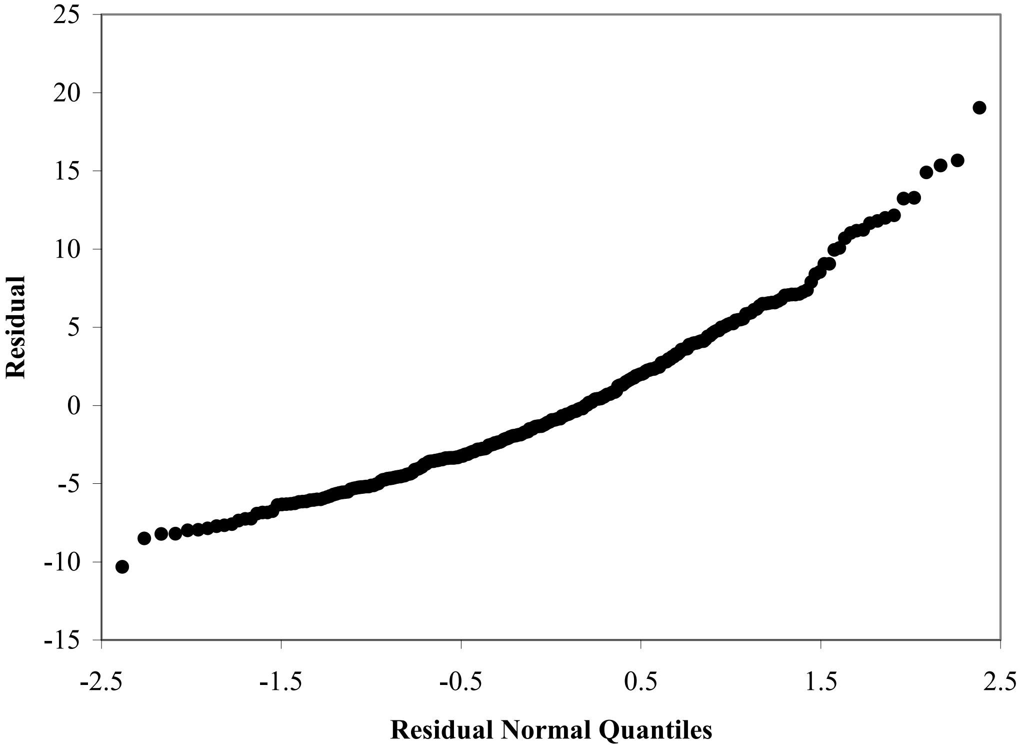
Appendix G.7. Residual vs. predicted plot for cherrybark oak 2004 Box-Cox transformed height increment model (3.8): $\Delta \text{ Ht}_{2004 \text{ Box-Cox}} = b_0 + b_1\text{Diam}_{\text{initial}} + b_2\text{CH}$



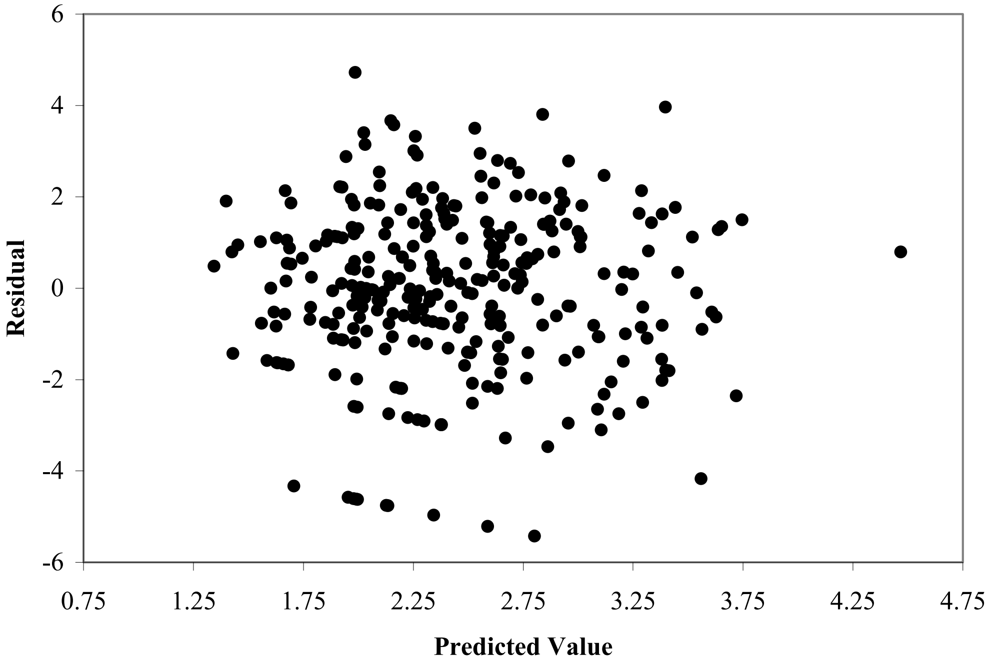
Appendix G.8. QQ-plot for cherrybark oak 2004 Box-Cox transformed height increment model (3.8): $\mathbf{\Delta}\ \mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Diam}_{\mathrm{initial}} + b_2\mathrm{CH}$



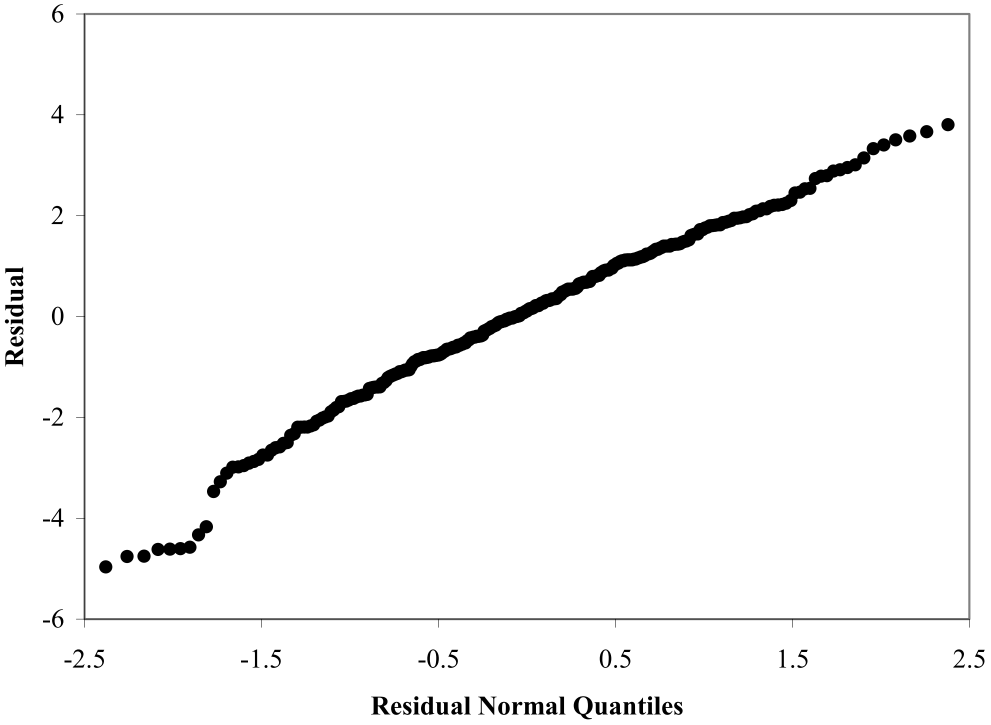
Appendix G.9. Residual vs. predicted plot for water oak 2004 untransformed height increment model: $\Delta \text{Ht}_{2004} = b_0 + b_1\text{Closure60} + b_2\text{Diam}_{\text{initial}}$



Appendix G.10. QQ-plot for water oak 2004 untransformed height increment model: **Δ** $Ht_{2004} = b_0 + b_1 Closure60 + b_2 Diam_{initial}$



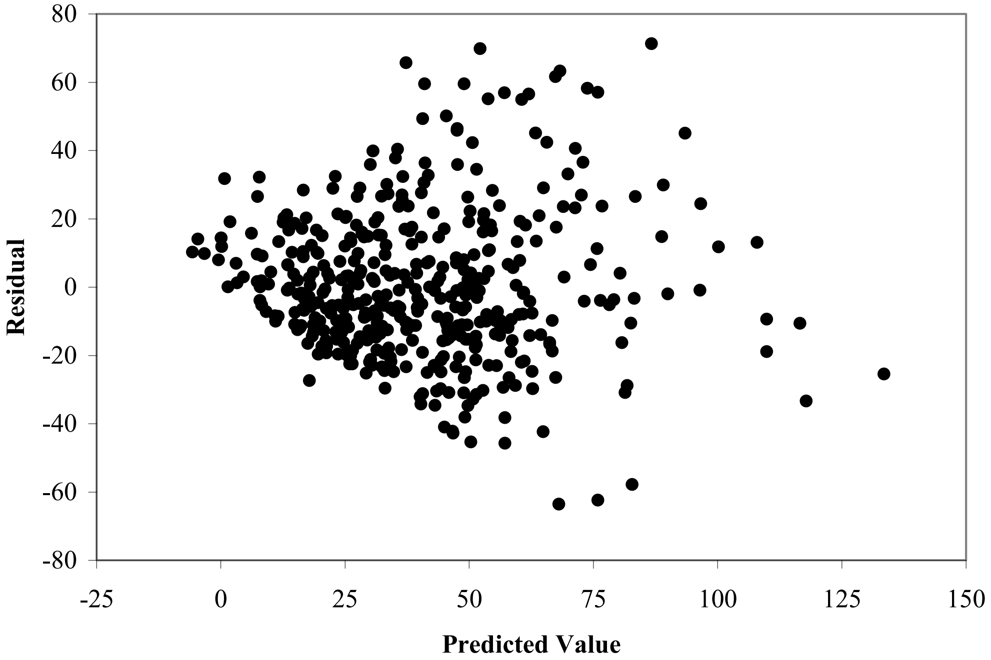
Appendix G.11. Residual vs. predicted plot for water oak 2004 Box-Cox transformed height increment model (3.9): $\mathbf{\Delta}$ $\mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Closure60} + b_2\mathrm{Diam}_{\mathrm{initial}}$



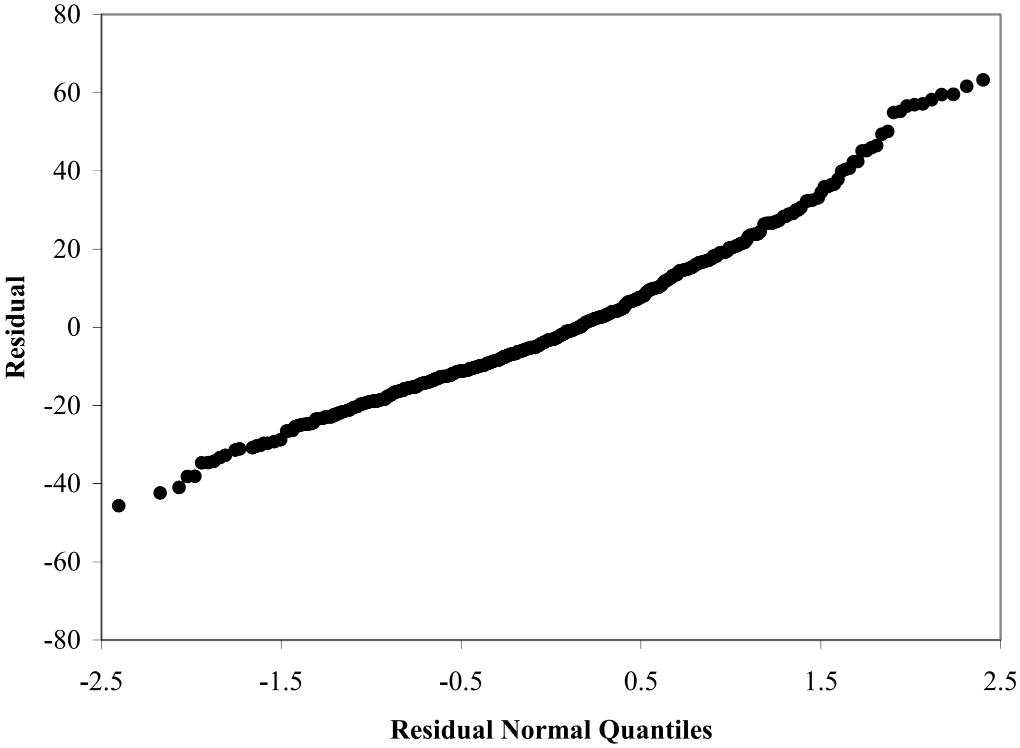
Appendix G.12. QQ-plot for water oak 2004 Box-Cox transformed height increment model (3.9): $\mathbf{\Delta}$ $\mathrm{Ht}_{2004\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Closure60} + b_2\mathrm{Diam}_{\mathrm{initial}}$

APPENDIX H

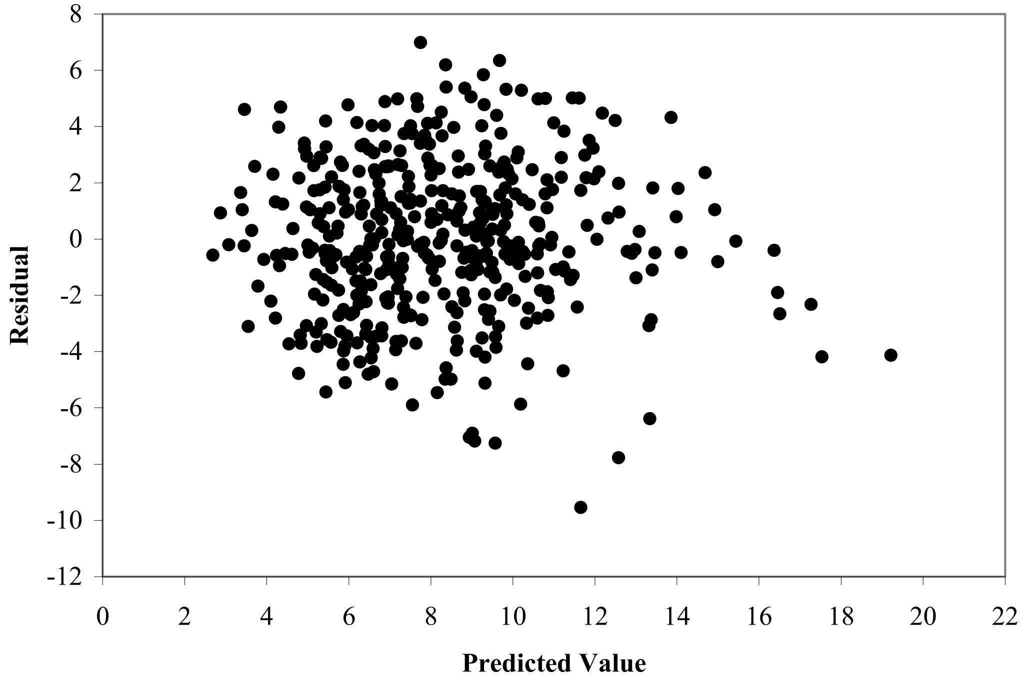
RESIDUAL ANALYSIS PLOTS FOR SPECIES-SPECIFIC 2005 UNTRANSFORMED AND BOX-COX TRANSFORMED HEIGHT INCREMENT MODELS



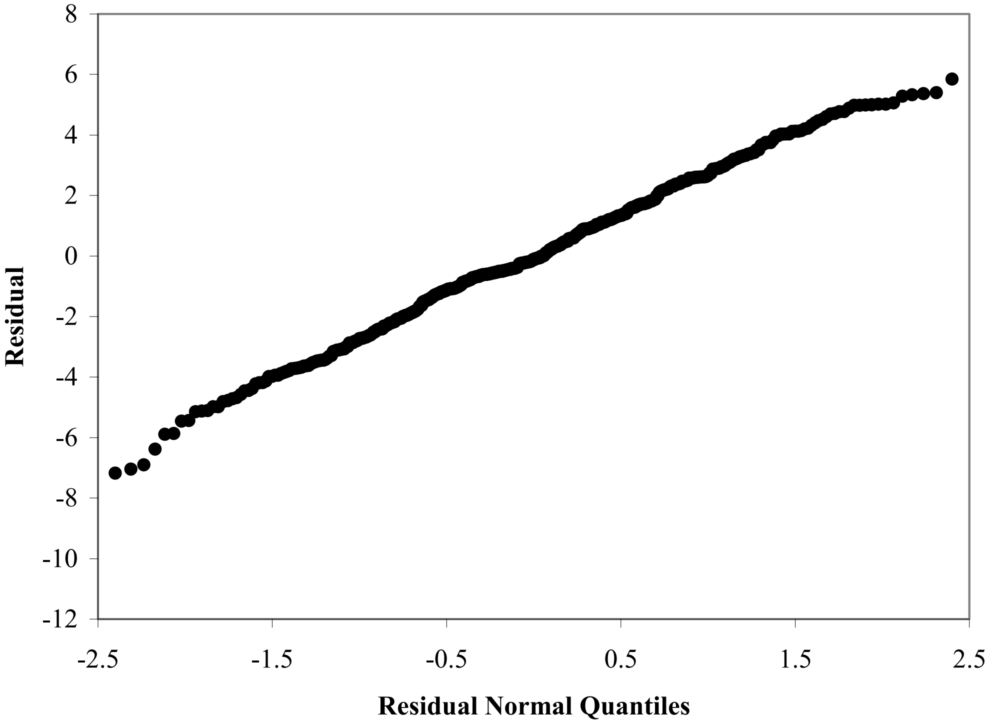
Appendix H.1. Residual vs. predicted plot for yellow-poplar 2005 untransformed height increment model: $\Delta \mathrm{Ht}_{2005} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Ht}_{2004} + b_3\mathrm{Closure120} + b_4\mathrm{Diam}_{2004}$



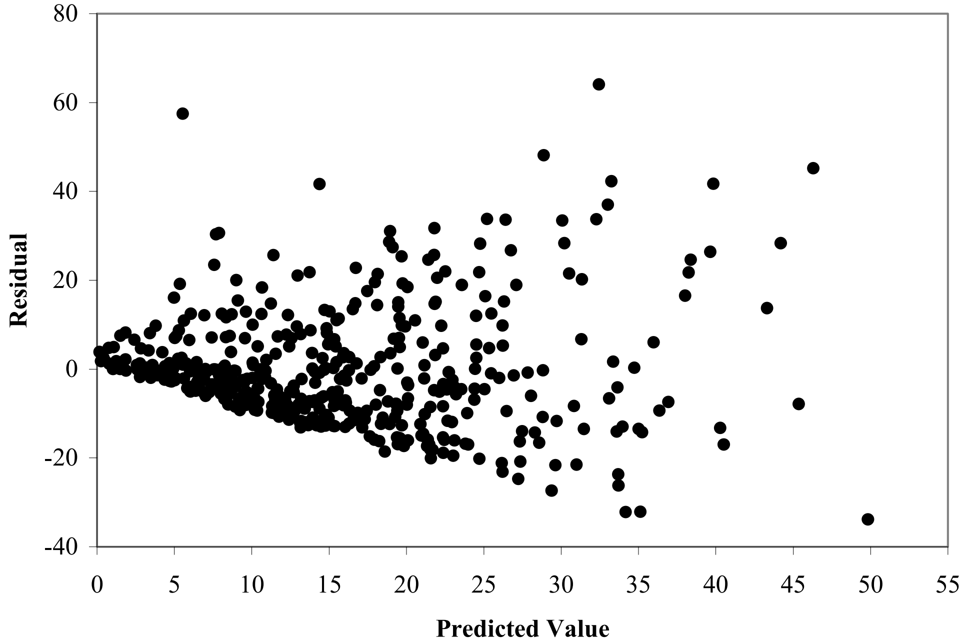
Appendix H.2. QQ-plot for yellow-poplar 2005 untransformed height increment model: $\Delta\ Ht_{2005} = b_0 + b_1CH + b_2Ht_{2004} + b_3Closure120 + b_4Diam_{2004}$



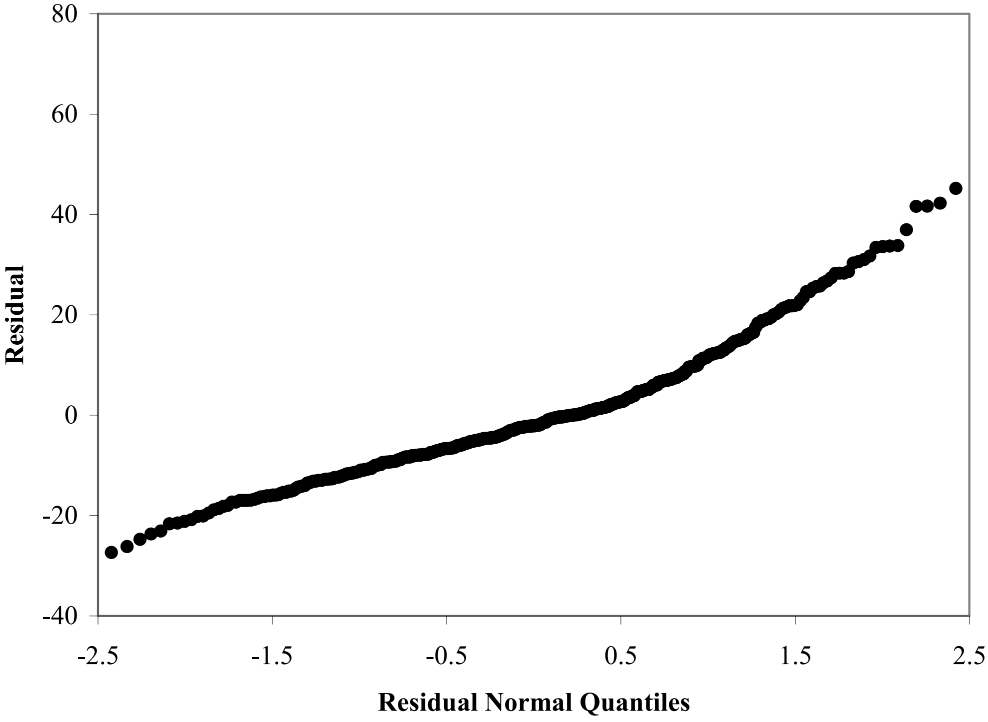
Appendix H.3. Residual vs. predicted plot for yellow-poplar 2005 Box-Cox transformed height increment model (3.10): $\mathbf{\Delta}$ $Ht_{2005\ Box\text{-}Cox} = b_0 + b_1CH + b_2Ht_{2004} + b_3Closure120 + b_4Diam_{2004}$



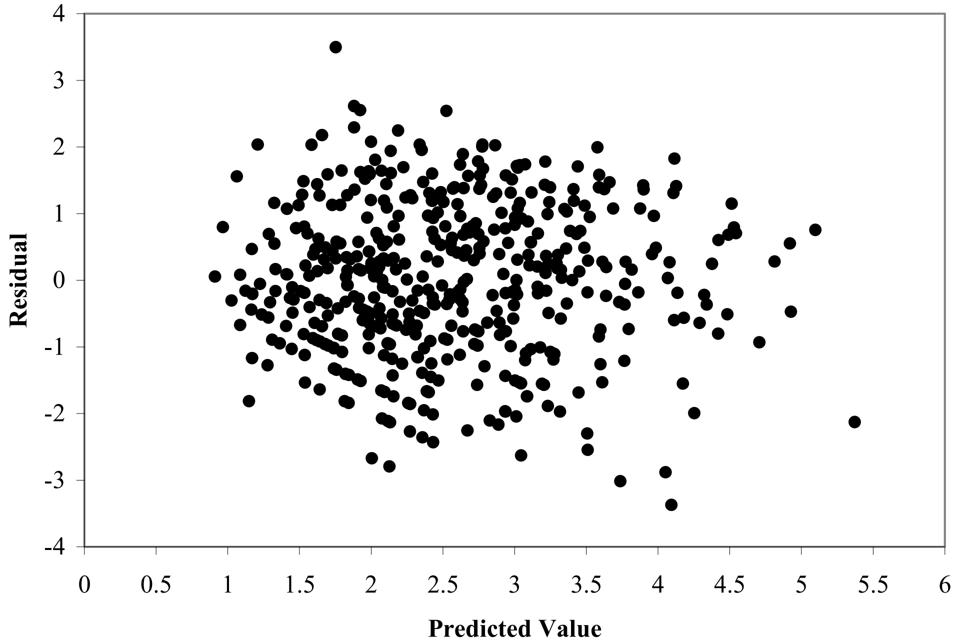
Appendix H.4. QQ-plot for plot for yellow-poplar 2005 Box-Cox transformed height increment model (3.10): $\mathbf{\Delta}$ $Ht_{2005\ Box\text{-}Cox} = b_0 + b_1CH + b_2Ht_{2004} + b_3Closure120 + b_4Diam_{2004}$



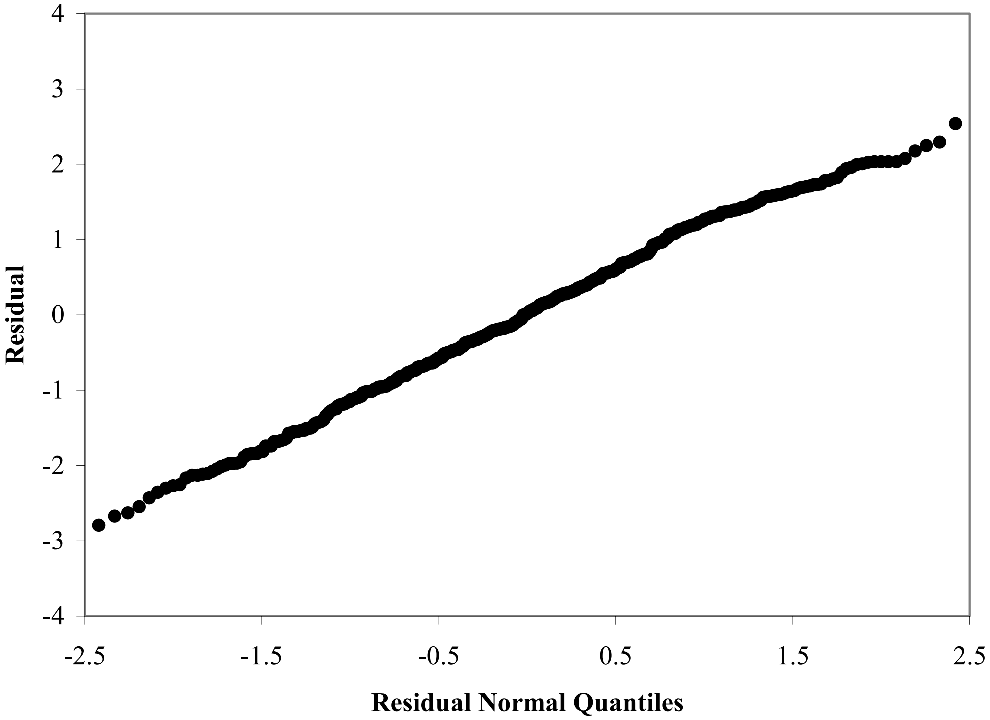
Appendix H.5. Residual vs. predicted plot for cherrybark oak 2005 untransformed height increment model: Δ $Ht_{2005\ \text{Box-Cox}} = b_0 + b_1 Diam_{2004} + b_2 CH + b_3 Closure120$



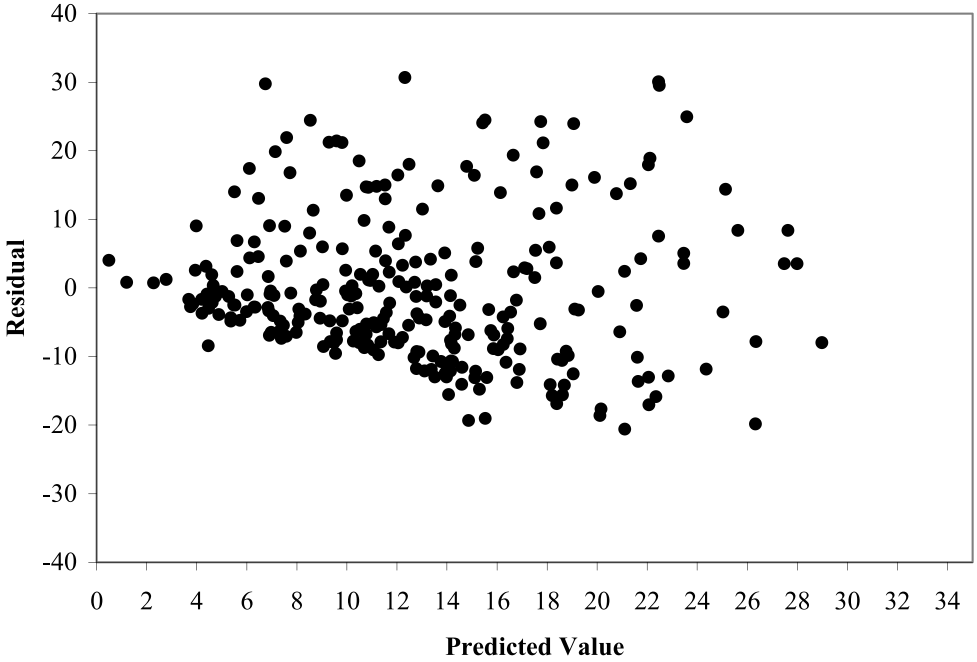
Appendix H.6. QQ-plot for cherrybark oak 2005 untransformed height increment model: **Δ** $\mathrm{Ht}_{2005\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Diam}_{2004} + b_2\mathrm{CH} + b_3\mathrm{Closure120}$



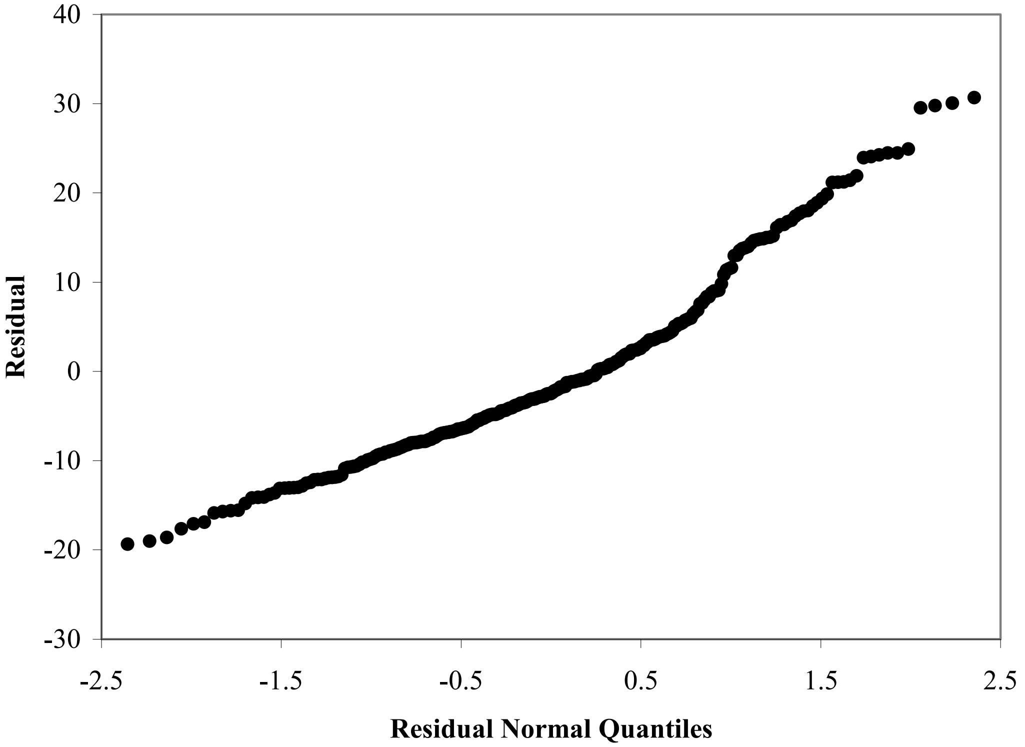
Appendix H.7. Residual vs. predicted plot for cherrybark oak 2005 Box-Cox transformed height increment model (3.11): Δ $Ht_{2005\ \text{Box-Cox}} = b_0 + b_1\text{Diam}_{2004} + b_2\text{CH} + b_3\text{Closure120}$



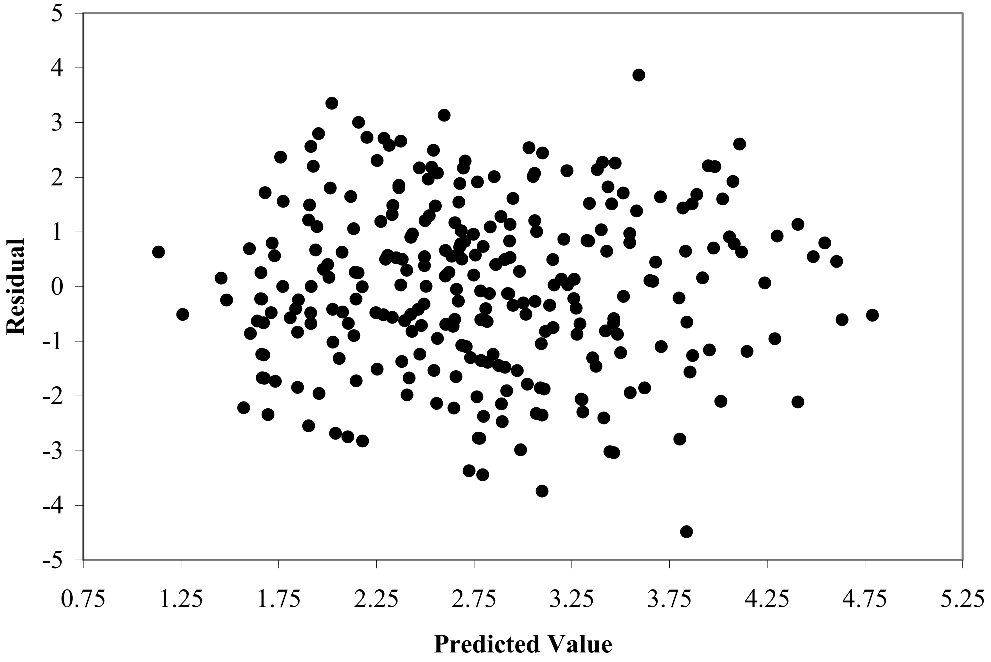
Appendix H.8. QQ-plot for cherrybark oak 2005 Box-Cox transformed height increment model (3.11): $\mathbf{\Delta}$ $\mathrm{Ht}_{2005\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Diam}_{2004} + b_2\mathrm{CH} + b_3\mathrm{Closure120}$



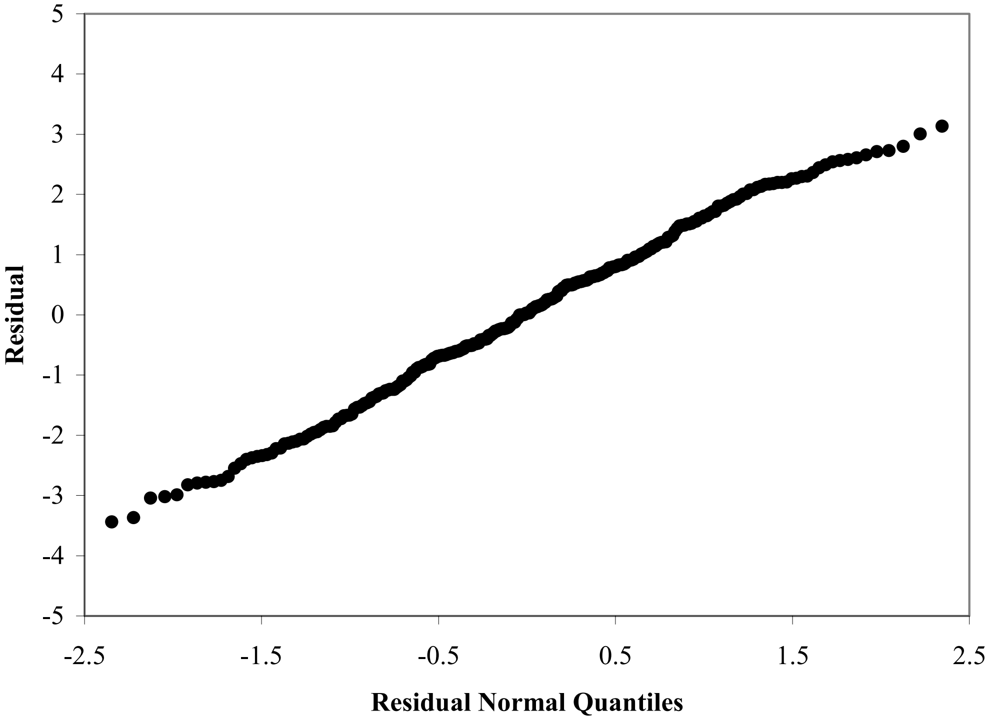
Appendix H.9. Residual vs. predicted plot for water oak 2005 untransformed height increment model: $\Delta \text{Ht}_{2005} = b_0 + b_1\text{Diam}_{2004} + b_2\text{CH} + b_3\text{Closure120}$



Appendix H.10. QQ-plot for water oak 2005 untransformed height increment model: **Δ** $Ht_{2005} = b_0 + b_1 Diam_{2004} + b_2 CH + b_3 Closure120$



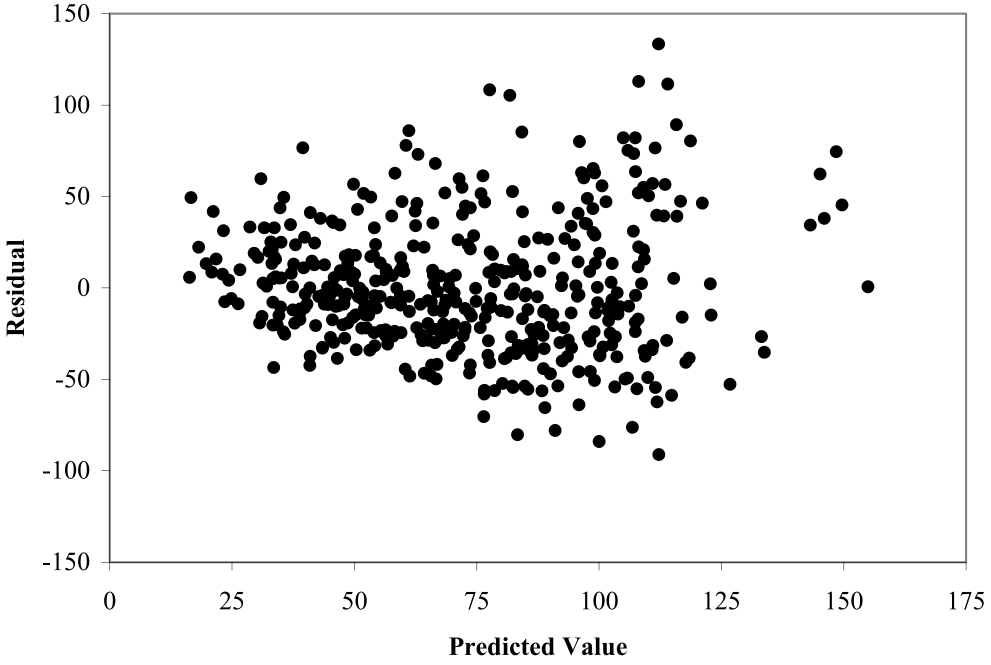
Appendix H.11. Residual vs. predicted plot for water oak 2005 Box-Cox transformed height increment model (3.12): $\Delta\ \mathrm{Ht}_{2005\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Diam}_{2004} + b_2\mathrm{CH} + b_3\mathrm{Closure120}$



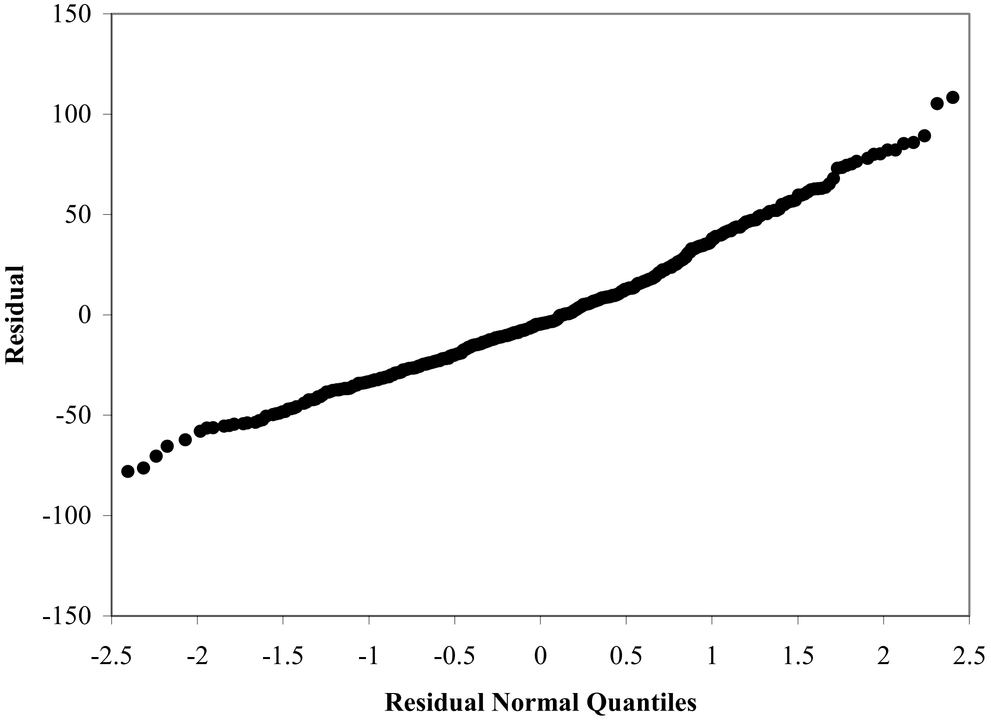
Appendix H.12. QQ-plot for water oak 2005 Box-Cox transformed height increment model (3.12): $\mathbf{\Delta}$ $\mathrm{Ht}_{2005\ \mathrm{Box\text{-}Cox}} = b_0 + b_1\mathrm{Diam}_{2004} + b_2\mathrm{CH} + b_3\mathrm{Closure120}$

APPENDIX I

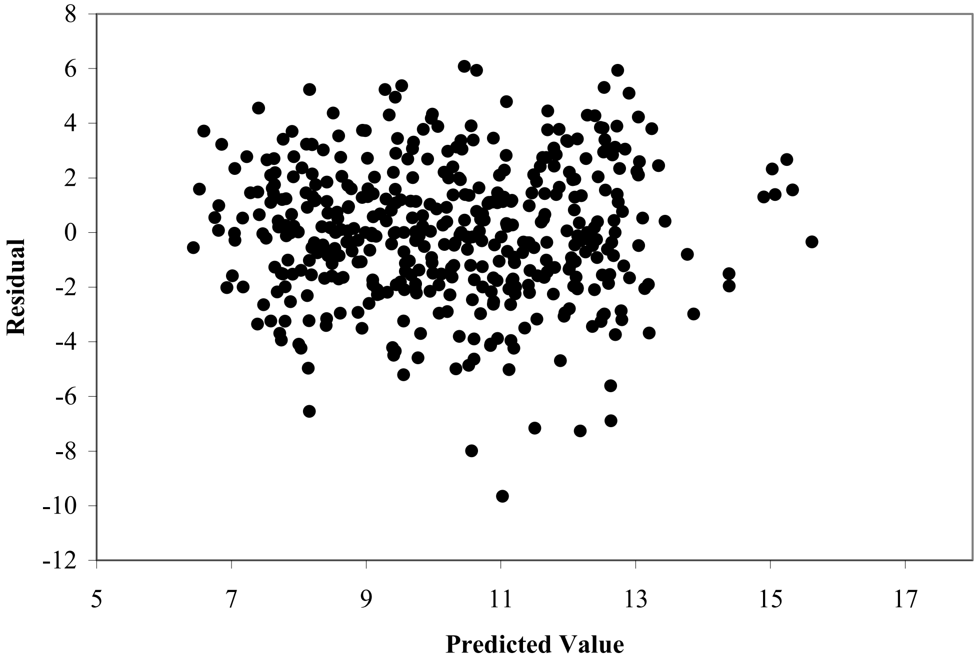
RESIDUAL ANALYSIS PLOTS FOR SPECIES-SPECIFIC TWO-YEAR (2004 TO 2005) UNTRANSFORMED AND BOX-COX TRANSFORMED HEIGHT INCREMENT MODELS



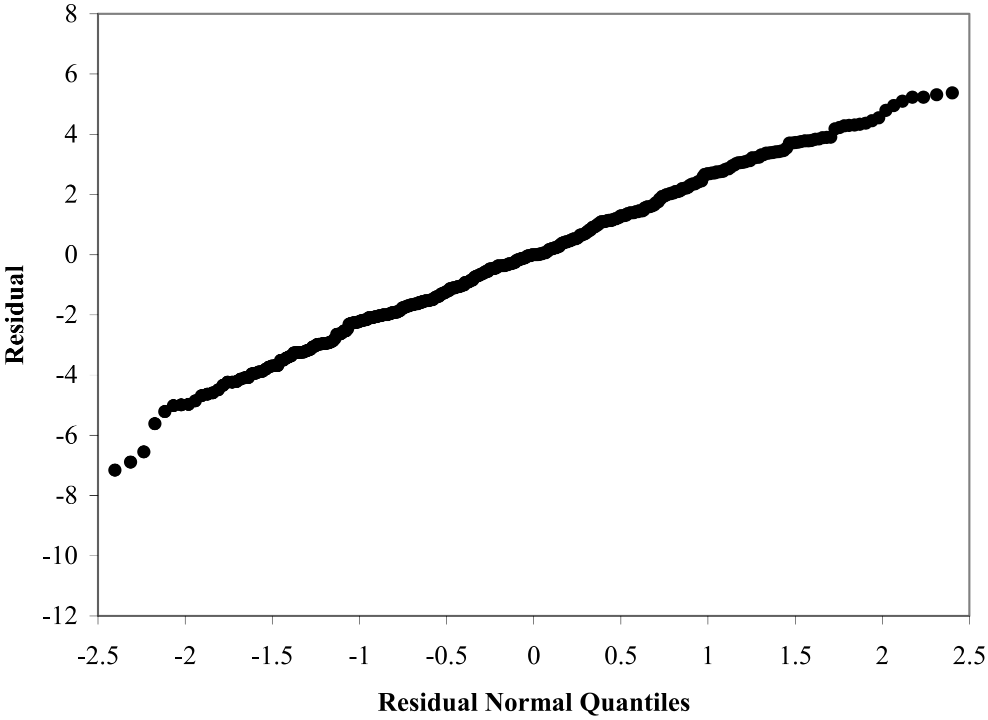
Appendix I.1. Residual vs. predicted plot for yellow-poplar Two-Year (2004 to 2005) untransformed height increment model: $\mathbf{\Delta}\ \mathrm{Ht}_{2yr} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Closure120} + b_3\mathrm{BA}$



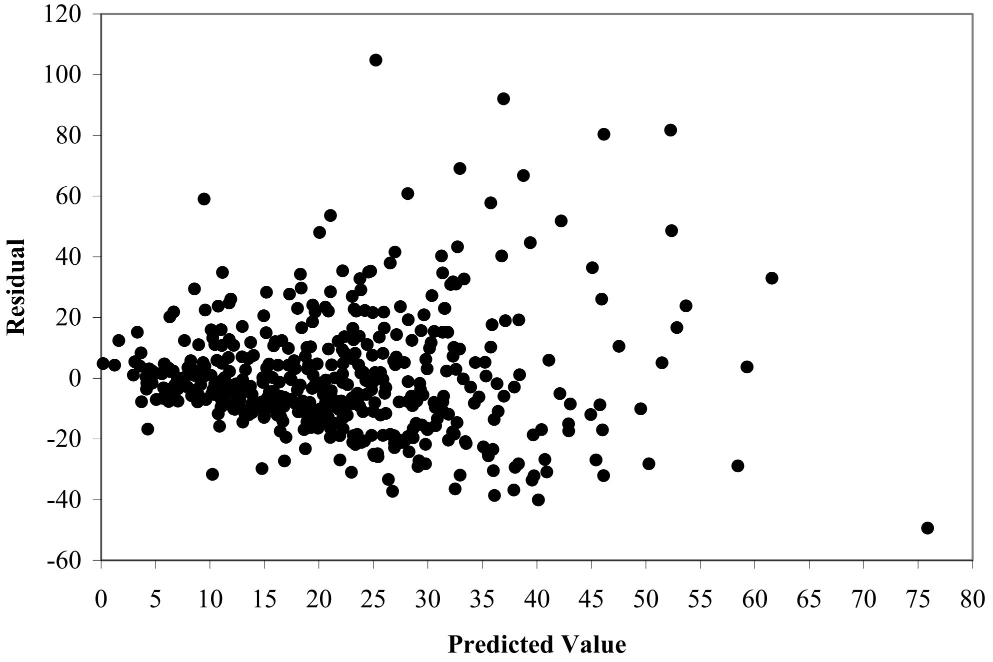
Appendix I.2. QQ-plot for yellow-poplar Two-Year (2004 to 2005) untransformed height increment model: $\mathbf{\Delta}\ Ht_{2yr} = b_0 + b_1CH + b_2Closure120 + b_3BA$



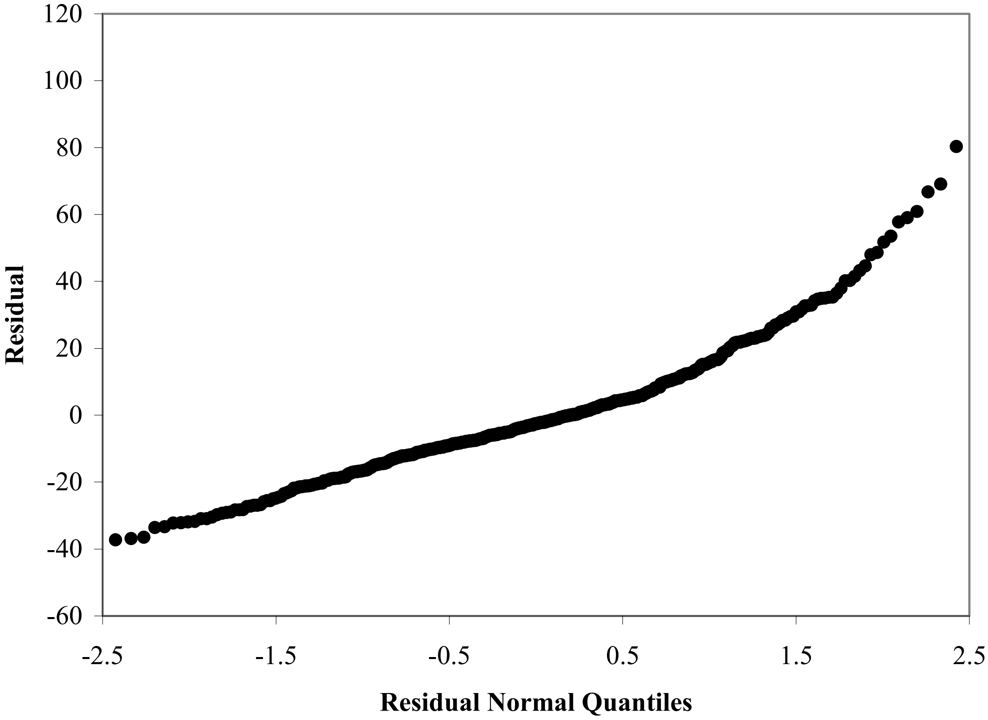
Appendix I.3. Residual vs. predicted plot for yellow-poplar Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.13): Δ $Ht_{2yr\ Box\text{-}Cox} = b_0 + b_1CH + b_2Closure120 + b_3BA$



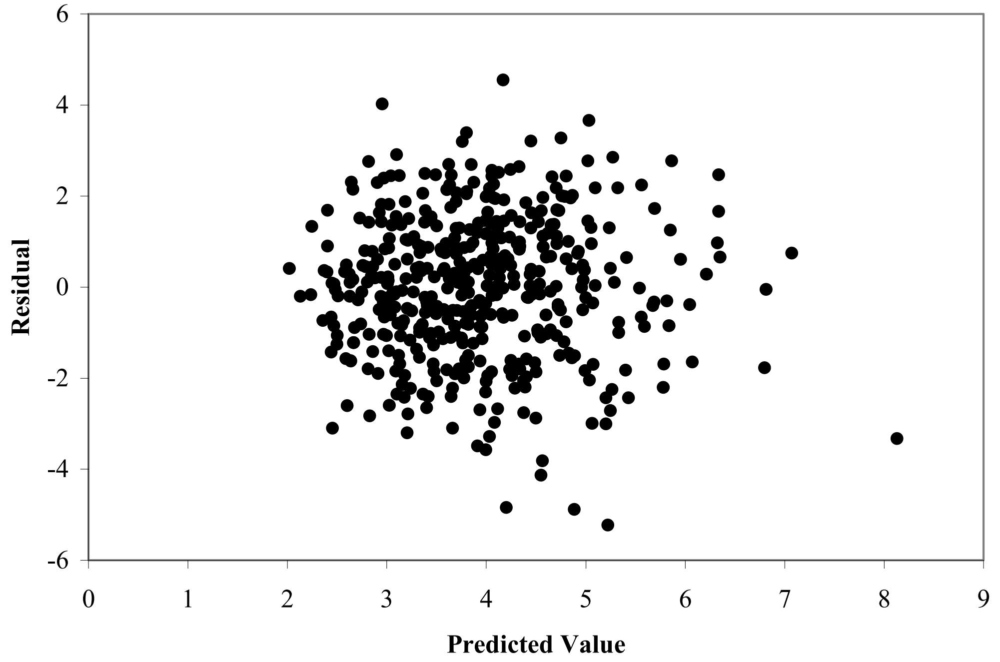
Appendix I.4. QQ-plot for plot for yellow-poplar Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.13): $\Delta \ \mathrm{Ht}_{2\mathrm{yr\ Box\text{-}Cox}} = b_0 + b_1\mathrm{CH} + b_2\mathrm{Closure120} + b_3\mathrm{BA}$



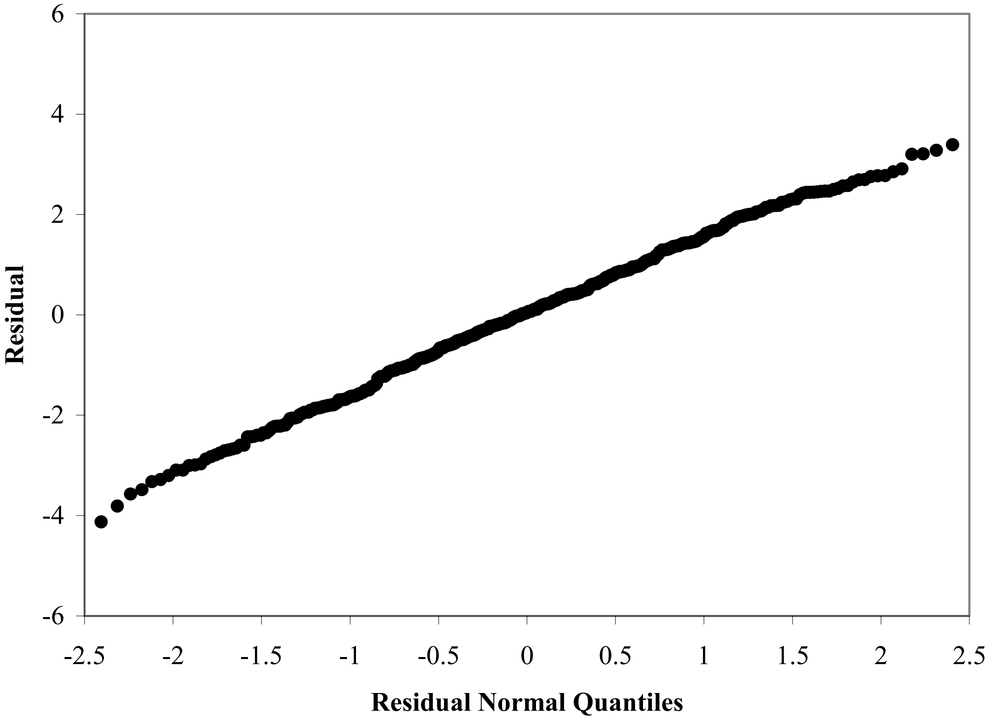
Appendix I.5. Residual vs. predicted plot for cherrybark oak Two-Year (2004 to 2005) untransformed height increment model: $\Delta \text{Ht}_{2yr} = b_0 + b_1\text{Diam}_{\text{initial}} + b_2\text{CH}$



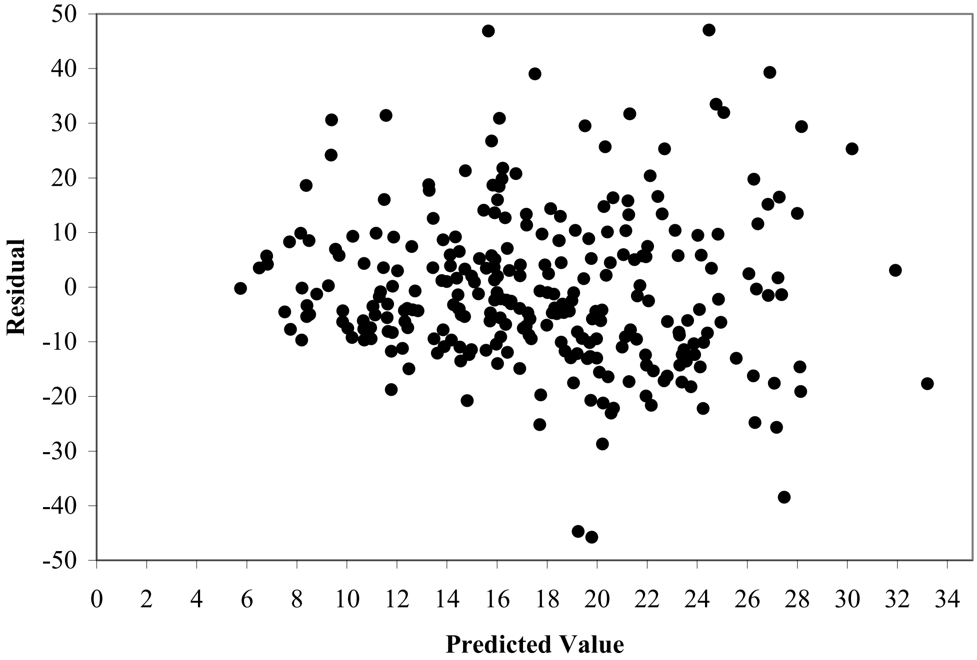
Appendix I.6. QQ-plot for cherrybark oak Two-Year (2004 to 2005) untransformed height increment model: $\mathbf{\Delta}\ \mathrm{Ht}_{2yr} = b_0 + b_1\mathrm{Diam}_{initial} + b_2\mathrm{CH}$



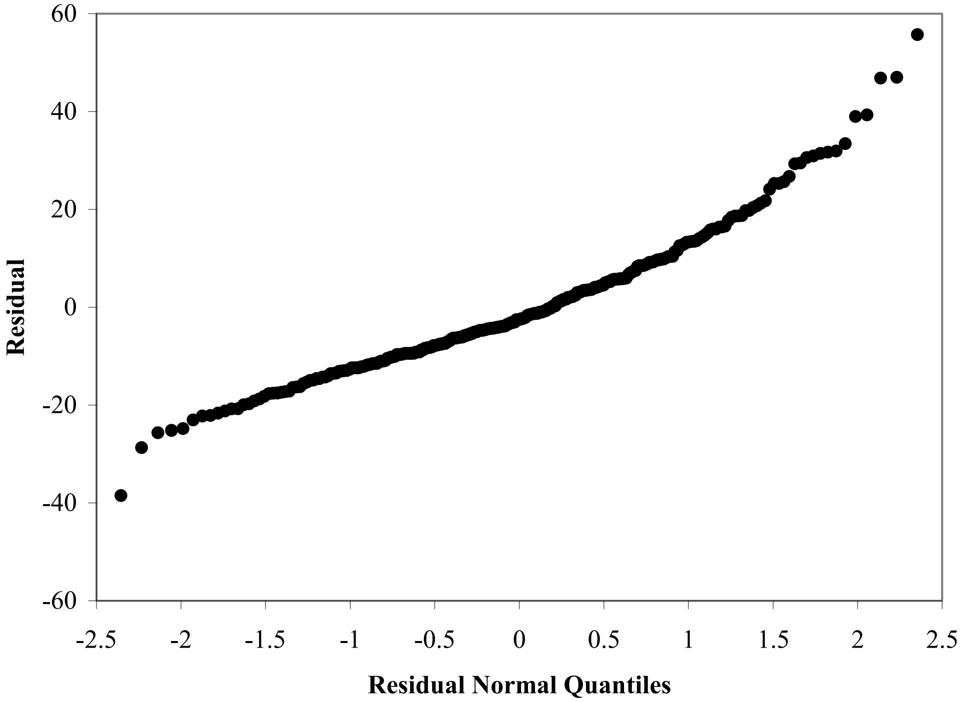
Appendix I.7. Residual vs. predicted plot for cherrybark oak Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.14): $\mathbf{\Delta}$ $\text{Ht}_{\text{2yr Box-Cox}} = b_0 + b_1\text{Diam}_{\text{initial}} + b_2\text{CH}$



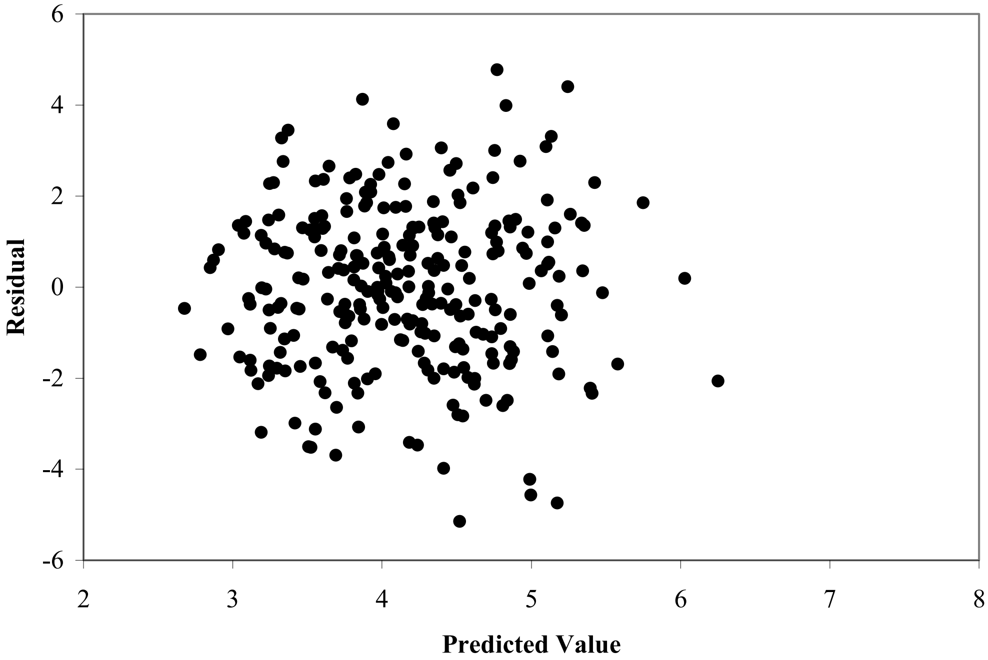
Appendix I.8. QQ-plot for cherrybark oak Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.14): Δ $Ht_{2yr\ Box\text{-}Cox} = b_0 + b_1 Diam_{initial} + b_2 CH$



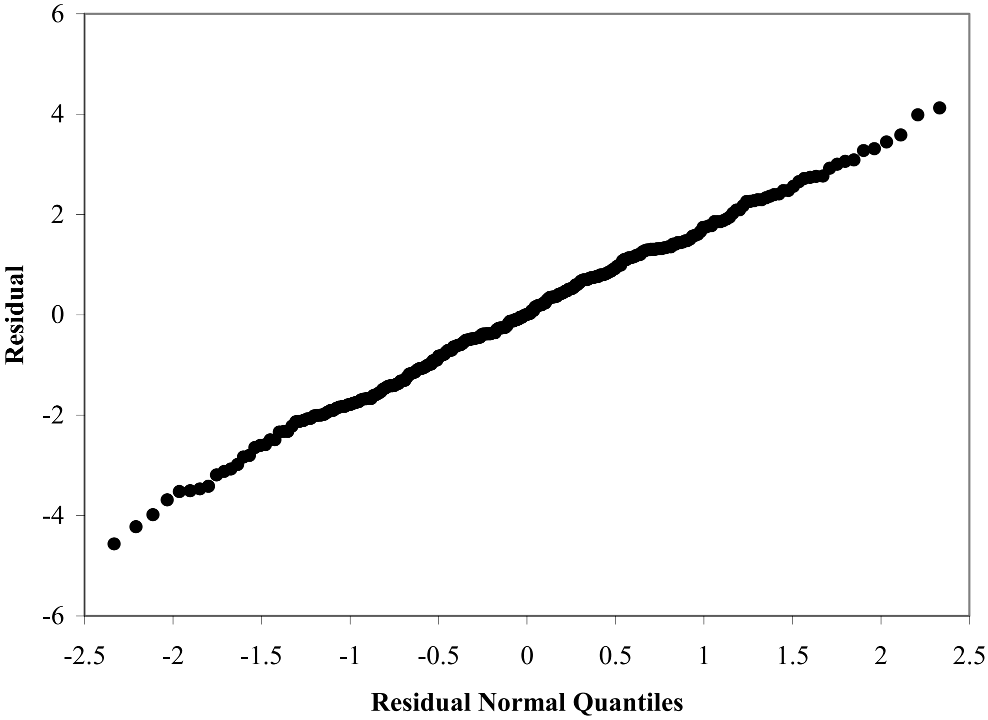
Appendix I.9. Residual vs. predicted plot for water oak Two-Year (2004 to 2005) untransformed height increment model: $\Delta \mathrm{Ht}_{2yr} = b_0 + b_1\mathrm{Closure60} + b_2\mathrm{CH} + b_3\mathrm{Diam}_{initial}$



Appendix I.10. QQ-plot for water oak Two-Year (2004 to 2005) untransformed height increment model: Δ $Ht_{2yr} = b_0 + b_1$Closure60+ b_2CH + b_3Diam$_{initial}$



Appendix I.11. Residual vs. predicted plot for water oak Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.15): Δ $Ht_{2yr\ Box\text{-}Cox} = b_0 + b_1Closure60 + b_2CH + b_3Diam_{initial}$



Appendix I.12. QQ-plot for water oak Two-Year (2004 to 2005) Box-Cox transformed height increment model (3.15): Δ $Ht_{2yr\ Box\text{-}Cox} = b_0 + b_1 Closure60 + b_2 CH + b_3 Diam_{initial}$