Relationships between Loblolly Pine (*Pinus taeda* L.) Yield and Woody Plant Diversity in Virginia Piedmont Plantations

by

Lisa E. Watson

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Approved:

Dr. Shepard M. Zedaker, Chairman

Dr. David Wm. Smith

Dr. James D. Fraser

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RELATIONSHIP BETWEEN LOBLOLLY PINE (*PINUS TAEDA* L.) YIELD AND WOODY PLANT DIVERSITY IN VIRGINIA PIEDMONT PLANTATIONS

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(ABSTRACT)

This study was established to determine the effects of competition control on loblolly pine (*Pinus taeda* L.), woody plant diversity, and wildlife habitat quality in Virginia Piedmont plantations 12-14 and 24-27 years of age. The responses of loblolly pine and competing woody vegetation in plantations 12-14 years of age were analyzed at 8 levels of competition control: total, 2/3, 1/3, or no woody stem control in combination with either total or no herbaceous vegetation control. As woody stem (plus herbaceous) control increased, pine yield increased, and percent hardwood basal area (PHWD BA) and overstory plant diversity (Shannon index (H')) decreased. Understory percent woody cover, and woody plant species richness, evenness, and diversity (H') were not affected at any of the competition control levels. Regression analysis was used to determine relationships between loblolly pine yield, hardwood dominance and overstory plant diversity. Pine yield was negatively correlated to PHWD BA (R^2=0.74), while overstory diversity (H') was proportional to PHWD BA (R^2=0.97) and inversely related to pine yield (R^2=0.77). The relationship between diversity and PHWD BA was consistent for plantations 12-14 and 24-27 years of age, while relationships of yield to PHWD BA and to diversity were altered in the older plantations.

In plantations 12-14 years, competition control reduced proportions of oak and hickory species and reduced canopy structural heterogeneity, but increased proportions of other fruit bearing plant species, and increased deer browse availability and ground stratum heterogeneity. In plantations 24-27 years, competition control altered plant species composition and increased structural heterogeneity.

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Introduction and Justification

Analyses of expected increases in population, economic activity, and timber product trends indicate that large increases in the demand for softwood timber in the United States will be met with only moderate increases in its supply (USDA 1982). While the majority of softwood inventory has, in the past, been supplied by the western United States, harvesting restrictions in the Pacific Northwest region should reduce federal harvest volumes. Washington, Oregon, and California contributions to federal harvest volumes are projected to be reduced by 52% to 76% between the years 1995 and 2000 (Wiedenbeck and Araman 1993). These trends illustrate the pressure that will be placed on the southeastern United States to supply a greater share of the softwood timber supply.

Approximately 61% of the softwood inventory in the South is under non-industrial private forest (NIPF) ownership, and a current lack of pine regeneration by this sector has contributed to a gradual decline in pine acreage in the South (Edwards and Dangerfield 1990). In Virginia, NIPF landowners control 68% of the pine acreage (Thompson and Johnson 1994) and provide 75% of the timber for Virginia's industrial market (Hodge and Southard 1992). The stability of Virginia's softwood inventory largely depends on sustained levels of pine regeneration and harvest by the NIPF sector (Thompson and Johnson 1994).

Because of the importance of the NIPF timber contribution, it is important to understand the NIPF landowners' objectives and motivations for owning forestland. From a recent survey, Hodge and Southard (1992) found that 44% of Virginia NIPF landowners have not harvested timber on their property, and 59% of those never plan to harvest. The survey also identified the top three reasons Virginia NIPF landowners feel it is important to own forestland: (1) preserving nature, (2) maintaining scenic beauty, and (3) viewing wildlife. Producing commercially saleable timber was cited as being not an important reason for owning forestland.

The Hodge and Southard survey reveals that non-commodity values of forests are important to forest landowners and these values are reflected in their forest management decisions. At the same time, timber demand and supply projections predict that these same landowners will soon be faced with economic pressure to produce higher timber yields. Therefore, there exist a need to represent the trade-off between the commodity benefits and the non-commodity benefits of forests so that NIPF landowners can make choices among management alternatives according to their own individual perspectives.

From a commodity perspective, loblolly pine (*Pinus taeda* L.) is the primary commercial softwood species in the Southeast. Because of its adaptability and commercial importance, loblolly pine is commonly planted in plantations within and along the periphery of its natural range. In unmanaged stands, loblolly pine is commonly found in association with a variety of hardwood and other pine species (Baker and Langdon 1990), and natural loblolly pine stand succession to hardwood forest cover occurs in plantations when no measure is taken to control competition (Felix et al. 1983). Even when silvicultural prescriptions are employed to control competition, a loblolly pine monoculture is rarely achieved.

Numerous studies indicate that loblolly pine growth and yield responses depend on the level of competition control achieved (Zutter et al. 1986, Bacon and Zedaker 1987, Swindel et al. 1989, Clason 1993, Glover and Zutter 1993, Lauer et al. 1993, Miller et al. 1991 and 1995). Competition control also has other effects. The gains in loblolly pine production are often met with changes in the plant diversity of young stands (Swindel et al. 1984, Zutter and Zedaker 1988, Neary et al. 1990, Edwards 1993, Reed et al. 1994), and compositional changes may persist 7 to 12 years after treatment (Harrington and Edwards 1994, Boyd et al. 1994). There are also indications that competition control can impact wildlife habitat, either favorably or adversely, depending on the type and intensity of the control treatment and the wildlife species of interest (Brooks et al. 1992, Leopold et al. 1994, Miller and Chapman 1995).

Although two bodies of research, one examining competition control effects on loblolly pine yield and one examining competition control effects on plant diversity, together suggest a relationship between loblolly pine yield and plant diversity, there is a lack of studies directly investigating this anticipated trade-off relationship. One approach to determining this relationship could utilize the established relationship between pine yield and canopy level competition.

Burkhart and Sprinz (1984) demonstrated that yield is negatively correlated to the percentage of total stand basal area in canopy hardwoods in hardwood-converted, site-prepared loblolly pine plantations. If basal area is inventoried by species, then it may be possible to describe a diversity -competition relationship. It follows, then, that if a diversity - competition relationship can be verified, a relationship between loblolly pine yield and woody plant diversity could be developed. Supplied with a quantified relationship between yield and plant diversity, forest resource managers would be better prepared to meet society's dual demands for timber and diversity conservation.

The purpose of this study was to test the hypothesis that a relationship exists between loblolly pine yield and woody plant diversity, quantify the relationship, and determine if the relationship persists through time and how it may affect wildlife habitat. Specific objectives of this study were to:

- Quantify the response of loblolly pine yield to eight levels of competition control.
- Quantify the response of canopy and woody understory species diversity to eight levels of competition control.
- Characterize the relationships between hardwood basal area, loblolly pine yield, and diversity.
- Compare the relationships found in plantations 12 to 14 years of age to trends found in plantations 24 to 27 years of age.
- Determine how competition control affects stand composition and structure, and relate these effects to wildlife habitat quality.

Literature Review

Loblolly Pine

Loblolly pine is an important plantation species in the Southeast. In Virginia, loblolly pine accounts for more than 60% of the acreage under pine plantation management (Thompson and Johnson 1992). It is generally accepted that the growth and yield of loblolly pine is negatively influenced by competing vegetation. Because of the economic importance of loblolly pine, numerous field studies have been established to quantity the effects of controlling competition on loblolly pine production. Fewer studies have examined the relationship dynamics of loblolly pine and competition. The following is a review of current work studying the influence of competition and its control on loblolly pine.

Responses to Competition Control

Competition control in pine plantations can be divided into three categories: control of herbaceous vegetation, control of non-crop woody vegetation, and control of both herbaceous and woody vegetation. Many studies involving herbaceous control have reported that herbaceous vegetation exerts negative influences on loblolly pine growth early in pine development, when moisture may be a limiting factor (Knowe et al. 1985, Zutter et al. 1986, Britt et al. 1990). Zutter et al. (1986) found that, during the first two growing seasons, soil moisture was negatively related to herbaceous vegetation levels.

There are indications that herbaceous control advances early pine growth (Knowe et al. 1985, Zutter et al. 1986, Bacon and Zedaker 1987, Miller et al. 1991). For instance, Knowe et al. (1985) reported the diameters and heights of loblolly pines in plots that received broadcast herbaceous control for two years were up to two times larger than in plots with no control. However, lack of height differences as early as age 5 (Miller et al. 1991) and by ages 7 to 9 (Lauer et al. 1993) indicate that the positive effects of herbaceous control on pine growth is realized early in development and may not persist as the plantation nears canopy closure (Miller et al. 1991). Miller et al. (1991) further found that while the influence of herbaceous competition decreased with stand age, the influence of woody competition was still increasing at age 5.

Loblolly pine responses to woody competition control has been well documented with positive growth responses occurring as early as 1 to 3 years after treatment (Bacon and Zedaker 1987, Zedaker et al. 1987, Perry et al. 1993) to 27 years after treatment (Glover and Zutter 1993). In those studies that have examined pine responses to varying levels of woody control (e.g., Bacon and Zedaker 1987, Clason 1993, Glover and Zutter 1993), loblolly pine growth and yield were generally shown to increase with increased treatment intensity. Only the Bacon and Zedaker (1987) study, however, was designed to investigate pine responses across a gradient of woody vegetation control intensities: controlling all, two-thirds, one-third, or none of the woody competition. Three years after treatment, control of all woody competition was shown to give no significant advantage to the pines over control of two-thirds, which averaged 150% higher in pine volume than no control.

In addition to the four levels of woody competition control, Bacon and Zedaker (1987) studied the combined effects of woody plus herbaceous control. They found that each level of woody control was more effective at increasing diameter and volume growth when combined with herbaceous control for plantations treated during the first and second growing season. Similar responses to combining woody and herbaceous control were detected in 5-year old plantations by Miller et al. (1991). Trends in this study continued to age 8, when loblolly pine cover in plots combining woody with herbaceous control was 28%, 30%, and 50% higher than in plots with herbaceous control alone, woody control alone, and no control, respectively (Miller et al. 1995).

Relationships to Competition

In order to best understand the relationship between loblolly pine and competition, pine responses should be examined over a gradient of competitive pressure. In a factorial experiment, Perry et al. (1993) subjected loblolly pine seedlings to various densities of broomsedge (*Andropogon virginicus* L.) and sweetgum (*Liquidambar styraciflua* L.) to determine the nature of the pine - competition relationship during the first growing season. They found that while the relationship of pine height response to competition was linear, diameter and volume responses to competition were curvilinear; that is, increases in early competition was found to decrease diameter and volume to a greater extent than height. This phenomenon has been observed by other researchers who noted that height was less responsive to competition control than were diameter or volume (Zutter et al. 1986, Bacon and Zedaker 1987, Miller et al. 1991, Lauer et al. 1993).

Perry et al. also found that growth responses to competition were not uniform across all density levels. Diameter and volume responses were highly influenced by changes in competition density at low densities but, at higher densities, responses became asymptotic. These results suggest that, once competition reaches some high level of intensity, early loblolly pine response will be relatively less affected by an increase in competition. Conversely, at lower levels of competition, a further reduction in competition results in relatively higher responses early in the development of loblolly pines.

This later conclusion, however, may not hold for loblolly pine response as a stand ages. The Burkhart and Sprinz (1984) model HDWD, predicts that as a stand ages the pine yield response is most sensitive within moderate ranges of competition and becomes asymptotic at very high and very low percentages of hardwood basal area. For example, at site index 60 ft (base age 25 for loblolly pine) and 800 planted pines per acre, the predicted response curves for loblolly pines at age 10, 30, and 50 become increasingly steep, respectively, at 60% to 20% hardwood basal area (Burkhart et al. 1987). As the percentage of total basal area in hardwoods decreases to 10% and below, the yield response pines 10 years of age continues to increase, while the responses for 30- and 50-year old pines increase at a slower rate (Burkhart et al. 1987).

Two important aspects are revealed from the work of Burkhart and Sprinz (1984). First, there is a strong relationship between loblolly pine yield and the percentage of total basal area in canopy hardwoods once a stand has reached canopy closure. And second, the nature of relationship can change as the stand ages.

Diversity

One rationale for monitoring the effects of competition control on plant diversity, among many proposed by conservationists and ecologists, is given by exiting and pending legislation (at least 29 federal statutes, Zedaker 1991) requiring that resource management objectives consider biological diversity. An important example of this is The National Forest Management Act of 1976 requiring the maintenance of forest ecosystem diversity as demonstrated by quantitative analysis. However, when quantifying diversity, it is necessary to define as clearly as possible the scope of the study's definition of diversity and to describe the methods used to quantify it. The following is a review of diversity types, their definitions, and quantification methods.

Definitions

Biological diversity has been defined by Giles and Overcash (1992) as "the variety of life and its processes." Diversity may be considered at different functional levels (e.g., diversity of an ecosystem to genetic diversity of a single species) as well as being considered within spatial and temporal bounds (Pielou 1975, Holland et al. 1994). Measures of diversity fall in to three broad categories: alpha, beta, and gamma. Alpha diversity refers to the composition within a defined community, beta diversity refers to composition differences between two communities, and gamma describes diversity on the landscape level (Kimmins 1987). This study restricts the term "diversity" to mean the alpha diversity of woody plants within the spatial and temporal bounds of a loblolly pine plantation stand of particular age classes.

Quantification

Alpha diversity measures seek to quantify the variability of qualitative characteristics occurring among species in a community (Pielou 1975). Of the alpha diversity measures, species abundance models provide a graphical description of a community's composition distribution, while models, or indices, based on the proportional abundance of species provide information about a community's population distribution (Pielou 1977, Magurran 1988). Another index, judged by Magurran (1988) as perhaps the simplest of the indices, is species richness.

Species richness (*S*) is merely a count of the number of species encountered in a given community (Pielou 1975, Magurran 1988). In combination with a list of species, this index provides information about the presence or absence of a species in a community and can be used to compare two or more communities of equal area.

Most ecologists include in their interpretation of community diversity a measure of the abundance of each species. Abundance is measured by the number of stems, cover, or some other measure of the quantity of a species (Pielou 1977, Swindel et al. 1987). The abundance of a species is commonly represented by its relative abundance or proportional abundance (p_i), where p_i is the proportion of the community belonging to the i^{th} species and $\sum p_i = 1$ (Pielou 1975 and 1977). When $p_1 = p_2 = \ldots = p_s = 1/s$, where $s =$ the number of species in the community, then the community is said to be proportionally even (Patil and Taillie 1982).

Indices based on proportional abundance have several characteristics that make them applicable for use in studies of forest diversity. These indices produce a single numerical value (or index) that, while alone may be difficult to interpret, can otherwise be used to determine differences in diversity between similar sites under different treatments or differences in the same site over time. Although these indices are traditionally calculated using the number of individuals present in a community (Pielou 1975), they are easily modified to incorporate basal area. By virtue of their proportionality, the indices produced from these models are unitless, making them dimensionally compatible with measures of yield.

While there is no consensus as to which diversity index is best, Margurran (1988) emphasizes a few of the more popular proportional abundance based indices: the Shannon evenness index, the Simpson dominance index, and the Berger-Parker dominance index. Dominance or evenness refers to which aspect of abundance distribution is given more weight in the model (Margurran 1988).

The forms of the indices are:

Shannon's index (H'): $H = -\sum p_i \ln(p_i)$

Simpson's index (C): $C = \sum p_i{}^2$

Berger-Parker (d): $d = N_{max} / N$

where: p_i = the proportion of individuals in the ith species or class
= the probability that a randomly selected individual will belong to the ith species or class

N = the total number of individuals

$Nmax$ = the number of individuals in the most abundant species or class

The Shannon and Simpson diversity indices are by far the most recognized and used among proportional abundance indices (Pielou 1977, Krebs 1985, Margurran 1988, Zedaker 1991).

Plant Diversity Responses to Competition Control

Interspecific competition has been defined by Radosevich and Osteryoung (1987) as the "adverse interference" among different species which contradicts with management objectives to optimize production of a single species that must pre-empt and dominate the resource. By this definition, competing vegetation is the adverse interference, but to a NIPF landowner it may be scenic beauty. Non-commodity benefits of forested land, such as scenic beauty and diversity, can be more important than commodity benefits, such as timber production, to a NIPF landowner (Hodge and

Southard 1992) or to the general public. Society's concern over the environment together with State and Federal statutes have prompted recent research into the effects of competition control on plant diversity.

It is expected that species richness and evenness decrease directly following release treatments but the magnitude, duration, and direction of the change in plant diversity remains to be more fully examined. Following a disturbance, secondary succession follows a shifting pattern of dominance throughout time. When release does not entirely eliminate residual competition, the appearance of early-successional species is expected, and, as Swindel et al. (1984) suggest, the initial decrease in plant species diversity caused by release may be viewed as merely a delay in the eventual increase in plant species diversity caused by early succession. However, if a release treatment occurs early enough and severe enough to either kill the rootstocks of the competition or bypass its successional stage, then the impact on plant diversity may last throughout the rotation period (Hunter 1990).

These conclusions point to two important factors that must be considered when examining the silvicultural effects on plant species diversity: first, the diversity affects should be related to the intensity of the treatment applied; and second, affects must be considered over time.

Numerous recent studies have explored silvicultural effects on plant diversity in loblolly pine plantations in the Southeast. Three studies, Swindel et al. (1984 and 1987) and Neary et al. (1990), were conducted in slash pine (*Pinus elliottii* var.

elliottii) stands but are worthy of inclusion because of their detailed work with plant diversity responses. A study by Edwards (1993) does not specifically mention loblolly pine; however, it provides interesting insight into plant diversity-treatment interactions in southeastern Piedmont pine stands. The majority of studies concerned with competition control impacts on plant diversity have concentrated on affects following site preparation (various mechanical, chemical, and combination treatments); however, two projects, Zutter and Zedaker (1988) and Boyd et al. (1994), studied release herbicide treatments and their effects on plant diversity.

No consistent diversity index was used across these various studies. Therefore, only general conclusions based on the researchers' interpretation of their results will be assessed in the following two sections.

Plant Diversity Responses: Time Considerations

Several of the studies evaluating the changes in plant diversity over time were conducted only within the first two years following silvicultural manipulation. First-year reductions in plant diversity following site preparation were detected by Reed et al. (1994) who examined growth forms ranging from herbs to trees and Edwards (1993) who concentrated on woody species only. Zutter and Zedaker (1988) also found decreases in woody plant diversity one year after herbicide treatment to release loblolly pine.

By the second year post-treatment, Reed et al. (1994) and Edwards (1993) found that diversity increased to levels nearly equal to non-treatment (check) and pre-treatment (antecedent) levels, respectively. Reed et al. stated that the overall increase in diversity was primarily due to increases in the herbaceous component.

In contrast to the decrease-recovery trends detected in the above studies, Swindel et al. (1984) reported continuous increases in species diversity of various vegetative growth forms from the first year to the third year post-treatment. Only one of their measures of diversity, second-year cover diversity by species, violated the increasing trend. It should be noted, however, that Swindel et al. (1984) used as their antecedent condition a 40-year-old second-growth forest.

A few studies have examined plant diversity responses to silvicultural treatments past the first few years; however, these studies contradict one another. Swindel et al. (1987), extending the 1984 study to 5 years post-treatment, confirmed the trends reported earlier and determined that these increasing trends in diversity continued to the fifth year. In a separate study, also concerned with site preparation for slash pine, Neary et al. (1990) found that plant species diversity was reduced 4 and 5 years post-treatment compared to pre-treatment levels.

Boyd et al. (1994) in a release study, determined that overstory and understory plant species diversity were not significantly effected 7 years after treatment; however, they did detect a shift in species composition and suggested that the difference was caused by using different herbicides.

Although the Miller et al. (1995) study did not investigate diversity per se, they did report compositional changes 8 years after intense chemical treatments. They found that herbaceous control decreased shrub density but increased the proportion of arborescent tree cover relative to no control treatment by the eighth year. Pine cover was not significantly different between woody alone and herbaceous alone treatments, but the woody component differed drastically between these to treatments, having a much higher proportion of woody cover in the herbaceous only treatment plots. Actual and relative semiwoody cover was higher in woody control than in no control, primarily due to the presence of blackberry (*Rubus* spp.).

Plant Diversity Responses: Composition Considerations

Of the site preparation studies that compared treatments, the majority determined that different treatments had differing effects on plant species diversity (Swindel et al. 1987, Neary et al. 1990, Harrington and Edwards 1994, Reed et al. 1994). The most commonly stated reason for these differences was observed shifts in species composition following treatment. Hurst et al. (1994), however, determined no significant difference in plant species richness among treatments; they did not state whether or not a species composition shift was detected.

Of the release studies, Zutter and Zedaker (1988) examined plant diversity responses to different rates of the same herbicide, while Boyd et al. (1994) examined the effects of different herbicides. Zutter and Zedaker found significant decreases in woody plant species diversity with increasing rates of hexazinone (3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione) application. Boyd et al. determined no significant treatment effects on total species diversity; however, by comparing importance values of species divided into growth forms, they found significant treatment effects with respect to semi-woody and legume growth forms.

Swindel et al. (1987) stated that cover of more "scarce" species in the minimum intensity site preparation plots had large initial increases followed by a slightly decreasing trend. Scarce species were those found in low proportional abundance. Maximum intensity treatments showed only small initial increases in scarce species followed by continued increasing trends toward the fifth year. Swindel et al. (1984), also observed these trends in an earlier study and concluded that intensive treatments had the effect of "delaying" increases in plant diversity.

Any discrepancies found between the results of the above studies may be due to the growth form(s) under investigation. For instance, Minogue et al. (1994) found that increased rates of imazapyr ((±)-2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) caused decreased broadleaf, non-arborescent, and arborescent hardwood species cover, but increased *Rubus* species cover; however, when imazapyr was combined with other site preparation treatments, *Rubus* decreased. Miller et al. (1995) reported that, in plots treated with triclopyr ([(3,5,6-tricloro-2-pyridinyl)oxy]acetic acid) and glyphosate (N-(phosphonomethyl)glycine) to control woody plants, erect *Rubus* spp. continued to increase in dominance for 8 years. Similar growth form shifts were detected by Zutter and Zedaker (1988) who confirmed blueberry's (*Vaccinium* spp.) resistance to hexazinone and found that Vacciniums increased in importance (average relative density and dominance) following treatment.

Because of the variable susceptibility of growth forms and species to different types, rates, and combinations of herbicides, there exists a need for a "measuring stick" that measures plant diversity responses to silvicultural prescriptions which includes more than just time and treatment. The logical addition to the measuring stick is pine yield. Comparing diversity responses directly to pine yield responses could lead to more direct and explicative conclusion about the impact of competition control; i.e., the possible trade-offs between commodity and non-commodity benefits could be more clearly represented.

Relationships between Loblolly Pine Yield and Plant Diversity

Only one study, to date, has addressed the trade-off between timber yield and diversity. In their study, Holland et al. (1994) incorporated measures of diversity into a linear programming harvest scheduling model to predict the effects of alternative regeneration methods on harvest volume, present net value (PNV), species diversity, and structural diversity over a 150-year planning period.

Using data collected by standard Forest Service inventory methods from the Cache National Forest in Utah, Holland et al. projected yield estimates with the single tree, distance independent growth and yield model, PROGNOSIS. Commercial trees of interest were spruce and fir species, lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*). The Shannon diversity index was used to calculate index values for three measures of diversity: species diversity; basal area diversity, an indication of horizontal structural diversity; and vertical diversity. The linear program, Industrial Lindo, was used for six runs depicting the following management objectives: 1) maximize harvest volume, 2) maximize PNV, 3) maximize species diversity, 4) maximize basal area diversity, 5) maximize vertical diversity, and 6) maximize average diversity.

From the simulated stand conditions generated from PROGNOSIS, Holland et al. determined that harvest volume maximization reduced basal area and vertical diversity by approximately 10% and species diversity declined by 24%. Under the diversity management objectives, harvest volume was reduced across all three diversity maximization scenarios by 17% to 20%.

Because the Holland et al. (1994) study is concerned with timber species and rotation periods typical of the western U.S. and utilized simulated data, its application may be limited. However, it does give insight into how quantifiable measures of diversity and timber yield can be used to demonstrate the trade-offs involved with different management objectives.

Effects of Competition Control on Wildlife

The primary way competition control affects wildlife is through its alteration of habitat. Because various types, rates, and combinations of control treatments affect plant growth forms and species differentially, the indirect effects of competition control (depending on the method and intensity) could drastically alter habitat characteristics. Depending on the wildlife species of interest, these habitat changes could be either beneficial or detrimental. Although the body of research aimed specifically at indirect effects on southeastern wildlife habitat is small, a few studies have investigated how plant compositional changes might affect wildlife. Other studies, unrelated to competition control effects, give insight into how wildlife respond to structural changes.

Studies specifically concerned with plant composition changes and its implication for wildlife report relatively short-term results, from 1 to 6 years post-treatment. Leopold et al. (1994) conducted a study in Mississippi to investigate the response of white-tailed deer forage to chemical and/or mechanical site-preparation for a pine plantation. They determined that, compared to mature pine-hardwood forest, woody forage was reduced by all treatments through the first 2 years following treatment, while forb and vine forage was higher. They found no differences in forage abundance and biomass between chemical and mechanical control methods. Comparing increasing intensities of mechanical site-preparation in the Georgia Piedmont, Locascio et al. (1990) found that the moderate to moderately high treatment intensities resulted in higher white-tailed deer forage diversity and biomass roughly 7 years after treatment.

In Georgia, Brooks et al. (1992) examined the effects of chemical site-preparation on vegetation composition and abundance as they related to wildlife food quality and availability 1 year after treatment with 3 different chemicals or chemical mixtures. They found that the selectivity of certain chemicals affected the plant species composition and, thus, habitat quality. For example, *Vaccinium* sp., an important food for numerous species of birds, white-tailed deer (*Odocoileus virginianus*), eastern cottontail rabbits (*Sylvilagus floridanus*), racoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and opossums (*Didelphis marsupialis*) (VanDersal 1939), was significantly reduced by imazapyr treatment and significantly increased by hexazinone treatment. Similar plant species shifts attributed to chemical susceptibility were noted for vine species that are important food sources for various wildlife species.

The selectivity effects of herbicides on wildlife habitat was also detected by Miller and Chapman (1995). In their study of site-preparation effects on southeastern avian communities, Miller and Chapman detected seasonal variation in avian communities. Although no significant difference between 3 different chemical treatments in songbird abundance was detected during winters, differences in songbird species richness and density did occur during summers for the first 3 years. Songbird density was found to be correlated to woody vegetation. Abundance of edge and shrub songbird species was highest in chemical treatments that increased the density of shrubs such as Vacciniums.

Miller and Chapman (1995) also investigated the effects of both chemical and mechanical competition control on small mammal communities through a period of five years. Small mammal capture rates declined the first year after treatment, were highest in mechanically treated areas in the second year, and by 5 years post-treatment there was no significant difference between treatments or pre-treatment capture rates.

The difference between the structure of a pre-harvest stand and its structure following harvest is obvious. As succession is initiated, structural and associated functional changes occur and much wildlife research has been devoted to better understanding wildlife assemblages through succession. Two studies have examined avian community dynamics in the succession of loblolly pine under natural conditions (Johnston and Odum 1975) and under plantation management (Childers et al. 1986).

Johnston and Odum (1956) investigated breeding bird pair densities on the Georgia Piedmont following natural succession of loblolly pine and shortleaf pine (*Pinus echinata* Mill.) in abandoned fields. The general trend found was that as stand development increased both bird density and species richness increased. Exceptions to this trend were a drop between the grass and shrub stages and in the young pine stage before hardwoods developed under the pines. Once a deciduous understory developed, avian species richness and density increased.

The work of Childers et al. (1986) provides valuable information on songbird community dynamics in developmental stages of Virginia Piedmont loblolly pine plantations. They sampled avifauna in 8 plantation age classes and in second-growth native forests and found the number of birds was highest in plantations 2 and 5 years, lower in plantations (7-11 years) and native forests (58-83 years), and lowest in plantations 17 to 24 years of age. Childers et al. attributed the decrease in bird density to canopy closure and decreased understory vegetation which had been previously determined and reported by Felix et al. (1983). Species richness and diversity, as measured by the Shannon diversity index, were higher in plantations 2 to 8 years than in plantations 11 to 24 years and comparable to values for the native forests. Early successional bird species were most prevalent in the young plantations, while those species found in the oldest native forest were also found in the older plantations.

Competition control can have the effect of delaying succession thereby influencing vertical growth and stratification. Documentation about the effects of competition control on vertical stratification is weak; therefore, its impact must be inferred from studies that have examined the effects of vertical stratification on avian assemblage.

The MacArthur and MacArthur (1961) study is the most commonly cited study in literature concerned with avian - forest strata relationships for their work in correlating avian species diversity with vertical stratification diversity. MacArthur and MacArthur predicted bird species diversity from foliage height diversity (both quantified with the Shannon diversity index). They further concluded that good predictions of bird diversity based on plant species diversity could be explained solely by vertical diversity; that is, habitats of similar vertical profile have similar bird diversity regardless of the number of plant species present. The 3 height classes used to compute the vertical diversity roughly corresponded to the qualitative classes of an herbaceous layer, a shrub to small tree layer, and a layer of larger trees (MacArthur and MacArthur 1961).

Dickson and Noble (1978), using MacArthur and MacArthur's (1961) methods for vertical diversity and the percent of bird sightings, determined that vertical resource partitioning occurred on the bottomland hardwood forests of Louisiana. They identified bird species that were specialists in one particular stratum, species that used 2 strata, and species that were generalists among the 3 strata. These results substantiate the hypothesis of resource partitioning and verify the importance of vertical stratification in forests, particularly for species that are not resource generalists. Another important finding of Dickson and Noble was that while the ground stratum (<0.6 m) represented only 2% of the total stand height it supported 31% of the bird sightings compared to 33% of the bird sightings in the canopy (7.6 - 25.9 m) which represented 71% of total stand height.

High avian use of the ground stratum was also observed by Yahner (1987) in even-aged stands of aspen (*Populus* sp.) and oak (*Quercus* sp.) in Pennsylvania. However, he found that bird species richness was highest in the lower midstory (1.1 -

6.0 m). Upper midstory (6.1 - 12.0 m) and canopy (> 12 m) layers were used least by birds and had the lowest bird species richness in the winter.

While the specific effects of competition control on vertical stratification in loblolly pine plantations is poorly documented, Miller et al. (1995) have reported that the type of competition control used can affect the distribution of shrubs versus trees. For example, they found that herbaceous control alone decreased shrub cover and increased arborescent tree cover, while woody control alone drastically decreased tree cover but increased shorter semiwoody cover.

In summary, the economic importance of loblolly pine has prompted research into the effects of competition control on loblolly pine, while the importance of biodiversity preservation has prompted recent research into the indirect effects of competition control on plant diversity and wildlife habitat quality. Much research into competition effects on pine response has led to the general acceptance that controlling competing vegetation results in improved loblolly pine growth and yield. However, studies investigating competition level effects (e.g. Burkhart and Sprinz 1984, Bacon and Zedaker 1987, and Perry et al. 1993) indicate that the relationship between loblolly pine and competing vegetation is dynamic and suggest that total control of competing vegetation may not be necessary in order to achieve high yield. This is particularly important in light of recent research indicating that plant diversity is likewise differentially affected by levels of competition control.

Though there is strong evidence that an apparent trade-off relationship exists between pine yield and plant diversity, this relationship has yet to be quantified for loblolly pine and plant diversity in the Southeast. Changes in plant diversity may not fully explain the extent of competition control effects, however, since compositional and structural changes can also impact wildlife habitat quality.

Methods

Site Descriptions

To characterize the relationship between loblolly pine yield and woody competition dominance and diversity, an effort was made to select study sites of different ages that would offer the widest possible range in competition dominance. A study by Bacon (1986) was installed in 1983 to compare the third-year growth response of loblolly pine to eight levels of release and, thus, offered a wide range of competition levels as well as a unique opportunity to examine the twelfth-year loblolly pine and competition responses to these levels of release. At the time of this current study these plantations were beginning their twelfth, thirteenth, and fourteenth growing seasons.

From release studies conducted by Thomas A. Dierauf for the Virginia Department of Forestry (some of which were published in Occasional Reports 1972-1989), plantations beginning their twenty-fourth to twenty-seventh growing seasons were selected to provide older sites with various levels of competing woody vegetation. Plantations were primarily on the Virginia Piedmont, had been converted from hardwood or mixed hardwood-pine stands, and were placed into one of two age categories: 12 to 14 years of age, or 24 to 27 years of age. Site-specific differences in site-preparation methods, release treatments, and plot sizes are summarized in Table 1.

Table 1. Description of study sites.

Location by Province	Soil Series	Previous Stand, Time of Planting	Site-Preparation	Release Treatment[1]	Plot Size (ha)	# Plots Sampled
Piedmont						
Appomattox-Buckingham State Forest, Stand 10-47	Tatum Manteo	hardwood, 1983	drum-chop, burn	• 2/3 woody + herbaceous	0.1	1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Appomattox-Buckingham State Forest, Stand 10-44	Tatum Manteo	hardwood, 1982	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 2/3 woody + herbaceous		1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Appomattox-Buckingham State Forest, Stand 10-19	Tatum Manteo	hardwood, 1981	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Dillwyn, VA Buckingham County	Tatum Manteo	hardwood, 1983	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Dillwyn, VA Buckingham County	Tatum Manteo	hardwood, 1982	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 2/3 woody + herbaceous		1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Dillwyn, VA Buckingham County	Tatum Manteo	hardwood, 1981	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 2/3 woody + herbaceous		1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1

Table 1. Continued

Location by Province	Soil Series	Previous Stand, Time of Planting	Site-Preparation	Release Treatment	Plot Size (ha)	# Plots Sampled
Piedmont						
Halifax County	Tatum Manteo	hardwood, 1983	drum-chop, burn	• total woody + herbaceous	0.1	1
				• 2/3 woody + herbaceous		1
				• 1/3 woody + herbaceous		1
				• no woody, herbaceous only		1
				• total woody only		1
				• 2/3 woody only		1
				• 1/3 woody only		1
				• check		1
Charlotte County	Tatum Manteo	hardwood, 1981	drum-chop, burn	• 2/3 woody + herbaceous	0.1	1
				• no woody, herbaceous only		1
				• 2/3 woody only		1
Prince Edward State Forest, Owens Unit	Cecil	mixed-hardwood 1969	burn	• hand-chop	0.04	4
				• mist-blow		1
				• basal spray		1
				• check		3
Prince Edward State Forest, Flippen 15 Unit	Cecil	hardwood 1972	drum-chop	• mist-blow	0.04	2
				• basal spray		3
				• check		3
				•		
Prince Edward State Forest, Flippen 16 Unit	Cecil	mixed-hardwood 1972	burn	• mist-blow	0.04	2
				• basal spray		2
				• check		3
Coastal Plain						
Caroline County	Unknown	hardwood 1970	drum-chop, burn	• aerial spray	0.04	3
				• check		3
				• Total number of stands 12 to 14 years of age	=	55
				• Total number of stands 24 to 27 years of age	=	30
				• Total number of stands sampled	=	85

[1] Some treatment plots were necessarily excluded because of accidental fires or excessive ice damage

Plantations beginning their fourteenth, fifteenth, and sixteenth growing seasons received drum-chop and burn site preparation and were machine-planted during the springs of 1981, 1982, and 1983, respectively. These sites were located in the counties of Buckingham, Charlotte, and Halifax on silt loam soils of the Tatum, Georgeville, Orange, and Manteo series. Tatum and Georgeville soil series are fairly deep and well drained, while the Orange series is fairly deep but poorly drained, and the Manteo series is shallow and excessively drained (Bacon 1986).

Plantations beginning their twenty-fourth and twenty-seventh growing seasons received either drum-chop only or burn only site preparation and were machine-planted in the winter of 1971/72 and in the spring of 1969, respectively. These plantations were located in Prince Edward County on fine sandy loams of the Cecil soil series, which are fairly deep and well drained. Six plots, in plantations beginning their twenty-fifth growing seasons, were located on the Upper Coastal Plain in Caroline County, two miles west of Carmel Church, Virginia. This site was drum-chopped and burned for site-preparation and was machine-planted in the winter of 1970/71. The soil series of this location is not available.

Although on the Virginia Coastal Plain, the Caroline County site was included in the study for two reasons. First, an effort was made to include sites that had received an overall wide array of release treatments to offer the widest possible percent hardwood distribution, and this site offered an additional release treatment not included on the Piedmont sites (Table 1). Second, there was a limited number of Piedmont sites ranging in age from 24 to 27 years that had not been thinned and were available for this study. The inclusion of this site is reasonably justified as studies that have included sites from both the Piedmont and Coastal Plain provinces have found that responses to chemical competition control (Lauer et al. 1993), mean loblolly pine yields (Burkhart et al. 1985), and successional trends (Miller et al. 1995) are similar across these two provinces.

Design and Treatments

Plantations Twelve to Fourteen Years of Age

In a split-plot design with three replications, release treatments were randomly assigned and applied in 1983 to square 0.1 hectare (ha) plots in plantations beginning their first, second, and third growing seasons. Treatments included total, two-thirds, one-third, or no woody stem control in combination with either total or no herbaceous vegetation control, for a total of 8 treatment levels. Woody stems received basal spray application of a 4% v/v solution of the ester formulation of triclopyr as Garlon 4 in diesel oil. Herbaceous vegetation was treated by broadcast application of sulfometuron (methyl-2 [[[[(4,6-dimethyl-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]benzoate) as Oust at 0.42 kg ai/ha in water, with follow-up directed applications of a 1% solution of glyphosate as Roundup in a water carrier.

Plantations Twenty-four to Twenty-seven years of age

Study sites in Prince Edward County were installed on Virginia State Forest Management Units between 1971 and 1974 by the Virginia Department of Forestry. Release treatments were applied to plantations beginning their first and third growing season in 40.3 meter (m) swaths and 0.04 ha square plots were installed in the center of each swath. Treatments included (1) hand-chopping, manually cutting down all hardwoods; (2) mist-blowing with 2,4,5-T (2,4,5-trichlorophenoxy)butoxyethanol ester) at 4.5 kg ai/ha in diesel oil and water at a rate of 56 liters mix per hectare using either a tractor-mounted Potts mist blower or a backpack sprayer; (3) basal spray application with a mixture of 3.8 liters of 2,4,5-T (4.5 kg ai/ha) in 10 gallons diesel oil; or (4) no vegetation control (check).

The study site in Caroline County was installed on a private industrial pine plantation in 1976 following a release treatment applied during the fifth growing season. Treatments here included an aerial spray of 2,4,5-T at 56 liters per hectare (carrier unknown), and check. A 30 m wide buffer strip separated the treatment from the check plots, each plot being 0.04 ha in area.

Data Collection

All data were collected during the summer of 1995 except for the heights of loblolly pines aged 24 to 26 years. Because vision of the pine tops was hindered by hardwood foliage, these heights were measured in the late fall of 1995 .

Loblolly Pine

Data collected for loblolly pine were used for estimates of yield on a per hectare basis. Pine ages were determined from planting records for all stands; however, some data collection methods differed for the two age categories because of differences in age and plot installation.

Plantations Twelve to Fourteen Years of Age

A total count of all live planted pines was taken in each 0.1 ha plot. Diameter at breast height (1.37 meters above ground level) and crown class were determined on 25 planted pines which were systematically located and tagged prior to release treatment. In cases where the originally tagged pines were dead or could not be relocated, randomly located pines were chosen for measurement without regard to their crown class. Diameter at breast height (DBH) was measured with a metric diameter tape to the nearest 0.1 centimeter (cm). Crown class determination followed the relative crown dominance guidelines described by Avery and Burkhart (1994). Four crown classes were recognized: dominant, codominant, intermediate, and suppressed. Total pine height to the tallest live bud was determined for three dominant and three codominant pines and measured with a metric telescoping height pole to the nearest 0.1 meter.

Plantations Twenty-four to Twenty-seven years of age

A total count of all live planted pines was taken for each 0.4 ha plot. Diameter and crown class were determined on 25 randomly located planted pines except for plots that contained less than 25 live planted pines (eight plots, 24 years of age, contained only 10 to 18 planted pines). Diameter at breast height and crown class were determined according to the same methods as described for the plantations 12 to 14 years of age. The total heights of three dominant and three codominant pines were determined to the nearest 0.3 m using a Suunto clinometer from a distance of 15 meters.

Canopy and Understory Woody Vegetation

The scope of this study restricts the term, competing vegetation, to mean only woody vegetation, which included all hardwood and non-loblolly pines trees, shrubs, and woody vines. Assessment of competing vegetation occurred on 2 strata levels: (1) canopy, or all woody stems of crown class intermediate or above (excluding climbing vines); and (2) understory, which included all suppressed woody cover (Avery and Burkhart 1994).

Since, hardwood basal area (including natural pines) in the main canopy has been shown to be useful as a predictor of loblolly pine yield (Burkhart and Sprinz

1984) and its use in calculating diversity indices does not violate model assumptions (Pielou 1975), canopy measurements were aimed at determining basal area by species. For each canopy stem in each plot, the genus and species, DBH to the nearest 0.1 cm, and crown class was determined.

Similar to canopy basal area as an estimate of occupied resource, percent understory cover estimates offer advantages over density estimates. Percent cover provides more structural information, and different species and growth forms can be comparatively evaluated using the same parameter (Gysel and Lyon 1980). As with basal area, percent cover is applicable to diversity evaluation (Pielou 1975). For estimates of understory cover by species, the line-intercept sampling method was used. Line intercept (often called line transect) has been shown to offer relatively rapid assessment of cover, is applicable in forest sampling where vegetation may be patchy, and is less effected by random error than quadrat sampling (DeVries 1979, Monkevich 1994).

A total line transect length of 60 m was determined to be adequate to estimate understory cover. Two 30 m line transects (in 0.1 ha plots) and three 20 m line transects (in 0.04 ha plots) were placed parallel, spaced 10 m apart, in each treatment plot. DeVries (1979) noted that the number of lines sampled is irrelevant as long as the total length remains constant. For each woody plant that intercepted the line, the length of the line (to the nearest 0.5 cm) intercepted by a living portion of the plant and the genus and species of the plant were recorded. Intercept lengths for tall vegetation were determined using the "stick method" (Andresen and McCormick 1962, cited and described in detail by Gysel and Lyon 1980). This method involves raising a stick through a vertical arc from the crown perimeter to the transect line, allowing accurate vertical projection of intercept lengths for taller vegetation. Plants belonging to the following genera were grouped by genus: *Vaccinium* sp., *Smilax* sp., *Crateagus* sp., *Rubus* sp., *Rosa* sp., *Rhododendron* (azalea species only).

Vertical Structure

Vertical line measurements were taken to describe the vertical profile of the plots. A telescoping height pole was erected at 6 randomly located points along the transect lines of each plot. At each point, the total height of each vegetation type in actual contact with the pole was recorded. Four vegetation types were recognized: shrub and/or vine, hardwood, conifer (other than loblolly pine), and hardwood-conifer mixtures.

Data Analysis

To quantify loblolly pine response to treatments, means for DBH, basal area (cu m/ha), height of dominant and codominant trees, and number of trees per hectare were computed for each treatment plot. The stand-level loblolly pine growth and yield model TAUYIELD (Amateis et al. 1995) was used to determine yield. TAUYIELD was developed using data collected from permanent remeasurement plots on the Coastal Plain and Piedmont throughout most of loblolly pine's natural range and is applicable under many stand conditions (Amateis et al. 1995). The form of the yield equation is:

$$\ln Y = b_0 + b_1(1/A) + b_2(\ln S) + b_3(HT_d/A) + b_4(A \ln N) + b_5(\ln BA)$$

where:	Y	= total outside bark yield (cu ft/ac)
	A	= stand age
	S	= site index (ft at age 25)
	HT_d	= average height of dominant and codominant trees (ft)
	N	= number of trees per acre
	BA	= basal area (sq ft/ac)
	$b_0, b_1, \ldots, b_5$	= model parameters (detailed by Amateis et al. 1995)

TAUYIELD simultaneously computes site index while computing yield. Metric - English conversions were computed where necessary.

Basal area (sq m/ha) by species was computed for canopy level hardwood and natural pine trees, hence termed hardwoods. The percentage of total stand basal in hardwoods (PHWD BA) was calculated by:

PHWD BA = hardwood basal area / hardwood + loblolly pine basal area

Understory percent woody cover (PWC) was estimated by the formula:

$$\text{PWC} = \sum l \,/\, L$$

where l = intercept length of the woody vegetation
L = total length of the transect line, in the case this study = 60 m

The Shannon diversity index, Evenness index, and species richness were calculated for the canopy and understory. Equation used followed Magurran (1988) and were:

Shannon index (H'): $H' = -\sum p_i \ln p_i$

Evenness index (E): $E = H' / \ln S$

Species richness (S): S = the number of species

where p_i = proportion of basal area for the ith species, in the canopy
= proportion of cover for the ith species, in the understory
S = number of species in the canopy per plot, for the canopy
= number of species per 60m transect line, for the understory

Data from stands 12 to 14 years of age were subjected to analysis of variance for a split-plot design and Duncan's Multiple Range Test (MRT) using the age*treatment interaction for the error term to determine the significance of treatment effects. The variable means tested were: number of loblolly pines per ha, loblolly pine HT_d, loblolly pine DBH (cm), yield (cu m/ha), PHWD BA, PWC, and the Shannon, Evenness, and species richness diversity indices.

Regressions were fit for plots 12 to 14 years of age using SAS (SAS Institute 1993) to describe the relationships between: (1) yield and PHWD BA, (2) diversity (as measured by indices) and PHWD BA, and (3) yield and diversity. Selection of the best regression models was based on analysis of variance and residual analysis. To determine the relevance of relationships found in the younger plantations to relationships in the plantations 24 to 27 years of age, dummy variables were incorporated into the models and used to test for intercept and slope coincidence between age classes.

To determine plant composition shifts, changes in the abundance of individual plant species were examined. The species or species groups chosen for examination were based on their relative abundance and/or importance (primarily food source) for wildlife and included: *Vaccinium* spp., greenbrier (*Smilax* spp.)., *Rubus* spp., grape (*Vitis* spp.), sumacs (*Rhus* spp.), Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Toxicodendron radicans*), oaks (*Quercus* spp.), hickories (*Carya* spp.), eastern redcedar (*Juniperus virginiana*), and black cherry (*Prunus serotina*). T-test analysis was used to test the null hypothesis that the mean PHWD BA and PWC for each species/group were the same in the competition control plots versus no competition control plots. Mean PHWD BA and PWC for each species/group were also plotted by control versus no control for visual representation of plant species compositional changes.

Vertical profiles for each plot were determined by calculating the percent of the total stand height (height of the tallest dominant loblolly pine sampled in the plot) and the percent frequency of each vegetation type in each height percentile. Graphical representations were made of the percent height against the percent frequency means by vegetation type and treatment for visual assessment of the vertical profile. Analysis of the vertical profiles and their implications for wildlife were based on visual assessment and were not subjected to statistical testing.

Results and Discussion

Effects of Eight Levels of Competition Control in Plantations Twelve to Fourteen Years of Age

The response of loblolly pine and competing woody vegetation in plantations 12 to 14 years of age was analyzed at 8 levels of competition control. Control levels included: total, 2/3, 1/3, or no woody stem control in combination with either total or no herbaceous vegetation control. Analysis of variance (ANOVA) was performed according to a simple split-plot design to determine significant main and interaction effects and in preparation for mean separation by the Duncan's multiple range test. The ANOVA results are summarized in Table 2.

There was some evidence that age or age at the time of treatment had a significant effect ($p \leq 0.05$) on some of the stand variables (Table 2). Because analysis was based on absolute measurement and not growth, it is difficult to distinguish between age versus age at treatment effects. In general, however, the pattern of effect for loblolly pine trees per hectare, HT_d, and yield, and species richness and Shannon diversity in the understory was: age 13 > 14 > 12 years. For loblolly pine DBH, the pattern was 12 > 13 > 14 years; and for canopy species richness and Shannon diversity the pattern was 14 $\geq$ 12 $\geq$ 13 years. These patterns do not follow the normal age sequence and, therefore, may be related to the treatment timing.

Table 2. Summary of ANOVA results for the significance of replicates, whole-plot factor (Age), control levels or split-plot factor (Treatment), and interactions for Virginia Piedmont loblolly pine plantations 12 to 14 years of age.

Stand Variable[1]		Significance values for main and interaction effects F statistics P-values				
		Rep	Age	R x A	Treatment	A x T
	df	2	2	3	7	14
Loblolly Pine:						
DBH		0.0001	0.0001	0.0001	0.0001	0.0003
HT_d		0.0001	0.0001	0.0001	0.0001	0.1257
# pines / ha		0.0001	0.0129	0.0858	0.4200	0.5165
Yield		0.0001	0.0222	0.0425	0.0276	0.7645
Canopy:						
PHWD BA		0.0001	0.1183	0.0692	0.0080	0.4549
Shannon (H')		0.0001	0.0373	0.0192	0.0017	0.5931
Evenness (E)		0.0001	0.0843	0.1556	0.0543	0.4043
Species (S)		0.0001	0.0156	0.0093	0.0011	0.4095
Understory:						
Woody Cover		0.2119	0.1905	0.0111	0.7823	0.2399
Shannon (H')		0.0433	0.0053	0.0085	0.9765	0.5631
Evenness (E)		0.0013	0.3645	0.0309	0.8263	0.4480
Species (S)		0.0219	0.0001	0.0003	0.8521	0.7367

[1] DBH, diameter at breast height; HT_d, average total height of dominant and codominant pines; Yield, total outside bark volume (cu m/ha); PHWD BA, percentage of hardwood basal area; Shannon diversity index (H') calculated from basal area proportions for canopy and from percent cover in the understory; Species richness (S) is the average number of species per 0.1 ha for canopy and average number of species per 60 m transect for the understory.

Bacon and Zedaker (1987) found that, 3 years post-treatment, the pines treated during the second-growing season (which corresponds to the 13-year old plantations) had the greatest percent volume growth over check, which is consistent with the age effects noted in this study. However, they reported the second highest percent volume growth for plantations treated during first-growing season (plantations now aged 12 years), which does not follow the pattern observed in this study. Bacon and Zedaker reported that greater diameter growth appeared to be related to herbaceous control treatments during the first- and second-growing seasons; this may have contributed to the age effects found for the twelfth-year DBH response, as it is unlikely that DBH would otherwise be greater in younger plantations.

Since the effect of age on evenness was not significant, the differences in Shannon diversity with age was likely the result of the differences in species richness with age. The age effect patterns differed for understory and canopy species richness and did not follow a normal age sequence. However, it is possible that treatment during the first growing season adversely affected twelfth-year understory species richness, while treatment during the second growing season adversely affected canopy species richness. While treatment level, rather treatment timing, was the focus of this current study, the results indicate that further study into treatment timing effects on loblolly pine as well as stand diversity is merited.

For all variables, with the exception of loblolly pine DBH, the treatment x age interaction was insignificant, indicating that treatment response did not change with plantation age or age at the time of treatment. Therefore, variable means were reported by control level (treatment) only and represent means across all ages. The responses of loblolly pine and of competing woody vegetation in both the canopy and understory are reported separately.

Loblolly Pine Response

The total and 2/3 woody stem control treatments, both with and without herbaceous control, resulted in the highest DBH responses compared to all other treatments (Table 3). Diameter was equally ($p > 0.05$) as large with the 2/3 woody control as with total woody stem control. Similar early groundline diameter growth responses to these treatment levels were detected by Bacon and Zedaker (1987) 3 years post-treatment. Their results also showed significant diameter growth with both 2/3 and total woody control.

The addition of herbaceous control to the 2/3 woody control treatment resulted in a significant difference in DBH, having a 5% increase over the same treatment without herbaceous control and a 17% increase over that of no competition control. One-third woody stem control alone was not significantly different from no woody control, but when combined with herbaceous control resulted in a significantly higher DBH response. In contrast, DBH did not significantly increase with the addition of herbaceous control for the highest and lowest levels of woody stem control (Table 3).

Bacon and Zedaker (1987), reporting the third-year responses to these treatment levels, stated that groundline diameter growth in stands treated during the first and second growing season was significantly increased at each level of woody stem control with the addition of herbaceous control. However, the results of this current study

Table 3. Loblolly pine means for diameter at breast height (DBH), height of dominants and codominants (HT_d), number of trees and cubic volume yield per hectare by treatment in loblolly pine plantations (ages 12-14 years) on the Virginia Piedmont, 1995.[1]

Treatment	DBH (cm)	HT_d (m)	Number / ha [2]	Yield [3] (cu m/ha)
Herbaceous + woody control:				
Total woody	16.2 [ab]	11.8 [a]	1092	125.0 [a]
2/3 woody	16.3 [a]	11.7 [ab]	1089	126.8 [a]
1/3 woody	14.8 [c]	11.4 [bc]	1250	120.4 [ab]
Herbaceous control only:	14.5 [cd]	11.1 [cd]	1035	94.0 [bc]
Woody control only:				
Total woody	16.1 [ab]	11.0 [cd]	1064	112.9 [abc]
2/3 woody	15.5 [b]	11.1 [cd]	1050	105.9 [abc]
1/3 woody	14.4 [cd]	10.7 [d]	1010	87.9 [c]
Check:	13.9 [d]	11.0 [cd]	1005	86.9 [c]

[1] Means within columns followed by the same letter are not significantly different at the 0.05 alpha level (Duncan's MRT procedure)

[2] Treatment effect not significant ($p = 0.4200$)

[3] Volume calculated with the TAUYIELD model (Amateis et al. 1995) using the formula:

$$\ln Y = 1.15173 - 9.33466(1/A) + 0.40538(\ln S) + 0.24032(HT_d/A) + 0.00321(A \ln N) + 0.96176(\ln BA)$$

where: Y = total yield outside bark (cu ft/ac); A = stand age; S = site index (ft at age 25); HT_d = ave. height of dominants and codominants; N = number of trees/ac; BA = basal area (sq ft/ac) indicate that, by the twelfth-year, the inclusion of herbaceous control does not significantly increase DBH at all levels of woody control.

Miller et al. (1991) found that the loblolly pine diameter response to treatments that combined woody and herbaceous control was most often greater than the average additive responses to control of these components separately. However, results of this current study indicate that this held true only for the 2/3 woody plus herbaceous treatment. The difference in the magnitude of diameter response to herbaceous control between this study and the Miller et al. (1991) study is most likely related to the amount of herbaceous competition present at the study locations. The majority (10 out of 13) of the study sites in the Miller et al. study were located on the Coastal Plain where herbaceous competition is expected to be more intense. One site in their study was located on the Virginia Piedmont (Appomattox, VA) and was found to differ from all other sites, having lower amounts of herbaceous vegetation and greater diameter growth following woody-only control compared to herbaceous-only control. Thus, herbaceous control may be expected to have relatively less effect on pine diameter when herbaceous competition is low, which is consistant with effects of woody plus herbaceous control on the twelfth-year DBH response found in this study.

There were fewer significant differences among treatments for the average height of dominant and codominant pines than for diameter (Table 3). This finding is consistent with other studies that found height to be comparatively less responsive to competition control (Zutter et al. 1986, Bacon and Zedaker 1987, Miller et al. 1991, Glover and Zutter 1993, Lauer et al. 1993). The only significant increases in heights were the result of herbaceous control in combination with 2/3 and total woody stem control, having 6 and 7% increases over the check response, respectively (Table 3).

There was no significant difference in the number of trees per hectare among treatment levels (Table 3). Although variance was relatively homogenous across treatment levels, the high variability (standard deviations of 348.5 to 542.4 pines/ha) may have contributed to no differentiation among treatment levels. The relatively small influence of competition control on pine density has been reported by Miller et al. (1991) who found only minor differences among check, woody, herbaceous, and woody plus herbaceous control in 5-year old stands. Lauer et al. (1993) did find a difference between check versus herbaceous control, but found no differences among broadcast versus banded applications at 2 different control durations by the ninth year.

Yield was significantly higher for plots with woody plus herbaceous competition control, while yield on plots that received woody only or herbaceous only control was not significantly different from yield on the check plots (Table 3). Relative to check, control of 2/3 and all of the woody stems in combination with herbaceous control resulted in 46 and 44% increases in yield, respectively. One-third woody plus herbaceous control resulted a 39% increase in yield relative to check. However, the significant difference ($p \leq 0.05$) in absolute yield between 1/3 woody plus herbaceous control and check may have been artifically induced by the number of trees/ha for this treatment which was numerically higher (1250/ha vs. 1005/ha for check), but not statistically higher ($p > 0.05$). Without the addition of herbaceous control, control of 1/3, 2/3, and all of the woody stems resulted in 1, 22, and 30% increases over check, respectively.

Bacon and Zedaker (1987) and Miller et al. (1991) found similar positive yield responses to woody plus herbaceous control 3 and 5 years post-treatment, respectively. Bacon and Zedaker found that the total and 2/3 woody plus herbaceous control treatments resulted in significantly better yield responses irrespective of treatment age. Results of this current study indicate that, by the twelfth-year, total and 2/3 woody plus herbaceous control has a continued positive effect on yield regardless of treatment age.

Because forest vegetation management may seek to increase pine yield while not unduly removing competing vegetation, it is useful to define the minimum threshold of competition control at which there is still a relative gain in yield. In this study, the minimum competition control level that significantly increased yield relative to no control was 2/3 woody plus herbaceous control. Furthermore, yield at this level was slightly higher than that achieved with total woody plus herbaceous control. Glover and Zutter (1993) determined that even small increases in the hardwood density of young plantations can have a strong negative effect on loblolly pine survival and basal area to 27 years of age. Thus, the residual hardwoods left by the 2/3 woody plus herbaceous control treatment may eventually reduce the relative gains in yield observed for this treatment as the plantations reach rotation age.

Canopy, Understory, and Diversity Responses

The percentage of total basal area in canopy hardwoods (PHWD BA) was highest (19%) in check plots, although this percentage was not significantly higher than that found in 1/3 woody with and without herbaceous control, 2/3 woody only, and herbaceous only treatment plots (Table 4). Treatments that resulted in significantly lower PHWD BA were: total woody without herbaceous control (8.8%), 2/3 woody plus herbaceous control (7.6%), and total woody plus herbaceous control (7.5%). Within each level of woody stem control, PHWD BA was numerically lower when the treatment included herbaceous control, although the differences were not significant.

The initial effect of total and 2/3 woody stem control in reducing hardwood basal area by 40 - 58% and 88 - 98%, respectively, over the first growing season (Bacon and Zedaker 1987) appears to have a continuing negative effect on twelfth-year PHWD BA. Bacon and Zedaker also noted a trend of greater hardwood basal area with herbaceous control and suggested there was a positive hardwood growth response to herbaceous control. That trend was no longer evident by the twelfth-year, as the faster growing pines that also responded positively following herbaceous control (Bacon and Zedaker 1987) likely dominated the resource more rapidly and displaced the hardwoods as the stands aged. Thus, by the twelfth-year herbaceous control resulted in lower absolute hardwood basal area and PHWD BA. Glover and Zutter (1993) have

Table 4. Percentage of total basal area in hardwoods (PHWD BA), and Shannon, evenness, and species richness[1] diversity indices of canopy by treatment in loblolly pine plantations (ages 12-14 years) on the Virginia Piedmont, 1995. [2]

Treatment	PHWD BA (%)	Shannon Diversity Index (H)	Evenness Diversity Index (E)	Species Richness (S)
Herbaceous + woody control:				
Total woody	7.5 a	0.329 a	0.199 ab	5.5 a
2/3 woody	7.6 a	0.359 a	0.158 a	8.4 bc
1/3 woody	12.1 ab	0.477 ab	0.231 ab	7.4 ab
Herbaceous control only:	15.4 ab	0.673 b	0.290 ab	9.5 bc
Woody control only:				
Total woody	8.8 a	0.331 a	0.212 ab	6.0 a
2/3 woody	12.5 ab	0.555 ab	0.234 ab	9.7 bc
1/3 woody	18.2 b	0.734 b	0.321 b	10.0 c
Check:	19.0 b	0.713 b	0.303 b	9.6 bc

1 Species richness is the average number of woody species of crown class intermediate or above in 0.1 hectare.

2 Means within columns followed by the same letter are not significantly different at the 0.05 alpha level (Duncan's MRT procedure)

demonstrated that there is a strong relationship between the percentages of hardwood basal area in loblolly pine plantations at age 6 and at age 27; therefore, it is reasonable to anticipate that the effects of these treatments on PHWD BA will continue past the twelfth-year post-treatment.

Woody plant species diversity in the canopy responded similar to PHWD BA among treatment levels with some exceptions. The treatment that controlled 1/3 of the woody stems resulted in the highest indices for species richness (10 per 0.1 ha), evenness (0.321; E is constrained between 0-1), and Shannon diversity (0.734; given 10 species, max. possible H' = 2.303) (Table 4). Statistically similar responses ($p > 0.05$) for all diversity indices occurred in the check, herbaceous only, 1/3 woody, and 2/3 woody control plots.

The inclusion of herbaceous control to 1/3 woody control significantly reduced species richness by 26%, while not significantly affecting the evenness and Shannon diversity indices. Conversely, 2/3 woody control in combination with herbaceous control did not significantly reduce species richness, but resulted in a lower Shannon index caused by the significant decrease in evenness. Alone or in combination with herbaceous control, total woody control resulted in significantly lower indices of species richness (5.5-6.0 per 0.1 ha) and Shannon diversity (0.329-0.330); however, evenness was not significantly affected by this level of control.

These results indicate that species richness and evenness, may respond differently and/or inconsistently to different levels of competition control. However, some general trends in the response of canopy species diversity were detected from the Shannon diversity index which takes into account both richness and evenness. Canopy diversity generally decreased with increasing control intensity. This trend is consistent with the results of Zutter and Zedaker (1988) 1 year post-treatment at 5 chemical rates, Neary et al. (1990) 5 years post-treatment at 2 chemical rates in slash pine stands, and Harrington and Edwards (1994) 12 years post-treatment at 6 various chemical and mechanical control intensities. Swindel et al. (1987), however, found that the diversity in 5-year old slash pine stands differed only slightly between 2 mechanical intensity levels of site-preparation, and Hurst et al. (1994) found no significant difference in species richness 2 years post-treatment at 3 intensity levels involving combinations of chemical and mechanical site-preparation.

The results of this study may help to explain some of the inconsistencies found among studies examining competition control impacts on plant diversity. While there was a general trend of decreased canopy diversity with increased treatment intensity, the significance of treatment level differences depends on the group of treatment levels under investigation. For instance, within the woody-only control levels, only the highest level of woody stem control resulted in a significant decrease in woody plant diversity; however, within the woody plus herbaceous control levels, both total and 2/3 woody control resulted in significantly lower diversity. Comparison of herbaceous control versus no herbaceous control showed no significant difference, yet there was a trend toward decreased diversity with herbaceous control within each level of woody control. Thus, studies of competition control effects on species diversity may conflict because the scope or range of the treatment level intensities may differ.

Understory percent woody cover and the species richness, evenness, and Shannon diversity indices showed no differentiation across control levels (Table 5), as analysis of variance revealed insignificant treatment effects on all understory measurement parameters (Table 2).

Across all control levels, mean percent cover of woody vegetation was ≥100%, indicating that none of the competition control levels substantially increased the proportion of open areas. Miller et al. (1995) found that woody, herbaceous, and woody plus herbaceous control resulted in respectively increasing proportions of open area, especially within the first 6 years, but this proportion decreased as the stands aged to 8 years. It should be noted, however, that the duration of control in the Miller et al. study exceeded the control duration in both this study (5 years vs. 1 year) and in normal operational management.

Although not significantly different from check plots, total woody control with and without herbaceous control had the lowest percentages of woody cover, having 10.5 and 20.5% less woody cover than check, respectively. Comparison of herbaceous control versus no herbaceous control yielded no clear trend. With the addition of herbaceous control, percent woody cover was slightly higher for no woody and total woody control, but slightly lower for the 1/3 and 2/3 woody control treatments; however these differences were not significant. Although the understory cover was not

Table 5. Percentage of woody cover, and Shannon, evenness, and species richness[1] diversity indices of the understory by treatment in loblolly pine plantations (ages 12-14 years) on the Virginia Piedmont, 1995.[2]

Treatment	Woody Cover (%)	Shannon Diversity Index (H)	Evenness Diversity Index (E)	Species Richness (S)
Herbaceous + woody control:				
Total woody	110.0	2.32	0.790	19.0
2/3 woody	111.1	2.45	0.815	20.7
1/3 woody	114.5	2.25	0.758	19.7
Herbaceous control only:	125.2	2.35	0.790	19.9
Woody control only:				
Total woody	100.0	2.27	0.764	20.0
2/3 woody	126.8	2.31	0.774	20.1
1/3 woody	120.7	2.33	0.767	21.0
Check:	120.5	2.26	0.768	19.0

1 Species richness is the average number of suppressed woody species per 60 m transect.

2 All means within columns are not significantly different at the 0.05 alpha level (Duncan's MRT procedure)

delineated into arborescent versus non-arborescent cover, the results are consistent with Miller et al. (1995) who found that herbaceous control decreased shrub cover but slightly increased arborescent cover relative to check, resulting in little change in total woody cover.

Relative to the canopy diversity indices, the understory diversity was higher, and, unlike canopy species diversity, there was no differentiation or trends across control levels. Given the highest species richness among treatment averages (21 per 60 m transect; Table 5), the maximum possible Shannon diversity index would be 3.04. For perspective, the lowest Shannon diversity index among treatment averages was 2.26, which was incidentally the average for the check plots. Evenness contributed to the relatively high Shannon diversity; no one species dominated greater than 28% of the total percent cover on any measurement plot.

Reports of competition control impacts on understory woody diversity are scarce; however, there is some evidence to support the findings of this study. Reed et al. (1994) examined species richness following thinning and herbicide applications in 15-year old loblolly pine plantations in Louisiana and found that woody vegetation was reduced in the first year following treatment but that species numbers returned to nearly pre-treatment levels by the second year. Following total, woody, and herbicide release treatments in 7-year old loblolly pine plantations in Louisiana, Clason (1993) determined that, at age 27, hardwood species richness and evenness in the understory (1.5-6 m) was unaffected by any of the treatments. Boyd et al. (1994), investigating plant diversity in Georgia loblolly pine plantations, reported no significant effect of chemical release on the Shannon diversity index for woody vegetation in the understory (< 1.5 m) 7 years after treatment.

In comparison to the yield threshold response at 2/3 woody plus herbaceous control, the maximum competition control threshold above which PHWD BA and species diversity (Shannon index) were reduced was 1/3 woody plus herbaceous control. Understory woody cover and species diversity were also unaffected at this level of competition control. These responses suggest that a level of competition control lower than total control, likely between 1/3 and 2/3 woody stem with herbaceous control, can achieve pine yield comparable to yield following total control while maintaining hardwood proportions, understory woody cover, and woody plant species diversity comparable to that with no competition control.

Relationships between Hardwood Dominance, Diversity, and Loblolly Pine Yield

Data from plantations 12 to 14 years of age were subjected to regression analysis to determine significant relationships among stand variables, irrespective of treatment level effects. Because analysis of understory variables yielded insignificant relationships to all other stand variables (P = 0.0522 to 0.9165), the understory component was not further analyzed. Regression models relating canopy diversity indices and loblolly pine yield to PHWD BA are given in Table 6.

The Shannon diversity index was deemed as the best diversity measure for modelling relationships and was, therefore, chosen above the other diversity indices for further analysis. The relationships determined for the plantations 12 to 14 years were projected onto data from plantations 24 to 27 years of age and comparisons were made.

Table 6. Regression models relating canopy diversity indices and loblolly pine yield (cu m/ha) to the percentage of hardwood basal (PHWD BA) in plantations (ages 12-14 years) on the Virginia Piedmont, 1995.

Model [1]	Root MSE	R^2
----- Shannon Diversity Index (H') -----		
$H' = 0.015901 + 0.047147(\text{PHWD BA}) - 0.000318(\text{PHWD BA})^2$	0.06864	0.9714
----- Evenness Diversity Index (E) -----		
$E = 0.048291 + 0.018613(\text{PHWD BA}) - 0.000147(\text{PHWD BA})^2$	0.04605	0.9134
----- Species Richness Diversity Index (S) -----		
$S = 3.966644 + 0.515240(\text{PHWD BA}) - 0.007739(\text{PHWD BA})^2$	2.57800	0.5373
----- Loblolly Pine Yield -----		
$\text{Yield} = 160.9455 \times e^{-0.041845(\text{PHWD BA})}$	0.27717	0.7394

[1] **All models are significant at $P < 0.0001$; all parameter estimates are significant at $p < 0.005$.**

Plantations Twelve to Fourteen Years of Age

There was a strong positive nonlinear correlation ($R^2 = 0.97$) between canopy species diversity, as measured by the Shannon diversity index, and PHWD BA in the plantations 12 to 14 years of age (Table 6). While no studies to date have reported this relationship, the positive correlation was expected because the nature of the Shannon diversity index formula. The formula assigns an index of zero to a community composed of only one species; the introduction of another species increases species richness, while the transfer of proportional abundance increases evenness (Patil and Taillie 1982). The relationship of PHWD BA to evenness was stronger ($R^2 = 0.91$) than its relationship to species richness ($R^2 = 0.54$) (Table 6), indicating that increases in PHWD BA influenced the Shannon diversity index primarily through the transference of proportional abundance from loblolly pine to hardwoods. The inclusion of site index into the regression models did not improve the fit of the relationships.

Total loblolly pine yield was negatively correlated to PHWD BA, and the form of the relationship was modelled with an exponential regression ($R^2 = 0.74$) (Table 6). The relationship between loblolly pine yield and the percentage of hardwood basal area has been confirmed by Burkhart and Sprinz (1984) and Knowe (1992) who have independently developed growth and yield models (each involving complex series of diameter distribution and survival functions) that utilize this relationship. The purpose of this current modelling effort was not to develop another model to predict yield, but rather to describe the shape of this relationship in the plantations under study. The soundness of the exponential model, however simple, is at least somewhat substantiated by the Knowe (1992) loblolly pine basal area prediction function that likewise utilizes the exponent of PHWD BA.

As with the diversity - PHWD BA relationships, the inclusion of site index did not significantly improve the regression model for the yield - PHWD BA relationship. The indication that site index does not influence the relationship between yield and PHWD BA was also observed by Burkhart et al. (1987) who stated that the relationship held regardless of site or stand conditions.

Figure 1 illustrates the relationships of PHWD BA to canopy species diversity (H') and to loblolly pine yield (cu m/ha). Species diversity was highly influenced by increases in PHWD BA at lower proportions; however, the parabolic shape of the relationship reduced the relative gains in diversity as PHWD BA continued to increase. Increases in PHWD BA from near zero to 5, 10, 20, and 40% were associated with respective 7, 14, 25, and 41-fold increases in H' relative to the minimum H' value.

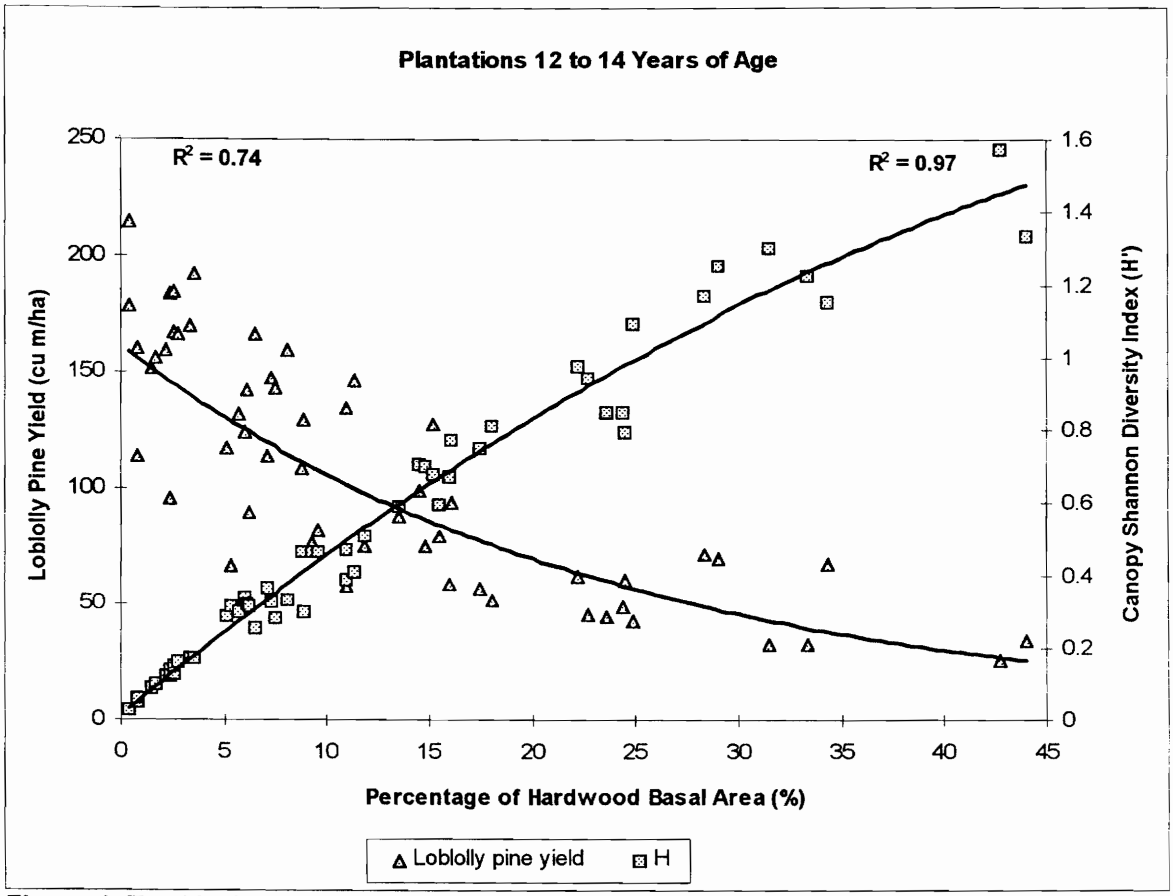

Figure 1. Total loblolly pine yield and the Shannon diversity index (H') for the canopy versus the percentage of hardwood basal area in Virginia Piedmont plantations 12 to 14 years of age. Regression lines for the modelled relationships and corresponding R-square values are given.

The large magnitude of relative increases in H' is related to the central tendency of the index scaling. For example, the model predicted a range in H' value from approximately 0.03 to 1.5; the median of the predicted data range is 0.43, which is 71% under the maximum value but >1000% over the minimum value. Thus, the central tendency of the data range is highly skewed to the right and, therefore, relative increases over the minimum H' value should be interpreted conservatively. Regardless of scale, the shape of the relationship clearly shows rapid increases in species diversity at low PHWD BA, followed by an asymptotic trend as the proportion of hardwood basal area nears the proportion of loblolly pine basal area.

The sharpest decline in loblolly pine yield also occurred within the lower range of PHWD BA. As PHWD BA increased from near zero to 15, 30, and 45%, yield decreased by approximately 44, 71, and 84%, respectively, below the maximum yield (Figure 1). Thus, roughly half of the total yield lost attributed to PHWD BA was lost within the first fifteenth percentile; however, as PHWD BA increased, the negative influence on yield was lessened. The declining influence of competition on loblolly pine yield has been documented by Perry et al. (1993) in their controlled study on the competition effects of broomsedge and sweetgum during the first growing season: pine growth was found to be strongly and negatively influenced at low densities, but growth became asymptotic at higher competitor densities.

Thus, in plantations 12 to 14 years of age, under conditions where the resource is heavily dominated by loblolly pine, even small increases in the proportion of hardwoods results in large increases in canopy species diversity and large decreases in pine yield. However, as the level of hardwood basal area approaches proportions close to that of the loblolly pine, both diversity and yield are relatively less sensitive to increases in the proportion of hardwoods.

The Shannon diversity index for the canopy was regressed against total loblolly pine yield to determine the shape of this relationship in Virginia Piedmont plantations

12 to 14 years of age (Figure 2). The shape of the relationship indicates that, within the range of this data, canopy diversity is negatively correlated to loblolly pine yield, and the relationship is curvilinear. The model accounted for 77% of the variation in H'; however, it should be noted that data outside of the range used to develop this model has the potential to illogically drive the Shannon diversity index below zero.

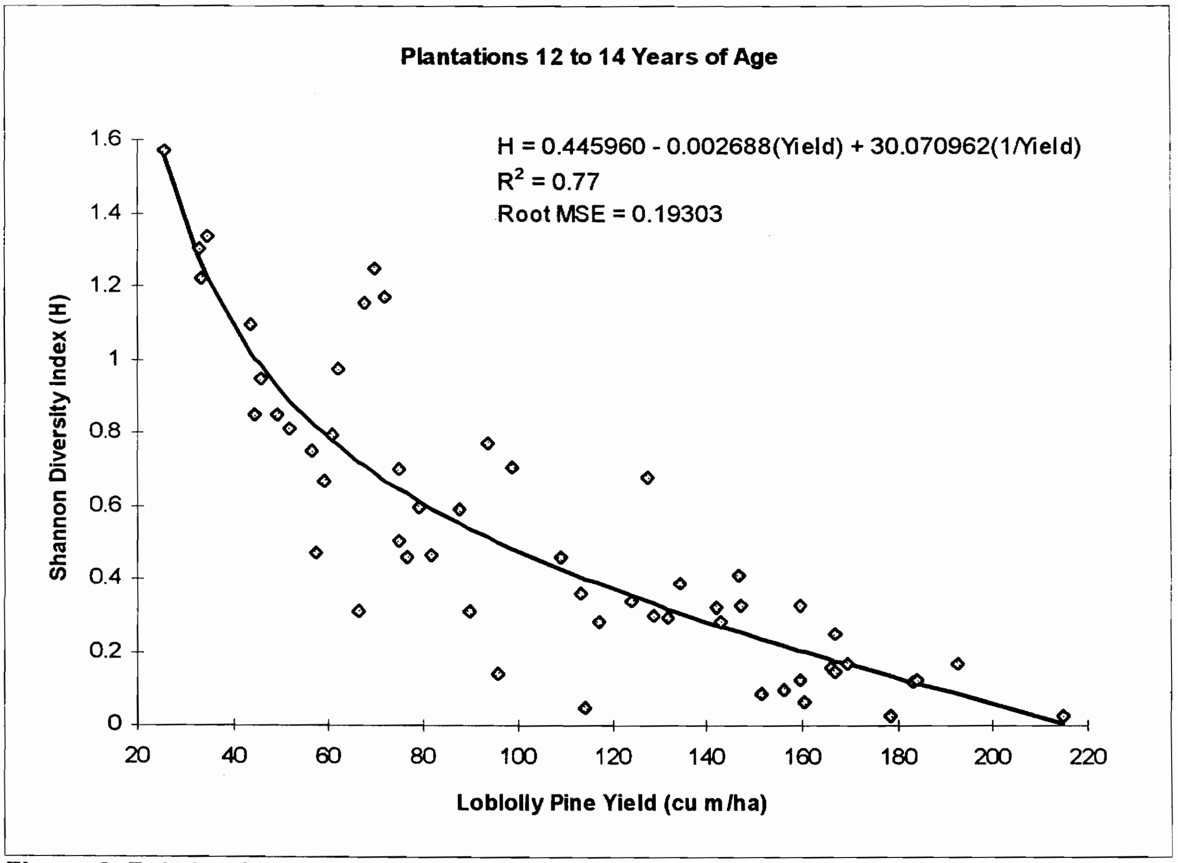

Figure 2. Relationship between the canopy Shannon diversity index (H') and total loblolly pine yield in Virginia Piedmont plantations 12 to 14 years of age.

The model uses the reciprocal of yield, which has a highly negative effect on H', but is tempered with a second yield term which reflects the decreased influence of yield on H' as yield increases. Following the relationships found between PHWD BA and yield and PHWD BA and H' (Figure 1), the pronounced decline of H' at low yield levels was not anticipated. Both the PHWD BA - yield and the PHWD BA - diversity relationships showed decreased sensitivity to changes in PHWD BA at high PHWD BA, which corresponds to low yield and high H'. However, upon inspection of the relationships in Figure 1, it can be seen that the distance between the highest H' and the lowest yield is great and the inverse bowed shapes of the relationship curves would likely cause high sensitivity at high diversity and low yield.

Because of the skewed central tendency of the Shannon index scaling, it is helpful to examine trade-offs between yield and diversity relative to the median values. The median values for yield and predicted H' were approximately 99 cu m/ha and 0.48, respectively. Relative decreases below median yield of 20, 40, and 60% were met with respective increases in H' of 27, 65, and 132% over the median H' value, which demonstrates the high sensitivity of diversity to changes in yield within the lower range of yield. However, relative increases above median yield of 20, 40, 60, 80, and 100% were met with respective decreases in H' of 21, 39, 56, 72, 86% below the median H' value. Thus, there was an approximately 1:1 trade-off between canopy diversity and yield within moderate yield levels, while there was disproportionately greater diversity trade-off at low yield and greater yield trade-off when yield was high.

The trade-off between species diversity and yield found by Holland et al. (1994) in the western Intermountain region corresponds most closely to the results found at moderate yield levels in this study. Because their linear programming model simulated stand responses over a 150-year planning period in 10 to 20-year increments, it is possible that increased diversity sensitivity at low yield levels was not detected by their method of analysis. The approach used in the current study should offer a better demonstration of relationship dynamics across a spectrum of yield levels which may be particularly important in the Southeast where rotation periods are far shorter than in the West.

The results of Perry et al. (1993) lend some validity to the inverse relationship found in this study. The reciprocal of their loblolly pine stem volume index ($SVI = HT(D^2)$) was significantly related to competition densities and their interactions. The Shannon diversity index takes into account the interaction of the number of species with the proportions of those species and, therefore, is at least somewhat comparable to the independent variables (sweetgum and broomsedge densities and their interactions) in the Perry et al. model. However, whereas Perry et al. found that the sweetgum per-plant effect was greater than broomsedge and competitor effects were not independent, the Shannon diversity index does not account for differential competitive effects nor effect dependence. For example, the Shannon index is incapable of differentiating between the effects of black locust (*Robinia psuedoacacia*) and sweetgum on loblolly pine when the proportions are equal; yet, loblolly pine and sweetgum have a competitive relationship (Perry et al. 1993), while loblolly pine and black locust have been shown to have a mutualistic relationship on poor sites (Frederickson et al. 1993).

The fact that the Shannon diversity index does not account for species composition or differential effects may limit its use in modelling diversity - yield relationships. This limitation is somewhat ameliorated by using basal area as the proportional unit for calculating the Shannon index, as was done in this study. Rather than viewing diversity and loblolly pine yield as direct competitors, it should be recognized that the relationship is dynamic and not independent of species composition.

Plantations Twenty-four to Twenty-seven Years of Age

Differences in canopy diversity, PHWD BA, and loblolly pine yield between the younger and older plantations were evident (Table 7). To determine if and how the these differences might alter the relationships found in the younger plantations, data from both age classes were pooled and dummy variables were incorporated in the relationship models. Model intercepts and slopes were tested for coincidence between the two age classes. Figures 3 and 4 illustrate the relationships predicted from the younger stands superimposed on the scatter plots of the older stands.

Table 7. Summary of percent hardwood basal area (PHWD BA), Shannon diversity index (H') for canopy, and loblolly pine yield (Yield) for Virginia Piedmont plantations by age classes.

Plantation Age Class (years)	PHWD BA (%)	Canopy (H') Mean (Range)	Yield (cu m/ha)
12 - 14	12.8 (0.38 - 43.9)	0.531 (0.027 - 1.574)	106.8 (25.5 - 215.0)
24 - 27	0.77 (0.0 - 4.2)	0.047 (0.0 - 0.201)	188.4 (93.7 - 275.9)

The diversity - PHWD BA relationship held reasonably constant between the age classes, having statistically similar intercepts ($p = 0.8446$) and slopes ($p = 0.5572$ (PHWD BA), $p = 0.6216$ (PHWD BA^2)) (Figure 3). Considering that PHWD BA and H' were much lower in the older plantations (Table 7), the validity of the model for both age classes, indicates that there is a strong and consistent relationship between canopy diversity and the proportion of hardwood basal area.

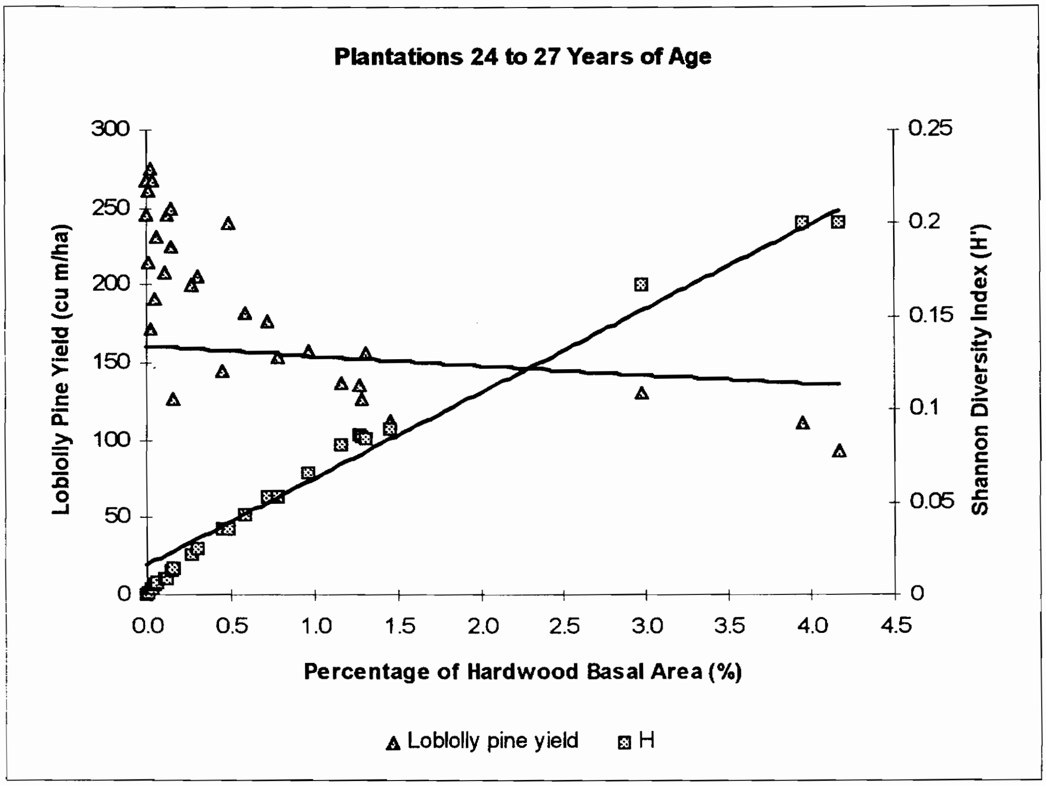

Figure 3. Loblolly pine yield and canopy Shannon diversity index (H') versus the percentage of hardwood basal area in Virginia Piedmont plantations 24 to 27 years of age. The lines represent the relationships predicted from relationships found in plantations 12 to 14 years of age.

The yield - PHWD BA relationship developed for the younger plantations did not adequately predict the relationship in the older plantations (Figure 3). Tests of coincidence revealed significantly different intercepts ($p = 0.005$) and slopes ($p = 0.0001$) between the age class relationships. The difference in intercepts was expected because of the higher yield in the older plantations. The slope of the relationship was steeper for the older plantations, indicating that the rate of yield decline with increasing PHWD BA was greater. More pronounced PHWD BA effects on pine yield with age have been illustrated by Burkhart et al. (1987). It should be noted, however, that the PHWD BA range in this study represents only a fraction of the range examined by Burkhart et al. (1987) (0 - 45% vs. 0 - 100%) to demonstrate yield - hardwood relationships over time.

Burkhart and Sprinz (1984) and Glover and Zutter (1993) have reported constant hardwood basal area proportions in loblolly pine plantations from ages 11 to 24 and 11 to 27 years, respectively. However, the PHWD BA between the younger and older plantations examined in this study were dramatically different (Table 7). It is possible that initial hardwood stocking was not equal across the age classes which could result in inconsistent PHWD BA (Burkhart et al. 1987). Regardless of the cause of disproportionate PHWD BA across age classes, the acute differences likely contributed to the apparent differences in the yield - PHWD BA relationships between age classes.

The relationship between diversity and yield in the older plantations was also significantly different from what the relationship in the younger plantations would predict (Figure 4). Most noticeably, the model developed for the younger stands illogically predicted negative H' values. This result, however, was not unexpected as the model had not been designed to constrain H' and was used outside of the data range which was used to construct it. Of more importance is the difference in relationship slopes ($p = 0.0408$ (yield), $p = 0.0001$ (1/yield)), which indicated that the model for the older plantations would have a flatter slope. There was slightly higher diversity sensitivity at the lower yield levels, but pronounced changes in H' were no longer evident in the older plantations and there was a much wider variation in yield within which diversity changed very little.

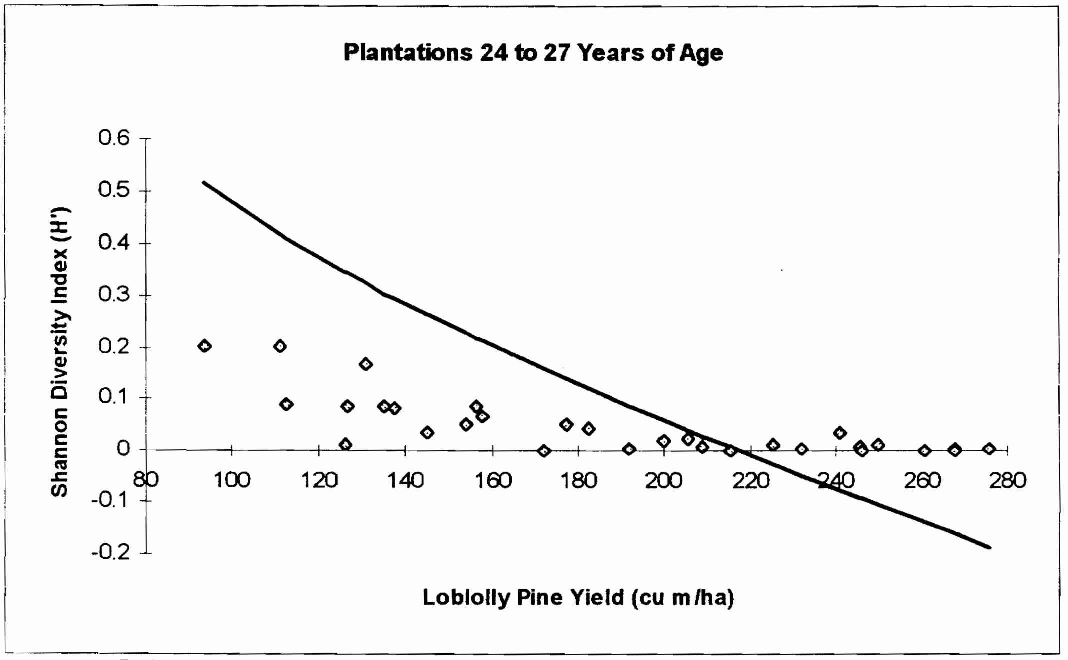

Figure 4. Relationship between the canopy Shannon diversity index (H) and total loblolly pine yield in Virginia Piedmont plantations 24 to 27 years of age. The line represents the relationship predicted from the relationship found in plantations 12 to 14 years of age.

The strong and consistent relationship between canopy diversity and PHWD BA suggests that low PHWD BA in the older plantations contributed to the lower diversity in the older plantations. Therefore, where constant PHWD BA over time can not be assumed, changes in the yield - PHWD BA relationship can be expected (Burkhart and Sprinz 1984) as well as changes in the yield - diversity relationship over time.

Effects of Competition Control on Wildlife Habitat Quality

Plant species composition and vertical structure responses to competition control were analyzed to determine possible impacts on wildlife habitat quality. Habitat response comparisons were made on the basis of: woody and woody plus herbaceous control versus check, in the younger plantations; and competition control versus check, in the older plantations. Impacts on plant species composition and vertical structure are reported and discussed separately for the two plantation age classes, and implications for wildlife are offered.

Plant Species Compositional Changes

Plantations Twelve to Fourteen Years of Age

Competition control had some effect of altering species composition in the canopy. Relative to no control, woody without herbaceous control had the effect of significantly decreasing ($p < 0.0001$) the basal area proportion of oak species (*Quercus* spp.) (Figure 5a). This same treatment slightly decreased hickory (*Carya* spp.), while slightly increasing the proportions of eastern redcedar (*Juniperus virginiana*) and black cherry (*Prunus serotina*) in the canopy, although these proportions were not significantly different ($p > 0.05$) from those found in the check plots.

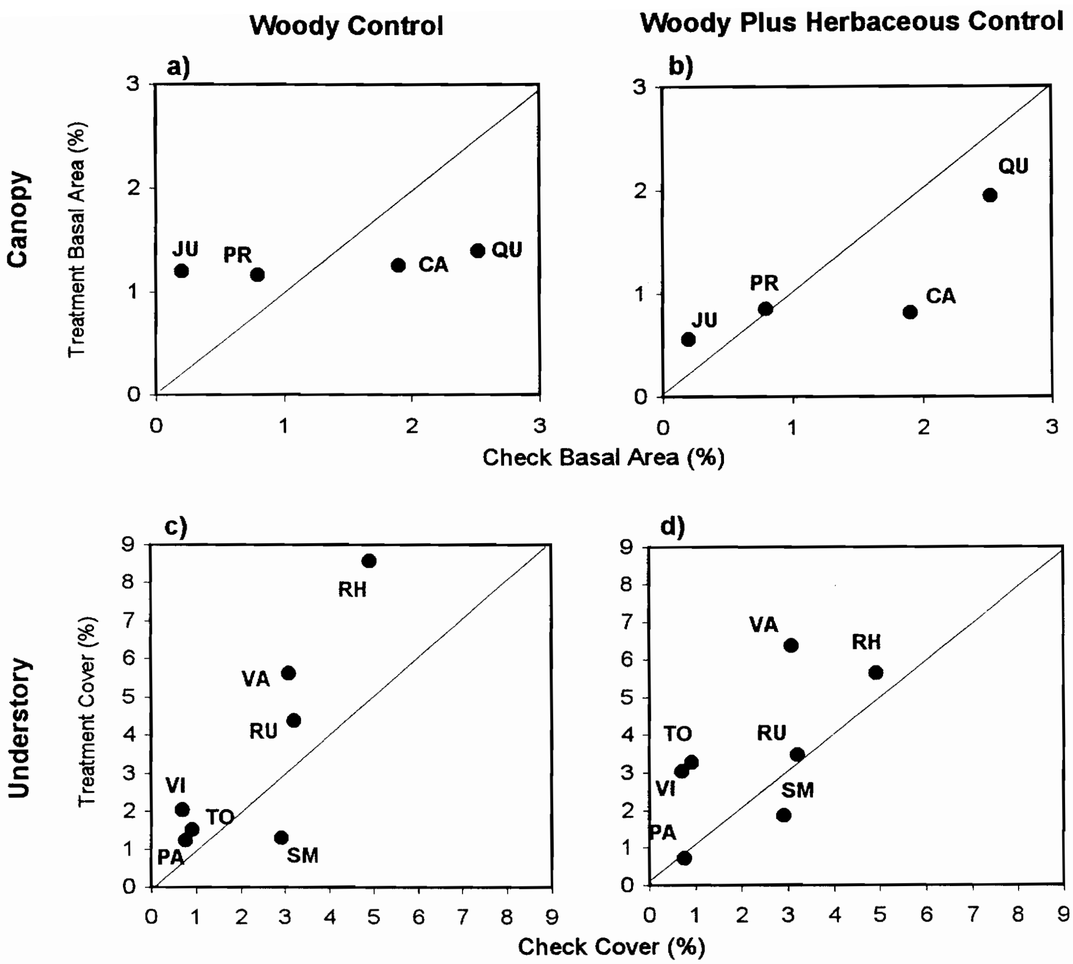

Figure 5. Comparisons of mean percent canopy basal area (top) and mean percent understory cover (bottom) of woody competition control (left) and woody plus herbaceous control (right) versus no competition control (check) for individual species in loblolly pine plantations 12 to 14 years of age. Shifts to the left or right of the diagonal line indicate compositional changes. Symbols represent the following species or genera:
CA = *Carya* spp., **JU** = *Juniperus virginiana,* **PR** = *Prunus serotina,* **QU** = *Quercus* spp., **PA** = *Parthenocissus quinquefolia,* **RH** = *Rhus* spp., **RU** = *Rubus* spp., **SM** = *Smilax* spp., **TO** = *Toxicodendron radicans,* **VA** = *Vaccinium* spp., **VI** = *Vitis* spp..

Woody plus herbaceous control also decreased the proportion of oak species, although not significantly ($p = 0.1109$), and significantly decreased ($p = 0.0092$) hickory proportions. Eastern redcedar and black cherry proportions were also slightly higher in the woody plus herbaceous control plots compared to check, although differences were not significant ($p > 0.05$). Thus, the additional use of sulfometuron and glyphosate to control herbaceous competition in combination with triclopyr to control woody competition resulted in relatively little difference in species composition changes compared to woody control alone.

Although black cherry and eastern redcedar are found under dense forest canopies, they are intolerant of over-topping competition and eventually decline and die (Marquis 1990, Harlow et al. 1991). Any increase in the proportions of these species is likely due to their incidental release from woody competition and rapid seeding following the release disturbance, as black cherry and eastern redcedar are pioneer species. In contrast, oaks and hickories are generally more tolerant of shade, slower growing, and are climax species. These genera would not likely respond to release in the same manner and, in fact, declined in proportions following competition control.

In the understory, woody-only control generally increased proportions of poison ivy (*Toxicodendron radicans*), *Rhus* spp. (primarily smooth and winged sumac), *Rubus* spp., *Vaccinium* spp. (including *Gaylussacia* spp.), and *Vitis* spp., but slightly decreased the proportion of *Smilax* species (Figure 5*c*). However, the only significant change ($p \leq 0.05$) in understory species composition with woody-only control was an increase in the proportion of Virginia creeper (*Parthenocissus quinquefolia*). The addition of herbaceous control to woody control slightly reduced the proportions of *Rhus* and *Rubus* and Virginia creeper relative to woody-only control, but did not reduce their proportions below that for check (Figure 5*d*). Woody plus herbaceous control significantly increased the proportion of poison ivy relative to check.

These results differ from the eighth-year results of Miller et. al (1995) in several respects. Although both studies used similar herbicides, Miller et al. found that woody control decreased poison ivy and increased *Smilax*, and herbaceous control decreased *Rhus* and *Vaccinium* species. Two factors could contribute to the discrepancies found between these results. First, Miller and other's COMP study controlled herbaceous vegetation for 4 years and woody vegetation for 5 years. The extreme duration of these treatments could dramatically decrease the abundance of particular species, while the single herbicide application used in this current study might have allowed the species to recover. Second, comparisons for *Rhus* and *Vaccinium* responses were based on herbaceous control alone versus check in the COMP study, but on woody plus herbicide control versus check in this study. It is possible that negative effects of herbaceous control on these genera may be amended by the positive effects of woody control by opening the canopy. The positive effect of woody control on *Rubus* species is in agreement with the results of the COMP study.

Plantations Twenty-four to Twenty-seven Years of Age

Eastern redcedar was not found in the overstory of plantations aged 24 to 27 years, but was present in the understory. Black cherry, hickory, and oak in the canopy were found in far lower proportions in the older plantations compared the younger plantations (0.03-0.38% vs. 0.20-2.5%, respectively). In contrast to the younger plantations, competition control (various methods of 2,4,5-T application and manual control) resulted in significantly increased ($p = 0.0005$) oak proportions relative to check, but did not significantly alter hickory proportions (Figure 6*a*). Similar to the younger plantations, the percentage of black cherry basal area was not significantly changed by competition control in the older plantations.

Many oak species have been shown to have high susceptibility to triclopyr (Payne and Bryant 1994), which was used to control woody stems in the younger plantations, and this may account for the relative increased proportions of oak in the older stands. However, the pattern observed is not unlike the pattern of old-field succession of a Piedmont hardwood-pine forests. Following the establishment of loblolly and shortleaf pine, various shrub, vine, and hardwood species invade the understory; as the stand ages, shade tolerant hardwoods, particularly oak and hickory species, eventually share dominance with the pines before becoming dominant and replacing the pines (Johnston and Odum 1956, Felix et al. 1983, Baker and Langdon 1990). Thus, the oak response in the older plantations was not unexpected.

The responses of *Vaccinium* and *Rhus* were similar to the responses in the younger plantations, with competition control resulting in slightly higher, but not significantly different ($p > 0.05$), proportions of these genera in the understory relative to check (Figure 6*b*). However, in contrast to the response in the younger plantations, the proportion of *Smilax* in the older plantations was significantly increased ($p \leq 0.05$) by competition control. Virginia creeper, poison ivy, *Rubus*, and *Vitis* cover were generally very low (0.05-0.48%) in the older plantations. While competition control significantly increased the proportion of *Rubus*, relative to check, it contributed to a significnatly negative effect on Virginia creeper and *Vitis* proportions.

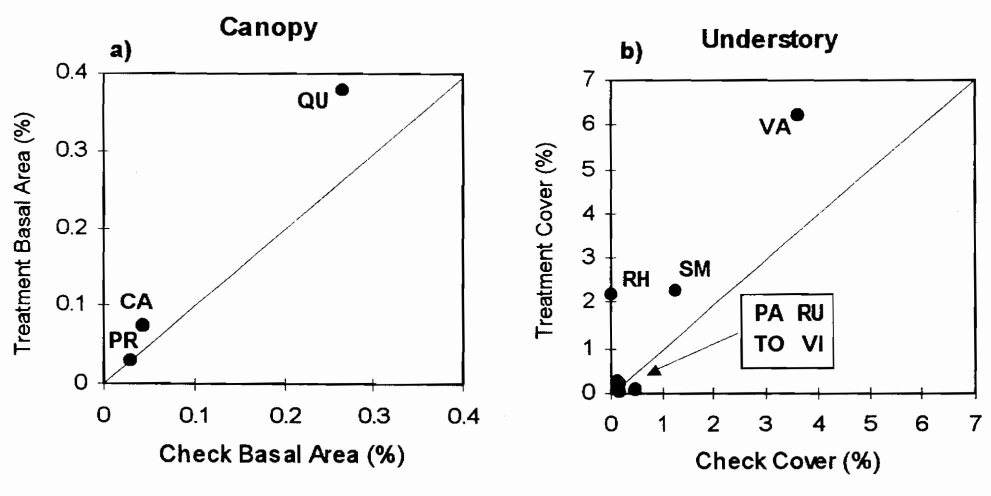

Figure 6. Comparisons of mean percent canopy basal area (left) and mean percent understory cover (right) of competition control versus no competition control (check) for individual species in loblolly pine plantations 24 to 27 years of age. Shifts to the left or right of the diagonal line indicate compositionsl changes.
Symbols represent the following species or genera:
CA = *Carya* spp., **PR** = *Prunus serotina*, **QU** = *Quercus* spp., **PA** = *Parthenocissus quinquefolia*, **RH** = *Rubus* spp., **SM** = *Smilax* spp., **TO** = *Toxicodendron radicans*, **VA** = *Vaccinium* spp., **VI** = *Vitis* spp..

Implications for Wildlife

Black cherry and eastern redcedar produce soft-mast as young as 10 years of age (Marquis 1990, Harlow et al. 1991); thus, their increased cover in competition controlled areas in the 12 to 14 year-old plantations are of current benefit to wildlife. Black cherry provides nectar to several species of flies and bees, and the drupes (available summer to early fall) are consumed by numerous small mammals, rodents, and least 33 species of birds (Van Dersal 1939, Marquis 1990). Black cherry sprouts prolifically even under dense canopies, providing browse for cottontail rabbits and white-tailed deer. The berry-like cone of the eastern redcedar provides a year-around food source for at least 52 species of birds (Van Dersal 1939).

Hard-mast produced by oaks and hickories is indisputably important to many wildlife species, and competition control induced reductions in the abundance of these genera could be a concern. Because these genera do not typically begin mast production until at least 20 to 50 years of age, the lower proportions in the competition controlled areas of the 12 to 14 year-old plantations may not be a major concern at this time. However, because stump sprouts may produce mast at much younger ages (*Q. prinus* as young as 3 years, McQuilkin 1990), and because oak species are highly susceptible to triclopyr (Payne and Bryant 1994), the reproductive origin and fate of the oaks and hickories in the plantations 12 to 14 years of age should be monitored.

Vaccinium cover was not significantly altered by competition control in either plantation age class. *Vaccinium* is an important shrub genus because it provides cover, browse, and fruit for numerous species of wildlife. The berries are eaten by raccoon, opossum, cottontail rabbit, skunk, white-tailed deer, and numerous species of birds including bobwhite quail (*Colinus virginianus*) which rely heavily on the berries as a major food source (Van Dersal 1939). White-tailed deer and cottontail rabbit also depend on *Vaccinium* species for winter browse. Miller and Chapman (1995), investigating the effects of herbicides on avian density and species diversity for the first 3 years post-treatment, found that dense *Vaccinium* cover was associated with greater densities of edge and shrub bird species.

Although not statistically higher, *Rhus* species cover was generally found in higher proportions in the treated plots of the younger plantations and found only the treated plots of the older plantations. Winged sumac (*R. copallina*) and smooth sumac (*R. glabra*), both prevalent at all of the younger plantation sites, produce large fruit clusters that are persistent year-around, providing a reliable food source for white-tailed deer and at least 20 species of birds. Smooth sumac is a preferred food source for wild turkey (*Meleagris gallopavo*) and cottontail rabbit (Van Dersal 1939).

The woody vines (including *Rubus*) investigated in this study play an important role in habitat quality. A variety of rodents, mammals, and birds depend on these vines for fruit, browse, and cover. To provide the greatest variety and cover of these vines, openings should be made in the canopy to emit more sunlight (Payne and Bryant 1994). While woody plus herbaceous control apparently provided the most favorable conditions for poison ivy, woody control alone provided more favorable conditions for

Virginia creeper. *Smilax* cover was decreased under both of these treatments relative to no competition control in the younger plantations, but was increased by competition control with 2,4,5-T in the older plantations.

Thus, even clear management objectives to improve wildlife habitat can lead to unclear management options, as not all plant species beneficial to wildlife respond to herbicides the same way, and since wildlife species requirements differ, plant species compositional changes will affect wildlife species in different ways. Furthermore, succession appears to have at least as great an influence as competition control on species composition, although competition control can have the effect of abbreviating natural succession (Felix et al. 1983).

Vertical Structure Changes

Vertical structure analysis was based on the relative height of competing vegetation and is presented as percentages of the total stand height (average height of dominant loblolly pines) to facilitate stand structure comparisons. Absolute heights tend to emphasis only distance from the ground, which could differ drastically between stands of different ages; percentage of total stand height gives a better estimate of relative changes in stand structure. The percent frequency of occurrence explains the distribution of the vegetation types (shrub and/or vine, hardwood, non-loblolly conifer, and hardwood-conifer mixes) throughout the length of the vertical stand profile.

Plantations Twelve to Fourteen Years of Age

In stands without competition control, shrubs and vines were distributed throughout the lower 15% of the total stand height (approximately $\leq$ 1.6 m) and vines reached up to 60% of the total height (Figure 7). The highest frequency (50%) of shrubs and/or vines were in the lowest height percentile (0-5%) at $\leq$ 0.55 m above ground. Hardwood foliage was not present in the lowest 15% and found only infrequently below 30% of the total stand height. Hardwoods alone, or in a mix with conifers, were fairly evenly distributed from 30 to 80% and solid pine foliage was restricted to the upper midstory at 80% of the total stand height.

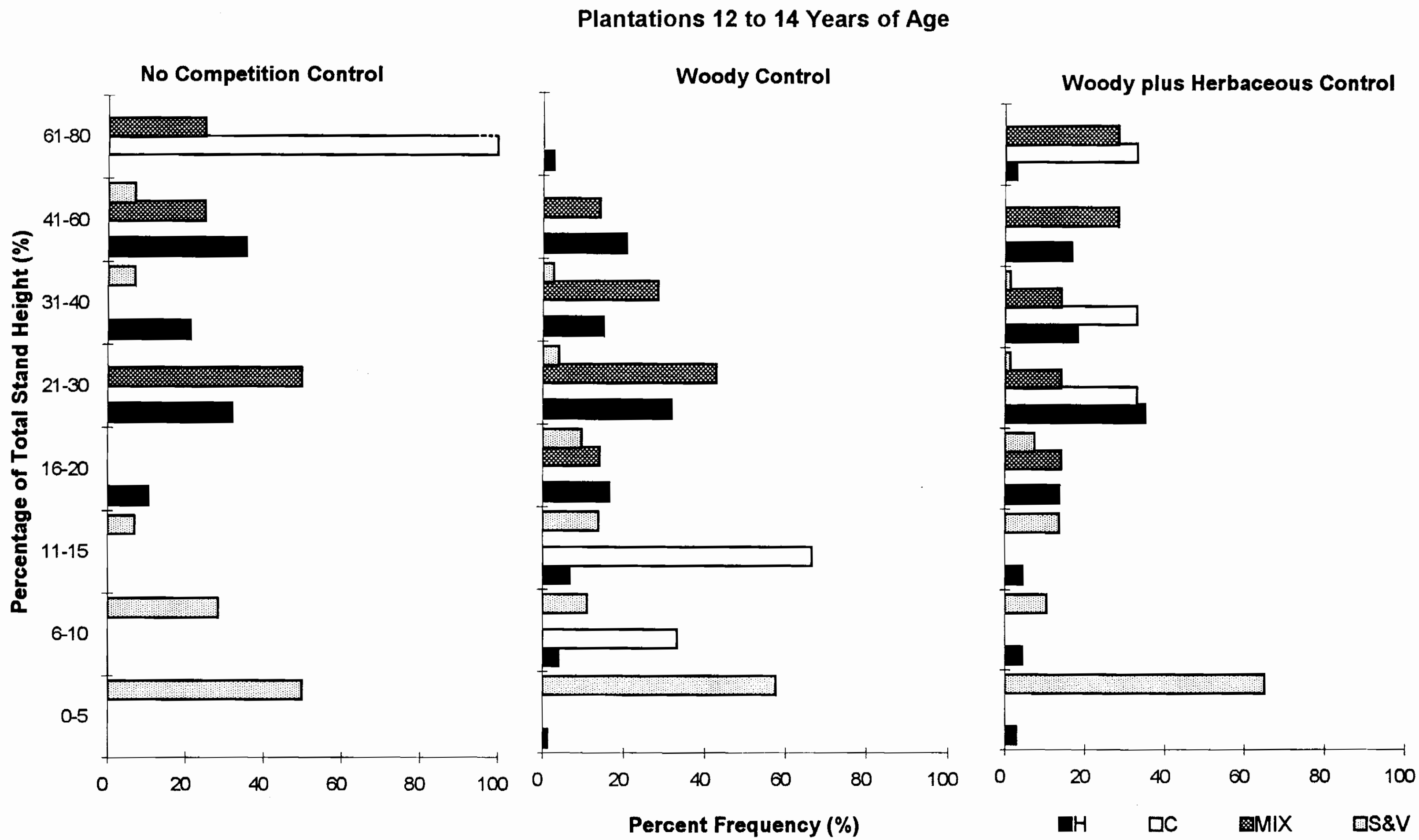

Figure 7. Representation of stand vertical profiles for stands 12 to 14 years of age. The percentage of total stand height is plotted against the percent frequency of occurrence within each height class percentile for hardwoods (H), non-loblolly pine conifers (C), hardwood-conifer mixes (MIX), and shrubs and/or woody vines (S&V) 12 years following: no competition control; woody without herbaceous control; and woody plus herbaceous control.

In the woody control and woody plus herbaceous control stands, shrub and vine cover was distributed from $\leq$ 0.55 m to 40 % of the stand height, with the highest frequency (approximately 60%) occurring near the ground (Figure 7). In comparison, vines occurred higher and more frequently in the upper midstory (approximately 41-80% of total height) of the check stands, while ground level shrub and vine frequencies were similar across all stands regardless of treatment. Hardwood sprouts were present in the lower strata (0-15%) of both woody and woody plus herbaceous control stands, but were absent in the lower stratum of the check stands.

The importance of the lower statum has been demonstrated by Dickson and Noble (1978) in their study of avian vertical distribution in mature hardwood forests of Louisiana. They observed that 31% of their bird sightings (out of 4103) occurred within the lowest 2% of the total stand height (0-0.6 m), indicating a large concentration of bird use of the lowest strata. Additionally, increased understory stratification of various vegetation types has been shown to increase bird species diversity (Johnston and Odum 1956, Childers et al. 1986), while hardwood sprouts at $<$1.5 m provides browse for deer (Lautenschlager 1993). Because a greater variety of vegetation types as well as hardwood sprouts were found in higher frequencies in the lower stratum of the woody control plots, this treatment should provide for greater bird diversity in the lower stratum and greater deer browse availability.

Increased plant species richness and structural heterogeneity in the mid- to upper-canopy levels contribute to increased bird species diversity in even-aged stands

(Johnston and Odum 1956, Childers et al. 1986, Yahner 1987). While conifer cover in the mid- to upper-canopy was primarily Virginia pine (*Pinus virginiana*), the hardwood component was comprised of a variety of species. Therefore, it is expected that an increase in hardwoods would increase the plant species richness of the canopy. Felix et al. (1983) found that the presence of hardwoods in the overstory of Piedmont loblolly plantations substantially increased the overstory species richness and evenness.

The distribution of vegetation types through out the canopy of all of the stands suggests that structural heterogeneity was preserved regardless of treatment. However, the higher frequency of hardwoods and vines in the canopy without competition control, suggest that this canopy could support a more diverse bird population.

There is good indication that birds use different forest strata at different times of the year (Dickson and Noble 1978, Yahner 1987). Dickson and Noble (1978), conducting their study in Louisiana uneven-aged hardwood stands, observed that the distribution of birds shifted from the highest strata in the summer, downward through the vertical profile in the fall, to the lowest strata in the winter. A nearly opposite trend was observed by Yahner (1987) who conducted his study in Pennsylvania even-aged hardwood stands. It is unknown if either resource use behavior exists in Virginia Piedmont bird populations; however, the possibility suggests that the canopy characteristics created by no competition control could provide for greater bird use during part of the year while the lower-strata conditions created by the woody control could be more beneficial for birds at other times of the year.

Plantations Twenty-four to Twenty-seven Years of Age

Childers et al. (1986) has documented bird population responses to loblolly pine succession on Virginia Piedmont plantations and determined that, in general, as plantations aged, the numbers of individuals and the number species decreased. They found that plantations 7 to 11 years of age supported a greater number of individual birds and bird species than plantations 17 to 24 years of age and attributed the difference to decreased understory cover resulting from canopy closure in older stands.

While the absolute frequencies of vegetation types in the older plantations were comparable to those in the younger plantations, the frequency distribution of the vegetation types along the vertical profile differed (Figure 8). The variety of vegetation types was less evenly distributed through out the vertical profile of the older stands. As the variety in vegetation is reduced, structural complexity or heterogeneity is reduced (Brown 1991).

Structural heterogeneity of a plant community is important because structural complexity provides greater opportunity for a variety of animal activities including feeding, resting, breeding, and hiding (Brown 1991) and has been associated with greater bird diversity in even-aged stands (Johnston and Odum 1956, Childers et al. 1986, Yahner 1987). In the older stands, competition control resulted in a more even distribution of more vegetation types throughout the vertical profile, creating a structurally more complex environment and, thus, should support a greater variety of wildife activities and greater bird diversity.

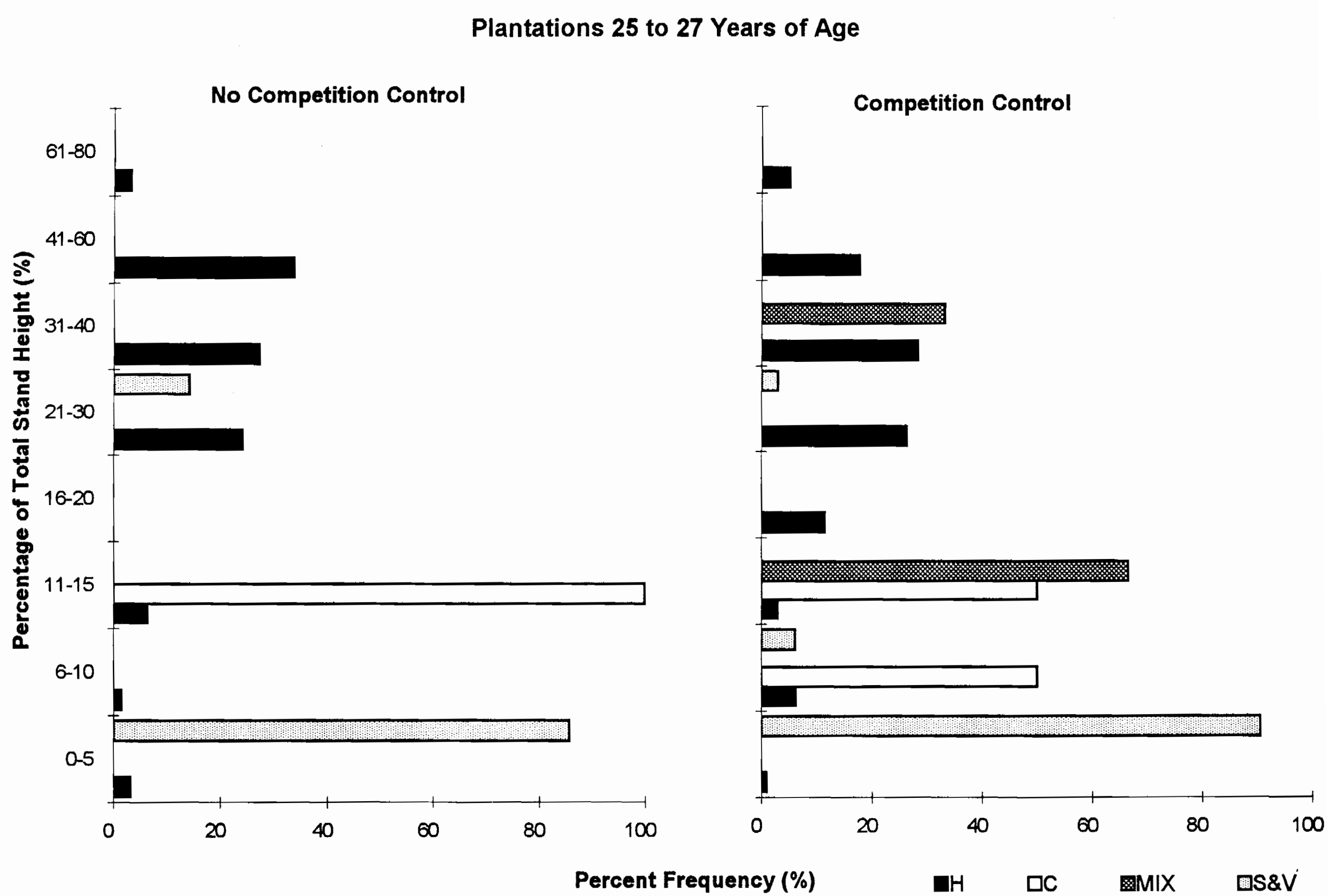

Figure 8. Representation of stand vertical profiles for stands 24 to 27 years of age. The percentage of total stand height and the percent frequency within each height class percentile for hardwoods (H), non-loblolly pine conifers (C), hardwood-conifer mixes (MIX), and shrubs and/or woody vines (S&V) for no competition control and competition control.

While the overall structural complexity of the older stands without competition control was decreased relative to the younger stands without competition control, coniferous and hardwood cover was shifted to the lower strata which should increase ground cover below 2.5 m, and browse availability below 1.7 meters.

Most investigations into the indirect effects of competition control on southeastern wildlife have been of the short-term (1 year, Brooks et al. 1992; 2 years, Leopold et al. 1994; 3-5 years, Miller and Chapman 1995). While this study by no means addresses all of the possible effects of competition control on all of the important aspects of wildlife habitat, the results should provide some indication of longer-term effects.

Summary and Conclusions

Twelve years after treatment, loblolly pine and canopy level hardwoods exhibited differential responses to competition control of varying intensity. In general, as control intensity increased, loblolly pine responded favorably while percent hardwood basal area and canopy species diversity decreased. The number of loblolly pines per hectare and average dominant height were less differentially affected by control levels than loblolly pine DBH. The diameter response indicated that the inclusion of herbaceous control to moderate levels of woody stem control resulted in improved growth; however, herbaceous control was ineffectual when combined with total woody stem control.

Total woody stem control with or without herbaceous control resulted in significant losses in the percentage of hardwood basal area as well as canopy species richness and diversity (H'), indicating that severe initial removal of hardwood stems at early plantation ages affect long-term (12 year) canopy species diversity. In contrast to the marked effects of competition control on canopy hardwood proportions and diversity, understory woody cover and species diversity was not effected at any level of competition control 12 years after treatment.

By examining stand responses to eight levels of competition control, it was possible to identify control level response thresholds. Two-thirds woody plus herbaceous control was determined to be the minimum control level that would significantly increase loblolly pine yield to a level comparable to that following total control. One-third woody plus herbaceous control was determined to be the maximum control level at which canopy hardwood proportions and species diversity (H') were not significantly reduced below that following no competition control. These threshold responses suggest that, in plantations as old as 14 years of age, there exist some level of competition control (most likely between 1/3 and 2/3 woody plus herbaceous control) at which it is possible to obtain high loblolly pine yield while not significantly altering woody plant diversity in the canopy.

This conclusion was supported by the relationship found between loblolly pine yield and canopy diversity in plantations 12 to 14 years of age, irrespective of treatment effect. The results of this investigation indicated that at low levels of loblolly pine yield, canopy diversity (H') was highly sensitive to changes in yield; that is, there was a disproportionate trade-off of species diversity when yield was only slightly increased above the minimum. Conversely, at high levels of yield, a small increase in species diversity was met with a disproportionate trade-off in yield. However, within the moderate ranges of both yield and diversity, there existed an approximately 1:1 trade-off, suggesting that moderate levels of yield could be achieved while conserving moderate levels of canopy species diversity.

A major limitation of the model developed to explain the relationship between yield and canopy diversity in plantations 12 to 14 years of age was its potential to illogically predict Shannon diversity index below zero. This limitation was evidenced when used to predict the relationship in plantations 24 to 27 years of age. Extremely low percentages of hardwood basal area in the older plantations appeared to contribute to a change in the relationship between yield and canopy diversity, but because the percent hardwood basal did not remain constant between the age classes, the mechanism of the change in the relationship over time was unclear.

However, the apparent strength and reasonableness of the model within the data range used to develop it suggests promise in future modelling efforts which should constrain H' to a minimum value of zero and investigate the relationship over time when the percent hardwood basal area remains constant. Until the development of such a model, the strong and consistent relationship between canopy diversity and the percent hardwood basal area demonstrated in this study could be used in conjunction with an existing loblolly pine growth and yield model that uses the percent hardwood basal as an input (e.g. Burkhart and Sprinz 1984 or Knowe 1992).

Regardless of the model used to describe the relationship between loblolly pine yield and diversity, the tendency to view diversity and yield as direct competitors should be avoided because indices of diversity do not account for species composition and differential relationship effects (e.g. mutualism vs. competition). Additionally, diversity indices do not account for compositional and structural changes that may have important impacts on wildlife habitat quality.

There was evidence that competition control adversely effected the proportions of oak and hickory species, and reduced canopy structural heterogeneity within the first

12 to 14 years. At the same time, however, competition control enhanced other aspects of wildlife habitat by increasing the proportions of other fruit bearing vegetation and increasing browse availability and ground stratum heterogeneity in younger plantations. While succession appeared to have at least as great of an effect on habitat quality, competition control generally increased structural heterogeneity in the older plantations.

The results of this study emphasize the relationship dynamics that can occur under management for loblolly pine production on the Virginia Piedmont. Further research into these relationship should enhance our understanding of the more subtle dynamics and better prepare forest resource managers for meeting increasing demands for sustainable timber supply, diversity, and wildlife conservation.

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Vitae

Lisa Elizabeth Watson, daughter of Duane and Lee Watson, was born May 15, 1959, in El Paso, Texas. Following her graduation, in 1977, from Midlothian High School, Virginia, she worked as a Veterinary Assistant until going to and subsequently graduating from Blue Ridge Community College, Virginia, in 1986 with an Associate in Applied Science degree. As a Licensed Veterinary Technician, she worked at Broad Street Veterinary Hospital in Richmond, Virginia, before coming to Virginia Polytechnic Institute and State University (Virginia Tech) to study Wildlife Sciences. In 1993, she graduated Cum Laude with a Bachelor of Science degree. Since August 1994, she has been a graduate research and teaching assistant for the Department of Forestry at Virginia Tech while working toward a Master of Science degree in forestry.