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Developing silvicultural protocols for longleaf pine (*Pinuspalustris*) restoration in loblolly pine (*P. taeda*) stands

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DEVELOPING SILVICULTURAL PROTOCOLS FOR LONGLEAF PINE (*Pinus palustris*) RESTORATION IN LOBLOLLY PINE (*P. taeda*) STANDS

A Dissertation
Presented to
the Graduate School of
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In Partial Fulfillment
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Doctor of Philosophy
Forest Resources

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by
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ABSTRACT

Throughout the southeastern United States, upland pine sites that were once dominated by longleaf pine (*Pinus palustris* Mill.) have been converted to faster growing species such as loblolly pine (*Pinus taeda* L.). This study was designed to determine optimal silvicultural techniques for restoring longleaf pine in existing loblolly pine stands while retaining canopy trees and enhancing desirable characteristics of the ground layer vegetation. We applied seven harvesting treatments to six loblolly pine stands at Fort Benning, GA, with treatments including four that created uniform canopy distribution (Control: uncut, with basal area > 14 m^2/ha; MedBA: residual basal area of ~ 9 m^2/ha; LowBA: residual basal area of ~ 5 m^2/ha; and Clearcut: complete canopy removal) and three that used group selection to create gaps of different sizes (SG: small-gap, ~ 0.12 ha; MG: medium-gap, ~ 0.25 ha; and LG: large-gap, ~ 0.50 ha). Additional cultural treatments were applied in a split-plot design, including an untreated control (NT), herbicide control of woody and herbaceous vegetation (H), and the herbicide treatment plus fertilizer (H+F). We monitored artificially regenerated longleaf pine seedling mortality and growth, measured the response of ground layer vegetation, and quantified resource availability over the first three growing seasons after harvesting.

Longleaf pine seedling mortality was highest in the first growing season, but by the end of three growing seasons mortality averaged 55%. Mortality was highest on Clearcut plots and increased from the forest edge to the gap interior in gap plots, demonstrating a facilitation effect of canopy trees on seedling survival in the first year after planting. Canopy trees showed a competition effect on seedling root collar diameter and the percentage of trees in height growth, with the highest growth rates on Clearcut plots and very little growth over three years on Control plots. Average seedling root collar diameter in gap plots did not differ from that in Clearcut plots, although seedling size increased from the forest edge to the gap interior. The H and H+F treatments did not affect cumulative mortality or seedling size after two or three growing seasons.

Canopy manipulation strongly affected light availability at the forest floor, with a negative exponential relationship between canopy density and canopy light transmittance and increasing light availability from the canopy edge to the gap center in each gap. Light transmittance was higher on the northern half of gaps than on the southern half of gaps, and average light transmittance increased with gap size. Soil moisture at 6 cm in the soil did not differ among canopy treatments or by within-gap position, but soil moisture at 60 and 100 cm in the soil profile was greater within canopy openings than beneath the canopy. Total soil nitrogen was highest north of gap center in LG plots, but there were no effects of within-gap position on foliar nitrogen of longleaf pine seedlings. Our results suggest that light is the most limiting resource for longleaf pine seedlings but that competition for below-ground resources, which is temporally more variable, also affects seedling response.

The ground layer was dominated by herbaceous vegetation in each growing season, and the study treatments did not affect the relative dominance of functional groups. In the uniform plots, vegetation cover increased following canopy removal, with the lowest cover of vegetation on Control plots and the highest cover on Clearcut and

LowBA plots in each growing season. Similar patterns were observed for woody vegetation, but cover of herbaceous vegetation was not significantly different among canopy treatments in the third growing season. Harvesting released woody stems into the midstory, with higher stem densities in Clearcut and LowBA plots than in MedBA and Control plots. The herbicide treatments reduced woody stems in the second growing season, but the effect was not significant after three years. Species richness did not differ among the study treatments, and patterns of species composition were most strongly affected by site-specific factors. At a local scale, species composition shifted to early successional species following harvesting.

To reduce the development of a woody midstory and retain canopy trees for other ecological services, we recommend using single-tree selection to thin stands to a residual basal area between 5 and 8 m^2/ha. Additionally, small gaps (0.1 ha) may be used to distribute local patches of longleaf pine regeneration throughout existing loblolly pine stands. In stands with high densities of woody stems, herbicides can be used to target hardwoods to improve the structure of the ground layer vegetation. Ultimately, frequent fire will be necessary to maintain the desired ecosystem structure over the long time periods.

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CHAPTER I: PROJECT DESCRIPTION AND LITERATURE REVIEW

1.1. Project overview and problem statement

The dramatic reduction in the distribution and extent of longleaf pine (*Pinus palustris* Mill.) ecosystems within the species' natural range has had widespread ecological, cultural, and economic impacts in the southeastern United States. In the time since European settlement, an estimated 97% of the longleaf pine forests and savannas have been 'lost', most commonly due to conversion to other land-use, timber practices that did not include attention to longleaf pine regeneration, and fire exclusion (Frost 1993, Outcalt 2000, Van Lear et al. 2005). As a result, longleaf pine ecosystems are considered to be among the most imperiled systems within the United States and were classified as critically endangered by Noss et al. (1995). Such loss and degradation has affected numerous other species associated with these habitats, resulting in an estimated 187 rare or threatened vascular plants associated with longleaf pine forests (Walker 1993) and 17 faunal species that are candidates for reintroduction through translocation, including 7 herps, 5 birds, and 5 mammals (Costa and DeLotelle 2006).

The structure and ecological function of the longleaf pine ecosystem provides unique habitats for the species that reside there. Longleaf pine forests are characterized by relatively open, and often monotypic, canopies over a ground layer component that is dominated by herbaceous vegetation. A conspicuous lack of a midstory layer creates a forest structure that has often been described as 'park-like' and aesthetically pleasing. This forest structure is associated with a frequent surface fire regime that eliminates hardwood encroachment, limits the regeneration of other pine species, and encourages the development of an herbaceous ground layer. The herbaceous ground layer supports very high floral diversity, with reports of up to 42 species at small spatial scales (0.25 m^2; Walker and Peet 1983) and over 100 species at the 1000 m^2 scale (Peet 2006). Sorrie and Weakley (2001) classified the Coastal Plain Floristic Province, in which the longleaf pine ecosystem historically dominated, as one of the most diverse floristic regions in North America. Fire is considered the most important ecological process within these systems and is critical to the restoration and management of longleaf pine forests (Barnett 1999, Mitchell et al. 2006).

The structure, composition, and function of longleaf pine forests are strongly linked through vegetation, fuels, and fire. The herbaceous ground layer component, often dominated by large bunchgrasses, provides well-aerated fuels for low-intensity surface fires. Longleaf pine needles are longer than other southern pines and have high resin content, and the needle-fall from canopy pines provides additional fuel to the ground layer. This fuel matrix is ideal for the frequent fire regime that is characteristic of the longleaf pine ecosystem, and in turn, frequent fire perpetuates the structure and composition of the ecosystem by eliminating hardwoods and increasing the dominance of herbaceous plants. In many cases, this cycle has been disrupted by historical land use and past forest management, and current restoration efforts require the re-establishment of the fire regime.

Longleaf pine restoration is currently a major objective of land managers throughout the southeastern United States, with motivation for restoration ranging from creating wildlife habitat to timber production (Lavoie et al. 2011). In many cases, protection of endangered species is a primary objective of land managers for longleaf pine forests. Such is the case for many lands that support the federally endangered red-cockaded woodpecker (RCW; *Picoides borealis* Vieillot), including many Department of Defense installations in the southeast. The RCW has been an important species for increasing awareness of the impacts of longleaf pine ecosystem loss and has led to important policy decisions that support or encourage longleaf pine restoration.

Regardless of the motivation, successful longleaf pine restoration requires that management transitions the stand from the starting conditions to the desired conditions. Although previous research has increased our understanding of natural longleaf pine regeneration and the management of existing longleaf pine forests, less is known about how to apply such techniques to longleaf pine restoration on sites currently dominated by other canopy species. Throughout much of the south, loblolly pine (*Pinus taeda* L.) was the favored species for regeneration following timber harvest in the 19th and 20th centuries; consequently, loblolly pine forests now occupy many sites that were once longleaf pine forestland (Schultz 1999). Fire exclusion and other management practices have resulted in the development of midstory hardwoods that strongly affect the fuels in the current stands. As the objectives of land owners have shifted to longleaf pine restoration, managers require information on how to convert existing loblolly pine forests to functioning longleaf pine ecosystems. Developing such guidelines requires an understanding of the biology of longleaf pine and how the interacting ecosystem components affect restoration outcomes. The overall goal of this research is to determine how silvicultural practices affect components of longleaf pine ecosystem restoration; results from this work will be used to develop silvicultural protocols for converting upland loblolly pine stands to longleaf pine forests on sites similar to those in this study.

1.2. Literature review

Longleaf pine natural range and history

At the time of European settlement in the southeastern United States, longleaf pine forests were among the most extensive cover types and occurred on sites that ranged from poorly-drained coastal flatwoods to dry mountain sites in northern Georgia and Alabama. The longleaf pine range stretched from southern Virginia to eastern Texas, reaching as far inland as northern Alabama and over halfway down the Florida peninsula to the south (Boyer 1990). In total, longleaf pine occurred within nine states and dominated an estimated 37 million hectares of forestland and savanna (Frost 1993; 2006). The large spatial extent of the natural longleaf pine range demonstrates the wide ecological amplitude of this species. In classifying ecological communities associated with longleaf pine, Peet (2006) separated the longleaf pine range into six broad ecoregions based on similarities in climate, soils, and physiography (Figure 1) and then further described six ecological groups that vary in soil type and landscape position: xeric sand barrens and uplands, subxeric sandy uplands, silty uplands, clayey and rocky uplands, flatwoods, and savannas and seeps. The occurrence of longleaf pine in such varied ecological conditions suggests that the species is tolerant of a variety of growing conditions and potential stressors. However, the historical dominance of longleaf pine is

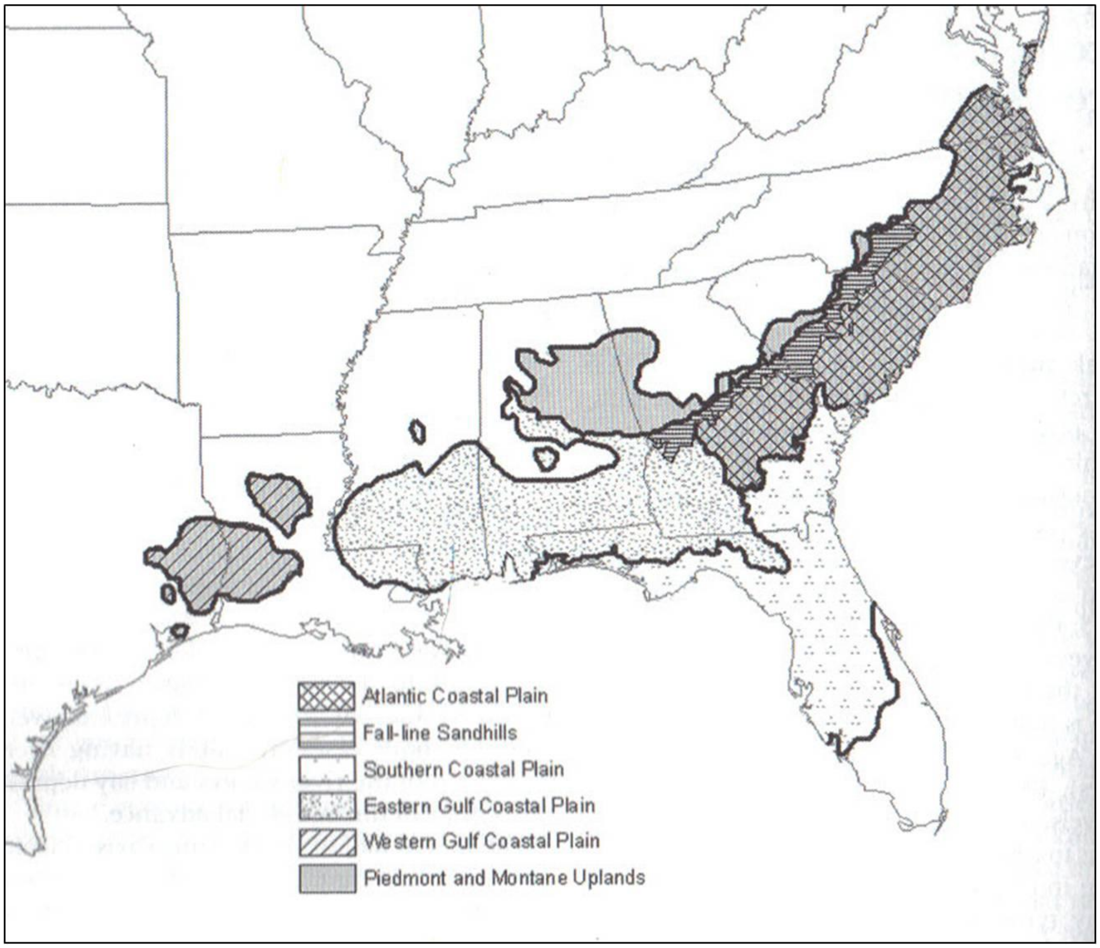

Figure 1.1. The natural longleaf pine range, separated into six ecoregions as defined by Peet (2006).

largely attributed to the historical prevalence of fire in the forest communities of the southeast. It is widely accepted that fire is a critical ecological process for perpetuating the longleaf pine ecosystem (e.g., Noss 1989, Landers et al. 1995, Van Lear et al. 2005, Mitchell et al. 2006), and the extensive historical range of longleaf pine has been attributed in part to frequent surface fires in the southeastern United States (Frost 2006). Throughout most of the natural longleaf pine range, pre-settlement fire frequencies have been estimated at 1-3 years for the Atlantic Coastal Plain and at 4-6 years for much of the Middle Coastal Plain (Frost 2006). Lightning strikes and burning by Native Americans were both important ignition sources (Komereck 1968, Croker 1979, Van Lear et al. 2005, Outcalt 2008), and in many cases these systems covered large spatial areas of continuous forest structure where a single fire could burn without interruption. In many areas, frequent surface fire continued following European settlement; for instance, Stambaugh et al. (2011) used dendrochronological evidence from remnant longleaf pines to show that the mean fire return interval from 1650 – 1905 averaged 2.2 years, with a maximum of 12 years, in the Kisatchie National Forest of central Louisiana, and Huffman (2006) reported an average fire return interval of 2 – 3 years from 1679 – 1868 in pine savannas of Gulf County, FL. In the early 20th century, however, a fire exclusion policy was implemented by the USDA Forest Service in response to large-scale wildfires (Van Lear et al. 2005). One result of the fire exclusion policy was the decoupling of important feedbacks among fuels, vegetation, and fire in longleaf pine forests. Changes in forest structure and fuels introduced different fire regimes to remaining longleaf pine forests, with the potential for overstory mortality or regeneration problems (e.g., Outcalt and Wade 2004, Varner et al. 2007).

While fire exclusion certainly contributed to the widespread decline of longleaf pine forests following European settlement, the forest products industry had a more direct effect on the fate of virgin longleaf pine. Longleaf pine was favored almost exclusively for the production of tar, pitch, rosin, and turpentine, which are collectively referred to as naval stores (Frost 2006). The naval stores industry was believed to have begun in

Virginia early in the 17th century. The process for extracting the gums and resins from living longleaf pine trees required that notches be cut into the bole of each pine, which often weakened the trees and resulted in mortality from fires or wind events. The industry quickly moved through the longleaf pine range, and almost all virgin stands had been affected by the end of the 19th century (Croker 1979). In addition to naval stores, longleaf pine was economically valuable as a timber species, and the invention of steam technology in the middle 19th century increased the efficiency of large-scale logging operations (Frost 2006). Many longleaf pine forests were clear-cut with little attention given to regeneration. Foresters that recognized a problem with longleaf pine regeneration often did not understand the ecosystem well enough to know how to successfully establish the species.

In addition to exploitation of longleaf pine by the naval stores and timber industries, land use changes converted productive sites to agriculture, and other forestlands were developed into urban areas as human population expanded. Many of the cutover forests were replanted with loblolly pine or slash pine (*Pinus elliottii* Engelm.), and the fire exclusion practices during the last century limited the regeneration potential for remaining longleaf pine. In 1995, Forest Inventory and Analysis (FIA) data indicated that only 1.2 million hectares of longleaf pine forest remained, representing about 3% of the original extent (Outcalt and Sheffield 1996). Additionally, much of the remaining habitat is fragmented and in various levels of degradation.

Factors affecting management decisions: restoration objectives and starting conditions

The objectives for longleaf pine restoration can be varied and often depend on the landowner. In 1995, about half (51%) of that total longleaf pine acreage was owned by non-industrial private landowners, with 33% owned by public agencies and the remaining 16% in forest industry (Outcalt and Sheffield 1996). Because forest management decisions are based on restoration objectives, it is important to understand landowner objectives for longleaf pine restoration. A recent survey of 75 private landowners, representing each state of the longleaf pine range except Virginia, was disseminated by The Longleaf Alliance to gain information about restoration goals (Lavoie et al. 2011). The survey indicated that the majority of private landowners restored longleaf pine forests for wildlife habitat (69.3%), while maintaining biological diversity (52%) and timber production (50.7%) were also listed as important reasons for restoration. The target stand condition for restoration for most landowners was a monotypic longleaf pine stand with an herbaceous understory (62.7% of respondents) (Lavoie et al. 2011).

On public and federal lands, restoration objectives are often motivated by habitat requirements for the federally endangered RCW. For example, many military installations in the southeast must manage their natural resources to meet RCW habitat requirements while supporting their military training missions (e.g., FBINRMP 2006, USMCB 2006). Although RCWs prefer longleaf pine forest for habitat, existing populations will use other pine forests (e.g., loblolly pine) for nesting and foraging; however, the longevity of loblolly pine stands is uncertain with frequent fire management. Red-cockaded woodpecker habitat guidelines generally require stand structure to be similar to that characteristic of longleaf pine forests: a pine canopy dominated by large trees, midstory hardwoods < 2.1 m tall, and ground cover of native bunchgrasses and herbs ≥ 40% and dense enough to carry fire at least once every five years (US FWS 2003). Although loblolly pine stands may currently support RCW populations, land managers are interested in converting these upland forests to longleaf pine.

Besides restoration objectives, management decisions depend strongly upon the starting conditions of the site. Sites in need of restoration often vary in their degree of degradation or divergence from target conditions. Differences in site history have important implications for the current stand conditions and the trajectory of stand development. The survey by Lavoie et al. (2011) described the range in stand histories of sites targeted for longleaf pine restoration by private landowners, reporting that 20% of landowners were converting other pine species to longleaf pine, 36% were restoring old field sites, 37% were restoring other, non-pine forest types, and 15% were restoring plantations. The structure and composition of these stands are likely to differ and therefore require different restoration approaches.

Longleaf pine ecosystem restoration: ecosystem components

Restoring a functional longleaf pine ecosystem requires attention to important ecosystem components, including establishing the proper canopy species, enhancing the ground layer vegetation, and reintroducing or maintaining the appropriate fire regime (Van Lear et al. 2005). In practice, researchers and land managers often focus on one particular aspect of longleaf pine restoration, whether that be establishing longleaf pine seedlings (e.g., Ramsey et al. 2003, Knapp et al. 2006) or manipulating vegetation dynamics (e.g., Brockway et al. 1998, Provencher et al. 2001, Mulligan and Kirkman 2002). Such approaches contribute important information for understanding ecological responses to management, but it is important to consider the effects of management practices on multiple ecosystem components when making management decisions (Kirkman and Mitchell 2006). By integrating management options that favor ecological function, managers may simultaneously achieve multiple restoration objectives (see Gilliam and Platt 2006, Kirkman et al. 2007).

Restoring longleaf pine as a canopy species

Seedling characteristics

Silvicultural prescriptions for restoration management must be based on the characteristics of the target species. Longleaf pine regeneration follows a unique life history, with seedlings existing in a 'grass stage' during initial establishment. During this stage, growth is primarily allocated to the root system, and the above-ground biomass consists of the terminal bud surrounded by a tuft of needles that resembles grass. The grass stage is believed to be an adaptation to fire because the long needles help to insulate the terminal bud from the heat of low intensity surface fires (Croker and Boyer 1975). Frequent surface fires reduce competition from surrounding vegetation, but longleaf pine seedlings are able to persist with minimal loss of carbohydrates during fire. In this stage, seedling growth is typically measured at the root collar, and longleaf pine seedlings initiate height growth when the root collar diameter (RCD) reaches a size of around 2.5 cm (Boyer 1990, Knapp et al. 2006), although growing conditions may also regulate grass stage emergence (Ramsey et al. 2003). Although seedlings may be vulnerable to fire during initial height growth, rapid vertical growth generally brings the terminal bud above flame height within one or two growing seasons.

Longleaf pine is traditionally considered to be intolerant of competition for resources from canopy trees and surrounding vegetation (Boyer 1990). Under unfavorable conditions, longleaf pine seedlings may remain in the grass stage for over a decade or never enter height growth at all (Pessin 1944), and numerous studies report that reduced competitive pressure results in increased growth of artificially regenerated seedlings (e.g., Boyer 1988, Palik et al. 1997, Ramsey et al. 2003, Knapp et al. 2008). In a greenhouse study, Jose et al. (2003) found that the availability of light, water, and nitrogen each regulated one-year-old longleaf pine seedling biomass and photosynthesis, although interactions among the measured resources suggest that seedling response to resource availability in natural conditions may be confounded by limitations in other resources. The perceptions that longleaf pine seedlings are slow-growing and require competition control have generally guided traditional longleaf pine management and restoration decisions.

Longleaf pine management and natural regeneration patterns

Early silvicultural prescriptions for managing existing longleaf pine stands included even-aged silvicultural techniques such as seed-tree and shelterwood systems (Boyer and Peterson 1983, Brockway et al. 2006, Mitchell et al. 2006). One of the challenges to natural regeneration management is the species' inconsistent seed production, with reports of good seed crops every 5 to 7 years (Wahlenberg 1946, Croker 1956, Croker and Boyer 1975). As a result, the seed-tree method does not typically leave enough trees on site for adequate regeneration (Boyer and Peterson 1983, Brockway et al. 2006). Moreover, the large seeds and cones of longleaf pine limit the dispersal distance and often require a higher density of seed producers to evenly distribute regeneration within the stand (Croker and Boyer 1975). To resolve these regeneration challenges, the shelterwood system was commonly recommended for natural longleaf pine management (Croker and Boyer 1975, Boyer 1979, Boyer and Peterson 1983). The general concept of this system is outlined with multiple management actions: 1) a preparatory cut to reduce stand basal area to around 15 m^2/ha of the best crop trees; 2) a seed cut reduces basal area to around 7 m^2/ha to encourage seeding and attain required stand density; 3) monitor the seed crop for a good seed year; 4) during a good seed year, prepare the site with prescribed fire; and 5) remove the overstory after successful establishment of a regeneration cohort (Boyer 1979). Variations of the shelterwood system may include the retention of the canopy for extended periods or for perpetuity, eventually creating two-aged or multi-aged stands, or modified distributions of residual canopy trees (Boyer 1993, Brockway et al. 2006).

Patterns of natural regeneration provide information about the establishment and growth requirements for longleaf pine seedlings, and natural longleaf pine regeneration is commonly observed to be concentrated in canopy gaps (Wahlenberg 1946, Platt et al. 1988). Grace and Platt (1995a) found that longleaf pine seedling survival and growth was higher in areas of low canopy pine density than in areas of high canopy pine density, resulting in the aggregation of longleaf pine seedlings within canopy openings. Gagnon et al. (2004) described natural longleaf pine regeneration in 141 canopy gaps in longleaf pine forests of the Apalachicola National Forest, FL and reported that distance of longleaf pine seedlings to canopy pines was positively related to both seedling density and RCD. Other studies have suggested that initial seedling establishment is less affected by proximity to canopy pines than subsequent growth. Boyer (1963) found that RCD of naturally regenerated seedlings significantly increased with distance from parent trees in a study in Escambia Experimental Forest, AL; however, seedling survival was not affected. In a survey of natural mortality from Eglin Air Force Base in northwest FL, Pecot et al. (2007) reported that the highest density of natural longleaf pine regeneration occurred within 5 m from the nearest overstory tree. These results suggest that the success of regeneration within canopy gaps may be related to factors controlling seedling growth rather than limitations on initial establishment.

Modeling silviculture after natural disturbance

In recent decades, forest managers have become increasingly interested in modeling forest management after patterns of natural disturbance in a variety of ecosystems (e.g., Hunter 1993, Attiwill 1994, Franklin et al. 2002, Bergeron et al. 2004). In longleaf pine ecosystems, the primary natural disturbances include large canopy events that occur infrequently (i.e., hurricanes or large wildfires), small canopy disturbances that occur relatively frequently (i.e., lightning strikes and windthrow), and widespread sub-canopy events that occur frequently (i.e., low-intensity surface fires) (Palik and Pederson

1996, Palik et al. 2002, Gilliam and Platt 2006). Given the infrequency of large-scale events and the importance of canopy gaps for longleaf pine natural regeneration, lightning and wind events are believed to be important drivers of longleaf pine regeneration. In southwestern Georgia, Palik and Pederson (1996) found that lightning was the most important source of canopy mortality on xeric longleaf pine sites, while windthrow was the most important source of mortality on more mesic sites. Over a five year period, mortality affected an average of 2.3 canopy pines per hectare, with an average of fewer than 2 trees per event. Similarly, Outcalt (2008) reported that lightning was the primary source of isolated mortality events in longleaf pine forests, with mortality rates of 1 tree per 3 hectares per year in Florida and 1 tree per 8 hectares per year in South Carolina. However, occasional strikes affected multiple trees and strikes often occurred on the edge of existing gaps; these mechanisms were capable of creating larger canopy openings within the forest matrix. As a result, natural disturbance patterns create an irregular mosaic of large and small canopy openings suitable for longleaf pine regeneration (Gilliam et al. 2006) and develop into an uneven-aged, old growth forest structure over time.

Modeling silviculture after natural disturbance is inherently complex, given the stochastic nature of disturbance events, but an underlying concept that commonly applies is the importance of some level of canopy retention (Guldin 1996, Palik et al. 2002, Franklin et al. 2007). Canopy retention provides multiple ecological benefits during regeneration, including structural heterogeneity, habitat for wildlife, and the maintenance of important ecological processes (Franklin et al. 2002). In longleaf pine ecosystems, a silvicultural system that implements canopy retention must balance creating suitable growing conditions for longleaf pine regeneration with maintaining the desired vegetation and promoting frequent fire (Palik et al. 2002, Mitchell et al. 2006). The group selection system has received the most attention for achieving variable retention objectives in longleaf pine ecosystems, although single-tree selection and variable harvest shelterwood systems have also been discussed (Palik et al. 2002, Pecot et al. 2007).

Effects of canopy pines on seedling response

To better understand how silvicultural techniques may be applied to longleaf pine management, multiple studies have been conducted on the regeneration dynamics of artificially regenerated (Palik et al. 1997, McGuire et al. 2001, Gagnon et al. 2003, Palik et al. 2003, Rodriguez-Trejo et al. 2003, Pecot et al. 2007) or naturally regenerated (Grace and Platt 1995a, Brockway and Outcalt 1998) longleaf pine seedlings in canopy openings or in uniformly distributed forest canopies (Boyer 1963, Harrington et al. 2003). Seedling growth responses were reported to generally follow the patterns expected from previous observations of gap regeneration, with seedling growth greater within canopy gaps than in the intact forest (McGuire et al. 2001, Palik et al. 2003, Rodriguez-Trejo et al. 2003, Pecot et al. 2007), with greater distance from canopy trees (McGuire et al. 2001, Gagnon et al. 2003, Pecot et al. 2007), or beneath lower stand level basal areas (Palik et al. 1997, Palik et al. 2003). Some of these studies also explored the mechanisms controlling gap dynamics of longleaf pine regeneration and have, in some cases, reported conflicting results. However, information from these studies provides a broad understanding of the factors affecting longleaf pine seedling dynamics. Canopy effects on regeneration are complex and include both direct effects (e.g., competition for resources) and indirect effects (e.g., controls on other ground layer plants or fire behavior). In addition, direct comparisons of the response of planted seedlings with the response of naturally regenerated seedlings may not be appropriate because mechanisms that affect germination and early seedling persistence in natural regeneration may not hold the same importance for planted seedlings.

The observed aggregation of natural longleaf pine regeneration within canopy gaps has generated two general hypotheses to explain the pattern: 1) the accumulation of pine litter beneath canopy trees increases fire intensity and consequently kills seedlings; and 2) competition for resources limits seedling establishment and development adjacent to adult trees (Boyer 1974, Platt et al. 1988, Grace and Platt 1995a, Brockway and Outcalt 1998). The first hypothesis comes from the findings that fires burn hotter with greater pine litter fuel loads and greater fuel loads are located beneath canopy pines (Williamson and Black 1981, Rebertus et al. 1989, Grace and Platt 1995a). Intense surface fires can kill longleaf pine seedlings, especially when seedlings are small (Jack et al. 2010). In a study from the Croatan National Forest in North Carolina, Avery et al. (2004) reported clustering of dead longleaf pine seedlings around mature trees following fire, with a greater likelihood of seedling mortality associated with increased needle litter around canopy trees. Brockway and Outcalt (1998) reported a lack of naturally regenerated longleaf pine seedlings up to 12-16 m from the forest edge in canopy gaps on the Ocala National Forest in Florida; however, they found that forest litter (i.e., fuel loads) was only greater within 4 m of canopy pines. Their results suggest that, while fuel inputs and fire effects likely contribute to the observed aggregation of longleaf pine regeneration in canopy openings, other mechanisms are also affecting regeneration patterns.

In considering the second hypothesis, it is well established that the presence of canopy trees controls resource availability in the ground layer. The forest canopy directly intercepts light, and strong relationships between canopy density and light availability have been established in different forest systems (e.g., Vales and Bunnell 1988, Canham et al. 1990). Longleaf pine ecosystems are characterized by relatively open canopies, and therefore light levels are typically higher than that of other forest types. Battaglia et al. (2002) reported a strong linear relationship between the canopy gap fraction (a measure of canopy openness) and light availability in longleaf pine forests in southwestern Georgia. The amount of canopy competition exhibits an exponential negative relationship with light availability in longleaf pine forests (Battaglia et al. 2003, Palik et al. 2003, Pecot et al. 2005).

While effects of canopy density on the quantity of available light are relatively straightforward, canopy trees often moderate below-ground resources in complex ways. Increases in soil moisture following canopy removal are associated with a reduction in uptake and evapotranspiration from canopy trees (e.g., Aussenac and Granier 1988, Elliot et al. 1998, Ma et al. 2004), but decreases in soil moisture have also been associated with drying effects from increased exposure to solar radiation (Redding et al. 2003). Effects of canopy density on soil nutrients are also complex; canopy trees provide nutrient inputs through litterfall, uptake nutrients for their own use, and affect microbial activity, litter decomposition, and nutrient release through the moderation of the soil moisture and temperature (Marshall 2000, Prescott 2002).

Given the importance of canopy gaps to ecological function in many different systems, previous research has often focused on determining effects of gap size and within-gap position on resource availability. In the northern hemisphere, the sun follows a southern trajectory through the sky and results in greater direct irradiance in the northern half of gaps than in the southern half of gaps (Canham et al. 1990, Gray et al. 2002, Ritter et al. 2005), and such patterns have been observed in canopy gaps of longleaf pine forests as well (McGuire et al. 2001, Gagnon et al. 2003). Forest canopy openings and within-gap position have also been shown to affect soil moisture (e.g., Gray et al. 2002) and nutrient concentrations (e.g., Denslow et al. 1998). The distribution of resources within canopy openings is an underlying concept of the gap partitioning hypothesis, in which the regeneration of many species occurs in forest openings that create suitable micro-habitats for establishment (Denslow 1980).

The role of resource availability in controlling longleaf pine seedling establishment and growth has been debated in previous studies. Brockway and Outcalt (1998) tested the hypothesis that within-gap variation in light availability was related to clustering of seedlings within canopy gaps and found that light levels did not differ across forest openings in a longleaf pine forest in north central Florida. As a result, they concluded that below-ground competition was more strongly related to seedling establishment than was light availability. However, subsequent research demonstrated strong relationships between the light environment and gap position (McGuire et al.

2001, Gagnon et al. 2003) and direct positive relationships between light availability and seedling size (Palik et al. 1997, McGuire et al. 2001, Pecot et al. 2007). The effects of canopy trees and gap position on soil moisture have been less clear. Harrington et al. (2003) found that soil moisture increased following canopy removal in longleaf pine plantation at Savannah River Site in Georgia, but gap studies in longleaf pine forests have reported no effects of gap position on soil moisture (Palik et al. 1997, McGuire et al. 2001, Gagnon et al. 2003). These studies were conducted on relatively dry sites and found no significant relationships between soil moisture and seedling growth. In a study of longleaf pine seedling growth relations on wet sites, Knapp et al. (2008) reported a negative relationship between seedling size and soil moisture. In contrast, Dyson (2010) found weak positive relationships between soil moisture and longleaf pine seedling growth in sites in FL and GA. Nitrogen availability has been reported to be positively related to seedling biomass (Palik et al. 1997, McGuire et al. 2001), although the effects of canopy density on available nitrogen may be variable. Generally, nitrogen availability in longleaf pine forests is negatively related to overstory density (Palik et al. 1997, Pecot et al. 2007) and positively related to distance from forest edge in canopy openings (McGuire et al. 2001); however, ground layer plants quickly fill root gaps following canopy removal (Jones et al. 2003) and may make nitrogen unavailable for longleaf pine seedlings (Pecot et al. 2007).

Results from these studies illustrate some general patterns of longleaf pine establishment in relation to canopy trees and resource availability. Consistent with the view of longleaf pine as intolerant of competition, seedling growth is negatively affected by canopy density; Palik et al. (1997) determined that seedling biomass had a negative exponential relationship with overstory basal area and that seedling size was strongly limited when basal areas were greater than 8 m^2/ha. Seedling growth was greater in canopy openings than beneath the intact forest, with the zone of influence from canopy trees to seedlings reported to range from around 15 to 18 m (Grace and Platt 1995b, McGuire et al. 2001). Increases in available light and available nitrogen are consistent with increases in seedling growth, although interactions with ground layer plants affect those relationships. However, patterns of survival for artificially regenerated seedlings have differed from patterns of growth, and many studies have reported evidence of facilitation from canopy trees on seedling survival, especially in years of drought (Palik et al. 1997, McGuire et al. 2001, Gagnon et al. 2003, Rodriguez-Trejo et al. 2003). Patterns of natural regeneration require both seedling establishment and growth, and canopy controls on fuels and fire behavior are additionally likely to regulate initial seedling establishment and persistence. Although the processes controlling seedling establishment in longleaf pine forests are strongly regulated by impacts from canopy pines, these relationships are complex and likely dependent on site- and stand-specific conditions.

Establishing longleaf pine in the absence of a longleaf pine canopy

With the widespread loss of longleaf pine from its natural range, many sites targeted for restoration are currently dominated by other canopy species or have been converted to other land uses. Traditional restoration efforts often used management prescriptions to maximize seedling growth and minimize the length of time seedlings were in the grass stage. Because longleaf pine seedlings are intolerant to competition, and given the observations of natural longleaf pine regeneration within canopy gaps, traditional canopy conversion practices included clearcutting followed by artificial regeneration of longleaf pine seedlings (e.g., Boyer 1988, Knapp et al. 2006, Freeman and Jose 2009). With the development of container-grown seedlings, artificial regeneration became a viable option for longleaf pine establishment (Barnett and McGilvray 2000, Barnett 2002). Depending on the condition of the stand, site preparation treatments or competition release treatments may be incorporated into management to improve growing conditions for seedlings.

Site preparation treatments are commonly used in southeastern forestry to modify the growing environment and favor target species (Burger and Pritchett 1988, Morris and Lowery 1988, Nilsson and Allen 2003). Such treatments are generally designed to change the abiotic growing environment (e.g., hydrology of the site, soil organic matter, soil temperature) or to control competing vegetation, and site preparation typically includes mechanical treatments, herbicides, and prescribed fire. Mechanical methods often manipulate the soil surface to change hydrology; for example, bedding raises the surface into continuous beds upon which seedlings are planted, and mounding creates individual mounds as planting sites. Other treatments, such as chopping or mowing, are primarily prescribed to remove standing vegetation. Generally, the intensity of the treatment is proportional to the growth response of the target seedling, although site preparation treatments can have lasting effects on other ecosystem components and should therefore be used with caution for longleaf pine ecosystem restoration because of potentially undesirable effects on fire management or ground layer vegetation.

Early research on longleaf pine regeneration found that site preparation treatments increased survival and growth of planted longleaf pine seedlings, and mechanical treatments were believed to be important for natural regeneration in the absence of prescribed burning (Croker 1975, Croker and Boyer 1975). Boyer (1988) reported that chopping, a mechanical form of vegetation control, increased seedling growth when compared to treatments with less vegetation control, and Hainds (2001) reported that scalping increased seedling survival relative to chemical site preparation or no treatment. On wet sites in the coastal plain of North Carolina, Knapp et al. (2006) found that bedding and mounding resulted in greater seedling growth than flat planting after two years of growth, but chopping did not increase seedling growth when compared to the untreated control. Changes in the planting site conditions by mechanical preparation can result in differences in the subsequent development of the plantation (Boyer 1983), although the long-term effects of site preparation on future stand conditions are not well understood (Boyer 1985, Boyer 1996).

The appropriateness of mechanical treatments such as bedding and mounding is largely dependent on the management objectives and the initial site conditions. On poorly drained sites, where excessive soil moisture limits seedling development, such treatments may improve seedling establishment by relieving excessive moisture (Knapp et al. 2008). Mechanical treatments that modify site hydrology may be less effective in naturally well-drained areas. For example, Loveless et al. (1989) also found that bedding resulted in only marginal increases in seedling growth and was less effective than herbicides for increasing growth on well drained sites in Florida. Mechanical treatments that manipulate the soil can have long-lasting impacts on the hydrology and vegetation of treated sites (Swindel et al. 1986), resulting in potentially irreversible changes to the trajectory of stand development (see Brudvig and Damschen 2011). Given the importance of maintaining or improving the ground-layer component during longleaf pine restoration, site preparation treatments are not generally used during longleaf pine establishment (Brockway et al. 2006). Walker and Cohen (2009) found that mechanical site preparation had few effects on vegetation cover and richness in flatwoods sites in the coastal plain of North Carolina, but changes in hydrology and micro-topography on bedded sites reduced the continuity and intensity of a prescribed fire. The long-term effects of such treatments on fire management are not known. Further, the effects of mechanical site preparation on rare or sensitive species are not understood, so the use of mechanical treatments that manipulate the soil may be more appropriate in heavily degraded sites than in areas with high-quality, remnant vegetation.

Chemical treatments can be an effective alternative to mechanical treatments for the control of competing vegetation and are often used alone or in combination with other treatments. Herbicides offer managers a wide variety of options for vegetation control, depending on the timing of application, the application method and rate, and the type of herbicide (Litt et al. 2001). As a result, herbicides have been recommended for longleaf pine management to improve seedling establishment (e.g., Ramsey et al. 2003, Haywood 2005, Knapp et al. 2008), to change the vegetation structure from woody to herbaceous species (e.g., Brockway et al. 1998, Jose et al. 2008, Freeman and Jose 2009), and to increase the effectiveness of fire management (e.g., Brockway and Outcalt 2000). However, because studies often apply herbicides to meet objectives that differ, comparing results from past research must be done within the context of the specific study objectives or design.

Land managers in the southeastern US commonly use herbicides as a site preparation treatment to reduce competing vegetation for the favored regeneration (Litt et al. 2001, Miller and Miller 2004). A variety of herbicides can be prescribed as site preparation for longleaf pine, including glyphosate, imazapyr, triclopyr, sulfometuron methyl, hexazinone, or picloram (Johnson and Gjerstad 2006). On poorly drained sites in the Coastal Plain of North Carolina, Knapp et al. (2006, 2008) found that a mixture of imazapyr and triclopyr reduced vegetation cover, and shrub cover in particular, resulting in increased seedling growth. Loveless et al. (1989) used a mixture of herbicides (triclopyr, sulfometuron methyl, glyphosate, and hexazinone) to achieve complete competition control on well drained sites in Florida and reported that herbicides increased longleaf pine seedling height and the rate of emergence from the grass stage. Herbicide application has also been applied as site preparation in other studies that were not designed to determine the effect of site preparation on longleaf pine seedling response (Knapp et al. 2011), suggesting that chemical site preparation is a common treatment associated with artificial regeneration. Although herbicide site preparation may be effective at improving longleaf pine seedling establishment, one potentially negative consequence of broadcast application is that the entire plant community and other biota are exposed to the herbicide application. Brockway et al. (1998) found that broadcast application of hexazinone decreased the cover, diversity, and richness of forbs, compared to an increase in herbaceous cover following a spot application of hexazinone. Hexazinone is commonly used to treat broadleaf hardwood species such as oaks and sweetgum but also affects the herbaceous plant community (Wilkins et al. 1993, Brockway et al. 1998, Provencher et al. 2001b). Non-selective herbicides, such as glyphosate, may additionally reduce the cover or diversity of desirable vegetation. As a result, previous studies have more commonly focused on the effects of herbicide release treatments, often (but not always) using band or spot spraying techniques, on longleaf pine establishment and growth.

Reports of increased longleaf pine seedling growth following herbicide release provide evidence of the sensitivity of longleaf pine seedlings to competition for resources. The type of herbicide used is largely dependent on the target vegetation, and previous studies have applied herbicides to control herbaceous species (Nelson et al. 1985, Haywood 2000, Ramsey et al. 2003), woody species (Jose et al. 2008, Haywood 2009, Freeman and Jose 2009), or complete control of both herbaceous and woody vegetation (e.g., Boyer 1988, Haywood 2007, Haywood 2011). In a restoration context, complete vegetation control is generally not desirable because of the risk to the ground layer community and the potential loss of fuels for fire management. Woody species are often targeted for chemical control because the development of a woody midstory poses a threat to long-term restoration goals (Boyer 1985, Provencher et al. 2001, Harrington 2011), and controlling woody vegetation has been found to increase longleaf pine seedling growth. In the coastal plain of North Carolina, Hu (2011) found that direct application of imazapyr to competing hardwood stems resulted in greater seedling growth through three years after planting. Similarly, imazapyr was found to increase seedling growth in the lower coastal plain of Florida (Jose et al. 2008, Freeman and Jose 2009). However, Haywood (2009) reported that control of woody vegetation with triclopyr resulted in no difference in seedling growth between treated areas and controls through eight years of growth on sites in the Kisatchie National Forest in Louisiana. In an earlier study on nearby sites, Haywood (2005) had reported that woody vegetation control with triclopyr had little effect on longleaf pine seedling growth through six growing seasons.

Although woody species are often targeted as a threat to long-term longleaf pine establishment, abundant herbaceous vegetation can also reduce seedling survival and decrease growth rates. Rodriguez-Trejo et al. (2003) found that grass cover had a negative effect on the survival of planted longleaf pine seedlings while shrub cover had a facilitative effect; similarly, Berrill and Dagley (2011) found that seedling survival was most strongly reduced by herbaceous vegetation. The root systems of herbaceous vegetation are often concentrated near the soil surface and are likely to provide strong competition for seedlings that have not developed extensive root systems. Haywood (2005) reported that seedling establishment was reduced by heavy competition with herbaceous vegetation, and seedling growth increased following herbaceous control with herbicides. In an old field site in Florida, Ramsey et al. (2003) used hexazinone and sulfometuron methyl to control competing herbaceous vegetation and found the highest survival, greatest height growth, and greatest root collar diameter on herbicide treatment plots.

The effectiveness of specific herbicide types is largely related to the species composition on the treatment site because of the selectivity of herbicide types. As a result, selecting the appropriate herbicide type and rate for the site conditions are critical for controlling the outcome. Freeman and Jose (2009) compared the effects of three herbicide types (imazapyr, sulfometuron methyl, hexazinone), one combination (hexazinone + sulfometuron methyl) and an untreated control on seedling response and found that imazapyr increased seedling growth but decreased survival relative to the control. On the other hand, hexazinone increased seedling growth with no additional mortality, suggesting that hexazinone may be better suited for their sites than imazapyr. Similarly, Ramsey et al. (2004) compared rates of hexazinone and sulfometuron methyl to determine the most effective treatment for increasing seedling establishment and found that seedling response varied with the rate of application. In general, determining the appropriate herbicide prescription requires an understanding of the existing vegetation structure and composition relative to the desired conditions.

Many of the sites on which longleaf pine naturally occurred are inherently low in nutrients, and fertilizers are commonly used to increase the growth potential of southern pine species (e.g., Colbert et al. 1990, Haywood and Tiarks 1990, Jokela et al. 2004). Past research on longleaf pine seedlings has shown that fertilizer amendments increased soil and foliar concentrations of P (Haywood 2007) and foliar concentrations of K (Bengtson 1976). Hu (2011) also found greater levels of foliar P following fertilizer use in the coastal plain of North Carolina, although the fertilizer effect depended on the density of canopy pines. Despite evidence of higher nutrient levels following fertilization, previous studies have generally reported few benefits of fertilizer to longleaf pine seedlings. Survival has been consistently reported to be lower on fertilized treatments than on control treatments when fertilizers are used alone or in combination with vegetation control (Bengston 1976, Loveless et al9 1988, Gagnon et al. 2003, Ramsey et al. 2003, Haywood 2007). Similarly, fertilizers can reduce seedling growth by increasing the abundance of competing vegetation (Ramsey et al. 2003, Haywood 2007), suggesting that surrounding vegetation may be more effective at acquiring nutrients than longleaf pine seedlings. When used in combination with competition control, fertilizer additions have increased seedling growth relative to fertilizers alone (Ramsey et al. 2003) but did not result in additional growth compared to competition control treatments alone (Loveless et al. 1989, Ramsey et al. 2003). Gagnon et al. (2003) found that fertilizer and competition control increased seedling size relative to untreated seedlings, but the fertilizer effect was not isolated from that of competition control.

Restoring the vegetation structure, fuels, and fire

Disruptions in the ecological processes associated with frequent disturbance regimes can alter the trajectory of ecosystem development and result in alternative ecological states (Groffman et al. 2006). This phenomenon is often associated with increasing the return intervals in systems where fire maintains ecological function (Menges et al. 1993, Nowacki and Abrams 2008, Martin and Kirkman 2009). In the longleaf pine system, the growth of woody vegetation associated with fire exclusion changes fuel dynamics and generally reduces the frequency or continuity of fire. Litter accumulation and the competitive effects of a hardwood mid-story reduce the abundance of herbaceous plants and decrease floristic diversity (Provencher et al. 2001a, Hiers et al. 2007). In the interest of conserving biodiversity, the appropriate vegetation structure must be maintained for fire management (Mitchell et al. 2006), and restoration of the longleaf pine ecosystem often includes treatments to promote the dominance of herbaceous species.

One approach to restoring the ground-layer vegetation of longleaf pine forests is to use herbicides or mechanical treatments to eliminate woody species in the midstory or understory layer (e.g., Harrington and Edwards 1999, Provencher et al. 2001a, Jose et al. 2008). Provencher et al. (2001b) reported that hexazinone was effective at reducing the density of oak seedlings and saplings in sandhill sites of Florida but concomitant increases in the abundance and richness of herbaceous plants were not observed (Provencher et al. 2001a). In another north Florida sandhill study, Brockway et al. (1998) reported that woody vegetation control with hexazinone led to increased cover of graminoids and forbs and resulted in the highest levels of species richness. Similar results were reported along the Gulf Coast in Florida, where reductions in woody vegetation on both hexazinone and imazapyr treatments led to increased herbaceous cover, with wiregrass abundance greater on treated plots than controls four years after treatment (Freeman and Jose 2009). Although past research indicates the potential for such treatments to change vegetation structure, long-term effects of chemical and mechanical treatments are rarely reported. Kush et al. (1999) found that a single treatment of 2, 4-D herbicide for woody vegetation control resulted in an increase in shrub biomass but no difference in herbaceous biomass when compared to control plots 23 years after treatment. To maintain or increase the herbaceous component over the long-term, repeated application of woody control treatments would be required during stand development (Harrington 2011).

In functioning longleaf pine systems, frequent fire acts to control woody species and promote the herbaceous ground layer component, and prescribed fire has been found to be more effective at enhancing the ground layer than chemical or mechanical control of woody vegetation. For example, woody vegetation control reduced woody stems from a sandhill site in Florida, but herbaceous species richness and abundance only increased in response to prescribed fire (Provencher et al. 2001a). The importance of fire in maintaining the desired vegetation community has been well established (e.g., Brockway and Lewis 1997, Haywood et al. 2001, Glitzenstein et al. 2003, Kirkman et al. 2004, Gilliam et al. 2006), and fire has commonly been found to accelerate the recovery of the ground layer community following herbicide or mechanical treatments (Brockway and Outcalt 2000, Outcalt and Brockway 2010, Haywood 2011). Therefore, fire management can be used to maintain initial shifts in vegetation structure caused by chemical or mechanical treatments, and frequent fire is critical to the long-term development of an herbaceous vegetation community (Freeman and Jose 2010).

With the overall objective of establishing an appropriate fire regime for maintaining the desired stand structure, chemical or mechanical treatments can be applied to degraded sites to change the fuel structure in such a way that prescribed fire can be re-introduced or applied more effectively. In longleaf pine forests of southwestern Georgia, Martin and Kirkman (2009) studied the effects of reintroducing fire to depressional wetlands that had become dominated by hardwoods. Chemical and mechanical removal of hardwoods caused a shift in the vegetation structure, with an increase in herbaceous species that allowed prescribed fires to carry through the depressions and further accelerate the recovery of an herbaceous ground layer community. In such cases, the initial intensive management (chemical or mechanical treatments) changes the trajectory of the community in such a way that an alternative structure can be maintained through less intensive management (prescribed fire) (Groffman et al. 2006). However, some treatments may have unintended effects on fire behavior and vegetation recovery. For instance, rotary mowing machines effectively remove dense, woody sub-canopy vegetation and redistribute potential ladder fuels as a mulch layer on the forest floor. Brockway et al. (2009) found that mulching resulted in short-term increases in herbaceous understory plants, but rapid regrowth of sprouting woody stems suggested that repeated prescribed fire would be necessary to control redevelopment of the woody midstory. However, the fuel complex created by mulching woody vegetation may reduce the efficiency of prescribed fire and hinder long-term management objectives (Glitzenstein et al. 2006). Therefore, more information is required to understand the effects of intensive mechanical treatments on fuels and fire management.

Although the re-introduction of fire is critical to longleaf pine restoration, changes in the vegetation structure, fuel accumulation, and fuel type can greatly alter fire behavior and the outcomes of prescribed fire during re-introduction. High mortality of longleaf pine trees has been observed following application of fire (both prescribed and wild) in stands that had not been burned for many years (Varner et al. 2005). The shift in vegetation from herbaceous ground layer plants to a woody midstory structure re-distributes fire spatially and can facilitate the movement of fire into the crown of canopy trees (Kush et al. 2004, Outcalt and Wade 2004). Previously discussed mechanical or chemical treatments can be used to change the fuel structure to reduce the risk of crown fires (Kush et al. 2004, Brockway et al. 2009, Stokes et al. 2010). However, fuel accumulation on the forest floor of stands with a history of fire exclusion also affects the movement of fire through the system and increases smoldering of the duff layer. The residence time of elevated soil and duff temperatures, particularly temperatures that exceed 60 °C, reduces root carbohydrates and resulting in lower growth or higher mortality of canopy pines (Kush et al. 2004, Varner et al. 2009). The moisture of the duff layer affects the smoldering rate and temperatures, and fuel moisture thresholds may be important for reducing overstory tree mortality (Varner et al. 2007). With the introduction of fire after 50 years of exclusion in the Horseshoe Bend National Military Park in Alabama, Hermann and Kush (2010) soaked the bases of longleaf pine canopy trees with water to reduce mortality. Although this method was expensive and not practical at a large scale, it demonstrates the importance of minimizing smoldering in the root zone when re-introducing fire to unburned longleaf pine stands.

Management approaches for restoration of stands with different histories

During restoration, the starting conditions of the stand and the land management objectives largely define the appropriate management practices. Generalizations in stand condition based on site history can guide management recommendations. Based on this literature review, there are different challenges for managers restoring the longleaf pine ecosystem on sites with different histories.

Existing longleaf pine stands

The restoration objectives in existing longleaf pine stands are frequently related to conservation of biodiversity and improving wildlife habitat (Mitchell et al. 2006, Lavoie et al. 2011). Existing longleaf pine stands can be classified as remnant old growth stands (e.g., Boyd tract or Wade tract; Gilliam et al. 2006), naturally regenerated second growth forests established after logging, or plantations (Outcalt and Sheffield 1996). Naturally regenerated stands are unlikely to have a history of mechanical disturbance, and changes in ground layer vegetation are most often associated with fire history. As a result, restoration concerns in naturally regenerated forests are commonly related to promoting natural regeneration and re-introducing or maintaining a frequent fire regime. Recent research emphasizes the importance of addressing both these objectives in forest management (Kirkman and Mitchell 2006, Mitchell et al. 2006). Gap-based silvicultural systems have been proposed for natural longleaf pine regeneration (Brockway et al. 2006, Palik et al. 2002), although small gaps (≤ 0.1 ha) or single-tree selection may also be appropriate for regenerating longleaf pine (McGuire et al. 2001, Pecot et al. 2007). In stands with a history of fire exclusion, initial herbicide or mechanical treatments may be important to alter fuel structure and accelerate the shift to herbaceous vegetation (e.g., Brockway and Outcalt 2000, Martin and Kirkman 2009). Once prescribed fire can be applied at the desired interval, additional treatments should not be needed for maintenance of ecosystem function.

Longleaf pine plantations often have lower levels of species richness than remnant stands (Walker et al. 2010), with decreases in herbaceous species associated with competition from densely planted longleaf pine trees or from hardwoods established in association with fire exclusion (Harrington and Edwards 1999, Harrington et al. 2003). In such cases, control of woody vegetation can increase resource availability and result in greater abundance and diversity of herbaceous plants that exist within the community or seedbank (Harrington 2011). Direct seeding or planting nursery grown ground layer plants can also increase the diversity and abundance of herbaceous plants within plantation (Glitzenstein et al. 2001, Aschenbach et al. 2009); however, canopy density and site conditions may affect establishment success (Outcalt et al. 1999, Mulligan et al. 2001). If timber production is the primary objective, longleaf pine plantations may require few additional management actions to ensure recruitment; however, the success of enhancing the ground layer of plantations increases with reductions in stand density, frequent use of prescribed fire, removal of competing vegetation, and establishment of native plant populations.

Restoring old-field sites

Given the common history of agriculture in the southeastern United States, a large proportion of the sites targeted for restoration are old-field sites (Outcalt and Sheffield

1999, Lavoie et al. 2011). Old-field sites present unique challenges to longleaf pine restoration. In recently abandoned fields, high densities of annual and perennial herbaceous species commonly associated with disturbance compete strongly with planted longleaf pine seedlings (Ramsey et al. 2004). The composition and density of herbaceous vegetation in these situations often differs from that in reference longleaf pine communities, and herbaceous vegetation control may be required to increase seedling growth and survival (Nelson et al. 1985, Ramsey et al. 2003). Hainds (2001) found that herbicide application increased seedling survival when compared to untreated seedlings on an old field site, but scalping resulted in the highest survival rates. On old field sites, where the legacies of tilling and agricultural treatments have greatly changed the ground layer vegetation, intensive site preparation treatments may be acceptable because little remnant vegetation remains. In fact, agricultural legacies introduce a major challenge to the restoration of ground layer vegetation in longleaf pine forests (Walker and Silletti 2006). Brudvig and Damschen (2011) found that land-use history drove patterns of richness and composition at the landscape scale in longleaf pine forests in southwestern South Carolina, with lower species richness and a loss of characteristic longleaf pine species on sites with a history of agriculture. While the loss of native species and an increase in early successional species is commonly observed, the mechanisms limiting the establishment of native communities are not fully understood and require additional research. Re-establishing fire in these stands may not be sufficient for ground layer recovery without additional planting or seeding of native species.

Restoring stands dominated by other canopy species

Following the historical logging of longleaf pine, reforestation efforts commonly focused on faster-growing tree species such as loblolly pine (Schultz 1999, Frost 2006). As a result, many of the stands targeted for restoration to longleaf pine require conversion of the canopy species (Lavoie et al. 2011). The ground layer component of these stands covers a gradient of degradation relative to reference conditions, primarily depending on site history prior to re-forestation and fire history. As a result, a combination of treatments may be appropriate for restoring the longleaf pine ecosystem, including treatments focused on shifting the vegetation to herbaceous species, treatments designed to improve fire management, and treatments designed to increase the establishment of longleaf pine seedlings. The application of these treatments can be done in such a way that existing ecological function is not disrupted. For example, needlefall from existing canopy pines may facilitate fire management objectives and thereby increase the success of restoration of other ecosystem components (Kirkman et al. 2007). Traditional conversion practices included clearcutting and planting, and we currently lack recommendations for restoring longleaf pine to existing pine forests while retaining canopy trees for other ecosystem services. The following chapters in this dissertation will describe the effects of different silvicultural treatments on longleaf pine restoration in loblolly pine stands, with a focus on planted longleaf pine seedling establishment and the response of ground layer vegetation. Results from this work will be used to develop silvicultural protocols for longleaf pine restoration in loblolly pine stands throughout the southeastern United States.

1.3. Study objectives

The overall goal of this research is to determine how silvicultural practices affect components of longleaf pine ecosystem restoration. Specifically, this research is designed to achieve the following objectives:

1) Determine the effects of canopy density and distribution on planted longleaf pine seedling survival and growth through three growing seasons
2) Determine the effects of cultural treatments (herbicides and fertilizer) on planted longleaf pine seedling survival and growth through three growing seasons
3) Determine the effects of canopy density on resource availability in relation to longleaf pine seedling survival and growth
4) Determine the effects of gap size and position on resource availability and longleaf pine seedling survival and growth
5) Determine the effects of canopy density and cultural treatments on ground layer vegetation response through three years
6) Determine effects of canopy density and cultural treatments on ground layer vegetation composition and richness

1.4. Study site

This study was conducted on Fort Benning Military Installation (~32.38º N, 84.88º W) in Muscogee and Chattahoochee Counties, GA and Russell County, AL. Fort Benning was acquired by the US Department of Defense as an Infantry School in 1918 and expanded to its current spatial extent by the early 1940s (FBINRMP 2006). Prior to establishment as a military installation, much of the land base was used by tenant farmers for cotton production until cotton farming was decimated by the boll weevil in the early 1900s. Following the abandonment of agricultural lands, many upland sites were reforested with loblolly pines. Currently, Fort Benning occupies approximately 74,000 ha, of which approximately one-third (22,500 ha) is dominated by loblolly pine and approximately 15,000 ha support pure or mixed longleaf pine stands (FBINRMP 2006).

Prior to European settlement, nearly half of the entire Fort Benning area and almost 60% of the upland sites were dominated by longleaf pine woodlands or savannas (Frost and Langley 2009). The longleaf pine ecosystems at Fort Benning fall within the Eastern Gulf Coast Plain and Fall-line Sandhills ecoregion classifications (Peet 2006). These forest types are dominated by longleaf pine or longleaf pine mixed with loblolly and shortleaf pines (*Pinus echinata* Mill.) in the overstory and an understory of herbaceous plants dominated by little bluestem (*Schizachyrium scoparium* Michx. (Nash)), arrowfeather threeawn (*Aristida purpurascens* Poir.), and Indiangrass (*Sorghastrum* spp.). Sites currently dominated by loblolly pine or upland oak species are currently targeted for restoration to longleaf pine woodlands by land managers at Fort Benning (TNC 2003). Many such sites have been managed for RCW habitat over the past few decades, with managers using frequent prescribed fire. Common understory species include bunchgrasses (e.g. *Andropogon* spp., *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum* spp.) and herbaceous species such as legumes (e.g. *Desmodium* spp., *Lespedeza* spp.) and composites (e.g. *Eupatorium* spp., *Solidago* spp.). Woody species, including sweetgum (*Liquidambar styraciflua* L.), persimmon (*Diospyros virginiana* L), oaks (*Quercus* spp.), and hickories (*Carya* spp.), are common in the understory and infrequent in the midstory.

Fort Benning is unique in that it is located at the interface of two ecoregions: the northeastern two-thirds of Fort Benning lies within the Sand Hills Subsection of the Lower Coastal Plains and Flatwoods Section ecoregion and the southwestern one-third of the installation falls within the Upper Loam Hills Subsection of the Middle Coastal Plain Section (Bailey 1995). Soils of the Sand Hills Subsection are generally deep, coarse-textured sands or loamy sands of Cretaceous origin, and common soil series include Ailey loamy coarse sand, Troup loamy fine sand, and Vaucluse sandy loam (TNC 2003). These soils are sandy in the surface layers and loamy in the subsoil, with low natural fertility and low organic matter content (Green 1997). Soils of the Upper Loam Hills are finer-textured and more productive, although they share the characteristics of being low in organic matter and natural fertility (Mason 2003). Common soils of the Upper Loam Hills include Maxton loamy sand and Wickham sandy loam. The terrain of Fort Benning is predominately rolling and highest in the Sand Hills of the northeast (225 m above sea level) and lowest near the Chattahoochee River in the southwest (58 m above sea level).

Mean annual precipitation at Fort Benning is 1230 mm with a mean temperature of 18.4 ºC (Garten et al. 2003).

The treatments were replicated in six mature loblolly pine stands located in areas targeted for longleaf pine restoration at Fort Benning (Figure 1.2). Three stands were in the Sand Hills and three stands were in the Upper Loam Hills. All study sites were dominated by 40 – 55 year old loblolly pines and had been burned with prescribed fire within three years prior to study initiation. Baseline soils information, including chemical and physical properties, was collected from each stand (Table 1.1). We obtained soil series information from Geographic Information Systems (GIS) provided by the Land Management Branch at Fort Benning (Appendices 1.1-1.7), and one soil sample was collected from each soil series that occurred in each plot. Soil chemistry, cation exchange capacity (CEC), organic matter (%), and soil pH were determined by the Agricultural Services Laboratory at Clemson University. Soil bulk density was determined gravimetrically from soil samples of known volume, and soil texture was calculated by the hydrometer method.

1.5. Experimental design and treatments

The experiment is a randomized, complete block split-plot design with location as the block factor. Each block was divided into seven main treatment plots and each main plot received an overstory treatment. Main plots were 100 x 100 m (1 ha), with the exception of the Clearcut plots, which were 141 x 141 m (2 ha) to create clearcut conditions in the plot center. The overstory treatments generate different competitive

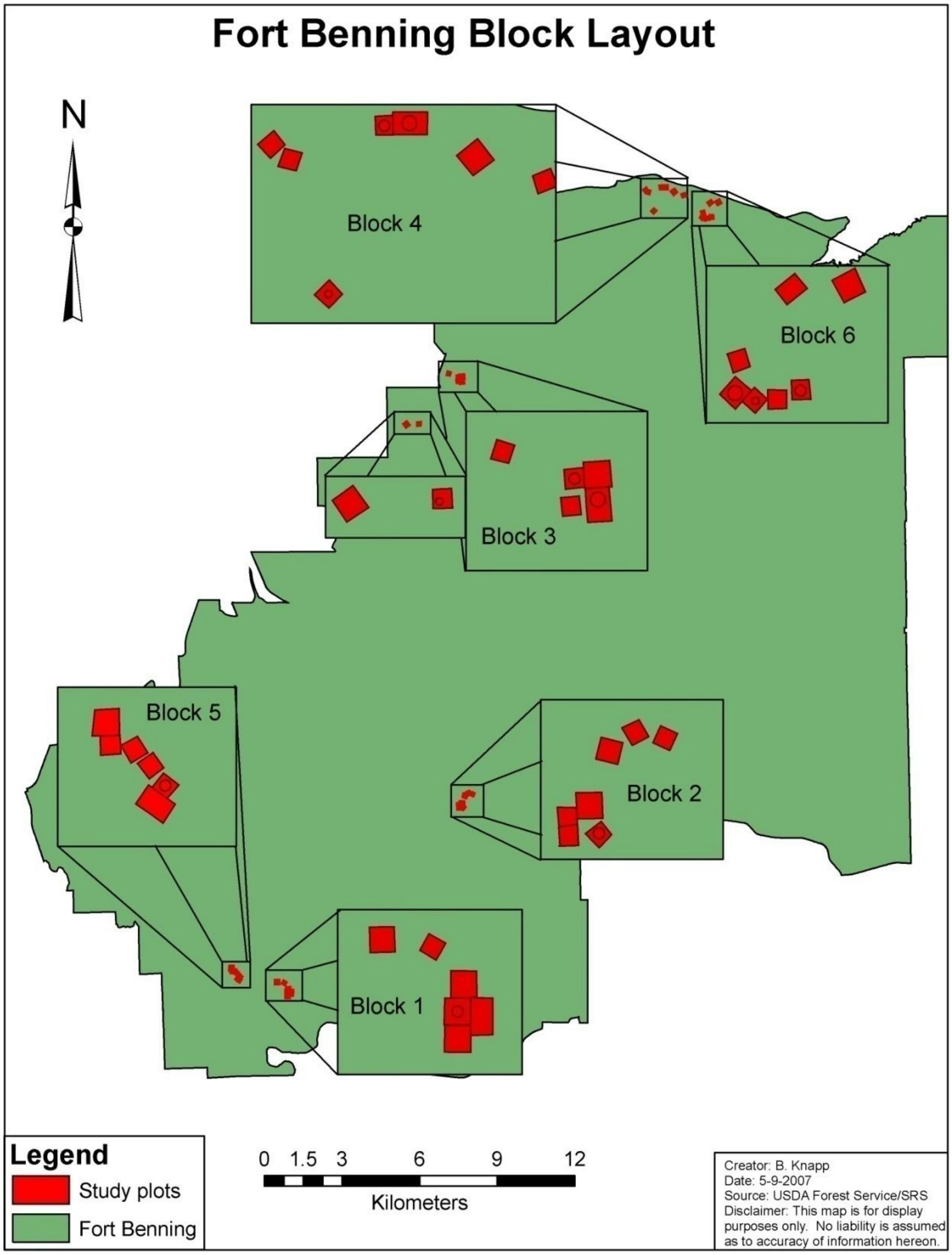

Figure 1.2. Map showing block and plot locations at Fort Benning, GA.

Table 1.1. Summary of chemical and physical properties of study blocks

	Block					
Variable	1	2	3	4	5	6
Total N (%)	0.05	0.06	0.03	0.02	0.04	0.02
Total C (%)	0.91	1.5	0.91	0.73	0.72	0.77
C:N ratio	16.26	25.76	32.67	28.98	17.82	34.61
Soil pH	5.41	4.73	5.01	4.93	4.96	5.08
Organic matter (%)	1.15	1.61	0.87	0.53	0.5	0.41
P (ppm)	26.25	5	8.22	10.11	7.56	8.25
K (ppm)	89.75	116.14	49.11	52.89	84.44	53.5
Mg (ppm)	119	239.57	31.33	25	191.33	38.13
Ca (ppm)	442.63	397	186.56	110.11	296.56	165.25
Cation exchange capacity	7.36	19.27	5.69	4.17	10.96	4.16
Bulk density (g/cm^3)	1.33	1.24	1.27	1.39	1.44	1.46
Sand (%)	71.8	73.2	88.1	88.9	68	88.5
Silt (%)	13.9	11.9	6.6	5.8	13	6.4
Clay (%)	14.3	14.9	5.3	5.3	19	5.1

conditions commonly created by silvicultural practices. Four treatments will henceforth be referred to as "Uniform" treatments because they resulted in the uniform distribution of canopy pines: Control (uncut; residual basal area ~ 16 m^2/ha); MedBA (single-tree selection to create a uniform canopy with the target basal area of 9 m^2/ha); LowBA (single-tree selection to create a uniform canopy with the target basal area of 5 m^2/ha);and Clearcut (all trees removed to basal area of 0 m^2/ha). Three additional treatments, referred to as "Gap" treatments, used group selection to create circular canopy gaps of different sizes: LG (large-sized gap; radius of 40 m and total area of approximately 5027 m^2); MG (medium-sized gap; radius of 30 m and total area of approximately 2827 m^2); and SG (small-sized gap; radius of 20 m and total area of approximately 1257 m^2).

Timber marking in uniform plots was done by land management personnel at Fort Benning, with the objective of thinning from below to uniformly distribute the canopy and reach the desired level of canopy density. To mark the trees for harvest within the gap plots, gap center was first determined, and the distance from gap center to each surrounding tree was measured with an Impulse 2000 laser hypsometer (Laser Technology, Inc., Centennial, CO). All trees with the center of the tree bole located within the defined gap radius were marked for harvest. The canopy treatments resulted in significantly different levels of basal area for the treatments at each location, with residual density around gaps not different from the Controls (Figure 1.3). More information on residual stand structure is provided in Appendices 1.8-1.13. The logging operations were completed following standard installation procedures, and operators were monitored to minimize damage to residual trees during logging. For the most part, tops and slash were removed from the experimental units during harvest. Harvesting was completed throughout 2007.

Following timber harvest, study sites were prepared in accordance with management procedures used for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-

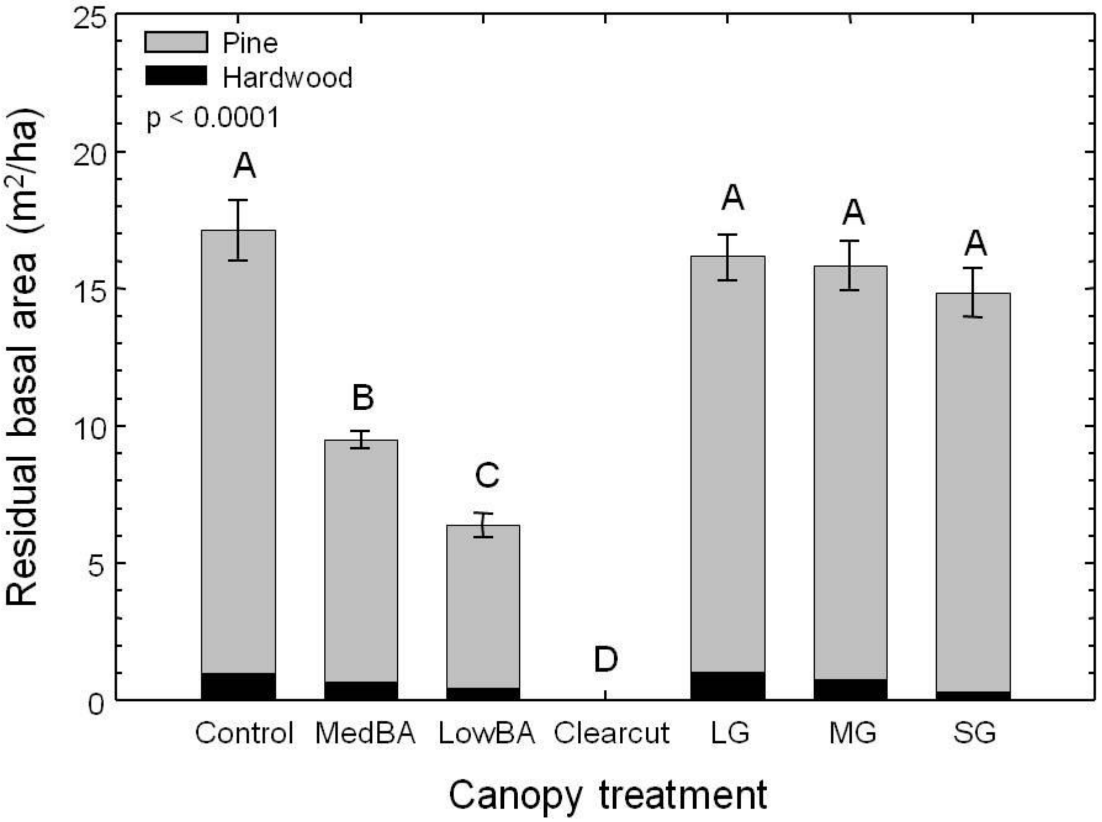

Figure 1.3. Residual basal area following harvest (mean ± one SE) by canopy treatment for pine and hardwood species. Similar letters indicate no significant differences for total basal area at $\alpha = 0.05$.

pyridinecarboxylic acid) mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pineseedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare, by contracted crews. Planting began in mid-November 2007 and was completed by January 2008.

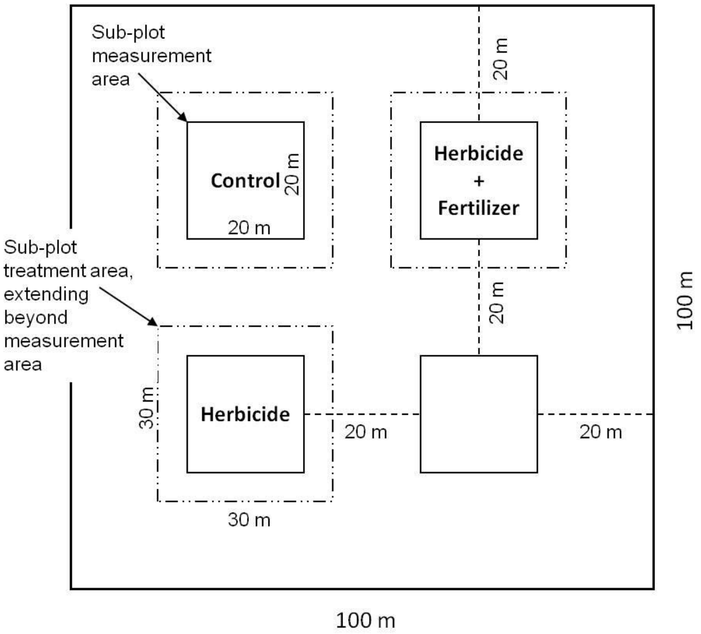

Figure 1.4. Example of sub-plot layout within uniform main plots. Note: Clearcut main plots are 141 x 141 m.

Sub-plot treatments include additional cultural practices designed to enhance ecosystem restoration, through either improvement of conditions for planted LLP seedlings or changes to the ground layer vegetation. The sub-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main plot treatments Control, MedBA, LowBA, and Clearcut were each divided into four equal sections for cultural treatment application (Figure 1.4). Within each section, sub-plot treatments were applied to a 30 x 30 m area centered on a 20 x 20 m measurement plot. Within each gap treatment sub-

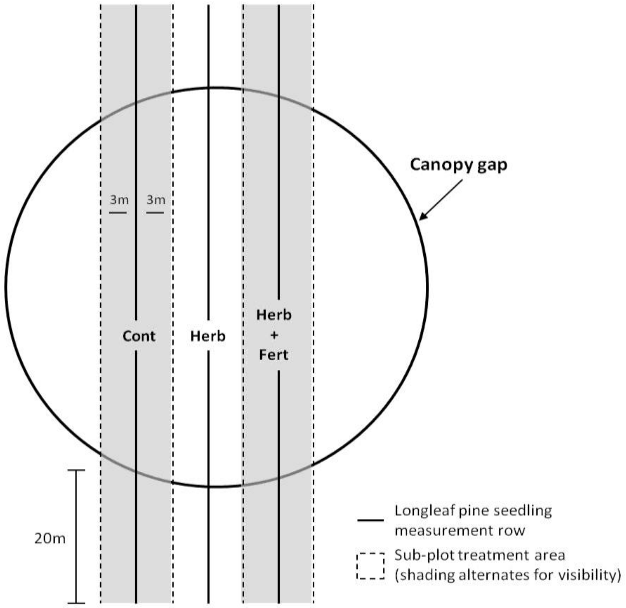

Figure 1.5. Example of sub-plot layout within gap main plots.

plot treatments were applied directly to four selected rows of planted LLP seedlings, each oriented along the north/south aspect (Figure 1.5).

The herbicide treatment was designed to improve conditions for planted longleaf pine seedlings by reducing competition from surrounding vegetation. We prescribed a direct spray of 1% imazapyr plus 0.25% non-ionic surfactant in October 2008 to control woody vegetation. Because herbaceous vegetation dominated most of the study sites, we applied an additional granular mix of 63.2%hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009, with care taken to evenly distribute the fertilizer throughout each treatment.

All study areas were burned with dormant season prescribed fire applied between the second and third growing season (January – April 2010). Prescribed fires were ignited by land management and The Natural Conservancy personnel using backing and strip-head firing techniques, and effort was made to completely burn the study plots; areas of patchy fire movement were re-ignited as needed. Weather conditions during the burns varied among the blocks (Table 1.2), but the study sites generally burned completely. The objective of the prescribed burns was to establish fire as an ecological process during longleaf pine restoration rather than to evaluate the role of fire as a restoration treatment. Therefore, all study areas were burned and this study was not designed to test the effects of fire on ecosystem response.

Table 1.2. Weather conditions during prescribed the 2009-2010 dormant season prescribed burns by block and plot

Site	Block	Treatment	Burn date	Temp. °C	Relative Humidity (%)	Average wind speed (km/hr)	Max gust wind speed (km/hr)	Wind direction
Fort Benning	1	All	7-Mar-10	16.7	15	7.9	17.6	West
	2	All	5-Apr-10	26.9	44	3.2	4.7	Southwest
	3	Clearcut	17-Feb-10	7.8	49	14.4	28.8	West
	3	LowBA, MedBA, Control, Gap	25-Feb-10	7.2	26	4.7	10.1	Northwest
	4	Clearcut, LowBA, Gap	18-Feb-10	12	28	4.7	11.2	West
	4	MedBA, Control	25-Feb-10	6.1	27	17.6	30.6	Northwest
	5	All	8-Mar-10	24.0	26	2.9	4.7	North
	6	All	18-Feb-10	14.4	26	6.5	13.0	Northwest

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CHAPTER II: EFFECTS OF CANOPY STRUCTURE AND CULTURAL TREATMENTS ON UNDERPLANTED LONGLEAF PINE SEEDLING SURVIVAL AND GROWTH

2.1. Introduction

The widespread shift in stand structure and composition of upland sites, from the historically dominant longleaf pine (*Pinus palustris* Mill.) ecosystem to loblolly pine (*P. taeda* L.) stands, has greatly changed the landscape of the southeastern United States. The longleaf pine ecosystem is characterized by a relatively open canopy, frequent surface fires that reduce or eliminate midstory species, and a diverse herbaceous community of ground layer vegetation (Walker and Peet 1983, Sorrie and Weakley 2001, Van Lear et al. 2005, Peet 2006), resulting in an open stand structure that provides high-quality habitat for threatened or endangered species such as the gopher tortoise (*Gopherus polyphemus*) and the red-cockaded woodpecker (RCW; *Picoides borealis*). Moreover, RCWs prefer large, long-lived longleaf pine trees for nesting (USFWS 2003), but in their absence will use other loblolly pines for habitat. To meet RCW recovery guidelines and to comply with the Endangered Species Act, land managers throughout the southeast are interested in improving RCW habitat by restoring longleaf pine to upland loblolly pine stands.

Longleaf pine seedlings are considered intolerant of competition for resources (Boyer 1990), and therefore traditional silviculture for stand conversion includes clearcutting the existing canopy followed by artificial regeneration (e.g., Boyer 1988, Brockway et al. 2006, Knapp et al. 2006, Freeman and Jose 2009). However, this approach is less desirable in stands that provide current RCW habitat or other ecological services that require the presence of canopy trees. Recently, the importance of canopy retention has been recognized for maintaining ecological function in a variety of forest systems (e.g., Attiwill 1994, Franklin et al. 2002, Palik et al. 2002), and variable canopy retention has been increasingly incorporated into forest management. When restoring the longleaf pine ecosystem, retaining canopy pines not only provides temporally continuous habitat for existing RCW populations but may also limit the development of a woody midstory layer and provide fine fuel inputs from needlefall of canopy pines, which is an important fuel source for fire management (Jack et al. 2006, Mitchell et al. 2006, Kirkman et al. 2007).

Recent studies that explored alternative silvicultural methods for regenerating longleaf pine within existing longleaf pine canopies report that seedling growth is reduced by the presence of canopy trees. Palik et al. (1997) determined a negative, exponential relationship between overstory density and seedlings size, and seedling size increased substantially with less than 8 m^2/ha of overstory basal area. Because it may be acceptable to meet ecological restoration objectives over a longer time period than that traditionally considered in plantation forestry, reduced seedling growth from canopy retention may not necessarily prohibit the use of single-tree selection for longleaf pine restoration (Kirkman and Mitchell 2006, Pecot et al. 2007). According to RCW habitat guidelines, optimal habitat requires overstory basal area between 9 to 14 m^2/ha (USFWS

2003), suggesting that balancing the two management objectives requires a better understanding of longleaf pine seedling responses to variable canopy densities.

Natural longleaf pine regeneration is commonly observed within canopy gaps (Plat et al. 1988, Grace and Platt 1995a, Gagnon et al. 2004) created by lightning strikes or other local disturbance events (Palik and Pederson 1996, Outcalt 2008). Consequently, a number of studies have explored regeneration dynamics within artificially or naturally created canopy gaps in longleaf pine forests (e.g. Brockway and Outcalt 1998, McGuire et al. 2001, Gagnon et al. 2003, Palik et al. 2003, Rodriguez-Trejo et al. 2003) and have generally recommended that gap sizes of 0.1 – 0.2 ha may be large enough to successfully establish longleaf pine seedlings (Brockway and Outcalt 1998, McGuire et al. 2001). However, the distribution of canopy trees within a stand also affects the competitive conditions they create; Palik et al. (2003) found that stand-level seedling size was larger in areas with large canopy gaps than in stands with evenly distributed trees at the same stand-level basal area, suggesting that a stand-level approach to longleaf pine management may incorporate different harvesting techniques. Because the majority of previous research was conducted within longleaf pine stands, however, it is unclear if the competitive effects of overstory loblolly pines will differ from those of longleaf pines.

In addition to competition from canopy trees, longleaf pine seedling establishment may be inhibited by competition from ground layer or midstory vegetation. Fast growing woody species threaten restoration efforts by outcompeting longleaf pine seedlings, with potentially long term consequences to stand structure and fire management. Herbicides may be used to control competing vegetation and generally improve seedling growth (Boyer 1985, Ramsey et al. 2003, Jose et al. 2008, Freeman and Jose 2009). In addition to controlling competition for longleaf pine seedlings, herbicides that target woody species may also improve the ground layer vegetation by increasing cover of herbaceous species (Haywood 2005). Because longleaf pine sites are generally nutrient poor, fertilizer has been suggested as an additional cultural treatment for increasing initial seedling growth (Gagnon et al. 2003).

To retain the desired stand structure and various benefits provided by canopy pines, new techniques are required for longleaf pine restoration beneath the canopy of other species. Underplanting is a technique that has been used in a variety of systems to establish forest regeneration beneath an existing canopy and is typically implemented either to increase the success of regeneration establishment or to maintain benefits from the existing canopy (Paquette et al. 2006). Underplanting has not traditionally been considered for longleaf pine because of the species' intolerance to competition (Brockway et al. 2005). However, recent research has discussed the potential application of single-tree selection methods for longleaf pine establishment within existing longleaf pine forests (Pecot et al. 2007). This study was designed to evaluate alternative silvicultural treatments for longleaf pine restoration on sites currently occupied by loblolly pine. Our specific objectives were to: 1) determine the effects of harvesting treatments that vary the distribution and density of residual canopy trees on planted longleaf pine seedling survival and growth; 2) determine the effects of cultural treatments on planted longleaf pine seedling survival and growth; and 3) determine the effects of within-gap position on planted longleaf pine seedling survival and growth.

2.2. Materials and methods

Study site and experimental treatments

This study was conducted at Fort Benning, GA and included all six study blocks described in Chapter 1.4. The experiment is a randomized, complete block, split-plot design, with the location of individual loblolly pine stands as the block factor. Each block was divided into seven main treatment plots and each main plot received an overstory treatment. Main plots were 100 x 100 m (1 ha), with the exception of the Clearcut plots, which were 141 x 141 m (2 ha) to create clearcut conditions in the plot center. The overstory treatments include four treatments that resulted in the uniform distribution of canopy pines: Control (uncut; residual basal area ~ 16 m^2/ha); MedBA (single-tree selection to create a uniform canopy with the target basal area of 9 m^2/ha); LowBA (single-tree selection to create a uniform canopy with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha). Three additional treatments, referred to as “gap” treatments, used group selection to create circular canopy gaps of different sizes: LG (large-sized gap; radius of 40 m and total area of approximately 5027 m^2); MG (medium-sized gap; radius of 30 m and total area of approximately 2827 m^2); and SG (small-sized gap; radius of 20 m and total area of approximately 1257 m^2).

Sub-plot treatments include additional cultural practices designed to enhance ecosystem restoration, through either improvement of growing conditions for planted LLP seedlings or changes to ground layer vegetation. The sub-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main plot treatments Control, MedBA, LowBA, and Clearcut were each divided into four equal sections for cultural treatment application. Within each section, sub-plot treatments were applied to a 30 x 30 m area centered on a 20 x 20 m measurement plot. Within each gap treatment, sub-plot treatments were applied directly to four selected rows of planted LLP seedlings, each oriented along the north/south aspect.

The herbicide treatment was designed to improve conditions for planted longleaf pine seedlings by reducing competition from surrounding vegetation and to improve the ground layer vegetation by eliminating hardwoods. We prescribed a direct spray of 1% imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid) plus 0.25% non-ionic surfactant in October 2008 to control woody vegetation. Because herbaceous vegetation dominated most of the study sites, we applied an additional granular mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione]and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha

10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009.

Following timber harvest, study sites were prepared in accordance with management procedures used for longleaf pine establishment at Fort Benning (INRMP 2006), with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pine seedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare, by contracted crews. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with prescribed fire applied in the dormant season between the second and third growing season (January – April 2010). Additional information on treatments, treatment application, site preparation, and prescribed burns is described in Chapter 1.5.

Data collection

In June 2008, we selected a sub-sample of longleaf pine seedlings in each sub-plot, and we marked each seedling with an aluminum tag. In uniform canopy plots (Control, MedBA, LowBA, and Clearcut), we randomly selected a sample of 30 seedlings (approximately half of what was planted in each 20 x 20 m measurement area), and in gap plots we tagged every seedling that occurred on each north/south sub-plot measurement row, extending 20 m into the forest on either end. Therefore, the total number of seedlings marked in each gap varied with gap size (average of 42, 34, and 23 seedlings/row in LG, MG, and SG, respectively).

We monitored seedling survival at the end of each of the first three growing seasons after planting (October 2008, 2009, and 2010). Root collar diameter (RCD) of each seedling was measured along two perpendicular axes with digital calipers, and the average of the two measurements was calculated to account for irregularity in root collar shape. Seedling height was measured as the distance from the root collar to the tip of the terminal bud. Because all seedlings were in the grass stage in 2008, seedling height was measured only in 2009 and 2010.

Data analysis

Treatment effects

We tested effects of management treatments on the average longleaf pine response at the plot level during each year. Mean mortality and growth variables (root collar diameter and the percentage of seedlings in height growth) were calculated at the main-plot level in 2008 and at the sub-plot level in 2009 and 2010. Incremental mortality was calculated as the percentage of seedlings that died between measurement periods. Seedlings were determined to be in height growth when the terminal bud was > 15 cm from the root collar, and we calculated the percentage of seedlings in height growth in 2009 and 2010 in two ways: 1) percent in height growth was calculated using the total number of surviving seedlings in the plot, and 2) percent in height growth was calculated using the total number of seedlings marked at the start of the study.

We used mixed-model Analysis of Variance (ANOVA) with a random block effect to determine significant treatment effects in each year, using one-way ANOVA for October 2008 data but split-plot ANOVA for October 2009 and 2010 data. We conducted repeated measures ANOVA using an unstructured covariance structure to determine the effect of time (measurement period) on longleaf pine mortality (all monitoring periods) and root collar diameter. The unstructured covariance structure was selected because it resulted in the lowest AICC values, indicating the best fit for the data. Because sub-plot treatments were applied during different years, we included only the control sub-plot (NT) data for the repeated measures analyses. Treatment differences were determined using Tukey’s Honestly Significant Difference (HSD) test, and degrees of freedom were calculated using the Satterthwaite approximation. When necessary, transformations were used to meet assumptions of normality and constant variance. Treatment effects were determined to be significant when the probability of a Type-I error was less than 0.05.

Effects of gap direction and position

In gap plots, we tested the effects of gap position on longleaf pine mortality and root collar diameter in two ways: 1) we compared seedling response in the northern vs. the southern portion of gaps, and 2) we tested the effect of gap position (in 10 m intervals) on seedling response along the north/south transects. We calculated mean values for each direction and 10 m interval position by grouping data into bins for analyses. Sub-plot data were grouped together for the analyses because we found no interactions between the sub-plot effects and gap position or direction effects.

We used an initial split-plot ANOVA with gap size as the main-plot effect and direction as the sub-plot effect to test for interactions between gap size and direction. Finding no interaction, we tested the effects of gap direction on response variables with data from all gaps combined. We used one-way ANOVA to test effects of gap position in 10 m intervals for each gap separately because gap size differed (and therefore the number of positions per gap differed). For the analyses, we used a repeated measures model with autoregressive order-one covariance structure to account for the spatial covariance in gap position. Treatment differences were determined using Tukey's HSD approach, and degrees of freedom were calculated using the Satterthwaite approximation. When necessary, transformations were used to meet assumptions of normality and constant variance. Treatment effects were determined to be significant when the probability of a Type-I error was less than 0.05.

2.3. Results

Treatment effects

Seedling mortality

The repeated measures analysis showed that there was no significant interaction between measurement period and canopy treatment ($F_{24, 35} = 1.78$; $p = 0.0589$). There was a significant effect of measurement period on cumulative seedling mortality ($F_{4, 35} = 55.80$; $p < 0.0001$), and cumulative mortality significantly increased every measurement period with exception of from October 2009 until May 2010 (Table 2.1). By the end of the third growing season, over half the planted seedlings had died, with the majority of mortality occurring in the first year. The canopy treatments also affected seedling mortality ($F_{6, 20.2} = 4.88$; $p = 0.0031$), with the highest mortality on the Clearcut plots and the lowest mortality on Control and MedBA plots (Table 2.1).

There were no significant interactions between the main-plot and sub-plot treatment effects on cumulative or incremental mortality in 2009 or 2010 (Table 2.2). We found significant treatment effects on cumulative mortality at the end of each growing season (Figure 2.1A), with general patterns similar to those found in the repeated measures analysis. After the first growing season, mortality on the Clearcut plot was near 50% of the planted seedlings and was significantly greater than that on the Control and MedBA plots. Cumulative mortality was similar after the second growing season, but by the end of the third growing season (2010) only mortality on the Control plots was significantly lower than that on the Clearcut and LG plots. There was no significant sub-plot effect in 2009 or 2010 (Table 2.2; Figure 2.1B). The incremental mortality was not significantly affected by the main-plot treatment between October 2008 and October 2009 or between October 2009 and October 2010. However, incremental mortality was higher on NT (control) sub-plots than on H (herbicide) sub-plots between the second and third growing seasons (Figure 2.2).

Seedling growth

Using only the NT sub-plot treatment, the repeated measures analysis showed that the interaction between year and canopy treatment was significant ($F_{12, 34} = 3.18$; $p =$

Table 2.1. Longleaf pine seedling cumulative mortality (%) by measurement period and canopy treatment; similar letters indicate no significant difference at α = 0.05

		Mortality	
Effect	Level	Mean	St. error
Measurement period	May 2008	6.77^{d}	(2.97)
	October 2008	29.05^{c}	(4.76)
	October 2009	36.25^{b}	(5.16)
	May 2010	41.21^{b}	(6.08)
	October 2010	55.00^{a}	(7.32)
Canopy treatment	Control	20.82^{b}	(4.20)
	MedBA	19.77^{b}	(3.15)
	LowBA	39.51^{a}	(7.51)
	Clearcut	47.02^{a}	(8.35)
	LG	38.00^{ab}	(5.03)
	MG	39.20^{a}	(5.98)
	SG	31.27^{ab}	(7.70)

0.0040), and therefore the means across years and across treatments are not presented. Root collar diameter increased over time on all treatments except the Control plots ($F_{2, 34}$ = 1.13; p = 0.3337), and there were significant treatment effects in each year ($p \leq$ 0.0391).

There were no significant interactions between main-plot and sub-plot effects on root collar diameter in 2009 or 2010 (Table 2.3). The main-plot treatment effect was significant in each year, and seedlings in the Control plots were significantly smaller than those in the Clearcut, LowBA, and SG plots in each year (Figure 2.3). After three growing seasons, seedlings in the Control were significantly smaller than those in each of

Table 2.2. Results of ANOVA to determine main-plot and split-plot treatment effects on longleaf pine cumulative and incremental mortality in October 2008, 2009, and 2010

Variable	Period	Effect	Num DF	Den DF	F-value	p-value	Transformation
Cumulative mortality	October 2008	main	6	30	8.59	<0.0001	
	October 2009	main	6	30	7.02	<0.0001	
		sub	2	70	0.37	0.6944	
		main*sub	12	70	0.73	0.7134	
	October 2010	main	6	30	3.97	0.0048	$\arcsin(x^{1/2})$
		sub	2	70	0.40	0.6714	$\arcsin(x^{1/2})$
		main*sub	12	70	0.83	0.6180	$\arcsin(x^{1/2})$
Incremental mortality	October 2008	main	6	30	8.59	<0.0001	
	October 2009	main	6	30	1.22	0.3236	$\arcsin(x^{1/2})$
		sub	2	70	0.94	0.3966	$\arcsin(x^{1/2})$
		main*sub	12	70	0.69	0.7530	$\arcsin(x^{1/2})$
	October 2010	main	6	30	0.64	0.7004	
		sub	2	70	5.19	0.0079	
		main*sub	12	70	1.00	0.4562	

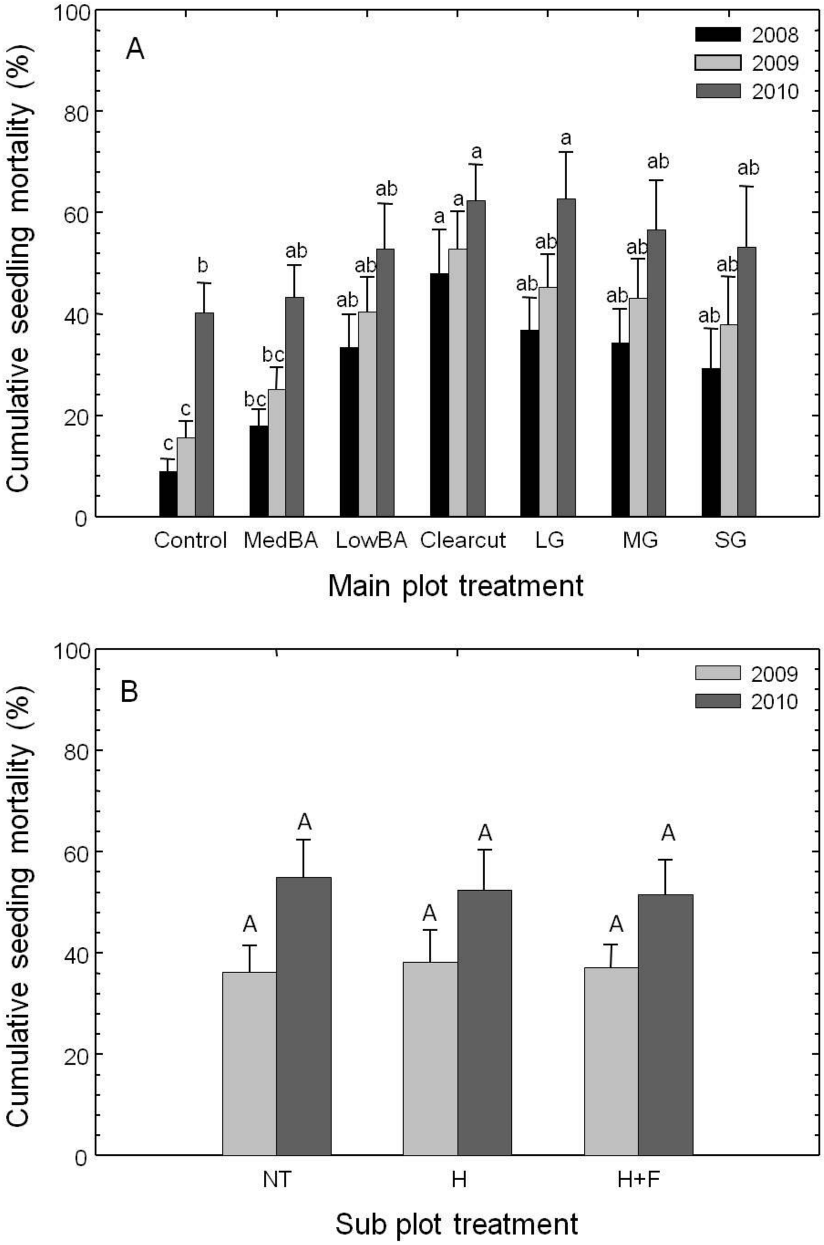

Figure 2.1. Cumulative seedling mortality (mean + one SE) by A) main-plot canopy treatment in October 2008, 2009, and 2010 and B) sub-plot cultural treatment in October 2009 and 2010. The same letter indicates pair-wise comparisons are not significantly different at α = 0.05.

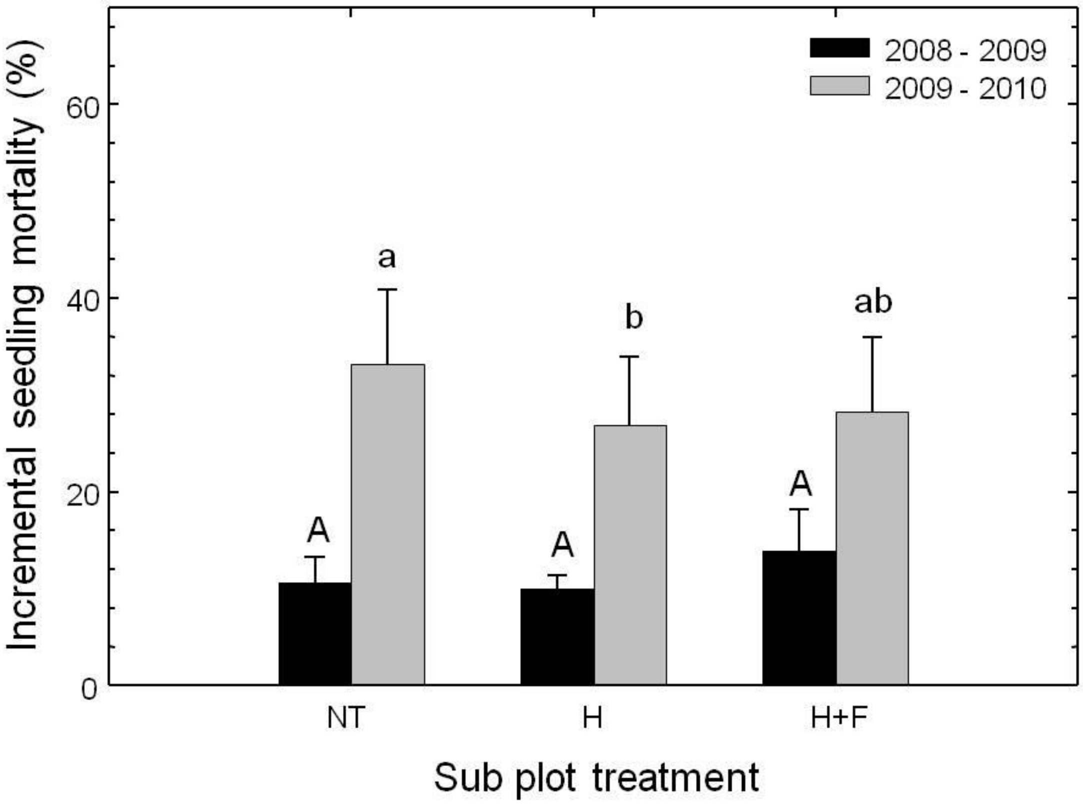

Figure 2.2. Incremental seedling mortality (mean + one SE) by sub-plot treatment from October 2008 – October 2009 and from October 2009 – October 2010. The same letter indicates pair-wise comparisons are not significantly different at α = 0.05.

the gap treatments, and there was a general pattern of increasing seedling size associated with canopy removal. The sub-plot treatments had no effect on seedling root collar diameter (Table 2.3, Figure 2.3).

The percentage of seedlings in height growth was not affected by an interaction between main-plot and sub-plot treatments when analyzed as the percentage of only live

Table 2.3. Results of ANOVA to determine main-plot and split-plot treatment effects on longleaf pine seedling root collar diameter and the percentage of seedlings in height growth in October 2008, 2009, and 2010

Variable	Year	Effect	Num DF	Den DF	F-value	P-value	Transformation
Root collar diameter	2008	main	6	114	7.21	< 0.0001	
	2009	main	6	30	8.94	< 0.0001	
		sub	2	70	1.65	0.2004	
		main*sub	12	70	1.27	0.2576	
	2010	main	6	30	8.75	< 0.0001	log(x)
		sub	2	67	1.25	0.2935	log(x)
		main*sub	12	67	1.87	0.0540	log(x)
Percentage in height growth out of living seedlings	2009	main	6	30.2	3.59	0.0083	log(x+1)
		sub	2	69.4	0.09	0.9127	log(x+1)
		main*sub	12	69.4	0.83	0.6172	log(x+1)
	2010	main	6	30.2	8.07	< 0.0001	arcsin($x^{1/2}$)
		sub	2	69.4	5.00	0.0093	arcsin($x^{1/2}$)
		main*sub	12	69.4	1.15	0.3326	arcsin($x^{1/2}$)
Percentage in height growth out of total seedlings planted	2009	main	6	30.2	3.44	0.0104	log(x+1)
		sub	2	69.4	0.12	0.8835	log(x+1)
		main*sub	12	69.4	0.73	0.7160	log(x+1)
	2010	main	6	30.2	7.08	< 0.0001	log(x+1)
		sub	2	69.4	3.29	0.0433	log(x+1)
		main*sub	12	69.3	0.92	0.5350	log(x+1)

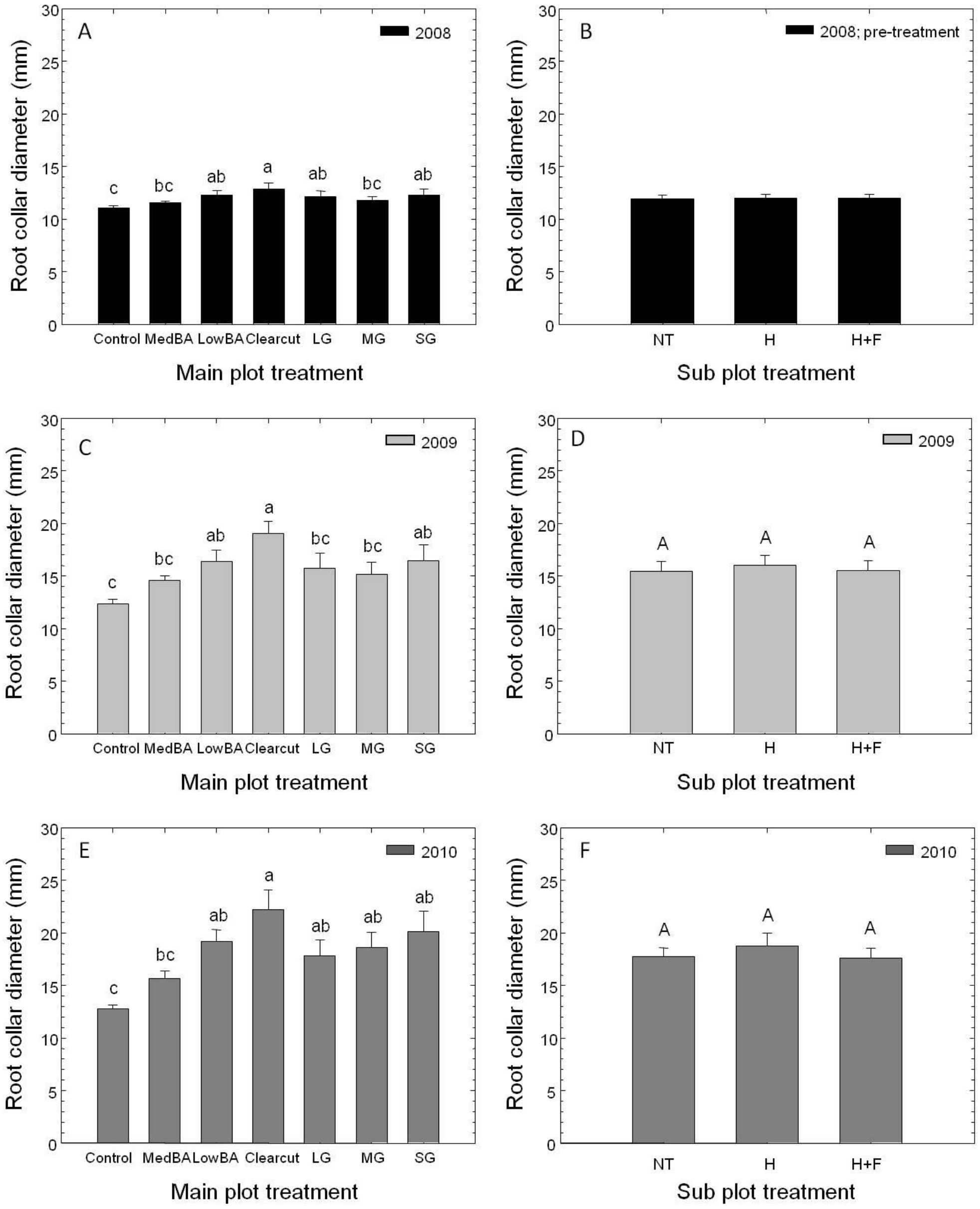

Figure 2.3. Longleaf pine seedling root collar diameter (mean + one SE) measured in October 2008, 2009, and 2010 by main-plot treatment (A, C, and E) and sub-plot treatment (B, D, and F). The same letter indicates pair-wise comparisons are not significantly different at α = 0.05. No analysis was performed on panel B because sub-plot treatments had not been applied in 2008.

seedlings or when analyzed as the percentage of the total number of seedlings sampled in 2008 (Table 2.3). The canopy treatments significantly affected both measures of seedlings in height growth in 2009 and 2010, with differences among treatments similar to the differences observed in root collar diameter (Table 2.4). The Control and MedBA plots generally had significantly fewer seedlings in height growth than the Clearcut and SG plots. Almost no seedlings had emerged from the grass stage on the Control treatments, but 35% of the remaining live seedlings were in height growth on the Clearcut plots. The sub-plot treatments had no effect on seedling emergence from the grass stage in 2009, but significantly more seedlings had emerged from the grass stage on the H than on the NT sub-plots in 2010. The calculation from the total number of seedlings planted resulted in lower percentages of seedlings in height growth because seedling mortality was factored into the calculation.

<u>Seedling response in canopy gaps</u>

Seedling mortality

There was not a significant interaction between gap size and direction on seedling mortality in 2008 ($F_{2,\,86.8} = 0.83$; $p = 0.4391$), 2009 ($F_{2,\,86.8} = 0.27$; $p = 0.7611$), or 2010 ($F_{2,\,85.8} = 1.81$; $p = 0.1704$). In each year, cumulative seedling mortality was significantly greater on the north half of gaps than on the south half of gaps (Figure 2.4A). Mortality rates generally increased from the forest edge to the gap center within each gap size and at each measurement period (Figure 2.5). By the end of the third growing season, however, significant differences in mortality by position were limited and included the

Table 2.4. The percentage of longleaf pine seedlings in height growth (mean + one SE) by main-plot and sub-plot treatments in 2009 and 2010, as calculated from only living seedlings and from all the seedlings initially sampled in 2008. Superscripts with the same letter indicate no significant differences within an effect and year at α = 0.05

		Height growth (%)							
		2009 - Live only		2009 - All		2010 - Live only		2010 - All	
Effect	Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot	Control	0.00^{b}	0.00	0.00^{c}	0.00	0.23^{c}	0.23	0.18^{c}	0.18
	MedBA	0.76^{b}	0.76	0.56^{bc}	0.56	3.38^{bc}	1.63	2.03^{bc}	1.01
	LowBA	3.31^{ab}	1.80	2.61^{abc}	1.51	16.04^{ab}	3.90	9.73^{ab}	3.30
	Clearcut	8.17^{a}	3.54	6.27^{a}	2.74	34.59^{a}	9.18	19.61^{a}	5.73
	LG	1.78^{ab}	1.24	1.10^{abc}	0.81	11.94^{abc}	5.33	6.49^{abc}	3.31
	MG	3.54^{ab}	1.98	2.27^{abc}	1.21	12.48^{abc}	5.90	7.07^{abc}	3.31
	SG	5.53^{a}	2.30	4.01^{ab}	1.95	23.31^{a}	8.59	15.53^{a}	6.38
	p-value	**0.0081**		**0.0103**		**<0.0001**		**0.0001**	
Sub-plot	NT	3.21	0.80	2.24	0.67	10.25^{b}	3.48	6.41	2.33
	H	3.28	1.49	2.40	1.09	18.14^{a}	5.78	10.74	3.83
	H+F	3.47	1.58	2.58	1.12	15.31^{ab}	4.40	8.84	2.98
	p-value	**0.9487**		**0.9211**		**0.0224**		**0.0587**	

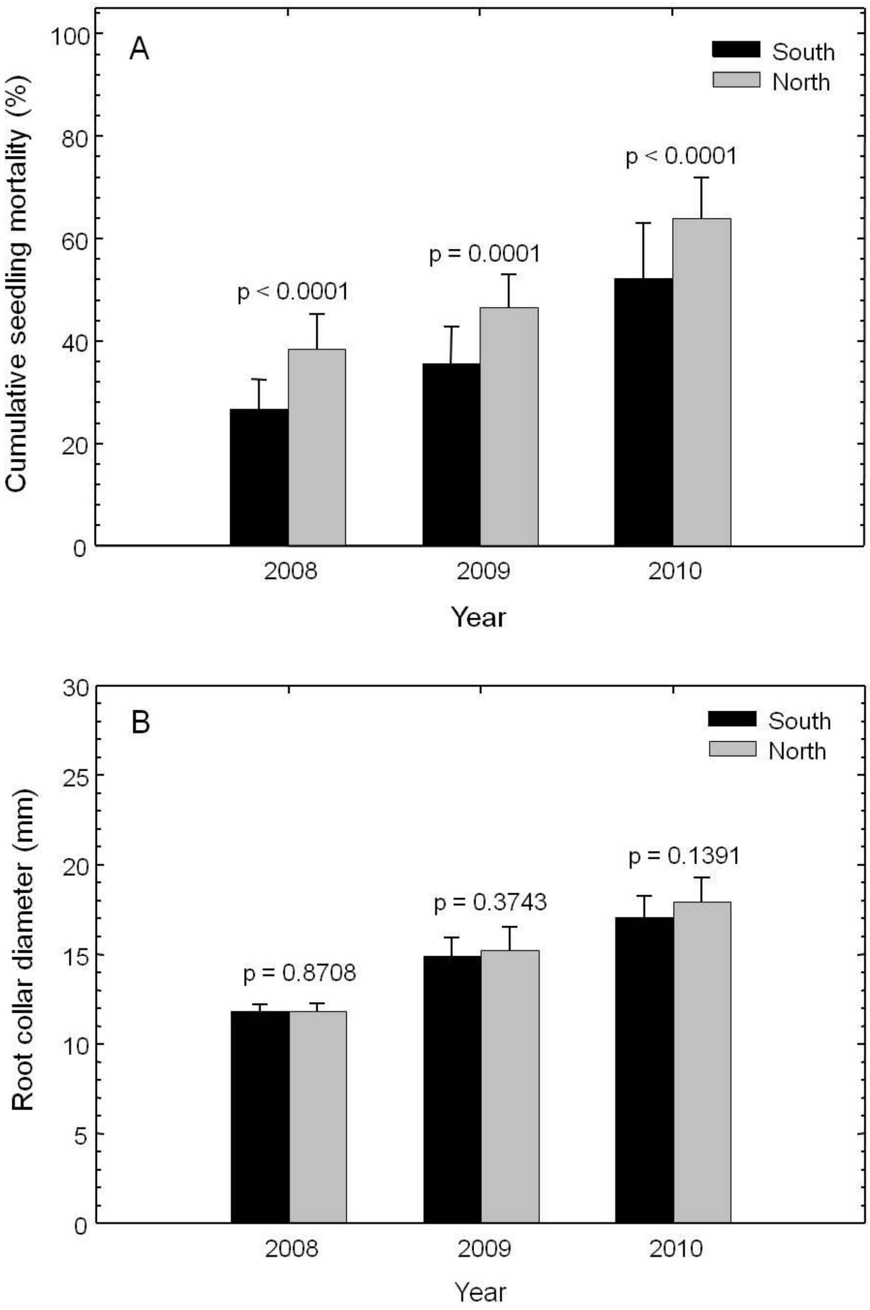

Figure 2.4. Effects of gap direction on A) cumulative seedling mortality (mean + one SE) and B) root collar diameter (mean + one SE) at the end of the first (2008), second (2009), and third (2010) growing seasons.

lowest mortality beneath the intact canopy. Mortality ranged from 40 to 70% in LG plots, from 31 to 61% in MG plots, and from 40 to 64% in SG plots at the end of the third growing season.

Seedling growth

We found no significant interaction between gap size and direction on seedling root collar diameter in 2008 ($F_{2,\ 87} = 0.10$; $p = 0.9055$), 2009 ($F_{2,\ 87} = 2.39$; $p = 0.0975$), or 2010 ($F_{2,\ 83.5} = 2.98$; $p = 0.0565$). Root collar diameter was not affected by gap direction in any measurement year (Figure 2.4) but generally increased from the forest edge to the gap center (Figure 2.5). There were no significant effects of gap position on seedling size after one growing season, but by the end of the third growing season root collar diameter was maximized at the center of each gap. However, seedling size did not significantly increase beyond 10 m from the forest edge in any gap.

2.4. Discussion

The widespread loss of longleaf pine from its natural range has made artificial regeneration necessary for converting existing forests to longleaf pine dominance, and early survival of planted seedlings is critical to the success of restoration efforts. The development of container-grown seedlings, as used in this study, has increased the success of artificial regeneration when compared to early attempts with bare-root seedlings (Boyer 1988, Barnett 2002, Rodriguez-Trejo et al. 2003). Many previous studies report that mortality is highest in the first year after planting because seedlings must adjust to the new growing environment (Boyer 1988, Haywood 2005, Knapp et al.

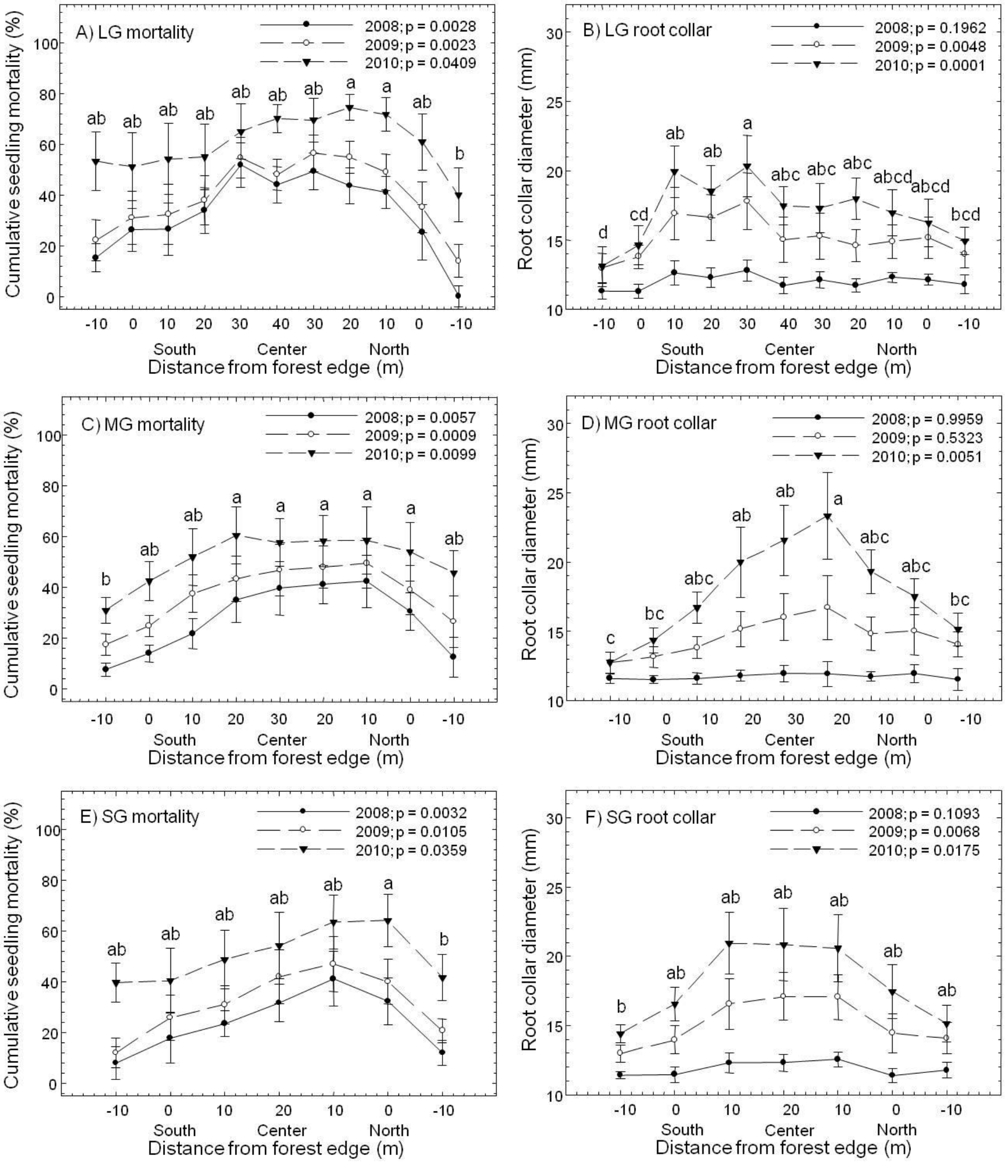

Figure 2.5. Effects of gap position on cumulative seedling mortality (A, C, and E) and root collar diameter (B, D, and F) at the end of the first (2008), second (2009), and third (2010) growing seasons for each gap size. The same letter within a panel indicates pair-wise comparisons are not significantly different at α = 0.05 (only shown for cumulative response in 2010).

2006), and our results indicate that the highest mortality period occurred during the first growing season (between May and October 2008). However, seedling survival is affected by initial growing conditions, including the degree of competition, climatic conditions, site quality and soil characteristics, planting quality, and seedling stock, and previous studies have reported a wide range of early longleaf pine seedling survival rates. For example, Palik et al. (1997) reported an average of 97% seedling survival one year after planting in canopy gaps ranging from around 0.1 to 0.2 ha in southwestern Georgia. In contrast, Rodriguez-Trejo et al. (2003) reported mean survival of only 25% for container-grown seedlings planted in canopy gaps and intact forest in a nearby study also located in southwestern Georgia. The early survival of planted longleaf pine seedlings appears to be related to climatic conditions during establishment, with increased mortality during periods of drought. Two related studies provide strong evidence of this pattern: the Rodriguez-Trejo et al. (2003) study planted seedlings in 1998 and reported high rates of first-year mortality following a year of drought, and McGuire et al. (2001) established a study at the same location one year earlier, with planting in 1997. First-year survival was higher (50–70%) in the McGuire et al. (2003) study, but by the end of the second growing season (1998) the survival had dropped to around 10%.

The role of drought conditions in longleaf pine seedling mortality is further supported by evidence of the facilitation of canopy pines on longleaf pine seedling survival. For example, Rodriguez-Trejo et al. (2003) reported that first-year seedling survival was over twice as high beneath intact forest (35.1%) than in large canopy gaps (15.4%). In a study from northwest Florida, Gagnon et al. (2003) found that initial seedling survival was higher at the edge of canopy gaps (51%) than at gap center (23%) and that survival was negatively correlated with exposure to solar radiation. Facilitation from canopy trees has commonly been observed for regeneration in dry or extreme habitats and is attributed to the alleviation of unfavorably harsh conditions (Holmgrem et al. 1997). Although longleaf pine is generally adapted to growing in dry environments, the additional stress of increased solar radiation may reduce seedling survival during drought years. Allen (1954) used palm fronds to shade longleaf pine seedlings and found that shaded seedlings had higher survival (83%) than exposed seedlings (27%) after one growing season on a dry sandy site in Mississippi. Our results support the presence of canopy facilitation on longleaf pine seedling survival, with gradually increasing mortality associated with the degree of canopy removal from the Control to Clearcut plots. Moreover, mortality was higher in gap centers than under the intact forest canopy at gap edges and significantly higher on the north half of gaps than on the south half, suggesting that increased exposure to solar radiation was related to seedling mortality. However, the importance of canopy trees for facilitation likely depends on the site conditions and weather patterns during seedling establishment. In a parallel study established with the same treatments and over the same time period at Camp Lejeune, North Carolina, Hu (2011) found that seedling survival was lowest on uncut Control plots and highest on Clearcut plots, with no effects of gap position on seedling survival. Therefore, the effects of canopy pines on seedling survival are likely to vary according to site-specific growing conditions and annual weather patterns.

Longleaf pine seedlings are generally considered to be resistant to mortality from low-intensity fires during the grass stage, but the specific interactions of fuel loads, fire intensity, and seedling response are not fully understood. Grace and Platt (1995a) attributed low density of naturally regenerated seedlings beneath canopy pines to increased fuel loads from pine litter and consequently hotter fires, and Boyer (1974) reported post-fire mortality rates of 41% for grass stage seedlings beneath canopy pines compared to 19% mortality of seedlings growing with no canopy above them. In a recent study from southwestern Georgia, Jack et al. (2010) experimentally manipulated fuel loads and found high fuel loads resulted in more intense fires and higher seedling mortality over the next two growing seasons. Although our study was not designed to test the effects of prescribed fire on seedling mortality, we observed that mortality in the third growing season (following the 2009-2010 burns) was higher than that in the second growing season. We did not find a significant effect of canopy density on incremental seedling mortality following the fire, but mortality on Control plots (where needle litter would be high) appeared to be higher than that on other treatments. In addition, incremental seedling mortality was higher on the untreated sub-plots than on the treatments with herbicide. It is possible that this higher level of mortality was related to greater competition on untreated plots, but there was no difference in incremental mortality the year before, suggesting that the mortality may be related to the prescribed burns.

In contrast to a facilitation effect of canopy pines on seedling survival, the canopy treatment effects on root collar diameter clearly indicated strong competition between overstory and understory trees. Given the intolerant nature of longleaf pine seedlings, such growth patterns are not unexpected, and many past studies have demonstrated the negative effect of canopy pines on longleaf pine seedling growth (e.g., Boyer 1963, Boyer 1993, Palik et al. 1997, Kirkman and Mitchell 2006, Mitchell et al. 2006, Pecot et al. 2007). The relationships between longleaf canopy trees and seedlings has been described as a negative exponential function (Palik et al. 1997, Mitchell et al. 2006), and Boyer (1993) reported drastic reductions in growth when canopy basal area exceeded 9 m^2/ha. In our study, only the uncut Control treatment (16 m^2/ha basal area) exceeded this level of stand density, and consequently we observed no measureable increase in seedling growth over three years from the repeated measures analysis. Mean root collar diameter in all other treatments increased over time, however, suggesting the potential of these alternatives for seedling establishment.

The average seedling sizes within canopy gaps of different size were no different from that within Clearcuts, despite significant effects of gap position on seedling root collar diameter. Generally, we found that seedling root collar diameter increased from the forest edge to 10 m within the gap, but seedling size was not significantly different among positions within the gap. In canopy gaps of different sizes in southwestern Georgia, McGuire et al. (2001) reported that seedling root collar diameter increased up to 18 m from the forest edge with no additional increases up to 72 m from the forest edge. Similarly, Grace and Platt (1995b) found that seedling growth was negatively affected by canopy trees within distances of 15 m. Our results corroborate those of previous studies that longleaf pine seedling growth is reduced near mature trees but quickly increases with distance from the canopy.

We found no effect of herbicide application on seedling root collar diameter at either measurement period. Previous studies have demonstrated that herbicides may be an effective management practice for controlling competing vegetation and increasing seedling growth, especially if fire management is restricted by fuels or other factors (Ramsey et al. 2003, Freeman and Jose 2009). Herbicide application during site preparation (Knapp et al. 2006) and as over-the-top release treatments (Nelson et al. 1985, Haywood 2000, Jose et al. 2008) have both been shown to increase seedling growth. However, the effectiveness of herbicide treatments is dependent on the dominant vegetation on the site and the type of herbicide used. Jose et al. (2008) tested the effects of four common herbicides used in longleaf pine restoration (imazapyr, hexaninone, sulfometuron methyl, and hexazinone + sulfometuron methyl) on planted seedling response and found all treatments increased seedling root collar diameter except sulfometuron methyl alone. The imazapyr treatment resulted in the greatest seedling volume growth, which was associated with better control of the dominant runner oak and gallberry on the site. In a study on herbicide use on longleaf pine establishment in Louisiana, Haywood (2005) found that herbaceous control was effective at increasing the percentage of seedlings in height growth through four years at a grass-dominated site but was only effective during the second growing season on a shrub-dominated site.

Despite having no effect on seedling root collar diameter, the herbicide treatment increased the percentage of seedlings in height growth two growing seasons after application in our study. Generally, the emergence of longleaf pine seedlings from the grass stage is believed to be related to seedling size, with emergence occurring when the root collar reaches a diameter of around 25 mm (Boyer 1990, Knapp et al. 2006). However, Ramsey et al. (2003) reported that vegetation control treatments may affect the timing of grass stage emergence by making the resources necessary for growth more readily available. The significant effect of herbicides on the percentage of seedlings in height growth in this study suggests that root collar alone may not be responsible for seedling emergence. Additional research is required to understand the mechanisms controlling the emergence of longleaf pine seedlings from the grass stage.

Longleaf pine forests commonly occur on sites with low nutrient holding capacity, and fertilization is a common practice for other southern pines on such sites (e.g., Haywood and Tiarks 1990, Jokela et al. 2004). Previous studies have reported beneficial or marginally beneficial effects of fertilizers used in combination with vegetation control during longleaf pine regeneration (Gagnon et al. 2003, Ramsey et al. 2003), but the effect is not easily attributable to the fertilizer alone because of the effects of competition removal. In fact, Ramsey et al. (2003) reported that fertilizer alone resulted in lower survival and root collar diameter than untreated plots. Other studies have also reported that fertilizers either reduced survival/growth when compared to untreated sites or had no effect (Bengtson 1976, Loveless et al. 1989, Haywood 2007). We combined fertilizer application with vegetation control to make the nutrient amendments available for longleaf pine seedlings by reducing immediate uptake from competing vegetation, but we did not observe benefits of the fertilizer treatment on longleaf pine seedling response.

2.5. Management implications

Our results demonstrate that longleaf pine establishment can be successfully accomplished using several silvicultural practices, suggesting that some flexibility can be used to meet different management objectives of stand conversion. The traditional practice of clearcutting resulted in the greatest seedling growth but came at the cost of seedling survival. As a result of high mortality, only 20% of the total number of seedlings planted was in height growth after three growing seasons, and only 40% of the planted seedlings remained alive. Landowner objectives will largely determine the target stand density; for instance, pine straw production requires higher density stands than is desirable for wildlife habitat or even sawtimber production (South 2006). When high initial density is desirable, managers may have to increase planting density to compensate for mortality, which increases planting costs.

Interest in maintaining ecological function, maximizing biological diversity, and providing habitat for existing wildlife species requires the retention of canopy pines and the underplanting of longleaf pine for restoration (Kirkman et al. 2007). Our results indicate that longleaf pine establishment can be accomplished following single-tree selection that reduces basal area to moderate levels in loblolly pine stands. The retention of canopy pines is expected to help maintain ecosystem function by providing fuels (needlefall) for fire management, reducing the release of hardwood species, reducing the growth potential of natural loblolly pine regeneration (Knapp et al. 2011), and improving planted seedling survival. Although these benefits come at the cost of longleaf pine seedling growth, it may be acceptable for a longer timeframe to meet restoration objectives than is used for traditional production forestry.

Longleaf pine restoration in loblolly pine stands that currently support the federally endangered red-cockaded woodpecker must be accomplished while meeting RCW recovery guidelines, which may restrict either the density or spatial arrangement of residual trees following harvest (USFWS 2003). Canopy gaps increase the flexibility of the spatial arrangement of regeneration within a stand and allow for the retention of large areas of uncut pine forest. Previous studies have recommended canopy gaps as small as 0.1 ha for longleaf pine establishment in longleaf pine forests (Brockway and Outcalt 1998, McGuire et al. 2001), and our results support the use of similar sized canopy gaps in loblolly pine forests. To reduce the negative effects of exposure to solar energy on seedling survival, Rodriguez-Trejo et al. (2003) suggested oval-shaped gaps oriented NW to SE may increase survival rates with minimal effects on seedling size. Given the higher mortality rates observed on the north half of canopy gaps in our study, additional research on canopy gap shape and orientation could result in improved longleaf pine seedling establishment in loblolly pine forests as well.

To convert loblolly pine forests to longleaf pine while retaining existing canopy pines to promote ecological function, we recommend the use of intermediate single-tree selection (residual basal area of 5 or up to 9 m^2/ha) or small canopy gaps (0.1 ha). Land managers using these methods should anticipate that seedling growth will be reduced by the presence of canopy pines, but longleaf pine seedlings should become established provided that hardwood encroachment and natural loblolly pine regeneration are limited by frequent fire management (Knapp et al. 2011). Although we found that herbicides did not improve seedling growth in our study, sites with aggressive herbaceous or woody competition may benefit from vegetation control. For example, in the replication of this study at Camp Lejeune, Hu (2011) found that woody vegetation control with herbicides increased longleaf pine seedling growth through three growing seasons. The condition of the ground layer vegetation should be considered when making management decisions. Furthermore, it is important to consider how silvicultural practices affect other ecosystem components during restoration, including the ground layer response, effects of treatments on fuel loads, and ability of land managers to effectively apply prescribed fires.

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CHAPTER III: EFFECTS OF CANOPY DENSITY, HERBICIDES, AND FERTILIZER ON RESOURCE AVAILABILTY AND LONGLEAF PINE SEEDLING RESPONSE

3.1. Introduction

The plant community within an ecosystem is controlled by many factors, including the regional species pool, dispersal limitations of individual species, disturbance frequency and intensity, interactions among species, and site suitability relative to species' biological requirements (e.g., Gleason 1926, Connell 1978, Vellend 2010). Land managers interested in promoting the establishment of particular species must control or alter several of these factors to ensure the success of the target species. In the southeastern United States, restoration of the longleaf pine (*Pinus palustris* Mill.) ecosystem to upland sites is an important objective shared by many land managers, particularly on lands that support the federally endangered red-cockaded woodpecker (*Picoides borealis*). In many cases, longleaf pines no longer occur as a canopy species in stands targeted for restoration, and therefore artificial regeneration is required for stand establishment. Because longleaf pine seedlings are intolerant to competition for resources (Boyer 1990) successful seedling establishment requires some degree of canopy removal to improve the suitability of the growing site (Palik et al. 1997, Palik et al. 2002, Pecot et al. 2007).

Land managers commonly use silvicultural techniques to manipulate growing conditions for target species or individuals, often through the removal of canopy trees. Canopy removal generally increases the availability of resources (light, nutrients, water) for planted seedlings and other vegetation by eliminating competition from the canopy (e.g. Smith et al. 1997). Light availability at the forest floor is closely related to canopy density because canopy trees are the primary source of light interception within most forest systems (Battaglia et al. 2002). However, increases in ground layer or midstory plants following canopy removal may redistribute the position of light interception. Effects of canopy removal on soil nutrients are more complex; canopy trees provide nutrient inputs through litterfall, uptake nutrients for their own use, and affect microbial activity, litter decomposition, and nutrient release through the moderation of soil moisture and temperature (Marshall 2000, Prescott 2002). Nitrogen is the most commonly studied nutrient of forest systems, and previous studies have reported increases in nitrogen following harvesting (Matson and Vitousek 1981, Attiwill and Adams 1993, Titus et al. 2006). Past research shows differing effects of canopy removal on soil moisture, with increases in soil moisture caused by reduced uptake and transpiration by canopy trees (Elliot et al. 1998, Harrington and Edwards 1999) and decreases in soil moisture associated with drying effects from increased exposure to solar radiation (Redding et al. 2003). Increased solar radiation also commonly results in increased soil temperatures following timber harvest (Londo et al. 1999, Redding et al. 2003, Moroni et al. 2009).

Additional management practices, including vegetation control or fertilization, are commonly used to improve the growing conditions for target species. Following timber harvest, understory vegetation quickly fills root gaps and reduces the availability of belowground resources for planted seedlings (Jones et al. 2003, Pecot et al. 2007).

During longleaf pine restoration, herbicides are often prescribed to reduce the competitive pressure of surrounding vegetation and have been reported to increase the growth response of planted seedlings (Ramsey et al. 2003, Haywood 2005, Jose et al. 2008). However, the mechanisms by which vegetation control results in improved seedling growth are not fully understood. In pine forests, controlling the understory vegetation has been associated with increased soil moisture availability (Zutter et al. 1986, Knapp et al. 2008) and increased nutrient availability (Nambiar and Sands 1993). Depending on the structure of the vegetation, the sub-canopy layers can have a considerable effect on light availability as well, with midstory development resulting in lower light transmittance to the ground layer. Fertilizers are commonly used to alleviate limitations on seedling establishment associated with nutrient deficiencies and have been found to increase the growth of southern pines (Colbert et al. 1990, Jokela et al. 2004). Haywood (2007) found that fertilizer amendments increased levels of phosphorus in the soil and in longleaf pine seedling foliage, although the fertilizer treatment did not increase seedling growth.

Developing prescriptions for longleaf pine restoration on sites dominated by loblolly pine requires an understanding of how management actions affect resource availability and how, in turn, resource availability affects longleaf pine seedling response. Previous studies on longleaf pine seedling response to growing conditions were primarily conducted within existing longleaf pine forests (Palik et al. 1997, McGuire et al. 2001, Pecot et al. 2007), in the absence of canopy trees (Knapp et al. 2008), or in a greenhouse setting (Jose et al. 2003). It is not clear if differences between loblolly and longleaf pines will result in different patterns of resource availability following management actions. This study was designed to quantify the effects of canopy density and management treatments that included herbicide and fertilizer (cultural treatments) on resource availability in relation to longleaf pine seedling response in loblolly pine forests. Our specific objectives are to: 1) determine the effects of canopy density and understory abundance on light availability; 2) determine the effects of canopy density on soil moisture, soil temperature, and longleaf pine foliar nutrients; 3) determine the effects of cultural treatments on light, soil moisture, soil temperature, and foliar nutrients; and 4) determine the effects of canopy density and resource availability on longleaf pine seedling response.

3.2. Materials and methods

Study site and experimental treatments

This study was conducted at Fort Benning, GA and included all six study blocks described in Chapter 1.4, but only the uniform main plots are used in this study. The experiment is a randomized, complete block, split-plot design, with the location of individual loblolly pine stands as the block factor. Each block was divided into four main treatment plots and each main plot received an overstory treatment. Main plots were 100 x 100 m (1 ha), with the exception of the Clearcut plots, which were 141 x 141 m (2 ha) to create clearcut conditions in the plot center. The overstory treatments manipulated the density of canopy pines: Control (uncut; residual basal area ~ 16 m^2/ha); MedBA (single-tree selection to create a uniform canopy with the target basal area of 9 m^2/ha); LowBA (single-tree selection to create a uniform canopy with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha).

Sub-plot treatments include additional cultural practices designed to enhance ecosystem restoration, through either improvement of conditions for planted LLP seedlings or changes to the ground layer vegetation. The sub-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main-plot treatments were each divided into four equal sections for cultural treatment application. Within each section, sub-plot treatments were applied to a 30 x 30 m area centered on a 20 x 20 m measurement plot. The herbicide treatment was designed to improve conditions for planted longleaf pine seedlings by reducing competition from surrounding vegetation. We prescribed a direct spray of 1% imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) plus 0.25% non-ionic surfactant in October 2008 to control woody vegetation. Because herbaceous vegetation dominated most of the study sites, we applied an additional granular mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione]and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009.

Following timber harvest, study sites were prepared in accordance with standard management procedures used for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pine seedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare, by contracted crews. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fire applied between the second and third growing seasons (January – April 2010). Additional information on treatments, treatment application, site preparation, and prescribed burns is described in Chapter 1.5.

Data collection

Longleaf pine seedlings

In each sub-plot, we randomly selected 30 longleaf pine seedlings for growth and survival measurements. We monitored seedling survival among the subsample of seedlings at the end of the first (October 2008), second (October 2009), and third (October 2010) growing seasons. At the time of survival surveys, we measured the root collar diameter of each seedling with digital calipers. Measurements were taken at two perpendicular directions to account for irregularity in the root collar form, and the average of the two measurements was used for calculations. In each sub-plot, the seedling nearest to each corner and nearest to the sub-plot center was selected for resource and competition measurements, for a total of five selected seedlings distributed throughout each sub-plot area.

Overstory and understory competition

We used an Overstory Abundance Index (OAI) to quantify the competitive effects of overstory pines on longleaf pine seedlings in the uniform plots. OAI is expressed as a unitless measure that integrates the distance and size of canopy trees surrounding target individuals and has been reported to capture the competitive effects of canopy pines better than traditional density measures such as basal area (Stoll et al. 1994, Pecot et al. 2007). We calculated OAI with the following formula:

$$OAI = \quad {}_{i=0}^{n} A/d$$

where A = the area of tree$_i$ in cm^2 and d = the distance from the target seedling in cm. Trees closer than one meter were given a value of d = 100 to limit excessive weight placed on trees in close proximity, and we measured all trees within a 15 m radius of each seedling targeted for resource and competition measurements (Palik et al. 2003, Pecot et al. 2007). We also calculated the basal area of trees within a 15 m radius of each target seedling to determine the relationship between OAI and basal area.

We measured the abundance of understory vegetation by recording vegetation cover in circular 1-m^2 sampling quadrats centered on each target seedling (n = 5 per sub-plot). Cover estimates were made as the percentage of the ground covered by a vertical projection of vegetation material. We recorded cover by functional group (graminoids, woody, forbs, ferns, woody vines) using cover classes (1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, and 10 = 95-100%), and total cover for a quadrat could sum to over 100% if vegetation overlapped.

Light

We used hemispherical photographs to quantify light availability in the summer of 2008. Within each sub-plot, we took hemispherical photographs directly above two target seedlings located at the corner closest to main-plot center and the other located diagonally across each sub-plot. We mounted a Nikon Coolpix 4500 digital camera that was equipped with a 180° fisheye lens on a self-leveling mount at a height of 1.4 m. The lens was adjusted to be level with the horizon, and an image of the canopy above each sampling point was captured. To prevent glare and light reflection off foliage, all hemispherical photographs were taken at dawn, dusk, or uniformly cloudy days when the sun was not directly in the image.

To determine effects of ground layer vegetation on light transmittance to longleaf pine seedlings, we quantified photosynthetically active radiation (PAR) at the ground level using an AccuPAR model LP-80 ceptometer (Decagon Devices, Inc.). At each target seedling per sub-plot, we measured PAR 15 cm above the ground directly adjacent to each selected seedling, with care taken to avoid shade provided by the target seedling. We recorded two PAR measurements at each seedling, with readings taken along perpendicular sides of each seedling. Immediately following seedling-level readings, we repeated PAR measurements at 1.4 m above each target seedling to determine the proportion of light that was penetrating the ground layer vegetation to reach the forest floor. Measurements were taken in June 2010 on uniformly cloudless days, and all measurements within a block were taken within a three hour period to reduce variability from the diurnal pattern of the sun.

Soil moisture and temperature

We measured the soil moisture and soil temperature adjacent to the 5 target seedlings in each sub-plot in May and September 2009 and in June, July, and August 2010. Volumetric soil moisture was measured in the upper 6 cm using a ML2 ThetaProbe moisture meter (Delta-T Devices, Ltd.). The ThetaProbe generates a 100 MHz signal between stainless steel rods extended into the soil, and the impedance of the signal between the rods is related to the water content of the soil. We took readings of soil moisture directly east and directly west of each selected seedling. Soil temperature was taken at a depth of 10 cm using a digital thermometer. All soil moisture and temperature measurements within a single block were taken within three hours to minimize the effects of diurnal fluctuations in weather or site conditions, and no measurements were taken within 24 hours of a precipitation event.

Longleaf pine foliar nutrients

To quantify the concentration of foliar nutrients in longleaf pine seedlings, we collected 12 needles (four fascicles) from the five target seedlings per sub-plot in 2009 and 2010. Foliar samples were collected between November and February because nutrient levels are the most stable during the dormant season (van den Driessche 1974). Foliar samples were composited for each sub-plot, placed into paper bags, and stored on ice in a cooler until they were processed in the lab. Upon return to the laboratory, foliar samples were over dried and analyzed for concentrations of N, P, K, Ca, Mg, S, Zn, Cu, Mn, Fe, and Na by the Agricultural Services Laboratory at Clemson University.

Data analysis

We used HemiView version 2.1 Canopy Analysis Software (Delta-T Devices, Ltd) to calculate light availability in each hemispherical photograph. HemiView uses the longitude and latitude for the study site to determine the diurnal and annual sunpath in each image. A user-defined threshold of light intensity classifies each pixel as open sky or sky obstruction, allowing HemiView to calculate gap fraction and the diffuse and direct solar radiation that reaches the photograph location. For each image, we then calculated the Gap Light Index (GLI) or the percentage of incident PAR transmitted to a point in the understory over the course of a growing season (Canham 1988), using the following equation:

$$GLI = [(T_{diffuse} * P_{diffuse}) + (T_{beam} * P_{beam})] * 100$$

where $P_{diffuse}$ and P_{beam} are proportions of incident seasonal PAR reaching the top of the canopy as diffuse and direct radiation, respectively, and $T_{diffuse}$ and T_{beam} are proportions of diffuse and direct radiation reaching the hemispherical photograph. We assume that $P_{diffuse}$ and P_{beam} are equal to 0.5 (Comeau et al. 1998, Gendron et al. 1998, Battaglia 2002). We used the PAR values measured with the ceptometer to calculate the percent light transmittance through the ground layer vegetation at each sampling position. Percent light transmittance was calculated as mean PAR at the ground level divided by mean PAR at 1.4 m (above ground layer vegetation) and converted to a percent. To integrate the interception of available light by canopy trees and the understory vegetation, we multiplied the percentage light penetration the canopy (GLI) by the percentage of light penetrating the understory (PAR) as a measure of total light availability at the seedling level.

We calculated sub-plot level averages of longleaf pine seedling response (root collar diameter and mortality), overstory competition (OAI and basal area), light availability (GLI and PAR), soil moisture, soil temperature, and longleaf pine seedling foliar nutrients for each measurement year. We used split-plot Analysis of Variance (ANOVA) with a random block effect to test effects of canopy density and cultural treatments on resource availability and competition. Effects of study treatments on longleaf pine seedling response have been previously reported (Chapter II). Data were transformed as necessary to satisfy assumptions of normality and constant variance, and degrees of freedom were calculated with the Satterthwaite approximation. We determined differences in least square means using post-hoc pairwise comparisons with Tukey’s Honestly Significant Difference (HSD) adjustment, and differences were considered significant if the probability of making a Type-I error was less than 0.05.

We used scatterplots to determine the type of relationships between independent competition variables (basal area, OAI, understory abundance) and dependent variables of resource availability and growing conditions (GLI, PAR, soil moisture, soil temperature, seedling foliar nutrients) and between independent variables of competition and resource availability (basal area, GLI, PAR, soil moisture, seedling foliar nutrients) and dependent variables of seedling response (mortality and root collar diameter). The appropriate models were fit to describe the data using linear or non-linear regression. For the analyses, we assume that overstory basal area and GLI values are stable for the duration of the study. However, because soil moisture and foliar nutrient concentrations are transient, we used the relative annual RCD growth as the longleaf pine growth response variable to test relationships with these independent variables. Incremental and cumulative mortality were tested with each independent variable in the analyses.

3.3. Results

Overstory and understory competition

The canopy density treatments applied in this study resulted in significantly different levels of residual basal area and OAI, but the canopy competition measures were not affected by the sub-plot treatments (Table 3.1). Although previous research suggests that OAI is a better metric for describing overstory competition than is basal area, we found that basal area explained 98% of the variation in OAI in a nearly one-to-one linear relationship (Figure 3.1). Therefore, only basal area is presented for the remaining results of this study because basal area is a more applicable measurement that is widely understood by land managers. The abundance of understory vegetation was significantly affected by canopy density, and total cover surrounding target seedlings was

Table 3.1. Overstory competition (basal area and OAI) and understory competition (% cover) by treatment; the same letter within a treatment effect indicates no significant difference at α = 0.05

		Basal area (m^2/ha)		OAI		Understory cover (%)	
Treatment	Level	Mean	St. Error	Mean	St. Error	Mean	St. Error
Main-plot	Control	17.50^a	0.67	16.39^a	0.81	20.89^b	3.60
	MedBA	10.06^b	0.76	9.13^b	0.63	36.03^a	1.30
	LowBA	5.51^c	0.76	5.22^c	0.64	38.22^a	5.75
	Clearcut	0.00^d	0.00	0.00^d	0.00	49.42^a	4.90
	p-value	**<0.0001**		**<0.0001**		**0.0003**	
Sub-plot	NT	8.25	0.49	7.72	0.42	44.54^a	2.23
	H	8.48	0.80	8.02	0.71	27.53^b	2.26
	H + F	8.08	0.36	7.32	0.39	36.35^a	4.45
	p-value	**0.8453**		**0.7621**		**<0.0001**	

significantly greater on plots that had been harvested than on the Control plots (Table 3.1). The sub-plot treatments also significantly affected understory vegetation cover, with significantly less cover on herbicide treatment plots than untreated or herbicide + fertilizer plots.

Light

Both measures of light transmittance were significantly affected by canopy density (GLI: $F_{3,\,15} = 393.56$; $p < 0.0001$, PAR: $F_{3,\,15} = 4.89$; $p = 0.0144$), although GLI increased with canopy removal and the percentage of available PAR penetrating the understory decreased with canopy removal (Figure 3.2A). The calculation of total light availability, as an integrated measure of canopy and understory transmittance, was lower

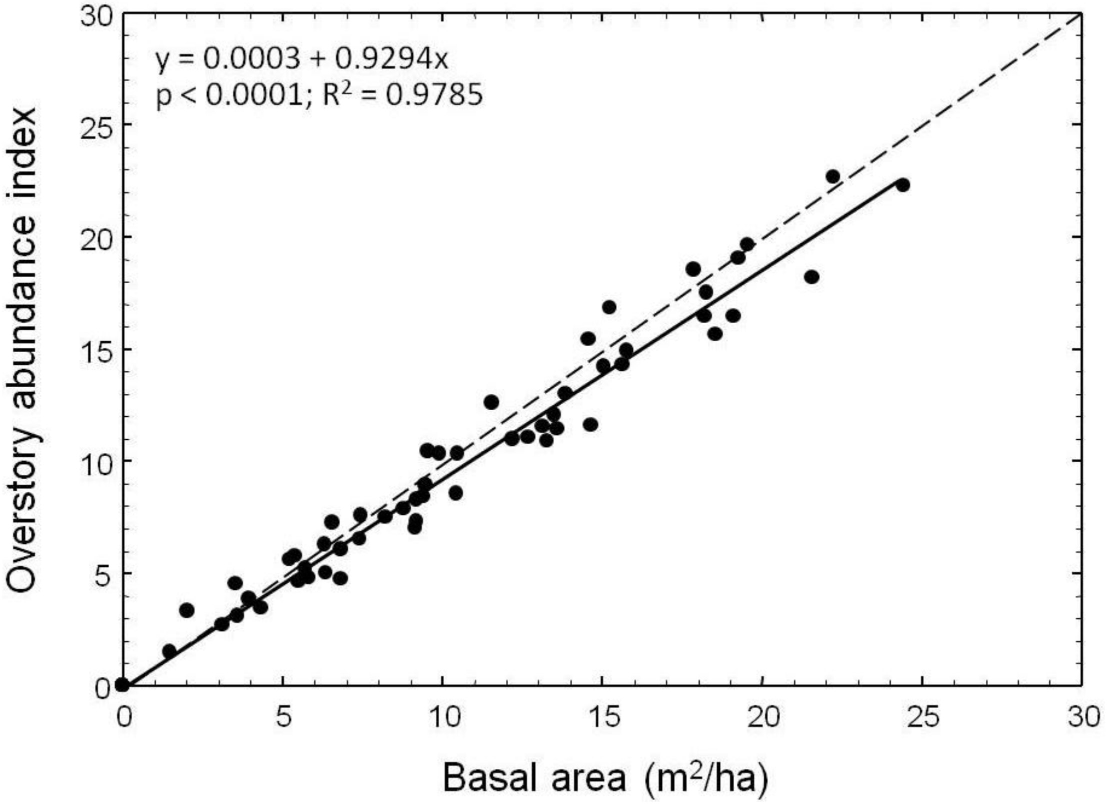

Figure 3.1. Relationship between stand basal area (m^2/ha) and overstory abundance index (OAI). The dotted line represents a one-to-one relationship.

than either individual light index. Total light transmittance to the forest floor increased with harvesting intensity but was moderated by the increase in understory vegetation following release by canopy removal. We found no effect of sub-plot treatments on light transmittance at either the canopy or understory level (Figure 3.2B). Canopy transmittance was strongly related to stand basal area, and a negative exponential relationship accounted for 95% of the variability in GLI (Figure 3.3A). The understory

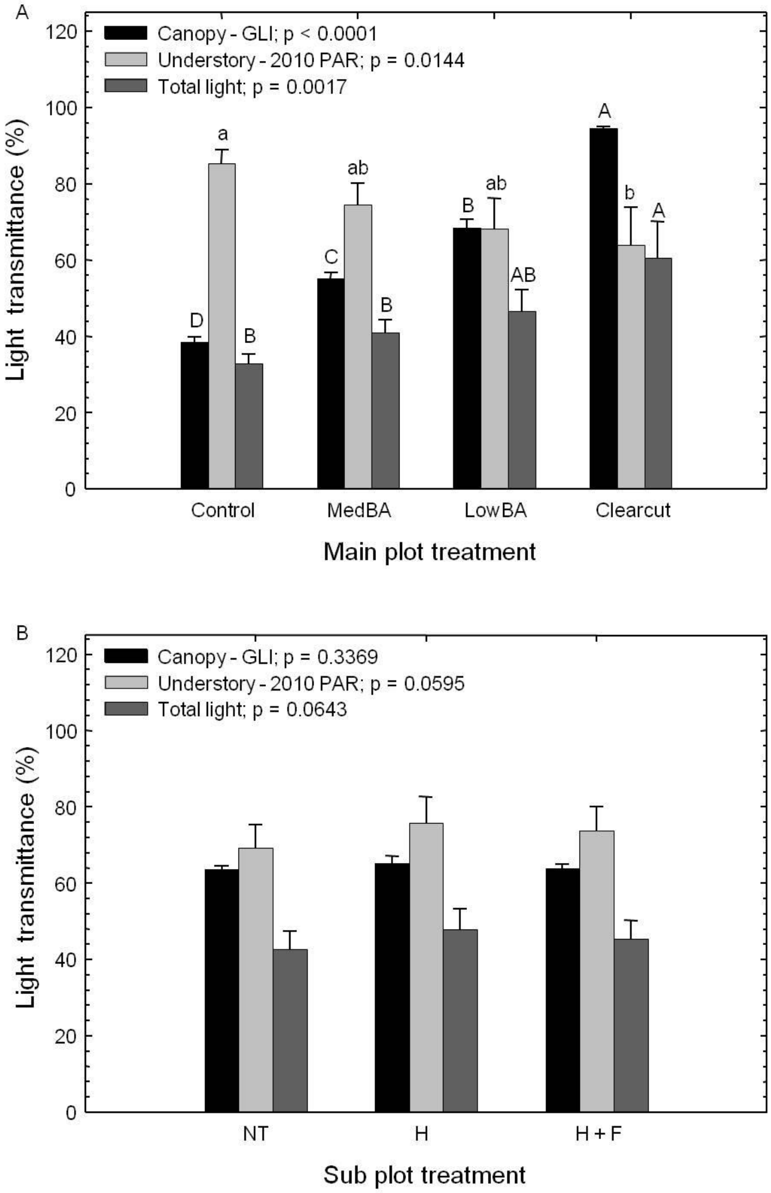

Figure 3.2. Light transmittance (through the canopy (GLI), through the understory (PAR) and the calculated total light transmittance) in 2010 by A) main-plot treatment and B) sub-plot treatment. The same letter within a light variable indicates no significant difference at α = 0.05.

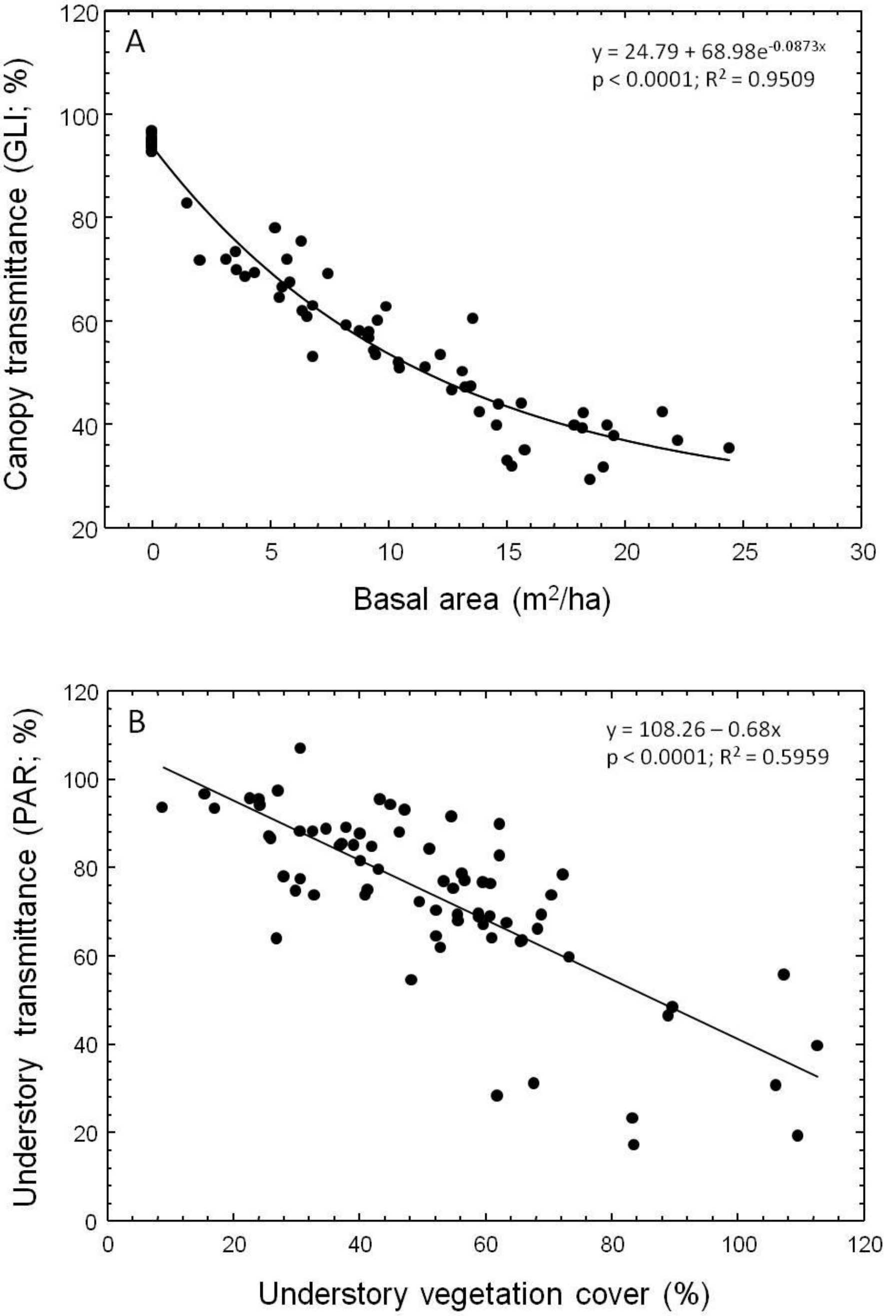

Figure 3.3. Relationship between A) overstory basal area (m^2/ha) and light availability (GLI; %) and B) understory vegetation cover (%) and light availability (PAR; %).

Table 3.2. Soil moisture and soil temperature in 2009 and 2010 by main-plot and sub-plot treatment; superscripts with the same letter indicate no significant difference within a treatment and variable at $\alpha = 0.05$

	2009				2010			
	Volumetric soil moisture (%)		Temperature °C		Volumetric soil moisture (%)		Temperature °C	
Effect	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Control	17.84	1.84	24.26^{b}	1.55	7.08	1.42	31.16^{b}	0.41
MedBA	16.47	3.00	24.56^{ab}	1.50	6.89	1.75	31.87^{ab}	0.55
LowBA	14.10	2.85	25.81^{a}	1.69	5.93	1.83	31.85^{b}	0.45
Clearcut	14.01	2.67	25.62^{a}	1.28	4.65	1.69	33.85^{a}	0.81
p-value	**0.0810**		**0.0078**		**0.3867**		**0.0056**	
NT	15.28	2.59	24.76^{b}	1.44	6.20	1.59	31.98	0.33
H	16.40	2.49	25.28^{a}	1.52	6.01	1.55	32.42	0.49
H+F	15.14	2.32	25.15^{a}	1.53	5.49	1.35	32.28	0.50
p-value	**0.2452**		**0.0053**		**0.4982**		**0.1674**	

cover explained 60% of the variability in understory light transmittance, with less than 50% light transmittance or greater found only with greater than 60% vegetation cover.

Soil moisture and temperature

We found no interactions between main-plot and sub-plot treatments for soil moisture in 2009 ($F_{6, 32} = 0.85$; p = 0.5418) or 2010 ($F_{6, 38} = 0.25$; p = 0.9575) or for soil temperature in 2009 ($F_{6, 32} = 0.81$; p = 0.5677) or 2010 ($F_{6, 36.2} = 1.28$; p = 0.2908). Neither canopy density nor the cultural treatments significantly affected soil moisture in either year, although mean soil moisture slightly increased with increasing basal area in

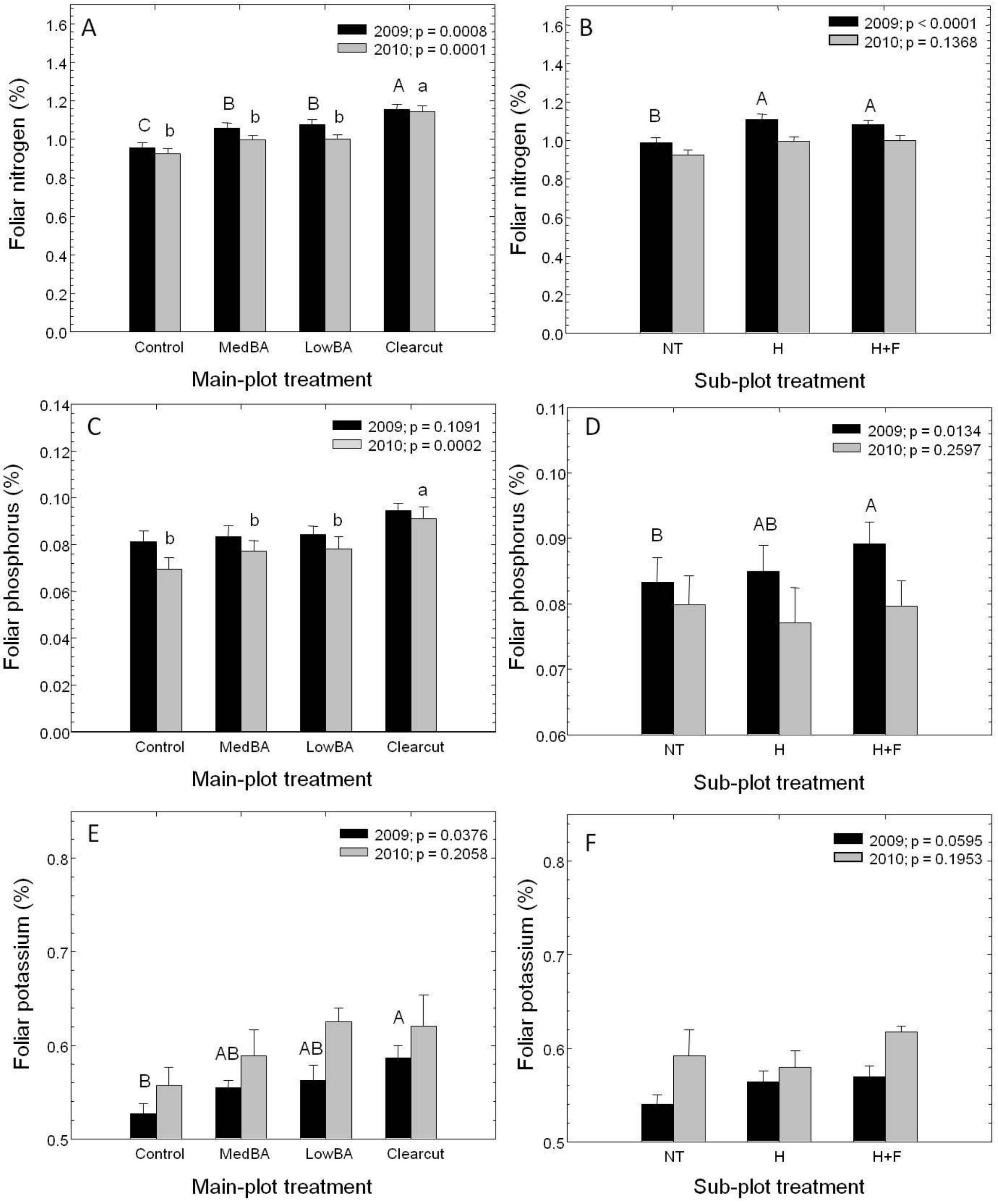

Figure 3.4. Main-plot and sub-plot treatment effects (mean + one SE) on foliar nitrogen (panels A and B), foliar phosphorus (panels C and D) and foliar potassium (panels E and F) in 2009 and 2010. The same letter indicates no significant difference within a year at $\alpha = 0.05$.

each year (Table 3.2). Mean soil moisture across study plots was 15.6% in 2009 and 6.1% in 2010. Soil temperature was significantly affected by canopy density in both years, with soil temperature highest on Clearcut plots and generally lowest on Control plots (Table 3.2). The cultural treatments significantly affected soil temperature only in 2009, when the NT plots had lower soil temperatures than the H and H+F plots.

Longleaf pine seedling foliar nutrients

There were no significant interactions among the main-plot and sub-plot treatments for N, P, of K in either 2009 or 2010 ($p \geq 0.1226$). Foliar nitrogen was significantly greater in Clearcut plots in both years when compared to the treatments with residual canopy density (Figure 3.4A). In 2009, the Control plots had the lowest foliar nitrogen concentration, but Clearcut plots were not different from the MedBA and LowBA plots in 2010. Although phosphorus concentrations were not significantly affected by canopy density in 2009, Clearcut plots had the highest P concentration in 2010, and treatments with residual pines had similar levels of P. Foliar potassium was greater in the Clearcut plots than in the Controls in 2009, but the differences were no longer significant in 2010. The sub-plot treatments only affected foliar nutrients in 2009. Foliar N was higher on the H and H+F plots than on the untreated NT plots, but there was no difference between the H and H+F plots. The H+F plots had higher levels of foliar P than the NT plots, and foliar P on the H plots was not different from either NT or H+F plots. There were no effects of the sub-plot treatments on foliar concentrations of K. Results for the other foliar nutrients analyzed are presented in Appendices A-3.1 and A-3.2.

Relationships between longleaf pine response and growing conditions

In 2008, longleaf pine seedling mortality was negatively related to overstory basal area, with an exponential relationship that explained 45% of the variability in mortality (Figure 3.5A). The mortality that occurred between 2008 and October 2009 was not significantly affected by the overstory basal area (Figure 3.5C), and a marginally significant positive relationship was observed between basal area and the seedling mortality that occurred between October 2009 and October 2010 (Figure 3.5E). In each sampling year, the cumulative root collar diameter was negatively affected by overstory basal area; the relationship only explained 31% of the variability in 2008 but improved to explain 62% of the variability in both 2009 and 2010.

The strong relationship between GLI and overstory basal area (Figure 3.3A) resulted in relationships between GLI and seedling response that were similar to those between overstory basal area and seedling response (Figure 3.6A). The GLI explained 60.2% of the variability in root collar diameter after three growing seasons, with seedling size strongly reduced by GLI levels below 60%. Total light transmittance in 2010, which incorporates effects of canopy and sub-canopy light competition on seedling size, was positively related to root collar diameter and explained 50.2% of the variability (Figure 3.6B).

Average soil moisture in 2009 was significantly, negatively related to relative seedling RCD growth from 2008 to 2009 ($p = 0.0234$), but the relationship only

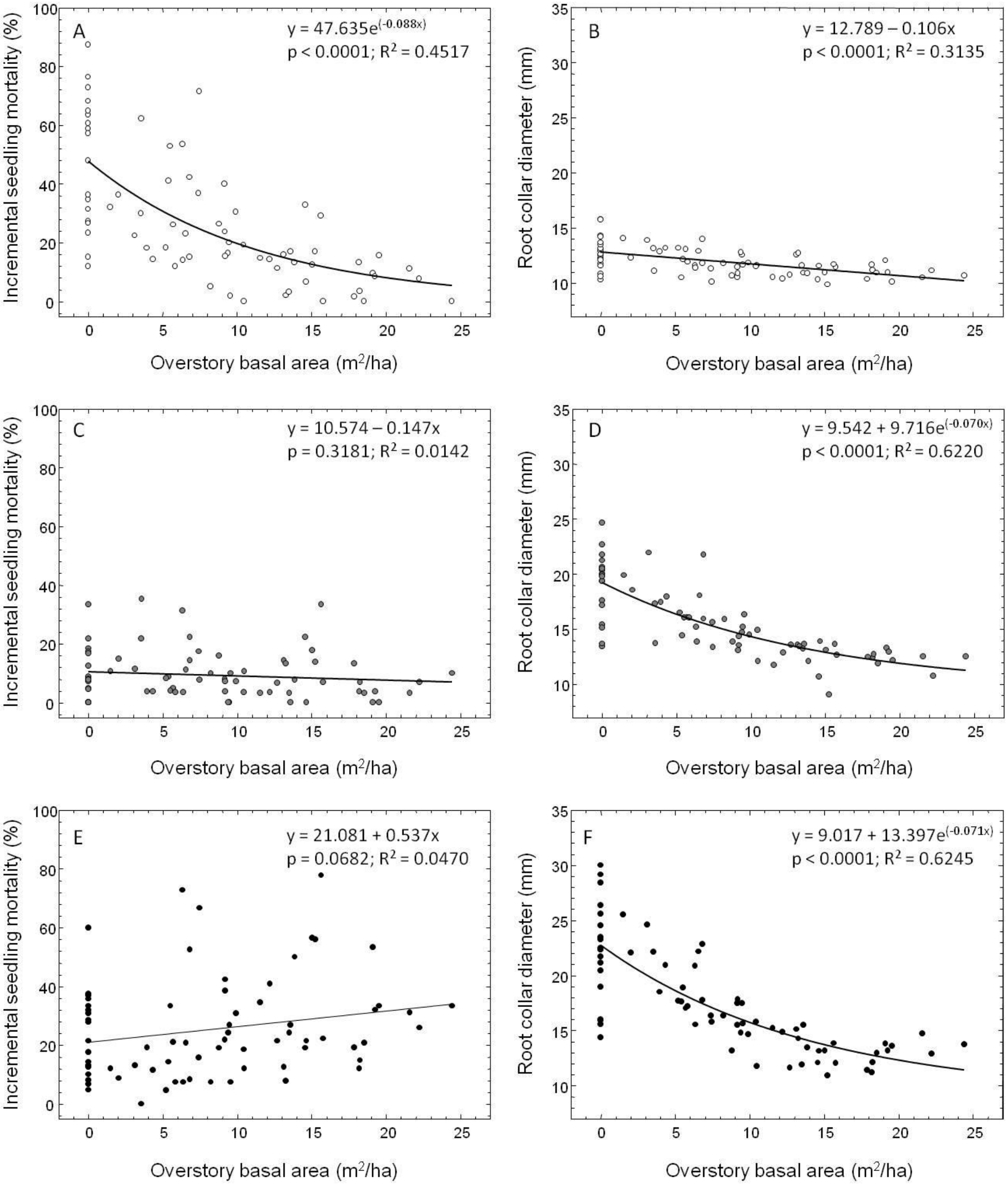

Figure 3.5. Relationships of overstory basal area to longleaf pine seedling mortality (panels A, C, and E) and to root collar diameter (panels B, D, and F) at the end of the 2008, 2009, and 2010 growing seasons.

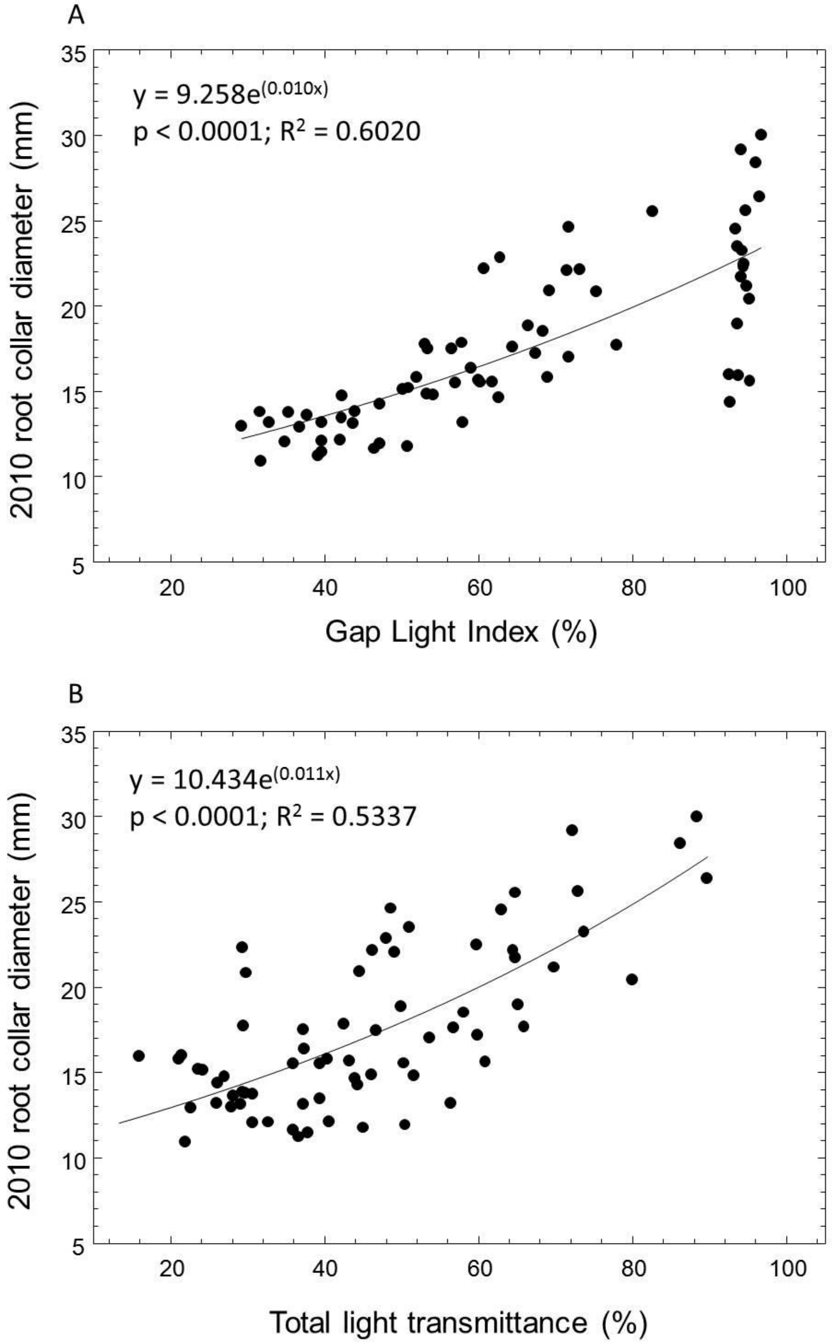

Figure 3.6. The relationships between 2010 root collar diameter and A) canopy transmittance (GLI) and B) total light transmittance based on the integration of GLI and 2010 PAR measurements.

explained 8.8% of the variability in seedling growth (Appendix A-3.3). There was no relationship between 2010 soil moisture and relative RCD growth between 2009 and 2010 ($p = 0.4475$). In both 2009 and 2010, root collar diameter was significantly, negatively related to soil moisture ($p \leq 0.0017$), explaining 27% of the variability in seedling size in 2009 and 13% of the variability in seedling size in 2010. Soil moisture was not related to incremental mortality or cumulative mortality in either year (Appendix A-3.4). The foliar nutrient concentrations for N and K in 2009 were significantly, positively related to relative seedling size in the same year (Figure 3.7). In 2010, there were no significant relationships between foliar nutrient concentrations and relative seedling growth.

3.4. Discussion

Competitive conditions and resource availability

The overstory abundance index has been used in longleaf pine forests (Battaglia et al. 2003, Palik et al. 2003, Pecot et al. 2007) and other forest types (Weiner 1984, Stoll et al. 1994) to quantify the level of competition provided by canopy trees to points in the understory because OAI incorporates both the tree size and distance of canopy trees into measures of competition. Our results suggest that stand-level measures of OAI do not vary from stand-level measures of basal area in uniformly-spaced loblolly pine stands. In naturally regenerated longleaf pine stands in southwestern Georgia, Palik et al. (2003) found that stand-level overstory abundance index was lowest for large aggregate retention harvesting and highest for single-tree selection, despite similar stand-

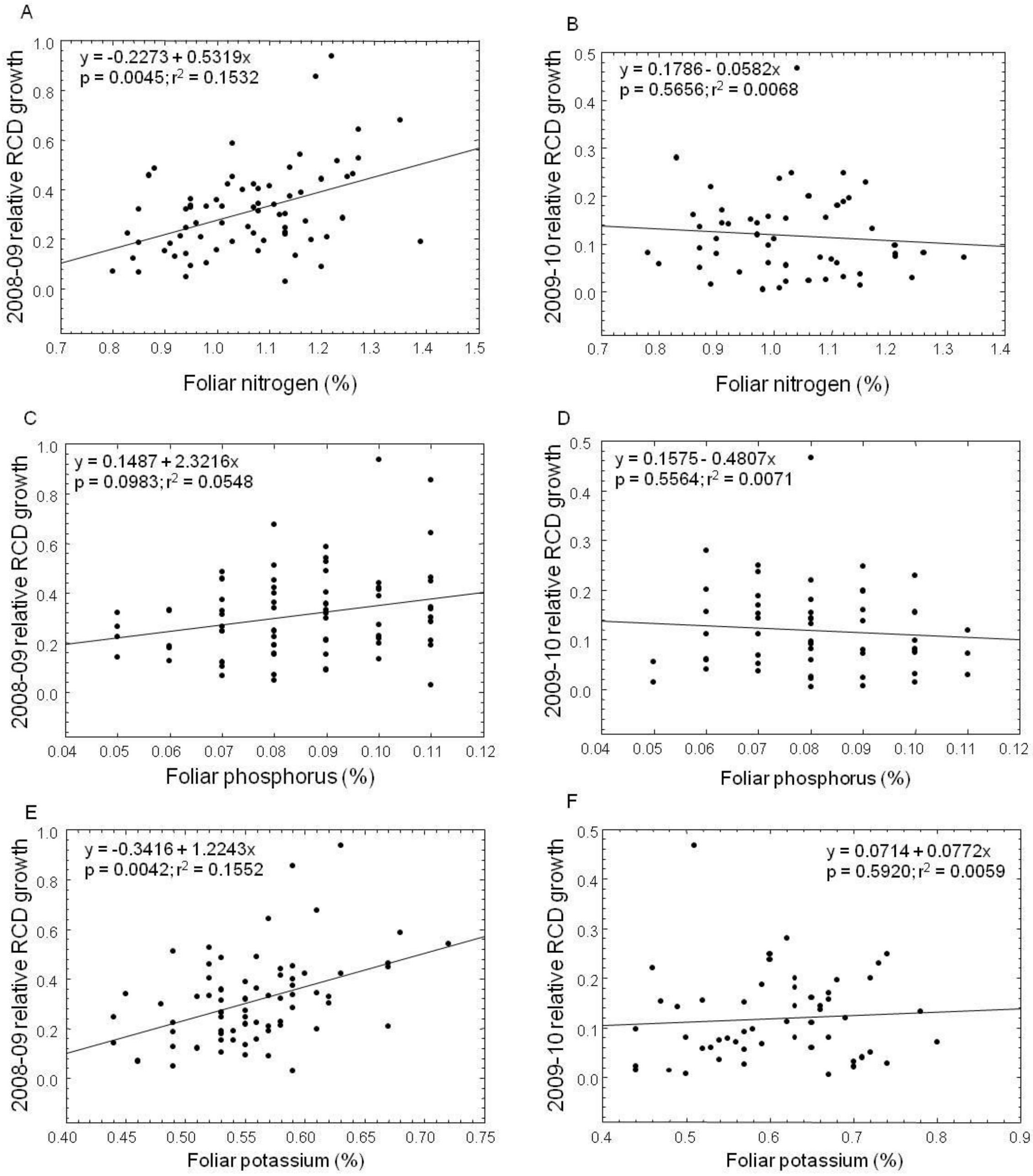

Figure 3.7. Relationships between foliar nutrients (N, P, and K) and relative seedling growth in 2009 and 2010.

level basal areas among the treatments. These findings suggest that incorporating tree size and distance from the sampling point into the OAI measurement is more important for describing the competitive effect of canopy trees as stand heterogeneity increases. We expect this to be true for the spatial heterogeneity in canopy distribution and as the range in the size of canopy trees increases.

Canopy effects on the availability of resources and growing conditions at the ground layer are strongly dependent on the density of canopy trees and on the species-specific morphological and physiological characteristics that define the competitive ability of canopy trees. For example, crown structure, leaf angle, and crown shape influence the transmission of light through a pine forest canopy (Stenberg et al. 1994). The generally open-canopy structure of many pine species results in relatively high levels of light penetration in pine forests compared to other closed canopy forest systems (e.g., Canham et al. 1990), although light availability at the forest floor is strongly regulated by canopy density. Young, densely planted loblolly pine plantations may intercept > 80% of available light (e.g., McCrady and Jokela 1998, Dalla-Tea and Jokela 1991). In contrast, longleaf pine forests have relatively open canopies and high levels of light transmittance (Battaglia et al. 2003). Palik and Pederson (1996) reported that canopy closure in second-growth longleaf pine stands averaged around 50%, and light transmittance remained over 25% beneath closed canopies (Palik et al. 1997). Our results suggest that the relationships between mature second-growth loblolly pine canopy density and canopy light transmission are similar to those in second-growth longleaf pine stands. Palik et al. (1997) found a negative exponential relationship between overstory basal area and light availability ($R^2 = 0.71$) that ranged from around 30% light at 25 m^2/ha to around 80% light at basal area < 5 m^2/ha. Similar relationships were reported between canopy transmittance and OAI in longleaf pine forests by Battaglia et al. (2003) and Pecot et al. (2005) and are expressed in the relationship between basal area and GLI in our study.

Reduced canopy density increases light availability for target species (e.g., planted longleaf pine seedlings) but also increases resource availability for other vegetation and often results in increased abundance of ground layer vegetation (Anderson et al. 1969, Grelen and Enghardt 1973). As a result, the interaction of canopy density and understory vegetation abundance regulates the net availability of resources for ground layer plants. Our results suggest that the greater abundance of ground layer vegetation on Clearcut plots may intercept nearly 40% of the available sunlight before it reaches the forest floor, and Knapp et al. (2008) found that competition for light can limit longleaf pine seedling growth following canopy removal. However, the effect of sub-canopy vegetation on light at the forest floor is dependent on the type of vegetation present and may change from year to year. Woody vegetation that puts on secondary growth and increases in stature each year decreases light levels over time; as a result, the presence of woody sub-canopy species can shade out low growing species that require high light levels (Brockway and Lewis 1997, Rogers and Provencher 1999, Lhotka and Lowenstein 2009). In contrast, herbaceous vegetation generally follows annual cycles of growth and die-back, with less potential for the interception of light to increase over time. Therefore, the role of canopy trees in controlling light levels at the forest floor is attenuated by the type and abundance of vegetation in the ground layer.

Soil moisture measurements reflect the combined effect of canopy and sub-canopy vegetation on water availability in the soil. Canopy removal may affect soil moisture through two primary processes: 1) a reduction in soil moisture associated with drying of the soil following increased exposure to solar radiation (Londo et al. 1999, Redding et al. 2003, Moroni et al. 2009); and 2) an increase in soil moisture in the absence of uptake and transpirational loss by canopy trees (Aussenac and Granier 1988, Breda et al. 1995, Elliot et al. 1998). However, ground layer plants quickly fill canopy gaps created by overstory removal (Jones et al. 2003) and provide an additional source of uptake of soil moisture. The distribution of root systems of ground layer plants within the soil profile varies by functional group; root systems of herbaceous plants are commonly concentrated at the soil surface, but woody plants are able to develop root systems deeper in the soil profile (Walter 1971). Therefore, the dynamics of overstory-understory interactions with soil moisture vary according to vegetation type and location within the soil profile (Knoop and Walker 1985, Pecot et al. 2007). We found no effect of canopy density on soil moisture at a depth of 6 cm, where competition with herbaceous vegetation is expected to be high, despite a slight pattern of increasing moisture with canopy density in both years. This pattern was associated with soil temperatures that increased with canopy removal, suggesting that the shade of canopy pines moderates soil heating and may affect the drying of the soil surface. However, we also found no effect of herbicide release on soil moisture, suggesting that competition from ground layer species, and herbaceous plants in particular, did not strongly affect soil moisture on these sites. It is not clear if patterns of soil moisture would differ at greater depths in the soil profile.

The competitive interactions of overstory and understory plants also affect nutrient availability in complex ways, and we quantified nutrient availability to longleaf pine seedlings through direct foliar nutrient analyses rather than quantification of soil nutrients. Previous studies have shown that overstory density is negatively related to the availability of nitrogen in the soil in the absence of understory competition in longleaf pine forests (Palik et al. 1997, Pecot et al. 2007) and that the presence of understory vegetation reduces nitrogen availability regardless of overstory density (Pecot et al. 2007). Our results indicate that canopy density negatively affected the concentration of foliar N in both years and negatively affected P and K in only one year. It is likely that competition from understory plants reduced foliar concentrations of N as well because the herbicide release treatment increased foliar N. In contrast, Haywood (2007) found that releasing longleaf pine seedling from competing vegetation did not significantly increase foliar N concentrations through six growing seasons. Previous studies have shown that foliar nutrients generally increase in response to fertilizer application for other southern pines (e.g., Valentine and Allen 1990, Murthy et al. 1996, Zhang and Allen 1996), but we found that the H+F treatment resulted in the increase of only P in the first year following application. Similarly, Haywood (2007) found that fertilizer application increased the foliar P concentration in two study sites in Louisiana. Blevins et al. (1996) list “sufficient” levels for longleaf pine foliar N, P, and K at 0.95, 0.08, and 0.30%, respectively, suggesting that retaining high levels of overstory density in loblolly pine stands will likely result in nutrient deficiencies of N and P for planted longleaf pine seedlings.

Longleaf pine seedling response

Canopy trees showed both facilitation and competition effects on longleaf pine seedlings. Seedling mortality in the first year after planting was negatively related to overstory density, suggesting that overstory retention may ameliorate harsh conditions of the growing site (Allen et al. 1954, McGuire et al. 2001, Rodriguez-Trejo et al. 2003, Gagnon et al. 2003). However, the relationship between longleaf pine seedling mortality and canopy density changed over time, with no significant canopy effect on mortality occurring between 2008 and 2009 but a marginally significant, positive effect of canopy density on seedling mortality between 2009 and 2010. These results suggest that the facilitation effect of canopy pines was transient and may have been associated with the specific weather patterns during 2008. For example, precipitation early in the first growing season (March – June 2008) was well below the 50-year average (343 vs. 442 mm, respectively). Mortality of out-planted plugs is often highest during the first year after planting (Boyer 1988, Knapp et al. 2006), and the facilitation effect of the canopy trees may have been most important during this establishment period.

In longleaf pine forests, the relationship between seedling size and canopy density is described by a negative exponential function in which seedling size is strongly reduced by canopy densities greater than 8 m^2/ha (Palik et al. 1997). Patterns of longleaf pine regeneration fit into a three-stage model of canopy density thresholds (Kirkman and Mitchell 2006, Mitchell et al. 2006). At high canopy densities (~17 m^2/ha) seedling establishment may occur, but survival through 5 years is not expected and regeneration is inhibited. Seedling are able to persist with moderate growth beneath stands with basal areas between 8 and 17 m^2/ha; however, grass stage emergence and subsequent height growth accelerates when basal area is less than ~ 8 m^2/ha (Mitchell et al. 2006). Our results generally support this model for longleaf pine seedling establishment in loblolly pine stands. Although we found that survival remained relatively high for seedlings beneath high canopy densities through three growing seasons, it is not clear how long seedlings will persist given the lack of seedling growth at high densities. Similar to the results from longleaf pine forests, we observed moderate increases in seedling growth between canopy densities of around 7 and 14 m^2/ha, with accelerated seedling growth with less than 7 m^2/ha basal area.

Interestingly, the clearcut plots in our study resulted in a large range in seedling sizes, suggesting that other factors are affecting seedling size in the absence of canopy competition. In clearcuts, canopy transmittance (GLI) was over 90% for each sub-plot, but seedling root collar diameters ranged from less than 15 to over 30 mm on plots with over 90% GLI. Such a wide range in seedling size was not observed at other levels of GLI, suggesting that canopy transmittance alone is not a good predictor of seedling size in clearcut plots (Figure 3.6). The abundance of ground layer vegetation was highest on the clearcut plots, resulting in high interception of light by the sub-canopy vegetation. The net competitive pressure experienced by longleaf pine seedlings is a combination of overstory and understory effects, and it is possible that competition for light by abundant ground layer vegetation contributed to the variability in seedling size in clearcuts. This result is supported by the relationship between total light reaching the understory and root collar diameter in 2010, which indicates that light availability in clearcut plots was lower than suggested by GLI.

Previous research suggests that the availability of below-ground resources regulates longleaf pine seedling establishment (Brockway and Outcalt 1998), and soil nitrogen has been found to be more closely related to longleaf pine seedling growth than soil moisture in field studies (Palik et al. 1997, McGuire et al. 2001). We found no evidence that soil water availability limited the growth or survival of longleaf pine seedlings in our study; in fact, we observed a negative relationship between soil moisture and seedling size. Knapp et al. (2008) reported that longleaf pine seedling size was negatively related to soil moisture after two growing seasons on wet flatwoods sites, where volumetric soil moisture ranged from around 10 to 40%. Our sites were considerably drier, ranging from 5 to 25% moisture by volume, and it is not clear if the observed relationship was due to direct effects of soil moisture on seedling growth or interactions between soil moisture and understory or overstory density. In contrast to soil moisture, we found that foliar N and K in 2009 were positively related to relative seedling growth, each accounting for 15% of the variability in growth during that year. It is often difficult to decouple the relationships of cause and effect between seedling size and nitrogen content. For example, large plants are often more competitive at acquiring resources (e.g., Schwinning and Weiner 1998), suggesting that nutrient levels may be dependent on seedling size; on the other hand, high nutrient levels, particularly nitrogen, are linked to increased photosynthesis and productivity (e.g., Evans 1989). However, the relationships among competitive pressure, foliar nutrients, and seedling response suggest that competition for N and P play an important role in controlling early longleaf pine seedling growth.

3.5. Conclusion

The presence of canopy pines regulates the growing conditions and distribution of resources at the ground level in forest ecosystems, and net resource availability for target plants is the result of interactions between overstory and understory plants. For example, although canopy transmittance was strongly related to overstory basal area, the total amount of light that was available at the forest floor was reduced by the increase of understory plants following canopy removal. Soil moisture at a 6 cm depth was not affected by canopy density or understory removal with herbicide, although canopy removal likely affected the magnitude of water uptake by plants and the patterns of evaporation from the soil. At the same time, the presence of canopy trees and understory plants reduced soil temperature. We quantified nutrient status through direct measures of foliar nutrient concentrations of longleaf pine seedlings and found that canopy removal increased foliar concentrations of N, P, and K. Understory removal also increased the availability of N, and fertilization increased the availability of P.

Recent interest in alternative silvicultural techniques for longleaf pine restoration suggest that canopy gaps or single-tree selection may be appropriate for seedling establishment in longleaf pine forests (McGuire et al. 2001, Pecot et al. 2007). Developing silvicultural protocols for restoration in loblolly pine stands requires an understanding of how stand conditions and resource availability affects seedling response, and we found that relationships between seedling size and overstory density in loblolly pine forests were similar to those previously published in longleaf pine forests. Given the interactions between competitive sources and the correlations among competitive pressures and resource availability, it is often difficult to isolate the effects of specific resources on seedling response under field conditions. Jose et al. (2003) found that interactions among resource limitations affect the relationships between longleaf pine seedling growth and resource availability. Despite these challenges, our results indicate that the availability of light strongly limits longleaf pine seedling growth in loblolly pine stands. Nitrogen and potassium limitations affected seedling growth to a lesser degree, but we found no evidence of water limitations to seedling growth. Establishing longleaf pine in loblolly pine stands can best be accomplished by reducing canopy density to ≤ 9 m^2/ha, although complete canopy removal will likely result in increased mortality and competition from understory vegetation.

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CHAPTER IV: CANOPY GAP SIZE AND WITHIN-GAP POSITION CONTROL GROWING CONDITIONS AND RESOURCE LIMITATIONS TO LONGLEAF PINE ESTABLISHMENT IN SOUTHERN PINE FORESTS

4.1. Introduction

Disturbance events are critical to the development and regeneration of forested ecosystems worldwide (Attiwill 1994), and the creation of canopy gaps following the mortality of canopy trees has been widely studied for its importance to ecological function in boreal (e.g., Dai 1996, Kneeshaw and Bergeron 1998, Hill et al. 2005), temperate (e.g., Busing and White 1997, Gray and Spies 1997, Coates 2000), and tropical (e.g., Lang and Knight 1983, Brokaw 1985, Denslow 1987) forest types. Canopy openings result in changes in the distribution of plant resources both spatially (Canham et al. 1990, Gray et al. 2002) and temporally (Poulson and Platt 1989). The growing conditions in canopy openings often favor species that differ from the species found beneath intact canopies, with an increase in shade-intolerant pioneer species within canopy openings (Whitmore 1989). Effects of gap size and within-gap position on growing conditions (e.g., micro-climate) have been demonstrated in a variety of habitats but often differ based on latitude, canopy density, and the tree height to gap size ratio (Runkle 1989, Canham et al. 1990, Yamamoto 2000, Gendreau-Berthiaume and Kneeshaw 2009). The spatial variation in resource availability and growing conditions allows different species to occur across canopy gaps and has been hypothesized to maintain species richness at large scales (Denslow 1980).

In longleaf pine (*Pinus palustris* Mill.) forests of the southeastern United States, canopy openings are important for regenerating the canopy species (Palik and Pederson 1996, Gilliam et al. 2006, Outcalt 2008). Observational studies report that natural regeneration of longleaf pine is often concentrated in canopy openings or locations with low canopy densities (Platt et al. 1988, Gagnon et al. 2004). Grace and Platt (1995b) found that overstory pines affected the survival of seedlings within distances of 18 m, and Brockway and Outcalt (1998) found a lack of longleaf pine regeneration within 12-16 m of canopy trees. However, other studies observed longleaf pine regeneration within 5 m of canopy trees, suggesting that patterns of longleaf pine establishment in canopy gaps may be related to persistence and growth rather than initial establishment (Pecot et al. 2007). Generally, two hypotheses have been proposed to explain gap-phase regeneration in longleaf pine ecosystems. In the first, what we refer to as the 'Fire Effects Hypothesis', the accumulation of fuels (pine litter) beneath canopies increases fire intensity (Williamson and Black 1981, Rebertus et al. 1989) and consequently increases seedling mortality (Boyer 1974, Platt et al. 1988, Grace and Platt 1995a, Brockway and Outcalt 1998, Jack et al. 2010). The second hypothesis, the 'Competition Hypothesis', relates competition from canopy trees to the observed patterns in longleaf pine regeneration, with increased competition from adult neighbors limiting seedling establishment and growth. Numerous studies have demonstrated that canopy pines limit the growth of longleaf pine seedlings (Palik et al. 1997, McGuire et al. 2001, Kirkman and Mitchell 2006, Chapters 2 and 3), but the distribution of resources within canopy gaps, and consequently the mechanisms controlling longleaf pine seedling response, have been debated (see Brockway and Outcalt 1998, McGuire et al. 2001, Pecot et al. 2007).

The longleaf pine ecosystem is considered to be among the most imperiled ecosystems in North America (Noss et al. 1995), and much of the current forested land within the historical range has been converted to other pine species such as loblolly pine (*Pinus taeda* L.) (Frost 2006). With a frequent surface fire regime, the longleaf pine ecosystem maintains an open stand structure that includes a highly diverse, herbaceous ground layer plant community (Walker and Peet 1983, Peet 2006) and supports several endangered faunal species (Van Lear et al. 2005). Interest in conserving biodiversity is currently high, and the conservation and restoration of the longleaf pine ecosystem is a major management objective of southeastern land managers. To maintain ecological function (e.g., frequent surface fire) and to conserve biodiversity, restoration of longleaf pine in stands occupied by other southern pines may require gradual conversion with canopy retention (Kirkman et al. 2007). Recent research suggests that canopy gaps as small as 0.1 ha result in increased seedling growth and may be appropriate for longleaf pine restoration (McGuire et al. 2001, Pecot et al. 2007, Chapter 2). Although past research has examined resource availability within canopy gaps in longleaf pine forests, it is not known if patterns will differ for longleaf pine seedlings planted in loblolly pine forests.

This study was established to determine the distribution of plant resources, growing conditions, and surface fuels and fire effects within experimentally created canopy gaps in loblolly pine forests targeted for restoration to longleaf pine. We used direct measurements of planted longleaf pine seedlings to determine effects of resource availability on resource limitation in plants. Our results will contribute to an understanding of the mechanisms controlling longleaf pine seedling establishment within canopy gaps in relation to the two hypotheses proposed in past research. Specifically, our objectives are to determine: 1) the effects of canopy gap size and within-gap position on microsite growing conditions (light, soil moisture, soil temperature, ground layer vegetation abundance, nitrogen availability); 2) the effects of within-gap position on direct measures of below-ground resource limitations for longleaf pine seedlings (xylem water potential and foliar nutrients); 3) relationships between below-ground resource availability and direct measures of resource limitations in longleaf pine seedling; and 4) effects of canopy gap size and within-gap position on fuels and fire effects on longleaf pine seedlings. Our study differs from previous work on longleaf pine regeneration in two important ways: 1) we measure artificially regenerated seedlings, so factors affecting germination and initial establishment are not assessed (compare to Grace and Platt 1995a, Brockway and Outcalt 1998, Gagnon et al. 2004); and 2) our study was established in a restoration context in existing loblolly pine stands, in contrast to previous gap studies in longleaf pine forests (e.g., Palik et al. 1997, McGuire et al. 2001, Gagnon et al. 2003, Pecot et al. 2007). Moreover, we attempt to get a more complete understanding of resource distribution and limitations to seedling establishment than previous studies by simultaneously quantifying multiple variables of resource availability and direct measures of seedling water or nutrient status.

4.2. Materials and methods

This study was conducted at Fort Benning, GA and included only the gap plots in all six study blocks. In each block, we used harvesting to create three canopy gap treatments that differed in size: SG (small gap, with a diameter of 40 m and total area of around 0.12 ha); MG (medium gap, with a diameter of 60 m and total area of around 0.25 ha); and LG (large gap, with a diameter of 80 m and total area of around 0.50 ha). Average tree height across the study blocks was 20.9 m, making the gap diameter to tree height ratio 2, 3, and 4 for SG, MG, and LG, respectively. Gaps were established by harvesting every tree with the center of its bole within the given radius from gap center, making the area of the gap defined as the 'extended gap' by Schliemman and Bockheim (2011). A matrix of uniform residual trees ≥ 30 m was maintained around each canopy gap.

Timber harvest was completed by the end of the summer of 2007 and was followed by site preparation in accordance with standard management procedures used for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1*H*-imidazol-2-yl]-3-pyridinecarboxylic acid) mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted in north/south rows with container-grown longleaf pine seedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare, by contracted crews. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fire applied between the second and third growing seasons (January – April 2010). Additional information on treatments, treatment application, site preparation, and prescribed burns is described in Chapter 1.5.

Data collection

We quantified resource availability across the north/south axis running through the center of each canopy gap to determine the effect of within-gap position on resources. The north/south axis was selected because the gradient of solar exposure is expected to be greatest along this axis. We established sampling points at 10 m intervals across each gap, extending 10 m into the forest on either side, with sampling points at gap center, each forest edge, and every 10 m in between. The number of sampling points depended on gap size, with 11 sampling points in LG plots, 9 sampling points in MG plots, and 7 sampling points in SG plots.

Light

In 2008, we used hemispherical photographs to quantify the amount of light at 1.4 m above the ground at each sampling point established in all study gaps. Hemispherical photographs use geographic information to calculate direct, diffuse, and total light levels that reach a given point throughout the year, and hemispherical photographs have been found to be an accurate assessment of light availability (Canham 1988, Comeau et al. 1998, Battaglia et al. 2003). At each sampling point, we mounted a Nikon Coolpix 4500 digital camera that was equipped with a 180° fisheye lens on a self-leveling mount at a height of 1.4 m. The lens was adjusted to be level with the horizon, and an image of the canopy above each sampling point was captured. To prevent glare and light reflection off foliage, all hemispherical photographs were taken at dawn, dusk, or uniformly cloudy days when the sun was not directly in the image.

To determine the effects of ground layer vegetation on light transmittance to the forest floor, we quantified photosynthetically active radiation (PAR) at the ground level using an AccuPAR model LP-80 ceptometer (Decagon Devices, Inc., Cambridge, UK). The ceptometer records PAR reaching a series of sensors located along a 1 m wand and calculates the mean PAR value. At each sampling point, we measured PAR 15 cm above the ground with the wand positioned at two perpendicular positions. Immediately following ground-level readings, we repeated PAR measurements at 1.4 m above the ground and then calculated the proportion of light that was penetrating the ground layer vegetation to reach the forest floor.

Ground layer vegetation

One transect was established along the north/south axis of each gap, extending 10 m into the forest on either end. Along the transect, we established twenty 1-m^2 sampling quadrats that were evenly spaced across the gap from the southern forest edge to the northern forest edge. The distance between sampling quadrats differed based on gap size, with 1 m between quadrats in SG, 2 m between quadrats in MG, and 3 m between quadrats in LG plots. At each 1-m^2 sampling quadrat, we recorded ocular estimates of percent cover for all vegetation < 1 m tall that occurred within or overlapped the quadrat in August 2009 and 2010. We estimated cover as the percentage of the plot that would be shaded if the sun was positioned directly overhead. Cover was recorded using the following cover classes: 1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, and 10 = 95-100%, and total cover for a quadrat could sum to over 100% if vegetation overlapped. We estimated cover by functional group (graminoids, ferns, forbs, woody shrubs/trees, and woody vines) and calculated total cover from the functional group data.

Soil temperature and soil moisture availability

We measured soil temperature and soil moisture at each sampling point along the north/south transect across each gap, extending 20 m into the forest on each end. At each location, soil temperature at a depth of 10 cm was measured with a Traceable® digital thermometer (Control Company, Friendswood, TX), and volumetric soil moisture was measured in the upper 6 cm of the soil using a ML2 ThetaProbe moisture meter (Delta-T Devices, Ltd., Cambridge, UK). The ThetaProbe generates a 100 MHz signal between stainless steel rods extended into the soil, and impedance of the signal between the rods is related to the water content of the soil. Soil moisture readings were taken in May and September 2009 and June and July 2010. Soil temperature readings were taken in June, July, and August 2010. In each LG plot, we used a PR2 Profile Probe (Delta-T Devices, Ltd., Cambridge, UK) to measure volumetric soil moisture at depths of 10, 20, 30, 40, 60, and 100 cm. At each 10 m sampling interval we installed a thin-walled fiberglass access tube into which the Profile Probe was inserted for measurement. The Profile Probe generates a 100 MHz signal that is applied to two stainless steel rings at each soil depth, and the stainless steel rings transmit an electromagnetic field that enters the soil around the access tube. The permittivity of the soil is determined by the water content, and an output reading of voltage is converted to volumetric soil moisture through a calibrated equation. Profile soil moisture was only measured within the large gaps, and no readings were recorded at a depth of 100 cm in the soil in 2010 due to problems with the equipment. Profile moisture readings were recorded in May and September 2009 and July, August, and September 2010. All soil temperature and soil moisture readings within a block were recorded within a two hour period to maintain consistent ambient conditions, and no readings were recorded within 24 hours of a precipitation event.

To directly quantify soil moisture availability for plants, we measured pre-dawn xylem water potential of longleaf pine seedlings in LG plots in July and September 2008, May, July, and September 2009, and July and September 2010. We first marked all seedling located within a 4 m wide belt running perpendicular to each sampling point along the north/south axis (2 m to the north and 2 m to the south of each sampling point), and seedlings within 15 m of the eastern or western gap edge were not included for sampling. During each sampling period, we removed one current-year fascicle from two randomly selected seedlings at each position, and individual seedlings were measured no more than once per year to minimize the impacts of tissue removal on seedling response. The foliar tissues were cleanly cut with a razor blade and needles were immediately loaded into a pressure chamber for water potential analysis (PMS Instruments, Corvallis, OR). All xylem water potential measurements were taken prior to sunrise, because tissue moisture is most strongly related to soil moisture conditions before light-dependent physiological processes are initiated. At the same time of xylem water potential measurements, we measured volumetric soil moisture in the upper 6 cm of soil with a ML2 ThetaProbe moisture meter.

Nitrogen availability

We used ion exchange resins (IER) to quantify available nitrogen at different positions within each large gap. The IER technique was developed by Binkley and Matson (1983) and is an effective method for measuring ammonium (NH_4^+) and nitrate (NO_3^-) that moves through the soil and is thus available to plants (Binkley 1984, Binkley et al. 1986). Each IER bag was prepared by mixing 10 g of IONAC C-249 cation (Sybron Chemicals, Inc.) and 10 g IONAC ASB-1P OH anion (Sybron Chemicals, Inc.) in a 5 x 5 cm nylon bag. Nylon bags were created from stocking material, and the edges of the nylon bags were sealed with a heat sealer to prohibit stretching and to maintain size and shape.

In each LG plot, we sampled available soil nitrogen at specific positions on both the north and south half of gaps: gap center (40 meters from forest edge), halfway between gap center and the forest edge (20 m from the forest edge), at the forest edge (0 m from the forest edge) and 10 m into the forest interior (-10 m from the forest edge). At each position, we sub-sampled soil N in three locations: along the central transect, approximately 10 m east of center, and approximately 10 m west of center. In July 2010, we buried one IER bag 5 cm below the soil surface at each sampling point. Care was taken to minimize impacts to the soil surface during installation. Resin bags were removed in October, after field incubation for 92 days. Following removal, IER bags were immediately placed in a cooler for transport to the laboratory and kept in cold storage until extraction. During extraction, each IER bag was placed in 100 ml of 2M KCl and placed on a shaker for 24 hours. The resulting solution was filtered through ashless filter paper and analyzed colorimetrically using a Lachat Auto-Analyzer (Lachat Instruments) by the USDA Forest Service Rocky Mountain Research Station water lab in Fort Collins, CO.

To quantify the concentration of foliar nitrogen in longleaf pine seedlings, we collected needles from at least five seedlings per position used for IER samples in LG plots in 2010. Seedlings that fell within the 4 m wide belt used for sampling xylem water potential were used for foliar sampling. Foliar samples were collected between November and February because nutrient levels are the most stable during the dormant season (van den Driessche 1974). All foliar samples were placed into paper bags and stored on ice in a cooler until processing. Upon return to the laboratory, foliar samples were oven dried at 70 °C and analyzed for concentrations of nitrogen by the Agricultural Services Laboratory at Clemson University.

Fuels and fire effects

We used data from the 2009 vegetation sampling to describe the standing fuels. In addition to vegetation cover, we estimated the cover of fallen pine needles in each 1 m^2 sampling quadrat. To determine the effects of fuel loading and fire effects on longleaf pine seedling mortality, we surveyed mortality of all seedlings planted along four rows oriented north/south across each gap. Rows were approximately 10 m apart and were systematically located from the center of each gap. We recorded seedling mortality at the end of the first growing season (October 2008), at the end of the second growing season

(October 2009), and following the prescribed fire (May 2010). Although we did not have an unburned treatment and therefore cannot determine if the prescribed fire caused patterns of seedling mortality, we assume that mortality in the dormant season (between October and May) was associated with the prescribed fire. We also use data from the previous year (with no prescribed fire) as a comparison of seedling mortality during a year without fire.

Data analysis

We used HemiView version 2.1 Canopy Analysis Software (Delta-T Devices, Ltd., Cambridge, UK) to calculate light availability for each hemispherical photograph. HemiView uses the longitude and latitude for the study site to determine the diurnal and annual sunpath in each image. A user-defined threshold of light intensity classifies each pixel as open sky or sky obstruction, allowing HemiView to calculate gap fraction and the diffuse and direct solar radiation that reaches the photograph location. For each image, we then calculated the Gap Light Index (GLI) or the percentage of incident PAR transmitted to a point in the understory over the course of a growing season (Canham 1988), using the following equation:

$$GLI = [(T_{diffuse} * P_{diffuse}) + (T_{beam} * P_{beam})] * 100$$

where $P_{diffuse}$ and P_{beam} are proportions of incident seasonal PAR reaching the top of the canopy as diffuse and direct radiation, respectively, and $T_{diffuse}$ and T_{beam} are proportions of diffuse and direct radiation reaching the hemispherical photograph. We assume that $P_{diffuse}$ and P_{beam} are equal to 0.5 (Comeau et al. 1998, Gendron et al. 1998, Battaglia 2002).

We used the PAR values measured with the ceptometer to calculate the percent light transmittance through the ground layer vegetation at each sampling position. Percent light transmittance was calculated as mean PAR at the ground level divided by mean PAR at 1.4 m (above ground layer vegetation) and converted to a percent.

To test the effects of gap size and gap direction (north vs. south) on response variables (GLI, PAR, total ground layer vegetation cover, soil moisture at 6 cm, soil temperature at 10 cm, and cover of pine straw and bunchgrasses), we used mixed model split-plot analysis of variance (ANOVA) in a randomized complete block design. The gap size was treated as the main-plot effect and the gap direction was treated as the split-plot effect. The block effect was the study site location and was treated as a random effect because the pine stands were selected as a random representation of pine stands targeted for restoration.

We additionally tested the effect of gap position on response variables (GLI, PAR, total ground layer vegetation cover, soil moisture at 6 cm, soil moisture at 10, 20, 30, 40, 60, and 100 cm, soil temperature at 10 cm, available NO_3^-, available NH_4^+, total available N, longleaf pine seedling foliar N, longleaf pine seedling mortality, and cover of pine straw and bunchgrass) for each gap separately because each gap size included a different number of positions. Because the sampling points were positioned linearly across the gaps, we used a repeated measures analysis with the autoregressive order-one covariance structure to account for spatial dependency. We used linear contrasts to compare the dependent variables at each specified 10 m interval in the north and south half of gaps (e.g., 20 m south of center vs. 20 m north of center) and to compare responses in the gap interior to those beneath the forest canopy (positions at the forest edge were not used in the analyses). Treatment differences were determined using Tukey's Honestly Significant Difference (HSD) approach, and degrees of freedom were calculated using the Satterthwaite approximation. The Shapiro-Wilk test was used to check the assumption of normality and Levene's test was used to check the assumption of constant variance; transformations were used as necessary to satisfy the statistical assumptions. Treatment effects were determined to be significant when the probability of a Type-I error was less than 0.05.

Incremental longleaf pine seedling mortality was calculated for the second growing season (mortality from October 2008 until October 2009) and for the dormant season of the prescribed fire (mortality from October 2009 until May 2010). We used repeated measures ANOVA to test the effect of monitoring period, canopy presence, and the interaction of monitoring period and canopy presence on incremental seedling mortality. In the presence of an interaction term, we tested for the effects of each treatment effect within each level of the other treatment effect (e.g., tested for an effect of canopy presence on mortality through October 2009 and mortality through May 2010 separately).

Scatterplots were used to determine the relationships between below-ground plant resources (soil moisture and nitrogen) and direct measures of resource limitation (xylem water potential and foliar nitrogen). We used linear regression to quantify the relationships, and transformations were used as needed to satisfy model assumptions. All statistical analyses were performed using SAS statistical software (version 9.1; SAS Institute, Inc., Cary, NC) and all figures were created using SigmaPlot (version 9.0; Systat Software, Inc., Point Richmond, CA).

4.3. Results

Light

There was no interaction between canopy gap size and direction for light transmitted through the canopy ($F_{2,\,132}$ = 0.59; p = 0.5554) or the ground-layer vegetation ($F_{2,\,103}$ = 1.38; p = 0.2455). The average light level transmitted through the canopy was greater on the LG plots than on the MG and SG plots (Table 4.1), although there was no difference in light transmittance on the two smaller gap sizes. Approximately 10% more light was available on the north half of gaps than on the south half of gaps, regardless of gap size (Table 4.1). Gap position significantly affected GLI in each of the gap sizes (Figure 4.1). Generally, light transmittance increased from the forest edge to gap center, with light levels maximized 10 m north of gap center. The lowest light levels were 10 m into the forest on the southern half of the gaps in MG and LG; in SG plots, light levels were lowest at the southern forest edge and 10 m into the forest in either direction. Linear contrasts indicated that light levels were higher in the northern half of gaps than in the southern half of gaps at every position except 10 m from center in LG plots; in SG

Table 4.1. Canopy transmittance (GLI (%)), ground-layer transmittance (PAR (%)) and ground-layer vegetation cover (%) by gap size and direction; the same letter within a treatment and response variable indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$

		Canopy transmittance (GLI)		Ground-layer transmittance (PAR)		Ground-layer cover (%)	
Effect	Level	Mean	SE	Mean	SE	Mean	SE
Main-plot	LG	73.2^a	1.9	61.4	6.1	70.2	7.8
	MG	65.8^b	1.4	57.3	10.7	52.2	8.0
	SG	60.1^b	1.6	66.6	8.0	50.7	7.7
	p-value	**< 0.0001**		**0.1457**		**0.1083**	
Split-plot	North	70.7^a	1.5	60.8	8.0	61.3	6.2
	South	60.8^b	1.7	62.2	8.6	56.7	5.9
	p-value	**< 0.0001**		**0.8295**		**0.0696**	

plots, GLI did not differ by direction at 10 m from center or 10 m into the forest (Figure 4.2).

Light transmittance through the ground-layer vegetation, measured as PAR, was not significantly affected by gap size ($F_{2, 14.1} = 2.22$; p = 0.1457) or by gap direction ($F_{2, 103} = 0.19$; p = 0.8295) (Table 4.1). Although PAR was generally reduced from forest edge to gap center, the effect of position was only significant in MG plots (Figure 4.3).

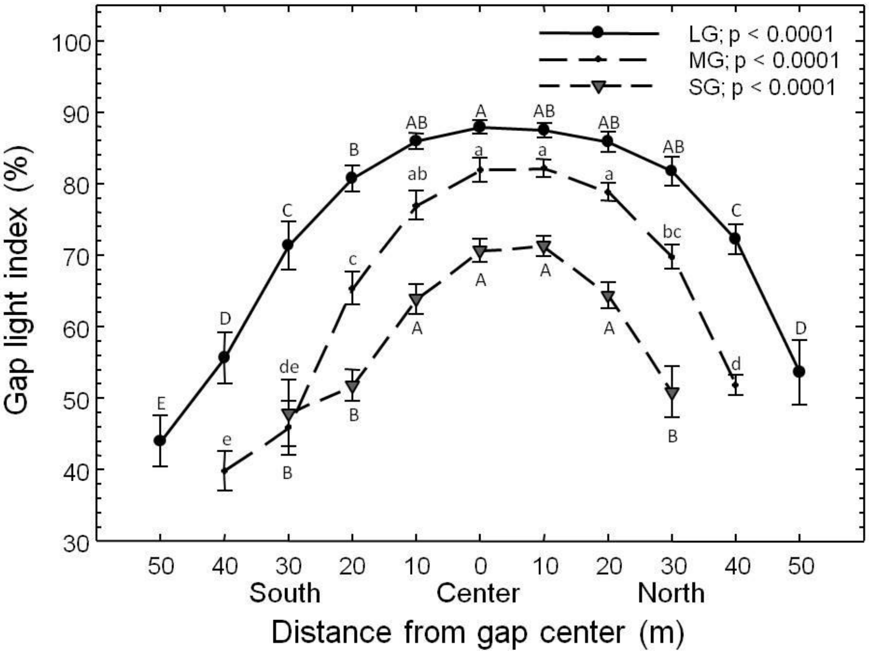

Figure 4.1. GLI (mean ± SE) by position from gap center in LG, MG, and SG. The same letter within a gap size indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.The forest edge is at 40 m in LG, 30 m in MG, and 20 m in SG.

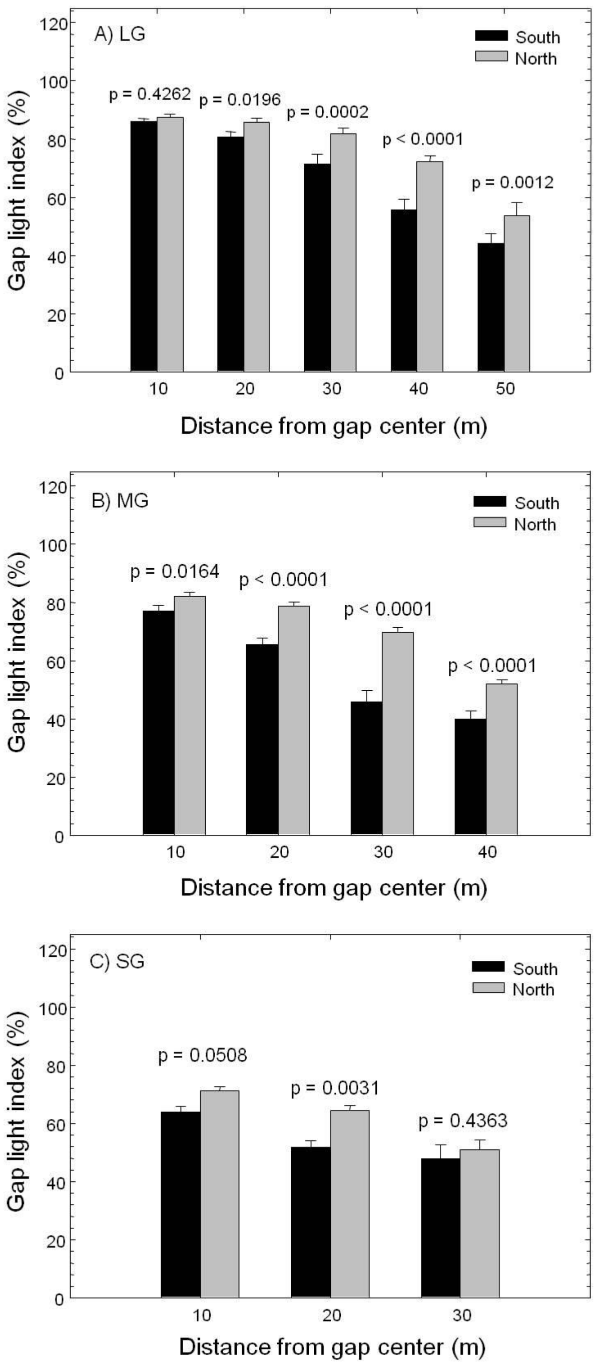

Figure 4.2. Gap light index (mean + SE) by distance from center to south and north in A) LG, B) MG, and C) SG plots; p-values are from linear contrasts that compare south and north directions.

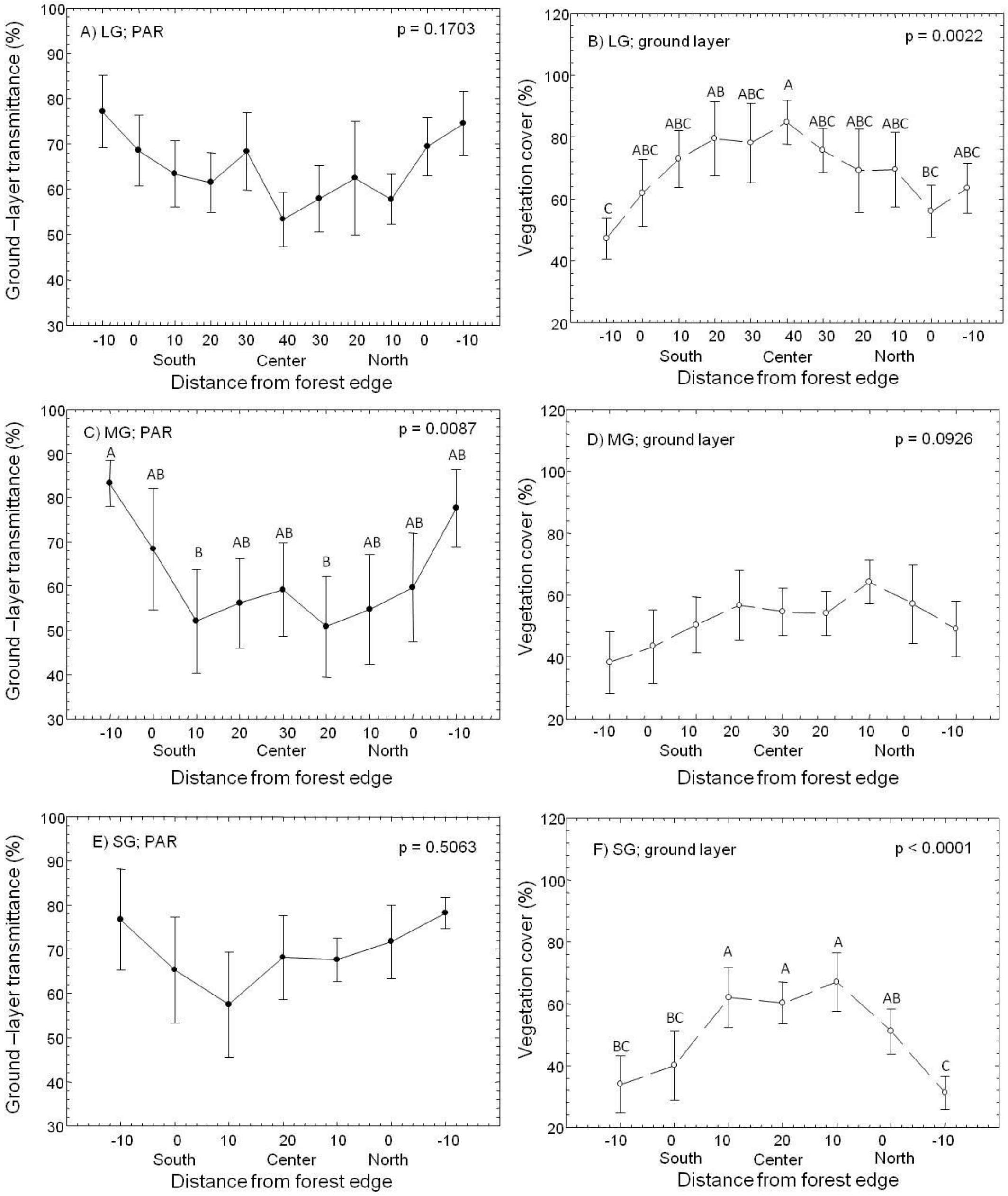

Figure 4.3. Ground layer light transmittance (PAR; %) (mean ± SE; panels A, C, and E) and ground layer vegetation cover (%) (mean ± SE; panels B, D, and F) in 2010 by gap position in each canopy gap. The same letter indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

Linear contrasts indicated that ground layer transmittance at positions beneath the canopy was significantly higher than ground layer transmittance within the gap interior in in LG ($F_{1, 32.2} = 10.08$; $p = 0.0033$) and MG ($F_{1, 25.9} = 26.31$; $p < 0.0001$) but not in SG ($F_{1, 18.3} = 3.10$; $p = 0.01947$).

Ground layer vegetation

In 2010, there was no interaction between gap size and gap direction on the cover of ground layer vegetation ($F_{2, 159} = 0.69$; $p = 0.5012$), and cover was not significantly affected by gap size or gap direction (Table 4.1). Total vegetation cover significantly increased from gap edge to gap center in LG plots and SG plots, but there was no effect of within-gap position on cover in MG plots (Figure 4.3). Linear contrasts indicated that the total vegetation cover was greater in the gap interior than beneath the intact forest for LG ($F_{1, 56} = 14.62$; $p = 0.0003$), MG ($F_{1, 46} = 6.78$; $p = 0.0124$), and SG ($F_{1, 36} = 67.29$; $p < 0.0001$).

Soil temperature and soil moisture

There was no interaction between gap size and gap direction for soil temperature ($F_{4, 101} = 0.90$; $p = 0.4682$), and we found no effect of gap size on average soil temperature at 10 cm (Table 4.2). Soil temperatures were significantly higher on the north half of gaps than on the south half of gaps, with a difference of almost one degree Celsius between the gap directions. Soil temperature increased from the forest edge to

Table 4.2. Volumetric soil moisture in 2009 and 2010 and soil temperature in 2010 by gap size and direction; the same letter within a treatment and response variable indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

		2009		2010			
		Volumetric soil moisture (%)		Soil temperature (°C)		Volumetric soil moisture (%)	
Effect	Level	Mean	SE	Mean	SE	Mean	SE
Main-plot	LG	15.51	2.06	32.84	0.49	6.74	1.80
	MG	15.27	2.91	32.66	0.61	7.20	2.30
	SG	14.02	3.76	32.09	0.67	6.31	2.21
	p-value	**0.8359**		**0.2953**		**0.8812**	
Split-plot	South	16.54^a	2.88	32.01^b	0.37	7.94^a	2.22
	North	13.50^b	2.10	33.02^a	0.67	5.64^b	1.43
	p-value	**0.0007**		**<0.0001**		**0.0041**	

gap center, with the highest temperatures slightly north of gap center in each gap size (Figure 4.4). Linear contrasts indicated that soil temperatures were significantly lower beneath the forest canopy than in the gap interior in LG plots ($F_{1, 23.4} = 29.35$; $p < 0.0001$; forest canopy = 30.5 °C and gap interior = 32.9 °C), in MG plots ($F_{1, 20.1} = 22.28$; $p = 0.0001$; forest canopy = 31.1 °C and gap interior = 32.9 °C), and in SG plots ($F_{1, 18.6} = 10.96$; $p = 0.0038$; forest canopy = 31.0 °C and gap interior = 32.1 °C).

Soil moisture at a depth of 6 cm was not significantly affected by gap size in 2009 or in 2010, but the south half of gaps had higher soil moisture than the north half of gaps in both years (Table 4.2). Using the profile access tubes installed in LG plots, we found that soil moisture was significantly greater in the south half of gaps than in the north half of

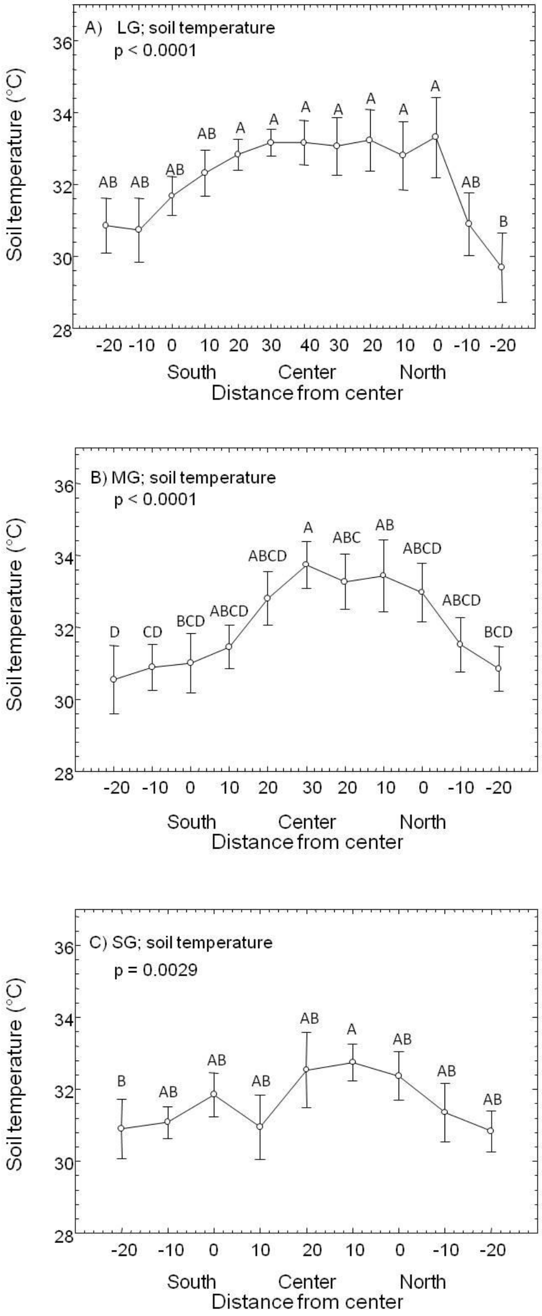

Figure 4.4. Soil temperature (°C; mean ± one SE) by gap position in A) LG, B) MG, and C) SG. The same letter indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

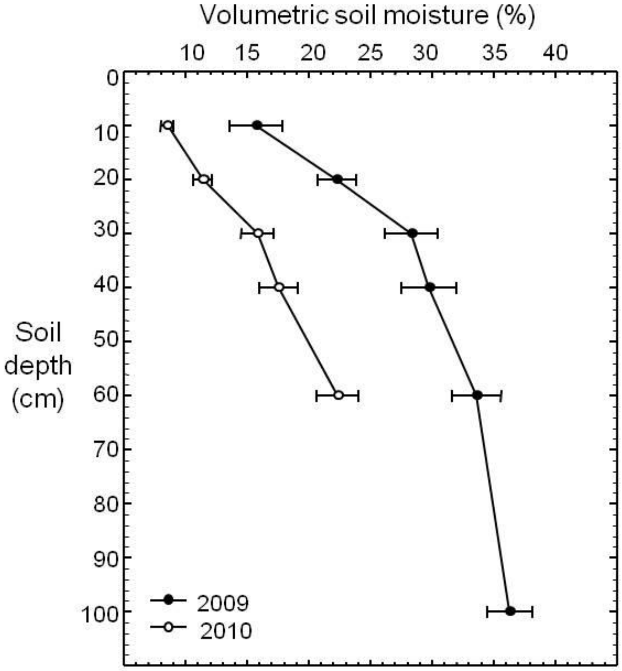

Figure 4.5. Volumetric soil moisture (mean ± one SE) by soil depth from LG plots in 2009 and 2010.

gaps in 2009 at depths of 10 cm ($F_{1,\,38.1}$ = 10.28; p = 0.0027; south = 18.9% and north = 13.7%) and 20 cm ($F_{1,\,38.1}$ = 8.84; p = 0.0051; south = 26.1% and north = 19.7%) in the soil profile; in 2010, soil moisture was significantly greater in the south half of gaps than in the north half of gaps only at 10 cm in the soil profile ($F_{1,\,53}$ = 8.21; p 0.0060; south = 9.6% and north = 7.5%). There were no significant effects of within-gap position on soil moisture at 6 cm in any gap size in either 2009 or 2010 ($p \geq 0.1071$). Likewise, we found no effects of within-gap position on soil moisture at 10, 20, 30, 40, 60, or 100 cm in the soil profile of LG plots in either year ($p \geq 0.0681$). Soil moisture did not significantly differ between sampling locations beneath intact canopy and the gap interior for any gap size in either year at a depth of 6 cm ($p \geq 0.0697$). In LG plots, soil moisture was significantly higher in the gap interior than beneath the forest canopy only at depths of 60 cm ($F_{1,\ 27.5} = 5.28$; $p = 0.0295$; forest = 33.1% and gap interior = 33.9%) and 100 cm ($F_{1,\ 27.7} = 6.79$; $p = 0.0146$; forest = 30.9% and gap interior = 37.6%) in 2009. Across the three gap sizes, soil moisture in the upper 6 cm of soil averaged 14.7% and 6.5% in 2009 and 2010, respectively. Soil moisture increased through the profile of LG plots, to a maximum of around 35% moisture by volume at 100 cm (Figure 4.5).

We measured xylem water potential of longleaf pine seedlings in LG plots as a direct quantification of water status. We found no effects of within-gap position or gap direction on xylem water potential in 2008, 2009, or 2010 (Figure 4.6). Xylem water potential of longleaf pine seedlings beneath intact forest canopy was lower than that of seedlings within the gap interior in 2009 ($F_{1,\ 17.3} = 13.7$; $p = 0.0017$; forest = -0.46 MPa and gap interior = -0.32 MPa), but this effect was not significant in any other year ($p \geq 0.4189$). Xylem water potential was never below -0.5 MPa when soil moisture levels were above 25% moisture by volume, and the lowest xylem water potentials occurred when soil moisture was near zero (Figure 4.7a). A linear relationship between the log of volumetric soil moisture and the log of the absolute value of xylem water potential explained 32.7% of the variability in xylem water potential (Figure 4.7b).

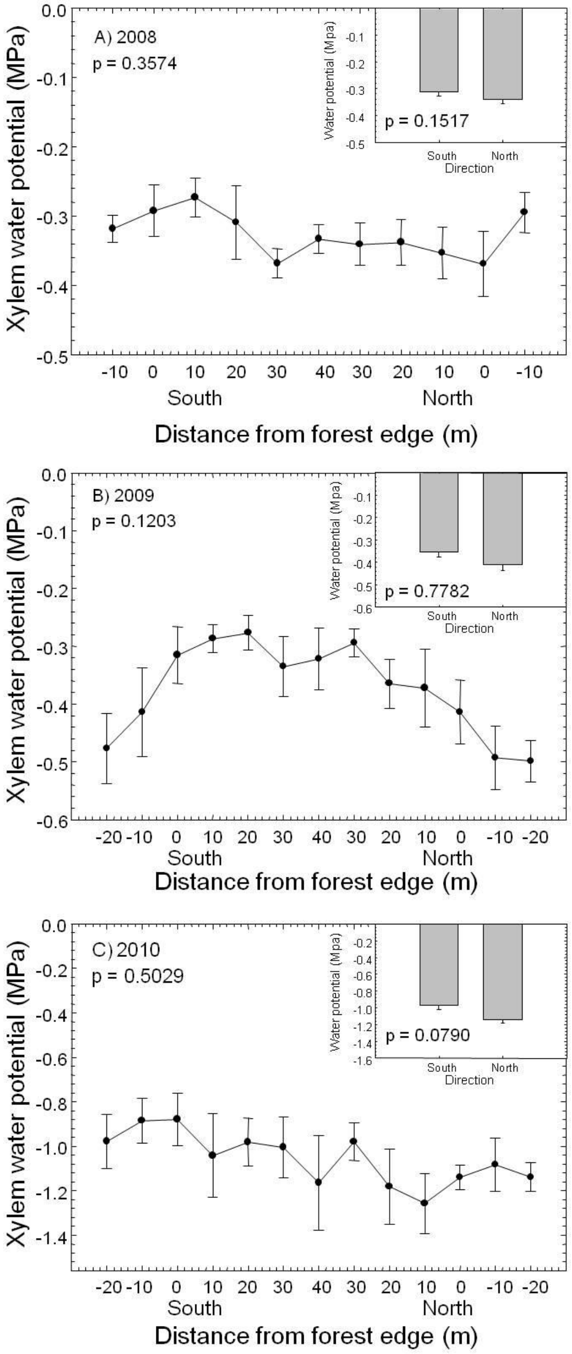

Figure 4.6. Xylem water potential (mean ± one SE) by gap position in A) 2008, B) 2009, and C) 2010. Inset: xylem water potential (mean + one SE) by gap direction in each year.

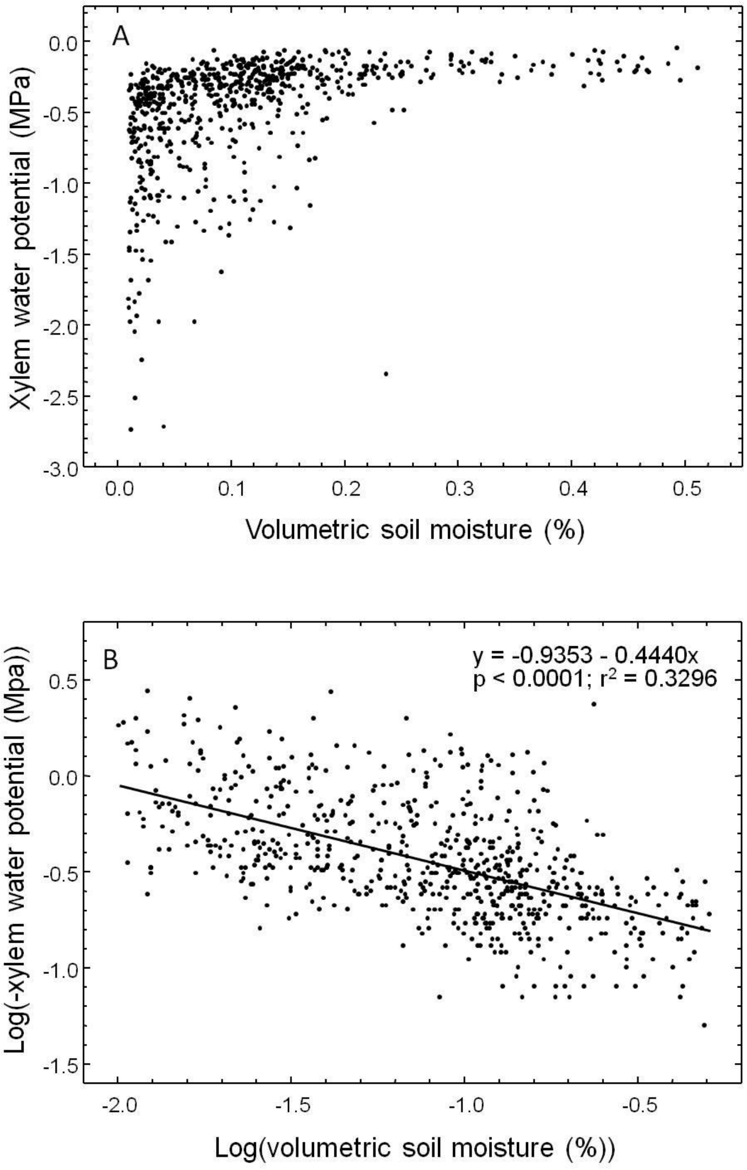

Figure 4.7. A) Scatterplot of xylem water potential by volumetric soil moisture for data from each sampling period in all years; B) relationship between log volumetric soil moisture and log of the absolute value of xylem water potential. The greatest water stress is represented by positive values on the y-axis; the lowest soil moisture is represented by negative values on the x-axis.

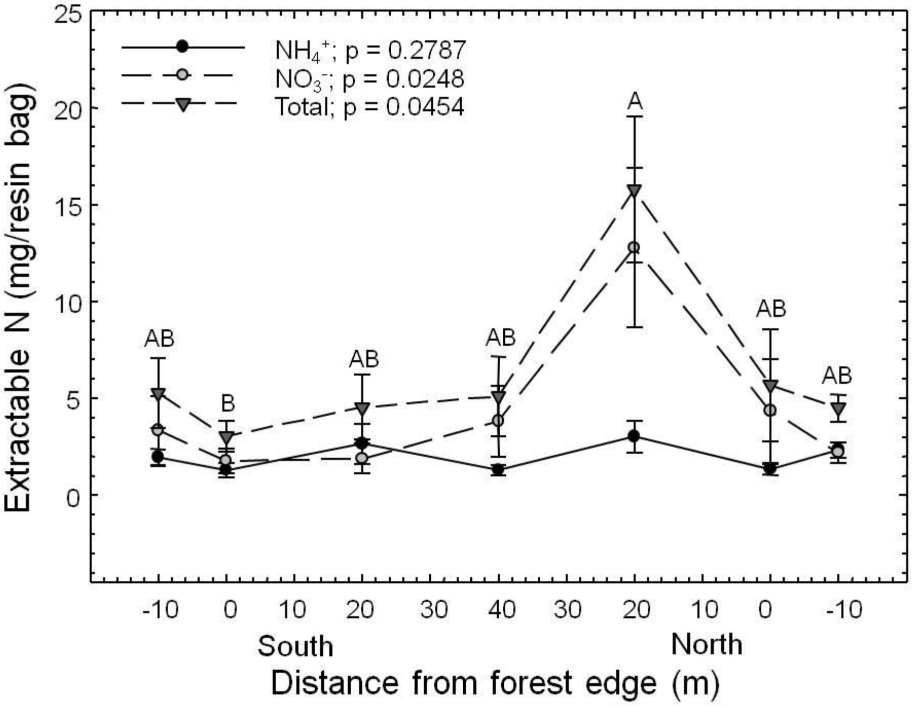

Figure 4.8. Nitrogen (NO_3^-, NH_4^+, and total N (sum of NO_3^- + NH_4^+)) extracted by ion exchange resins (mean ± one SE) by gap position in LG plots; the same letter for values of total N indicates that pair-wise comparisons are not significantly different at $\alpha = 0.05$.

Nitrogen availability

There was no effect of within-gap position on available NH_4^+ adsorbed by the resin bags ($F_{6,\,33} = 1.31$; $p = 0.2787$), but there was a significant effect of within-gap position on NO_3^- ($F_{6,\,28} = 2.91$; $p = 0.0248$) and total nitrogen availability (NH_4^+ + NO_3^-; $F_{6,\,28.1} = 2.51$; $p = 0.0454$). At 20 m north of gap center, there was a spike in NO_3^- availability that drove the pattern in total nitrogen availability. Total nitrogen was significantly higher at 20 m north of gap center than at the southern forest edge, and NO_3^- was significantly greater at 20 m north of gap center than at the southern forest edge, 20 m south of gap center, and 10 m north of the northern forest edge (Figure 4.7). Because of the higher level of NO_3^- at 20 m north of gap center, levels of both NO_3^- ($F_{1, 28.1} = 4.42$; $p = 0.0446$) and total nitrogen ($F_{1, 28.1} = 4.58$; $p = 0.0412$) were significantly higher in the northern half of gaps than in the southern half of gaps, but there was no effect of gap direction on NH_4^+ ($F_{1, 28.4} = 0.57$; $p = 0.4560$).

Foliar nitrogen concentration was not significantly affected by within-gap position ($F_{7, 20.5} = 0.71$; $p = 0.6625$) and there was no effect of gap direction on foliar nitrogen ($F_{1, 21.6} = 1.93$; $p = 0.1793$). Foliar nitrogen concentration averaged 0.99% across blocks and gap positions. Using linear regression, we found no significant relationship between total extractable soil N and foliar nitrogen concentrations ($p = 0.1248$; $r^2 = 0.0660$).

Fuels and fire effects

We found no effects of gap size ($F_{2, 9.87} = 1.89$; $p = 0.2013$), gap direction ($F_{1, 146} = 0.08$; $p = 0.7755$), or interactions between gap size and direction ($F_{2, 146} = 0.09$; $p = 0.9114$) on the cover of pine straw in 2009. For all gap sizes, pine straw cover decreased from the gap edge to gap center, with no differences in pine straw cover from 10 m from the forest edge to gap center (Figure 4.9). As a result, the linear contrasts showed that pine straw cover was significantly higher beneath the intact forest canopy than in the gap

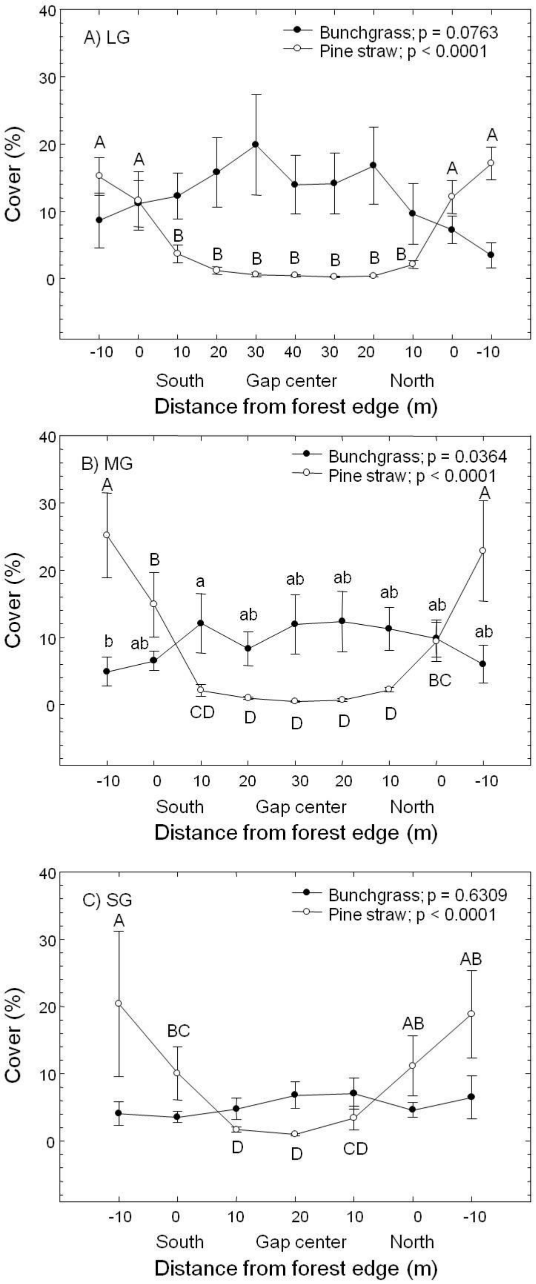

Figure 4.9. Cover of important fuel components (pine straw and bunchgrasses) by gap position for A) LG plots, B) MG plots, and C) SG plots. The same letter within cover types indicates that pair-wise comparisons are not significantly different at α = 0.05.

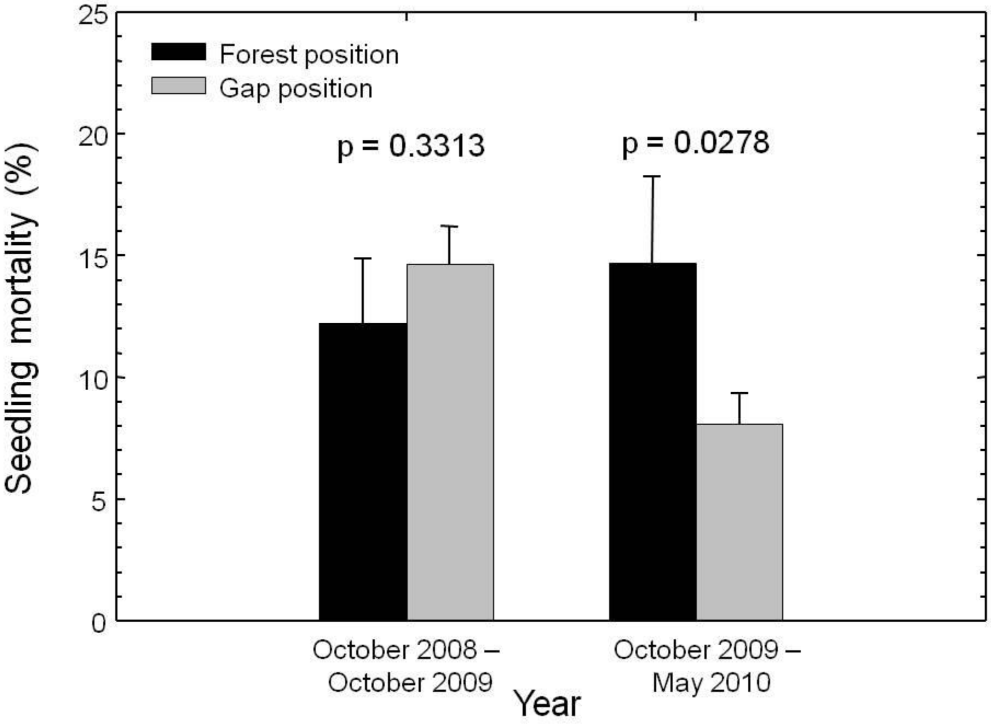

Figure 4.10. Results from repeated measures ANOVA for incremental seedling mortality (mean + one SE) beneath the forest canopy and within the gap interior in October 2009 and May 2010; p-values refer to significant differences between seedling location for each measurement period.

interior for LG plots ($F_{1,\,22.2} = 182.18$; $p < 0.0001$), MG plots ($F_{1,\,35.4} = 139.27$; $p < 0.0001$), and SG plots ($F_{1,\,29.9} = 83.42$; $p < 0.0001$). For bunchgrass cover, we found a significant effect of gap size ($F_{1,\,9.9} = 4.42$; $p = 0.0424$), with bunchgrass cover higher on LG plots than on SG plots. There was no effect of gap direction on bunchgrass cover ($F_{1,\,147} = 0.09$; $p = 0.7643$). Although bunchgrass cover generally increased from forest edge to gap center, the effect was only significant in MG plots, where the position 10 m into the gap on the southern half had higher bunchgrass cover than 10 m into the forest on the southern side (Figure 4.9).

There were no effects of within-gap position on seedling mortality between October 2009 and May 2010 in LG plots ($F_{10, 24.1}$ = 1.89; p = 0.0980), MG plots ($F_{8, 21}$ = 1.54; p = 0.2040); or SG plots ($F_{1, 6}$ = 0.69; p = 0.6592). The repeated measures test resulted in a significant interaction between mortality period and seedling position ($F_{1, 243}$ = 5.08; p = 0.0251), with significant differences in mortality by seedling position in the May 2010 survey but not in the October 2009 mortality survey (Figure 4.10).

4.4. Discussion

Resource availability and growing conditions in canopy gaps

Canopy removal influences growing conditions at the ground level through a variety of mechanisms and their interactions, including the release of limiting resources, changes in the abundance of ground layer plants, modification of the micro-climate, and changes to the seedbed and soil substrate (Canham et al. 1990, Denslow and Spies 1990, Brosofsky et al. 1997, Prescott 1997, Roberts 2004). There have been many studies on the effects of canopy gaps on resource distribution and ecosystem response, but the magnitude of these effects are often dependent on site conditions (e.g., topography, latitude, soil properties) and stand structure (e.g., tree height to gap size ratio). For example, Canham et al. (1990) compared light penetration in canopy gaps of five forest types that ranged in latitude from tropical rain forests (latitude of 10 °N) to boreal forests (latitude of 44.3 °N) and demonstrated the importance of latitudinal effects on solar angle for determining patterns of available light in canopy gaps, with areas of high light transmittance shifted further north from gap center in northern latitudes. Past research has been conducted in a wide range of canopy gap sizes, and differences in gap size affect competition thresholds as well as patterns of resource availability (Schliemann and Bockheim 2011). Gendreau-Berthiaume and Kneeshaw (2009) discussed the importance of the tree height-to-gap size ratio in controlling the distribution of light availability in canopy gaps of different sizes, suggesting that inconsistencies in previous studies may be related to comparisons of gaps of different sizes or differences in surrounding tree height. Understanding the factors that influence canopy gap dynamics in different ecosystems is important for comparing results of gap studies across ecosystems.

Pine forests of the southeastern United States have relatively open canopies compared to many other forest systems, resulting in relatively high levels of light transmittance to the understory even beneath intact forest canopies (Canham et al. 1990, Endler 1993, Battaglia et al. 2003). However, species-specific morphology affects the efficiency of light interception by the forest canopy of different pine species (Stenberg et al. 1994). For a given basal area, slash pine (*Pinus elliottii* Engelm.) forests have lower canopy transmittance than longleaf pine forests (Kirkman et al. 2007), and Hu (2011) reported slightly higher levels of canopy transmittance for loblolly pine forests than that previously reported in longleaf pine forests. Results from our study suggest that canopy light transmittance within canopy gaps in loblolly pine forests are similar to light levels in canopy gaps of similar size in longleaf pine forests. In longleaf pine forests, McGuire et al. (2001) reported an average of 67% light in 0.10 ha gaps (similar to our SG plots) and an average of 79% light in 0.41 ha gaps (slightly smaller than our LG treatment). Likewise, relationships between canopy density and light availability have been reported to be similar in second-growth loblolly pine forests and longleaf pine stands (Chapter 3).

In the northern hemisphere, where the sun moves across the southern portion of the sky, solar radiation is predictably greater on the northern half of gaps than on the southern half of gaps due to shade provided by trees along the southern gap edge (Canham 1988, Gray et al. 2002, Ritter et al. 2005, Gálhidy et al. 2006). This pattern has been reported in canopy openings ranging from 0.10 ha to 1.63 ha in longleaf pine forests (McGuire et al. 2001, Gagnon et al. 2003). Regardless of gap size, we found that canopy light transmittance was maximized slightly north of gap center, but maximum light levels increased with gap size. Gendreau-Berthiaume and Kneeshaw (2009) discussed the importance of gap size-to-tree height for determining the position of maximum light within canopy openings, with light maximized near the northern edge in small gaps (diameter of 0.5 times tree height) but shifting to gap center in larger openings (diameters up to 1.5 times tree height). All gaps used in our study were larger than those discussed by Gendreau-Berthiaume and Kneeshaw (2009), perhaps explaining the high light levels observed slightly north of center in all gaps of our study. Differences in canopy light transmittance between the north and south half of gaps were greatest at the forest edge for all gap sizes, suggesting that gap partitioning related to light availability may result in habitats with varying suitability for plant species at each respective gap edge.

Canopy removal often results in the release of sub-canopy vegetation and subsequent spatial and temporal variability of resource gradients within canopy openings. Three years after gap formation, the abundance of ground layer plants in our study increased from forest edge to gap center, generally resulting in greater interception of light by sub-canopy vegetation within the gap interior. Poulson and Platt (1989) reported that high light levels in the northern half of gaps resulted in rapid growth of understory and midstory vegetation, and 13 years after gap formation the higher density of woody species resulted in lower light levels in the northern portions of canopy openings than in the southern portion. In many longleaf pine habitats, canopy openings release hardwood species such as oaks (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua* L.) if fire management is not effective (Jack et al. 2006, Pecot et al. 2007). Creating canopy openings for longleaf pine restoration in stands dominated by other pine species enables the establishment of natural regeneration of the canopy species, with greater growth observed in canopy openings than beneath intact forest (Knapp et al. 2011). The development of the regeneration layer largely determines species dominance of the gap-filling cohort, with the interception of light shifting from the canopy layer to the developing sub-canopy layer over time.

Increased exposure to solar radiation following canopy removal has been associated with greater soil temperature extremes in clearcut areas than beneath intact forests (Hungerford and Babbitt 1987, Brosofske et al. 1997). Similar results have been reported in canopy openings, with higher summer soil temperatures in the northern half of gaps than in the southern half of gaps in different forest systems (Gray et al. 2002, Wright et al 1998). However, other studies have reported the opposite pattern, finding lower soil temperatures in the northern half than in the southern half of canopy openings (Ritter et al. 2005). Because soil temperatures are strongly controlled by the direct exposure to solar radiation, the development of midstory vegetation can moderate soil temperature increases. In our study, the higher temperatures in the northern half of gaps are likely associated with patterns of canopy transmittance but are likely to change through stand development and canopy closure. Our results suggest that gap size is important to the magnitude of within-gap position effects on soil temperature, with few differences in small gaps. Similarly, Gray et al. (2002) found no effect of gap position on soil temperature in small gaps (~10 m diameter) in Douglas-fir forests, but soil temperatures were higher in northern than southern gap portions in gaps with > 20 m diameters.

The effects of canopy gap formation on soil moisture include interacting factors that may increase or decrease soil moisture through the soil profile. Canopy removal changes the pathway of precipitation to the forest floor from drip, stemflow, and evaporation with an intact canopy to direct throughfall in canopy openings (Moore and Vankat 1986). Root gaps in the soil profile (e.g., Ostertag 1998) and reductions in evapotranspiration have been associated with increased levels of soil moisture beneath canopy openings when compared to the intact canopy (Moore and Vankat 1986, Denslow et al. 1998, Gray et al. 2002). However, increased exposure to solar radiation can result in drier soil conditions following canopy removal (Londo et al. 1999, Redding et al. 2003, Moroni et al. 2009), and the soil moisture in the northern half of canopy openings has been reported to be lower than that in the southern half, even in studies with higher soil moisture beneath canopy openings than beneath intact canopies (Wright et al. 1998, Gray et al. 2002). The evaporative effect of solar radiation on soil moisture would be strongest near the soil surface, and we found that soil moisture was significantly higher in the southern half of gaps than in the northern half of gaps through 20 cm in the soil in 2009 and through 10 cm of the soil surface in 2010. Interestingly, we found that soil moisture was higher beneath the canopy openings than beneath the intact forest at depths of 60 and 100 cm in the soil profile, suggesting that the evaporative effect of solar radiation was more important in determining soil moisture differences at the soil surface and root gap competition was more important for controlling soil moisture deeper in the profile.

Nitrogen availability within the soil is strongly controlled by soil moisture, soil temperature, the microbial community, and the quality of the organic substrate within the soil (e.g. Keeney 1980, Myers et al. 1992, Knoepp and Swank 2002), with increases in any of the variables generally resulting in increased mineralization and nitrogen availability. Canopy removal has been shown to increase nitrogen mineralization in the soil following clearcutting (Matson and Vitousek 1981, Kim et al. 1995, Prescott 1997), and Palik et al. (1997) found that decreasing overstory basal area through thinning resulted in increased nitrogen availability in the mineral soil of longleaf pine forests in southwestern Georgia. The conditions created by patch-cutting are often similar to those created by clearcutting, especially in the LG plots used for N analysis in this study. In a study in a longleaf pine forest in southwestern Georgia, McGuire et al. (2001) reported that nitrification generally increased from the forest edge to 10-20 m into canopy gaps of different sizes, although total mineralization was maximized in the smallest gaps of their study (~ 0.1 ha). Both the mineralization and nitrification of organic N in the mineral soil are positively related to soil temperature (Matson and Vitousek 1981, Knoepp and Swank 2002), and it is likely that the higher soil temperatures in the northern portion of canopy openings resulted in greater nitrification. The differences in extractable NO_3^- and total extractable N between the north and south half of gaps in our study were primarily driven by the spike in NO_3^- observed 20 m from the north forest edge. NO_3^- is more mobile than NH_4^+ and may have transported more readily to the IER bags (Binkley et al. 1986), resulting in the greater contribution of NO_3^- to the total extractable N. However, it should be noted that variability in NO_3^- concentrations at 20 m from the northern forest edge was generally high, resulting in a significant difference only with the location at the southern forest edge, and our results do not suggest a general increase in soil N from beneath the forest canopy to the gap interior.

Limitations to longleaf pine establishment and gap-phase regeneration

Canopy disturbances are understood to be important drivers of longleaf pine regeneration and are critical for ecosystem persistence through time (Palik et al. 2002, Gilliam et al. 2006). Observational studies have consistently demonstrated the aggregation of natural regeneration within canopy openings or areas of low canopy density (e.g., Platt et al. 1988, Grace and Platt 1995a, Brockway and Outcalt 1998, Gagnon et al. 2004), and artificial regeneration generally shows greater growth within canopy gaps than beneath canopy trees (e.g., McGuire et al. 2001, Gagnon et al. 2003, Palik et al. 2003, Chapter 2). The results of previous research have generated two main hypotheses describing the patterns of seedling aggregation in canopy openings (the Fire Effects Hypothesis and the Competition Hypothesis), and our results suggest that these processes are not mutually exclusive but rather that both hypotheses control regeneration success. Three primary requirements must be met for successful regeneration: 1) the establishment of new individuals (germination in natural regeneration or planting in artificial regeneration), 2) the persistence of new individuals (survival), and 3) the growth and development of established seedlings. Each of these stages of regeneration success is affected by the mechanisms of these two hypotheses, and although canopy gap formation may have interacting effects on these requirements, the net effect of these processes determines the regeneration outcome.

Our results show differences in the distribution of fuels, with an increase in bunchgrasses within canopy openings but higher cover of pine needles beneath the forest canopy. Pine needles increase fire temperatures and are essential for fire continuity, especially when the ground layer vegetation and other fuels have patchy distribution (O’Brien et al. 2008). The greater abundance of pine needles beneath canopy pines has been shown to increase fire intensity and result in greater longleaf pine seedling mortality (Grace and Platt 1995a, Jack et al. 2010). In a study from the Croatan National Forest in North Carolina, Avery et al. (2004) reported clustering of dead longleaf pine seedlings around mature trees following fire and found that the likelihood of seedling mortality was associated with increased needle litter around canopy trees. The prescribed fires in our study burned more uniformly and with generally higher temperatures beneath the forest canopy than within canopy gaps (Knapp et al. 2011, Tennant 2011). Although the effects of the prescribed fire cannot be compared to an unburned treatment in our study, it is likely that the greater seedling mortality that occurred beneath the forest canopy was associated with effects of the prescribed fire for the following reasons: 1) there was no difference in mortality between forest and gap positions the year prior to the prescribed fire; and 2) post-fire mortality was monitored in May, before growing season competition affected seedling survival.

The importance of fire in regulating gap-phase regeneration is likely different for naturally vs. artificially regenerated longleaf pine because seedling size affects the vulnerability to mortality from fire. O'Brien et al. (2008) reported that seedlings < 0.2 m in height had the highest mortality following experimentally manipulated fire when compared to larger longleaf pine seedlings and saplings. The competitive effects of canopy pines on seedling growth results in smaller, more vulnerable seedlings occurring in locations with higher fuel loads and more intense fires (Grace and Platt 1995a). During natural regeneration, the small, newly germinated seedlings are most susceptible to mortality from fire and are likely to be eliminated from the regeneration pool, increasing the importance of synchronizing fire management with the timing of natural regeneration to ensure that seedlings are large enough to survive surface fires. In contrast, artificial regeneration controls the establishment phase of regeneration and allows managers to time prescribed fire application after seedlings have grown for a few years. However, our results indicate that fire management plays a role in seedling persistence following underplanting and that more research is required to understand the fine-scale effects of fire on restoration objectives following artificial regeneration.

In addition to influencing fuels and fire effects, canopy pines affect the persistence of longleaf pine regeneration through both facilitation and competition. Previous studies have reported higher early survival of artificially regenerated seedlings beneath canopy pines than in canopy openings, typically in years of drought (McGuire et al. 2001, Gagnon et al. 2003, Rodriguez-Trejo et al. 2003, Pecot et al. 2007). Experimental shade provided by palm fronds was found to reduce mortality in dry sandy sites of Mississippi (Allen 1953), suggesting that exposure to high levels of solar radiation may increase desiccation of planted seedlings. Patterns of seedling mortality from our study support these findings, with increased mortality in the interior of canopy gaps and higher mortality on the north half of gaps than on the south half (Chapter 2). In a replication of this study at Camp Lejeune, NC, however, Hu (2011) found no effect of within-gap position on seedling survival, suggesting that facilitation effects on longleaf pine seedling persistence may be associated with site conditions or climatic patterns.

The role of canopy competition in controlling seedling size in longleaf pine forests has been well established (e.g., Palik et al. 1997, Kirkman and Mitchell 2006, Mitchell et al. 2006), but the resources limiting growth and long-term regeneration persistence have been debated. Positive relationships have commonly been reported between light availability and seedling growth, with the strongest limitations to seedling growth observed below light levels of 65% full light (Palik et al. 1997, McGuire et al. 2001, Knapp et al. 2008, Chapter 3). In our study, seedling size generally increased from the forest edge to gap center but did not differ between the north and south half of gaps (Chapter 2). Average light levels within canopy openings exceeded 60% for all gap sizes in our study, suggesting that light levels were high enough throughout gaps that seedling growth was not strongly limited by the directional effect of light distribution. In contrast to our results, Brockway and Outcalt (1998) found no effect of canopy position on light levels in canopy gaps in a longleaf forest in northern Florida and proposed that the open canopy of the forest resulted in high light levels regardless of position. It is possible that differences in the measurement technique (instantaneous PAR measurements by Brockway and Outcalt (1998) vs. hemispherical photographs in this study) led to the different results, as instantaneous measurements have been found to be less sensitive to differences in light availability than hemispherical photographs (Battaglia et al. 2003, Pecot et al. 2007, Gendreau-Berthiaume and Kneeshaw 2009).

Competition for below-ground resources has also been shown to regulate longleaf pine seedling growth, and Brockway and Outcalt (1998) proposed that root gaps within canopy openings were the primary driver of gap-phase regeneration in natural forests. However, the increase in the abundance of ground-layer plants following canopy removal can quickly fill root gaps (McGuire et al. 2001, Jones et al. 2003), resulting in only transient increases in below-ground resources in the presence of ground layer vegetation. For example, Pecot et al. (2007) found that longleaf pine seedlings responded to increased soil nitrogen availability at a depth of 5 cm with greater growth when understory plants were removed, but nitrogen availability decreased strongly and was not related to longleaf pine seedling size when the understory was intact. Our results suggest that root gaps may be present at depths > 50 cm in the soil profile, because we found greater soil moisture concentrations in canopy gaps than beneath the forest canopy at 60 and 100 cm in the soil profile. The distribution of roots in the soil profile differs for herbaceous and woody species, with the concentration of herbaceous roots within the soil surface (Walter 1971, Knoop and Walter 1985). As a result, it is likely that the lower soil moisture levels relatively deep in the soil profile beneath the intact canopy were caused by water use by the canopy trees.

We found little evidence that below-ground resource availability (soil water or nitrogen) was driving the patterns of seedling growth within gaps. Soil water content did not differ across canopy gap positions at any soil depth, and the direct measures of plant moisture stress (i.e., xylem water potential) did not vary across canopy gaps. In 2009, however, xylem water potential was more negative beneath the canopy than in the gap interior, suggesting that competition for soil water between seedlings and canopy trees increased water stress. However, the scatterplot of xylem water potential and soil water content (Figure 4.7A) indicated that plant water stress was not common when soil moisture at 6 cm exceeded 20%. Although longleaf pine is better suited to dry conditions than other southern pines, water stress limits root growth (Prior et al. 1997, Sword Sayer et al. 2005), changes needle chemistry (Pritchard et al. 1997), and can ultimately limit biomass production (Prior et al. 1997). Studies that have experimentally manipulated water stress of longleaf pine seedlings have applied 'stressed' treatments with levels of xylem water potential that fall within the range measured in our study (Prior et al. 1997, Sword Sayer et al. 2005); therefore, water stress was likely affecting seedling growth.

However, because the annual variability in soil moisture was higher than that within canopy gaps, it is likely that plant water stress was more strongly associated with precipitation patterns than with competition from surrounding vegetation.

Previous studies have reported positive relationships between nitrogen availability in the soil and longleaf pine seedling growth (Palik et al. 1997, McGuire et al. 2001), but the increased nitrogen availability observed on the northern half of canopy gaps did not result in greater foliar nitrogen concentrations in longleaf pine seedlings at the same position. Because nitrogen availability was not higher at other gap positions when compared to beneath the forest canopy, it is unlikely that canopy removal eliminated the competition for soil nitrogen. Pecot et al. (2007) found that soil nitrogen was only related to canopy density in the absence of understory vegetation and that understory plants replaced the competitive pressure of canopy trees following harvesting. It is likely that increases in soil nitrogen following gap formation were not made available for seedlings because of competition with other vegetation.

4.5. Conclusions

Canopy gaps play an important role in resource distribution and regeneration dynamics across forested ecosystems, and our study demonstrates several effects of canopy openings on the microsite conditions in gaps of different sizes in southern pine forests. Despite the relatively open stand structure, light transmittance in canopy openings was highest to the north of gap center, with greater light levels in the northern half of gaps than the southern half of gaps regardless of gap size. Canopy removal increased the abundance of ground layer vegetation, which in turn increased the competition for light at the forest floor. Soil temperatures were highest within the gap interior, with higher temperatures in the northern half of gaps where solar radiation was the highest. The observed increases in soil nitrogen north of gap center may have been associated with higher soil temperatures. However, we found no effects of gap size or position on soil moisture near the surface; at greater depths in the soil profile, the presence of canopy trees reduced soil moisture relative to canopy openings.

We contend that the two hypotheses generated by past research are both important for controlling the aggregation of longleaf pine seedlings within canopy gaps. The effects of fuel loads and fire intensity on seedling persistence is likely more important in regulating the establishment and early persistence of longleaf pine seedlings during natural regeneration than during artificial regeneration because of the control managers have on seedling establishment and the timing of prescribed fire during artificial regeneration. The factors controlling seedling growth within canopy openings are complex, with interplay and feedbacks among limiting resources (Prior et al. 1997, Jose et al. 2003) that make decoupling the effects *in situ* difficult. The availability of below-ground resources can be quite variable through time, depending on weather conditions, microbial activity, and vegetation dynamics. Increased nitrogen in the northern half of canopy gaps did not result in higher foliar nitrogen content in longleaf pine seedlings, suggesting that the nitrogen may have been used by other ground layer plants or quickly moved through the soil. Differences in soil moisture between areas beneath the canopy and the gap interior indicate that competition for water is more prevalent below 50 cm in the soil profile than closer to the surface and that competition at that depth is driven by the presence of canopy trees. However, soil moisture did not appear to be a strong regulator of the spatial patterns of seedling size within canopy openings. Similar to previous research (Palik et al. 1997, McGuire et al. 2001), results from this study and from Chapter 3 indicate that light is the most limiting factor for seedling growth of longleaf pine seedlings that have become established in canopy openings.

Regenerating longleaf pine seedlings in canopy gaps requires seedling establishment, persistence, and growth. The establishment stage differs between artificial and natural regeneration, and our study was not designed to determine the factors that control germination and initial seedling establishment in natural regeneration. Following establishment, canopy pines may facilitate early seedling persistence by alleviating harsh conditions or limit seedling persistence by changing fuels and fire effects or through competitive pressures. Seedling development is strongly controlled by competition with canopy trees, and light appears to be the major driver of seedling response. Small gaps (0.1 ha) create light conditions ≥ 60% within 10 m of the forest edge, suggesting that large forest openings are not necessary for longleaf pine restoration.

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CHAPTER V: IMPLICATIONS OF FOREST MANAGEMENT FOR THE RESTORATION OF VEGETATION STRUCTURE IN OPEN-CANOPIED PINE FORESTS

5.1. Introduction

The historical conversion of upland sites from longleaf pine (*Pinus palustris* Mill.) to loblolly pine (*Pinus taeda* L.) forests has been largely associated with land use legacies (e.g. timber clearing, agriculture) and management decisions (e.g. plantation forestry, fire exclusion) (Frost 1993, Van Lear et al. 2005). As a result, there has been a notable change in the dominant pine species across the southeastern landscape. However, the differences between the forest types are not limited to canopy composition; the stand structure of upland loblolly pine plantations is often quite different from that of the fire-maintained longleaf pine ecosystem, with important implications for biodiversity, ecological function, and endangered species management.

The characteristic stand structure of frequently burned longleaf pine forests includes an open canopy dominated by longleaf pine, a poorly developed or no midstory layer, and a ground layer that is dominated by herbaceous species. This structure is important to the ecosystem by providing high quality habitat for many of the endangered faunal species associated with longleaf pine. For example, the gopher tortoise (*Gopherus polyphemus*) and many other reptile specialists in longleaf pine habitats require open stands for foraging herbaceous ground layer plants (Guyer and Bailey 1993). Perhaps the most well-known faunal species associated with the longleaf pine ecosystem is the red-cockaded woodpecker (*Picoides borealis*), which uses live longleaf pine trees for nesting cavities and prefers open stands for foraging (USFWS 2003). Recent reports suggest that RCWs living in habitats dominated by herbaceous plants have higher reproductive potential than those in habitats dominated by shrubs (James et al. 1997), in part due to the diverse arthropod community supported by herbaceous ground layers plants (Folkerts et al. 1993, Hanula and Engstrom 2000).

Functionally, the ground layer vegetation serves as a critical fuel source for maintaining the frequent fire regime required to sustain the longleaf pine ecosystem. The ‘canopy’ of the ground layer is typically dominated by large bunchgrasses that create a matrix of overlapping plant tissue and form an often continuous layer of well-aerated fuels. When combined with needlefall from canopy pines, this fuel layer burns readily as low-intensity surface fires (e.g. Clewell 1989, Noss 1989). Frequent surface fire reduces the growth from hardwood species and maintains the dominance of herbaceous species (Glitzenstein et al. 1995, Brockway and Lewis 1997). The importance of ground-layer vegetation (particularly large bunchgrasses) as a fuel source, coupled with the dependence of the structure of the vegetation layer on a frequent fire regime for self-perpetuation, represents a positive feedback system that becomes difficult to re-establish once disrupted.

Although fire maintained longleaf pine forests may provide a reference for desirable stand structure, existing loblolly pine stands often appear very different from the desirable target conditions. Midstory encroachment by hardwoods is a common occurrence in the absence of frequent fire, and the presence of a midstory component can further reduce the pyrogenicity of a pine dominated forest (Mitchell et al. 2006). As hardwood species gain dominance, herbaceous species such as grasses and forbs are often shaded out and their contribution as fine fuels is reduced. In such cases, management objectives must include the control of midstory hardwoods to shift the balance to an herbaceous dominated ground layer.

Despite an understanding of the importance of ground layer vegetation in this system, longleaf pine restoration efforts often focus on successful establishment of longleaf pine seedlings. Restoration must also consider other aspects of stand structure, and a complete understanding of how management actions prescribed to improve longleaf pine seedling establishment will affect overall stand structure is required. This study was designed to determine how longleaf pine restoration management affects ground layer vegetation during the first few years after treatment. Our specific objectives are to determine: 1) how manipulation of canopy density affects ground layer vegetation cover by functional group; 2) how cultural treatments used for longleaf pine ecosystem restoration affect ground layer cover by functional group; and 3) how ground layer vegetation cover changes through time in response to canopy density manipulation and prescribe fire. We are additionally interested in determining how woody vegetation develops following longleaf pine restoration treatments, as well as how management actions affect fine fuel sources that are important to fire management.

5.2. Materials and methods

Study site and experimental treatments

This study was conducted at Fort Benning, GA and included all six study blocks described in Chapter 1.4, but only the uniform main plots are used in this study. The experiment is a randomized, complete block, split-plot design, with the location of individual loblolly pine stands as the block factor. Each block was divided into four main treatment plots and each main plot received an overstory treatment. Main plots were 100 x 100 m (1 ha), with the exception of the Clearcut plots, which were 141 x 141 m (2 ha) to create clearcut conditions in the plot center. The overstory treatments include four treatments that resulted in the uniform distribution of canopy pines: Control (uncut; residual basal area ~ 16 m^2/ha); MedBA (single-tree selection to create a uniform canopy with the target basal area of 9 m^2/ha); LowBA (single-tree selection to create a uniform canopy with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha).

Sub-plot treatments included additional cultural practices designed to enhance ecosystem restoration, through either improvement of conditions for planted LLP seedlings or changes to ground layer vegetation. The sub-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main-plot treatments were each divided into four equal sections for cultural treatment application. Within each section, sub-plot treatments were applied to a 30 x 30 m area centered on a 20 x 20 m measurement plot. The herbicide treatment was designed to improve conditions for planted longleaf pine seedlings by reducing competition from surrounding vegetation. We prescribed a direct spray of 1% imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) plus 0.25% non-ionic surfactant in October 2008 to control woody vegetation. Because herbaceous vegetation dominated most of the study sites, we applied an additional granular mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009.

Following timber harvest, study sites were prepared in accordance with standard management procedures used for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted with container-grown longleaf pine seedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare, by contracted crews. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fire, applied between the second and third growing seasons (January – April 2010). Additional information on treatments, treatment application, site preparation, and prescribed burns is described in Chapter 1.5.

Data collection

In the sub-plots of each main-plot, we randomly located the starting points of two transects (each 20 m in length) that ran parallel to one sub-plot boundary (Figure 5.1). Along each transect, we randomly selected 10 numbers ranging from 2 to 17 to serve as starting points for sampling quadrats. Each randomly selected number represented a distance (m) from the start of the transect (0 m). We did not sample from the edges of the transects to avoid potential disturbance from transect establishment and plot layout.

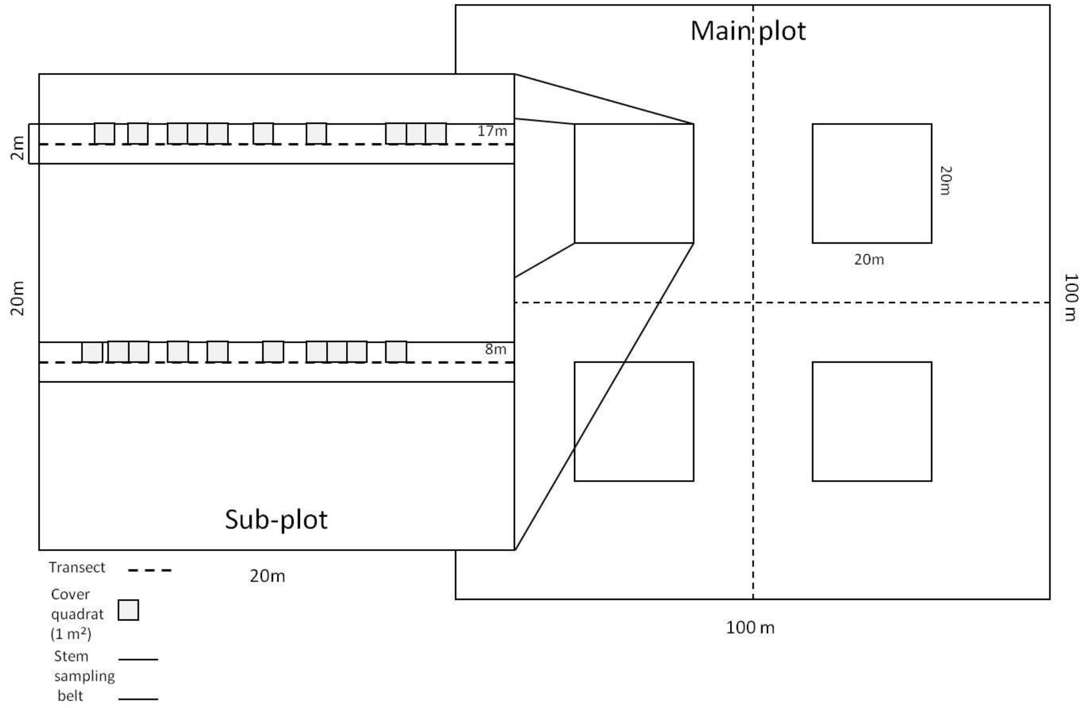

Figure 5.1. Layout of main- and sub-plots for ground layer vegetation sampling.

At each randomly selected sampling location along the transects, we established a 1 x 1 m sampling quadrat and recorded ocular estimates of percent cover of all vegetation < 1 m tall that occurred within the quadrat. We estimated cover as the percentage of the plot that would be shaded if the sun was positioned directly overhead. Cover was recorded using the following cover classes: 1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, and 10 = 95-100%, and total cover for a quadrat could sum to over 100% if vegetation overlapped. We estimated cover by functional group (bunchgrasses, other graminoids, ferns, forbs, woody shrubs/trees, and woody vines) and by selected species of interest (e.g., *P. taeda*, *Liquidambar styraciflua* L., *Rubus* spp.). Ground layer vegetation cover was recorded in October 2008, 2009, and 2010.

We used each transect as the center of a 2-m wide belt transect for sampling woody stems > 1 m tall but < 10 cm in diameter at breast height (DBH). Within each belt transect, we tallied all woody stems by species in October 2008, 2009, and 2010. A prescribed fire, described in Section 1.4, was applied to all study plots in the dormant season before the 2010 growing season.

Data analysis

Cover data were converted to the mid-point of each class, and we calculated mean values at the sub-plot level for analyses. We used split-plot Analysis of Variance (ANOVA) with a random block effect to test for main-plot effects, sub-plot effects, and main*sub-plot interaction effects on total vegetation cover, herbaceous vegetation cover, woody vegetation cover, and vegetation cover by functional group. Analyses were conducted for each year separately because the timing of sub-plot treatment application differed. In 2008, no sub-plot treatments had been applied, and we tested for only main-plot effects; by 2009, we had applied the herbicide and fertilizer treatments and compared NT, H, and H+F treatments. We used repeated measures ANOVA with an autoregressive order-one covariance structure to test for year effects and year*main-plot treatment effects. For the repeated measures test we used only NT sub-plot treatments because the sub-plots were applied at different times.

We determined the average number of woody stems per hectare at the sub-plot level by species and by the total number of stems. We used split-plot ANOVA with a random block effect to test for main-plot effects, sub-plot effects, and main*sub-plot interaction effects on woody stem density in each year. For each test, we used transformations as necessary to satisfy assumptions of constant variance and normality. Treatment differences were determined using Tukey's Honestly Significant Difference (HSD) approach, and degrees of freedom were calculated using the Satterthwaite approximation. We determined statistical significance when the probability of making a Type-I error was less than 0.05.

5.3. Results

There was no interaction between main-plot and sub-plot effects on total vegetation cover in 2009 or 2010 ($p \geq 0.2734$), but total vegetation cover was

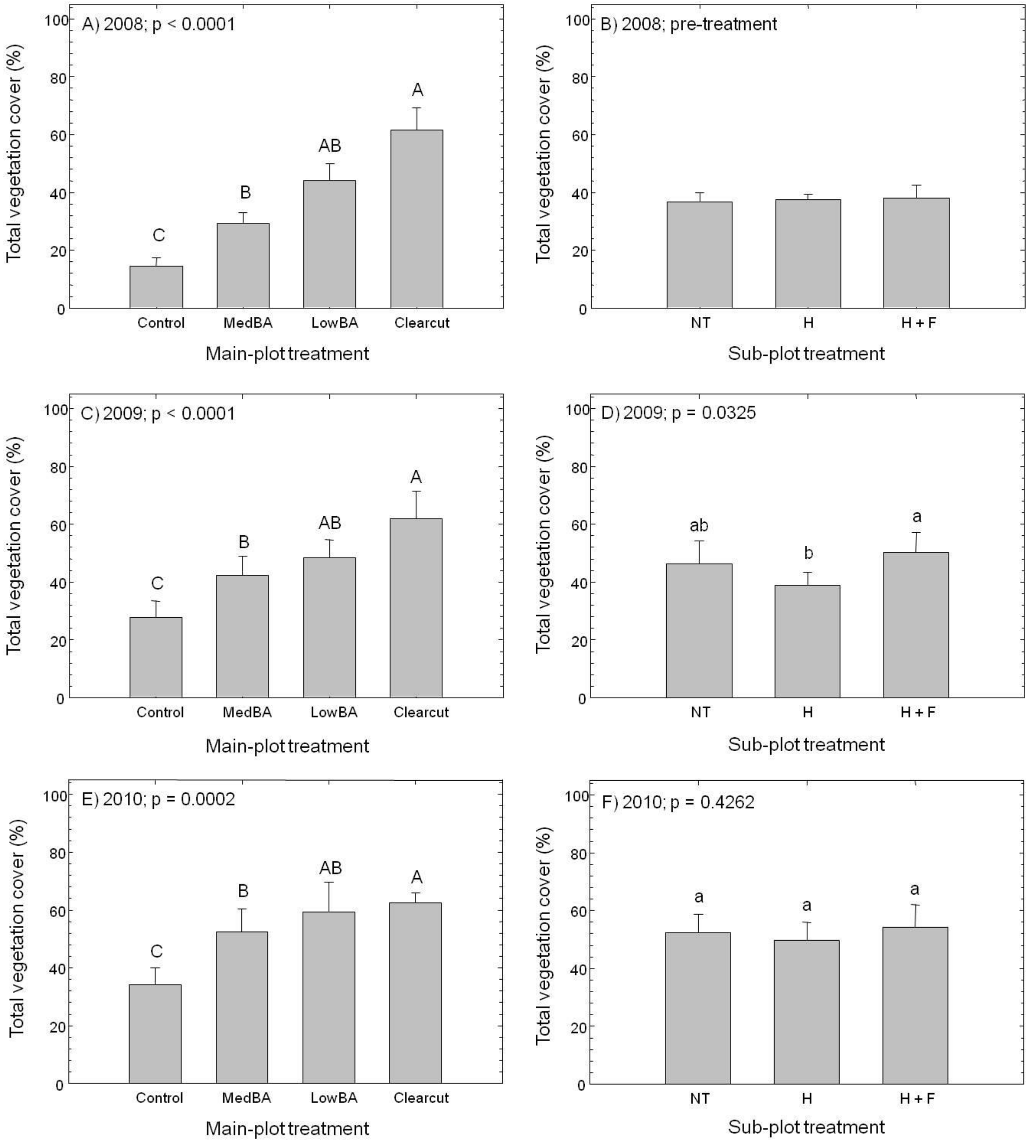

Figure 5.2. Total vegetation cover (mean + one SE) by main-plot treatment (panels A, C, and E) and sub-plot treatment (panels B, D, and F) in 2008, 2009, and 2010. The same letter indicates pair-wise comparisons are not significantly different at α = 0.05. No analysis was performed on panel B because sub-plot treatments had not been applied in 2008.

significantly affected by the main-plot treatments in each year (Figure 5.2). Generally, total vegetation cover increased with decreasing overstory density, although total vegetation cover was not significantly different between Clearcut and LowBA plots or between LowBA and MedBA plots. The uncut Control plots had the least amount of vegetation cover in each year. The sub-plot treatments had a significant effect on total vegetation cover in 2009 ($F_{2, 10}$ = 4.92; p = 0.0325), when the H+F plots had higher total cover than the H plots. The sub-plot effect was no longer significant in 2010 ($F_{2, 40}$ = 0.87; p = 0.4262).

Regardless of the treatment applied, herbaceous vegetation dominated the ground layer, with more than twice as much cover as woody species in all years (Figure 5.3). In 2008, the canopy treatment effect was significant for herbaceous ($F_{3, 15}$ = 13.6; p = 0.0001) and woody ($F_{3, 15}$ = 6.05; p = 0.0066) vegetation, with the pattern in vegetation response similar to that for total cover for each group. The greatest cover of herbaceous and woody vegetation was on Clearcut plots, and the least cover was on Control plots. In 2009, there was a significant interaction between the main-plot and sub-plot effects ($F_{6, 40}$ = 2.39; p = 0.0459). The sub-plot treatment effect was only significant on MedBA plots ($F_{2, 40}$ = 9.86; p = 0.0003), and the canopy treatment effect was significant on NT ($F_{3, 30.9}$ = 6.40; p = 0.0017) and H ($F_{3, 30.9}$ = 5.43; p = 0.0040) plots. Within the main-plot treatments, herbaceous cover in MedBA plots was significantly lower in H plots than in H + F plots; within the sub-plot treatments, the Clearcuts plots had greater vegetation cover than the Control plots on NT and H plots (Table 5.1). There was no interaction

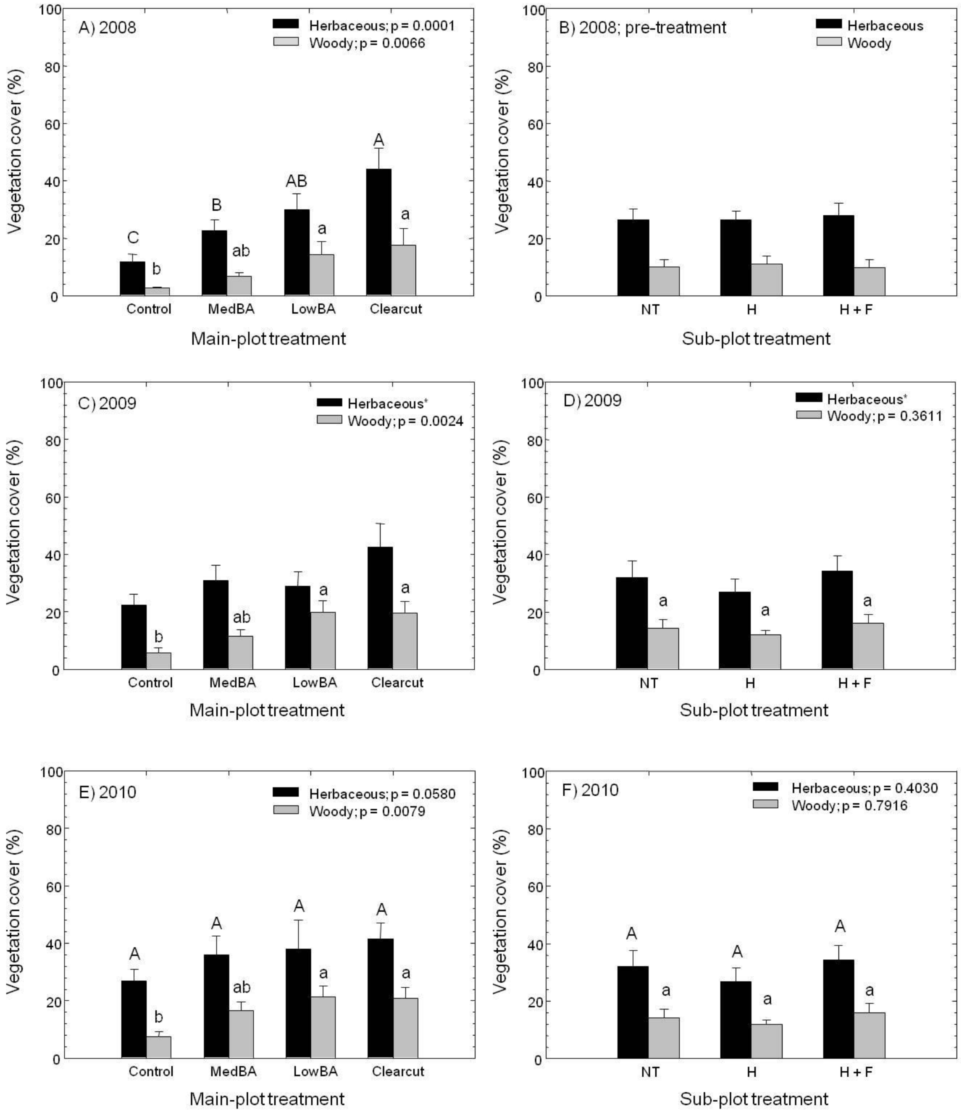

Figure 5.3. Herbaceous and woody vegetation cover (mean + one SE) by main-plot treatment (panels A, C, and E) and sub-plot treatment (panels B, D, and F) in 2008, 2009, and 2010. The same letter indicates pair-wise comparisons are not significantly different at α = 0.05. No analysis was performed on panel B because sub-plot treatments had not been applied in 2008. *Results are not presented for herbaceous cover in 2009 because there was an interaction between main-plot and sub-plot treatments.

Table 5.1. Results of significant interaction between main-plot and sub-plot effects for herbaceous vegetation cover in 2009; the same upper-case letters indicate no significant differences within columns and the same lower-case letters indicate no significant differences within row at α = 0.05

	Sub-plot						
	NT		H		H + F		
Main-plot	Mean	SE	Mean	SE	Mean	SE	**p-value**
Control	$^{B}20.9$	(4.5)	$^{B}20.1$	(5.2)	25.8	(4.1)	**0.3614**
MedBA	$^{AB}34.4^{ab}$	(7.2)	$^{B}20.2^{b}$	(2.6)	38.1^{a}	(7.4)	**0.0003**
LowBA	$^{AB}27.0$	(4.5)	$^{AB}26.1$	(5.2)	33.3	(6.4)	**0.1991**
Clearcut	$^{A}45.9$	(10.3)	$^{A}41.1$	(8.1)	40.2	(6.9)	**0.3691**
p-value	**0.0017**		**0.0040**		**0.1001**		

effect for woody vegetation in 2009 ($F_{6, 30}$ = 0.47; p = 0.8241), and the Clearcut and LowBA plots had significantly greater woody vegetation cover than the Control plots. Sub-plot treatments did not significantly affect woody vegetation cover in 2009 ($F_{2, 10}$ = 1.13; p = 0.3611). In 2010, there was no significant interaction effect for herbaceous ($F_{6, 40}$ = 1.57; p = 0.1825) or woody ($F_{6, 40}$ = 0.55; p = 0.7670) vegetation. There was no longer a significant main-plot treatment effect on herbaceous vegetation ($F_{3, 15}$ = 3.11; p = 0.0580), but woody cover was significantly greater on Clearcut and LowBA plots than on Control plots (Figure 5.3E). We found no significant effect of the sub-plot treatments on herbaceous ($F_{2, 40}$ = 0.93; p = 0.4030) or woody ($F_{2, 40}$ = 0.24; p = 0.7916) vegetation.

There were no interactions between main-plot and sub-plot treatment effects for any functional group in any year. In 2008, the canopy density treatments significantly

Table 5.2. Effects of main-plot and sub-plot treatments on vegetation cover by functional group in 2008; the sub-plot effect was not included in the analysis because treatments were not applied until 2009

2008		Graminoids		Forbs		Ferns		Woody stems		Woody vines	
Effect	Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot	Control	3.4^{b}	(0.7)	7.9^{b}	(2.4)	0.4	(0.2)	2.5^{b}	(0.4)	0.2	(0.1)
	MedBA	5.5^{b}	(0.9)	15.5^{ab}	(2.3)	1.6	(1.6)	6.2^{ab}	(1.2)	0.5	(0.1)
	LowBA	6.5^{b}	(1.1)	21.3^{ab}	(5.3)	2.0	(1.2)	13.8^{a}	(4.6)	0.6	(0.4)
	Clearcut	18.1^{a}	(4.7)	25.3^{a}	(5.0)	0.5	(0.3)	16.8^{a}	(5.8)	0.7	(0.4)
	p-value	**0.0006**		**0.0072**		**0.4723**		**0.0074**		**0.3334**	
Sub-plot	NT	8.3	(1.4)	17.1	(3.0)	1.2	(0.7)	9.4	(2.8)	0.6	(0.4)
	H	7.3	(1.1)	17.6	(2.4)	1.5	(1.0)	10.5	(2.7)	0.6	(0.2)
	H + F	9.5	(1.1)	17.9	(3.6)	0.8	(0.4)	9.5	(2.9)	0.3	(0.1)

Table 5.3. Effects of main-plot and sub-plot treatments on vegetation cover by functional group in 2009

2009		Graminoids		Forbs		Ferns		Woody		Woody vine	
Effect	Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot	Control	11.5^{b}	(3.0)	10.4	(2.1)	0.4	(0.2)	5.2^{b}	(1.9)	0.4	(0.2)
	MedBA	14.6^{ab}	(3.3)	15.9	(2.3)	0.5	(0.4)	10.4^{ab}	(2.0)	1.0	(0.6)
	LowBA	10.9^{b}	(1.6)	16.1	(3.7)	1.9	(1.5)	18.7^{a}	(4.4)	0.5	(0.2)
	Clearcut	23.6^{a}	(5.9)	18.1	(3.4)	0.7	(0.3)	18.4^{a}	(4.2)	1.1	(0.8)
	p-value	**0.0235**		**0.1240**		**0.5646**		**0.0056**		**0.6198**	
Sub-plot	NT	15.9	(3.9)	15.0	(2.0)	1.1	(0.6)	13.2	(3.2)	0.7	(0.3)
	H	12.7	(3.2)	13.4	(1.6)	0.8	(0.4)	11.0	(1.7)	1.0	(0.4)
	H+F	16.9	(2.1)	16.9	(3.3)	0.6	(0.4)	15.3	(3.1)	0.6	(0.4)
	p-value	**0.1522**		**0.1668**		**0.5312**		**0.3048**		**0.3462**	

Table 5.4. Effects of main-plot and sub-plot treatments on vegetation cover by functional group in 2010

2010		Graminoids		Forbs		Ferns		Woody		Woody vine	
Effect	Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Main-plot	Control	13.2^{b}	(2.7)	12.6	(3.0)	1.5	(0.9)	6.3^{b}	(1.6)	0.7	(0.4)
	MedBA	18.5^{ab}	(3.9)	16.9	(3.2)	1.2	(0.9)	15.6^{ab}	(2.7)	2.2	(1.0)
	LowBA	16.7^{ab}	(3.8)	17.8	(5.3)	3.8	(2.7)	18.3^{a}	(4.0)	1.1	(0.7)
	Clearcut	23.6^{a}	(4.6)	16.7	(2.6)	1.3	(0.7)	22.3^{a}	(3.4)	1.1	(0.6)
	p-value	**0.0172**		**0.2044**		**0.5920**		**0.0093**		**0.5840**	
Sub-pot	NT	18.4	(3.2)	16.0	(3.1)	2.1	(1.1)	14.9	(2.4)	1.0	(0.8)
	H	16.5	(3.7)	15.2	(2.9)	2.1	(1.0)	14.5	(2.4)	1.4	(0.6)
	H+F	18.3	(3.0)	16.8	(4.0)	1.2	(0.6)	17.0	(2.7)	0.9	(0.5)
	p-value	**0.3547**		**0.8075**		**0.5251**		**0.6754**		**0.2092**	

affected the cover of graminoids ($F_{3, 15}$ = 10.27; p = 0.0006), forbs ($F_{3, 15}$ = 5.90; p = 0.0072), and woody stems ($F_{3, 15}$ = 5.84; p = 0.0075). For each functional group, the greatest amount of cover was on the Clearcut plots and the least amount of cover was on the Control plots (Table 5.2). For forbs and woody stems, the intermediate density treatments (MedBA and LowBA) resulted in intermediate vegetation cover; for graminoids, cover was similar among all treatments that retained canopy trees but greater on Clearcut plots. In 2009 and 2010, the patterns of vegetation response were similar to that in 2008, but only the graminoid and woody stem groups were significantly affected by the canopy density treatments. In both years, the Clearcut plots had greater cover of graminoids and woody stems than the Control plots. There were no sub-plot treatment effects on any functional group in either 2009 or 2010 (Tables 5.3 and 5.4).

Results from the repeated measures analysis indicate that total vegetation cover increased over time ($F_{2, 38.5}$ = 16.91; $p < 0.0001$), with no interaction between year and treatment effects ($F_{6, 38.5}$ = 1.85; p = 0.1147). Total cover was significantly higher in 2010 than in 2008, but total cover in 2009 was not significantly different from either other year (Figure 5.4). Ferns, woody stems, and woody vines followed similar patterns as total vegetation cover over time, but there was an interaction between treatment and year effects for forbs ($F_{6, 39.6}$ = 2.5; p = 0.0383). Forb cover did not change over time on the Control, MedBA or LowBA plots, but forb cover decreased over time on Clearcut plots (Figure 5.5).

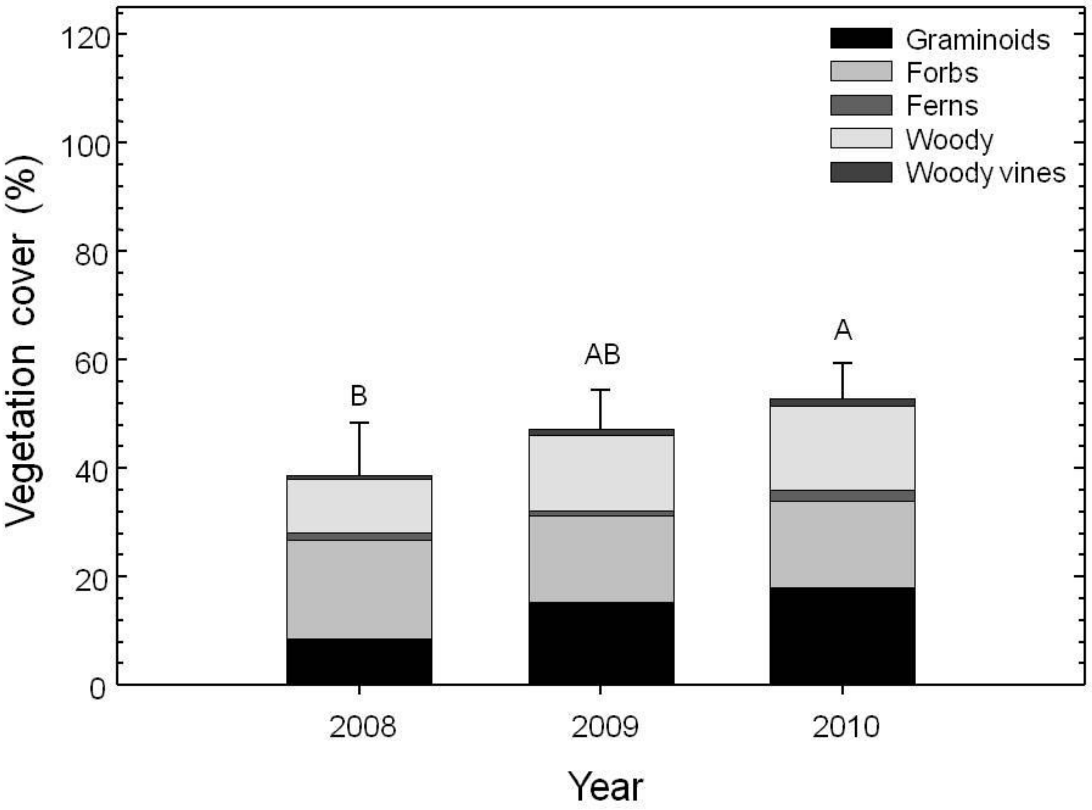

Figure 5.4. Vegetation cover (%) by functional group in 2008, 2009, and 2010. Only NT sub-plots were used for the analysis because sub-plot treatments were applied in 2009. Error bars are one standard error of the mean total cover, and the same letter indicates pair-wise comparisons are not significantly different at α = 0.05.

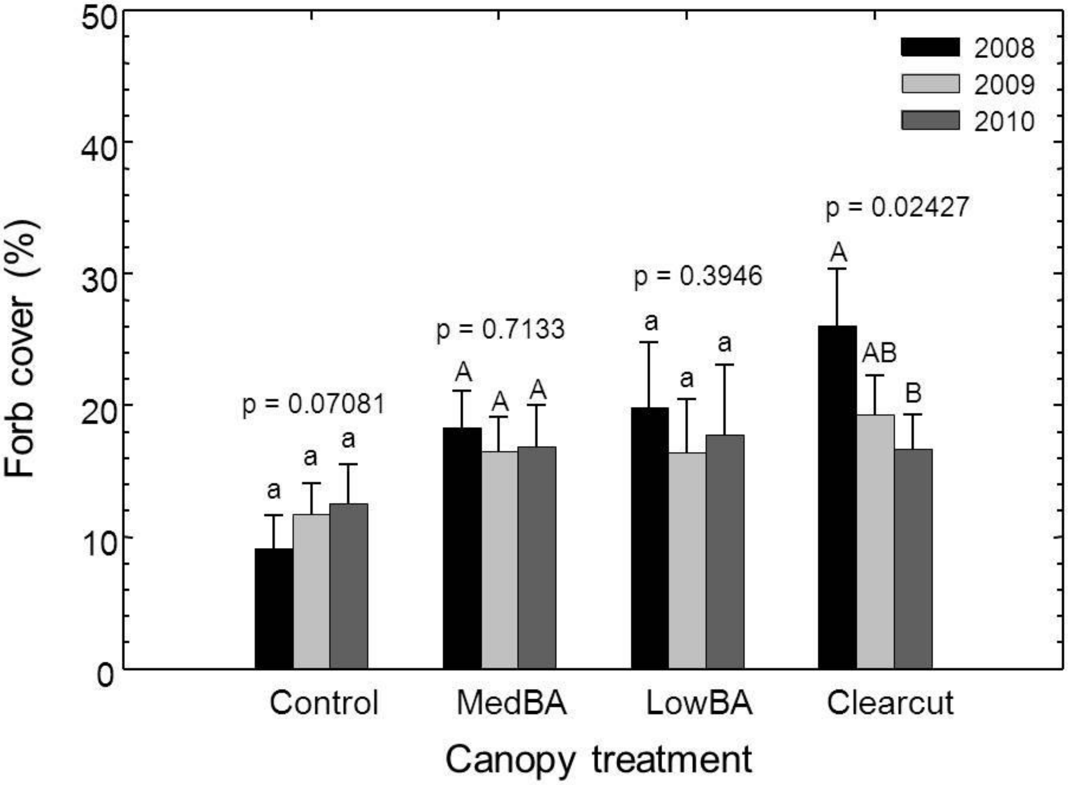

Figure 5.5. Results of repeated measures ANOVA showing the significant year by treatment interaction for mean cover (+ one SE) for forbs. P-values relate to year effects within each treatment, and the same letter indicates pair-wise comparisons among years within each treatment are not significantly different at α = 0.05.

Changes in vegetation structure may have large implications for fuels and fire management. We found no interactions between main-plot and sub-plot treatments on cover of bunchgrasses or pinestraw in either 2009 or 2010 ($p \geq 0.1499$). The main-plot treatments significantly affected the cover of pinestraw in 2009 ($F_{3, 15} = 71.25$; $p < 0.0001$) and 2010 ($F_{3, 15} = 44.40$; $p < 0.0001$), with greater pine straw associated with the density of the canopy (Figure 5.6). Although bunchgrasses appeared slightly more

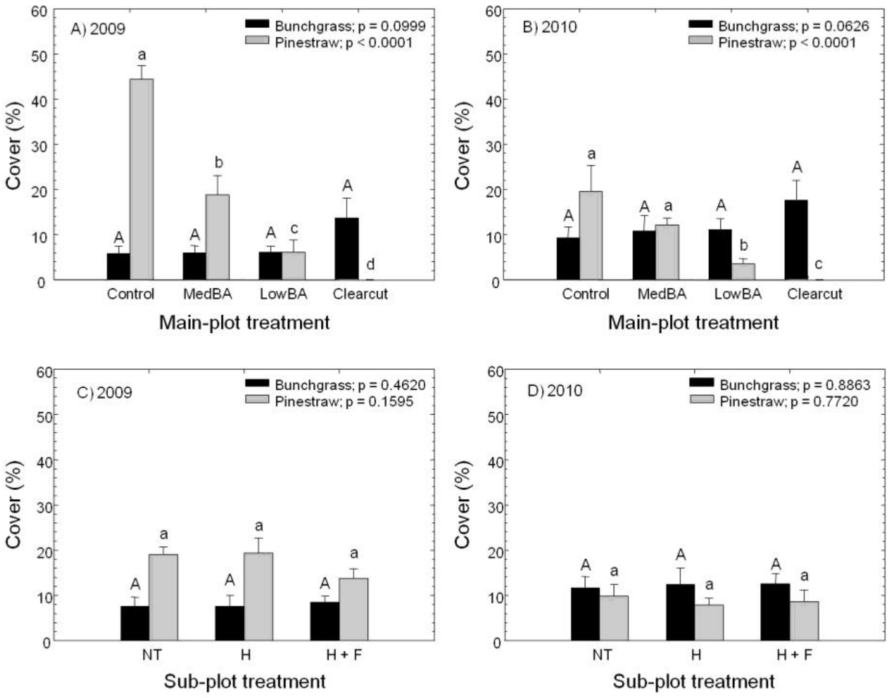

Figure 5.6. Cover of important fine fuels (bunchgrasses and pine straw) by main-plot (panels A and B) and sub-plot (panels C and D) treatment in 2009 and 2010. The same letter within a response variable indicates pair-wise comparisons are not significantly different at $\alpha = 0.05$.

abundant on Clearcut plots in both years, there were no significant main-plot effects on bunchgrass cover in 2009 ($F_{3,\,15}$ = 2.49; p = 0.0999) or 2010 ($F_{3,\,15}$ = 3.02; p = 0.0626). The sub-plot treatments did not significantly affect either bunchgrasses or pine straw in 2009 or 2010. Although woody vegetation cover did not dominate the ground layer in any year, the release and development of woody vegetation into the midstory layer could threaten restoration efforts. In 2010, the majority of the woody vegetation cover was *Rubus* spp. for all treatments (Figure 5.6). Loblolly pine and sweetgum made only minor contributions to the woody species cover. Sub-plot treatments did not significantly affect the cover of *Rubus* spp. ($F_{2,\,40}$ = 0.94; p = 0.3989) or loblolly pine ($F_{2,\,40}$ = 1.72; p = 0.1918) by the end of the third growing season, but sweetgum ($F_{2,\,40}$ = 4.71; p = 0.0145) had significantly greater cover on NT plots than on H+F plots.

The number of woody stems in the midstory layer was significantly affected by canopy density in 2008 ($F_{3,\,63}$ = 5.32; p = 0.0025), with greater stem density on the Clearcut and LowBA plots than on the Control and MedBA plots (Figure 5.8). There were no interactions between main-plot and sub-plot effects in 2009 or 2010 ($p \geq 0.1560$). Stem density increased with canopy removal in 2009 and 2010, and by the end of the 2010 growing season the Clearcut plots averaged 1222 stems per hectare and the Control plots averaged 42 stems per hectare. The sub-plot treatment effect was significant in 2009 ($F_{2,\,40}$ = 8.31; p = 0.0010), with higher stem density on the Control plots than on H and H+F plots. In 2010, the sub-plot treatment effect was not significant ($F_{2,\,40}$ = 0.54; p = 0.5861), despite a range of 548 stems per hectare on the NT plots to 48

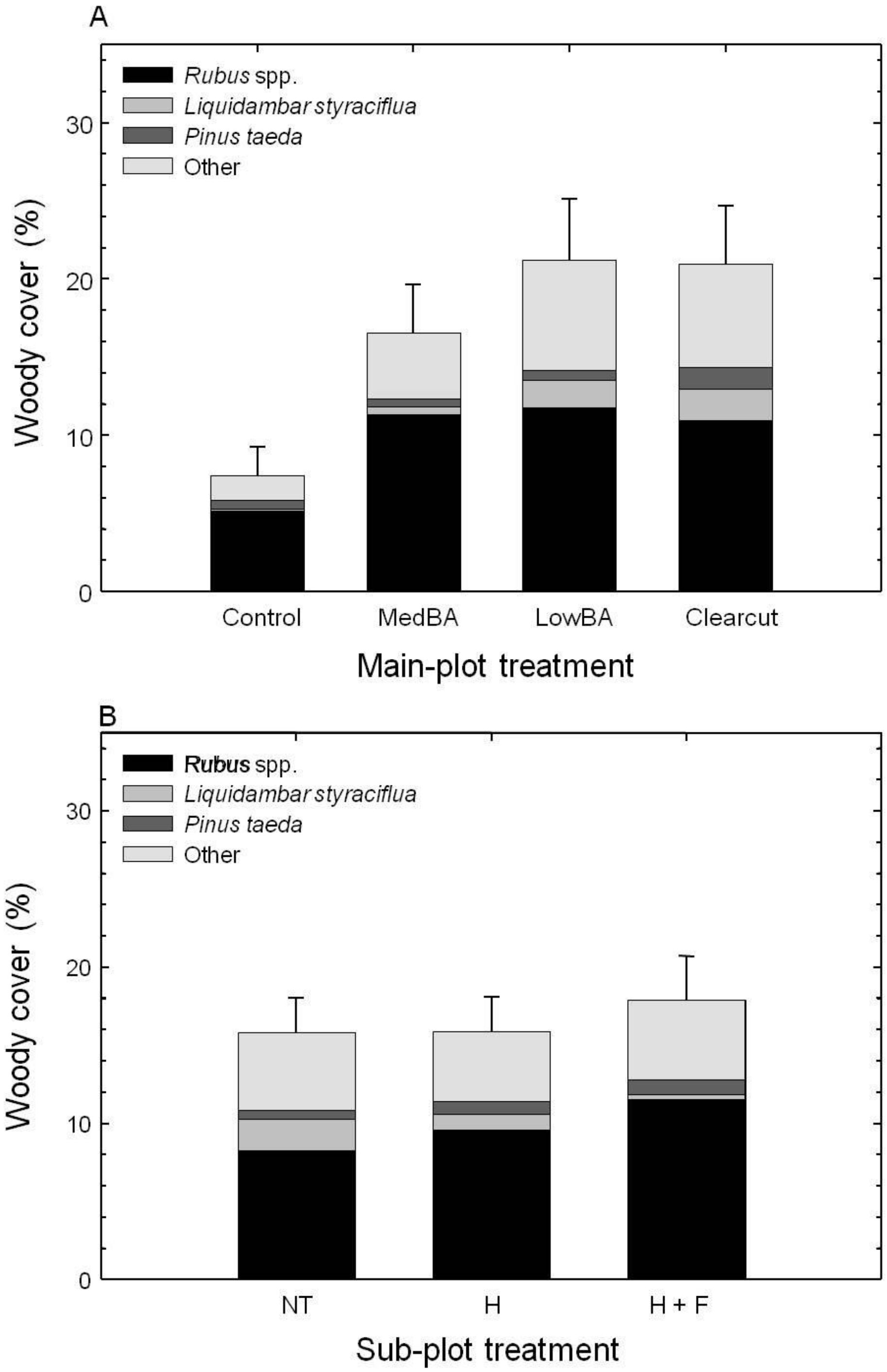

Figure 5.7. Total woody cover in 2010 (mean + one SE) by contributing woody species of interest for A) main-plot treatments and B) sub-plot treatments.

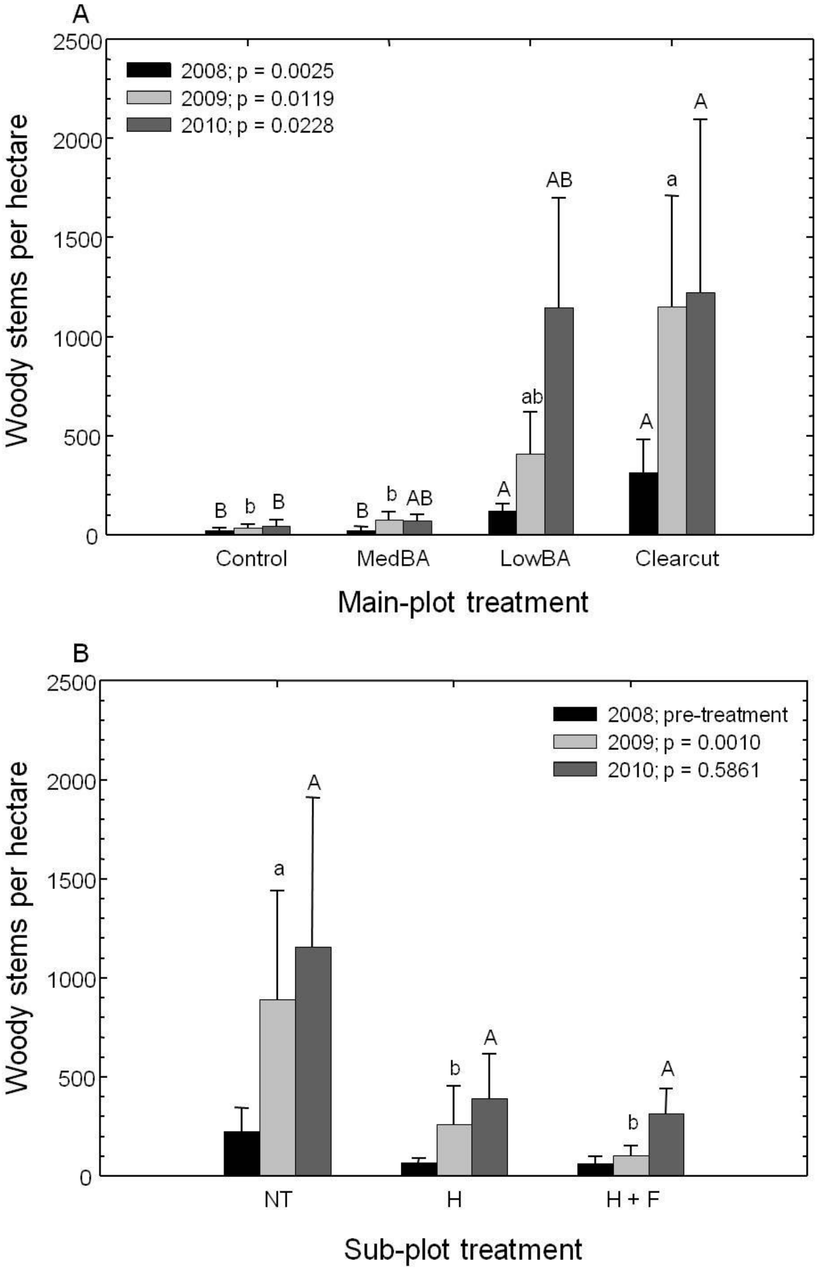

Figure 5.8. Woody stem density in the midstory layer (mean + one SE) in 2008, 2009, and 2010 by A) main-plot treatment and B) sub-plot treatment. The same letter indicates pair-wise comparisons among treatments within each year are not significantly different at $\alpha = 0.05$.

stems per hectare on the H + F plots. The number of stems per hectare for the five most common species is shown in Appendices A-5.1 and A-5.2.

5.4. Discussion

Canopy trees moderate the understory community by regulating abiotic conditions and competing for limited resources (Anderson et al. 1968, Roberts 2004, Wagner et al. 2010). The release of nutrients (light, nutrients, water) following canopy removal is generally associated with increases in ground layer plants, and thinning disturbances have commonly been reported to increase the abundance of ground layer vegetation in a variety of ecosystems (e.g., Frederickson et al. 1999, Harrington and Edwards 1999, Zenner et al. 2006, Wilson et al. 2009, Ares et al. 2010). Grelen and Enghardt (1973) reported increases in herbaceous vegetation of longleaf pine communities that was proportional to the intensity of canopy thinning. In 8- to 11-year old longleaf pine plantations at the Savannah River Site, GA, Harrington and Edwards (1999) found that forb, grass, vine, and shrub cover increased following experimental reductions of canopy density. They determined that the increased light availability strongly controlled increases in herbaceous vegetation but that increased soil moisture was also important.

Our results demonstrate a consistent increase in vegetation cover following canopy removal, although response patterns differed across functional groups and over time. We observed that total vegetation cover and woody vegetation cover increased as canopy decreased from uncut Control plots to Clearcut plots, which was consistent in each year. However, the response of herbaceous vegetation changed over time; in the first year following treatment, herbaceous cover appeared strongly linked to canopy density, but by the third growing season there were no longer significant effects of canopy density on herbaceous vegetation cover. Moreover, the presence of canopy trees at any density (Control, MedBA, or LowBA) limited bunchgrass cover in 2008 and 2009, but only bunchgrass cover on Control plots was different from Clearcut plots in 2010.

Differences in the response of herbaceous and woody vegetation may be related to several factors. Competitive strategies, including trade-offs between the ability to tolerate limiting resources and the ability to utilize resources rapidly for growth, often differ among individual species but may be grouped according to similar growth patterns (Smith and Huston 1989). Although herbaceous and woody species have been shown to exhibit wide ranges of competitive abilities (Grime 1977), spatial variability in the distribution of above- and below-ground biomass affects resource availability for different vegetation types. Models of root partitioning suggest that the root systems of woody plants often extend deeper in the soil profile than those of herbaceous plants (Walter 1971, Schenk and Jackson 2002). In longleaf pine forests of southwestern Georgia, Pecot et al. (2007) reported that differences in rooting depth affected the response of understory plants to increases in resource availability; herbaceous plants responded strongly to increases in light availability and woody plants responded to increases in below-ground resources. The differential response was attributed to strong root competition between woody vegetation and canopy trees deeper in the soil profile, as well as differences in shade tolerance between the woody and herbaceous vegetation. The consistent response of woody vegetation to canopy release over time in our study suggests that overstory competition strongly controls woody cover, but changes in the patterns of herbaceous cover over time indicate that other factors are affecting herbaceous response.

Effects of the prescribed fire between the second and third growing seasons on the vegetation response likely contributed to the response patterns in 2010. It is widely reported that repeated burning with low-intensity surface fires reduces the presence of woody vegetation and enhances herbaceous species abundance (Gilliam and Christensen 1986, Waldrop et al. 1992, Peterson and Reich 2001, Reich et al. 2001). In longleaf pine systems, repeated burning eliminates woody midstory density and increases the biomass of grasses and forbs (Brockway and Lewis 1997). Haywood et al. (2001) reported that herbaceous biomass ranged from 12 kg/ha in unburned longleaf pine plots to 1113 kg/ha in plots that had received biennial burning for a 37 year period in central Louisiana. We found that the cover of herbaceous vegetation was no longer significantly affected by canopy density in 2010, suggesting that the prescribed fire may have stimulated regrowth of herbaceous plants regardless of canopy density. However, the effects of a single fire on woody vegetation may be more variable (Arthur et al. 1998), and our results show that the prescribed fire did not reduce the cover of woody vegetation the year following burning. The number of woody stems in the midstory layer did not decrease between 2009 and 2010, suggesting that the single prescribed fire had little overall effect on woody plant structure. Although it is likely that the prescribed fire contributed to the vegetation response patterns observed in 2010, our study was not designed to test effects of a single fire and we cannot make conclusive interpretations about the role of fire on the observed vegetation response.

Objectives of longleaf pine ecosystem restoration commonly include reducing dominance of woody vegetation in the ground layer, especially when site history includes fire exclusion and the stand has developed a hardwood layer (Provencher et al. 2001, Mitchell et al. 2006, Brockway et al. 2009). Our results indicate that the development of woody species is not currently a major challenge for restoration on these particular sites. Of the woody species within the ground layer, the majority of the cover was from *Rubus* spp. rather than tree seedlings that could threaten restoration over time. In particular, natural loblolly pine regeneration could potentially dominate the understory of stands restored using loblolly pine canopy retention (Knapp et al. 2011), but we observed that loblolly pine regeneration was only a very minor component of the ground layer cover. Although sweetgum was the most commonly occurring species in the midstory layer, we found that it did not contribute more than 5% cover to the ground layer vegetation. Previous researchers have discussed concerns with gap-based longleaf pine restoration management because canopy removal can result in the release and rapid growth of woody stems (Jack et al. 2006, Pecot et al. 2007). Our results support this finding, suggesting that clearcutting may result in the development of a woody midstory layer without additional herbicide control.

Given the threat of hardwoods to longleaf pine restoration, herbicides have been studied as a technique to rapidly change vegetation structure by reducing woody stem density and improving fire management options (e.g., Kush et al. 1999, Provencher et al.

2001, Freeman and Jose 2009, Haywood 2009, Jose et al. 2010). The appropriate herbicide type is largely dependent on the initial vegetation density and composition, and therefore past studies commonly tested different herbicide prescriptions. Herbicides that target woody vegetation, including imazapyr, hexazinone, and triclopyr, have been reported to reduce the abundance of woody species and often increase longleaf pine seedling growth (Knapp et al. 2006, Freeman and Jose 2009, Jose et al. 2010) or the cover of herbaceous vegetation (Brockway et al. 1998, Freeman and Jose 2009). In our study, herbicides significantly reduced midstory woody stem density in the first year following application, but high variability in stem densities resulted in no significant differences two years after treatment. The long-term effects of herbicides on stand structure are not well understood, but Kush et al. (1999) reported that the understory biomass of woody vegetation was higher on plots treated with a single herbicide application than on untreated controls 23 years after treatment, suggesting that herbicide effects may be transient and require multiple applications. Provencher et al. (2001) found that prescribed fire was more effective at increasing herbaceous plant densities than herbicide control of woody vegetation, and it is not likely that short-term improvements in ground layer vegetation structure caused by herbicides can be maintained without frequent fire management (Brockway and Outcalt 2000, Freeman and Jose 2009). Therefore, initial herbicide applications may be used to change the vegetation structure in such a way that the fuel matrix can support frequent surface fire; once fire management can be applied, additional herbicide treatments may not be needed. It should also be noted that we targeted woody vegetation with herbicides during site preparation in this study. Therefore, the treatment effects on woody vegetation represent control of vegetation not killed by the site preparation treatments and are likely an underestimation of herbicide effects in the absence of site preparation.

Because the establishment success of artificially regenerated longleaf pine seedlings may be reduced by competition with dense herbaceous vegetation, herbaceous control is commonly used for longleaf pine establishment (Haywood 2000, Ramsey et al. 2003, Haywood 2005). In our study, herbaceous vegetation control was applied in bands over the rows of longleaf pine seedlings, with the objective of localizing herbicide effects around seedlings. As a result, approximately 30% of the study plots were treated with the herbaceous vegetation control treatment, and we found few effects of the herbicide treatment on herbaceous vegetation at the stand level. Targeted application of herbicides is often favored over broadcast application for restoration of sensitive plant communities and has been found to result in greater species richness and diversity than broadcast application in longleaf pine forests in Florida (Brockway and Outcalt 2000). Therefore, in situations when herbaceous vegetation is dense enough to affect seedling performance, we recommend using band-spray herbicide application to reduce the stand-level effects on the herbaceous plant community.

5.5. Management implications

Converting loblolly pine stands to the longleaf pine ecosystem requires attention to the ground layer vegetation, which is a critical component of the system that strongly controls ecosystem function and diversity. The target stand conditions for longleaf pine restoration include a ground-layer that is dominated by herbaceous species, with a minor component of hardwoods and few midstory stems; the desired herbaceous layer includes large bunchgrasses that serve as fine fuels for frequent surface fire and forbs that support high levels of floral diversity. The structure and condition of ground layer vegetation at a given time are the reflection of land use history and management legacies, in addition to biotic and abiotic controls on plant establishment and persistence (Brudvig and Damschen 2011). Therefore, the initial conditions of the stand will largely affect the magnitude of response of the vegetation community to canopy removal. On our study sites, herbaceous plants dominated the ground layer vegetation, and both herbaceous and woody vegetation increased following canopy removal. Woody vegetation cover was strongly controlled by canopy density through three years after harvesting, but the effects of canopy density on herbaceous plant cover were transient.

Clearcutting is traditionally used for establishing longleaf pine seedlings on sites occupied by other pine species, and past studies have demonstrated rapid seedling growth in the absence of canopy trees (e.g., Haywood 2005, Knapp et al. 2006, Freeman and Jose 2009, Hu et al. 2011). Despite potential short-term increases in seedling growth on clearcut plots, the long-term effects of clearcutting on the vegetation structure may conflict with restoration objectives (Mitchell et al. 2006, Kirkman et al. 2007). For example, the characteristically high level of floral diversity in the longleaf pine ecosystem is largely found among the forb group. We found few effects of our treatments on forb cover throughout this study, except for a decrease in forb cover from

2008 to 2010 on the Clearcut plots. The reason for the decrease is not clear, but it is possible that an increase in woody vegetation began to out-compete the forbs. Although species richness and composition are not reported here, it is likely that floral diversity will decrease on Clearcut plots if forb cover continues to decline. In addition, a frequent fire regime is critical to maintain the desired vegetation structure, and fine fuels provided by bunchgrasses and pine needles from canopy trees are important fuels. Previous studies have demonstrated that prescribed fires burn hotter and more completely beneath canopy trees, where pine needle inputs increase fuel loads (Williamson and Black 1981, Grace and Platt 1995), and our study supports these findings. We found that pine needle cover was higher on plots with higher stand basal area, while bunchgrass cover was not significantly affected by canopy density. Previously, Knapp et al. (2011) found that the prescribed fires burned more completely on Control and MedBA plots than on the Clearcut plots. These results, along with the increased density of midstory stems on Clearcut plots, suggest that clearcutting may have important, undesirable long-term effects on the development of these stands.

Our results indicate that low-to-moderate canopy removal can be used to encourage the development of herbaceous vegetation while limiting release of woody species into the midstory during longleaf pine restoration. If dense woody stems are present, herbicides that target arborescent vegetation are recommended to reduce the midstory layer. We found no effects of fertilizer or herbaceous vegetation control (applied in bands) on stand-level vegetation structure, suggesting that these treatments may be applied to improve longleaf pine seedling establishment as needed. However, it is not clear how the short-term results presented here may change throughout stand development. Continued management with frequent prescribed fire will ultimately be necessary to achieve and maintain the desired stand structure of the longleaf pine ecosystem.

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CHAPTER VI: SPECIES RICHNESS AND COMPOSITION OF UPLAND PINE FORESTS FOLLOWING LONGLEAF PINE RESTORATION

6.1. Introduction

The contribution of species richness to ecosystem stability and ecological function (Tilman 1996, Loreau et al. 2001) has resulted in the conservation of biodiversity becoming a major objective for ecosystem restoration (Mitchell et al. 2006). The longleaf pine (*Pinus palustris* Mill.) ecosystem of the southeastern United States is recognized as one of the most floristically diverse ecosystems in North America (Sorrie and Weakley 2001, Peet 2006). The characteristic stand structure of fire-maintained longleaf pine forests includes a canopy dominated by longleaf pine with little to no mid-story layer, and the exceptional diversity of this system is found primarily in the ground layer vegetation. For example, Walker and Peet (1983) identified over 40 species within 0.25 m^2 in the Green Swamp of the lower coastal plain of North Carolina, and Peet (2006) described many areas with greater than 100 species occurring within 1000 m^2. Such levels of diversity are comparable with those found in cove forests of the Great Smoky Mountains (Mitchell et al. 2006) and contribute to a unique biological legacy of the longleaf pine ecosystem.

Patterns of floristic diversity in longleaf pine ecosystems are largely associated with gradients of soil moisture and soil texture and are maintained by frequent surface fire (Walker and Peet 1983, Kirkman et al. 2001, Kirkman et al. 2004). The wide ecological amplitude of longleaf pine encompasses habitats that range from xeric sandhill sites to wet or even hydric flatwoods and savannas, often within relatively small spatial extent, providing the opportunity to determine richness levels across gradients of soil conditions. Peet (2006) developed a model that categorizes longleaf pine communities in relation to soil texture and soil moisture, with species richness increasing in association with increases in both moisture and silt content. The role of disturbance in maintaining species diversity has been widely discussed in ecology (Connell 1978, Denslow 1980), and fire has been shown to increase species richness in a number of different ecosystems (Tester 1989, Arthur et al. 1998, Peterson and Reich 2008). In longleaf pine forests, frequent fires limit the development of hardwood species (Waldrop et al. 1992, Provencher et al. 2001, Kirkman et al. 2004) and increase the reproductive potential of many herbaceous species (Platt et al. 1988, Streng et al. 1993, Mulligan and Kirkman 2002, Shepherd et al. 2011). Previous studies have shown that floral diversity of pine woodlands and savannas increases with frequent fire (Walker and Peet 1983, Gilliam and Christiansen 1986, Mehlman 1992, Brockway and Lewis 1997).

A variety of anthropogenic influences have resulted in reductions in biological diversity globally (Butchart et al. 2010) and led to increased interest in the conservation of biological diversity in managed and restored communities (Rudd 2011). Land-use legacies, management history, and landscape patterns of fragmentation each contribute to current patterns of biological diversity (Hedman et al. 2000, Walker and Silletti 2006, Brudvig and Damschen 2011). A history of fire exclusion and changes in land use have resulted in widespread reduction and fragmentation of the longleaf pine ecosystem, with many upland sites converted from longleaf pine to loblolly pine (Frost 1993, Schultz

1999). As a result, the diversity of many of these communities has decreased and numerous species have become rare or threatened and pose concerns for regional conservation of biodiversity (Sorrie and Weakley 2006). Walker (1993) identified 187 species associated with the longleaf pine ecosystem that are currently considered rare, threatened or endangered, and Glitzenstein et al. (2001) updated this list with over 200 additional species. The large number of endemic plants within the longleaf pine range suggests that continued habitat loss and fragmentation will result in the risk of future species extinctions without significant conservation efforts (Walker 1993, Sorrie and Weakley 2001, Sorrie and Weakley 2006).

The widespread reduction in the longleaf pine ecosystem and habitat pressures for endangered species that rely on the ecosystem, such as the red-cockaded woodpecker (RCW; *Picoides borealis*), have resulted in recent interest in longleaf pine restoration on sites that currently support other southern pines. In many cases, recent management that includes fire exclusion has drastically altered the structure of these stands, resulting in higher densities of woody species and lower floristic diversity than found on remnant stands (Walker et al. 2010). Ecosystem restoration requires successful establishment of longleaf pine and the re-establishment of the ground layer community associated with this system (Walker and Silletti 2006). However, because longleaf pine seedling growth can be strongly reduced by competition from canopy pines (e.g. Palik 1997, Mitchell et al. 2006), some degree of canopy removal will likely be required for seedling growth, and managers need information on how longleaf pine establishment affects ground layer vegetation. Additional forest management practices, including herbicides or fertilizers, are commonly applied to improve planted longleaf pine seedling success (e.g., Ramsey et al. 2003, Gagnon et al. 2003, Haywood 2005) or to improve the structure and composition of the ground layer vegetation (e.g., Brockway et al. 1998, Freeman and Jose 2009, Jose et al. 2010).

Conserving biological diversity is an important objective of longleaf pine management (Mitchell et al. 2006), and land managers need information about how restoration management affects species composition and richness. Past research demonstrates that canopy removal and associated management actions can have significant effects on the ground layer plant community in other ecosystems (e.g., Gilliam 2002, Roberts 2002, Zenner et al. 2006). This study was established to determine how longleaf pine restoration management affects the richness and composition of ground layer vegetation in existing loblolly pine stands. Our study included pine stands located in two adjacent ecoregions, and differences in soil texture among the sites allowed us to measure the effects of soil texture on plant communities in response to management treatments. Our specific objectives were to: 1) determine the effects of thinning intensity and herbicide/fertilizer on species richness at different scales; 2) determine effects of soil texture on species richness in relation to restoration treatments; and 3) explore the site factors controlling patterns of species composition during longleaf pine restoration in loblolly pine stands located along the Fall Line in Georgia and Alabama.

6.2. Materials and methods

Study site and experimental treatments

This study was conducted at Fort Benning, GA and included the uniform plots in all six blocks described in Chapter 1.4. The study includes three blocks that are located on loam soils in the Upper Loam Hills (Blocks 1, 2, and 5) and three blocks located on sand soils in the Sandhills (Blocks 3, 4, and 6). The blocks were selected to minimize between-block heterogeneity of stand structure and to minimize within-block heterogeneity of soil properties; however, soil properties were similar among the blocks in each respective ecoregion (Table 6.1). We compiled data on land-use and management history from the Fort Benning Land Management Division, but study areas were not selected to represent specific criteria related to site history.

The experiment is a randomized, complete block, split-split-plot design, with the location of individual loblolly pine stands as the random block factor nested within soil type. Each block was divided into four main treatment plots and each main plot received an overstory treatment. Main plots were 100 x 100 m (1 ha), with the exception of the Clearcut plots, which were 141 x 141 m (2 ha) to create clearcut conditions in the plot center. The four overstory treatments resulted in the uniform distribution of canopy pines at different densities: Control (uncut; residual basal area ~ 16 m^2/ha); MedBA (single-tree selection to create a uniform canopy with the target basal area of 9 m^2/ha); LowBA (single-tree selection to create a uniform canopy with the target basal area of 5 m^2/ha); and Clearcut (all trees removed to basal area of 0 m^2/ha).

Table 6.1. Summary of stand structure, soil texture, and site history by study block

		Block					
Type	Variable	1	2	3	4	5	6
Stand structure	BA (m^2/ha)	8.9	8.3	7.9	7.3	9.8	7.3
	DBH (cm)	38.0	29.2	25.7	33.9	41.5	32.4
	Total ground-layer vegetation cover (%)	73.6	48.2	31.8	34.2	45.0	38.2
Soil texture	Sand content (%)	66.7	75.9	87.2	88.7	76.1	86.9
	Silt content (%)	17.2	14.0	5.3	5.5	14.0	6.3
	Clay content (%)	16.1	10.1	7.5	5.8	9.9	6.8
	Texture class	sandy loam	sandy loam	loamy sand	sand	sandy loam	loamy sand
Site history	Land use in 1944*	agriculture	forested	forested	mixture	agriculture	agriculture
	Prescribed burns since 1981	7	6	11	9	6	7
	Wildfires since 1981	3	1	4	0	3	1
	Total burns since 1981	10	7	15	9	9	8

*Land use was determined by visual inspection of aerial photographs from 1944. ‘Mixture’ indicates that part of the block was in agriculture and part of the block was forested.

Sub-plot treatments include additional cultural practices designed to enhance ecosystem restoration, through either improvement of conditions for planted LLP seedlings or changes to ground layer vegetation. The sub-plot treatments included an untreated control (NT), competition control with herbicide (H), and competition control with herbicide combined with fertilizer (H+F). Main-plot treatments were each divided into four equal sections for cultural treatment application. Within each section, sub-plot treatments were applied to a 30 x 30 m area centered on a 20 x 20 m measurement plot. The herbicide treatment was designed to improve conditions for planted longleaf pine seedlings by reducing competition from surrounding vegetation and to eliminate encroachment from woody species. We prescribed a direct spray of 1% imazapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid) plus 0.25% non-ionic surfactant in October 2008 to control woody vegetation. Because herbaceous vegetation dominated most of the study sites, we applied an additional granular mix of 63.2% hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and 11.8% sulfometuron methyl {Methyl 2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]-carbonyl]amino]sulfonyl]benzoate} at a rate of 0.84 kg/ha, sprayed in approximately 1 m wide bands over top of longleaf pine seedlings in March 2009. The H+F treatment included the herbicide treatments described above as well as an application of 280 kg/ha 10-10-10 NPK granular fertilizer. The fertilizer treatment was broadcast by hand in April 2009.

Following timber harvest, study sites were prepared in accordance with standard management procedures used for longleaf pine establishment at Fort Benning, with the objectives of removing woody competitors and preparing the sites for planting container-grown longleaf pine seedlings. Site preparation included an herbicide treatment of 2.34 l/ha imazapyr mixed with 2.24 kg/ha glyphosate (N-(phosphonomethyl) glycine, isopropylamine salt) and applied in September 2007, followed by prescribed fire in November 2007. Study sites were planted by contracted crews with container-grown longleaf pine seedlings at 1.8 x 3.7 m spacing, for a total of 1495 seedlings per hectare. Planting began in mid-November 2007 and was completed by January 2008. All study areas were burned with dormant season prescribed fires that were applied between the second and third growing seasons (January – April 2010). Additional information on treatments, treatment application, site preparation, and prescribed burns is described in Chapter 1.5.

Data collection

Vegetation sampling

We used a nested sampling design to quantify species richness and composition at different scales. In each sub-plot measurement area, we randomly located one transect running parallel with the measurement plot boundary and established a 10 x 10 m (100 m^2) sampling plot at a random starting location along the transect (Figure 6.1). Within each corner of the 10 x 10 m sampling area, we established nested sampling areas that were 0.316 x 0.316 m (0.1 m^2), 1 x 1 m (1 m^2) and 3.16 x 3.16 m (10 m^2). In August 2010, we recorded the presence of each species occurring in the smallest scale and additional species at each subsequent scale for each corner of the sampling area (n = 4 for the 0.1, 1, and 10 m^2 sampling scales and n = 1 for the 100 m^2 sampling scale in each sub-plot).

Species that could not be positively identified in the field were collected (from outside study plots when possible) and immediately pressed for laboratory identification. We worked with personnel of the Clemson University Herbarium to identify unknowns. Some species could not be positively identified because they lacked the required features (e.g. flowering or seed structures). In such cases, species were identified to the genus and grouped for analyses; this was most common for functionally similar genera such as *Dichanthelium* spp., *Rhychospora* spp., and *Solidago* spp. Taxonomy followed Weakley (2010) and functional groups were assigned to each species based on classifications from the USDA PLANTS Database (http://plants.usda.gov/java/). A complete list of species identified and used in analyses is included in Appendix A-6.1.

Stand and site data

We described stand and soil characteristics to determine factors controlling patterns in vegetation composition. In 2008, diameter at breast height (DBH; cm) of all trees within each sub-plot measurement area was recorded, and mean DBH and basal area (BA; m^2/ha) were determined at the sub-plot level. We used hemispherical photographs to quantify light availability (measured as gap light index; GLI) at the sub-plot level (for additional details, see Chapter 3). Volumetric soil moisture at a depth of 6 cm and soil temperature at a depth of 10 cm were measured in June, July, and August 2010 from five points systematically located throughout each sub-plot. In September

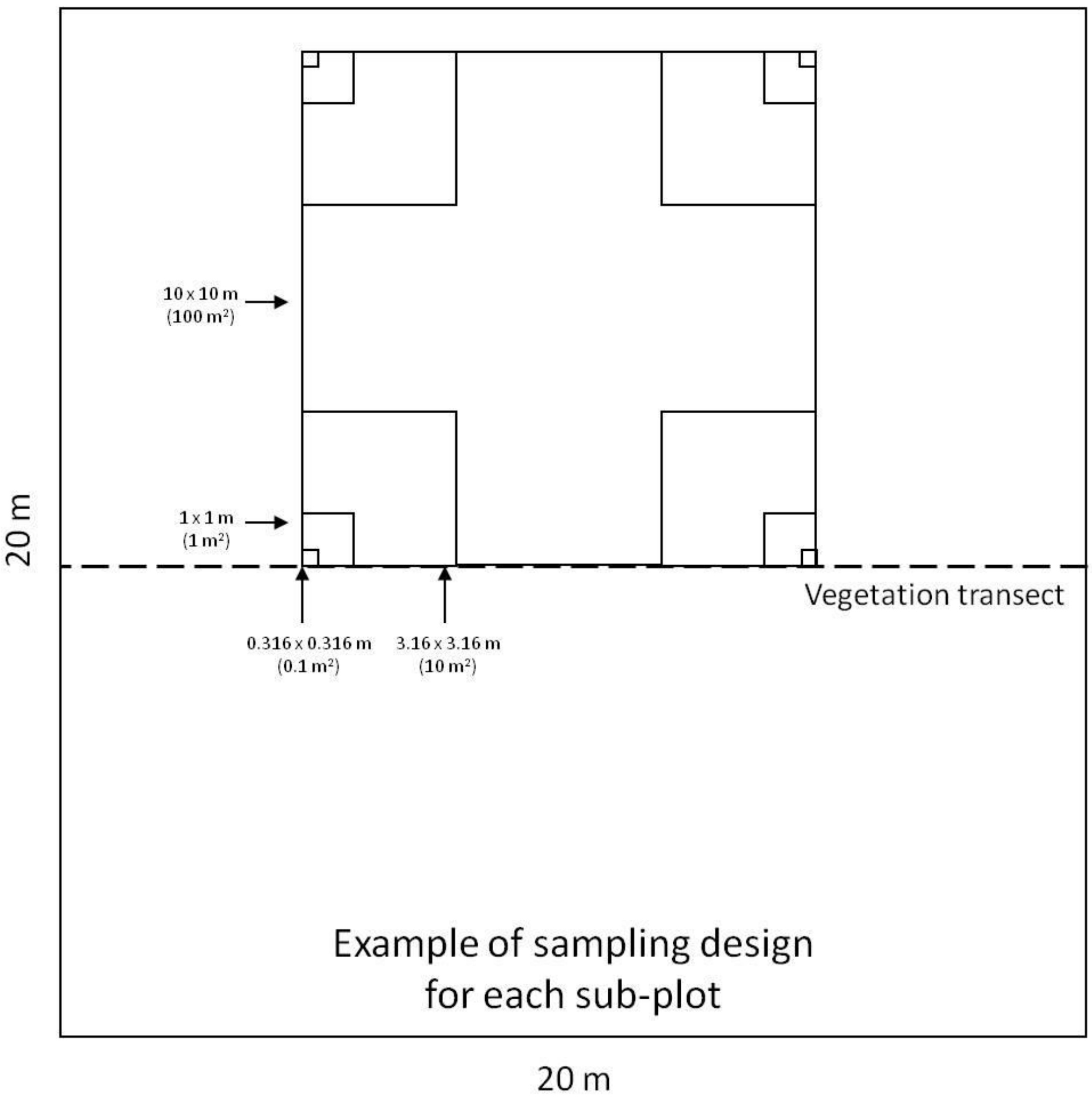

Figure 6.1. Example of sampling design for quantifying species richness at spaces of 0.1 m^2, 1 m^2, 10 m^2, and 100 m^2.

2010, the cover of ground layer vegetation (< 1 m tall) was recorded by functional group (graminoids, forbs, ferns, woody stems, and woody vines) in twenty 1-m^2 quadrats randomly located in each sub-plot (for additional details, see Chapter 5). Mean vegetation cover was calculated by functional group, for total herbaceous cover, for total woody cover, and for total vegetation cover at the sub-plot level. We quantified physical and chemical properties of the soil on the main-plot level in 2008. In each plot, five randomly located soil samples were extracted with a slide hammer, and samples were composited at the main-plot level. For each soil sample, we determined soil texture (percent sand, silt, and clay) using the hydrometer method. Soil samples were analyzed for total nitrogen (%), total carbon (%), phosphorus (ppm), potassium (ppm), soil pH, organic matter (%), and cation exchange capacity (CEC) by the Agricultural Services Laboratory at Clemson University.

Data analysis

We calculated the total number of species (species richness) occurring at each scale for all species, all woody species, all herbaceous species, and for each of the functional groups. Functional groups were assigned to each species based on classifications from the USDA PLANTS Database (http://plants.usda.gov/java/). We used split-split-plot Analysis of Variance (ANOVA) to test for effects of soil type, main-plot treatments, sub-plot treatments, and interaction treatments using Proc Mixed with a random block effect in SAS statistical software (version 9.1; SAS Institute, Inc., Cary, NC). The block factor was nested in the soil type. The data did not violate assumptions of normality or constant variance and no transformations were needed. We determined statistical significance when the probability of making a Type-I error was less than 0.05.

Non-metric multidimensional scaling (NMS) was used to identify patterns in species composition relative to our study treatments and stand or site characteristics. The NMS procedure is an iterative process that orients data in ordination space to minimize the dissimilarity between the original data and the data in the reduced ordination space (McCune and Grace 2002). At the largest scale (100 m^2), each sub-plot represented one point in ordination space (n = 72 total); at each other scale, we sampled four locations within each 100 m^2 area, resulting in 288 total sampled points. The NMS analyses included secondary matrices of explanatory variables, including stand structure variables (basal area, DBH, ground layer vegetation cover by functional group), abiotic factors (light availability, soil moisture, soil temperature), and soil physical and chemical properties (percent sand, silt, and clay, concentrations of N, C, P, and K, soil pH, organic matter (%), and cation exchange capacity). We used bi-plot overlays to represent the strength of the correlations between continuous explanatory variables and the ordination groups. For each ordination, we used the Sorensen distance measure with random starting coordinates, 40 runs with real data, and 400 iterations for each run. We analyzed all data together at the 100 m^2 scale at each location but found that the strong effect of the study blocks (site/location) on composition masked main and sub-plot treatment effects on composition. Consequently, we analyzed data for each block separately at the 10 m^2 scale to demonstrate localized effects of study treatments on composition.

We used the non-parametric multi-response permutation procedure (MRPP) to determine differences in species composition based on study block, main-plot treatment, and sub-plot treatment at each location. When interpreting results from the MRPP analyses, it is important to consider the A-statistic as well as the significance value (p-value) from the T-statistic. The A-statistic describes the within-group homogeneity of the group, with A = 1 when all items in the group are identical and A = 0 when the heterogeneity in the group is equal to that expected by chance. In ecology, values of A that are greater than 0.3 are considered fairly high (McCune and Grace 2002). To determine the degree of similarity in the composition between blocks and treatments, Sorensen's similarity coefficient was calculated for each pairwise block and treatment combination. Indicator species analyses were used to identify species with high importance values for treatments for each block at the 10 m^2 scale, and species that were significant indicators of each canopy treatment in two or more blocks are presented.

6.3. Results

In total, we recorded 286 species throughout the study plots, with 221 species on the sandy loam soils and 224 species on the sand and loamy sand soils. There were no effects of soil texture on species richness at any scale for all species, all herbaceous species, all woody species, or any functional groups. At the 100 m^2 scale, total species richness was 52.9 species on loam soils and 59.0 species on sand soils ($F_{1, 4} = 0.61$; p = 0.4781), total herbaceous richness was 37.9 species on loam soils and 44.8 species on sand soils ($F_{1, 4} = 1.96$; p = 0.2341), and total woody richness was 15.0 species on loam soils and 14.2 species on sand soils ($F_{1, 4} = 0.08$; $p = 0.7888$). There were no interactions between soils and main-plot treatment effects or between soils and sub-plot treatment effects.

There were no significant main-plot treatment effects or main*sub-plot treatment interactions on total species richness at any sampling scale ($p \geq 0.4523$). Mean species richness across treatments was 5.3 species at 0.1 m^2, 12.6 species at 1 m^2, 27.3 species at 10 m^2, and 55.9 species at 100 m^2 (Figure 6.2A). At each scale, herbaceous species dominated the local richness, representing between 74 and 78% of the number of species encountered. Around half of the total floristic diversity was within the forb group, with no treatment effects on richness and an average of 2.6 species at 0.1 m^2, 6.7 species at 1 m^2, 14.6 species at 10 m^2, and 29.6 species at 100 m^2. There were no main-plot effects or main*sub-plot interaction effects on richness of herbaceous or woody species at any scale (Table 6.2). We found a significant sub-plot treatment effect on total species richness at the largest sampling scale (100 m^2), in which species richness was higher on H plots (57.8 species) than on NT plots (52.7 species; Figure 6.2B). The difference was associated with a significant sub-plot treatment effect on total woody species at the 100 m^2 scale (Table 6.3). The same pattern in species richness was observed for herbaceous species, although the sub-plot treatment effect was not significant. There were no sub-plot treatment effects on the richness of the forb functional group ($F_{2, 40} = 0.59$; $p = 0.5601$), but graminoid richness was significantly higher on the H+F plots (12.1 species) than on the NT plots (10.5 species) at the 100 m^2 scale ($F_{2, 40} = 3.59$; $p = 0.0368$).

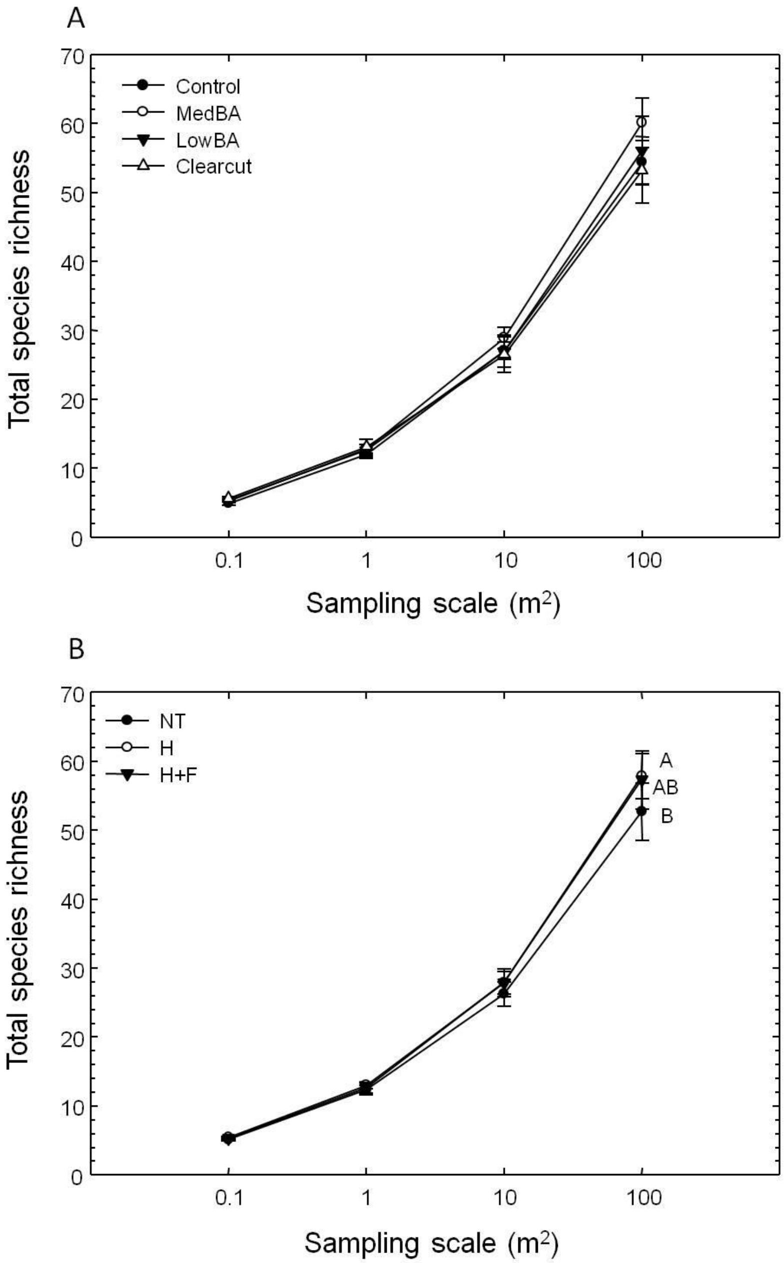

Figure 6.2. Total species richness at each sampling scale by A) main-plot treatment and B) sub-plot treatment. The same letter indicates pair-wise comparisons within each scale are not significantly different at $\alpha = 0.05$.

Table 6.2. Herbaceous and woody species richness by main-plot treatment at each sampling scale

		Control		MedBA		LowBA		Clearcut		
Group	Scale	Mean	SE	Mean	SE	Mean	SE	Mean	SE	**p-value**
Herbaceous	0.1 m^2	4.1	(0.3)	4.0	(0.2)	4.0	(0.2)	4.4	(0.4)	**0.8133**
	1 m^2	9.8	(0.6)	9.9	(0.4)	9.7	(0.8)	10.2	(1.1)	**0.9788**
	10 m^2	21.0	(1.0)	21.9	(1.0)	19.8	(1.9)	20.0	(1.9)	**0.6034**
	100 m^2	41.2	(2.2)	45.3	(2.3)	40.3	(4.1)	38.6	(3.8)	**0.2028**
Woody	0.1 m^2	0.8	(0.2)	1.3	(0.2)	1.3	(0.1)	1.3	(0.3)	**0.2477**
	1 m^2	2.2	(0.4)	2.9	(0.4)	2.9	(0.3)	2.9	(0.7)	**0.4682**
	10 m^2	6.0	(0.7)	7.0	(0.8)	7.1	(0.8)	6.5	(1.2)	**0.5586**
	100 m^2	13.2	(1.8)	14.8	(1.7)	15.7	(1.4)	14.7	(1.8)	**0.5001**

Table 6.3. Herbaceous and woody species richness by sub-plot treatment at each sampling scale; the same letter indicates pair-wise comparisons within each scale are not significantly different at α = 0.05

		NT		H		H+F		
Group	Scale	Mean	SE	Mean	SE	Mean	SE	**p-value**
Herbaceous	0.1 m^2	4.0	(0.1)	4.2	(0.2)	4.1	(0.2)	**0.8657**
	1 m^2	9.8	(0.4)	10.1	(0.4)	9.8	(0.6)	**0.7223**
	10 m^2	20.1	(1.2)	20.8	(1.2)	21.2	(1.4)	**0.3903**
	100 m^2	39.5	(3.1)	42.1	(2.4)	42.4	(3.1)	**0.1866**
Woody	0.1 m^2	1.1	(0.2)	1.3	(0.2)	1.1	(0.2)	**0.7039**
	1 m^2	2.6	(0.4)	2.8	(0.3)	2.8	(0.4)	**0.5550**
	10 m^2	6.2	(0.7)	7.1	(0.7)	6.7	(0.9)	**0.0891**
	100 m^2	13.2^{B}	(1.3)	15.8^{A}	(1.4)	14.9^{AB}	(1.6)	**0.0106**

The results of the NMS analysis indicated that a 2-dimensional solution was most appropriate for ordination of the composition data at the 100 m^2 scale. Axis 1 explained 63.4% of the variability in species composition and Axis 2 explained 17.8% of the variability in species composition. When plotted in ordination space, the sampling plot data was strongly grouped by study block, and we found that the data did not separate by main-plot treatment or sub-plot treatment (Figure 6.3). The MRPP test confirmed these results, with a significant effect of study block on species composition ($A = 0.2071$; $p < 0.0001$), but no significant effects of main-plot treatment ($A = 0.0058$; $p = 0.1326$) or sub-plot treatment ($A = 0.0003$; $p = 0.4141$). The variable from the secondary matrix that most strongly affected the compositional similarity of study plots was the percent sand content, accounting for 37.7% of the variability in Axis 2 (Table 6.4). Sorenson's similarity coefficients support the results of the ordination and show that compositional similarity was highest between Blocks 4 and 6 and that Blocks 1 and 3 were the most dissimilar (Table 6.5).

When we analyzed each study block separately, the ordinations suggested that study treatments were important in determining the local composition of the plant community. The MRPP analysis shows that both main-plot and sub-plot treatments had significant effects on the composition of the sampled plots, although the effect of canopy density (main-plot treatment) was consistently stronger than that of the cultural treatments (sub-plot treatments; Table 6.6). Sorensen's similarity coefficients indicated that the Control plots were most similar to MedBA ($QS = 0.851$) and least similar to the

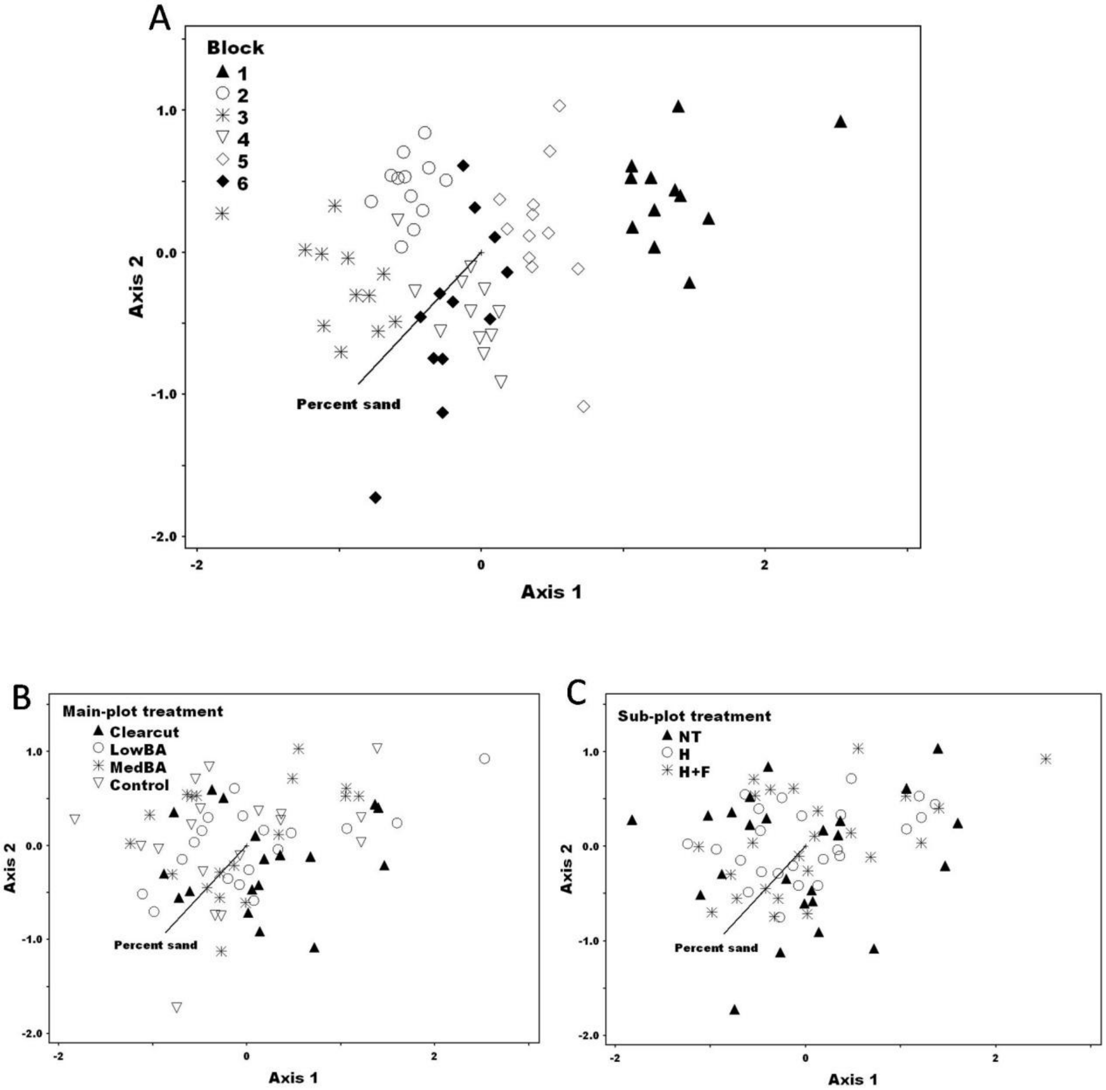

Figure 6.3. NMS ordination of species composition at 100 m^2 scale classified by A) study block (location), B) main-plot treatment, and C) sub-plot treatment.

Table 6.4. Summary of Pearson and Kendall tau correlations with ordination axes at the 100 m^2 scale

	Axis 1			Axis 2		
Variable	r	r-square	tau	r	r-square	tau
Basal area (m/ha)	-0.107	0.012	-0.084	0.220	0.048	0.187
DBH (cm)	0.091	0.008	0.205	0.182	0.033	0.113
Gap light index (%)	0.116	0.014	0.054	-0.249	0.062	-0.205
Soil moisture	0.497	0.247	0.301	0.516	0.266	0.392
Soil temperature	-0.085	0.007	-0.264	-0.010	0.000	-0.210
Total vegetation cover (%)	0.608	0.370	0.355	0.359	0.129	0.202
Herbaceous vegetation cover (%)	0.512	0.262	0.242	0.277	0.077	0.171
Woody vegetation cover (%)	0.443	0.196	0.317	0.297	0.088	0.192
Graminoid cover (%)	0.380	0.144	0.232	0.235	0.055	0.219
Forb cover (%)	0.507	0.257	0.197	0.180	0.032	0.030
Fern cover (%)	-0.125	0.016	-0.059	0.163	0.027	0.194
Shrub cover (%)	0.462	0.214	0.319	0.251	0.063	0.161
Woody vine cover (%)	-0.082	0.007	-0.027	0.338	0.114	0.268
Clay content (%)	0.594	0.353	0.288	0.555	0.308	0.457
Sand content (%)	-0.587	0.344	-0.344	-0.608	0.377	-0.515
Silt content (%)	0.554	0.306	0.380	0.614	0.370	0.497
Total soil N (%)	0.332	0.110	0.259	0.631	0.375	0.546
Total soil C (%)	-0.102	0.010	-0.114	0.397	0.157	0.267
Soil P (ppm)	0.572	0.327	0.349	-0.042	0.002	-0.160
Soil K (ppm)	0.183	0.034	0.309	0.467	0.218	0.442
Soil pH	0.595	0.354	0.407	-0.021	0.000	-0.074
Soil organic matter (%)	0.074	0.005	-0.025	0.463	0.214	0.332
Cation exchange capacity	-0.059	0.003	0.057	0.519	0.270	0.474

Table 6.5. Sorensen’s similarity coefficient for species composition among study blocks

Sorensen's similarity coefficient	Richness	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
Block 1	109	.					
Block 2	151	0.538	.				
Block 3	145	0.465	0.655	.			
Block 4	153	0.557	0.704	0.691	.		
Block 5	132	0.680	0.657	0.563	0.681	.	
Block 6	152	0.559	0.693	0.707	0.800	0.683	.

Clearcut plots (*QS* = 0.764), although the similarity in composition among treatments was higher than that among most blocks. Among the sub-plot treatments, NT and HF had the lowest similarity index (*QS* = 0.833) and H and HF had the highest (QS = 0.883). The indicator species analysis did not find any species that were significantly associated with any canopy treatment in more than two study blocks (Table 6.7). In the Control plots, indicator species were primarily perennial forbs, as well as the perennial grass *Danthonia sericea*. In contrast, species associated with the Clearcut plots primarily included annuals that are common following disturbance events. The most common indicator species were *Desmodium ciliare* in Control plots, with a frequency of 58% of sampled plots, and *Eupatorium hyssopifolium* in MedBA plots, also with a frequency of 58%.

Table 6.6. Results from the MRPP testing the effects of main-plot and sub-plot treatments on community composition for each block

Block	Effect	A	p-value
1	main	0.139	<0.0001
	sub	0.077	<0.0001
2	main	0.118	<0.0001
	sub	0.017	0.0081
3	main	0.128	<0.0001
	sub	0.024	0.0011
4	main	0.136	<0.0001
	sub	0.036	<0.0001
5	main	0.119	<0.0001
	sub	0.018	0.0081
6	main	0.166	<0.0001
	sub	0.024	0.0092

6.4. Discussion

Levels of species richness are often used as a metric of ecosystem functionality and serve as a target for restoration objectives relative to reference conditions (Hedman et al. 2000, Provencher et al. 2001, Walker et al. 2010). The development of dense longleaf pine plantations reduces species richness over time (Harrington 2011) in comparison to naturally regenerated reference sites (Smith et al. 2002, Walker et al. 2010). Although we did not measure reference sites, species richness from our study sites was similar at small scales to that reported for reference longleaf pine communities at Fort Benning, with

Table 6.7. Significant indicator species that occurred in more than one study block for each main-plot treatment and the frequency (%) of occurrence out of all sampled plots (n = 72 for each treatment)

Treatment	Species	Growth form	Duration	No. of blocks	Frequency (%)
Control	*Ageratina aromatica*	Forb/herb	Perennial	2	26
	Danthonia sericea	Graminoid	Perennial	2	49
	Desmodium ciliare	Forb/herb	Perennial	2	58
	Elephantopus tomentosus	Forb/herb	Perennial	2	26
	Tephrosia spicata	Forb/herb	Perennial	2	21
MedBA	*Saccharum alepecuroides*	Graminoid	Perennial	3	26
	Ambrosia artemisiifolia	Forb/herb	Annual	2	25
	Campsis radicans	Vine	Perennial	2	22
	Eupatorium hyssopifolium	Forb/herb	Perennial	2	58
LowBA	*Campsis radicans*	Vine	Perennial	2	14
	Dichanthelium acuminatum	Graminoid	Perennial	2	25
	Liquidambar styraciflua	Tree	Perennial	2	35
	Smilax glauca	Shrub/vine	Perennial	2	32
Clearcut	*Agalinis fasciculata*	Forb/herb	Annual	2	17
	Hypericum gentianoides	Forb/herb	Annual	2	36
	Lespedeza stuevei	Forb/herb	Perennial	2	22
	Polypremum procumbens	Forb/herb	Annual	2	36

between 12 and 15 species at the 1 m^2 scale on soils representative of the Upper Loam Hills (Nankin sandy clay loam) and the Sandhills (Troup loamy sand) (Mulligan and Hermann 2004). At larger scales (100 m^2), however, our study sites had lower species richness than those of reference longleaf pine stands (Mulligan and Hermann 2004). Comparing species richness from our study to that reported in previous studies is complicated by the wide range of site types where other studies have been conducted. For example, Glitzenstein et al. (2003) reported species richness that ranged less than 40 species per 100 m^2 at a site in northeast Florida to almost 80 species per 100 m^2 in South Carolina, and Kirkman et al. (2001) found that species richness was 25 and 56 species at the 100 m^2 scale on xeric and wet-mesic sites, respectively, in southwestern Georgia. Many other studies report species richness at scales that differ from those reported in this study (e.g., Brockway and Lewis 1997, Provencher et al. 2003), making direct comparisons difficult to interpret. However, species richness from our study was comparable to that reported for longleaf pine habitats on similar site types by Peet (2006), indicating that the existing loblolly pine forests support reasonably diverse ground layer communities.

Past research has established that soil moisture and soil texture are important correlates of species richness in longleaf pine woodlands and savannas (Peet 2006). The highest levels of species richness along soil moisture gradients have been found in mesic habitats in coastal North Carolina (Walker and Peet 1983) and in southwestern Georgia (Kirkman 2001). In the sandhills of northwestern Florida, Provencher et al. (2003) found that silt and clay content, which increased soil fertility and water retention, were positively related to species richness at large scales. Interestingly, we found more herbaceous and total species on sandy soils than on sandy loam soils, although the effect of soil texture was not significant at any scale. Similarly, Dilustro et al. (2002) found no differences in richness between clayey and sandy soils at Fort Benning, although clayey soils were expected to have higher species richness. Although soil texture and moisture may define the richness potential in these ecosystems, fire is a critical process that is required for increasing or maintaining species richness (Walker and Peet 1983, Mehlman 1992, Kirkman et al. 2001). It has been suggested that species richness is maximized by burning as frequently as fuels will allow (Glitzenstein et al. 2003), and indirect effects of soil characteristics on fire frequency may more strongly control species richness than direct effects of soil properties (Kirkman et al 2004). Our study sites have been burned regularly, on a three year burn cycle since 1985, with the most recent burns in 2005, 2007, and 2010 (prior to sampling). Therefore, it is possible that the effects of the recent fire regime allowed for similar levels of species richness to develop among the study blocks.

Canopy removal increases resource availability to ground layer plants and commonly results in the release of ground layer vegetation (see Chapter 5, Grelen and Enghardt 1973, Frederickson et al. 1999, Ares et al. 2010). The response of species richness to canopy removal, however, has been reported to be variable in many ecosystems, with decreases in richness following harvesting (Halpern and Spies 1995, Meier 1995), no change in species richness following harvesting (e.g., Gilliam 2002, Roberts 2002) or increased species richness following harvest (Roberts and Zhu 2002, Battles et al. 2001, Schumann et al. 2003, Zenner et al. 2003). We found no significant effects of harvesting intensity on species richness of the ground layer three years after harvest at any of the scales measured. In young longleaf pine plantations in South Carolina, Harrington and Edwards (1999) reported that herbaceous species richness was higher five years after thinning than on uncut plots. By year 14, species richness was negatively correlated to the total density of trees, suggesting that open conditions encourage the development of biodiversity in such stands (Harrington 2011). Beckage and Stout (2000) speculate that fire helps to indirectly increase species richness by maintaining an open canopy structure, which in turn increases the availability of light and soil resources. Although we found no short-term differences in species richness in this study, it is not known if the reduced canopy density created by thinning, combined with a frequent fire regime, will affect patterns of species richness over the long term.

Herbicides are often applied during management of southern pine forests for a variety of reasons, including improving the growth of planted tree seedlings and changing the structure of the ground layer vegetation. In a review of the use of herbicides in southern pinelands, Litt et al. (2001) reported that herbicides generally reduced species richness when compared to untreated areas. However, the effects of herbicides are largely dependent on the herbicide type, the method of application, and the management objectives guiding those decisions. The primary objective of competition control for plantation establishment often results in reduced species richness (e.g. Blake et al. 1987, Zutter and Zedaker 1988), in part because managers attempt to maximize reductions in vegetation (i.e., competition for planted seedlings), and herbicides are often broadcast at highly effective rates. Brockway et al. (1998) found that broadcast application of hexazinone in second-growth longleaf pine forests in central Georgia decreased forb richness over the short-term, whereas spot applications resulted in increased herbaceous species richness. As a result, they suggested that spot application is more effective for longleaf pine restoration because localized reductions in woody vegetation reduced competition with herbaceous plants and enhanced the ground layer vegetation at the stand level. Similarly, Harrington and Edwards (1999) found that woody control with herbicides increased herbaceous species richness through five years and 14 years (Harrington 2011) after application. Similar results were reported by Freeman and Jose (2010) for imazapyr and sulfometuron methyl through four years after application. In our study, the herbicide treatment resulted in greater total species richness than the untreated control only at the largest scale. Both herbaceous and woody species richness were greater on the herbicide plots than on the control plots, but only woody species richness was significantly increased by herbicides. Other studies have associated increases in herbaceous species richness with control of woody species, and our results may appear to contradict that mechanism because of the increase in woody species richness; however, control of competitively dominant species (both herbaceous and woody) may have increased resource availability for less competitive species. This effect would likely have been reinforced by the prescribed fires in the dormant season of 2010, prior to sampling for species richness. Provencher et al. (2001) found that prescribed fire increased herbaceous species richness in longleaf pine sandhill sites in Florida, whereas woody vegetation control with herbicides resulted in short-term decreases in richness.

Although results from our study and previous research generally indicate that selective herbicides may be used to increase species richness of ground layer vegetation, the importance of fire in maintaining diversity in these habitats should not be discounted when making management decisions.

When we considered all the study blocks together, our results show that the composition of the ground layer was more strongly associated with the particular study site than with the restoration treatments. Sorensen's similarity coefficient was highest among the blocks that with common soil texture (Blocks 1, 2 and 5 were sandy loams; Blocks 3, 4, and 6 were sands or loamy sands), suggesting the importance of soil texture in defining community composition. In addition to the effects of environmental filters (e.g., soil texture, topography, resource availability) on local plant communities, differences in the community history also affect local plant composition, even when site conditions are similar (Chase 2003). Brudvig and Damschen (2011) recently evaluated the effects of land-use history, landscape-scale connectivity, and local land management on species richness and composition and found that land-use history was the foremost driver controlling the plant communities, with lower richness and a different suite of species present on sites formerly in agriculture than on sites with a forested history. Forestlands on military installations often have unique land-use histories that include the impacts of military training in addition to land-use prior to military acquisition. The combination of historical and recent land-use has important effects on soil properties and plant communities, with reductions in species richness and major changes in composition associated with the intensity of military training (Dale et al. 2002, Dilustro et al. 2002, Garten et al. 2003, Maloney et al. 2008). Although our study design does not allow for the evaluation of historical legacies on the current ground layer communities, our results support the strong effect of site-specific characteristics (conditions and history) on current ground layer composition.

At the local, stand-level scale, the management treatments affected ground layer plant composition, with harvesting treatments more strongly altering species composition than herbicide or fertilizer. The response of the ground layer community is related to the intensity of a disturbance event and its effect on the forest canopy, the forest floor and soils, and the ground layer structure (Roberts 2004). Harvesting has the potential to greatly modify each of these components and has been shown to result in major changes in species composition, often with shifts to early successional or ruderal species (e.g., Roberts 2002, Roberts and Zhu 2002, Zenner et al. 2006). Based on Sorensen's similarity coefficients, we found that compositional similarity between the uncut Control plots and each other treatment decreased as thinning intensity increased. The indicator species analysis identified perennial forbs and one perennial graminoid, species that are generally found in woodlands (Weakley 2010), as associates of the uncut forestlands. In addition, Mulligan and Hermann (2004) identified one associate of uncut plots, *Tephrosia spicata*, as a potential indicator of high quality habitat at Fort Benning. In contrast, three of the four species associated with the Clearcut plots are annual forbs that are associated with fields or disturbed areas (Weakley 2010). Generally, the composition of the ground layer shifted from woodland species to disturbance species as harvesting intensity increased in our study. Past work suggests that compositional shifts may not persist over long-term stand development (e.g., Halpern and Spies 1995, Kern et al. 2006), but the potential loss of individual species following compositional shifts could threaten long-term restoration objectives (Roberts 2004). The long-term effects of forest management on ground layer composition needs additional research, especially in habitats that support sensitive species.

6.5. Conclusions

Our results suggest that canopy removal during longleaf pine restoration in loblolly pine stands that currently support a relatively diverse ground layer community will not affect species richness in the short-term but will shift species composition to early successional species. Herbicides had little effect on species composition, but slight increases in species richness following herbicide application may have been associated with a reduction in dominance of highly competitive species. At larger spatial scales, composition was strongly controlled by site-specific factors, including soil texture, and although an analysis of the effects of historical and recent land-use history is beyond the scope of this study, our results indirectly support the importance of legacy factors in controlling current species composition. At local spatial scales, land management practices affected species composition. Our results suggest that the restoration practices used in this study can be applied for converting loblolly pine stands to longleaf pine with minimal impacts on the ground layer vegetation. However, it is not known if the short-term shifts in species composition associated with canopy removal will result in long-term species loss; therefore, retaining moderate to low levels of canopy trees may reduce the risk of species loss while providing other ecosystem services to maintain ecological function during restoration.

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CHAPTER VII: SILVICULTURAL RECOMMENDATIONS FOR LONGLEAF PINE RESTORATION IN LOBLOLLY PINE STANDS

7.1. Problem statement

The historical conversion of pine forests from longleaf pine to loblolly pine throughout the southeastern United States has greatly changed the landscape and has resulted in a shift in stand structure and composition. The longleaf pine ecosystem is associated with high floral diversity and supports a large number of endemic species. As a result of habitat loss and fragmentation, numerous plant and animal species have recently been identified as rare or threatened, and longleaf pine restoration has become a major conservation objective in the southeastern United States. Specific restoration objectives vary among land owners, but desired outcomes generally include establishing longleaf pine as the canopy species, changing the vegetation structure to that of reference longleaf pine communities, and re-introducing a frequent fire regime. These three components are synergistic in that longleaf pines and herbaceous vegetation provide suitable fuels for frequent surface fires, and frequent surface fires eliminate woody competition and sustain the desired stand structure.

Targeting the restoration of these ecosystem components can simultaneously address several management objectives, including increasing biodiversity and providing habitat for wildlife. In particular, the federally endangered red-cockaded woodpecker (RCW) prefers open pine stands dominated by large, old longleaf pine trees for nesting and foraging but will use loblolly pine stands if needed. For many landowners interested in longleaf pine restoration, including land managers on US Department of Defense installations, RCW recovery and management is a primary objective. In areas currently supporting RCW populations, restoration protocols require canopy retention that is consistent with stand-level RCW recovery guidelines.

7.2. Forest management for RCW habitat

Forest management for RCW populations must comply with RCW recovery guidelines, and converting loblolly pine stands to longleaf pine forests requires a balance between canopy retention and longleaf pine seedling establishment. The US Fish and Wildlife Service recovery guidelines define good-quality RCW foraging habitat as having the following characteristics (USFWS 2003):

- 45 stems per acre > 60 years in age and ≥ 35 cm in DBH, with minimum basal area of 4.6 m^2/ha
- Basal area of pines 25.4 – 35 cm DBH is between 0 and 9.2 m^2/ha
- Basal area of pines < 25.4 cm DBH is below 2.3 m^2/ha and below 50 stems/ha
- Basal area of all pines ≥ 25.4 cm is at least 9.2 m^2/ha
- Groundcover of native bunchgrasses and/or herbs ≥ 40% and are dense enough to carry fire once every 5 years
- No hardwood midstory exists or is less than 2.1 m tall
- Canopy hardwoods are absent or < 10% the number of canopy trees in longleaf pine forests and < 30% the number of canopy trees in loblolly pine or shortleaf pine forests

- All this habitat is within 0.8 km of the center of the cluster, and preferably 50 percent or more is within 0.4 km of the center of the cluster

The proximity of a given stand to an active RCW cluster determines the application of these guidelines, suggesting that silvicultural techniques for stand conversion may differ depending on RCW habitat use.

7.3. Longleaf pine establishment with alternative silvicultural techniques

On many sites requiring conversion from loblolly pine to longleaf pine, artificial regeneration is necessary because there are no longleaf pines in the canopy to provide seed for natural regeneration. Our results confirm a strong relationship between overstory competition and longleaf pine seedling growth in loblolly pine forests, but canopy trees had variable effects on the survival of planted longleaf pine seedlings; in the first year after planting we observed a facilitation effect of canopy pines that was not evident in the following years. These results indicate that canopy retention may additionally benefit restoration by reducing first-year mortality that was likely associated with desiccation of the out-planted seedling during the adjustment period immediately following planting.

Based on results from our study, underplanting longleaf pine seedlings beneath uncut loblolly pine stands (basal area ~ 14 m^2/ha or higher) is not a feasible option for establishing longleaf pine because seedling growth was strongly limited and there were no seedlings in height growth after three growing seasons. Height growth was observed on all other study treatments (although not common on MedBA plots), suggesting that grass stage emergence can be expected at some point in the future on those treatments. In many cases, it may be acceptable for the objectives of restoration forestry to be met on a timescale that is different from that of traditional forestry, contingent on eventual seedling emergence and stand establishment.

In natural stands, longleaf pine regeneration is often observed within canopy gaps, and patch cutting has been proposed as a silvicultural technique for establishing longleaf pine seedlings while retaining canopy pines (McGuire et al. 2001, Palik et al. 2002). Seedling growth increased from the forest edge to the gap interior and was generally maximized within 10 m from the forest edge in our study, and gaps resulted in greater mean seedling growth than uncut plots. However, greater seedling mortality on the north half compared to south half of gaps further supports that first-year mortality may be associated with the desiccation of planted seedlings caused by increased exposure to solar radiation. Previous research suggests that varying the shape and orientation of canopy openings may be a viable option for reducing first-year seedling mortality (Rodriguez-Trejo et al. 2003), and our results indicate that more research into gap shape is warranted.

Results from our study do not support the use of fertilizer for improving longleaf pine seedling establishment, despite the low nutrient status of our study sites. Generally, we found that foliar nutrients (N, P, and K) remained above sufficiency levels and that fertilizers did not increase growth. Likewise, we found no effects of the herbicide release treatment on seedling root collar diameter, although the herbicide plots had a higher percentage of seedlings in height growth than the control plots did in 2009. Interestingly, Hu (2011) reported that herbicide release increased seedling RCD in a parallel study at Camp Lejeune, NC. The herbicide prescriptions differed at the two study locations because woody vegetation was dominant at Camp Lejeune but herbaceous vegetation was more common at Fort Benning. Herbicide release prescriptions must be made on a site-specific basis to address differences in initial conditions and competitive pressures. Additionally, the site preparation treatment at Fort Benning included herbicide control of common woody competitors, and it is not clear if an herbicide release treatment would have affected seedling response differently if site preparation had not been used.

7.4. Factors regulating longleaf pine seedling establishment

Two hypotheses have commonly been discussed to describe the factors controlling longleaf pine establishment in canopy openings. The ‘Fire Effects Hypothesis’ proposes that interactions between fuels and fire effects create hotter fires beneath canopy trees and consequently increase seedling mortality; the ‘Competition Hypothesis’ proposes that because longleaf pine seedlings are intolerant of competition for resources, seedling establishment in gaps is regulated by competition with canopy trees. Our results suggest that processes from both hypotheses act on longleaf pine seedling establishment, and it is likely that the importance of each mechanism differs for natural and artificial regeneration. However, our project was designed to primarily test the effects of management treatments on resource availability and seedling response of artificially regenerated longleaf pine.

Canopy removal changes the spatial and temporal distribution of resources required for plant growth. We found that light availability was strongly regulated by canopy density and increased from the southern edge of canopy openings to slightly north of gap center. Similar to most other studies from the northern hemisphere, canopy transmittance was higher on the northern half of gaps than on the southern half of gaps, and canopy transmittance was similar to that reported in studies from longleaf pine forests. However, the cover of ground layer vegetation increased with the intensity of canopy removal, with concomitant increases in the interception of light by the understory. Such changes in light availability at the ground layer may affect seedling establishment, especially when seedlings remain in the grass stage, but have not been accounted for in previous studies. Greater exposure to solar radiation following canopy removal increased soil temperatures at a depth of 10 cm in uniform plots and across canopy openings, but we found no effect of canopy density on soil moisture at 6 cm. It is possible that any increases in soil moisture associated with reduced uptake and transpiration from canopy trees were offset by the increased uptake by understory vegetation or by evaporative effects of increased temperatures and solar radiation. However, at greater depths in the soil (60 and 100 cm) we observed higher soil moisture in canopy openings than beneath the forest, suggesting that root gaps are present beneath the ground-layer root zone following canopy removal. Soil nitrogen was measured only in the LG plots, and we found that NO_3^- and total nitrogen ($NO_3^- + NH_4^+$) were higher 20 m north of gap center than at the southern edge of the gap. The increase in available nitrogen may have been related to greater soil temperatures north of gap center.

Interactions among the resources that limit longleaf pine seedling growth, and the temporal variability of resource availability, make it difficult to isolate the effects of resource availability on *in situ* seedling response. Canopy density was negatively related to seedling size through three growing seasons, with strong limitations to growth at canopy densities > 7 m^2/ha basal area. Because light transmittance through the canopy was strongly related to canopy density, light was also related to seedling size. However, the variability in seedling response increased for plots with complete canopy removal, suggesting that other factors were also limiting seedling growth in clearcut plots. Foliar nutrients (N, P, K) in longleaf pine seedlings increased with canopy removal, although nutrients were higher than the previously published sufficiency levels and were not strongly related to seedling growth. Likewise, direct measures of water status through xylem water potential suggested that water stress did not strongly limit seedling growth in canopy openings, although we did observe higher water stress beneath canopy trees than in gap openings in 2009. In general, xylem water potential appeared more closely related to annual variability in precipitation and soil moisture than to spatial variability in soil moisture. Overall, our results support that light is the most limiting resource for longleaf pine seedling growth.

7.5. Enhancing the condition of the ground layer vegetation

Our results support previous findings that ground layer vegetation is released by canopy removal, and we found that cover of both herbaceous and woody vegetation increased with thinning intensity. Generally, vegetation cover increased to the maximum within 10-20 m from the forest edge in canopy gaps but was significantly lower beneath the intact canopy. Although vegetation cover increased following harvesting, we did not observe changes in the proportional abundance of vegetation groups; in particular, woody vegetation did not dominate the understory following canopy removal. The proportional composition by functional group was similar in each year of the study, suggesting that the initial condition of the ground layer strongly regulates the ground layer response over time. Therefore, decisions for management of the ground layer must be made based on the initial conditions relative to restoration objectives. We did observe an increase in the number of woody stems in the midstory following canopy removal, supporting previous work finding that clearcuts or large canopy gaps encourage development of midstory hardwoods (Kirkman and Mitchell 2006, Pecot et al. 2007). Herbicides were an effective method for reducing woody stem density, and sites with abundant woody vegetation may require herbicides for short-term improvements in vegetation structure that can be maintained with frequent fire management.

Species richness of the ground layer vegetation was not strongly affected by canopy treatments in our study. The composition of the study plots was more strongly controlled by the stand location than by the study treatments, suggesting that stand/site histories regulate current stand composition (Hedman et al. 2000, Walker and Silletti 2006, Brudvig and Damschen 2011). However, the canopy treatments affected composition at the local scale, and we observed shifts in composition from perennial woodland forbs in uncut plots to early successional species in clearcut plots. The shifts in composition did not affect species richness, but it is not clear if sensitive species will be lost from the community over longer timescales than considered in this study.

7.6. Managing restored stands with frequent surface fire

The fuel complexes created by inputs of highly flammable longleaf pine needles that fall onto a well-aerated bed of bunchgrass-dominated herbaceous vegetation are ideal from maintaining the high-frequency surface fires that perpetuate the longleaf pine ecosystem. The ability for land managers to apply effective prescribed fires depends largely on fuel conditions. In many stands requiring restoration, the ground layer vegetation includes a hardwood component that may inhibit the use of prescribed fire. Canopy removal reduces the input of needles as a source of fine fuels, creating concerns about fire movement throughout gaps following the use of patch-cutting for longleaf pine restoration (Mitchell et al. 2006).

A complete analysis of the effects of restoration management on fuels and fire behavior/effects was beyond the scope of this dissertation but has been presented elsewhere (Tennant 2011). However, our results demonstrate changes in the fuel complexes following manipulation of canopy density and distribution. Generally, we found that pine needle inputs decreased and herbaceous plant cover, including bunchgrasses, increased with canopy removal. Pine straw cover decreased rapidly from the forest edge to gap center, but bunchgrass cover did not strongly increase across canopy gap positions. Fuel dynamics have important implications for the maintenance of the longleaf pine ecosystem, and trade-offs between needle inputs from canopy pines and the release of herbaceous or woody vegetation following canopy removal must be considered when making management decisions.

7.7. Management recommendations for longleaf pine restoration in loblolly pine stands

Management objectives and the starting conditions of the stand will determine the appropriate silvicultural practices for converting loblolly pine stands to the longleaf pine ecosystem. If maximizing longleaf pine seedling growth is the only objective, eliminating competition from canopy trees and ground layer vegetation would be appropriate. However, seedling survival would likely be reduced following complete canopy removal, especially in years of drought. Commonly, restoration objectives include conserving biodiversity and providing habitat for wildlife. In such cases, complete canopy removal conflicts with long-term goals by changing the composition of the ground layer vegetation and disrupting ecosystem function. We recommend using single-tree selection with residual basal areas between 5 and 8 m^2/ha to encourage longleaf pine seedling establishment, limit encroachment by hardwoods, reduce compositional shifts of ground-layer vegetation to ruderal species, and maintain fuels for fire management. In some cases, particularly if management is constrained by spatial requirements for RCW habitat, group selection can be used to initiate longleaf pine establishment in discrete locations within a stand while maintaining existing RCW habitat in critical areas. We recommend using small gaps (0.1 ha) to reduce seedling mortality and maintain the desirable structure of the ground layer vegetation structure.

Cultural treatments should be considered on a site-specific basis, although we do not recommend using fertilizers for improving longleaf pine establishment on sites similar to those in this study. Herbicides can be prescribed for woody or herbaceous control but may not be necessary if the ground layer is in good condition. If woody vegetation has developed, herbicides can be used to reduce midstory abundance, release herbaceous vegetation, and improve fire management. On sites with high abundance of herbaceous vegetation, such as old field sites, herbaceous control may improve longleaf pine seedling establishment. We recommend that herbaceous control be applied in bands or spot treatments to localize effects around longleaf pine seedlings and to minimize stand-level effects on remnant vegetation.

Results from this research demonstrate that longleaf pine restoration can be initiated in loblolly pine stands without complete canopy removal, which has been the traditional method for stand conversion. Our results describe ecosystem responses through only three years after treatment, and we lack important information on long-term stand development. In particular, longleaf pine restoration requires the establishment of a frequent fire regime, and it is not clear how changes in stand conditions will affect fire management in the future. By prescribing frequent fire, we anticipate that the ground layer structure and composition will be maintained or improved, but specific effects of fire season and frequency are not fully understood in a restoration context. Moreover, the persistence and development of longleaf pine seedlings are essential for canopy conversion. Short-term differences in seedling growth may not be maintained over longer timeframes; for instance, it is not known if seedlings on uncut plots will eventually emerge from the grass stage or be suppressed until eventual mortality. We recommend that a long-term monitoring program be designed for these study sites to improve our understanding of longleaf pine ecosystem development over time.

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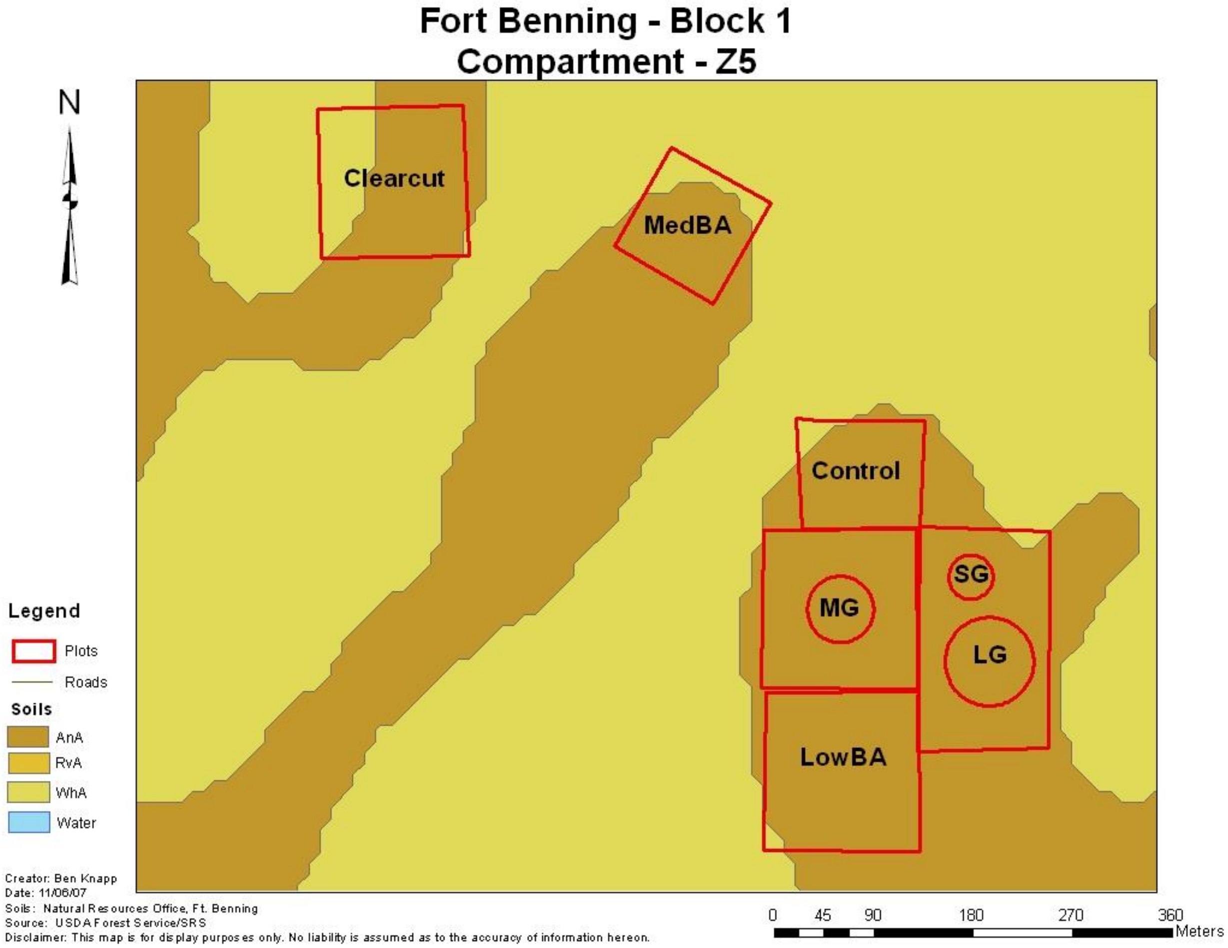
APPENDICES

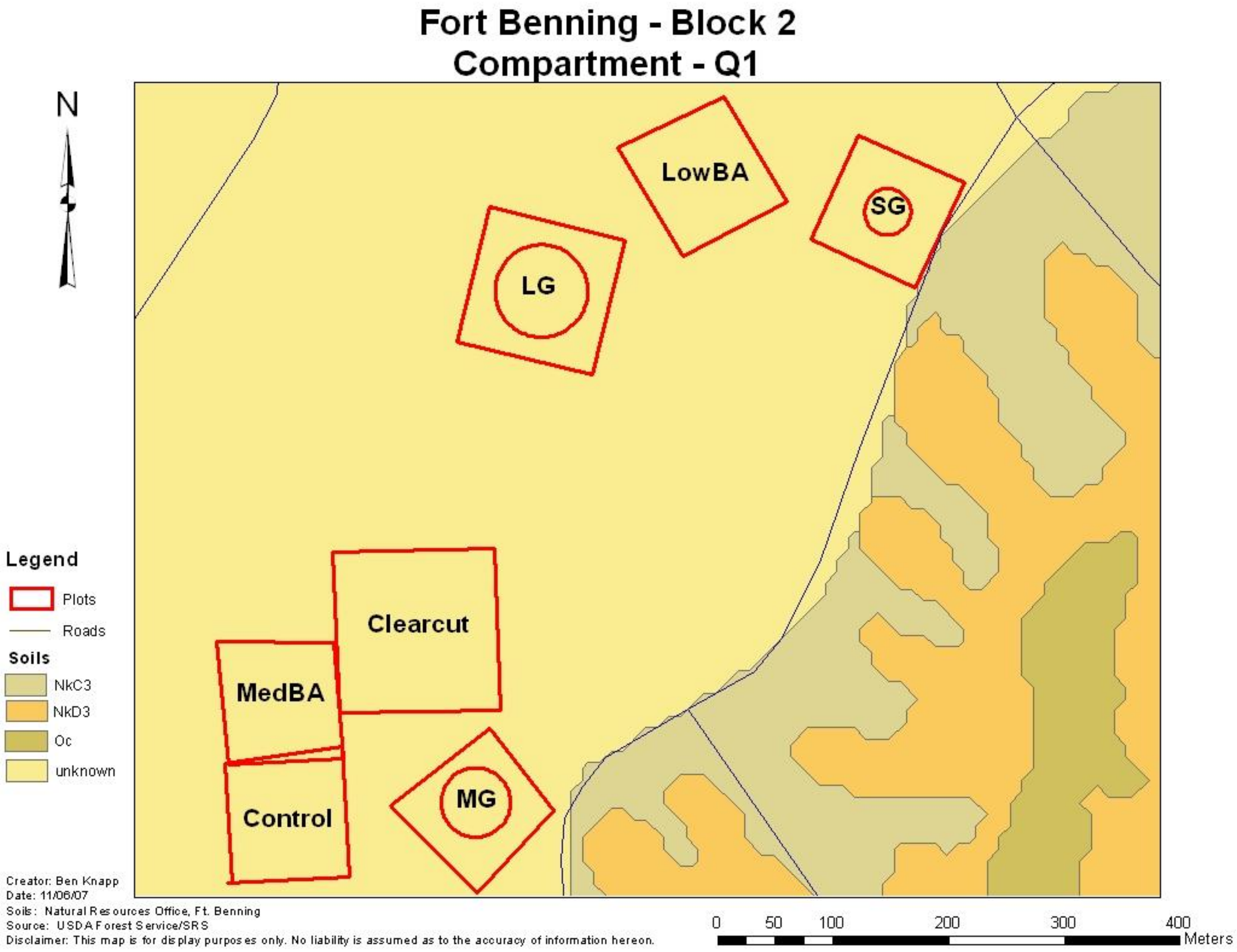
A-1.1. Key to soil names associated with study plots.

Soil Type	Soil Name	Slope
AaB	Ailey loamy course sand	2 to 5
AaC	Ailey loamy course sand	5 to 8
AnA	Annemaine fine sandy loam	0 to 2
BeA	Bladen loam	0 to 1
Bh	Bibb sandy loam	0
CaA	.	.
EmB	Esto sandy loam	2 to 5
EtA	Eunola sandy loam	0 to 3
NaB	Nankin sandy loam	2 to 5
NkC3	Nankin sandy clay loam	5 to 12
NkD3	Nankin sandy clay loam	12 to 18
Oc	Ochlockonee sandy loam	0
Pm	Pelham loamy sand	0 to 2
SuB	Susquehanna sandy loam	2 to 5
SuC	Susquehanna sandy loam	5 to 8
TrB	Troup loamy sand	2 to 5
TrC	Troup loamy sand	5 to 12
TSD	Troup and Esto loamy sands	5 to 15
TVD	Troup, Vaucluse, and Pelion loamy sands	8 to 12
VeC	Vaucluse sandy loam	5 to 8
VeD	Vaucluse sandy loam	8 to 15
WaC	Wagram loamy sand	5 to 8
WhA	Wickham fine sandy loam	0 to 2

A-1.2. Study site and associated soils of Block 1. Soils information is shown for reference but is not updated with the 2003 Russell County Soil Survey.

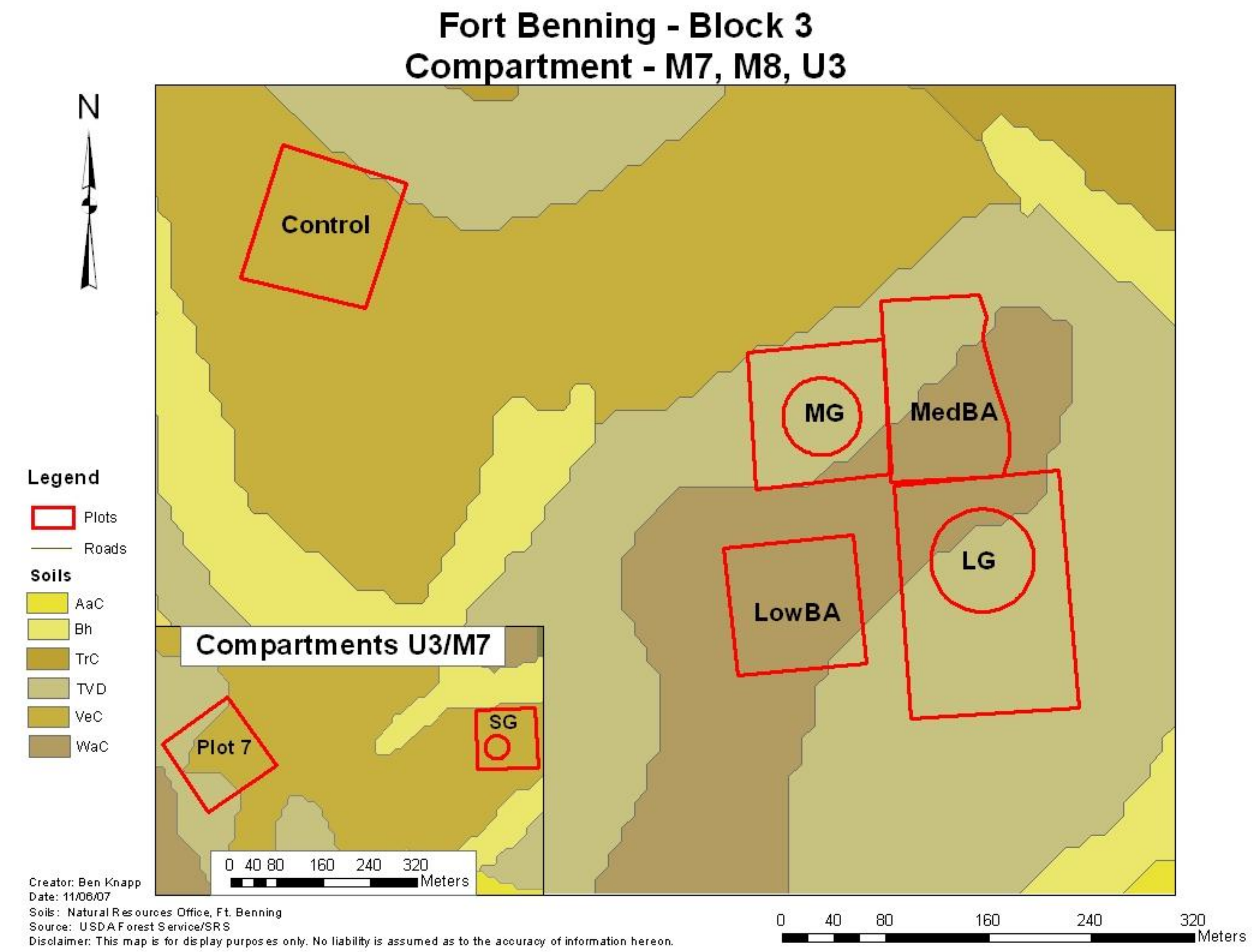


A-1.3. Study site and associated soils of Block 2.


Fort Benning - Block 2
Compartment - Q1

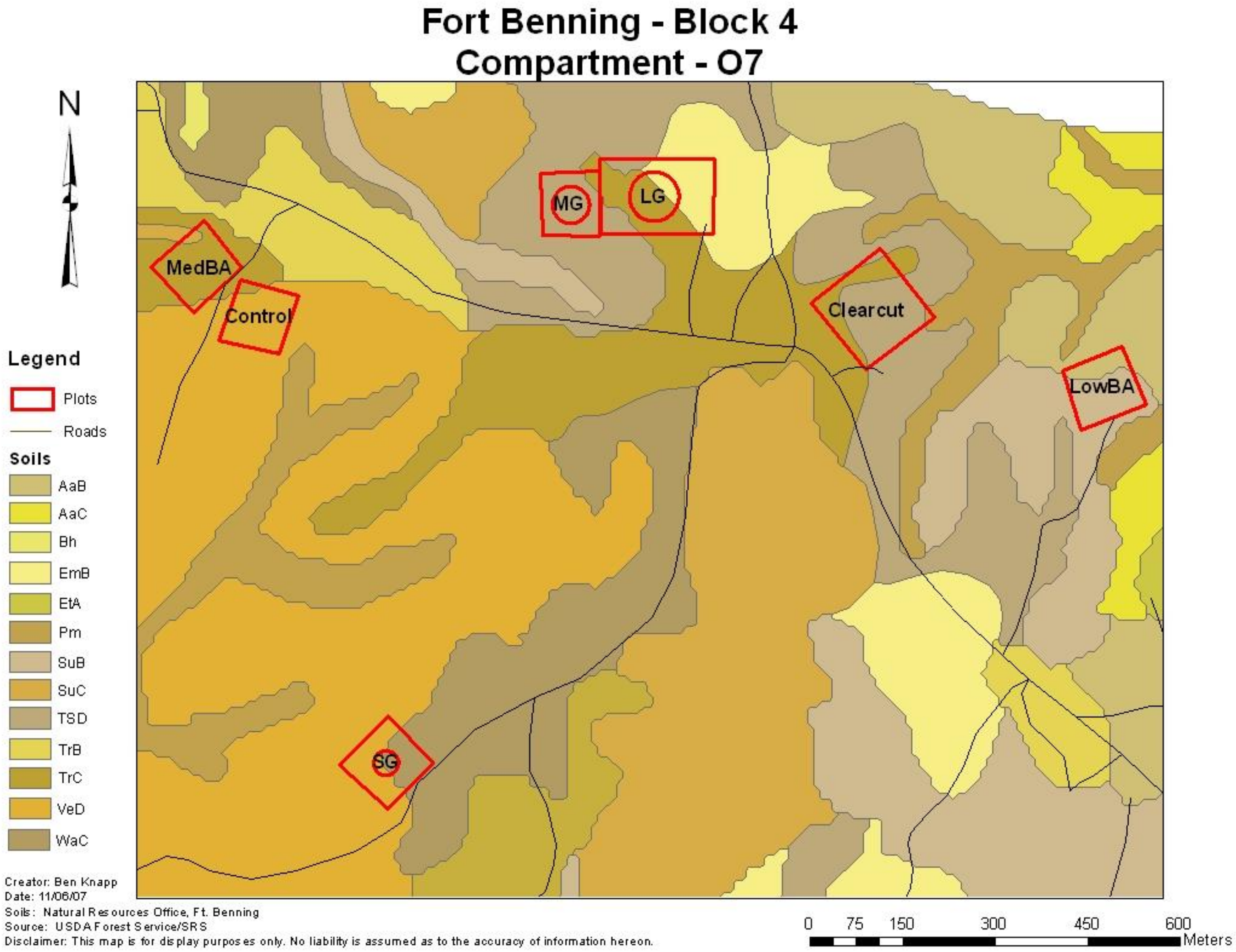
Creator: Ben Knapp
Date: 11/06/07
Soils: Natural Resources Office, Ft. Benning
Source: USDA Forest Service/SRS
Disclaimer: This map is for display purposes only. No liability is assumed as to the accuracy of information hereon.

A-1.4. Study site and associated soils of Block 3.

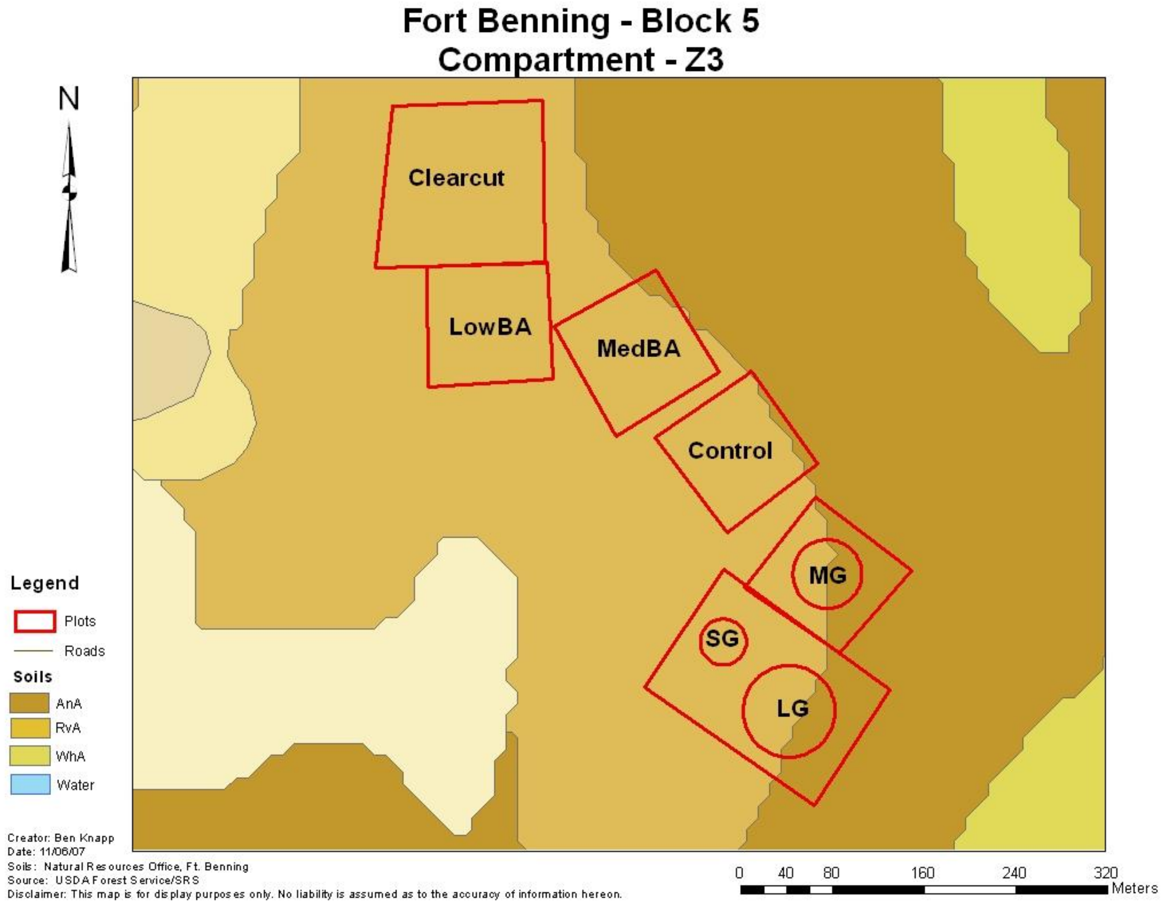


Creator: Ben Knapp
Date: 11/06/07
Soils: Natural Resources Office, Ft. Benning
Source: USDA Forest Service/SRS
Disclaimer: This map is for display purposes only. No liability is assumed as to the accuracy of information hereon.

A-1.5. Study site and associated soils of Block 4.

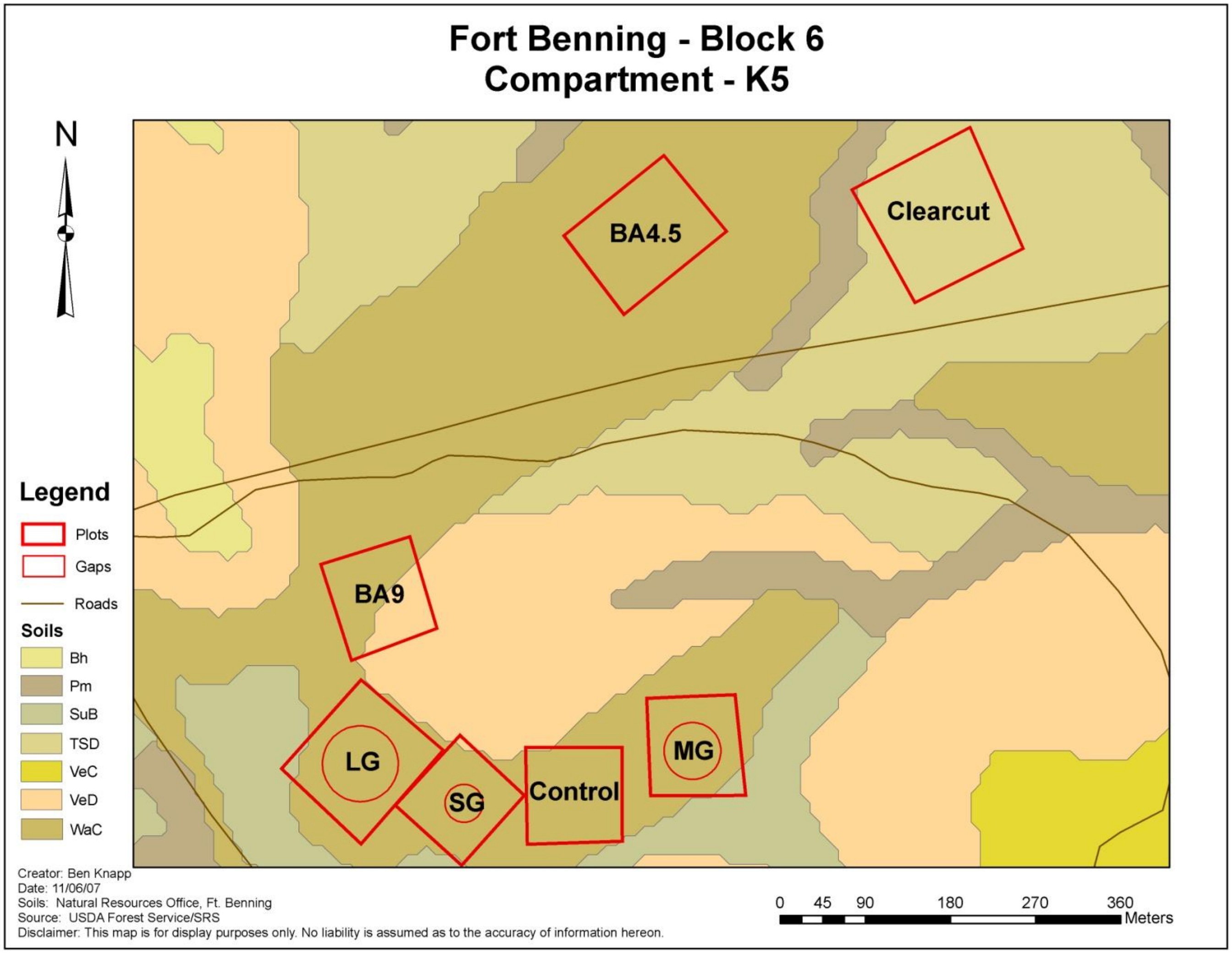


A-1.6. Study site and associated soils of Block 5. Soils information is shown for reference but is not updated with the 2003 Russell County Soil Survey.


Fort Benning - Block 5
Compartment - Z3

Creator: Ben Knapp
Date: 11/06/07
Soils: Natural Resources Office, Ft. Benning
Source: USDA Forest Service/SRS
Disclaimer: This map is for display purposes only. No liability is assumed as to the accuracy of information hereon.

A-1.7. Study site and associated soils of Block 6.



A-1.8. Description of post-harvest structure of Control plots for each study block.

Control			**Block**					
			1	2	3	4	5	6
	Plot Size (ha)		1.09	1.10	1.06	1.01	1.02	1.02
	TPH	Pine	146.00	147.13	470.43	307.08	176.23	153.44
		Hardwood	0.00	89.91	68.15	35.78	6.89	11.80
		Total	146.00	237.04	538.58	342.85	183.12	165.25
BA	**(m^2/ha)**	Pine	15.14	11.08	19.24	17.36	18.97	14.94
		Hardwood	0.00	3.32	1.91	0.61	0.07	0.17
		Total	15.14	14.39	21.15	17.97	19.04	15.12
DBH	**(cm)**	Pine	34.32	29.94	21.58	25.93	36.40	34.44
		Hardwood	0.00	19.99	17.01	14.32	11.66	13.35
Height	**(m)**	Pine	25.67	21.58	18.29	18.46	25.87	22.05

A-1.9. Description of post-harvest structure of MedBA plots for each study block.

MedBA			**Block**					
			1	2	3	4	5	6
	Plot Size (ha)		1.08	1.04	1.21	1.10	1.11	1.01
	TPH	Pine	76.96	110.61	159.14	86.10	78.51	117.89
		Hardwood	0.93	28.85	49.73	5.44	2.71	43.59
		Total	77.88	139.46	208.88	91.54	81.22	161.47
BA	**(m^2/ha)**	Pine	9.93	8.87	8.14	7.62	9.93	8.32
		Hardwood	0.01	0.83	1.87	0.35	0.03	1.04
		Total	9.94	9.70	10.01	7.97	9.96	9.36
DBH	**(cm)**	Pine	39.96	31.16	24.38	31.97	39.30	29.00
		Hardwood	11.50	18.08	20.52	25.93	11.63	15.96
Height	**(m)**	Pine	25.32	23.04	16.76	20.31	25.49	19.54

A-1.10. Description of post-harvest structure of LowBA plots for each study block.

LowBA			**Block**					
			1	2	3	4	5	6
		Plot Size (ha)	2.01	1.10	1.00	1.09	1.11	1.43
	TPH	Pine	53.64	138.29	80.76	64.17	52.37	47.48
		Hardwood	18.38	23.65	18.94	40.33	4.51	2.09
		Total	72.02	161.94	99.71	104.50	56.88	49.57
BA	**(m^2/ha)**	Pine	5.91	7.56	4.78	5.33	6.89	5.08
		Hardwood	0.30	0.62	0.88	0.84	0.09	0.03
		Total	6.20	8.18	5.66	6.17	6.98	5.11
DBH	**(cm)**	Pine	35.07	24.84	26.29	30.20	40.57	34.99
		Hardwood	13.85	16.91	21.49	15.59	15.66	13.23
Height	**(m)**	Pine	21.33	18.90	17.35	20.36	25.84	21.78

A-1.11. Description of post-harvest structure of LG plots for each study block.

LG			**Block**					
			1	2	3	4	5	6
		Plot size (ha)	2.36	2.23	2.37	2.25	2.18	1.48
	TPH	Pine	133.69	305.58	237.14	208.49	187.80	176.66
		Hardwood	3.18	41.38	93.90	71.62	22.28	9.55
		Total	136.87	342.18	331.04	280.11	210.08	186.21
BA	**(m^2/ha)**	Pine	14.17	14.60	12.05	15.69	19.12	15.10
		Hardwood	0.06	0.78	2.85	1.82	0.47	0.30
		Total	14.23	15.18	14.90	17.51	19.60	15.41
DBH	**(cm)**	Pine	35.08	23.39	24.01	30.00	35.25	32.03
		Hardwood	15.75	14.90	18.21	17.24	15.89	17.78
Height	**(m)**	Pine	24.18	18.05	17.72	19.51	26.00	21.66

A-1.12. Description of post-harvest structure of MG plots for each study block.

MG			**Block**					
			1	2	3	4	5	6
	Plot size (ha)		2.01	1.01	1.12	0.97	1.01	1.02
	TPH	Pine	230.77	175.07	204.91	272.55	161.14	183.03
		Hardwood	7.96	13.93	87.54	43.77	13.93	7.96
		Total	238.73	189.00	292.45	316.32	175.07	190.99
BA	**(m^2/ha)**	Pine	13.71	14.44	11.23	15.43	17.88	17.87
		Hardwood	0.30	0.34	1.96	1.26	0.21	0.38
		Total	14.01	14.78	13.19	16.69	18.09	18.26
DBH	**(cm)**	Pine	24.10	31.55	25.49	25.21	36.96	34.14
		Hardwood	18.65	17.24	15.26	18.37	13.56	21.35
Height	**(m)**	Pine	18.32	22.47	18.76	17.32	24.89	21.64

A-1.13. Description of post-harvest structure of SG plots for each study block.

SG			**Block**					
			1	2	3	4	5	6
	Plot size (ha)		1.13	1.13	1.06	1.13	2.18	0.94
	TPH	Pine	108.76	169.77	145.89	307.70	161.81	183.03
		Hardwood	37.14	29.18	0.00	2.65	13.26	5.31
		Total	145.89	198.94	145.89	310.35	175.07	188.33
BA	**(m^2/ha)**	Pine	13.65	13.44	12.35	13.36	16.74	17.52
		Hardwood	0.66	0.60	0.00	0.03	0.71	0.09
		Total	14.31	14.04	12.35	13.39	17.44	17.61
DBH	**(cm)**	Pine	39.67	30.63	31.35	22.47	34.54	33.73
		Hardwood	14.64	15.32	0.00	11.00	22.82	14.50
Height	**(m)**	Pine	25.01	22.38	20.59	15.77	26.99	22.70

A-3.1. Results of foliar nutrient analysis by main-plot and sub-plot treatments in 2009; the same letter indicates no significant difference within a treatment and nutrient at α = 0.05

2009

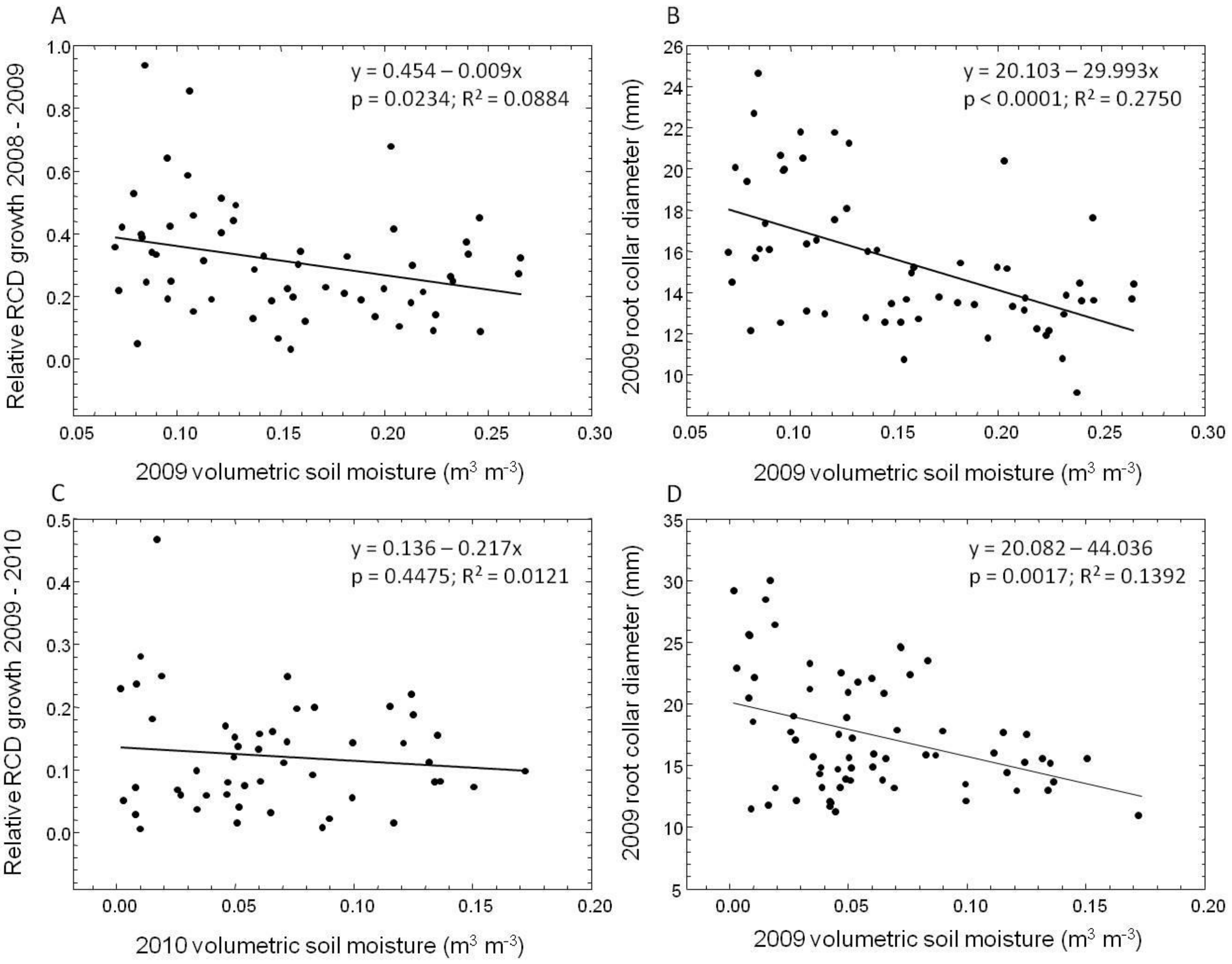
Effect	Treatment	Ca (%)	Mg (%)	S (%)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Fe (ppm)	Na (ppm)
Main	Control	0.121^{b}	0.090^{a}	0.076	34.2^{b}	3.3	347.1	46.1	35.1
plot	MedBA	0.131^{b}	0.082^{b}	0.077	38.1^{ab}	3.6	374.7	45.6	31.5
	LowBA	0.134^{b}	0.078^{b}	0.072	40.2^{a}	3.7	289.4	58.5	27.8
	Clearcut	0.172^{a}	0.081^{b}	0.083	41.2^{a}	3.6	386.8	39.8	30.1
	p-value	**0.0017**	**0.0036**	**0.0775**	**0.0488**	**0.2837**	**0.1881**	**0.3427**	**0.3470**
Sub	NT	0.142	0.085	0.075	37.8	3.4	355.6	40.1	31.7
plot	H	0.140	0.083	0.080	39.9	3.6	329.4	51.8	30.5
	H+F	0.136	0.080	0.076	37.5	3.5	363.5	50.5	31.2
	p-value	**0.5917**	**0.0613**	**0.2166**	**0.2689**	**0.5318**	**0.4832**	**0.2317**	**0.8693**

A-3.2. Results of foliar nutrient analysis by main-plot and sub-plot treatments in 2010; the same letter indicates no significant difference within a treatment and nutrient at $\alpha = 0.05$

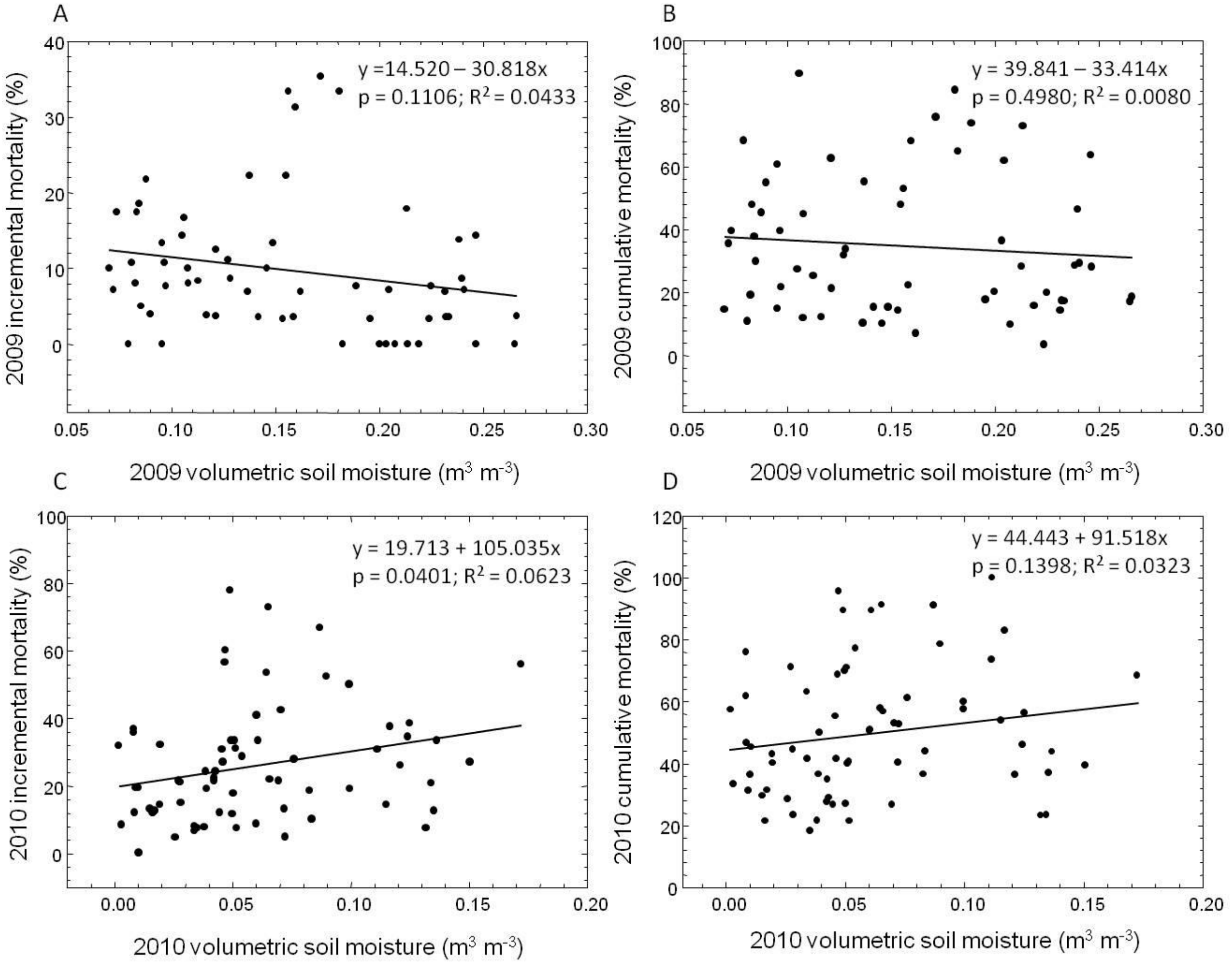
2010

Effect	Treatment	Ca (%)	Mg (%)	S (%)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Fe (ppm)	Na (ppm)
Main plot	Control	0.148^{b}	0.102	0.084	29.9	2.3^{b}	323.8	47.1	23.5
	MedBA	0.164^{ab}	0.098	0.086	35.8	2.8^{b}	376.2	49.0	20.1
	LowBA	0.169^{ab}	0.094	0.081	35.7	2.6^{b}	242.1	45.1	22.5
	Clearcut	0.197^{a}	0.088	0.088	37.8	3.9^{a}	315.6	41.6	24.1
	p-value	**0.0122**	**0.0655**	**0.5607**	**0.1066**	**0.0003**	**0.0688**	**0.5490**	**0.6680**
Sub plot	NT	0.166	0.095	0.087	33.3^{b}	2.8	321.3	44.3	22.2
	H	0.175	0.100	0.084	37.2^{a}	3.0	311.0	48.4	23.8
	H+F	0.166	0.093	0.083	33.4^{ab}	2.9	315.2	44.4	21.1
	p-value	**0.4651**	**0.3532**	**0.2210**	**0.0302**	**0.7945**	**0.9250**	**0.4230**	**0.4585**

A-3.3. Relationships between seedling size and soil moisture in 2009 and 2010



A-3.4. Relationships between seedling mortality and soil moisture in 2009 and 2010.



A-5.1. Woody stem density by main-plot treatment for the five most common species encountered in the midstory layer

		Control		MedBA		LowBA		Clearcut	
Year	Species	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2008	*Liquidambar styraciflua*	14	(14)	21	(21)	69	(33)	236	(172)
	Quercus spp.	0	(0)	0	(0)	7	(7)	42	(7)
	Morella cerifera	0	(0)	0	(0)	28	(28)	0	(0)
	Diospyros virginiana	0	(0)	0	(0)	0	(0)	28	(21)
	Carya spp.	0	(0)	0	(0)	7	(7)	7	(7)
2009	*Liquidambar styraciflua*	0	(0)	28	(18)	354	(193)	708	(534)
	Pinus taeda	14	(14)	7	(7)	7	(7)	285	(276)
	Quercus spp.	7	(7)	7	(7)	7	(7)	111	(50)
	Morella cerifera	14	(9)	7	(7)	14	(9)	7	(7)
	Diospyros virginiana	0	(0)	0	(0)	0	(0)	35	(27)
2010	*Liquidambar styraciflua*	7	(7)	14	(9)	590	(351)	674	(585)
	Morella cerifera	0	(0)	14	(14)	139	(103)	222	(214)
	Pinus taeda	35	(35)	21	(14)	69	(46)	111	(58)
	Quercus spp.	0	(0)	7	(7)	83	(62)	104	(48)
	Rhus copallina	0	(0)	0	(0)	118	(73)	28	(21)

A-5.2. Woody stem density by sub-plot treatment for the five most common species encountered in the midstory layer by sub-plot treatment

		NT		H		H + F	
Year	Species	Mean	SE	Mean	SE	Mean	SE
2008	*Liquidambar styraciflua*	182	(118)	52	(26)	21	(15)
	Quercus spp.	16	(11)	5	(5)	16	(11)
	Morella cerifera	21	(21)	0	(0)	0	(0)
	Diospyros virginiana	5	(5)	5	(5)	10	(10)
	Carya spp.	0	(0)	0	(0)	14	(7)
2009	*Liquidambar styraciflua*	714	(511)	57	(51)	47	(26)
	Pinus taeda	26	(17)	198	(198)	10	(10)
	Quercus spp.	31	(35)	0	(0)	5	(7)
	Morella cerifera	21	(10)	5	(5)	5	(5)
	Diospyros virginiana	21	(21)	0	(0)	5	(5)
2010	*Liquidambar styraciflua*	693	(539)	146	(88)	125	(79)
	Morella cerifera	167	(148)	89	(82)	26	(15)
	Pinus taeda	10	(10)	68	(27)	99	(51)
	Quercus spp.	57	(31)	73	(46)	16	(11)
	Rhus copallina	89	(60)	0	(0)	21	(15)

A-6.1. Complete species list with functional group classifications

Section	Family	Genus	species	Common name	Functional group
PTERIDOPHYTES					
	Dennstaedtiaceae	*Pteridium*	*aquilinum*	western brackenfern	fern/herb
	Lygodiaceae	*Lygodium*	*japonicum*	Japanese climbing fern	fern/herb
GYMNOSPERMS					
	Cupressaceae	*Juniperus*	*virginiana*	eastern redcedar	woody/woody
	Pinaceae	*Pinus*	*palustris*	longleaf pine	woody/woody
		Pinus	*taeda*	loblolly pine	woody/woody
ANGIOSPERMS					
DICOTS					
	Acanthaceae	*Ruellia*	*caroliniensis*	Carolina wild petunia	forb/ herb
	Aceraceae	*Acer*	*rubrum*	red maple	woody/woody
	Anacardiaceae	*Rhus*	*copallinum*	winged sumac	woody/woody
		Toxicodendron	*pubescens*	Atlantic poison oak	woody/woody
		Toxicodendron	*radicans*	eastern poison ivy	woody vine/woody
	Aquifoliaceae	*Ilex*	*glabra*	inkberry	woody/woody
		Ilex	*opaca*	American holly	woody/woody
	Asclepiadaceae	*Asclepias*	*amplexicaulis*	clasping milkweed	forb/ herb
		Asclepias	*obovata*	pineland milkweed	forb/ herb
		Asclepias	*tuberosa*	butterfly milkweed	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
<u>DICOTS</u>					
	Asclepiadaceae	*Asclepias*	*tuberosa*	butterfly milkweed	forb/ herb
	Asteraceae	*Ageratina*	*altissima*	white snakeroot	forb/ herb
		Ageratina	*aromatica*	lesser snakeroot	forb/ herb
		Ambrosia	*artemisiifolia*	annual ragweed	forb/ herb
		Baccharis	*halimifolia*	eastern baccharis	forb/herb
		Boltonia	*asteroides*	white doll's daisy	forb/ herb
		Brickellia	*eupatorioides*	false boneset	forb/herb
		Chrysopsis	*mariana*	maryland goldnaster	forb/ herb
		Chrysopsis	*gossypina*	cottony goldnaster	forb/ herb
		Cirsium	*vulgare*	Bull thistle	forb/ herb
		Conoclinium	*coelestinum*	blue mistflower	forb/ herb
		Conyza	*canadensis*	Canadian horseweed	forb/ herb
		Coreopsis	*major*	greater tickseed	forb/ herb
		Croptilon	*divaricatum*	slender scratchdaisy	forb/ herb
		Elephantopus	*nudatus*	smooth elephantsfoot	forb/ herb
		Elephantopus	*tomentosus*	devil's grandmother	forb/ herb
		Erechtites	*hieraciifolia*	American burnweed	forb/ herb
		Erigeron	*strigosus*	prairie fleabane	forb/ herb
		Eupatorium	*album*	white thoroughwort	forb/ herb
		Eupatorium	*capillifolium*	dogfennel	forb/ herb
		Eupatorium	*compositifolium*	yankeeweed	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Asteraceae	*Eupatorium*	*glaucescens*	waxy thoroughwort	forb/ herb
		Eupatorium	*hyssopifolium*	hyssopleaf thoroughwort	forb/ herb
		Eupatorium	*rotundifolium*	roundleaf thoroughwort	forb/ herb
		Eupatorium	*serotinum*	lateflowering thoroughwort	forb/ herb
		Gamochaeta	*purpurea*	spoonleaf purple everlasting	forb/ herb
		Helianthus	*angustifolius*	swamp sunflower	forb/ herb
		Helianthus	*hirsutus*	hairy sunflower	forb/ herb
		Helianthus	*longifolius*	longleaf sunflower	forb/ herb
		Helianthus	*resinosus*	resindot sunflower	forb/ herb
		Hieracium	*gronovii*	queendevil	forb/ herb
		Ionactis	*linariifolius*	flaxleaf whitetop aster	forb/ herb
		Lactuca	*canadensis*	Canada lettuce	forb/ herb
		Lactuca	*graminifolia*	grassleaf lettuce	forb/ herb
		Liatris	*elegans*	pinkscale blazing star	forb/ herb
		Liatris	*pilosa*	shaggy blazing star	forb/ herb
		Liatris	*spp*	blazing star	forb/ herb
		Liatris	*tenuifolia*	shortleaf blazing star	forb/ herb
		Pachera	*tomentosa*	woolly ragwort	forb/ herb
		Pityopsis	*aspera*	pineland silkgrass	forb/ herb
		Pityopsis	*graminifolia*	narrowleaf silkgrass	forb/ herb
		Pluchea	*camphorata*	camphor pluchea	forb/ herb
		Pseudognaphalium	*obtusifolium*	rabbit-tobacco	forb/ herb
		Rudbeckia	*hirta*	blackeyed Susan	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Asteraceae	*Sericocarpus*	*asteroides*	toothed whitetop aster	forb/ herb
		Sericocarpus	*tortifolius*	Dixie whitetop aster	forb/ herb
		Silphium	*compositum*	kidneyleaf rosinweed	forb/ herb
		Solidago	*altissima*	Canada goldenrod	forb/ herb
		Solidago	*nemoralis*	gray goldenrod	forb/ herb
		Solidago	*odora*	anisescented goldenrod	forb/ herb
		Solidago	*rugosa*	wrinkleleaf goldenrod	forb/ herb
		Solidago	*spp.*	goldenrod	forb/ herb
		Symphyotrichum	*concolor*	eastern silver aster	forb/ herb
		Symphyotrichum	*dumosum*	rice button aster	forb/ herb
		Symphyotrichum	*patens*	late purple aster	forb/ herb
		Vernonia	*angustifolia*	tall ironweed	forb/ herb
		Vernonia	*gigantea*	giant ironweed	forb/ herb
	Bignoniaceae	*Campsis*	*radicans*	trumpet creeper	woody vine/woody
	Buddlejaceae	*Polypremum*	*procumbens*	juniper leaf	forb/ herb
	Cactaceae	*Opuntia*	*humifusa*	devil's-tongue	woody/woody
	Campanulaceae	*Lobelia*	*puberula*	downy lobelia	forb/ herb
		Wahlenbergia	*marginata*	southern rockbell	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
<u>DICOTS</u>					
	Bignoniaceae	*Campsis*	*radicans*	trumpet creeper	woody vine/woody
	Buddlejaceae	*Polypremum*	*procumbens*	juniper leaf	forb/ herb
	Cactaceae	*Opuntia*	*humifusa*	devil's-tongue	woody/woody
	Campanulaceae	*Lobelia*	*puberula*	downy lobelia	forb/ herb
		Wahlenbergia	*marginata*	southern rockbell	forb/ herb
	Caprifoliaceae	*Lonicera*	*japonica*	Japanese honeysuckle	woody vine/woody
	Cistaceae	*Lechea*	*minor*	thymeleaf pinweed	forb/ herb
		Lechea	*mucronata*	hairy pinweed	forb/ herb
		Lechea	*sessiliflora*	pineland pinweed	forb/ herb
	Clusiaceae	*Hypericum*	*crux-andreae*	St. Peterswort	forb/ herb
		Hypericum	*hypericoides*	St. Andrew's cross	forb/ herb
		Hypericum	*gentianoides*	orangegrass	forb/ herb
	Convolvulaceae	*Ipomoea*	*pandurata*	man of the earth	forb/herb
		Jacquemontia	*tamnifolia*	hairy cluservine	forb/herb
		Stylisma	*patens*	coastal plain dawnflower	forb/herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
<u>DICOTS</u>					
	Cornaceae	*Cornus*	*florida*	flowering dogwood	woody/woody
		Nyssa	*sylvatica*	blackgum	woody/woody
	Ebenaceae	*Diospyros*	*virginiana*	common persimmon	woody/woody
	Ericaceae	*Gaylussacia*	*dumosa*	dwarf huckleberry	woody/woody
		Vaccinium	*arboreum*	farkleberry	woody/woody
		Vaccinium	*myrsinites*	shiny blueberry	woody/woody
		Vaccinium	*spp.*	blueberry	woody/woody
		Vaccinium	*stamineum*	deerberry	woody/woody
		Vaccinium	*tenellum*	small black blueberry	woody/woody
	Euphorbiaceae	*Acalypha*	*gracilens*	slender threeseed mercury	forb/ herb
		Chamaesyce	*nutans*	eyebane	forb/ herb
		Cnidoscolus	*stimulosus*	finger rot	forb/ herb
		Croton	*glandulosus*	vente conmigo	forb/ herb
		Euphorbia	*pubentissima*	false flowering spurge	forb/ herb
		Tragia	*urens*	wavyleaf noseburn	forb/ herb
		Tragia	*urticifolia*	nettleleaf noseburn	forb/ herb
	Fabaceae	*Albizia*	*julibrissin*	silktree	woody/woody
		Centrosema	*virginiana*	spurred butterfly pea	forb/ herb
		Chamaecrista	*fasciculata*	partridge pea	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Fabaceae	*Chamaecrista*	*nictitans*	sensitive partridge pea	forb/ herb
		Clitoria	*mariana*	Atlantic pigeonwings	forb/ herb
		Crotalaria	*rotundifolia*	rabbitbells	forb/ herb
		Crotalaria	*purshii*	Pursh's rattlebox	forb/ herb
		Dalea	*carnea*	whitetassels	forb/ herb
		Dalea	*pinnata*	summer farewell	forb/ herb
		Desmodium	*obtusum*	stiff ticktrefoil	forb/ herb
		Desmodium	*ciliare*	hairy small-leaf ticktrefoil	forb/ herb
		Desmodium	*laevigatum*	smooth tricktrefoil	forb/ herb
		Desmodium	*lineatum*	sand tricktrefoil	forb/ herb
		Desmodium	*marilandicum*	smooth small leaf ticktrefoil	forb/ herb
		Desmodium	*nuttallii*	Nuttail's ticktrefoil	forb/ herb
		Desmodium	*paniculatum*	panicledleaf ticktrefoil	forb/ herb
		Desmodium	*rotundifolium*	prostrate ticktrefoil	forb/ herb
		Desmodium	*spp.*	ticktrefoil	forb/ herb
		Desmodium	*strictum*	pine barren ticktrefoil	forb/ herb
		Desmodium	*viridiflorum*	velvetleaf ticktrefoil	forb/ herb
		Desmodium	*glabellum*	Dillenius' ticktrefoil	forb/ herb
		Galactia	*regularis*	eastern milkpea	forb/ herb
		Galactia	*volubilis*	downy milkpea	forb/ herb
		Kummerowia	*striata*	Japanese clover	forb/ herb
		Lespedeza	*angustifolia*	narrowleaf lespedeza	forb/ herb
		Lespedeza	*bicolor*	shrub lespedeza	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Fabaceae	*Lespedeza*	*capitata*	roundhead lespedeza	forb/ herb
		Lespedeza	*cuneata*	sericea lespedeza	forb/ herb
		Lespedeza	*hirta*	hairy lespedeza	forb/ herb
		Lespedeza	*procumbens*	trailing lespedeza	forb/ herb
		Lespedeza	*repens*	creeping lespedeza	forb/ herb
		Lespedeza	*stuevei*	tall lespedeza	forb/ herb
		Lespedeza	*virginica*	slender lespedeza	forb/ herb
		Mimosa	*quadrivalvis*	fourvalve mimosa	forb/ herb
		Phaseolus	*polystachois*	thicket bean	forb/ herb
		Pueraria	*montana*	kudzu	forb/ herb
		Rhynchosia	*reniformis*	dollarleaf	forb/ herb
		Rhynchosia	*tomentosa*	twining snoutbean	forb/ herb
		Strophostyles	*umbellata*	pink fuzzybean	forb/ herb
	Fabaceae	*Stylosanthes*	*biflora*	sidebeak pencilflower	forb/ herb
		Tephrosia	*florida*	Florida hoarypea	forb/ herb
		Tephrosia	*spicata*	spiked hoarypea	forb/ herb
		Tephrosia	*virginiana*	Virginia tephrosia	forb/ herb
	Fagaceae	*Quercus*	*falcata*	southern red oak	woody/woody
		Quercus	*hemisphaerica*	laural oak	woody/woody
		Quercus	*laevis*	turkey oak	woody/woody
		Quercus	*marilandica*	blackjack oak	woody/woody
		Quercus	*nigra*	water oak	woody/woody

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
<u>DICOTS</u>					
	Fagaceae	*Quercus*	*phellos*	willow oak	woody/woody
		Quercus	*spp.*	oak	woody/woody
		Quercus	*velutina*	black oak	woody/woody
		Quercus	*stellata*	post oak	woody/woody
	Hamamelidaceae	*Liquidambar*	*styraciflua*	sweetgum	woody/woody
	Hippocastanaceae	*Aesculus*	*pavia*	red buckeye	woody/woody
	Juglandaceae	*Carya*	*alba*	Mockernut Hickory	woody/woody
		Carya	*cordiformis*	butternut hickory	woody/woody
		Carya	*glabra*	pignut hickory	woody/woody
		Carya	*illinoinensis*	pecan	woody/woody
		Carya	*ovata*	shagbark hickory	woody/woody
	Lamiaceae	*Pycnanthemum*	*loomisii*	Loomis' mountainmint	forb/ herb
		Scutellaria	*elliptica*	hairy skullcap	forb/ herb
	Lamiaceae	*Scutellaria*	*integrifolia*	helmet flower	forb/ herb
		Trichostema	*dichotomum*	forked bluecurls	forb/ herb
		Trichostema	*setaceum*	narrowleaf bluecurls	forb/ herb
	Lauraceae	*Sassafras*	*albidum*	sassafras	woody/woody

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Linaceae	*Linum*	*medium*	stiff yellow flax	forb/ herb
	Loganiaceae	*Gelsemium*	*sempervirens*	evening trumpetflower	woody vine/woody
	Malvaceae	*Sida*	*elliottii*	Elliott's fanpetals	forb/ herb
	Melastomataceae	*Rhexia*	*mariana*	Maryland meadowbeauty	forb/ herb
	Meliaceae	*Melia*	*azedarach*	Chinaberrytree	woody/woody
	Myricaceae	*Morella*	*cerifera*	wax myrtle	woody/woody
	Onagraceae	*Gaura*	*filipes*	slenderstalk beeblossom	forb/ herb
		Oenothera	*biennis*	common evening primrose	forb/ herb
	Oxalidaceae	*Oxalis*	*spp.*	woodsorrel	
		Oxalis	*stricta*	common yellow oxalis	forb/ herb
	Passifloraceae	*Passiflora*	*incarnata*	purple passionflower	forb/ herb
	Polygalaceae	*Polygala*	*mariana*	Maryland milkwort	forb/ herb
		Polygala	*nana*	candyroot	forb/ herb
		Eriogonum	*tomentosum*	dogtongue buckwheat	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
<u>DICOTS</u>					
	Rosaceae	*Crataegus*	*flava*	yellowleaf hawthorn	woody/woody
		Crataegus	*spathulata*	Littlehip hawthorn	woody/woody
		Crataegus	*spp.*	hawthorn	woody/woody
		Prunus	*angustifolia*	Chickasaw plum	woody/woody
		Prunus	*serotina*	black cherry	woody/woody
		Rubus	*argutus*	sawtooth blackberry	woody/woody
		Rubus	*cuneifolius*	sand blackberry	woody/woody
		Rubus	*flagellaris*	northern dewberry	woody/woody
		Rubus	*trivialis*	southern dewberry	woody/woody
	Rubiaceae	*Diodia*	*teres*	poorjoe	forb/ herb
		Galium	*hispidulum*	coastal bedstraw	forb/herb
		Galium	*pilosum*	hairy bedstraw	forb/ herb
		Galium	*uniflorum*	oneflower bedstraw	forb/ herb
		Mitchella	*repens*	partridgeberry	forb/ herb
	Scrophulariaceae	*Agalinis*	*fasciculata*	beach false foxglove	forb/ herb
		Agalinis	*purpurea*	purple false foxglove	forb/ herb
		Aureolaris	*virginica*	downy yellow false foxglove	forb/ herb
		Nuttallanthus	*canadensis*	Canada toadflax	forb/ herb
		Penstemon	*australis*	Eustis Lake beardtongue	forb/ herb

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
DICOTS					
	Scrophulariaceae	*Seymeria*	*cassioides*	yaupon blacksenna	forb/ herb
	Solanaceae	*Solanum*	*carolinense*	Carolina horsenettle	forb/ herb
	Ulmaceae	*Celtis*	*laevigata*	sugarberry	woody/woody
		Ulmus	*alata*	winged elm	woody/woody
		Ulmus	*rubra*	slippery elm	woody/woody
	Verbenaceae	*Callicarpa*	*americana*	american beautyberry	forb/ herb
		Verbena	*brasiliensis*	Brazilian vervain	forb/ herb
	Violaceae	*Viola*	*pedata*	birdfoot violet	forb/ herb
	Vitaceae	*Ampelopsis*	*arborea*	peppervine	woody vine/woody
		Parthenocissus	*quinquefolia*	Virginia creeper	woody vine/woody
		Vitis	*rotundifolia*	muscadine	woody vine/woody
ANGIOSPERMS	Agavaceae	*Manfreda*	*virginica*	false aloe	forb/herb
MONOCOTS		*Yucca*	*filamentosa*	Adam's needle	forb/herb
	Cyperaceae	*Bulbostylis*	*capillaris*	densetuft hairsedge	graminoid
		Bulbostylis	*ciliatifolia*	capillary hairsedge	graminoid

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
MONOCOTS					
	Cyperaceae	*Cyperus*	*odoratus*	fragrant flatsedge	graminoid
		Cyperus	*plukenetii*	Plukenet's flatsedge	graminoid
		Cyperus	*spp.*	flatsedge	
		Cyperus	*strigosus*	strawcolored flatsedge	graminoid
		Rhynchospora	*harveyi*	Harvey's beaksedge	graminoid
		Rhynchospora	*rariflora*	fewflower beaksedge	graminoid
		Rhynchospora	*spp.*	beaksedge	
		Scleria	*ciliata*	fringed nutrush	graminoid
		Scleria	*pauciflora*	fewflower nutrush	graminoid
		Scleria	*spp.*	nutrush	
		Scleria	*triglomerata*	whip nutrush	graminoid
	Juncaceae	*Juncus*	*spp.*	rush	graminoid
	Liliaceae	*Aletris*	*farinosa*	white colicroot	forb/ herb
	Orchidaceae	*Spiranthes*	*praecox*	greenvein lady's tresses	forb/ herb
	Poaceae	*Andropogon*	*glomeratus*	bushy bluestem	graminoid
		Andropogon	*ternarius*	splitbeard bluestem	graminoid
		Andropogon	*virginicus*	broomsedge bluestem	graminoid
		Aristida	*dichotoma*	churchmouse threeawn	graminoid
		Aristida	*gyrans*	corkscrew threeawn	graminoid

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
MONOCOTS					
	Poaceae	*Aristida*	*lanosa*	woolysheath threeawn	graminoid
		Aristida	*longespica*	slimspike threeawn	graminoid
		Aristida	*oligantha*	prairie threeawn	graminoid
		Aristida	*purpurascens*	arrowfeather threeawn	graminoid
		Aristida	*spp*		graminoid
		Chasmanthium	*laxum*	slender woodoats	graminoid
		Chasmanthium	*sessiliflorum*	longleaf woodoats	graminoid
		Danthonia	*sericea*	Downy danthonia	graminoid
		Dichanthelium	*dichotomum*	cypress panicgrass	graminoid
		Dichanthelium	*aciculare*	needleleaf rosette grass	graminoid
		Dichanthelium	*acuminatum*	tapered rosette grass	graminoid
		Dichanthelium	*boscii*	Boscs panicgrass	graminoid
		Dichanthelium	*laxiflorum*	openflower rosette grass	graminoid
		Dichanthelium	*oligosanthes*	Heller's rosette grass	graminoid
		Dichanthelium	*ravenelii*	Ravenel's rosette grass	graminoid
		Dichanthelium	*scoparium*	velvet panicum	graminoid
		Dichanthelium	*sphaerocarpon*	roundseed panicgrass	graminoid
		Dichanthelium	*spp.*	rosette grass	graminoid
		Dichanthelium	*strigosum*	roughair rosette grass	graminoid
		Digitaria	*violascens*	violet crabgrass	graminoid
		Digitaria	*ciliaris*	southern crabgrass	graminoid
		Digitaria	*spp.*	crabgrass	graminoid
		Digitaria	*villosa*	shaggy crabgrass	graminoid

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
MONOCOTS					
	Poaceae	*Eragrostis*	*curvula*	weeping lovegrass	graminoid
		Eragrostis	*hirsuta*	bigtop lovegrass	graminoid
		Eragrostis	*spectabilis*	purple lovegrass	graminoid
		Eragrostis	*spp.*	lovegrass	graminoid
		Gymnopogon	*ambiguus*	bearded skeletongrass	graminoid
		Gymnopogon	*spp.*	skeletongrass	graminoid
		Panicum	*anceps*	beaked panicgrass	graminoid
		Panicum	*verrucosum*	warty panicgrass	graminoid
		Paspalum	*laeve*	field paspalum	graminoid
		Paspalum	*notatum*	bahiagrass	graminoid
		Paspalum	*setaceum*	thin paspalum	graminoid
		Paspalum	*urvillei*	Vasey's grass	graminoid
		Saccharum	*alopecuroides*	silver plumegrass	graminoid
		Saccharum	*giganteium*	sugercane plumegrass	graminoid
		Saccharum	*spp.*	sugercane	graminoid
		Schizachyrium	*scoparium*	little bluestem	graminoid
		Setaria	*parviflora*	marsh bristlegrass	graminoid
		Setaria	*pumila*	yellow foxtail	graminoid
		Sorghastrum	*elliottii*	slender Indiangrass	graminoid
		Sorghastrum	*nutans*	Indiangrass	graminoid
		Sorghastrum	*secundum*	lopsided Indiangrass	graminoid
		Sorghum	*halepense*	Johnsongrass	graminoid
		Tridens	*flavus*	purpletop tridens	graminoid

A-6.1 (cont). Complete species list with functional group classifications from Fort Benning

Section	Family	Genus	species	Common name	Functional group
MONOCOTS					
	Smilacaceae	*Smilax*	*bona-nox*	saw greenbrier	woody vine/woody
		Smilax	*glauca*	cat greenbrier	woody vine/woody
		Smilax	*laurifolia*	laurel greenbrier	woody vine/woody
		Smilax	*rotundifolia*	roundleaf greenbrier	woody vine/woody