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Introduction

Upland forests of the Southeastern United States Coastal Plain range from Virginia to Texas and include a rich array of woody species (Braun 1950, USDA Forest Service 1988). Due to a cycle of clearing, farming, and farm abandonment followed by reforestation, early-succession forests have come to dominate much of the region (USDA Forest Service 1988, Workman and McLeod 1990, Walker and Oswald 2000). Consequently, some late successional hardwood species, especially those with large seeds, may be less prominent or less widely dispersed than during pre-European settlement times. This under representation of large-seeded hardwoods may be due to low abundance and a narrow distribution of seed dispersal limiting the rate of re-invasion into the landscape (Guo et al. 2000), resource poor soils slowing the rate of establishment (Workman and McLeod 1990) or herbivory inhibiting growth and subsequent survival (Sork 1983).

Conditions that influence woody plant regeneration vary across forest stands, and also within forest stands at scales as small as one meter or less (i.e., the microsite scale). For the regeneration phase, however, studies at the microsite scale reveal the most about underlying cause and effect relationships (Grubb 1977, Harper 1977, Sork 1983). For example, in old-fields of the southeastern United States, DeSteven (1991) used experiments at the microsite scale to show that life history traits, competition, herbivory and abiotic environmental stresses interact in complex ways to influence hardwood establishment. Her study as well as data from other studies show that hardwood regeneration is influenced by biotic factors, including browsing, competition, or microbial pests; resources, such as light, water and nutrient availability; and conditions, including temperature, and flooding (Kramer et al. 1952, Ferrell 1953, Carvell and Tryon 1961, Grubb 1977, Sork 1983, Wright et al. 1984, Brose and Van Lear 1998, Buckley et al. 1998).

Many have attempted to determine the single most important variable for survival and growth, centering on two primary environmental stressors, light and water limitations. Whether light or water is the most influential variable for seedlings is a constant source of debate and not necessarily the focus of our study. Wenger (1952) stated that soil moisture was the most limiting factor for both seedling growth and

survival in the well-drained sands of the Upper Coastal Plain. However, separating water from light effects is difficult because the two interact. For example, shading may decrease water loss and thereby mask negative impacts of shade on growth rate. Furthermore, the importance of water and light may co-vary. For pines in the Upper Coastal Plain, the influence of one factor on biomass growth of *Pinus* species may increase as that for the other factor decreases (Mitchell et al. 1999). The importance of the two factors also varies with respect to life history. Water may be key for initial establishment while light may be the most important variable for long-term persistence (Ferrell 1953, Wright et al. 1984, Horn 1985).

For hardwood seedlings in the coastal plain, the effects of light and water on seedlings are confounded by nutrient availability, soil organic matter content, and herbivory. Organic matter content and nutrient levels are typically low as a result of degrading land practices, such as cotton farming (Workman and McLeod 1990). When these low levels are combined with low light or water availability, seedling establishment is hindered. Herbivory obviously has negative impacts on growth; however, the level of herbivory is not easily predicted, partly because humans have had profound impacts on populations and spatial distributions of herbivores and their predators. All of these studies have indicated that the determination of the one limiting factor is a complex issue confounded by the many interactions between resources. Therefore, the determination of that one limiting factor is an almost impossible and unnecessary problem. Instead, the focus should be on determining the overall influence of variables on seedlings.

Resources are generally greater in open gaps and clearcuts than under the canopy, because there is less interception, transpiration and consumption by overstory vegetation. This implies that hardwood regeneration should be more favorable in old-fields or recently clearcut forests than in the understory. However, experiments with natural regeneration (De Steven 1991) and experience with artificial regeneration of bottomland hardwoods suggest otherwise. For example, oaks often grow too slowly to survive and gain dominance unless they first develop a pool of relatively large seedlings (advance regeneration) prior to removal of the overstory (Sander et al. 1976, Wright et al. 1984, Brose and Van Lear 1998) or benefit from artificial reduction of competing vegetation (Beck and Hooper 1986, Crow 1988). Underplanting, or natural regeneration is

therefore recommended as the method for gaining successful regeneration of oaks and other large-seeded hardwood species (Beck and Hooper 1986, Crow 1988, Buckley et al. 1998) with increased site preparation by burning or coppicing understory vegetation (Wright et al. 1984, Brose and Van Lear 1998). However, these recommendations are derived from studies with relatively productive non-agricultural sites where competition with small-seeded hardwoods and herbs is likely to be strong. In coastal plain uplands, hardwood regeneration in clearcuts may not be as strongly influenced by competition. Comparisons of oak regeneration across site productivity gradients suggest that regeneration in clearcuts may be increasingly successful as overall site productivity declines (Carvell and Tryon 1961, Buckley et al. 1998).

This project focuses on factors that influence the long-term success of planted *Q. alba* L. and *C. florida* L. seedlings in pine-dominated landscapes of the Coastal Plain region. Brand (1991) stated that projects focusing on growth and survival do not provide an explanation of the causal, or limiting factors. Chapin et al. (1987), on the other hand, pointed out that in order to study such limiting factors, one must have a range of environmental variables that may cause variation in growth and survival responses. From there, one can make conclusions based upon the environmental stresses present. Our project focuses on the latter idea, and thus, uses a mechanistic model to determine the impacts of environmental variables on seedling growth and survival from the environmental stress perspective.

Objectives and hypotheses

The main goal of this research was to determine the environmental factors affecting regeneration, and then establish which of these ecological factors are influential to re-invasion of large-seeded hardwood seedlings in former agricultural sites of the Upper Coastal Plain of South Carolina. White oak (*Quercus alba*) and flowering dogwood (*Cornus florida*) were the two species chosen for study. Practical reasons for using these species included their potential value for wood products and food for wildlife (Oosting 1942, Good and Good 1972, Lesser and Wistendahl 1974, Roberts et al. 1979, Jones et al. 1984, McLemore 1990). Both species' susceptibility to water and light

limitations (Ferrell 1953; McLemore 1990) as well as the impact herbivory has on *C. florida* (Crawley 1983) provided us with ecological reasons to study these two particular species. The study incorporated three different sites across a moisture gradient and two cutting treatments (clearcut and understory) to produce a wide range of resources and conditions. This increased the chances for observing impacts of the various environmental factors on seedling performance.

A second goal of this research was to determine which of several artificial regeneration methods is best for restoring large-seeded hardwoods. Specifically, we wanted to determine if planting seedlings in the understory was the most feasible option for the restoration of these hardwoods. Most restoration literature has found that the facilitative effects of the understory are stronger than the negative impact of shade on survival and growth (Beck and Hooper 1986, Crow 1988, Buckley et al. 1998). By utilizing the two cutting treatments, our study focused on the differences between the two management plans.

Specific hypotheses that will be tested for our specific sites are:

- 1) For large-seeded hardwood species, seedling growth and survival will respond to low soil moisture during the first two years after planting.
- 2) Light availability will have a large impact on growth responses for *Q. alba* and *C. florida* seedlings.
- 3) Herbivory will have a significant impact on growth and survival in seedlings of large-seeded hardwood species.

Literature Review

Establishment and Persistence

Two life stages are particularly critical for hardwood regeneration: establishment (i.e. germination, emergence, and survival through the first growing season or year), and long-term persistence of seedlings or saplings (i.e. elongation, biomass growth, and long-

term survival). In the southeastern United States, seed rain, life history traits, plant competition, herbivory, and abiotic environmental stresses interact in complex ways to influence hardwood establishment in old-field habitats (De Steven 1991). Furthermore, biotic factors, such as selective browsing, competition, or the selective effects of microbial pests, can actually halt the seedling's transition to the sapling stage (Grubb 1977; Sork 1983).

For *Quercus* species, establishment is influenced most strongly by biotic factors while long-term persistence is more strongly controlled by abiotic conditions (Carvell and Tryon 1961, Stebbins 1971). This can be attributed to the evolutionary development of large seeds, implying they have large cotyledon reserves to tolerate low light or resource availability (Salisbury 1942, Baker 1972, Bonfil 1998, Hewitt 1998). However, *Quercus* species are typically light demanding. More than likely, their large seeds have actually evolved due to their occupation of dry sites and the advantage of a deep taproot (Ferrell 1953, Grubb 1977). Therefore, the carbon reservoirs in the seed buffer *Quercus* seedlings from abiotic stress during the first growing season. Later, when the carbon reservoirs have been depleted, access to light may be critical for survival (Grime and Jeffrey 1965, Hodges and Gardiner 1992). For *Cornus* seedlings, abiotic stress is important during both establishment and long-term persistence. *Cornus* species have smaller-sized seeds and therefore less carbon reserves in the cotyledons than *Quercus*, so the effect of light is typically stronger. *Cornus* seeds usually show early and rapid root growth (Lesser and Wistendahl 1974), but their shallow root systems make it difficult to survive on dry soils (McLemore 1990). On the other hand, once established, *Cornus* seedlings may need less light than *Quercus* seedlings to persist for long periods of time, because *Cornus* species are more shade-tolerant than *Quercus* seedlings (Hewitt 1998).

Light or Water?

Several tree regeneration and population dynamics studies have shown greater survival to be expected in open spaces, whether they are gaps or clearcut areas (Good and Good 1972, Ehrenfeld 1980, Crow 1992). This implies that light may be a principal limiting factor (Kramer et al. 1952, Grubb 1977, Wright et al. 1984, Williston et al. 1986, Crow 1992). However, initial survival of planted seedlings may be better in shaded

understories (See Results from Previous Work Section), possibly because heat loads or too much direct light may be harmful to early seedling development. Korstian and Coile (1938) suggested that drought is the cause of high mortality in highly competitive clearings, not light. Because of this, some believe that water is the primary limitation to the growth of hardwood seedlings (Grubb 1977, Wright et al. 1984, Horn 1985).

The debate over which factor, water or light, is more limiting to survival and growth is still ongoing. To have this debate may not be necessary or pertinent to our study, but the conclusions drawn from these deterministic studies are. Specifically, many researchers have suggested considering these two major factors together rather than separately. Kozlowski (1949) pointed out that light and water are not separable. Mitchell et al. (1999) found that light and water stress explain survival and growth variability better together as combined factors than as individual limiting factors. Ferrell (1953), a proponent of water as the limiting factor, noted that when dealing with any environmental complex, all major factors must be considered before any conclusions can be made. Maximizing the growth and survival of planted conifers (Brand 1991) and mixed oak stands (Carvell and Tryon 1961) required studying all resources and their interactions, especially water and light. From these studies, no definitive conclusion on which environmental factor was more limiting could be made, thereby indicating a complex relationship between the two resources. Because the environmental resources are heavily dependent on site conditions, species needs and climatic conditions, the depiction of one resource being the most limiting is unlikely.

Some have argued that light is more limiting than water. In most cases, these researchers did stress the interaction between the two factors, but they concluded that water's effect on seedlings is mediated by light. For example, adequate light allows for better water uptake (Shirley 1929, Rice and Bazaaz 1989) and nutrient uptake and use (Phares 1971, Sork 1983, Brand 1991). Inadequate light levels also condition seedlings over a long period of time and reduce their vigor, rendering them susceptible to drought and water stress (Smith 1940, Kozlowski 1949). Specifically, light is important for the survival of our two study species, *Q. alba* and *C. florida*, and *Pinus taeda* L. (loblolly pine), a major overstory tree at our study site. For these species, researchers found that inadequate light levels could not be overcome by high soil moisture (Moore 1926, Wood

1938, Smith 1940, Lutz 1945). All of these studies suggest water stress effects are mediated by light limitations, suggesting a synergistic relationship between the two resources when the seedling is stressed.

Some propose that water is the principal limiting factor, especially during the early and juvenile stages of the seedlings. Low available water lowers overall survival, because it directly lowers germination and increases root competition (Moore 1926, Toumey and Kienholz 1931). Kramer et al. (1952) found that increasing water levels significantly increased overall survival for some species. However, in certain species, such as *C. florida*, moisture levels are especially important, because they greatly moderate the influence of light (Horn 1985). Horn found greater growth responses to a trenching treatment than an increased light level treatment. In fact, correlations of significantly greater growth and higher light levels were only found within trenched plots, not without, emphasizing the complex relationship of *C. florida* with moisture availability. These results could not be exclusively attributed to moisture availability, however, because trenching also changes nutrient availability and resource competition. This further indicates that environmental variables cannot be truly separated.

The debate about water versus light is now focusing more on responses during different life stages of seedlings, specifically the germinant versus juvenile stages. Light proponents believe light intensity becomes the major limiting factor to seedling survival once the carbon reserves in the cotyledons are gone (Grime and Jeffrey 1965, Hodges and Gardiner 1992). This covers everything after emergence in the seedling's life. The other side of the debate does not directly counter this. Instead, water proponents believe water is more related to overall survival than growth while light is more associated with growth than survival (Korstian and Coile 1938, Ferrell 1953, Myers et al. 1989). Thus, a distinction between the factors and their limiting ability on seedlings is not completely clear in the literature.

This debate is a starting point for our project, meaning that the determination of the one principal limiting factor is not of primary importance. Instead, our intent is to describe and quantify the seedling responses to environmental variables in the Upper Coastal Plain of South Carolina. Soils of the Upper Coastal Plain are typically very sandy and well drained, so the assumption that available soil moisture might be a very

important factor is valid. Wenger (1952) found this for both seedling growth and survival.

If water is at a premium, shading can decrease water loss from evaporation and transpiration, benefiting seedlings at their initial, vulnerable stages. Therefore, shading can allow for better establishment if drought does not lessen the water availability of the area. These shading responses were shown in biomass responses of *Pinus* species in the Coastal Plain province of Alabama (Mitchell et al. 1999). Biomass varied across a range of water stress and light availability as one of the resources increased while the other decreased, and vice versa. Light availability still remained the critical factor in the long run even though there was obviously less light available in the shaded understories than in the clearcuts. Shaded understories, therefore, lessened the long-term persistence of seedlings (Mitchell et al. 1999). These findings support the idea of a distinction between the limitations of the two factors, which is where the debate remains.

Environmental Stressors

In addition to light and water stress, low organic matter or low quality organic matter content in the soil may be a barrier to establishment of *Q. alba* and *C. florida* in the Upper Coastal Plain. Farming practices that degrade soil organic matter, such as cotton farming, have caused the soil organic matter at the Savannah River Site, which is located in the Upper Coastal Plain, to remain fairly low, approximately 0.5-3% (Rogers 1990). Even in the absence of degrading practices, organic matter percentage is typically low in upland forests dominated by *P. taeda* and other southern pines, the sites of study for this project. Thus, nutrient availability and water holding capacity of the soil may be low enough to stress hardwood seedlings.

Quantity and quality are the two more important characteristics of organic matter. Quantity of organic matter affects the water holding capacity, cation exchange capacity, and the source of mineralizable nutrients, estimated by measuring total carbon (Burger 1998). Because of the past land practices, the soils in the Southeastern United States generally have high carbon/nitrogen ratios of approximately 22:1 (Korstian and Coile 1938), implying that the quality of the organic matter is poor in the Upper Coastal Plain of South Carolina, or it has not decomposed very quickly. It also suggests that there will

be low quantities of organic nitrogen present. Low quality organic matter results in low mineralization rates, keeping the quantity of available nitrogen consistently low.

Another major barrier to establishment is herbivory. Herbivores have strong influences on the survival of seedlings (Grubb 1977, Buckley et al. 1998) and may have their greatest impact after seedlings have survived the initial mortality risks during germination or emergence (Streng et al. 1989). Herbivory may not necessarily kill an individual plant, but it will prevent or delay the plant from entering the next size category (Sork 1983). However, the consumption of enough of the seedling can possibly lead to death (Janzen 1970). In nature, large herbivores such as deer frequently take 100% of the shoot, forcing regrowth from lower buds (Crawley 1983). Herbivory can reduce photosynthetic capacity, stressing the plant and predisposing it to other stress factors, such as drought or competition (Sork 1983).

The effect an herbivore will have on a seedling is determined by seed size (Bonfil 1998). Bonfil showed high levels of herbivory are more influential on small-seeded seedlings than larger-seeded seedlings. Small-seeded seedling survival was decreased 13% while large-seeded species' survival decreased by only 0.6%. Thus, larger seeds have a greater chance to survive shoot removal due to their larger cotyledon reserves (Bonfil 1998).

Other factors affecting seedling establishment and long-term survival

The two major barriers to seedling establishment and survival not tested in this project are seed dispersal and fire. The first barrier, seed dispersal, may increase seed and seedling survival by carrying seeds to better habitats (Schupp 1988). *Quercus alba* is a large-seeded and *C. florida* a smaller-seeded hardwood species, but both rely primarily on animal dispersal (Stebbins 1971, McLemore 1990). Streng et al. (1989) found that smaller-seeded species have larger seed crops. However, they tend to have more mortality and smaller germination percentages than larger-seeded species, making smaller-seeded species' populations unstable when compared to large seed crops (Lesser and Wistendahl 1974, McLemore 1990). Animal dispersal frequently transports seeds from favorable sites to other favorable sites, possibly removing the seed from heavy herbivory pressure. Wind dispersal, on the other hand, puts the seeds in favorable as well

as many unfavorable sites (Stebbins 1971). In the pine-dominated uplands of the Coastal Plain, wide seed dispersal may be necessary for the seed to reach a “safe site” (Harper 1977); i.e. one where the propagule can germinate and grow without mortality occurring because of herbivory or other barriers to establishment and survival.

The second untested factor in the establishment of seedlings is fire. *Quercus alba* is not a fire-adapted species, but it can tolerate surface fires as an adult. Fire can slow *Quercus* establishment if it is severe and if it occurs while seedlings are young. However, fire may be needed to lessen competition for the initiation and emergence of *Quercus* regeneration (Carvell and Tryon 1961, Good and Good 1972, Beck and Hooper 1986, Crow 1988). During the seedling stage, *Q. alba* dies back after fire and can re-sprout during the same or the next growing season due to its habit of building large root systems with adventitious buds. Many *Q. alba* competitors emphasize shoot growth and so lose relatively more production than *Q. alba* when burned (Kelty 1989, Kolb and Steiner 1990, Lorimer et al. 1994, Brose and Van Lear 1998). *Cornus florida* has relatively thin bark, which makes it less tolerant to fire than *Q. alba* (McLemore 1990). It can tolerate infrequent burns of low intensity once stems reach 3 to 5 m in height (Lesser and Wistendahl 1974).

Results from Previous Work

Three other projects have been established at the Savannah River Site (SRS) to determine the feasibility of artificially regenerating hardwood species in old-field *Pinus* plantations and to determine the barriers to their regeneration. The first study was initiated in 1997 and consists of four plots, two recent clearcuts and two adjacent forest understories, planted with seeds of white oak (*Q. alba*), flowering dogwood (*C. florida*), black gum (*Nyssa sylvatica* Marsh.), pignut hickory (*Carya glabra* (Mill.) Sweet), and sand hickory (*Carya pallida* (Ashe) Eng. & Graebn.). First-year emergence rates were low, with an average of 30% for the larger-seeded species (*Q. alba*, *C. glabra*, and *C. pallida*) and an average of 6% for the smaller-seeded species (*C. florida* and *N. sylvatica*; Jones and Riley, 1999). In one forest understory plot, squirrels ate all but one of the

Carya nuts, illustrating the potential importance of seed predation on large-seeded species. This was comparable to a study performed by Buckley et al. (1998) on northern red oak (*Quercus rubra* L.) seedlings. They found direct-seeded seedlings had high mortality, especially in the clearcut plots, stating that direct seeding is not a preferred option for artificial regeneration.

In the second study, *Q. alba*, *C. florida*, *C. glabra*, and *C. pallida* seedlings were planted in four pine-dominated sites in the spring of 1998. A total of 23 plots, 16 in the understory and 7 in recently clearcut areas, were established. Seedling survival during the first growing season in the understory (overall mean of 75%) was greater than the survival for the clearcut plots (47.5%) (Jones and Riley 1999). The species that fared best overall was *Q. alba*, and the worst was *C. glabra*.

The third study was a trenched plot experiment. In 1998, seedlings of *Q. alba* and *C. florida* were planted in a *P. taeda* understory, half in trenched plots and the other half untrenched. Trenched plots were weeded consistently in order to minimize potential effects of belowground competition. This study's main objective was to test the influence of soil resource availability, primarily water, on seedling establishment and long-term performance. Overall, growth for both species in the trenched plots was consistently greater than in the untrenched plots (personal observations).

Seed planting was deemed to be an inefficient method for regeneration of these hardwoods, because there were low emergence rates and very slow growth rates as well as the seed predation problem (Jones and Riley 1999). However, the fact that many plants survived for two years suggests that seed dispersal is one barrier to re-invasion of large-seeded species into upland forest communities of the Upper Coastal Plain. It was obvious from the second experiment's data that once seedlings reach some critical size, they are capable of long-term persistence. Because of low soil moisture conditions correlating with high mortality, the seedling planting study indicates water availability may be a key factor in establishment. The trenched plot project further indicates that soil resource availability is a major barrier to growth. This does not mean that soil moisture is the sole limiting factor, because the effect of soil moisture cannot be teased apart from other soil resource effects. However, it does strengthen our hypothesis concerning the impact water availability will have on seedling responses.

Methods

Site Description

The Savannah River Site (SRS) (33.15°N latitude, 81.30°W longitude) is a 78,000-hectare area in west central South Carolina, 32 km south of Aiken (Jones et al. 1984, Rogers 1990). SRS is included within the Upper Coastal Plain Physiographic Province (Odum 1960) (Figure 1), and has two subprovinces within it: upland areas characterized by sand hills (Aiken Plateau) and Pleistocene coastal terraces ("low country") that roughly parallel the Savannah River (Odum 1960, Workman and McLeod 1990) (Figure 2).

In 1950, the Atomic Energy Commission (AEC) acquired the area. SRS was originally chosen for its relative distance from large populations, its access to adequate transportation, its fairly level topography, its large supply of water, and its well-drained soils. After purchasing the land for nearly \$19 million, the AEC contracted E.I. DuPont de Nemours, Inc., to create, design, and construct facilities to produce nuclear materials for national defense (Rogers 1990, D.O.E. 1996).

Since 1951, SRS has had three missions: 1) production of nuclear materials, 2) production of forest products, and 3) environmental research. Construction of reactors and waste management facilities accomplished the goals of the first mission. The second mission began soon after construction with the accelerated cutting of the forests on site with subsequent planting beginning in 1952 as part of the timber management plan. The design called for watershed stabilization (Langley and Marter 1973), which led to a reforestation of nearly forty percent of the old-fields with short rotation, highly productive southern pines (Jones et al. 1984). In 1972, SRS was classified as the first National Environmental Research Park (NERP) to serve as a testing ground for basic and applied questions concerning ecology and multiple use forest resource management (Langley and Marter 1973, D.O.E. 1996). Further steps were taken in 1981 toward the preservation of the SRS environment when an environmental cleanup program was initiated, and the site was included on the National Priority List in 1989. Since that time, the EPA has regulated SRS (D.O.E. 1996), illustrating the Savannah River Site's dedication to environmental awareness and research.

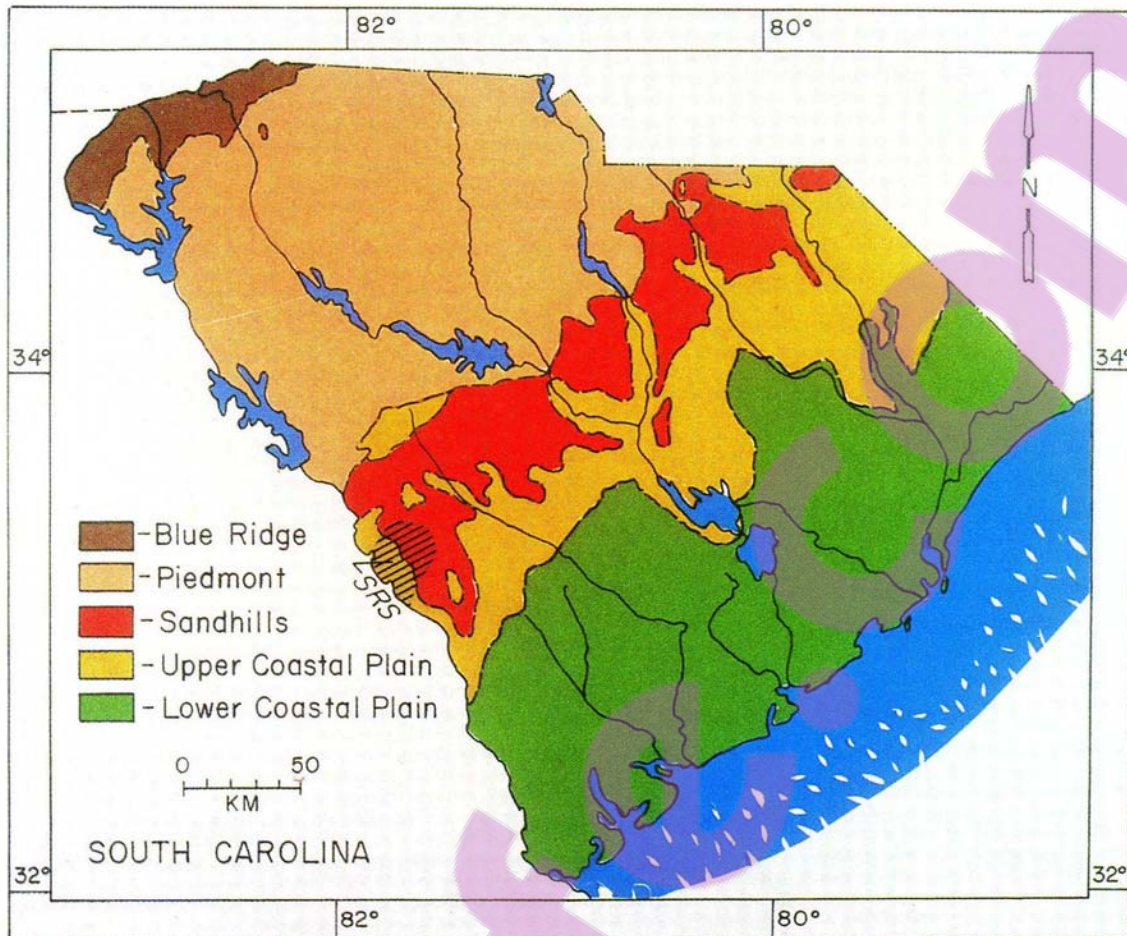


Figure 1. The Savannah River Site in relation to the physiographic provinces of South Carolina (taken from Workman and McLeod 1990).

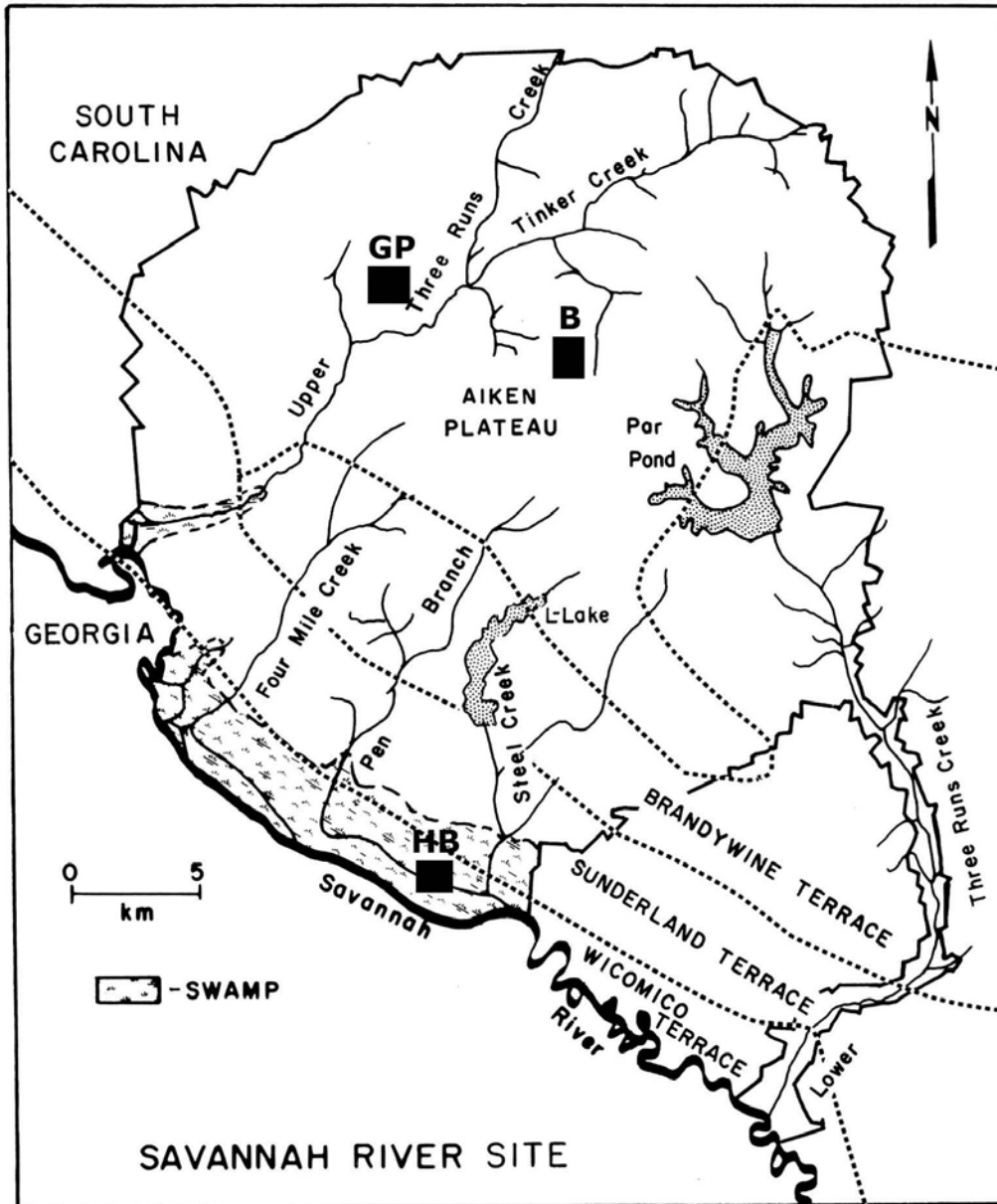


Figure 2. Map of SRS showing the Aiken Plateau and coastal terraces. B= Beaufort; GP=Green Pond; HB=Hog Barn (taken from Langley and Marter 1973).

Braun (1950) classified SRS as part of the Southeastern Evergreen Forest Region, which includes three broad forest types occurring throughout:

- 1) Pine and oak-pine forest communities including *P. palustris* Mill., *P. elliotti* Engelm., *P. taeda* and pine-hardwood forests.
- 2) Bottomland forests such as swamp forests, bottomland hardwoods, and ridge bottoms.
- 3) Hardwood forests of uplands and slopes, including oak-hickory forests.

At each of our experimental sites, the predominant forest type before European settlement was most likely *P. palustris* or pine-hardwood communities. General plot and soil information of our sites are included in Table 1. Data in this table include density and basal diameter of overstory trees (>5 cm dbh) and understory woody plants (<5 cm dbh). This data was obtained by plotting four 100 m² circular areas within each forest stand, collecting the necessary data within each area, averaging the values over the four areas, and then extrapolating them to quantities per hectare.

Plot Selection

Three sites within the larger Savannah River Site were selected to provide a wide range in environmental conditions and are labeled in Figure 2. One site (Beaufort) is a dry upland with Fuquay and Dothan soils and sparse understory vegetation. Another upland site (Green Pond) has a thinner sandy epipedon but denser understory than the Beaufort site. The wettest of the three sites (Hog Barn) was located on the coastal terraces near the Savannah River swamp. This Hog Barn site has Hornsville and Smithboro soils, and a dense understory. Water drainage was greatest at Beaufort, followed by Green Pond and Hog Barn. At the Hog Barn site, puddles frequently formed after rainfall, because the soil had over 30% clay and had relatively poor drainage. The three sites were also different in overall productivity, resource levels, and possibly in competition and herbivory (Rogers 1990, Rogers 1990). One point in common at each of the three sites was the presence of a clearcut adjacent to a 40-50 year old pine forest with the same soil types in both. Another distinction between the Hog Barn site and the two upland sites was the absence of *Pinus* planting. Both of the upland sites (Green Pond

Table 1. Soil and vegetation properties of three selected sites within the Savannah River Site in South Carolina. Superscripts correspond to specific soil type descriptions. Four 100 m² plots were used at each site to determine the tree species, densities and basal areas. The results were averaged and extrapolated into the units meter squared per hectare (m²/ha).

SITE	Green Pond	Hog Barn	Beaufort
Soil Type (Series)	Neeses B	^a Hornsville, ^b Smithboro	^c Fuquay B, ^d Dothan B
Soil Description	Fine, kaolinitic, thermic, Typic Hapludults	^a Fine, kaolinitic, thermic Aquic Hapludults ^b Fine, kaolinitic, thermic Aeric Paleaquults	^c Loamy, kaolinitic, thermic Arenic Plinthic Kandiudults ^d Fine-loamy, kaolinitic, thermic Plinthic Kandiudults
Dominant Tree Species	<i>P. elliottii</i> (Slash pine)	<i>P. taeda</i> (Loblolly pine)	<i>P. elliottii</i> (Slash pine)
Basal Area of dominant species (m ² /ha)	20.8	18.4	12.3
Density of dominant species (no./ha)	290	135	190
Total Tree Basal Area (m²/ha)	27.21	29.19	19.05
Total Tree Density/ha (≥ 5cm dbh)	510	415	380
% Bare Ground in Clearcuts	57.88	7.75	81.63

and Beaufort) were planted with *P. elliotii* while the Hog Barn site was allowed to progress as an old-field without planting. The term “site” refers to the three specific areas (Green Pond, Hog Barn, and Beaufort) used in this study, not the entire Savannah River Site.

At each of the three sites, four 30 x 30 m plots were laid out in the understory and two 30 x 30 m plots were placed in the recently clearcut areas adjacent to the understory (total of eighteen plots). Each plot included 216 pin-flagged grid points (2 x 2 m spacing). One understory and one clearcut plot was chosen by a random number generator at each site (a total of six plots). These plots were made larger to accommodate an additional 60 planting locations that were used for measures of environmental factors and seedling performance at the microsite scale. These six chosen plots (two for each site) are the experimental units referred to throughout the study as whole-plot and within-plot scales (See *Methods—Analysis*).

Seedling Planting

Quercus alba 1-0 bare root stock seedlings were obtained from Flint River Nursery in South Carolina (seed source primarily South Carolina, but also Georgia). *Cornus florida* 1-0 bare root stock seedlings were obtained from Hillis Nursery in McMinnville, Tennessee (seed source Georgia). One-year-old seedlings were culled to include only those that were relatively large (≈ 30 cm in height for white oaks; ≈ 40 cm or more for dogwoods) with numerous lateral roots. Very large seedlings with 40-50 lateral roots were also culled to improve uniformity of planted seedlings. We chose bare root stock, because they are produced cheaply and are also easy to plant.

Over a span of two days in March 1999, the seedlings were planted one per grid location (randomly assigned species at each location), resulting in a density of 138 seedlings per species per plot in each of the six plots chosen for microsite measurements.

Thirty seedlings per species per plot were randomly chosen by random-number generator for measurement and analysis of environmental factors (i.e., water, nutrients, light, and herbivory) and seedling performance. At the time of planting, basal diameter and stem height were measured and the number of first order lateral roots was counted in order to have values for initial size. Also at the time of planting, thirty seedlings of each

species were randomly drawn from the seedling stock after culling for dimension analysis. Shoot length and stem basal diameter were measured, and the number of lateral roots was counted (Table 2). Roots and shoots were dried to constant weight at 60°C and weighed. The root samples were ashed at 500°C overnight and weighed to correct for mineral soil that adhered to roots. These samples were used to predict initial biomass of planted seedlings using a regression of dry mass on diameter squared times height (d^2h ; Table 3) (Parresol 1999).

Water Measurements

Rain gauges were installed in the clearcuts at each site to estimate monthly precipitation. The precipitation values are presented in Figures 3a-b and show that there was little precipitation in March through May of each year, causing relatively dry conditions during a period when seedlings normally achieve much of the year's growth.

In May 1999, we placed pairs of 32 cm stainless steel rods within 10-20 cm of every experimental seedling to measure available soil moisture by Time Domain Reflectometry (TDR). The TDR technique gives an integrated average of the volumetric soil water content from 0-30 cm by determining the dielectric constant of the media. The dielectric constant is calculated by measuring the travel time of an electromagnetic pulse through the stainless steel rods (Topp et al. 1980, Topp et al. 1982, Dasberg and Dalton 1985, Dalton 1987). An initial reading was taken upon installation and biweekly sampling followed during the summer of each growing season.

TDR calibration and measurement had been used principally in rocky, clayey Piedmont soils (Topp et al. 1980, Topp et al. 1982). Because of the many differences in soil characteristics and properties between the Piedmont soils and our sandy soils, the calibration curves and equations derived from previous studies did not fully explain the volumetric water content of our soils. It was evident after calculating the water contents from TDR measurements that the values were not true representations of the available water.

Therefore, we conducted a small laboratory experiment, much like the study by Topp et al. (1982). Samples were taken from the top 30 cm of soil of the Hog Barn site

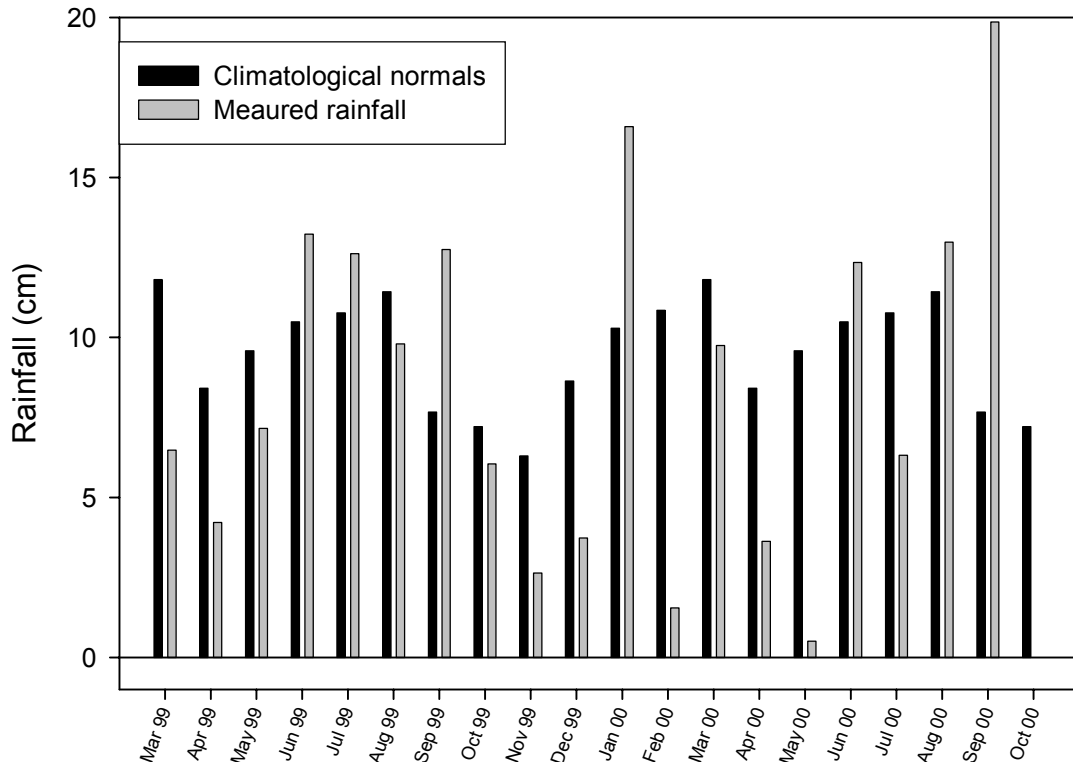


Figure 3. Rainfall measured by the USDA Forest Service Savannah River vs. climatological normals for both growing seasons at the Savannah River Site in South Carolina for 1999 and 2000.

Table 2. Mean size and morphology measures for 30 seedlings per species collected at the time of planting for dimension analysis at Savannah River Site in South Carolina. OD Bio = Oven-dried Biomass.

Species	Height (cm)	Basal Diam (cm)	# of Root laterals	Root OD Bio (g)	Shoot OD Bio (g)	Total OD Bio (g)
<i>Q. alba</i>	28.07	0.72	7.87	13.07	3.54	16.61
<i>C. florida</i>	51.60	0.73	5.60	4.46	4.83	9.28

Table 3. Regressions used to predict the total biomass at the time of planting for 1-0 bare root seedlings at the Savannah River Site in South Carolina. Z = total biomass (without leaves) at the time of initial planting; d²h = diameter in squared cm times height in cm.

Species	Total biomass regression equation	R²
<i>Q. alba</i>	$Z = 8.169 + 0.523d^2h$	0.742
<i>C. florida</i>	$Z = 0.094 + 0.303d^2h$	0.717

and one of the two dry sites (Green Pond), returned to the laboratory, dried, and sieved to 2 mm particle size. The soil was divided into three replicates of 3800 cm³ volume samples for each site. The samples were then placed into plastic containers and covered to lessen evaporative loss. A pair of TDR rods was placed into each container to a depth of 30 cm, and an initial reading was taken. After the initial reading, a 5% increase by volume of water was added to each container. The soils were mixed, allowed to settle, and a second reading of each container was taken. These steps were repeated at 5% by volume increments until the soils reached saturation (water puddling on top without draining).

We proceeded to calibrate the TDR for each type of soil using a 3rd order polynomial regression. A fully additive design of regression analyses was used to calculate the experimental TDR values with different physical constants, Topp et al.'s (1980) calibration curve, and our calibration curve. Regression and graphing of the data showed that the Topp et al. (1980) calibration underestimated the data for our soil, while our calibration curve explained 99% and 98% of the variation at the dry site and moist site, respectively.

Gray and Spies (1995) pointed out that in some cases, 1st order regressions explained as much variation as 3rd order, but we found otherwise. A 1st order calibration of our data explained 98% and 91% compared to 99% and 98% in the 3rd order polynomial regression). Dielectric constants (K_a) were calculated for input into the 3rd order calibration curves to determine actual values:

$$K_a = (\text{TDR reading}/(0.66 \times 0.32))^2$$

$$\text{Dry site: Vol. Water \%} = (-0.109 + 0.119K_a - 0.0105K_a^2 + 0.000431K_a^3) \times 100\%$$

$$\text{Wet site: Vol. Water \%} = (-0.108 + 0.149K_a - 0.0156K_a^2 + 0.000622K_a^3) \times 100\%$$

There were many aspects of this experiment and its design that may provide reasons for miscalculation including: 1) the disturbance of soils by mixing and the TDR rods themselves causing a loss of contact between the soils and rods; 2) the sieved soil not being a true representation of the variable particle size of the soil in the field; 3) the soil lacking the true porosity and bulk density, two major factors in the determination of

dielectric constants; and 4) the water loss from mixing, evaporation, and other miscellaneous procedures. Cassell et al. (1994) suggested this type of calibration curve experiment if the soil's available water was questionable. However, they stated that the application of derived calibration curves should be for the intended experiment only.

Nutrient Measurements

To estimate the available nutrients for each seedling, resin impregnated membranes were placed in the soil within 10 cm of each experimental seedling. We assessed nitrate, ammonium, and phosphate concentrations. One cation and two anion 3 x 3 cm resin impregnated membranes were inserted into the top 10 cm of mineral soil. After a 6-10 day incubation period in the field, the membranes were taken from the soil and the ions extracted from them (Jarrell 1996, Jones Ecological Research Center 1998) to give an index of available nitrogen and phosphorus next to each seedling. For nitrogen, this procedure was conducted twice during the growing season, once in the middle of summer and once again at the end of the growing season. Phosphate levels were calculated during the first growing season only, because logistic limitations during the second growing season restricted us from acquiring the second season's phosphate levels. Laboratory soil extractions of the nutrients were a possibility for more accurate nutrient determination, but the large amount of time required convinced us that the faster membrane method was preferable.

Total Carbon Analysis

The quantity of organic matter was assessed once during the first growing season. Soil auger samples of the top 10 cm of mineral soil were taken within a 10-20 cm radius of each experimental seedling. Because soil carbon content does not change rapidly, one sample was sufficient to describe the carbon content of the soils for both growing seasons. The samples were analyzed for total carbon on the LECO CR-12 Carbon System (LECO, Inc., St. Joe, Michigan), giving a measure of the total carbon and an estimation of the quantity of organic matter around each experimental seedling.

Available Light Measurements

We used the hemispherical (180°) canopy photography technique for each experimental seedling during the 1999 growing season. Only understory seedlings were measured for light availability, because clearcut seedlings were assumed to have 100% full sunlight (Canham 1988). The photographs were developed and scanned into the computer for analysis. The pictures were digitally sharpened to make the contrast between sky and vegetation obvious. This enabled the computer to estimate the light environment of the growing season with the use of the software package HemiView (Delta-T Devices Ltd., Cambridge, UK). HemiView calculated gap light index (GLI) by using estimates of sun tracts and the Standard Overcast Sky (SOC) model. GLI is an integration of the seasonal and diurnal movements of the sun, direct and indirect radiation, and the distribution of canopy openness in units of percent full sun (Canham 1988, Pacala et al. 1994):

$$\text{GLI} = \{(0.5 \times \text{Direct Radiation}) + (0.5 \times \text{Indirect Radiation})\} \times 100\%$$

A value of 0% meant there was no available light able to penetrate the forest overstory over the span of one year, and a value of 100% meant there was nothing blocking or intercepting the sunlight from the seedling.

Herbivory Treatment and Measures

All biotic causes of leaf area damage, including insects and microbes, were counted as leaf herbivory. We defined stem herbivory as any loss of stem tissue. Small mammals and white-tailed deer caused most stem herbivory.

In order to facilitate differences between seedlings concerning the degree of herbivory, half of the extra experimental seedlings in each randomly chosen plot (15 seedlings of each species) were sprayed individually with the insecticide Malathion and the broad-spectrum fungicide chlorothalonil (Daconil) simultaneously at levels recommended by the biocide labels. This was conducted in a split-plot design with one-half of the plots sprayed and the other half not sprayed.

The pesticides were applied once during May 1999 but had undesirable effects on the seedlings. In some cases, 25-50% of the total leaf area of each seedling died back early in the growing season, and in other cases the pesticides appeared to increase insect herbivory (personal observations). The spraying was deemed ineffective, and so was discontinued after only one treatment. The survival status and resource measurements of the once-sprayed seedlings were kept separately in case there were any residual effects by the pesticides on the seedlings, but there proved to be no lasting effect.

Once the decision to discontinue the spraying was made, the methodology of measuring leaf and stem herbivory became the primary issue. During the summers of 1999 and 2000, percent leaf area and stem tissue lost to herbivory were assessed monthly. The primary drawback to monthly measures versus one final measure was the amount of time spent. However, the primary benefit to this method was that it allowed for decreased measurement error, because the frequent sampling interval could capture more herbivory occurrences than the yearly measures. Several methods to measure leaf area were attempted before settling on the best one. Each of the first two attempted methods required the use of three representative random leaves from each experimental seedling. The first method involved taking digital pictures of each of the three representative leaves. These images were to have their outlines and area eaten traced later on the computer and those areas computed. It would give the total area, the area lost to herbivory, and, by subtraction, the total leaf area. This digital tracing method seemed unreasonable, because the consistent glare from the leaves made the pictures difficult to analyze, and the creation of a suitable background for the camera was also difficult. The second method employed a transparent plastic grid sheet to estimate area, much like the grids used by previous researchers (Aide and Zimmerman 1990, Marquis and Whelan 1994, Aizen and Patterson 1995, Wold and Marquis 1997). Our grid sheet had the capability of estimating area to the nearest cm^2 . The sheet was placed over each of the three representative leaves, and the total leaf area was counted in grid squares. Theoretically, the squares were small enough to adequately measure both the total leaf area and the area eaten by herbivores, but large enough to quickly and efficiently count the squares for total leaf area. This second method was also inefficient, because the time required to count the squares for one leaf was excessive. Both of these methods suffered

an additional drawback: it was difficult to determine a method to consistently choose three leaves that would be representative of a seedling, especially for *Q. alba*.

The final method involved surveying the percentage of overall leaf herbivory of each experimental seedling through a visual estimation technique. Several studies have used this same technique (Hunter 1987, Hunter and Schultz 1993, Hunter and Schultz 1995, Humphrey and Swaine 1997, Hunter and Forkner 1999) and have grouped leaf defoliation into either five or seven classes of defoliation. For practical purposes, we assigned the level of herbivory into one of five categorical rankings (0-20, 20-40, 40-60, 60-80, 80-100% of leaf are killed by herbivores) for each seedling and recorded the level of herbivory as the midpoint of each category for each seedling, making an arc sine transformation unnecessary. Even with the averaging of herbivory values over both seasons, 10% was the lowest possible value, and so the ranges and error bars could not fall below 10%. When the benefits of quicker measurement time were weighed against the costs of less accuracy and lost precision, this third method still seemed the most efficient and the best choice.

During each herbivory survey, the total number of leaves was also counted. The leaf count for the first growing season was problematic, because it was pseudo-quantitative. It assumed the leaves counted at each survey were the same leaves present during the preceding month's survey. This could have been an erroneous assumption. Some of the leaves may have fallen, some may have been eaten, and others may have replaced them between the monthly measurements. Therefore, in the second growing season, we attempted to measure the true leaf production of these seedlings. Each measurement included a categorization of each leaf as a new or old leaf (first or later flush) by dabbing a small bit of paint on the base of the petiole of each new leaf. This marking method easily distinguished between newly emerged leaves and old leaves already counted. In order to obtain a valid initial count, this marking was performed in the beginning of the growing season when the leaves first flushed. At the end of each growing season, all of the leaves were harvested. Each leaf was counted, run through a LI-COR 3200 leaf area meter (LI-COR, Inc., Lincoln, Nebraska), and its area summed with the seedling's other leaves to estimate total leaf area per plant.

The chosen visual technique of herbivory measurement was also used to determine stem herbivory from small mammals and deer. Stem herbivory was recorded as the percent of the stem eaten, typically from the top to the bottom. From previous studies, small mammals seemed to only cause survival problems during germination and emergence (Finegan 1984, Hodges and Gardiner 1992, Jones and Riley 1999). Deer, however, have caused problems for some seedlings during the establishment phase by breaking off the top of the stem (Crawley 1983, McLemore 1990), but these herbivory events were typically sporadic.

Growth and Survival Measurements

Height, basal diameter and survival status (alive or dead) were noted for all seedlings at the end of each growing season. The experimental seedlings that were still alive after the second growing season were harvested in the fall of 2000. Each seedling was separated into root and shoot portions, washed, dried, weighed and ashed to obtain aboveground, belowground, and total biomass values.

Analysis

Because our experimental design emphasized differences between sites and treatments as well as seedlings, we needed two different scales at which to make comparisons. The larger whole plot scale was used to test the general assumption that sites and treatments were different. This involved Chi-square (for survival data) and one-way ANOVA tests (for all other data) to analyze for differences among the environmental variables between treatments (clearcut and understory) and sites. The level of significance, α , was set at 0.05. For the survival data, we tested independent effects of site, treatment and their interaction. For all other data, we analyzed for site and treatment differences, but not the interaction because of limited degrees of freedom ($n=6$ observations, each corresponding to a mean for a site X treatment combination). Our aim in these tests was to determine if sites or treatments could be combined for our regression analyses (see below). Our expectation was that sites and treatments would be different, and therefore would require separate regressions.

Survival was analyzed for each year and each species separately. Environmental data analyzed included mean percent soil water for each growing season, nitrate and ammonium availability for each season, phosphorus availability for the first year only, GLI, and percent soil carbon. Total carbon content and the nutrient variables (nitrogen and phosphorus) were each natural log-transformed to ensure normal distributions. GLI could only be tested for site differences because the well-known differences between clearcuts and forest understories don't need to be tested. Each herbivory variable (leaf and stem) was tested for treatment and site differences within species using ANOVA. Seedling responses analyzed included diameter growth, height growth, leaf area growth, and total biomass growth for each species. Diameter and height growth were calculated as differences between measurements at planting and at final harvest. Total leaf area growth was calculated as the difference between the first and second growing seasons. Total biomass growth was the difference between biomass predicted at planting (from the regressions in Table 3) and biomass measured at final harvest.

The more specific, or within plot scale, involved multiple regression analysis of the independent variables to best explain survival and growth within each site/treatment combination. The seven major factors—water, nitrogen, phosphorus and light availability, total carbon content, and leaf and stem herbivory—were the independent random variables regressed against the dependent variables of survival and growth using a forward selection model and the SAS statistical package (SAS 1988). Leaf area and total biomass growth over both years were the only growth responses used and were modeled for each species via linear regression. First and second year survival were analyzed by logistic regression. The final sample population ranged from 8-29 due to mortality during the study. Each herbivory and soil moisture interval measure was compared individually against growth responses in a simple linear regression to determine which interval reading best explained the variation. The leaf and stem herbivory interval measure that best explained variation was the third measure of the second growing season (mid-June), while the best soil moisture interval measure was the fourth measure of the first growing season (mid-July). Even though this was a high soil moisture period, it best explained the variation caused by soil moisture within the simple linear regression. Once the optimum readings were established, they were included in the

multiple regression models along with the other environmental variables. Because these analyses were used to not only test, but also generate hypotheses, we used the 15% statistical probability as the cut-off point instead of the default 5%, allowing additional variables to enter the regression equations. Light was assumed 100% in all clearcuts, and was therefore excluded from analysis of clearcuts. Thus, the all-inclusive models for survival (y_1) and growth (y_2) responses were:

$$\text{UNDERSTORY: } y_{1ij} \text{ or } y_{2ij} = \mu + \beta_1 w_{1ij} + \beta_2 n_{2ij} + \beta_3 p_{3ij} + \beta_4 l_{4ij} + \beta_5 h_{5ij} + \beta_6 s_{6ij} + \beta_7 o_{7ij} + \epsilon_{ij}$$

$$\text{CLEARCUT: } y_{1ij} \text{ or } y_{2ij} = \mu + \beta_1 w_{1ij} + \beta_2 n_{2ij} + \beta_3 p_{3ij} + \beta_4 h_{4ij} + \beta_5 s_{5ij} + \beta_6 o_{6ij} + \epsilon_{ij}$$

μ is the overall mean of y . The subscripts “i” and “j” represent the species and site levels, respectively. β_{1-7} are the coefficients for the seven predictor variable, which are represented as **w** (water availability), **n** (nitrogen availability), **p** (phosphorus availability), **l** (light availability), **h** (leaf herbivory), **s** (stem herbivory) and **o** (organic matter content).

To determine which factors were most important, we tallied the number of models in which each was significant. We also conducted a correlation analysis among the independent factors to determine if there was any substantial multicollinearity present.

Results

Site and cutting treatment effects on environmental conditions and herbivory

At the scale of whole plots, significant site differences were detected for all five environmental resources measured (Table 4). The Hog Barn site had two times the water availability of the other two sites and greater total carbon content than the other two sites (Figure 4). The Beaufort site had the greatest available phosphorus and nitrogen of the three sites, although these were more strongly affected by cutting treatment than site (Figure 4). Understory GLI was greatest at the Beaufort site ($35.59 \pm$ standard error 1.04%), intermediate at Green Pond ($23.52 \pm 1.09\%$) and lowest at Hog Barn ($16.21 \pm 0.89\%$).

Significant treatment effects at the plot level were also detected for all environmental measures (Table 4). At each site, clearcut plots had significantly more available water, phosphorus, and nitrogen than the understory plots (except for phosphorus at the Hog Barn site) (Table 4; Figure 4). Clearcut plots, however, had significantly less soil carbon ($21.00 \pm 0.84\%$) than in the understory plots ($17.53 \pm 0.65\%$; Table 4).

Leaf herbivory was also strongly affected by site (Table 5). The only exception was the non-significant site differences for leaf herbivory in *C. florida* seedlings during the first growing season (Figure 5; Table 5). Overall, *C. florida* leaves were most damaged by herbivory at the Green Pond site ($22.00 \pm 2.24\%$) versus $20.00 \pm 2.58\%$ at the Hog Barn site and $18.67 \pm 1.71\%$ at the Beaufort site, while *Q. alba* leaves were damaged more at the Beaufort site ($30.40 \pm 2.46\%$) than either the Hog Barn ($18.92 \pm 1.81\%$) or Green Pond site ($16.40 \pm 1.10\%$). Treatment differences were also found. Understory plots had significantly greater leaf herbivory than clearcut plots (mean of $14.72 \pm 1.16\%$ for *C. florida* in clearcuts; $24.89 \pm 1.82\%$ for *C. florida* in the understory; $15.22 \pm 1.08\%$ for *Q. alba* in clearcuts; and $29.26 \pm 1.83\%$ for *Q. alba* in the understory; Table 5).

For stem herbivory, there were no significant site or treatment differences at the scale of whole plots for either species (Table 5). Mean stem herbivory for *C. florida* was $20.63 \pm 2.66\%$, $20.29 \pm 1.76\%$ and $20.00 \pm 1.44\%$ for the Hog Barn, Green pond and Beaufort sites, respectively. The corresponding numbers for *Q. alba* were $13.51 \pm 0.88\%$, $12.80 \pm 0.81\%$ and $12.80 \pm 0.70\%$ (Figure 5). There was a slight, but non-significant trend for more stem herbivory in the understory ($21.33 \pm 1.51\%$) than in the clearcuts ($18.89 \pm 1.42\%$) for *C. florida*, and more stem herbivory in the clearcuts ($13.53 \pm 0.65\%$) than in the understory ($12.46 \pm 0.63\%$) for *Q. alba*.

Because we had differences among our biotic and abiotic variables at the whole plot scale, we could not analyze all of the data in one multiple regression. We had to conduct multiple regressions at the more specific within plot scale to test for significant individual seedling responses to these variables; one regression would not be able to explain all of the variation amongst all of the sites and treatments (See *Within Site Seedling Responses*).

Table 4. ANOVA to assess effects of sites and treatments on environmental variables at the Savannah River Site in South Carolina. Gap Light Index (GLI) was only tested for site differences within the understory treatments. Significant values ($\alpha = 0.05$) are in bold type. The degrees of freedom were 2 for site, 1 for treatment and 2 for error.

Variable	Factor	F-Ratio	P-Value
1 st year Water Availability	Site	521.59	< 0.0001
	Trt	40.33	< 0.0001
2 nd year Water Availability	Site	55.82	< 0.0001
	Trt	4.27	0.0395
Total Carbon	Site	150.75	< 0.0001
	Trt	95.01	< 0.0001
Available Phosphate	Site	55.72	< 0.0001
	Trt	26.92	< 0.0001
1 st year Available Nitrogen	Site	35.58	< 0.0001
	Trt	454.87	< 0.0001
2 nd year Available Nitrogen	Site	12.99	< 0.0001
	Trt	3.91	0.0491
GLI	Site	96.60	< 0.0001

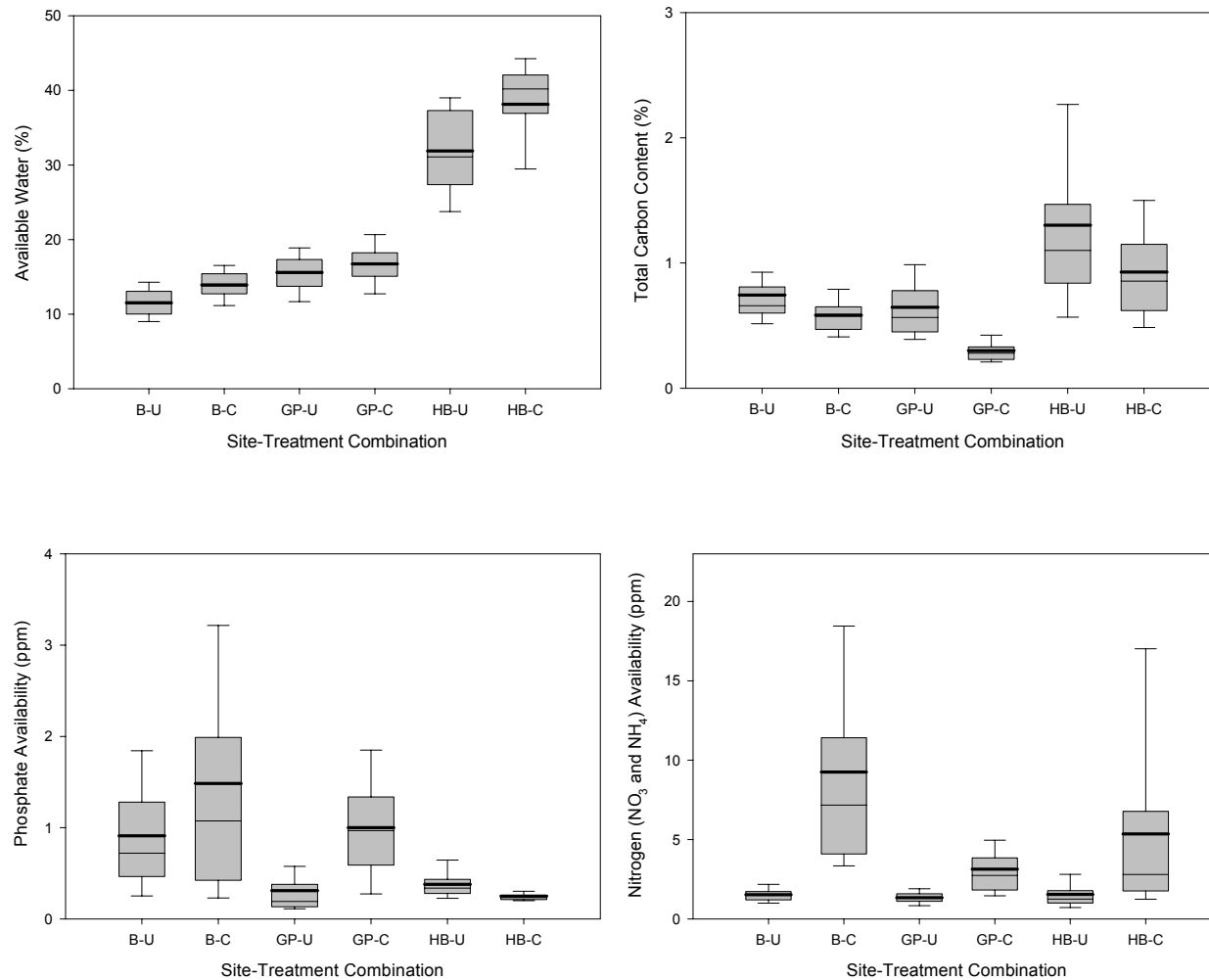


Figure 4. Box plots of environmental conditions in all six of the site/treatment combinations on the Savannah River Site in South Carolina. The thick solid line is the mean, the thin solid line is the median, and the error bars show the 10-90% quantile range. The box represents the 25-75% quantile range. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory).

Table 5. ANOVA to assess the effects of sites and treatments on leaf and stem herbivory of 1-0 bare root seedlings at the Savannah River Site in South Carolina. Significant values ($\alpha = 0.05$) are in bold type. The degrees of freedom were 2 for site, 1 for treatment, and 2 for error.

Species	Variable	Factor	F-Ratio	P-Value
<i>C. florida</i>	1 st year Leaf Herbivory	Site	1.81	0.1666
		Trt	23.56	<0.0001
	2 nd year Leaf Herbivory	Site	3.11	0.0492
		Trt	5.29	0.0238
	1 st year Stem Herbivory	Site	2.54	0.0815
		Trt	0.80	0.3724
	2 nd year Stem Herbivory	Site	0.36	0.7003
		Trt	3.19	0.0772
<i>Q. alba</i>	1 st year Leaf Herbivory	Site	17.48	<0.0001
		Trt	53.64	<0.0001
	2 nd year Leaf Herbivory	Site	4.98	0.0081
		Trt	17.63	<0.0001
	1 st year Stem Herbivory	Site	0.98	0.3768
		Trt	0.07	0.7887
	2 nd year Stem Herbivory	Site	2.10	0.1258
		Trt	0.00	0.9541

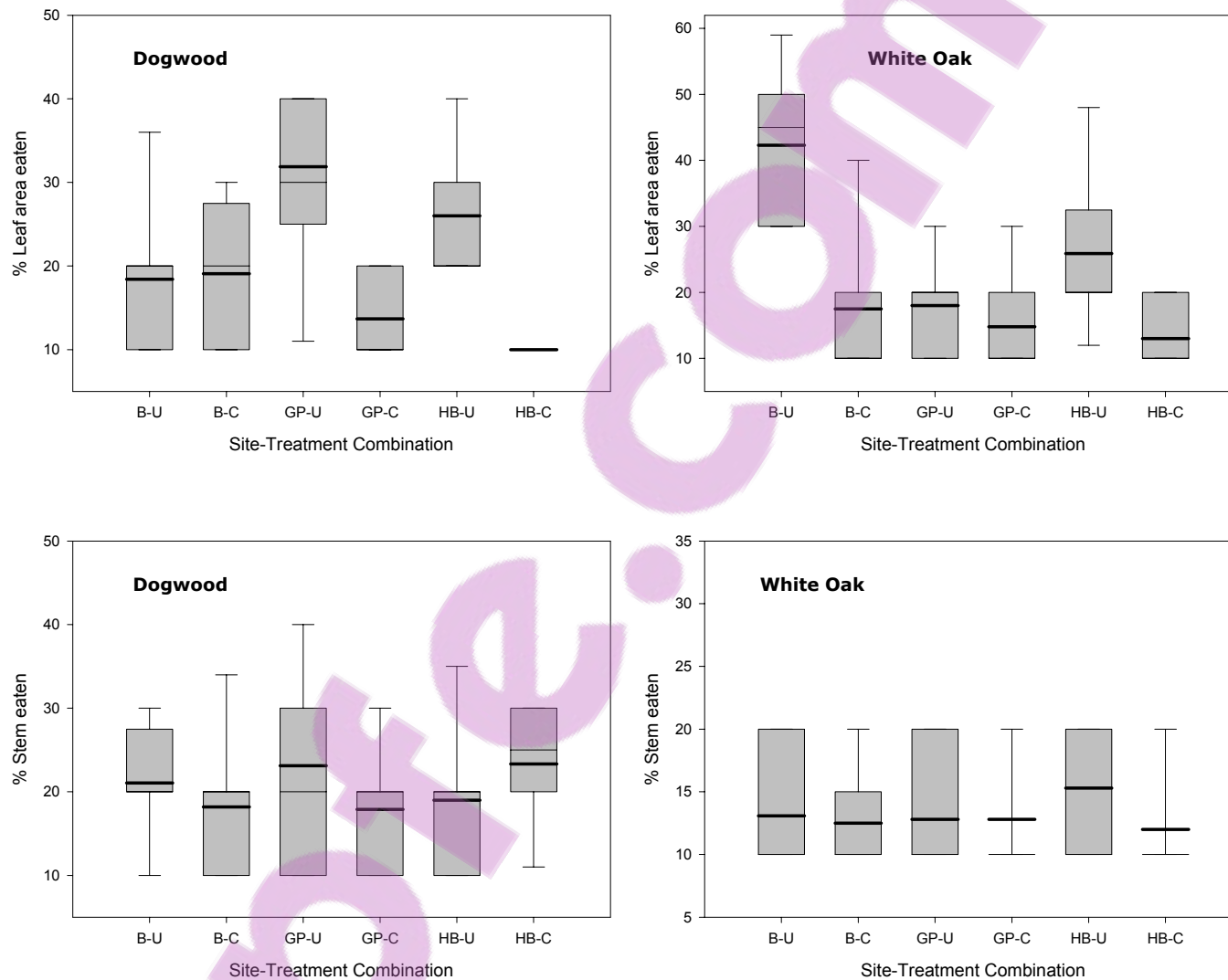


Figure 5. Box plots of mean two-year herbivory by species in all six of the site/treatment combinations on the Savannah River Site in South Carolina. This thick solid line is the mean, the thin solid line is the median, and the error bars show the 10-90% quantile range. The box represents the 25-75% quantile range. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory).

Site and cutting treatment effects on seedling survival and growth

Survival was lower at the Hog Barn site than at the other two sites (Figure 6), but these site differences were only significant for *C. florida* (Table 6). This indicated that *Q. alba* seedlings were either more tolerant to the range of environmental variables present or less responsive to the added resource than *C. florida*. Gross mortality of *C. florida* in the first year was distinctly greater than the second year whereas *Q. alba* had more constant annual mortality (Figure 6). There were no significant treatment or site X treatment interaction effects on survival detected for either species at the scale of whole plots (Table 6).

All *Q. alba* growth responses were significantly influenced by site differences at the whole plot level, but only two of the five growth variables for *C. florida* were affected (Table 7). In both species, no one site had consistently greater growth than another (Figures 7-8). Cutting treatment had a much stronger and more consistent influence on growth than did site. For example, *Q. alba* growth in clearcuts was significantly greater than *Q. alba* growth in the understory at each of the three sites (Table 7, Figures 7-8). However, the same could not be said for *C. florida* as its first year total leaf area was not significantly affected by treatment (Table 7), and its second year height growth in the understory was greater than its clearcut second year height growth at each site (Figure 7). All other growth measures for *C. florida* in the clearcut plots were greater than the values in the understory plots (Figures 7-8).

Within-site seedling responses

Many of the abiotic and biotic environmental factors used as independent variables in the multiple regression analyses were correlated with one another, but most correlations were weak; the strongest correlation being $r=0.32$ between light and water (Table 8). Therefore, we assumed that problems with multicollinearity were minor or non-existent. The strongest correlations were between nitrogen availability and phosphorus availability, water availability and GLI, and total carbon content and water availability. Within sites, the largest values occurred at Hog Barn (generally the largest value shown for the ranges in Table 8).

Table 6. χ^2 tests to assess the effects of sites, treatments, and their interactions on first and second year survival of 1-0 bare root seedlings at the Savannah River Site in South Carolina. Significant values ($\alpha = 0.05$) are in bold type. The degrees of freedom are 2 for site, 1 for treatment, and 2 for the site*treatment interaction.

Species	Variable	Factor	χ^2	P-Value
<i>C. florida</i>	1 st year Survival	Site	7.81	0.0202
		Trt	0.01	0.9174
		Site*Trt	3.29	0.1926
	2 nd year Survival	Site	7.19	0.0275
		Trt	1.00	0.3173
		Site*Trt	2.42	0.2981
<i>Q. alba</i>	1 st year Survival	Site	0.34	0.3378
		Trt	0.27	0.8694
		Site*Trt	0.92	0.9189
	2 nd year Survival	Site	2.47	0.2912
		Trt	0.01	0.9319
		Site*Trt	0.85	0.8539

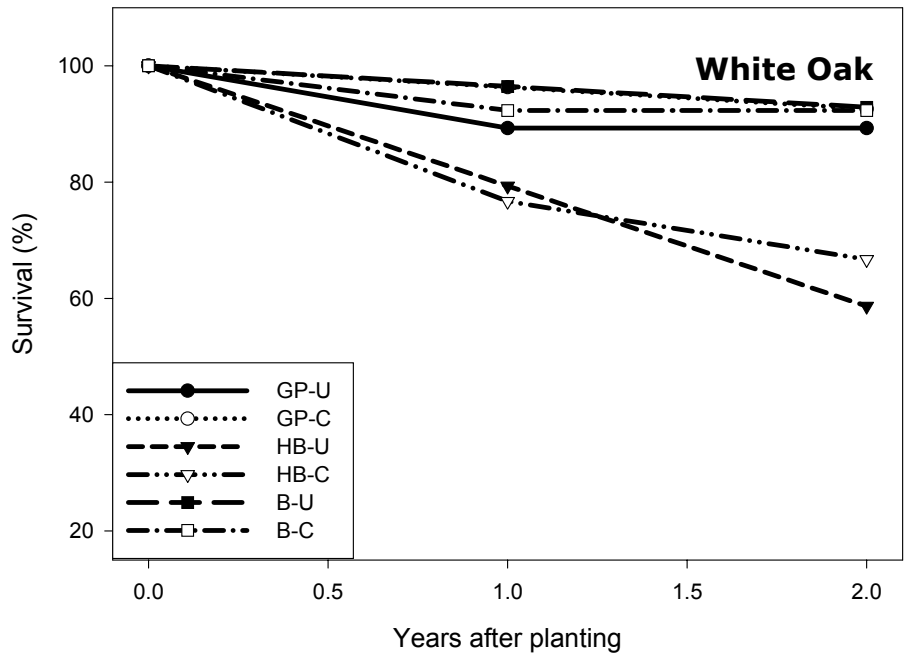
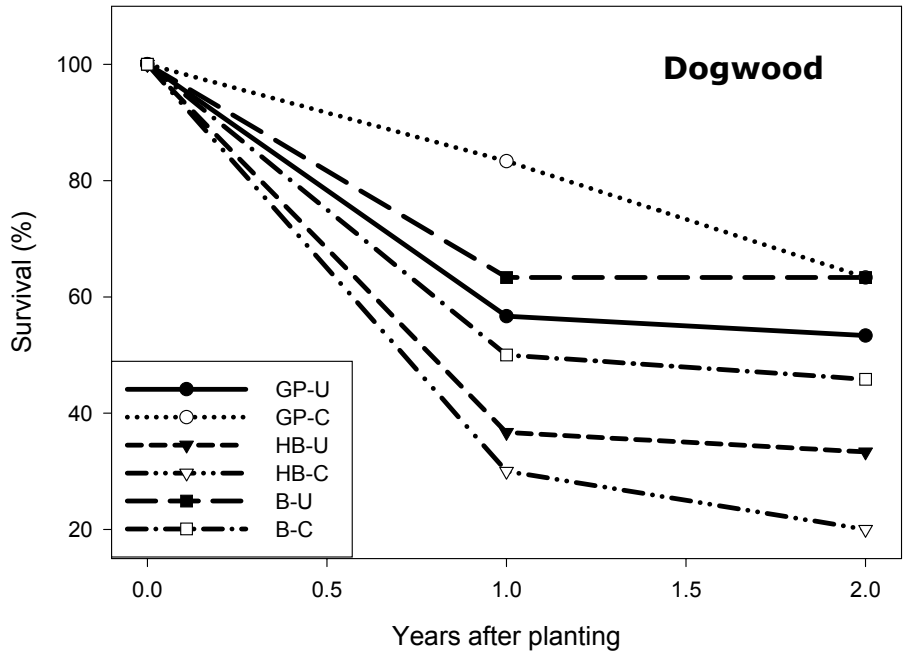


Figure 6. Survival of 1-0 bare root seedlings planted in the understory of *P. elliotti* (slash pine) or *P. taeda* (loblolly pine) stands or in adjacent clearcuts on the Savannah River Site in South Carolina of each species by year and species/site combination. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory).

Table 7. ANOVA to assess the effects of sites and treatments on growth responses of 1-0 bare root seedlings at the Savannah River Site in South Carolina by species. Significant values ($\alpha = 0.05$) are in bold. The degrees of freedom for the tests were 2 for site, 1 for treatment, and 2 for error.

Species	Response	Factor	F-Ratio	P-Value
<i>C. florida</i>	Stem Height Growth	Site	0.17	0.8472
		Trt	6.91	0.0104
	Basal Diameter Growth	Site	3.25	0.0441
		Trt	22.51	<0.0001
	1 st year Total Leaf Area	Site	4.62	0.0123
		Trt	0.79	0.3778
	2 nd year Total Leaf Area	Site	1.21	0.3031
		Trt	8.50	0.0047
	Total Biomass Growth	Site	1.64	0.2013
		Trt	21.39	<0.0001
<i>Q. alba</i>	Stem Height Growth	Site	3.73	0.0265
		Trt	17.13	<0.0001
	Basal Diameter Growth	Site	6.61	0.0018
		Trt	131.41	<0.0001
	1 st year Total Leaf Area	Site	5.84	0.0036
		Trt	32.52	<0.0001
	2 nd year Total Leaf Area	Site	7.08	0.0012
		Trt	71.52	<0.0001
	Total Biomass Growth	Site	9.16	0.0002
		Trt	87.25	<0.0001

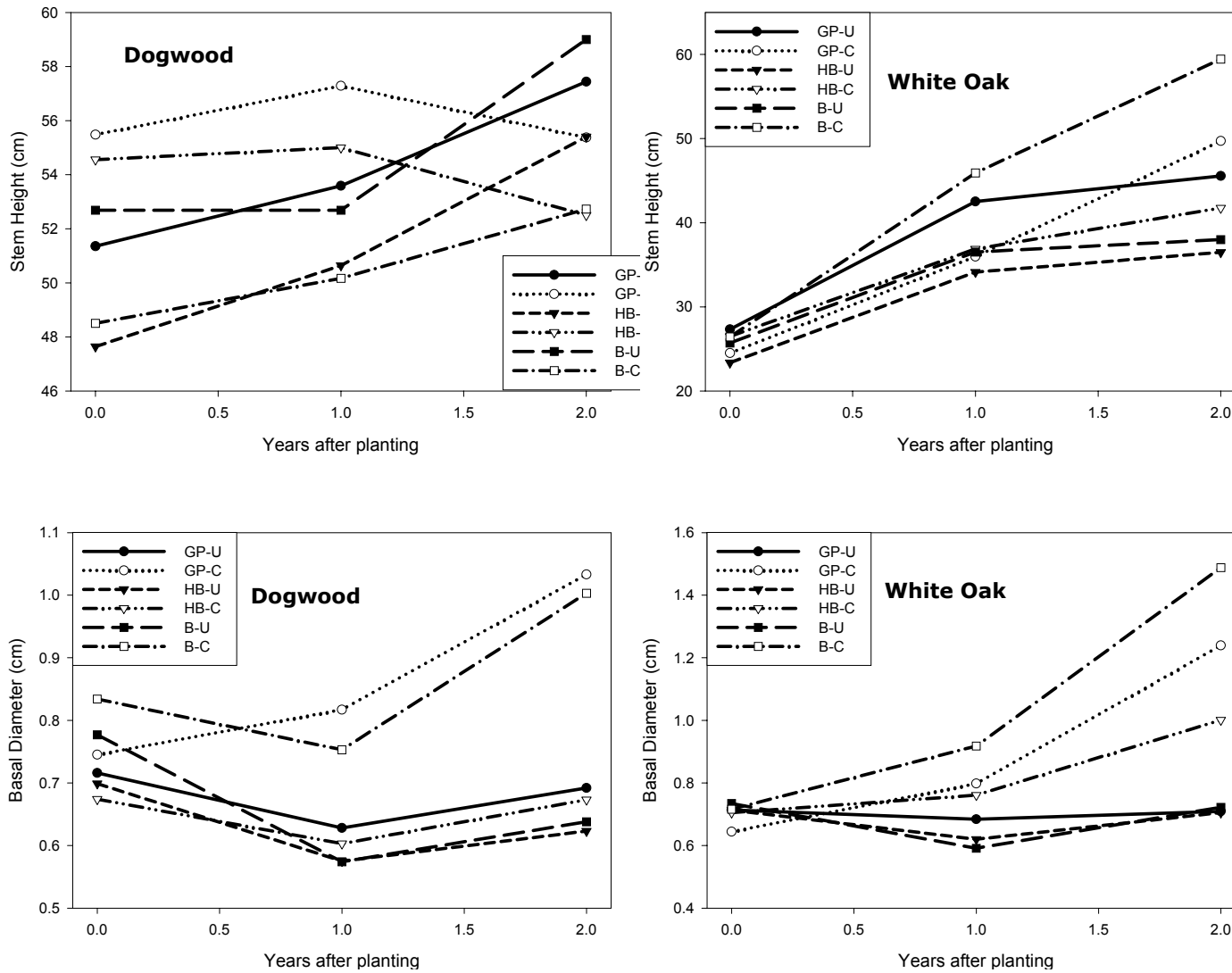


Figure 7. Height and diameter growth responses of 1-0 bare root seedlings planted in the understory of *P. elliotti* (slash pine) or *P. taeda* (loblolly pine) stands or in adjacent clearcuts on the Savannah River Site in South Carolina (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory)

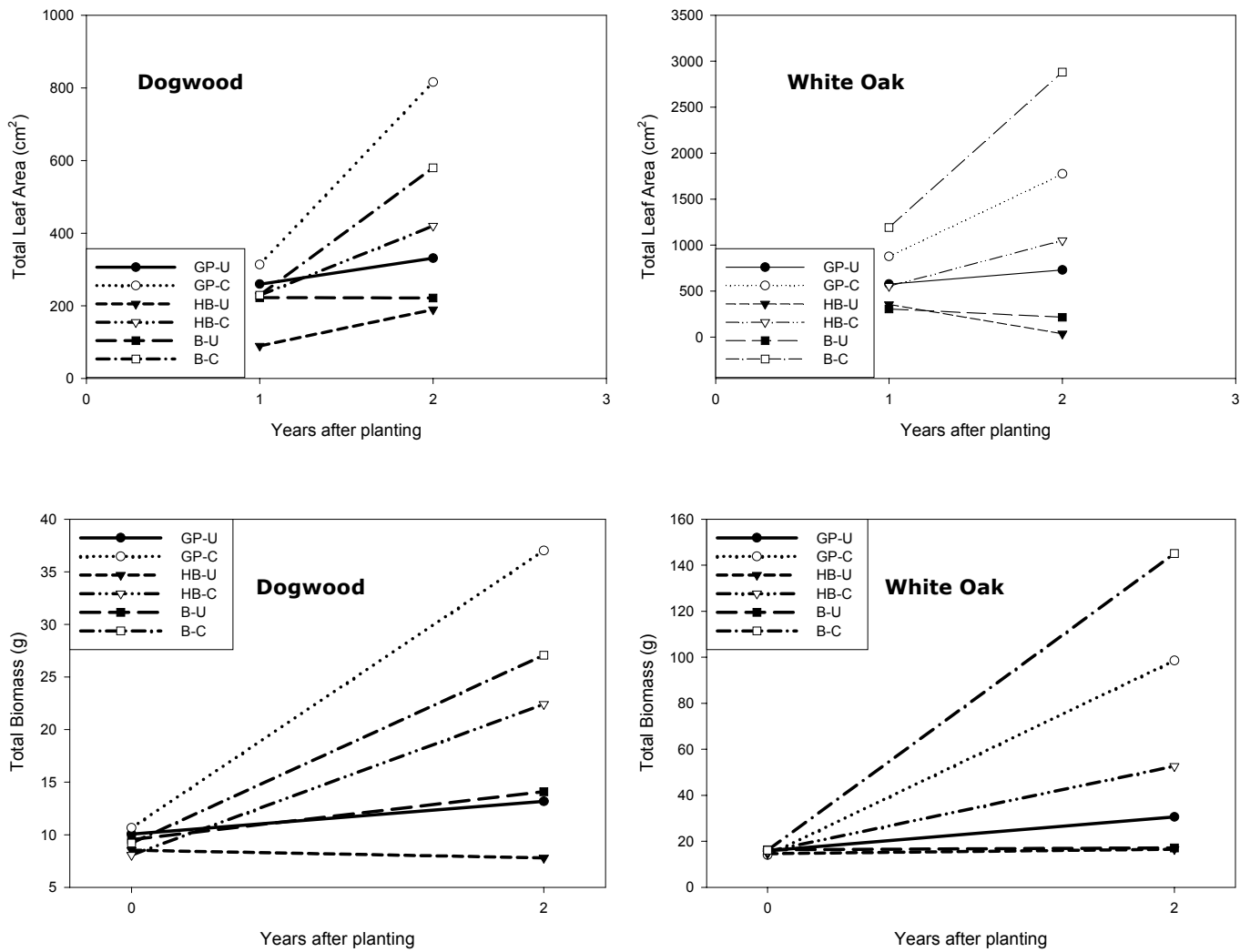


Figure 8. Total leaf area and biomass growth responses of 1-0 bare root seedlings planted in *P. elliotii* (slash pine) or *P. taeda* (loblolly pine) stands and in adjacent clearcuts on the Savannah River Site in South Carolina (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory)

In general, seedling growth and survival were weakly related to the environmental variables we measured, and usually just one or two variables were significant. Out of the 48 tests in total (including survival and growth), 37 of them included only one variable or no variables. There was only one case where there were four significant variables, the Beaufort understory plot. Variation explained by the multiple regression models never exceeded 70%.

For survival responses, there was no one environmental variable that was very important (Table 9). The possible outcome for each cell in Table 9 was three, corresponding to each of the three sites for the species/treatment combinations. Thus, total carbon content and nitrogen availability were both the most significant for seedling survival in the clearcut plots, but even they were significant in only 2 out of the 12 possible situations. In the understory, water availability and leaf herbivory were significant most frequently but were significant in only 2 out of the 12 possible situations.

Leaf and stem herbivory were the most dominant variables affecting seedling growth. Leaf and stem herbivory, therefore, were significant ($P < 0.15$) in 10 out of 24 multiple regression models (Table 10). Across both species, leaf and stem herbivory had a mean partial r^2 value of 0.208 for biomass growth and 0.153 for total leaf area growth. Stem herbivory was included in the models twice as frequently in the understory for total biomass growth than in the clearcut plots (Table 10). As expected, more herbivory equated to less growth, but there was considerable scatter in the data (Figure 9). Herbivory was a stronger factor for *Q. alba* than for *C. florida*.

After herbivory, no other environmental variable had a particularly strong effect on seedling growth. For biomass growth, no variable was significant more than once out of 12 possible site/treatment combinations. This included water, which was barely related to growth as seen by a very shallow slope in the regression line (Figure 10). For carbon, there were two significant relationships, but one of these barely had a positive slope (Figure 11). There was only one significant relationship between GLI and biomass growth (Figure 12). For total leaf area growth, light availability was the next most important variable after herbivory. GLI was significant in three tests (out of six possible). None of the other variables significantly explained leaf area growth variation more than once.

Table 8. Mean and range of Pearson correlation coefficients between each of the seven environmental variables measured at the Savannah River Site in South Carolina. The means were calculated from each combination of three sites and two treatments (N = 6). The five greatest mean (absolute value) correlation coefficients are asterisked.

1 st Variable	2 nd Variable	<i>First Year</i>		<i>Second Year</i>	
		Mean	Range (Low↔High)	Mean	Range (Low↔High)
Leaf Herb.	Stem Herb.	0.08	-0.21 ↔ 0.27	0.11	-0.22 ↔ 0.63
	LN Carbon	-0.09	-0.17 ↔ 0.13	0.11	-0.26 ↔ 0.29
	Water	0.15*	-0.01 ↔ 0.34	-0.04	-0.16 ↔ 0.16
	LN Nitrogen	0.07	-0.07 ↔ 0.25	-0.13	-0.29 ↔ 0.00
	LN Phosphorus	-0.11	-0.39 ↔ 0.04	NA	NA
	GLI	-0.03	-0.15 ↔ 0.06	0.01	-0.02 ↔ 0.03
Stem Herb.	LN Carbon	-0.01	-0.26 ↔ 0.37	-0.07	-0.26 ↔ 0.03
	Water	-0.13	-0.34 ↔ 0.09	0.10	-0.08 ↔ 0.36
	LN Nitrogen	-0.10	-0.45 ↔ 0.16	0.02	-0.12 ↔ 0.23
	LN Phosphorus	-0.14	-0.38 ↔ 0.10	NA	NA
	GLI	0.02	-0.09 ↔ 0.21	-0.11	-0.30 ↔ 0.11
LN Carbon	Water	-0.17*	-0.49 ↔ 0.09	-0.22*	-0.50 ↔ 0.02
	LN Nitrogen	0.06	-0.08 ↔ 0.16	0.14	-0.15 ↔ 0.30
	LN Phosphorus	0.13	-0.09 ↔ 0.38	NA	NA
	GLI	0.08	-0.23 ↔ 0.33	NA	NA
Water	LN Nitrogen	-0.06	-0.16 ↔ 0.10	-0.02	-0.27 ↔ 0.29
	LN Phosphorus	-0.07	-0.26 ↔ 0.20	NA	NA
	GLI	-0.32*	-0.46 ↔ -0.06	-0.06	-0.43 ↔ 0.19
LN Nitrogen	LN Phosphorus	0.21*	0.02 ↔ 0.54	NA	NA
	GLI	-0.10	-0.27 ↔ 0.06	0.13	-0.05 ↔ 0.25
LN Phosphorus	GLI	-0.02	-0.11 ↔ 0.03	NA	NA

Table 9. Frequency of significance of environmental variables in the multiple regression of first and second year survival of 1-0 bare root seedlings at the Savannah River Site in South Carolina for DW (*C. florida*) and WO (*Q. alba*) and the two treatments, clearcut and understory. Maximum number possible for each cell is 3. GLI was not placed into the clearcut regressions, because it was not relevant for those tests.

Trt	Species	Response	L. Herb.	S. Herb.	Carbon	Phosp.	Water	GLI	Nitrogen
Clearcut	DW	1 st year survival	0	0	0	0	0	--	1
		2 nd year survival	0	0	1	0	1	--	0
	WO	1 st year survival	0	0	1	1	0	--	1
		2 nd year survival	1	1	0	0	0	--	0
	SUM	1	1	2	1	1	1	--	2
Understory	DW	1 st year survival	0	0	0	0	1	0	1
		2 nd year survival	1	0	0	1	0	0	0
	WO	1 st year survival	0	0	0	0	1	1	0
		2 nd year survival	1	0	0	0	0	0	0
	SUM	2	0	0	1	2	1	1	

Table 10. Frequency of significance of environmental variables in the multiple regression equations of the growth response variables total biomass and total leaf area for 1-0 bare root seedlings at the Savannah River Site in South Carolina for DW (*C. florida*) and WO (*Q. alba*) and the two treatments, clearcut and understory. The maximum number possible for each cell is 3. GLI was not placed into the clearcut regressions, because it was not relevant for those tests.

Trt	Species	Response	L. Herb.	S. Herb.	Carbon	Phosp.	Water	GLI	Nitrogen
Clearcut	DW	Total Biomass	0	0	1	1	0	--	0
	WO	Total Biomass	1	3	0	1	0	--	0
		SUM	1	3	1	2	0	--	0
Understory	DW	Total Biomass	2	1	0	0	0	0	1
	WO	Total Biomass	1	2	1	1	1	1	0
		SUM	3	3	1	1	1	1	1
Clearcut	DW	Leaf Area	1	0	1	0	0	--	0
	WO	Leaf Area	1	0	0	0	0	--	0
		SUM	2	0	1	0	0	--	0
Understory	DW	Leaf Area	2	0	0	0	0	1	1
	WO	Leaf Area	1	1	0	0	0	2	0
		SUM	3	1	0	0	0	3	1

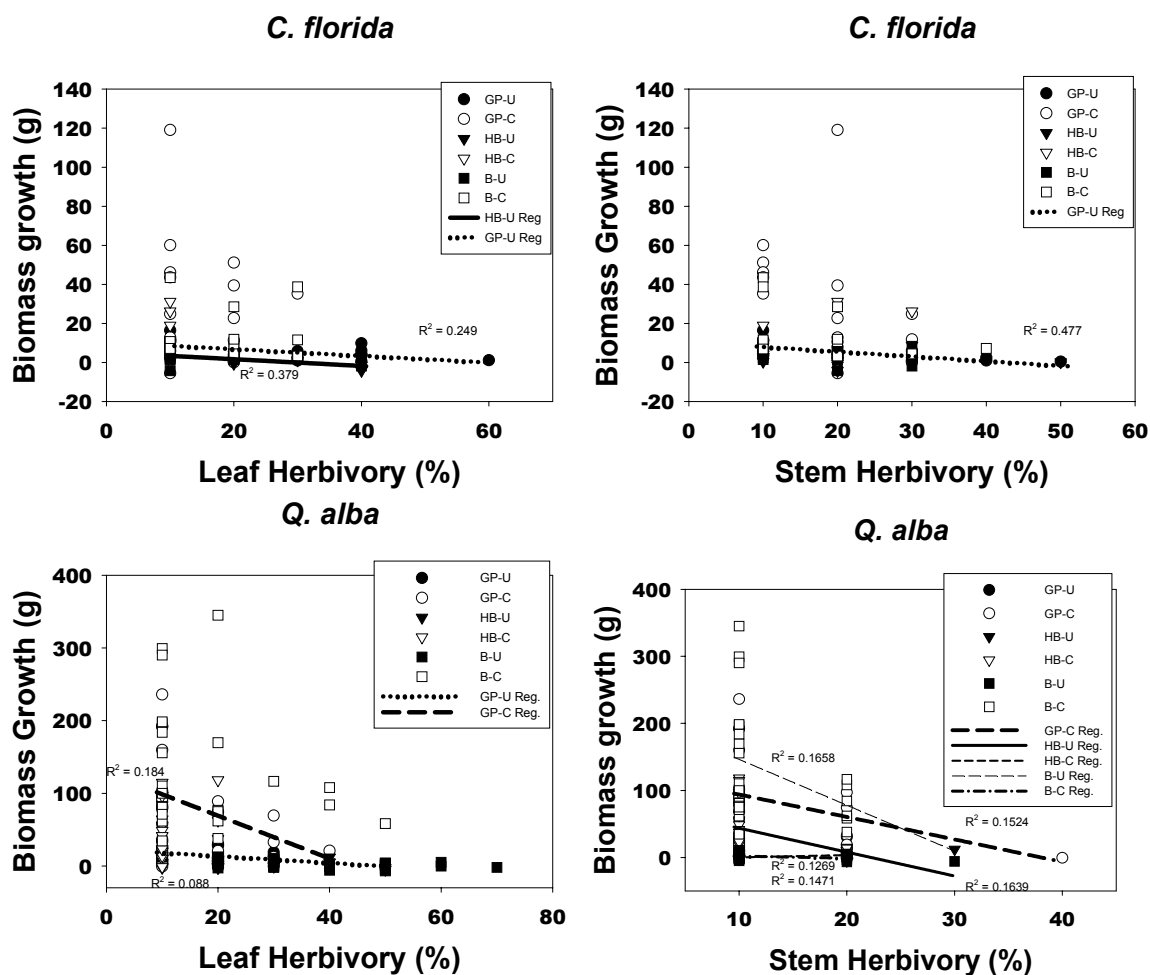


Figure 9. Biomass growth responses vs. leaf and stem herbivory for 1-0 bare root seedlings planted in *P. elliotii* (slash pine) stands on the Savannah River Site in South Carolina. The biomass growth scales are different for the two species. Monthly measures of leaf and stem herbivory were taken; the third measure of the second growing season best explained the most variation in seedling biomass growth responses, and so was used. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory) The regression lines represent the **significant** site/treatment combinations with their R² values.

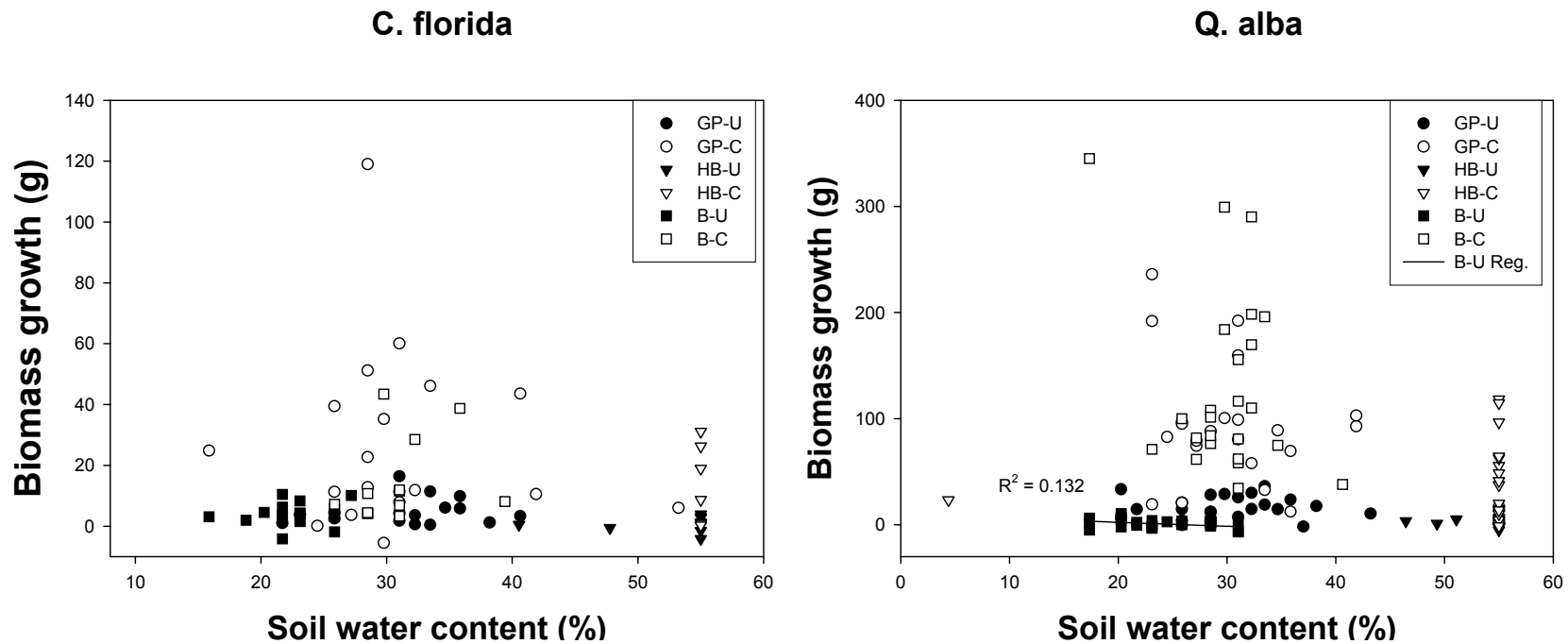
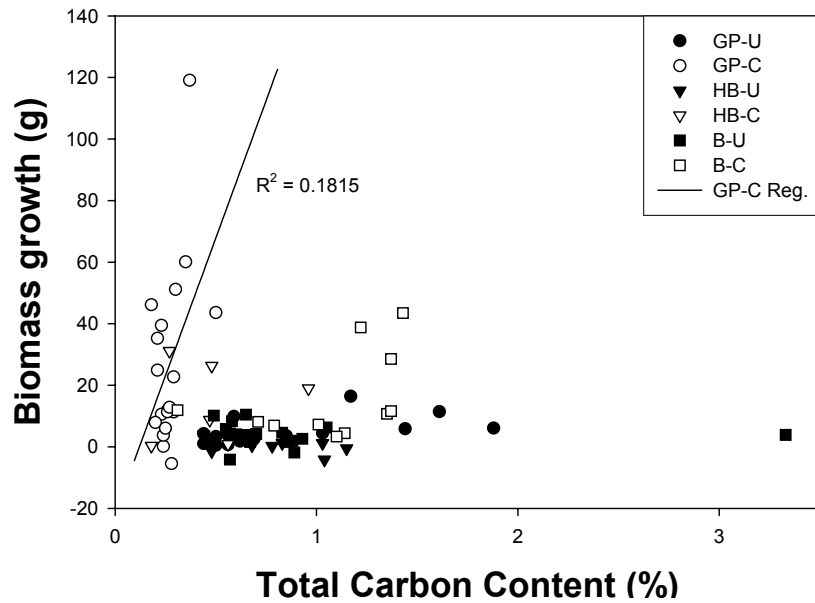


Figure 10. Biomass growth responses vs. percent soil water content for 1-0 bare root seedlings planted in *P. elliotti* (slash pine) stands on the Savannah River Site in South Carolina. The biomass growth scales are different for the two species. Bimonthly measures of water content were taken; the fourth measure (mid-July) of the first growing season best explained the most variation in seedling biomass growth responses, and so was chosen. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory) The regression line represents the **significant** site/treatment combinations with its R^2 value.

C. florida



Q. alba

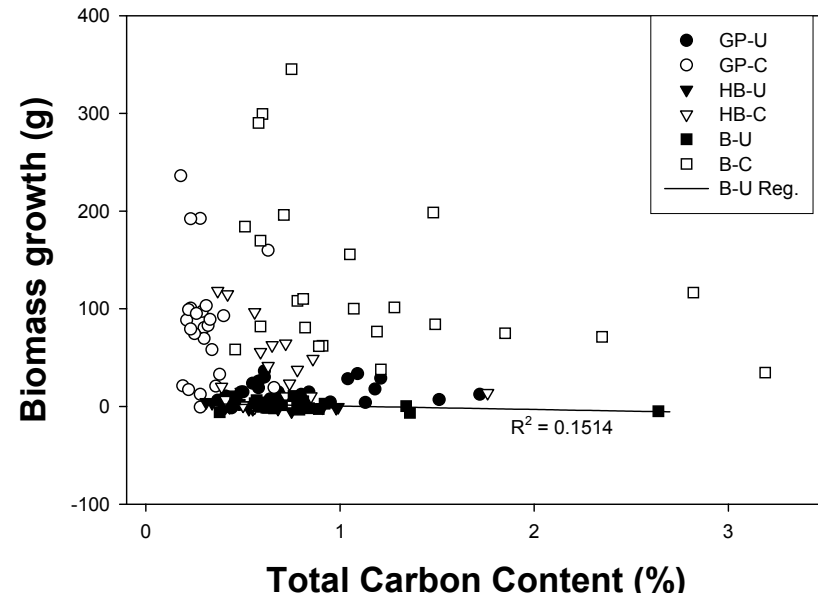
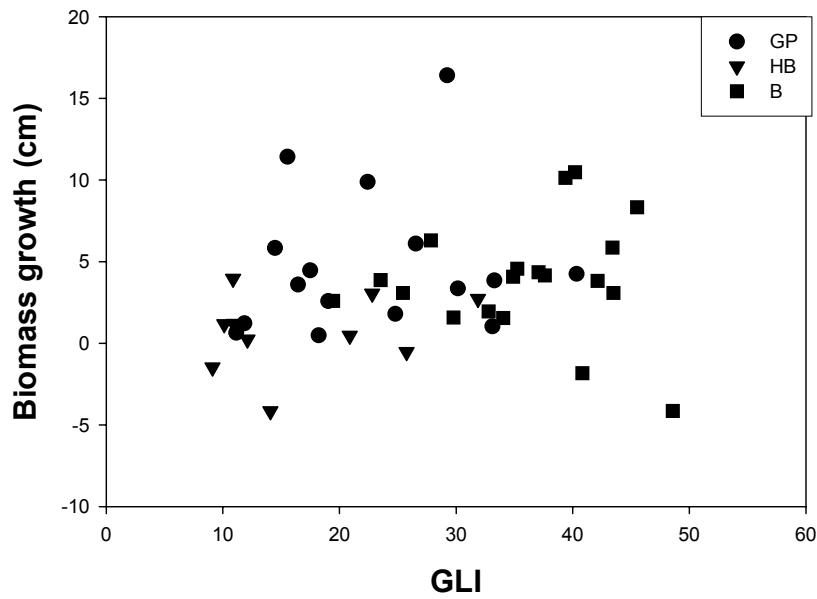


Figure 11. Biomass growth responses vs. percent soil carbon content for 1-0 bare root seedlings planted in *P. elliotti* (slash pine) stands on the Savannah River Site in South Carolina. The biomass growth scales are different for the two species. (B = Beaufort; GP = Green Pond; HB = Hog Barn; C = Clearcut; U = Understory) The regression lines represent the **significant** site/treatment combinations with their R^2 values.

C. florida



Q. alba

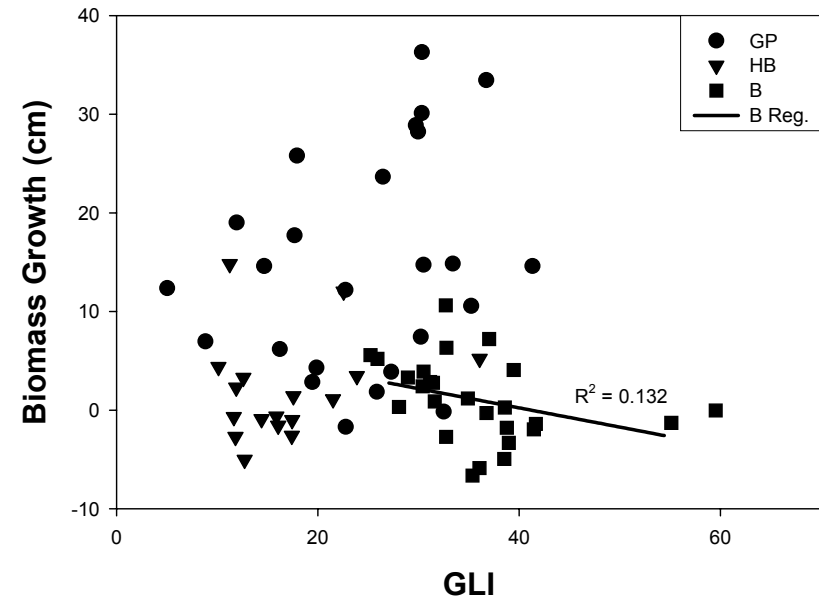


Figure 12. Biomass growth responses vs. Gap Light Index for 1-0 bare root seedlings planted in *P. ellioti* (slash pine) stands on the Savannah River Site in South Carolina. The biomass growth scales are different for the two species. Only the seedlings in the understory were included for this analysis. (B = Beaufort; GP =Green Pond; HB =Hog Barn) The regression line represents the **significant** site/treatment combination with its R^2 values.

Discussion

Resource availability

Our first hypothesis predicted that low soil moisture would have a large influence on two-year survival and growth of *C. florida* and *Q. alba* seedlings. Even though soil moisture was an important factor, this hypothesis was rejected, because water did not have the large impact expected for first or second year survival, or for growth. Analysis at the whole plot scale indicated that there were broad differences in water availability across sites and treatments, but the analyses of seedling responses within plots revealed that water availability explained seedling responses very infrequently. At the scale of whole plots, both species had greater survival at the two xeric sites than at the mesic site (Figure 6), even though the difference between xeric and mesic sites was significant only for *C. florida* (Table 6). Height, diameter and biomass growth were affected by site differences (Table 7); however, there was no consistent pattern in the differences attributable to site moisture (Figures 4, 7; Table 10). Since the lowest mean and extreme soil moisture measures occurred at the xeric sites, roughly half those for the mesic site (Figure 4), we concluded that the effects of low water availability on survival and growth did not exceed the influence of other plot-scale factors. Further evidence at the scale of whole plots was shown in the comparison of cutting treatments. The clearcut plots had significantly greater water availability than the understory plots (Table 4), but there were no significant differences in seedling survival for either species between the two treatments. All growth responses were significantly different between cutting treatments; however, it could not be stated unequivocally that soil moisture availability was the lone reason for these differences, because clearcut plots also had greater availability of nutrients and light than the understory plots. At the within-plot scale, water was seldom a significant factor explaining variability of survival in the clearcut plots, although it was one of the most frequently identified variables affecting first year survival in the understory plots (Table 9). Water significantly affected growth in only 1 out of the 24 tests performed (Table 10); however, that one significant growth response to microsite variation in water availability was positive (i.e., positive regression coefficient). It was barely positive, illustrating that increased water had only a slight positive effect on *Q. alba* biomass growth (Figure 10), not the large positive relationship we expected.

Although not a dominant factor, water was clearly important. In fact, the presence of excess water (flooding) was likely the most important factor for survival in both *C. florida* and *Q. alba* seedlings. Numerous puddles caused by poor drainage were present at the Hog Barn site and were the principal cause for the significant water availability differences between sites (Figure 4; Table 4). Virtually all seedlings, most notably *C. florida*, located in these puddles died. In effect, we may have been looking at the water availability from the wrong direction. The seedlings may not have been able to respond to added resources, because they could not tolerate high water availability, implying that water may truly have been more important than our data led us to believe.

In addition to water, nutrient availability and light were correlated with seedling performance, but none of these variables stood out as the principal limitation to seedling survival or growth. At the whole plot scale, sites and treatments differed significantly in nitrogen and phosphorus availability (Table 4), but the largest differences were between the clearcut and understory treatments. Furthermore, light was obviously much greater in clearcuts than in the understory (full sunlight in clearcut versus a mean of $25.13 \pm 1.01\%$ of full sunlight in the understory). As reported earlier, most growth parameters for both species in the clearcut plots were also significantly greater than in the understory plots. Because of this, the facilitative effects of the understory did not show much of an impact on these seedlings. Facilitation may have occurred, but it was not rapid enough to compensate for the losses from increased shade and decreased resources to compare the understory seedlings with their clearcut counterparts. Since water, nutrients and light were all least in the understory, we were unable to determine which factor, at the scale of whole plots, was the catalyst for such differences.

Analysis within plots was less ambiguous. Nitrogen availability was significant two times (out of a possible 12 regressions) for survival in the clearcut plots, and phosphorus was significant one time (Table 9). In the understory, phosphorus and nitrogen availability each significantly impacted survival only one time (out of a possible 12 regressions). All five of these significant situations occurred at the Hog Barn site. For growth, phosphorus availability was significant in three regressions, and nitrogen in two (Table 10). Nitrogen was only significant for growth in the understory, possibly because nitrogen availability was much more abundant in the clearcut plots (Figure 4).

Phosphorus was a limiting factor at the Hog Barn site, because that site had the lowest mean phosphorus levels (Figure 4).

Total carbon content at the whole plot scale was greatest at the Hog Barn site (Figure 4) where survival was poor (Figure 6) and growth was modest or low (Figures 7-8). As expected, total carbon was also significantly greater in the understory plots than the clearcut plots (Table 4). When analyzed at the whole plot scale, total carbon content had an apparent negative effect, because increased levels of total carbon content were associated with decreased survival and growth. An exception to this rule was the positive relationship of the *C. florida* Green Pond clearcut combination (Figure 11), indicating a strong association between increased growth response and increased total carbon content. Within plots, however, the apparent effect of total carbon content was complex. Survival was significantly affected by total carbon content only twice (out of a possible 24 regressions; Table 9). In both cases, which occurred at the Hog Barn site, increased carbon was associated with decreased survival. Growth was significantly related to total carbon content in three cases (out of a possible 24 regressions; Table 10) spread across both species, both treatments and two sites (Green Pond and Beaufort). Only in one case, however, was there an obvious positive relationship between carbon and biomass growth; i.e., for *C. florida* at the Green Pond clearcut plot. This was the result we expected, but it happened rarely. We concluded that carbon was relatively unimportant, but it could also be concluded that points of lesser total carbon content could be places of increased mineralization leading to increased nutrient content. From this perspective, seedlings should respond better to lesser total carbon content and have a negative relationship, making total carbon content an important variable.

Effect of light

Our second hypothesis involved the effect of light on growth during the duration of the study. We cannot reject or accept this hypothesis; however, we suspect that it is incorrect. Growth at the clearcut sites was clearly greater than at the understory sites where light was much greater as compared to the understory. As stated above, however, clearcut plots also had more available water and nutrients than understory plots, possibly confounding the effect light may have on growth and vice versa. In the understory,

where variation in light levels might be expected to play a role in growth, the role of light was weak or undetectable. There was a significant difference in understory light availability among sites (Table 5), but growth parameters did not parallel these differences. For example, the Beaufort site had the greatest mean understory light availability, yet seedling growth there was not distinctly greater than either of the other two sites (Figure 7). Within each understory site, light was identified by multiple regressions as a factor affecting growth, but it was not very influential when compared to the other environmental factors (Table 10). Light was significant for only 4 out of 24 (16.7%) tests. Leaf area was the growth parameter most affected by light; the two sites with the greatest light availability in the understory (Beaufort and Green Pond) had the greatest total leaf area. Light availability only affected biomass growth in 1 out of 6 site/treatment combinations (Figure 12). Although light was not the principal limiting factor affecting seedling performance during the first two growing seasons, it is assumed that it will have a much greater impact in the near future.

Effects of herbivory

Our third hypothesis stated that herbivory will have a significant impact on seedling survival and growth. At the whole plot scale, evidence to support this hypothesis was weak. First, no significant differences in stem herbivory were detected among sites in either species (Table 5). Second, in the sites where leaf herbivory was particularly heavy, survival was not particularly low (Figure 6). For example, leaf herbivory of *Q. alba* was greatest in the Beaufort understory site (Figure 5), but *Q. alba* survival was very good at this site (Figure 6). The same pattern was seen for *C. florida* at the Green Pond understory site; i.e., high leaf herbivory yet good survival (Figures 5-6). At the Beaufort understory site, *Q. alba* growth was low while leaf herbivory was at its greatest among all site/treatment combinations. This relationship between leaf herbivory and growth was not as evident for *C. florida*. Leaf herbivory was greatest for *C. florida* at the Hog Barn understory plot (Figure 5), but growth was not consistently the smallest at this site. Within plots, evidence for herbivory effects was much stronger. Leaf herbivory was a significant factor in the survival analyses for just 3 out of 24 tests (Table 9) and stem herbivory was significant only once (Table 9); however, both leaf and stem

herbivory were significant factors in many of the growth analyses. In fact, leaf and stem herbivory were the two most frequently identified variables affecting responses within plots (Table 10). Leaf herbivory was significant 9 times and stem herbivory 7 times, each out of a possible 24 regressions (Table 10). In models where they were significant, both forms of herbivory were inhibitors to total leaf area growth (average r^2 for 1st year = 0.190; average r^2 for 2nd year = 0.205) as well as total biomass growth (average r^2 = 0.189). They explained the most variation in both of these growth responses among all of the environmental variables, including water and light. They were also present in every case where there were two or more variables included, and occurred together in four separate regressions. Because of this and the fact that herbivores consumed 40-60% of the leaf area or stem in some plants (Figure 9), herbivory was a strong factor. However, the importance of herbivory may have been overstated by the data. The herbivores may have selected either slow-growing or weak plants, indicating a greater effect on survival than would generally be present.

Generally, deciduous species can overcome modest degrees of defoliation (Krause and Raffa 1996). Krause and Raffa found that deciduous larch (*Larix deciduas*) defoliated by 33% and 66% recovered their aboveground biomass growth to near control values within one year. Recovery, however, varies among species. Many species have been known to compensate for losses to herbivores up to about 75% (Risley 1993) while 25% defoliation may fatally inhibit plant function in other species (Verkaar 1987). Beyond these threshold values, growth losses due to early abscission are likely (Risley 1993). Hardwood growth after defoliation, or recovery, is accomplished by returning to as nearly normal a photosynthetic machinery as possible, taking advantage of its ability of multiple flushes and allowing the plant to survive until more favorable times (Hodkinson and Hughes 1982). Therefore, much of this recovery ability is species-driven. Many of these herbivory studies were performed by mechanical defoliation or in greenhouse studies. Plants grown in natural environments where stress factors are present may be much less capable of overcoming leaf tissue losses as compared to greenhouse seedlings. One field experiment used a random sample of 50 leaves of 52 plant species, giving a mean defoliation of 10.46%, much higher than our results (de la Cruz and Dirzo 1987), but recovery was not measured. Linit et al. (1986) also had field

experiment leaf area losses of 20-24%, but the impact on survival and growth was not measured; it was only assumed that the defoliation was not detrimental. This is very common among herbivory experiments. Either the biology of recovery via mechanical defoliation studies or the quantification of leaf herbivory via field studies is the main goal of these studies, not both.

Practical implications

One important goal was to develop effective and cost efficient methods to artificially regenerate large-seeded hardwoods in pine-dominated landscapes of the coastal plain. In a preliminary experiment at Savannah River Site, we found that direct seeding of *Q. alba* and *C. florida* into pine understories or recently clearcut pine forests resulted in poor survival (less than 10% of planted *C. florida* seeds and approximately 25-30% of planted *Q. alba* seeds) and very poor growth (generally less than 10 cm of height growth) four years after planting. In this study, we evaluated the planting of one-year-old, bare-root seedlings directly into the understory, or in clearcut plots during the first dormant season after harvest and site preparation. We conclude that planting in the clearcut plots is the most effective method, principally because there was no significant difference in survival between cutting treatments (Table 4); however, in most cases, growth in the clearcut treatments was significantly greater than in the understory (Table 5). The large differences in growth between the treatments also proved that the two-year duration of the study was long enough for us to detect effects of our proposed environmental factors on seedling performance.

Our recommendation contrasts with general guidelines for hardwood regeneration that emphasize establishment of advance regeneration in the understory followed by release. These guidelines are based on studies that show positive effects of clearcutting on herbaceous and non-crop woody species, and subsequent strong impacts of these competitors on crop species (Sander et al. 1976, Wright et al. 1984, Beck and Hooper 1986, Crow 1988, Brose and Van Lear 1998). However, these studies also show that competition problems are much less in the understory than in the clearcuts, and regeneration is easier on poor quality versus high quality sites. Our two driest sites certainly qualify as unproductive relative to most eastern US hardwood-dominated

forests, and survival was much greater at these sites than at our more productive Hog Barn Site. Standing water may have complicated the Hog Barn site's productivity, but in general, our results seem consistent with the literature. On the other hand, our sites had few hardwoods in the understory prior to harvest. Site preparation (including burning and herbicide) was also used to reduce competing vegetation. These caveats should be considered before upland hardwood seedlings are planted into recently clearcut forests.

Conclusions

Our intent in this study was to determine which of several environmental factors have the greatest influence on survival and growth of *Quercus alba* and *Cornus florida* seedlings. Since the environmental factors varied both among and within plots, teasing apart the influence of individual factors was difficult. However, some important key points emerged.

First, variation among seedlings was quite high, and very few of our models were capable of explaining more than 40% of the variation in survival and growth. Thus, there are clearly other variables, such as genetic differences among the seedlings that affect seedling performance not accounted for in our study. This is not an unusual finding; virtually all studies of seedlings planted in natural conditions have found a substantial background variability that is not accounted for by measured variables. A greenhouse study might better quantify our limiting factors, but it would eliminate the stochastic factors present among the natural environment. Analysis of allometric relationships, e.g., between leaf weight and shoot weight, might also better show how the environmental variables, specifically light and water, impacted the seedlings.

Second, we found that herbivory was the most important variable among those that we measured. Within sites, herbivory had strong impacts. Among sites that had conditions potentially favorable for seedling performance, leaf herbivory made some sites appear inadequate for establishment, especially *Q. alba*. Thus, we found that herbivory varied at multiple spatial scales and that the nature of this variation was important to hardwood seedlings. Our study adds to a growing literature that has demonstrated strong herbivore influences on tree regeneration and patterns of forest succession (Streng et al.

1989, Hodges and Gardiner 1992, Pope 1992, Krause and Raffa 1996, Buckley et al. 1998).

Third, we found that virtually all of the resource and environmental conditions we measured had influences on at least some survival and growth parameters, but none stood out as an overriding factor. Water was the most prevalent of these conditions. It did factor into the growth and survival of our seedlings, but not in the manner expected. Instead of a large positive effect on growth and survival, a negative impact of water was found due to the effects of excessive water on survival at the Hog Barn site.

Finally, because factors such as herbivory, soil moisture, and nutrients operate at more than one scale (i.e., both within and among plots), it is important to note that planting success will likely vary across the landscape despite apparent similarities among sites. In our study, large differences in resources at the whole plot scale were obvious and expected, but substantial microsite variation was also present.

Chapin et al. (1987) stated that the future direction for understanding plant responses to environmental stresses is to establish mechanistic studies of responses to multiple environmental stresses or responses of species mixtures to environmental variation. Our study does not reveal mechanisms underlying seedling performance; however, we have shown that plants respond significantly to multiple factors, including some that we did not measure, all of which vary at multiple scales. Furthermore, resources, conditions, and interspecific interactions such as herbivory, vary more or less independently across natural landscapes. Gaining a truly mechanistic understanding of seedling responses will therefore be a tremendous challenge, but if we knew all of the answers already, regeneration ecology would not be necessary.

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Curriculum Vitae

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Education

- B.S. Biology and Chemistry, Western Kentucky University (WKU)
- M.S. Biology, Virginia Polytechnic Institute and State University (VPI & SU)
- Pursuing Ph.D. Forestry, University of Missouri-Columbia (MU)
- Expected Completion: Spring 2005
- GPA: 3.85

Objectives and Interests

My goal is to obtain my Ph.D. in forestry with an emphasis on forest ecology and plant physiology. My academic interests are primarily population and physiological biology of forest stands. I also wish to focus on the impacts the environment can have on old field succession.

Honors/Activities

- 2nd Place Undergraduate Research Presentation Competition of the 83rd Annual Kentucky Academy of Science Meeting
- President's List (Fall 1996-Fall 1997). Dean's List (Fall 1994-Spring 1996)—WKU
- Ogden Research Scholarship, Hallmark Scholarship, Schoenbaum Foundation Scholarship, Caveland Classic Scholarship—WKU
- Ogden College, Department of Chemistry, Chemistry Student of the Year (1998)

Grants/Funding

- Graduate Student Assembly Travel Fund Program (1999, 2000, and 2001)
- Graduate Research Development Project (1999)
- Sigma Xi Grants-in-Aid of Research (2000)
- University of Missouri-Columbia Life Sciences Fellowship (2001-2005)

Career Related/Research Experience

- Employed for four years in the Materials Characterization Center at Western Kentucky University (July 1994-May 1998)
- Analyzed various materials including coals, ashes, soils, steels, biological samples, etc. with an Inductively-Coupled Plasma Atomic Emission Spectrometer (ICP-AES) and other elemental analyzers
- Oversaw several hardwood seedling regeneration projects at the Savannah River Site (1999-2001) through the USDA Forest Service

Presentations (Underline name was presenter)

- J.T. Riley, B. Wang, M.B. Renfrow, and J.M. Riley, Jr. ICP-AES Analysis of Solids/Water Slurries. Pittsburgh Conference on Analytical Chemistry and Applied Spectroscopy. New Orleans, LA. March 5-10, 1995.
- K.B. Kleeman, D.E. Edmonds, K.E. Prow, D.B. Wilhite, X. Fan, Q. Cao, J.M. Riley, Jr., M.B. Renfrow, L.B. Hughes, E. Gray, J.T. Riley. Major, Minor and Trace Element Analysis of Compost Mixtures. WKU Sigma Xi Research Conference, April 15, 1995.
- M.B. Renfrow, J.M. Riley, Jr., and J.T. Riley. Slurry Injection ICP-AES Analysis of Solids. WKU Sigma Xi Research Conference, April 15, 1995.
- K.B. Kleeman, K.E. Prow, Q. Cao, J.M. Riley, Jr., J.T. Riley, L.B. Hughes and E. Gray. Evaluation of Composting Processes Using Elemental Analysis Data. KAS/TAS Joint Meeting, Bowling Green, KY, November 16-18, 1995.
- J.M. Riley, Jr., Q. Cao, M.B. Renfrow, J.T. Riley, D.L. Harper, J. Adair, and D. Jedrejic. Selection and Analysis of Samples for Calibration of a Glow Discharge-Atomic Emission Spectrometer. KAS/TAS Joint Meeting, Bowling Green, KY, November 16-18, 1995.
- J. Adair, D. Jedrejic, D.L. Harper, J.T. Riley, J.M. Riley, Jr., and Q. Cao. Depth Profile and Bulk Analysis of Raw Steels Using Glow Discharge-Atomic Emission Spectroscopy. KAS/TAS Joint Meeting, Bowling Green, KY, November 16-18, 1995.
- John T. Riley, Joseph M. Riley, Jr., Q. Cao, Douglas L. Harper, Janet Adair, and Dave Jedrejic. Calibration of a Glow Discharge-Atomic Emission Spectrometer for Quantitative Depth Profile and Bulk Analysis. Pittsburgh Conference on Analytical Chemistry and Applied Spectroscopy, Chicago, IL, March 3-8, 1996.
- Douglas L. Harper, Janet Adair, Dave Jedrejic, John T. Riley, Joseph M. Riley, Jr., and Q. Cao. Use of Glow Discharge-Atomic Emission Spectroscopy for Quality Control. Pittsburgh Conference on Analytical Chemistry and Applied Spectroscopy, Chicago, IL, March 3-8, 1996.
- Enrique Yanes, David Wilhite, Joseph M. Riley, Jr., Dong Li, Wei-Ping Pan, and John T. Riley. A Study of the Volatile Matter of Coal as a Function of the Heating Rate. 12th International Coal Testing Conference, Cincinnati, OH, September 8-11, 1996.
- M.B. Renfrow, J.M. Riley, Jr., X. Chi, J. Adair, J.T. Riley, and D.L. Harper. Development of Calibration Standards for a Glow Discharge-Atomic Emission Spectrometer. WKU Sigma Xi Research Conference, March 30, 1996.
- Enrique Yanes, David Wilhite, Joseph M. Riley, Jr., Dong Li, John T. Riley, and Wei-Ping Pan. A Study of the Volatile Matter of Coal as a Function of the Heating Rate. 82nd Annual KAS Meeting, Frankfort, KY, November 14-16, 1996.
- Joseph M. Riley, Jr., Dong Li, Ming Ji, and John T. Riley. Development of an ASTM Standard Test Method for the Determination of Major and Minor Elements in Combustion Residues. 83rd Annual KAS Meeting, Morehead, KY, November 13-14, 1997.
- Jones, R.H. and J. M. Riley, Jr. Limits on invasion of upland hardwood tree species into pine-dominated landscapes. 84th Annual ESA Meeting, Spokane, WA, August 8-12, 1999.

- Jones, R.H. and J.M. Riley, Jr. Limits on invasion of upland hardwood tree species into pine-dominated landscapes. 16th Annual Research Symposium of Virginia Tech, Blacksburg, VA, March 27, 2000.
- Riley, J.M., Jr. and R.H. Jones. Limiting factors to regeneration of large-seeded hardwoods in the Upper Coastal Plain of South Carolina. 85th Annual ESA Meeting, Snowbird, UT, August 6-10, 2000.
- Riley, J.M., Jr. and R.H. Jones. Factors limiting regeneration of upland hardwoods. 86th Annual ESA Meeting, Madison, WI, August 5-10, 2001.

Publications

- Riley, J.T., M.B. Renfrow, and J.M. Riley, Jr. 1995. ICP Analysis of Water Slurries of Ashes. Proceedings of the 11th Annual International Coal Testing Conference. Lexington, KY, 58-66.
- Yanes, E., D. Wilhite, J.M. Riley, Jr., D. Li, W. Pan, and J.T. Riley. 1996. A Study of the Volatile Matter of Coal as a Function of the Heating Rate. Proceedings of the 12th International Coal Testing Conference. Cincinnati, OH, 87-96.
- Renfrow, M.B., J.M. Riley, Jr. and J.T. Riley. 1997. ICP Analysis of Aqueous Slurries of Solids. Microchemical Journal 56: 30-39.

Related Course Work

Biol. Concepts	General Chem. I/II	Comparative Anatomy
Molecular Biology	Organic Chem. I/II	Ecosystem Dynamics
Botany	Quantitative Chem.	Statistics in Research I/II
Zoology	Physical Chem.	Advanced Forest Soils
Ecology	Biochemistry	Plant/Water Relations
Genetics	Biophysics I/II	Community Ecology
Calculus I	Methods in Regression Analysis	

Instrumentation

LECO ICP-AES	Atomic Absorption Spectrometer
Thermogravimetric Analyzer (TGA)	Bomb Calorimeter
Carbon, Hydrogen, and Nitrogen Analyzer	LECO CR-12 Carbon Analyzer

Professional Meetings

Pittsburgh Conference: 1996, 1997, and 1998
 Kentucky Academy of Science: 1996 and 1997
 Ecological Society of America: 1999, 2000, and 2001
 Research Symposium of Virginia Tech: 2000

Employment

- Laboratory Technician at the Materials Characterization Center of WKU (July 1994-May 1998)
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