I. INTRODUCTION

A key component of forest succession is the development of a seedling bank in the understory prior to disturbance of the overstory (i.e., advance regeneration). Understory seedling banks are typically dominated by mid- to late-successional tree species. It has been theorized that early successional species are excluded from the advance regeneration pool because they are intolerant of shade (Walker and Chapin 1986) or root competition (Jones et al. 1989). However, other organisms may also influence advance regeneration.

Aside from plants, the predominant organisms in the forest soil community are often fungi (Ingham et al. 1991, Anderson and Domsch 1975). Yet, the influences of fungi on species composition of advance regeneration are poorly understood. Studies are needed to elucidate: a) the mechanisms by which fungi mediate differential plant fitness and competition; and b) the importance of fungal effects relative to shade tolerance and root competition.

The net effect of fungi on tree seedlings may be difficult to predict because fungi have diverse functions. All fungi are heterotrophic for carbon and obtain required organic compounds from autotrophs. Saprophytes obtain nutrients from degradation and perform the important facilitative function of converting recalcitrant compounds to energy and nutrient sources for use by plants. Pathogens divert active resources from living plants for their own use to the detriment of the plant. Mutualists (e.g., mycorrhizal fungi) also divert resources from living plants, but the plant also benefits by drawing resources from the fungi.

Recent studies have shown that soil microbiota can mediate succession in grasslands (Wilson and Harnett 1997; Bever 1994) and sand dune communities (Van der Puten et al. 1993). Both inhibitory and facilitative effects have been reported. Van der Puten et al. (1993) found that soil organisms present in the later stages of succession can inhibit establishment of plants found in earlier successional stages. Bever (1994) found an inhibitory feedback between plants and the soil microbial community that develops in the plant's presence. This negative feedback may be a product of accumulation of pathogens where high density of hosts are present (Burdon 1987). Wilson and Hartnett (1997) found that when fungi were suppressed in grassland microcosms, relative dominance between the

different grasses shifted. These studies have identified soil microbiota as a key part of succession. However, no studies have yet attempted to uncover this type of influence on advance regeneration dynamics in forests.

Understanding fungal effects on tree seedlings may have practical importance to forest restoration efforts. The southeastern coastal plain landscape is defined by a cycle of land use that began with the clearing of forests by European settlers. The land was subsequently used for cotton and tobacco agriculture with unarable land left to regenerate timber. In the 20th century, large areas of cropland were abandoned and left to regenerate naturally or planted with various pine species (Turner and Ruscher 1988). It was predicted that upland hardwood species would eventually appear in those new forests as part of the normal succession process (Odum 1960). This has not occurred with the frequency predicted (Golley and Gentry 1966, Thompson and Lloyd 1995).

Potential limitations to upland hardwood re-establishment in coastal plain forests include lack of seeds, poor seed dispersal, limited availability of nutrients and water, negative interactions with soil biota, and for planted seedlings, initial seedling size. The role of fungi (either inhibitory or facilitative) may be an important factor limiting hardwood regeneration. Particularly in nutrient poor sites, mycorrhizal inoculations can boost survivorship and growth of tree species (Kormanik 1985, Haselwandter and Bowen 1996). Fungi may also determine which tree species are capable of becoming established in a given forest understory.

II. REVIEW OF PLANT-FUNGI INTERACTIONS

INDIRECT INHIBITORY INTERACTIONS

Few documented indirect inhibitory effects of fungi on plants have been reported. However, nutrient immobilization by some fungi may bind limiting resources reducing the ability of a plant to maximize its growth (Richards1974). Fungal competition may mediate the competition of the plants with which they are associated. An example of this potential mechanism of indirect inhibition was shown by Mitchell et al. (1992). They cultured the ericaceous mycorrhizae *Hymenoscyphus ericae* (Read) Korf and Kernan with a number of

ectomycorrhizal Basidiomycetes from *Picea sitchensis* (Bong.) Carr. (Sitka spruce) and showed an antagonistic effect of the ericaceous on spruce mycorrhizae (Mitchell et al. 1992). This has not been tested in the field but it shows that possible allelopathic interactions between fungi associated with different plant species can influence plant interactions and, potentially, successional dynamics and community structure.

DIRECT INHIBITORY INTERACTIONS

Direct inhibitory effects of fungi on plants are common and well documented owing to the direct economic impact of these interactions on forestry and agriculture. Inhibitory effects have also produced dramatic changes in forest composition in America, Europe and Australia (Dobson and Cawley 1994; Castello et al. 1995). In America *Cryphonectria parasitica* (Murr.) wiped out the dominance of American Chestnut over vast sections of the eastern U.S. *Ceratocystis ulmi* (Buisman) had similar effects on elms in the U.S. and western Europe, and in Australia the eucalypt forests have been hard hit by the fungal parasite *Phytopthora cinnamomi* Rands. But a number of studies have shown pathogens also work at more subtle levels in shaping community properties (Van Der Puten et al. 1993, Bever 1994).

Fungal pathogens obtain their nutrition from a host plant to its detriment. Fungi are not chlorophyllous and must tap their hosts photosynthetic capacity. K-strategist pathogens have poor dispersal and are not mortal infections for the host plant. Their 'strategy' is to siphon off the 'fat' but not to kill the host. R-strategists, on the other hand, cause the rapid deterioration of their host and survive by means of an efficient dispersal mechanism (Newman 1978). Pathogens often affect the flow of resources by synthesizing and releasing plant growth hormones - indole auxins, cytokinins, gibberellins and ethylene - disrupting the hosts internal balance of these compounds (Isaac 1992). The fungi can then exploit the chaos, and often increased growth of the plant. Foolish rice disease is an example of this phenomenon. *Gibberella fujikuroi* (Swada) Ito causes rice seedlings to grow twice as long as uninfected plants but the stem is weak and eventually collapses and dies (Stern 1991). By the time the plant dies the fungus has completed its reproductive cycle.

Light has a well known effect on seedling establishment (Ferrell 1953). Augspurger (1984) found that fungi can interact with light. She showed that mortality due to pathogenic fungal disease was greater in shaded sites than in light gaps. Pathogen activity has a strong influence on seedling survival in specific microhabitats. This finding suggest that shade intolerance may be partially due to a pathogenic effect in addition to physiological effects.

Van der Puten et al. (1993) showed in a set of experiments that the growth of plants of different successional associations were differentially effected by the pathogens of adjacent successional stages. Pathogens of an earlier successional stage had little effect on plants of the next successional stage. However, pathogens of the successor stage negatively affected growth of plants from previous stages. Although they did not distinguish fungal pathogens from other pathogens, they did show that the soil biota shaped successional processes of sand dune plant species. This phenomenon has also been noted in old field succession (Bever 1994).

Pathogen regulation of community structure has received much attention recently (Dobson and Crawley 1994, Castello et al. 1995). Pathogens can restrict the growth rate of dominant plants allowing others to gain a foothold, thus increasing diversity. Wilbur (1972) showed that a predatory salamander could exert top down control by restricting the population growth rate of a dominant that competitively excludes another species in the absence of the predator. Pathogens can function similarly as top predators in many ecosystems (Dobson and Crawley 1994). Dickman and Cook (1989) studied mechanisms by which diversity is maintained in pure old growth stands of mountain hemlock (*Tsuga mertensiana* (Bong.) Carriore). Between periodic fires, the fungal pathogen *Phellinus weirii* (Murrill) R.L. Gilbertson (root rot) is a major mechanism whereby openings are formed. In these openings lay the opportunity for diversity in this community.

Soil fungi can become a conduit for source-sink relationships between plants. Mycorrhizal fungi can link different plant species through a common mycelial association, and can transfer carbon (Björkman 1960). Björkman injected ^{14}C into pine and spruce trees and traced it to nearby achlorophyllous *Monotropa* plants which are dependent on a mycorrhizal symbiont for carbon. This early work demonstrated the phenomenon of source-sink relationships mediated by fungi.

More interesting effects on community structure may be derived from the linking of chlorophyllous plants to other individuals of the same or even different species. Given that fungal mycelium can spread for many meters and many species of mycorrhizae are not highly host specific (Molina et al. 1992), it seems likely that plants are linked. This physical linkage has been demonstrated in the laboratory, as has been the transfer of water, carbon, phosphorus and cations (Miller and Allen 1992). Field data have shown physical connections between lodgepole pines (Miller et al. 1989) but the frequency and extent of these connections has not yet been well established.

The possibility that established trees 'donate' or lose carbon to seedlings or shaded trees could be an important mechanism by which seedling dynamics and advance regeneration niches are structured. Trappe and Luoma(1992) speculated on ways seedlings might benefit from carbon 'sharing' via mycorrhizae mycelium. Seedlings can link into established mycelial networks and potentially pick up carbon from overstory plants that have a much higher photosynthetic capacity and access to light. Weakened or dying overstory trees may 'retranslocate' mobile nutrients to other plants connected to the same mycelial web. Mycorrhizae may exert a pathogic influence on a given tree which is weakened and exploit as many resources from the plant as it can before the plant dies (Trappe 1992). This could be a mechanism for species with similar fungal symbionts that share mycelium to maintain dominance over other species with less developed mycelial networks.

INDIRECT FACILITATIVE INTERACTIONS

Many indirect facilitative effects of fungi on plants result from inhibitory effects on neighboring plants. The hemlock root rot inhibits hemlock yet facilitates the establishment of species that utilize the gap opened up by the dead hemlock. R-strategist pathogens often are indirectly facilitative to the competitors of the host. Often, the indirect effect of pathogens on the community is more diversity (Dickman and Cook 1989).

Saprophytes are important members of the soil community. Unlike the mutualist and pathogens, they obtain their nutrition from dead organic material so they do not directly affect living plants but decompose organic matter in the soil. The decomposing

biota take organic materials and mineralize them increasing the available nutrient pool for all organisms in the community. An example is the decomposition of amino rich chitin (Mitchell et al. 1992). The nitrogen bound in chitin is unavailable to plants for uptake. The soil fungi can degrade this chitin and (in conjunction with other members of the soil biotic community) fuel a series of soil biota exchanges that eventually converts the chitin's nitrogen into ammonium or nitrate which is then available for plant uptake. This allows a system to recycle nutrients, maintaining a resource base from which resident plants can draw for nutrition.

If the system has enough available energy and substrate, however, the soil biotic community can actually immobilize nutrients effectively competing with plants for the available resources. Richards (1974) illustrated this phenomenon with a study measuring plant available nitrogen in two soils, one of which had sugar added to represent a high energy substrate. In the soil without the added sugar, the plant available nitrogen was nearly 5 times greater. The net immobilization/net mineralization status of a soil may change over the course of the year. Again we see the fine line that often separates a facilitative from an inhibitory relationship among plants and the soil biota.

Mutualists are commonly thought of for their direct effects on plants, however their indirect effects are also substantial. In course-grained sand dune soil, soil aggregation occurred only around endomycorrhizal hyphae (Rose 1988). The soil structure provides the capacity to store water and retain nutrients. Without the mycelium the soil would support a smaller resource base thus limiting biomass production and affecting community structure by allowing only plants that could survive low resource stress. The course of succession could be significantly altered if no aggregation was initiated by the fungal hyphae.

Ectomycorrhizae may also be a barrier to other pathogenic fungi (Newman 1978, Azcon-Aguilar and Barea 1992). There are three proposed mechanism's by which this may occur (Marx 1975). First, they may provide a physical barrier to infection sites for other fungi. Secondly, they also are dominant competitors for rhizosphere nutrient resources. Lastly, and finally they may produce inhibitory compounds (Leake 1987, Mitchell et al. 1992). By decreasing a plant's susceptibility to disease, ectomycorrhizae may increase an ectomycorrhizal plant's chance of survival over other non-ecto plants.

Many forest trees have ectomycorrhizal associations which may help them avoid disease over the course of their long life.

Aside from cycling nitrogen, fungi also play an important role in the fixation of atmospheric nitrogen. Brill (1979) estimates that sixty percent of some plant communities' nitrogen originates through biological fixation. One of the main sources of fixed nitrogen in some systems is rhizobial bacteria infecting legumes. Rhizobial N-fixation can be limited by phosphorus availability (Shulka and Yadav 1982). Endomycorrhizae enhance phosphorus availability via a tripartite relationship with the host plant and the N-fixing bacteria, and facilitate N-fixation which is often phosphorus limited (Barea and Azcon-Aguilar 1983). Another source of nitrogen are lichens which have a cyanobacterium in cephaloidia that carry out N-fixation (Galun and Bubrick 1984). As resources increase, different species may be able to dominate and take the place of N-fixing plants which are usually abundant in early successional stages. Thus fungal enhanced N-fixation can set the resource stage for the progression of succession.

The demands of the fungi for carbon have important community consequences. Quantifying carbon flow to mycorrhizae is difficult but a number of studies have established estimates. Vogt et al. (1982) determined that 70- 80 % of net primary production is allocated to below ground tissue in a Pacific silver fir forest, approximately 15% of that goes to mycorrhizae. Other studies have found that 10-40% of total photosynthate can be allocated to mycorrhizae (Finlay and Söderström 1992). This provides a large carbon base for the soil biotic community.

The soil biota in turn decompose organic matter and make nutrients available. Griffiths and Caldwell (1992) showed a difference in decomposing enzymes in early vs. late successional mycorrhizae species. Later successional mycorrhizal species produced enzymes more adept at degrading humic acid. This may be the mechanism where by nitrogen and phosphorus in recalcitrant organic matter are accessed by the fungi and plant.

DIRECT FACILITATIVE INTERACTIONS

The two main types of mycorrhizae are ecto- and endo-mycorrhizae. Ectomycorrhizae are characterized by a hyphal sheath surrounding the host root. By the

formation of a hartig net which directly contacts host cortical cells both symbionts are able to exchange resources culminating in the well known mutual relationship. Ectomycorrhizal associations are common for woody plants. Endomycorrhizal (most commonly vesicular arbuscular mycorrhizae) fungi physically penetrate the host root and form arbuscules inside the host's cells where resource exchange takes place. Endomycorrhizae are formed with bryophytes, pteridophytes, gymnosperms and many woody and herbaceous angiosperms.

Mycorrhizae are key factors in the structuring of plant communities (Perry et al. 1989a; Perry et al. 1989b; Trappe and Luoma 1992). They increase the plant's access to soil nutrient resources in exchange for some of the hosts photosynthetic resources. It is estimated that nearly 80% of angiosperm families and nearly 100% of gymnosperm families have members that form mycorrhizal associations (Trappe 1987). The vast majority of these associations are successful because they form obligate mutualisms. There can be temporal variations in which one member of the symbiosis is actually gaining more benefit than the other and, thus, the relationship may vary between mutualistic, parasitic or commensal (Bethenfalvay et al. 1982). By virtue of their sheer abundance, mycorrhizae have profound influences on community structure and may even regulate the functioning of almost all plant communities (Allen 1991).

Phosphorus is often a limiting plant resource. Mycorrhizae exude acid phosphotases that can mobilize unavailable phosphorus increasing the plant's ability to obtain phosphorus (Gianinazzi-Pearson and Gianinazzi 1989). As mentioned previously, early successional mycorrhizae function differently in the types of materials they, and thus the host, can obtain. Griffiths and Caldwell (1992) found more than twice the phosphotase and nearly an order of magnitude more lignolytic peroxidases in later successional mycorrhizal mats. These compounds facilitate the exploitation of otherwise unavailable nutrients.

This absorption of phosphorus is the crux of the association for the plant infected with a mycorrhizal fungus. If resources are not limiting, mycorrhizal plants may do no better and possible even lose fitness because of the infection. Increased phosphorus allows the plant to improve its water relations as phosphorus improves membrane control of absorption (Fitter 1991). The cost in carbon to obtain extra phosphorus may be regained

in the potential increase in photosynthetic ability because of improved phosphorus nutrition (Herod 1980).

Many mycorrhizal species have a broad range of hosts. But only form mycorrhizae with specific hosts (Molina et al. 1992). Specificity may give some plants advantages over others and thus a differential species performance. Mycorrhizae can regulate the flow of nutrients and distribute carbon through a plant community thus regulating the performance of interacting plants (Allen 1991). This clearly has important ramifications for the structuring and dynamics of plant communities under almost any environmental conditions.

III. OBJECTIVES AND HYPOTHESES

The first objective of the study is to determine if soil fungi have an important influence on differential species performance of understory seedlings in forest communities. To test this theory a fungicide is used to shift fungal community composition in forest understories, and then seedling survivorship and growth were assessed for three tree species with different successional status.

The second objective was to determine if an advance regeneration pool of upland hardwood seedlings can be established successfully in the understory of upland pine and hardwood forests in the coastal plain.

From these objectives follow four hypotheses:

1. ***Fungal community structure has a significant effect on tree seedling survival and growth***.
   Therefore, if fungal community structure is altered, growth and survival of advance regeneration will also be altered.

2. ***Tree species will have different sensitivity to fungal community shifts***.
   Affects of fungal community structure on growth and survival of different tree species will be related to successional status (i.e. early or late) or physiological tolerance (i.e. shade or drought tolerance).

3. ***Advance regeneration can be established in the understory of an upland coastal plain forest***.
   3a. Survival and growth of planted seedlings will be greater in early-successional than in late-successional forests.

3b. Larger seedlings will have greater survival and growth.

IV. MATERIALS AND METHODS

SITE DESCRIPTION

The study was located at the Department of Energy's Savannah River Site (SRS) in Aiken county, South Carolina. SRS has approximately 800 km^2 of forest managed by the USDA Forest Service (FS) and is located within the Coastal Plain province. Average daily temperatures range from 7.8 º C in January to 27.2 º C in July. The site receives approximately 120 cm rain yearly with Oct and Nov (6.3 and 5.9 cm) being the driest months and March (12.9 cm) being the wettest (Rogers 1990). The first spring after I planted seedlings was unusually dry with rainfall totals for April (5.0 cm) and May (7.2 cm) well below the ten year averages (8.9 cm and 10.8 cm respectively,unpublished data, Savannah River Forest Station). The first week of June was also without any rain, but by mid June rainfall was up to the ten year average.

A number of forests were surveyed to find sites that had a pine stand directly adjacent to a hardwood stand (i.e. two different seral stages) on similar soil types. In addition, the stands had to be at least 40 years old. Our strategy was to test how seral stage might affect seedlings directly or alter fungi effects on tree seedlings while reducing variance in other environmental factors.

Two sites with these characteristics were chosen (Table 1). Site 1 was in the northeast sector of SRS in FS management compartment 30. The Blanton soil at Site 1 is classified as a loamy, silicaceous, thermic, Grossarenic Paleudult. Site 2 was on the west side of the SRS in compartment 7. The Fuquay series soil at Site 2 is classified as a loamy, silicaceous, thermic, arenic, Plinthic Paleudult. The sites included four upland stands, two late-successional hardwood stands (oak-hickory) and two early successional (loblolly pine) stands (Table 1). The organic matter at both hardwood stands were twice as high as the adjacent pine stands (Table 1).

The sites varied somewhat in overstory density and basal area (Table 2). Site 2 had higher density and basal area in both the hardwood and pine stands. Both pine stands were dominated by *Pinus taeda* L. (loblolly pine), but Pine 2 had a significant *P. palustris* Mill. (longleaf pine) component which was absent in Pine 1. Pine 2 also had a far higher density of trees. Both hardwood stands were dominated by oaks and *Quercus stellata* Wangenh.

(post oak) was a dominant or codominant. *Carya tomentosa* (Poir.) Nutt. (mockernut hickory) was a major codominant at Hardwood 1 while *Q. falcata* Michx. (southern red oak) was the major codominant at Hardwood 2. Pine stands had lower woody species diversity than the adjacent hardwood stands at both sites (Table 2).

PLOT DESIGN AND TREATMENTS

In each of the four stands, ten 2 x 2 meter plots were randomly located within a 30 x 40 meter area (Figure 1). Five were randomly designated for fungicide treatment and the other five were control plots.

Ten one-year-old seedlings for each of the three tree species were planted in each plot on February 24, 1996, for a total of 1200 seedlings. Seedlings were planted in a 35 x 35 cm grid. Randomization of the seedlings was done by counting out 10 of each species for each plot and randomly pulling them out of a plastic bag.

Captan, a broad spectrum fungicide, was used to reduce fungal activity. Captan was chosen because it has a fairly long soil retention time (Brown 1978). It also has little or no effect on soil invertebrates and is thus fairly specific for fungi (Brown 1978; Ingham 1985).

Treatments consisted of applying 75 g of captan mixed with 8 l of water evenly over the treatment plots. The captan was mixed with water in the field in 5 gallon buckets. It was then poured into water cans and applied in a systematic and even sprinkle over the 2 x 2 meter plots. Control plots received 8 l of tap water. The treatment was repeated every six weeks from April 1996 through August 1997 - a total of 12 treatments. This application rate of 175 kg (80 % a.i./ha) is nearly double the rate used by Beare et al. (1993) in another study in a field crop setting that resulted in the reduction of hyphal densities.

TREE SPECIES

Tree species were chosen to represent different successional status and to compliment another study of hardwood regeneration at SRS (Jones and Waldrop 1995). *Cornus florida* L. and *Quercus alba* L. are later succession plants on these sites while *P.*

taeda is an earlier colonizer. The *Q. alba* seedlings were supplied by the Virginia Department of Forestry nursery in Augusta county from Virginia seed sources. *Cornus florida* were procured from a Tennessee nursery from an unknown seed sources. *Pinus taeda* seedlings came from commercial stock grown at the International Forest Seed Company in Statesboro, GA from seed collected at the Francis Marion and Sumter National Forest within the South Carolina coastal plain.

MEASUREMENTS

Pre-Planting harvest data and regression

Initial biomass of seedlings was estimated from 25-35 seedlings of each species removed from the planting pool. Basal diameter, shoot length and dry weight biomass (60 ^{o}C for 72 hours) were measured for each sampled seedling. A linear regression was performed using dry weight (wt) as the response variable and two independent variables: shoot length (sl) and diameter (d). The regression model was $wt = d^2sl$. Biomass was seperated into root biomass and shoot biomass. The regression yielded $r^2 \geq 0.72$ for roots and shoots of each of the species. All seedlings that were planted had basal diameter and shoot length measurements which were converted to dry weight with the regression. These initial biomass estimates were then compared to final biomass to determine biomass growth.

Fungal Assessments

- Plate Counts

Soil samples were collected from each plot at each site on May 5, 1997. Five 2.5 cm diameter plugs 5 cm deep were taken from each plot and bulked by treatment, forest and site. The soil was sifted through a 0.2 mm sieve. One to ten dilutions were prepared by suspending 10.0 g of each soil in 95 ml distilled and sterilized water. Additional ten-fold dilutions were made ranging from 10^{-2} to 10^{-6} by successively transferring 10 ml into 90 ml sterile water blanks. Dilutions from 10^{-3} to 10^{-6} were plated out on a standard rose bengal-streptomycin agar in triplicate and the counts of fungal colonies from the three plates were averaged (Wollum 1982, Beare et al. 1993).

The plates were incubated at 30º C for 7 days. Total fungal colonies on each plate were counted and recorded for the dilutions $10^{-4} – 10^{-6}$. These colonies included Deuteromycetes, Zygomycetes, yeasts and molds. The 10^{-3} plates were overgrown with colonies and could not be accurately counted.

Subsamples of the soils were weighed wet and then dried at 80° C for 48 hours and weighed again. Dry weight was divided by wet weight to yield a conversion factor. Wet weight of the soil sample used for the initial dilution was divided by the conversion factor to yield the dry weight of the sample. The following formula was then used to convert the plate counts to a standard unit of colony forming units (CFU) / g of soil (dry weight):

$$\text{CFU/g} = \frac{[\text{(mean of the three plate counts)} \times \text{(dilution factor)}]}{\text{Dry weight of soil used for the initial dilution}}$$

- Root Tip Counts

Root tip counts were used to assess the effects of the fungicide on colonization of seedling root tips by mycorrhizal symbionts (Poder 1996). Counts were made in the spring of the second growing season (May 29, 1997) and again from samples taken during the final harvest (September 22, 1997). Sixteen *Q. alba* seedlings were sampled in May from Hardwood 1 and Pine 1 stands. Seedlings were carefully harvested to obtain all root material for each plant. Roots were then washed in shallow tubs to tease out loose soil and other roots that had tangled with the sample plant. Three 10 cm segments of secondary root were removed from the root material and stored in plastic bags with water at 3º C. During the final harvest, 3-5 seedlings of each species were selected from each treatment within each stand (except Pine 1 from which not enough seedlings were available) and set aside to analyze root tips.

Samples were observed under a dissecting scope at 3X power. Each root tip was tallied. Then root tips with mycorrhizal infections were also tallied. Swollen and suberized tips indicated a mycorrhizal mantle (Walker et al. 1998). Questionable tips were crushed and observed under compound scope for hyphae. Results are reported in a percentage of root tips colonized. For the final harvest, infections with the *Ceonococcum* morphotype (Walker 1998) were noted for each sample.

Seedling Responses

Survival was assessed at the end of the first growing season after planting (September 21, 1996) and again at the time of harvest (September 22, 1997). Seedlings were considered alive if they held green leaves or had living stems. Separate survival rates were calculated for: 1) planting to the end of the first season, 2) planting to the end of the second season , and 3) end of first to end of second season.

Seedlings were harvested September 22, 1997 and maintained at 3º C until basal diameter and shoot length were recorded the following week. The seedlings were then separated into root, shoot and leaf components. These parts were dried at 60º C for 72 hours and then weighed. The initial estimate of root, shoot and total dry mass (from the regression) was then subtracted from the root, shoot and total final dry mass to determine dry mass growth. Growth was calculated only for seedlings alive at the end of the study.

Pine 1 was partially destroyed by a thinning operation approximately two months before the final harvest. This disturbance completely destroyed 3 fungicide treatment plots and 2 control plots. It is assumed that the effects of the disturbance (increased light, increased litter) on the remaining plots was minimal due to the short time the remaining plants were in the field before harvest. Growth and survival data for the five destroyed plots could not be measured for the final harvest, but survival was measured for the first growing season.

STATISTICAL ANALYSIS

Hypotheses concerning mycorrhizal infection rates, seedling survival and seedling growth were tested using an ANOVA for a split-split plot design. Forest type and treatment were the split factors. The GLM procedure of SAS (SAS 1985) was used to handle the unbalanced design caused by unequal mortality and the loss of five plots in Pine 1 to a thinning cut in the stand. The response variables tested were percent survival and biomass growth (g). Survival data is often arcsin transformed to normalize the distribution if the percentages are less than 30 or greater than 70 (Underwood 1997). Since the data for this study were within this range I chose not to transform them. Differences were considered significant at the $p < 0.05$ level.

Relationships between survival and initial seedling biomass were calculated using logistic regression. Linear regression was used to analyze the relationship between initial biomass and growth. For plate count data, paired t-tests were used to analyze differences in CFU by treatment. Four pairs corresponding to each combination of forest and site were used in the comparison.

V. RESULTS

FUNGAL COMMUNITY RESPONSES

Colony forming unit (CFU) counts were nearly twice as great in plates from control plots than in plates from treatment plots ($p= 0.02$; Figure 2). Root tip counts, however, did not show differences between the control and fungicide plots. For the spring sample of *Q. alba* seedlings (25 days after a treatment) there was a significant difference in colonization between the hardwood and pine forests ($p< 0.05$), but no significant difference between control and fungicide treatments (Figure 3). In year two, neither *P. taeda* or *Q. alba* seedlings showed differences between the hardwood and pine forests or between the control and fungicide treatments (Figure 3) .

SEEDLING RESPONSES

Overall, seedlings grew very little and survival was modest to poor. The early growing-season dry period that occurred immediately after planting resulted in visible wilting, especially among *C. florida* seedlings. Throughout the two growing seasons of this study virtually all *Q. alba* and *C. florida* seedlings had some leaf and stem herbivory. The stem herbivory was most noticeable in *Q. alba*. Some *Q. alba* and *P. taeda* had many leaves and large leaf area at the end of the study, others had few or no leaves as did most of the *C. florida*.

Total survival for each species ranged from 31 – 62 % at the final harvest (Table 3). *Quercus alba* and *P. taeda* had significantly greater survival than *C. florida* (Figure 4a). Though not statistically different, the survival in hardwood forests was higher after year one (data not shown) and at final harvest (Figure 4b) than for corresponding times in the pine forests. Fungicide treatment effects were not significant, nor were site effects.

However, mean survival was slightly higher at site 1 than at site 2 (Figure 4b). Suvival of oak seedlings alive after the end of the first growing season until the end of the study was higher in fungicide treated plots than in the control plots (Table 4).

According to logistic regression, initial biomass had a significant influence on survival for *C. florida* seedlings ($p < 0.01$) with larger seedlings having higher survival (Table 4). No significant influence of size on survival was detected for *Q. alba* and *P. taeda*.

Mean biomass growth (Figure 5) was greatest in *Q. alba* seedlings (9.5 g) followed by *P. taeda* (3.3 g) and *C. florida* (0.8 g). Some individuals had negative growth values, due to post planting die back. No significant site or forest differences were found, though *P. taeda* mean biomass was slightly greater in site 1 than site 2 (Figure 5).

Fungicide treatment impacts were nearly significant for total ($p = 0.0594$) and root ($p = 0.0583$) but not for shoot ($p = 0.485$) biomass growth (Tables 6-8). Separate analysis by species revealed that the fungicide treatment significantly increased growth of *Q. alba* seedlings but not in seedlings of the other two species (Table 5). *Q. alba* had greater growth in treatment plots in all stands except for Pine 2 (Figure 5). An opposite trend, though not significant, occurred in *C. florida*. *C. florida* seedlings had reduced growth in treatment plots in all stands except for Pine 2.

C. florida and *P. taeda* growth had a significant positive linear relationship with initial seedling size ($p < 0.01$), but *Q. alba* did not. The relationship between initial seedling size and growth for *Q. alba* may have been obscured by herbivory, dieback and resprouting which affected roughly half of the *Q. alba* seedlings.

Table 1. General forest characteristics of the four sites used in this study. Forest characteristics were compiled from the USFS Savanah River Station data base. Soil type was obtained from the SCS soil survey of the Savanah River Site (Rogers 1990). Carbon content (% carbon) in the top 5 cm of soil was measured by a Leco Carbon Analyzer (Stevens and Jones, unpublished data).

Site	Stand	Forest Type	Age	Regeneration	% Carbon	Soil Series	SRS unit
1	Hardwood 1	Oak-Hickory	74	Natural	1.53	Blanton	Compartment 30 Stand 38
	Pine 1	Loblolly	46	Planted	0.70	Blanton	Compartment 30 Stand 67
2	Hardwood 2	Oak-Hickory	65	Natural	1.15	Fuquay	Compartment 7 Stand 19
	Pine 2	Loblolly	47	Planted	0.56	Fuquay	Compartment 7 Stand 18

Table 2. Overstory (trees ≥ 10cm dbh) vegetation characteristics measured within a single 0.1 ha sampling plot within each stand. D = density (stems/ha) BA = basal area (m^2/ha).

Species	**Hardwood 1**		**Hardwood 2**		**PINE 1**		**PINE 2**	
	D	BA	D	BA	D	BA	D	BA
Carya pallida	40	0.70						
Carya alba	160	8.07	50	1.89				
Cornus florida			10	0.11				
Ilex opaca			30	0.57				
Liquidamber			30	1.52				
Myrica cerifera					10	0.13		
Nyssa sylvatica	40	1.11						
Pinus palustris	10	0.52	20	0.86			40	5.94
Pinus taeda			10	0.53	200	20.32	440	17.04
Prunus serotina					10	0.19	30	0.65
Quercus falcata	20	0.61	140	7.82			10	0.11
Quercus stellata	210	5.31	120	8.86				
Quercus velutina	10	0.22	40	1.36				
Ulmus alata			10	0.10			10	0.22
TOTAL	240	16.54	310	23.62	220	20.64	530	23.96

Table 3. Survival rates from planting to year one (a), year one to year two (b), and from planting to final harvest (c). Data are for all four forests combined.

	YEAR ONE (A)		**YEAR TWO (B)**		**FINAL (C)**	
Species	Fungicide	Control	Fungicide	Control	Fungicide	Control
C. florida	44.8 ± 3.8	50.6 ± 3.7	67.8 ± 7.1	68.8 ± 6.1	31.0 ± 3.5	32.8 ± 3.5
P. taeda	65.3 ± 3.7	70.6 ± 3.4	83.1 ± 6.3	83.3 ± 5.1	57.1 ± 3.8	59.4 ± 3.7
Q. alba	77.6 ± 3.2	77.9 ± 3.1	80.6 ± 3.8	66.7 ± 5.5	62.4 ± 3.7	51.2 ± 3.7

Table 4. Mean initial biomass ± standard error of seedlings for each survival category. Data for all forests and treatments combined.

Species	Survived	Died
C. florida	0.47 ± .02 *	0.39 ± .01
P. taeda	2.21 ± .06	2.01 ± .07
Q. alba	8.57 ± .42	9.19 ± .61

*Mean initial seedling biomass significantly ($p < 0.05$) different between individual seedlings surviving than those not surviving according to t-test.

Table 5. Biomass growth (g) accrued over two seasons broken down developmentally and by treatment for each species.Data are for all forests combined.

Species	Treatment	Root	Shoot	Total
C. florida	Fungicide	0.45 ± 0.06	0.25 ± 0.04	0.71 ± 0.09
	Control	0.53 ± 0.04	0.35 ± 0.03	0.89 ± 0.06
P. taeda	Fungicide	0.31 ± 0.05	0.81 ± 0.06	3.25 ± 0.19
	Control	0.36 ± 0.04	0.87 ± 0.08	3.29 ± 0.20
Q. alba	Fungicide	8.54 ± 0.65	2.15 ± 0.19	*10.77 ± 0.80
	Control	6.73 ± 0.63	1.96 ± 0.19	8.78 ± 0.79

*Mean biomass change significantly ($p < 0.05$) different between seedlings in fungicide treated plots and in control plots according to ANOVA.

Table 6. ANOVA for total biomass change over the entire course of the study.

SOURCE	DF	MS	Pr > F
Species	2	2987.2	0.0001
Species*Forest	2	13.8	0.5822
Species*Treat	2	51.9	0.1309
Species*Forest*Treat	2	13.1	0.5983
Error 1	467	25.4	
Forest	1	5.5	0.8586
Error 2	1	108.7	
Treatment	1	77.2	0.0594
Treatment*Forest	1	0.1	0.9544
Error 3	27	19.9	

Table 7. ANOVA for shoot biomass change over the entire course of the study.

Source	DF	MS	Pr > F
Species	2	113.1	0.001
Species*Forest	2	0.3	0.8105
Species*Treat	2	1.3	0.4487
Species*Forest*Treat	2	0.2	0.8801
Error 1	467	1.6	
Forest	1	0.4	0.8536
Error 2	1	7.8	
Treatment	1	0.7	0.4849
Treatment*Forest	1	0.1	0.8102
Error 3	27		

Table 8. ANOVA for root biomass change over the entire course of the study.

Source	DF	MS	Pr > F
Species	2	2642.3	0.001
Species*Forest	2	12.3	0.4487
Species*Treat	2	37.3	0.0889
Species*Forest*Treat	2	14.9	0.3785
Error 1	467	15.3	
Forest	1	0.4	0.9339
Error 2	1	38.7	
Treatment	1	55.7	0.0583
Treatment*Forest	1	0.5	0.8595
Error 3	27	14.3	

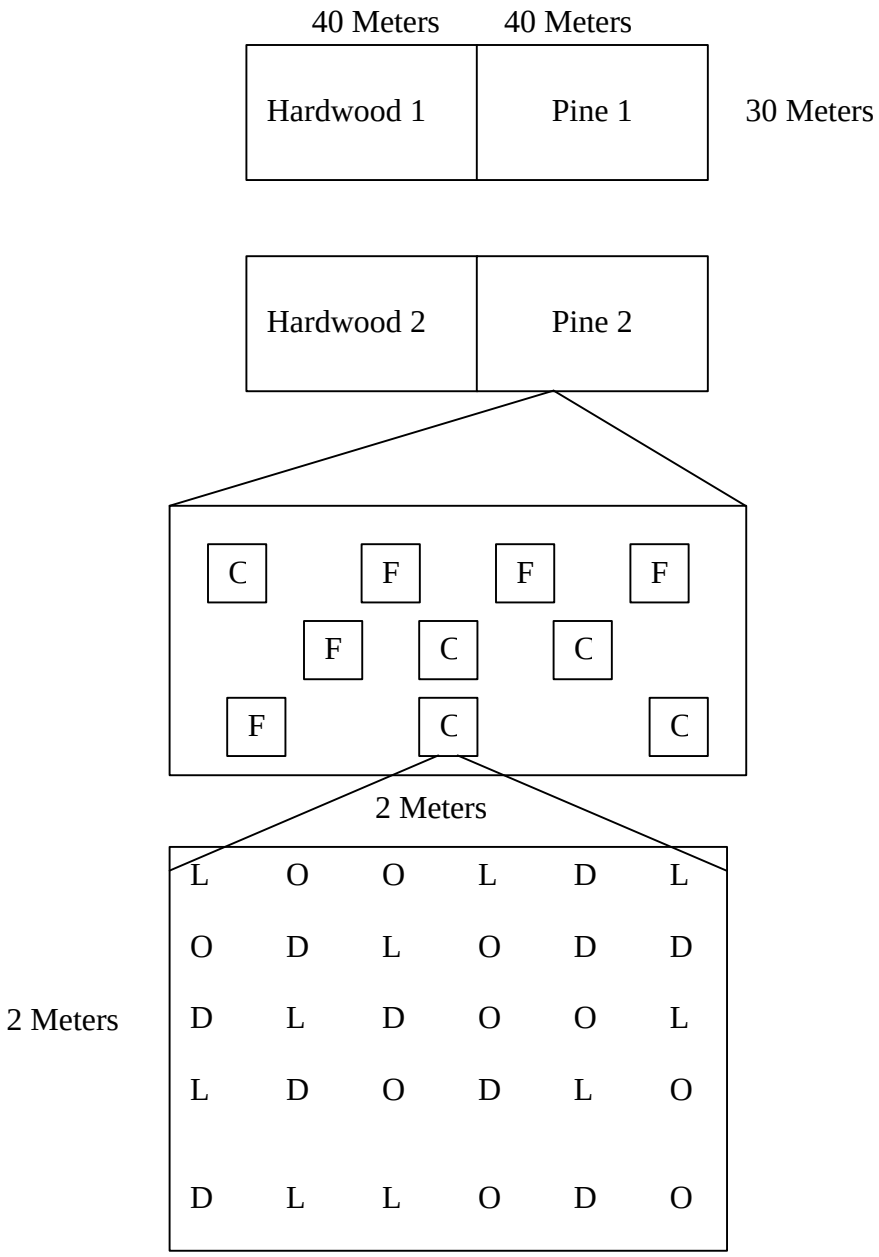

Figure 1. Schematic of plot design and layout. Treatments and seedlings were randomly mixed in stands and plots. F=Fungicide treatment, C=Control treatment; D=*Cornus florida*, L=*Pinus taeda*, O=*Quercus alba*. Each of the 4 stands had ten 2x2 meter plots – five control and five fungicide treatment. Ten seedlings of each species were randomly located in each plot.

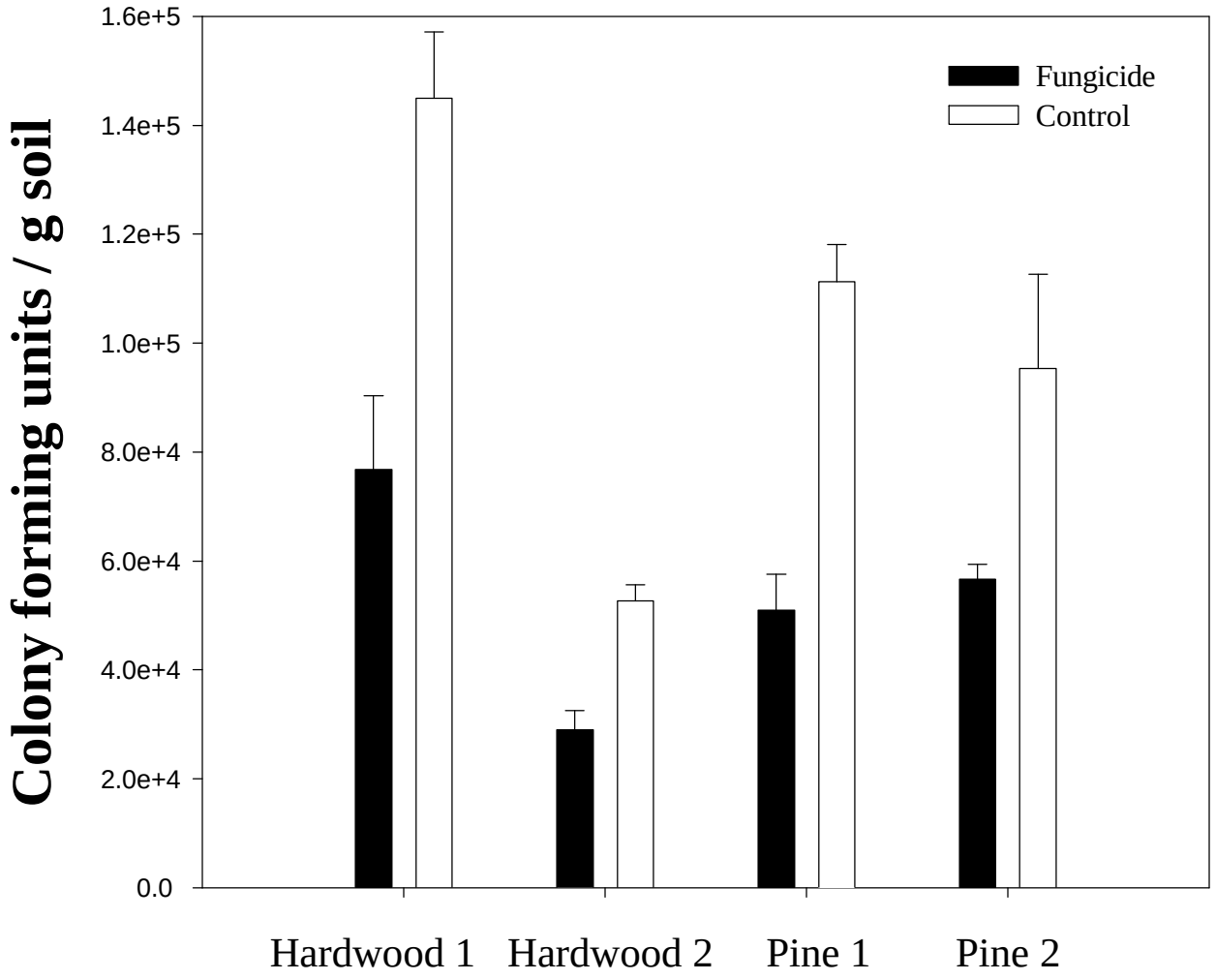

Figure 2. Plate count totals for each stand by treatment. Error bars are standard errors for three determinations.

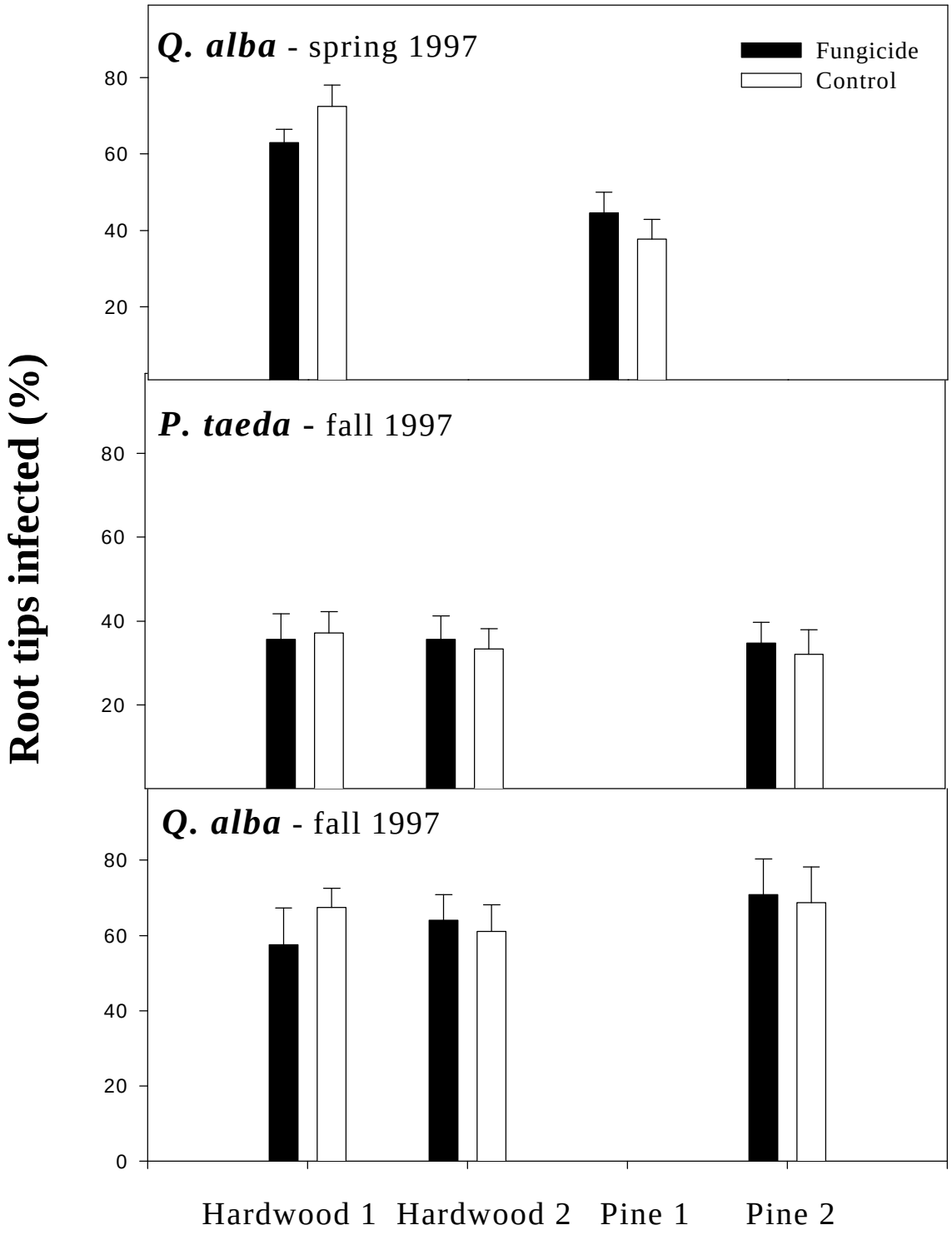

Figure 3. Percentage of root tips colonized by mycorrhizal fungi by treatment.

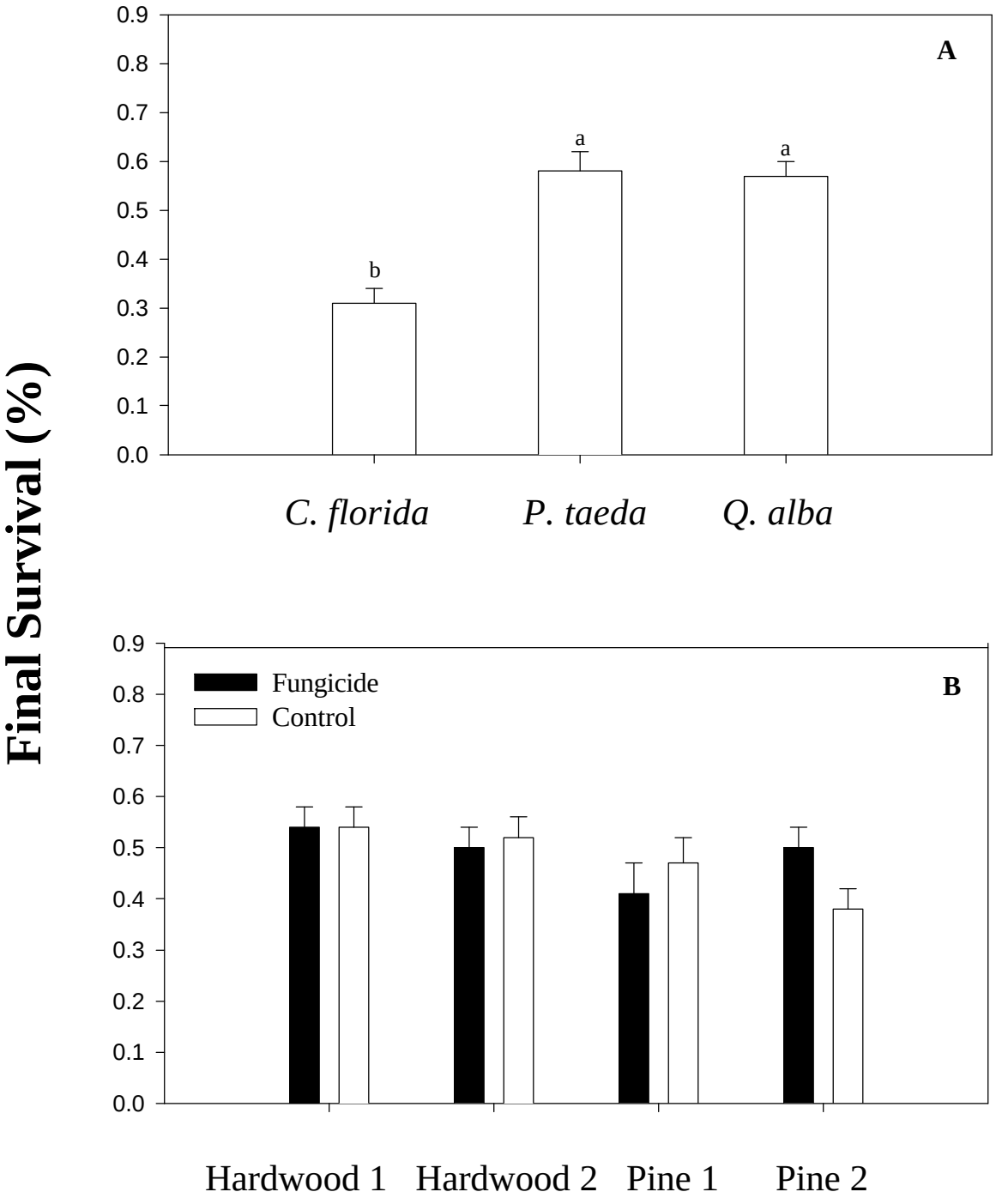

Figure 4. Mean survival in plots from initial planting to final harvest. A; for each species, data and treatments combined; B, for each stand and treatment with all species combined. Bars with different small letters are significantly different ($p < 0.05$).

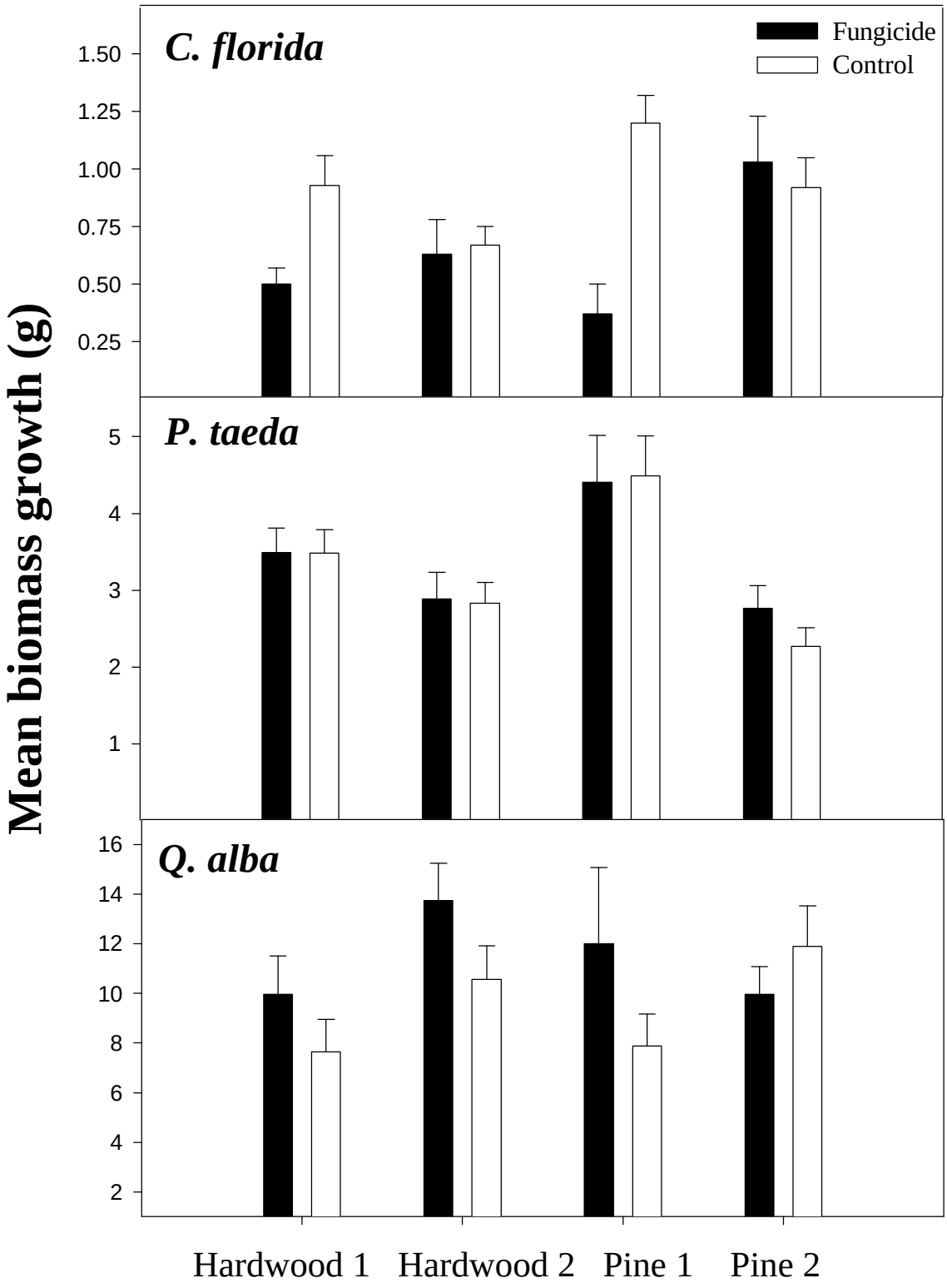

Figure 5. Mean biomass growth for each species by forest, site and treatment from initial planting to final harvest.

VI. DISCUSSION

It is clear that the fungicide treatment impacted fungal community structure; however the nature of the impact is incompletely known. Plate counts showed a reduction in fungal density within treated plots. Since captan is commonly used to protect plants against plant pathogens, this may indicate a reduction in biomass or diversity of pathogenic fungi. Mycorrhizal root tip counts, on the other hand, were unchanged by the treatment. This suggests that either ectomycorrhizal fungi were unaffected by the captan treatment or that the mycorrhizal community shifted in composition but not in abundance. Since root tip counts of the *Ceonococcum* morphotype were unchanged by the treatment, it is more likely that the mycorrhizae were simply unaffected. This is not surprising since captan is a relatively weak fungicide (Brown 1978). Furthermore, the plant hosts may afford protection from the effects of a fungicide on mycorrhizae.

Despite causing a shift in the fungal community, the fungicide treatment had no effect on seedling survival and had a significant effect on growth in just one of the three species tested. Thus, my first hypothesis concerning fungal community effects on seedling establishment was not supported by this study. However, if only the pathogen part of the community was effected, the question of mycorrhizal community effects on seedling establishment in this system remains unresolved by this study.

Much larger impacts of the soil biotic community have been demonstrated in other studies (Van Der Puten et al. 1993, Bever 1994, Wilson and Hartnett 1997). The degree of impact from the treatment may explain the differences between previous studies and this one. The other studies had much more aggressive treatment regimes such as soil sterilization (Van Der Puten et al. 1993, Bever 1994) or more toxic fungicides such as benomyl (Wilson and Hartnett 1997). These more powerful fungicides have effects on non-target organisms such as nematodes, earthworms, and nitrification bacteria (Brown 1978). Captan is a relatively mild fungicide with much milder effects on these non-target organisms. In this respect, I believe that my approach provides a more targeted test of fungal community influences. It is also possible that our results were less dramatic than in other studies because fungi may have a smaller role in mediating succession shifts in forest understories than in other types of systems.

Species were effected differentially by treatment lending support to the second hypothesis. Although the fungicide treatment had only small effects on seedlings during

the two years of this study, fungal community structure may have long-term impacts on tree species composition in the forests studied. *Q. alba* seedlings grown in fungicide treated plots had significantly greater growth (10.4g) than those grown in control plots (8.5g). Results for *C. florida*, though not statistically significant, suggested a reduction of growth in the treated plots. These apparently opposite responses to the treatment may indicate either different susceptibility to fungal community shifts or a reduction of endomycorrhizal infection on *C. florida*. Over time, this effect may not control the presence or absence of tree species in a community, but it could have important impacts on relative abundances of the two species and competitive interactions between them and other plant species.

It is clear that mycorrhizal fungi were not affected by the fungicide treatment. The specific fungi affected by the treatment (Figure 2) was not clearly identified by the tests conducted in this study. However, captan is used effectively against root pathogens in fruit tree nurseries. Though captan may also affect decomposers and thus nutrient availability I suspect that differences in growth between treated and untreated seedlings would most likely be due to affects on root pathogens.

Pathogenic fungi may be the key to different responses of the two hardwood species (*Q. alba and C. florida*). Density of pathogens tends to follow density of the host (Burdon 1987). *Quercus sp*. had far higher densities in the forests in and around the plots than *C. florida*. *Quercus alba* pathogens may therefore have had higher densities and a higher probability of influencing the growth of seedlings than *C. florida* pathogens. The probability that captan influenced pathogens, and that *Q. alba* root systems grew much larger in treated plots (i.e., root/shoot ratio increased) also suggest that pathogenic fungi may be the key to growth differences seen in this study.

The third hypothesis, that advance regeneration can be successfully established in closed canopy understories, was supported by this study. The commercial species (*Q. alba* and *P. taeda*) both had modest survival and at least some growth. This adds to the body of evidence suggesting the establishment of advance regeneration is an effective means of stand regeneration (Hodges and Jenzen 1987, Chambers and Henkel 1989, Marquis et al.1992, Sander and Graney 1993.). The effectiveness of this method will require following stand development over a longer time period and through overstory removal.

Though survival rates were lower than previously reported for *P. taeda* (Gresham 1984, Venator and Barnett 1984, South et al. 1985) and *Quercus* species (Tworkoski et al. 1986, Chambers and Henkel 1988, Jones and Sharitz 1990) each species had nearly 60 % survival after two years (Table 4). Little is known about *C. florida* survival in forest settings for comparison. Given the understory conditions and the dry spring following planting, higher survival rates may be possible.

Large differences among species in terms of survival and growth were expected (Tables 4 and 5). *C. florida* is very shade tolerant, but it is also shallow rooted and intolerant of drought (Burns and Honkala 1990). The low survival in this species is therefore not surprising given the sandy soils of the study site and the low rain fall in spring following planting. *P. taeda* is relatively drought tolerant and was probably not as affected by the first dry spring. However the low survival for *P. taeda* compared to plantation studies (South et al. 1985; Tuttle et al. 1987) in open conditions was not unexpected since it is intolerant of shade and it was actually higher than I would have predicted given the conditions. *Q. alba* is intermediate in drought and shade tolerance (Burns and Honkala 1990), thus its intermediate survival was not unexpected.

The fact that forest type had no significant influence on growth or survival was unexpected. Successional models (Connell and Slatyer 1977, Grime 1979) would predict large differences between forests since the three species have different successional status and tolerances for various stresses (e.g., light and drought). This difference was particularly unexpected for *P. taeda* which, as an early succession plant, would be expected to perform poorly in a later successional hardwood stand.

Initial seedling size was related to growth ($p < 0.01$) for *P. taeda* and *C. florida*, and to survival ($p < 0.01$) in *C. florida.* The relationship between 1-0 seedling size and survival of *P. taeda* is consistent with other studies (South et al. 1985, Tuttle et al. 1987). The analysis of *Q. alba* seedlings showed no significant results for either survival or growth. However, the analysis of growth may have been affected by herbivory or dieback and resprouting which yielded more negative growth values for *Q. alba* than the other two species. Though no data were recorded on this herbivory or dieback, we observed these phenomenon in an estimated fifty percent of the *Q. alba* seedlings over the course of the study.

It is clear that fungi have influences on plant communities. Results from this study show that effects may be subtle in forests. More targeted tests of fungi may reveal clearer information on the role of fungi in forest communities, succession and artificial regeneration.

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Plant Taxonomy (1 semester – 2 sections)
Plant Biology labs (2 semesters – 2 sections)

Research Technician : Joseph Jones Ecological Research Center (Georgia) 1995
Nutrient dynamic studies in Longleaf Pine

Preserve Steward : Texas Nature Conservancy 1994
Managed preserve and implemented visitor education at James River Bat Cave

Research Technician : Institute of Ecology, University of Georgia 1993
Riparian forest nutrient uptake study

Research Technician : Ferrum Life Science Department/USFS 1993
Bat summer habitat study

MEMBERSHIPS IN PROFESSIONAL ASSOCIATIONS

Ecological Society of America
Virginia Academy of Science
American Society of Microbiology

GRANTS FUNDED

West, L. 1996(May). The Effects of Soil Fungi on Seedling Establishment in a South Eastern Coastal Plain Forest. VA Tech Graduate Research Development Project for $250.

Abstracts

West, L. and R.H. Jones. 1997. Effects of soil fungi and overstory composition on seedling establishment in a Southeastern U.S. Coastal Plain forest. Bull. of Ecology Society of America 78 (4) : 329.

West, L. and R.H. Jones. 1997. Effects of fungi establishment for oak, loblolly and dogwood seedlings. VA Academy of Science 48(2) : 92.

PROFESSIONAL ACTIVITIES

Treasurer - Graduate Student Assembly 1997-8
GSA Representative - University Commission of Graduate Studies and Policy 1997
Chair - Graduate Student Assembly Research Development Project 1997
Graduate Student Assembly Delegate from Biology Dept. 1996
Co-Chair - Biology Graduate Student Association Speaker Committee 1996