

INTERFERENCE INTERACTIONS IN EXPERIMENTAL PINE-HARDWOOD STANDS

by

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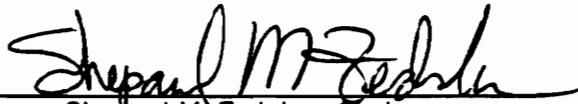
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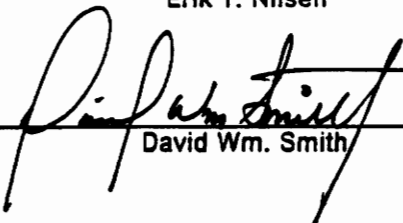
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(ABSTRACT)

Competition for resources and other interference from non-crop vegetation often limits the productivity of pine and pine-hardwood forest stands in the southern United States. However, forest researchers have yet to fully quantify the effect of this interference on forest tree yield and there is an incomplete understanding of the biological mechanisms of interference. To better quantify the effects of interference interactions and elucidate their mechanisms, a field replacement series experiment and two supporting greenhouse experiments were carried out using loblolly pine (*Pinus taeda* L.), red maple (*Acer rubrum* L.), black locust (*Robinia pseudoacacia* L.), and herbaceous vegetation. Interference between pine, hardwood species, and herbaceous vegetation significantly impacted the growth and yield of young experimental pine-hardwood stands. While herbaceous vegetation significantly affected all stands, it reduced the yield of hardwood species more than loblolly pine. Loblolly pine appeared to ameliorate the effect of herbaceous vegetation on hardwoods in some stands. Interference outcomes were site- and scale-dependent. In field stands, synergistic adjustment in total yield due to pine-hardwood interference was not observed, except for loblolly pine-black locust mixtures on lower site quality replicates. Hardwood species suppressed the growth of pine in seedling stands planted at very close spacing in greenhouse boxes, while the yield at age three of less densely-planted field stands was positively related to the proportion of pine in the stand. Close spacing increased the ability of wide-spreading hardwood crowns to overtop and restrict light availability to conically-shaped pine crowns. Interference outcomes were related to the interactive effect of light, soil moisture, and soil nitrogen resources on tree growth and competitive ability. If not overtopped by hardwoods, loblolly pine had high yields in mixtures with hardwoods and competed effectively for soil moisture and

nitrogen through efficient use of these resources. Changes in allometric relationships were observed for tree species in response to interference including root-shoot ratios, crown dimensions, and specific leaf areas. Tall fescue (*Festuca arundinacea* Schreb.), the principal herbaceous species in the field study, appeared to affect the physiology and yield of all species through allelopathy in a greenhouse experiment, suggesting that reduced yield in herbaceous plots may be due to direct chemical effects in addition to resource competition.

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Chapter I

INTRODUCTION AND LITERATURE REVIEW

A large share of the forest materials produced in the United States is contributed by southeastern forests. In 1984, these forests were the source of two-thirds of the pulpwood, one-half of the plywood, and two-fifths of the hardwood lumber in the United States. The total value of all delivered forest products in 1984 was \$6.1 billion and demand for these products is expected to increase in the future (Robertson 1988). Considering this increased demand for southeastern forest products, and the relatively fixed land base from which they must be secured, forests in the Southeast will have to be more efficiently managed to increase yields and improve utilization. The potential for increasing forest production is great, however, considering that less than half of southeastern forests are currently under the management of trained silviculturalists (Boyce et al. 1986).

Apart from the inherent limitations of site quality and genetic composition, forest productivity in the Southeast is most limited biologically by the presence of non-crop vegetation which competes for site resources, or otherwise interferes with the growth of crop tree species (Farnum et al. 1983, Boyce et al. 1986). There is extensive literature documenting the

deleterious effects of this interference on forest productivity, but its underlying mechanisms are still not completely understood.

Except in mountain regions and bottomland sites in the Piedmont and Coastal Plain, the principal crop tree species in the Southeast are southern yellow pines, particularly loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm.) pines. There also exists a rich hardwood tree component, but this has been underutilized due to economic and management constraints. In southern pine stands, these hardwoods have largely been regarded as weeds and great effort has been expended towards their removal from pine stands.

While short-term hardwood control has often been effective, hardwood encroachment is increasing on a long-term scale (Boyce and Knight 1980, Zahner 1982) which will require increased financial outlays for competition control in the future. The projected cost of controlling encroaching hardwoods, combined with the effects of other social and economic factors, has aroused an interest in the possibility of growing pines and hardwoods in mixed stands. Little is known, however, regarding the management of pine-hardwood mixtures due to the dearth of knowledge concerning the mechanisms of pine-hardwood interference.

To manage pine-hardwood mixtures efficiently, as well as to better control interference in pine monocultures, research is needed to quantify the effects of pine-hardwood competition and to better understand the mechanisms of interference interactions. It will also be important to understand the impact of herbaceous vegetation on interference mechanisms in mixed stands. Planned experimental plantings of pines and hardwoods with and without herbaceous vegetation will be necessary in order to predict the relative yields which can be obtained from mixed stands. Particular attention should be focused on young stands before the period of canopy closure, when early growth and interference interactions determine the future course of stand development (Boyer 1987).

Objectives

1. To estimate the relative yields and assess the compatibility of pure stands and mixtures of loblolly pine, red maple (*Acer rubrum* L.), and black locust (*Robinia pseudoacacia* L.) grown with and without herbaceous vegetation.
2. To examine the dynamics of canopy and root morphology and allocation patterns as they relate to the interference process.
3. To investigate the nature of competition mechanisms and other interference interactions which determine the early growth of pure and mixed stands.

Definitions

Competition has been defined by plant ecologists as the mutually adverse effects on plants which utilize a resource in short supply (Barbour et al. 1987). These resources generally include nutrients, light, and soil moisture; although Harper (1977) cites evidence of competition for carbon dioxide under some conditions as well. Competition, may be intraspecific (between individuals of the same species) or interspecific (between individuals of different species). Competition is one of the many interactions between individual plants or plant species which Harper (1964) defined as "interference". Interference interactions may be positive, such as increased fertility derived from nearby nitrogen fixing plants; or negative, such as competition or root parasitism. Some interactions may be positive and/or negative, such as allelochemic interactions (Rice 1984). Some researchers (e.g., Levine 1976, Keddy 1989) use the term "exploitative competition" where resources (such as light, nutrients, and water) are involved, and "interference competition" otherwise. The distinction between the terms

"competition" and "interference" is useful for separating references to negative effects due to resource consumption from general references to any effects due to presence of neighbors. In the literature, however, the terms "competition" and "interference" have often been used synonymously, as well as by their more rigid definitions (Radosevich and Osteryoung 1987). In order to avoid confusion, particularly with the older literature, the two terms will generally be considered as synonyms in this literature review.

The Early Development of Competition Theory

According to Miller (1967), competition theory has developed in the following sequence: 1. Inferences drawn from observation of natural populations. 2. Construction of mathematical models. 3. Experiments designed to test elements of competition interaction in controlled environments. Studies of competition in the forest environment have generally followed this sequence, although much of plant competition theory has been borrowed from equilibrium and niche theories of animal studies.

Since competition was proposed as the basis of natural selection by Darwin (1858), numerous studies, dealing largely with animals, have theorized the role of competition in speciation and community structure. Lotka's (1925) and Volterra's (1926) theories of competitive equilibrium and Gause's (1934) competitive exclusion principle set the stage for studies describing the role of competition in niche partitioning, character displacement, and community dynamics (Lack 1947, Brown and Wilson 1956, MacArthur 1958, Hutchinson 1961, Lubchenco 1978). However, the magnitude of importance ascribed to competition in the evolution and structure of natural communities is still the subject of lively debate (Grubb 1977, Schoener 1982, Lewin 1983).

While equilibrium and niche theory is similar for all types of interspecific competition, there are many features unique to the study of competition in plant communities. Due to these

unique characteristics, little attempt has been made to develop Lotka-Volterra type analogs for plant competition (Silander and Pacala 1990). Because plants cannot generally use mobility to escape competition, their root systems and crowns possess great morphological and physiological plasticity and elasticity in growth response (Grime et al. 1986). As opposed to individual animals, each individual plant may actually be viewed as a metapopulation of individual units (branches) each with a separate fate in the process of competition (Harper 1977). The sum of all competition outcomes among these metapopulations determines the plastic response for the whole plant. While plants may adjust plastically to competition, temporary or elastic physiological responses, such as stomatal closure, are also important avoidance and tolerance strategies in plants which may affect competitive ability.

Another result of being relatively immobile in the soil matrix is that the impact of competition for any individual plant is determined by the summary influence of its neighbors. Studies in natural herbaceous communities (Silvertown 1982, Goldberg and Werner 1983) indicate that competitive relationships in these plant communities are generally diffuse, with specific and unique interactions (at least in natural populations) being relatively rare. This diffuse competition results because herbaceous species generally require the same types and similar amounts of resources. Moreover, the probability of repeated encounters with the same species for any individual plant is low. However, with temperate tree species, repeated species-specific encounters are possible in many environments where local tree species richness and diversity is not high. Furthermore, tree species show a great deal of difference in their use of resources, as exhibited by differences in growth rates, shade tolerance, and potential to attain biomass (Kolb et al. 1990). Morris et al. (1991) have also demonstrated that different herbaceous species may have dramatically different interference effects on tree species.

Methods of Forest Competition Assessment

Studies of competition in forest communities are particularly unique in that the large size and long lifespan of trees means that competition relationships are often played out over long periods of time under a variety of dynamic biotic and abiotic conditions. Indeed, much of the early study of competition in forests was closely linked to the study of forest succession (Clements et al. 1929).

Competition is a phenomenon which cannot be measured directly and thus can only be detected by its effects. Hence, competition studies have been conducted primarily with the use of bioassays (Zedaker 1983). While the effects of competition are often readily apparent, difficulty in measuring the causal agents and interactions between them has prevented a better understanding of competition mechanisms (See later section on investigating mechanisms of competition).

In pure stands, morphological and physiological characteristics of trees within the population are relatively similar and, therefore, the intensity and outcomes of intraspecific competition are largely determined by the size of individuals and the density of the stand. Numerous indices of competition have been developed on the basis of these size-density measures to predict the effects of intraspecific competition (See Daniels et al. 1986 for a review of indices for loblolly pine).

Interspecific Competition Indices

For determining interspecific effects of competition in mixed stands, size-density measures are less accurate because morphological and physiological differences between species result in differential utilization of site resources (Zedaker 1983). In addition, the outcome of competition will also be affected by differences in the intrinsic rate of growth for the individual species (Vandermeer 1975). However, because these species differences have been difficult to separate and quantify, forest researchers have still relied on index measures, such as size, number, basal area, and mass of competing vegetation to predict interspecific

competition outcomes and effects. These indices have been used to evaluate the effectiveness of site preparation, assess the need for release, and provide information for growth and yield models (Burkhart and Sprinz 1984, Zutter et al. 1985, Weise and Glover 1987).

Biomass has been a common index of competing vegetation influence in many studies, but biomass measures are destructive and often time-consuming to obtain. Byrne and Wentworth (1988) found that measures of competing plant canopy volumes provided an accurate, non-destructive, and easily-obtained field estimate of competition intensity which was highly correlated with competing plant biomass ($r = .88$ for grasses, $r = .97$ for tree vegetation). Dierauf (1977) developed a simple index of competition intensity used for determining the need for release in pine stands. Using this index, pines were classified as "free-to-grow" or as overtopped based upon the size and distance of surrounding vegetation. Fifteen years after assessment, pine cordwood yield was positively related to the free-to-grow index ($r^2 = .672$) (Dierauf 1990).

Cain (1989) developed a competition assessment system for natural loblolly and shortleaf pine stands based on recurring observations of groundline diameter-height relationships of pine seedlings under competitive stress. It was concluded that pine seedlings showed a positive growth response to competition control if their groundline diameters when multiplied by 10 were not at least within 10 mm of their total height in feet.

Because it is an integrative measure of resource use, leaf area has been advocated for use as an index of competing vegetation intensity in coniferous plantations (Zedaker 1983, Brand 1986a, Zutter et al. 1986a, Aldrich 1987). However, it is difficult to measure or estimate leaf area in the field and its use is dependent on the development of good allometric relationships with other more easily obtained measures. Specific leaf area (leaf area per unit weight of foliage) is one such measure. However, specific leaf area variability within the forest canopy is often high and needs to be accounted for in sampling (Shelton and Switzer 1984). The close correlation between sapwood area and leaf area also makes stem cross-sectional area a possible surrogate measure (Grier and Waring 1974, Shelton and Switzer 1984, Johnson et al. 1985). In the Virginia Piedmont, Bacon and Zedaker (1986) have developed

equations for obtaining the leaf area index from stem cross-sectional area for sixteen common hardwood competitors. Still, allometric relationships, such as those used to obtain estimates of leaf area, have been shown to vary with competitive regime (Shainsky 1988) which further complicates the use of this and other competition indices.

Waring (1983) proposed the use of wood production per unit leaf area as a growth efficiency index (GEI) and indicated that it may be useful to gauge stress due to interspecific competition. Binkley (1984) found that GEI increased for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in plantation with red alder (*Alnus rubra* Bong.) and sitka alder (*Alnus sinuata* (Regel.) Rydb.) as compared to pure Douglas-fir stands due to an increase in soil fertility from alders which allowed a shift from root to stem growth. Britt et al. (1990) found GEI increased for trees growing without herbaceous vegetation when leaf area index was less than 0.2, but this trend was reversed for leaf area indices greater than 0.2.

Because they are derived from the results of controlled competition experiments, some indices of interspecific competition have been rarely used in forest competition studies. These indices have been employed extensively in field crop competition studies. The relative crowding coefficient and relative yield total developed by de Wit (1960) and Harper (1977) are commonly employed to assess competition for field crops, but not in forestry, perhaps because of the long time required to observe competition outcomes. Austin (1982) proposed a relative physiological performance value for predicting the performance of species in multi-species mixtures vs. monocultures. Predictions using this index performed generally well ($r = .74$), but values have been shown to be age-dependent (Grace 1988). Research involving indices of threshold response have been commonly employed in agriculture in the form of additive experiments (Harper 1977). Zimdahl (1980) found that the response of field crops to competition was sigmoidal in shape with well-defined thresholds indicating a range of competing plant densities where crop yield began to rapidly decrease or ceased to respond to competition. Working with pine species and competing vegetation, Wagner et al. (1989) advocated the use of minimum and maximum response thresholds for quantifying competitive intensity and its affect on forest crop yield. The maximum response threshold corresponds to

the level of competition where additional weed control measures will not improve performance of crop species, while minimum thresholds describe the level of vegetation that must be reached before any control measures will improve crop performance.

Experimental Designs for Competition Study

Many studies of competition have documented the response of planted or naturally-regenerated pines to competition control (detailed in the following section) without the use of any specific experimental competition design. These studies have largely involved measuring the growth response of pines after site preparation or release, often without measurement of the actual levels of competing vegetation.

Other studies have followed established experimental designs borrowed from weed studies in agriculture, which manipulate the density, spatial arrangement, and/or proportion of competitors. A great deal of information exists regarding the design and analysis of competition experiments (Harper 1961, McGilchrist 1965, Baeumer and de Wit 1968, McGilchrist and Trenbath 1971, Mead 1968, 1979, Radosevich and Osteryoung 1987, Cousens 1991). Radosevich (1987) recently reviewed the major types of experimental designs used to study interspecific plant competition, all of which have been used, to some extent, in forestry. They include neighborhood, additive, substitutive, and additive designs.

Neighborhood designs are used primarily to determine the effect of competition on individual plants due to the summary effect of neighboring plants. In these designs, the response of the target plant is measured and related to the size, number, cover, or distance to its neighbors. The development of neighborhood designs may be credited to Pielou (1962) and Mack and Harper (1977), but at least one earlier forest competition study employed something similar to the neighborhood concept (Roberts 1960). More recently, Carter et al. (1984), Nusser and Wentworth (1987), Everett (1987), and Fredericksen et al. (1991) used the neighborhood design to study competing vegetation in loblolly pine stands.

In **additive designs**, the density of the non-crop species is varied while the density of the crop species is held constant. These designs are useful in determining the threshold re-

sponse level of the crop species to the presence of weeds. The interpretation of competition interactions in additive designs, however, is difficult since the effects of species proportion and density are confounded. Additive designs have only been infrequently used in the study of forest competition in the form of comparisons of different levels of competition control on the growth of crop tree species. Examples of the use of additive competition designs in forestry include Nelson et al. (1981) and Bacon and Zedaker (1987).

Substitutive (replacement) designs, pioneered by De Wit (1960), eliminate the confounding of density and proportion effects by maintaining constant density. This density, however, is assumed to be high enough to be past the point of constant final yield, so that yield is unaffected by density. Proportions of two species are then varied in a series to test whether interspecific competition effects will substitute for, or replace, the effects of competition from pure monocultures. This testing is based upon the yield totals obtained from the various mixtures. Relative yield totals, based upon the growth of the species in mixed vs. pure stands, can be calculated to assess whether the relationship between the two species is antagonistic (competition), symbiotic, or neutral (Harper 1977). Yield ratios or indices of competitiveness (such as the relative crowding coefficient) can also be calculated from pure stands and 50-50 mixtures to assess the competitive ability of species and to determine patterns of resource utilization. Connolly (1987) proposed the use of relative resource totals, which utilize information from all proportions of the replacement series, as an index of whether species in mixtures are capturing the same resource amounts as in pure stands.

While useful as a predictive tool, substitutive designs have been criticized (Jolliffe et al. 1984, Firbank and Watkinson 1985, Connolly 1986, Law and Watkinson 1987) primarily because the relative yields of the replacement series are dependent on the initial density chosen for the study and because differences in initial size of the two species may bias results. These disadvantages may be lessened, however, if the density chosen is high enough or the duration of the experiment is long enough to reach the range of constant final yield (Radosevich 1987). Species should also be evenly matched in size at the outset of the experiment. Ideally, the density of replacement series experiments should allow each component yield to attain the

constant final yield of that attained by a monoculture at that density (Taylor and Aarssen 1989). An additional problem with the replacement series experiments is that comparing actual vs. expected yields that would occur if competitive interactions between the two species were equal does not assess the relative importance of interspecific vs. intraspecific competitive effects. If space and resources are available it is desirable to repeat replacement series over a range of densities (Roush et al. 1989).

In contrast with its use in agronomic studies, the replacement series design has scarcely been used in the study of forest competition. Shainsky and Radosevich (1986) have used the design to assess competition between Ponderosa pine (*Pinus ponderosa* Dougl. ex D. Don) and greenleaf manzanita (*Arctostaphylos patula* Greene) in the Pacific Northwest, but no other studies are known.

Systematic designs include Nelder plots and addition series experiments. Originally developed for the study of intraspecific competition (Nelder 1962), Nelder plots consist of a grid of plants arranged in radiating sectors, the end result resembling a wagon wheel. While density decreases moving outwards in a sector, planting arrangement remains constant. Interspecific competition can be studied by varying species proportions among sectors. Nelder plots allow for the study of competition over a wide range of densities while achieving economy of space. Disadvantages include difficulty with installing plots in the field, as well as difficulty in separating intraspecific from interspecific effects. In forestry applications, Nelder plots have been used by Zedaker (1981) and Cole and Newton (1986) to study interspecific competition between Douglas-fir, red alder, and grass.

Another type of systematic design, the addition series, represents a combination of additive and substitutive designs in that competition between two species is examined using an array of species densities and proportions. Using this design, intraspecific and interspecific competition effects can be readily separated. One disadvantage to the design is that it requires a relatively large study area. Shainsky and Radosevich (1991) used the addition series design to study competition intensity between Douglas-fir and red alder. Mitchell et al.

(1991) have employed the addition series to study competitive relationships between loblolly pine, sweetgum (*Liquidambar styraciflua* L.), and broomsedge (*Andropogon virginicus* L.).

The design of competition experiments typically neglects the spatio-temporal structure of plant communities (Austin 1990). Resources vary along a spatial continuum in the environment and will also change with time along with plant resource requirements (Ares 1972). It is thus necessary to consider that outcomes of competition experiments are thus dependent on the chosen scales (Hanski 1983, Grace 1990). Most competition experiments are also somewhat artificial in that they employ a limited number of species, often reduced to two-species trials. Experiments should move towards multi-species experiments, more closely approximating the multiple competitive relationships of natural communities (Keddy 1989).

Studies Documenting Competition Response in Pine Forests

Competition has long been recognized as a natural ongoing process in forest ecosystems. The large size and lifespan of forest communities promotes the perpetual existence of competition and other interference interactions. In pure stands, intraspecific competition has been studied extensively in an effort to determine optimum density-yield relationships for the stocking of crop tree species, from which have arisen the laws of self-thinning and reciprocal yield (Kira et al. 1953, Yoda et al. 1963, Westoby 1984).

Response of Older Crop Trees to Hardwood Competition Control

Interspecific competition has also received considerably more attention due to the decline in yield of crop tree species (almost exclusively pines) caused by non-crop vegetation. An extensive compilation of abstracts on the subject is provided by Stewart et al. (1984). Early studies dealt largely with the effect of hardwood tree competition on pine growth response. Studies by Bull (1945) and Freese (1950) showed that pine growth could be dramatically im-

proved by cutting or girdling large hardwoods. In mature pine stands it was demonstrated that pine growth could also be improved through the removal of understory hardwoods (Lange 1951, Bower and Ferguson 1968, Grano 1970, D'Anieri et al. 1986.) However, on a good site (Site index 90 at base age 50), Russell (1961) found no growth response in loblolly pine upon removal of the hardwood understory.

Trenching and shading studies (Fricke 1904, Toumey and Kienholz 1931, Korstian and Coile 1938, Shirley 1945, Kozlowski 1949) provided more detailed information about the objects of competition, revealing both the importance of determining the limiting factors and competition mechanisms, as well as the difficulty in separating aboveground from belowground competition effects.

Early Studies of Hardwood Competition Control in Young Pine Stands

As the practice of artificial pine regeneration increased and the importance of the early establishment period in determining the future course of the rotation was recognized, researchers began to focus attention on competition in young stands.

In a seven-year-old stand of loblolly pine in the North Carolina Piedmont, Korstian and Bilan (1957) demonstrated the existence of light and moisture competition between young pines and surrounding hardwood vegetation. Ferguson (1958) reported that the survival and growth of young pines in East Texas was improved by reduction of moisture competition caused by surrounding hardwood vegetation.

While many other studies report a significant response by pine seedlings to release (e.g., Shipman 1954, Miller and Tissue 1956, Yocum 1962, Grano 1965), only a few early studies provided detailed quantitative information concerning competing vegetation or offered specific recommendations for its control. Wenger (1955) studied the growth of loblolly pines in competition with sprout clumps of five hardwood species during the period preceding canopy closure. Relative growth rates of pine vs. sprout clumps were documented and projections for pine dominance were derived based on heights achieved by a certain age. Roberts (1960) also studied loblolly pine seedlings in competition with hardwood sprouts for seven growing

seasons. He found that the degree of competition was related to size of pine seedlings, the hardwood species competitor, and the distance and direction of hardwoods from the pines. Release recommendations were based on the relative size and distance of hardwood competitors to the pines.

Recent Studies of the Response of Young Pines to Hardwood Control

Numerous studies of hardwood competition in pine stands were conducted in the wake of the large-scale employment of mechanical site preparation and chemical release treatments, particularly in the southeastern U.S. Substantial improvement of pine growth after mechanical or chemical control of surrounding hardwood vegetation has been reported by Dierauf (1977), Clason (1978, 1984), Hunt and Cleveland (1978), Loyd et al. (1978), Cain and Mann (1980), De Wit and Terry (1983), Pienarr et al. (1983), Pehl and Bailey (1983), Haywood (1986), Slay et al. (1987), Zedaker et al. (1989), and Shiver et al. (1990, 1991). In one economic analysis, Balmer et al. (1978) reported that control of large hardwoods alone, doubled pine production and increased financial returns by 200% by age twenty. This increase was even more dramatic when combined with precommercial thinning.

Pine Response to Herbaceous Competition

Compared to studies dealing with hardwood competition, studies of pine response to herbaceous competition control have, with few exceptions (Pearson 1923, Pessin 1938, Larson and Schubert 1969), been conducted only recently (within the past ten years). Research conducted by the Auburn University Herbicide Research Cooperative (Knowe et al. 1985, Zutter et al. 1986b, Creighton et al. 1987) has shown that substantial pine growth increases can be obtained by herbaceous weed control in the first two years after planting. Furthermore, these growth gains appear to be maintained for at least twelve years on both poor and high quality sites (Glover et al. 1989).

Herbaceous weeds have repeatedly been implicated as competitors with pines for soil moisture (Nelson et al. 1981, Sands and Nambiar 1984, Carter et al. 1984, Zutter et al.

1986b, Creighton et al. 1987). Elliot and White (1987) found that herbaceous vegetation competed for both moisture and soil nitrogen with ponderosa pine seedlings. In addition to their role as competitors, many common herbaceous weeds have also been implicated as allelopathic agents (Walters and Gilmore 1976, Horsley 1977, Priester and Pennington 1978, Larson and Schwarz 1980, Hollis et al. 1982, Rice 1984, Smith 1989).

Studies of Pine Response to both Woody and Herbaceous Competition

In an attempt to synthesize the effect of the entire competing plant community on crop tree species, many recent studies have simultaneously investigated the effects of controlling both herbaceous and woody competition.

Glover (1982) attempted to quantify competition relationships between hardwood and herbaceous vegetation and loblolly pine seedling growth in the Georgia Piedmont through correlation study. Hardwood height and number of hardwood rootstocks were significant variables impacting pine growth. Pine diameter growth was affected more than height growth. Herbaceous competition effects were relatively minor, being overshadowed by the effect of hardwood competitors. The need for long-term studies of competition and the determination of the relative competitiveness of different hardwood species was stressed.

In five-year-old loblolly pine stands in the Piedmont and Coastal Plain, Carter et al. (1984) found that removing tree vegetation reduced pine water stress one-half as much as removing all vegetation, indicating an equivalence of herbaceous and hardwood competition effects.

Bacon and Zedaker (1987) conducted a release study in a three-year-old loblolly pine plantation in the Virginia Piedmont which combined elements of woody and herbaceous control. Hardwood competition was removed in 33% increments both with and without herbaceous control to produce a total of eight treatments. It was reported that long-term benefits were achievable by controlling both types of competitors; however, total eradication of woody competition produced no significant benefits over two-thirds control. Total control was thus unnecessary and also economically undesirable.

During the first six years of growth of a loblolly pine plantation in the North Carolina Piedmont, Nusser and Wentworth (1987) and Fredericksen et al. (1991) studied the effects of specific components of plant communities on the growth of pines. These components included hardwood trees, woody shrubs and vines, grasses, and herbaceous forbs. While herbaceous vegetation had an important effect in the first two years after planting, hardwood competitors accounted for most of the difference in pine growth by year six. Tiarks and Haywood (1986) reported similar results in a young loblolly pine plantation in the Louisiana Coastal Plain. Herbaceous vegetation control was deemed necessary for the first four years after pine establishment, while hardwood competition control became important after three-to-four years.

Since forest trees are affected by interactions with the entire plant community, the assessment of competition on a community-wide basis is essential for predicting the magnitude of crop tree response to competing vegetation. Miller et al. (1987) describe a cooperative effort to determine the response of both planted loblolly pine and competing vegetation throughout the Southeast to total control, woody vegetation control only, herbaceous control only, and no control. During the first two years, herbaceous vegetation exerted a greater influence on pine growth than woody vegetation. Total control of all competing vegetation increased pine height by 50% and pine diameter by 1.5x that of no vegetation control. After five years, pine volume in stands receiving total competition control averaged approximately 4x those receiving no competition control (Miller et al. 1991). On average, pine volume was increased more by herbaceous control (171%) than woody control (67%), but this response varied by site. Using the same experimental design with naturally-regenerated loblolly and shortleaf pine seedlings, Cain (1991) found similar results, except that the pine response to woody control was not different from the untreated check.

The above studies depict the increasing detail of investigations into the effects of competition. Competition study in pine stands has moved from examining only the effects of large hardwood competitors to the detailed analysis of the entire competing plant community.

Increasing emphasis is placed on determining the relative effects of individual species and to optimizing competition control in terms of cost and the maintenance of ecological integrity.

Investigating the Mechanisms of Competition

While there is a rather large body of response data defining the importance of competition in forest stands, considerably less attention has been paid in forest competition research, and in the study of competition in general, to understanding the actual process of competition (Weldon and Slauson 1986, Tilman 1987a, Radosevich 1987). Gaudet and Keddy (1988) point out that studies of interspecific competition have yielded a large number of special cases, but few general principles, largely due to the phenomenological approach to the subject. Connell (1990) adds that because few competition studies have demonstrated underlying mechanisms, these cases of competition may be more apparent than real. For example, pathogens or herbivores could be the major influence in some plant competitive relationships by decreasing the competitive ability of one or more of the species involved. The implication for forest competition study is that eventual outcomes of competition are determined by the physiological and morphological responses of trees to processes occurring within their operational environments. The ability of silviculturalists to direct these outcomes can only come from an understanding of the mechanisms of competitive interactions. Much of the theory concerning the mechanisms of competition has revolved around two themes: the importance of growing space in the competition process and the search for limiting resource factors which determine the basis of competition.

Competition for Space vs. Resources

Whether competition for space can be considered as an object of competition along with other environmental resource factors has been debated in the literature. Werner (1979)

argued that since plants are sessile and basically require the same set of resources, they are essentially in competition for space. Much of competition is determined by preempting this space, before competition for other resource factors begins.

However, plant population dynamics are not generally thought to involve territoriality, as in animal populations (although increasing knowledge of allelochemic influences may disprove this). Mack and Harper (1977) point out that the summary effect of one's neighbors, not density per se, is what determines the course of competition. The use of terminology in the literature such as occupation of biological space (Ross and Harper 1972) and zones of exploitation (Fisher and Miles 1973) appears, at first, to imply competition for space in the literature. However, this terminology has been adopted largely for convenience sake with "space" actually referring to the resources that space contains and not space itself (Donald 1963, Hall 1974, Zedaker 1983). One instance where space may be the actual object of competition among plants is evidenced by mechanical abrasion and "crown shyness" which exists in some forest communities (Putz et al. 1984, Shainsky 1988). More recently, McConnaughay and Bazzaz (1991) provided evidence that plants may compete for physical space belowground in addition to other resources if plant densities are high enough to affect the normal development of roots.

The reason why density and space are of lesser importance in plant vs. animal competition is due to the plastic growth response of plants. As a substitute for mobility, most plants possess the ability to undergo great modifications in canopy and root morphology in response to competitive stress. This plasticity is of vital importance in resource acquisition. Indeed, aside from the ability to maximize dry matter production, the best plant competitors are those which can undergo rapid morphological adjustments in their allocation of resources (Grime et al. 1986, Tilman 1988). During competition, a plant will die only after its capacity to withstand competition by plastic response is exceeded (Hutchings and Budd 1981).

The Search for Limiting Factors

Since the creation of Liebig's (1840) law of the minimum, it has been widely accepted in both agriculture and ecology that plant growth is restricted by the one resource factor that is least available in amount. Again, the resources under consideration are generally light, moisture, and nutrients; although carbon dioxide and soil oxygen can be limited in supply. In forest competition study, much effort has been expended in attempts to determine which factor is most limiting, and, supposedly, the object of competition.

The large number of studies citing soil moisture as the most limiting factor, particularly in the Southeast (Korstian and Coile 1938, Ferguson 1958, Pienarr et al. 1983, Zutter et al. 1986b, Byrne et al. 1987) indicate the relative importance of this factor in competition. However, light will generally always become limiting at canopy closure, and nutrient limitations are known to be common, for phosphorus in the Coastal Plain and for nitrogen in the Piedmont of the Southeast (Allen et al. 1990).

The Integration of Environmental Factors in Competition

While a knowledge of the factors limiting growth may be desirable for determining the main object of competition and for ameliorating site deficiencies, a better understanding of competition also requires the detection of synergistic interactions between environmental factors (Chapin et al. 1987). According to Aspinall (1960), an interaction occurs when "a decrease in the level of one factor in the immediate environment of a less successful competitor, results in the more rapid reduction in the level of another factor available to it". Examples of such interactive effects abound in the literature. Pharis and Kramer (1964) found that the drought resistance of loblolly pines was dependent on soil nitrogen concentrations. A common response to allelopathic agents is reduced nitrogen uptake (Hollis et al. 1982, Rice 1984). Harper (1977) cited several examples of interactions. For instance, nitrogen uptake, particularly nitrate, is dependent to a large extent on water movement to the roots. Also, lower light levels which decrease root-shoot ratios may decrease water and nutrient uptake.

Because interactive effects are so common, some researchers have questioned the wisdom of trying to separate out the effects of individual factors from the environmental complex. De Wit (1960) asserted that this subdivision of the resource complex is "not necessary, always inaccurate, and therefore unadvisable". Glover (1982) agreed, stating that the individual factors of competition were not independent and treating them as such would be artificial. Hall (1974), however, questioned whether it was possible to determine if competition effects were interactions or merely additive.

Whether the effects are additive or interactive, it is clear that causation is difficult to determine in any study of competition. While it is possible to test specific hypotheses concerning the various individual environmental factors, it is not usually possible to separate their effects on the competition process from the integrated effect of all other factors without disturbing the system. Because of this difficulty, researchers have relied heavily on correlative studies (Harper 1977), and attempts to explain the process of competition or predict its outcomes will continue to be based more on deduction than hypothesis testing. Still, much knowledge can be gained from detecting and quantifying the mechanisms of competitive interactions by collecting data on as many of the parameters within the environmental complex as possible that are likely to play a role in the competition process (Aldrich 1987, Chapin et al. 1987).

The inclusion of many environmental parameters in competition experiments becomes more important as the complexity of the plant community under study increases. In field studies with natural communities, competition interactions typically occur simultaneously between the entire matrix of species in the community (Tilman 1987a, Fowler 1990). As a simple example, in an Oregon study, Cole and Newton (1986) found that Douglas-fir and grasses were competing for soil moisture, while Douglas-fir and red alder were competing for both nutrients and light. As more species are added to the experiment, a condition similar to the diffuse competition of many natural communities develops and more information is needed to overcome the large variance which obscures competition mechanisms. One potentially useful approach is the ecological field theory (EFT) approach summarized by Walker

et al. (1989). EFT is an expansion of the neighborhood approach to competition study where primary environmental resource factors (water, light, and nutrients) are combined into a multi-resource index to model community dynamics. Instead of relating competition intensity to size and distance of neighbors, like ordinary neighborhood studies, EFT makes spatial interactions a function of plant size and resource demand.

Finally, it is important to note that not only are environmental factors integrated in competition, but plant communities themselves integrate. In general, there has been a long-standing assumption about forest competition that trees function as discrete physiological units (Graham and Bormann 1966). However, phenomena such as intraspecific and interspecific root grafting (Graham and Bormann 1966, Kozlowski and Cooley 1961, Stone and Stone 1975), and allelochemic effects in forest communities (Priester and Pennington 1978, Hollis et al. 1982), brings into question the view that each individual plant, or plant species, functions as an individual entity.

Resource Partitioning and Competition Mechanisms in Mixed Stands

Mechanisms of Resource Use

The use of growth-limiting resources (light, moisture, nutrients) is a fundamental aspect of plant competition. Plants species may vary in the manner and efficiency at which they use resources. Researchers studying nutrient use (Chapin 1980, Vitousek 1982, Nambiar 1985) proposed that there are different ways to view the efficiency of resource use by plant species. One measure, "uptake efficiency" is the ability of a plant to rapidly exploit available resources, which for nutrients is related to the physiological and morphological properties of root systems. This efficiency in uptake also appears to be related to plant growth rates (Miller 1984). Another measure of nutrient-use efficiency is the productivity of a plant per unit of nutrient absorbed, or the "internal-use efficiency". Internal resource use could be increased by re-

quiring fewer resources to produce an equivalent amount of tissue, or by more efficient recycling of nutrients already absorbed. Canham and Marks (1985) combined uptake efficiency with internal-use efficiency into a single index termed "growth efficiency". Growth efficiency = resource uptake efficiency x internal-use efficiency and thus represents the amount of biomass produced per unit of available resource. They also proposed that growth efficiency may be used to make predictions about species competitive abilities. Growth efficiencies of species, however, are likely to vary in different environments. For example, a tree species may display foliage in a manner which maximizes resource uptake efficiency at high light levels and results in high growth efficiency. However, growth efficiency may be low at low light levels due to low internal-use efficiency.

Using algal species, Tilman (1982) was one of the first ecological researchers to model population size and competition from the standpoint of resource dynamics. On the basis of this mechanistic model, Tilman (1987b, 1988) generalized that the competitive superiority of a species is determined by its ability to reduce resources below levels needed to support competitors. This explanation of competitive ability soon generated a debate about what constitutes a good competitor, which is still unresolved today (Aerts et al. 1991, Grace 1991). Grime (1979) and Grime and Hodgson (1987) propose that many plant characteristics confer high competitive ability including the potential to exploit large volumes of space both above- and belowground, rapid conversion of resources to the production of new leaves and roots, high morphological plasticity, and high turnover rates for leaves and roots.

Goldberg (1990) proposed an effect-reponse model for resource use and competition. Plants may respond to limiting resources by altering the efficiency by which they take up or internally use resources. Plants also affect resources by uptake, reducing resource availability to other plants. However, plants may also increase or decrease the resource availability or uptake rates of other plants through other mechanisms not related to uptake. These "non-uptake" mechanisms include increased addition of nutrients through litter, exudates, or nitrogen fixation; or by modification of the physical or biological environment. Hunter and

Aarssen (1988) cited many ways in which plants have a positive net effect on other plants through compensatory mechanisms that outweigh competitive depletion of resources.

Competition for Soil Moisture

Soil moisture is thought to be the single most important factor affecting the natural distribution and growth of trees (Shoulders and Tiarks 1980) and its importance in forest competition is evident from the large number of studies (previously cited) in which it was found to be the factor most limiting to growth.

Previous work regarding the physiological basis of moisture competition between pines and hardwoods appears to provide evidence for superior competitive ability of many hardwood tree species with loblolly pine. While loblolly pine reaches its threshold leaf water potential for stomatal closure at -0.9 to -1.8 Mpa, many hardwoods can go to -2.3 to -3.0 Mpa before stomatal closure (Teskey and Hinckley 1981). Similar results were reported by Kozlowski (1949) with loblolly pine and oak. Pines had lower water absorption capacity than oak at lower soil moisture levels due to a lower rooting intensity. For drought-adapted hardwood species, Bunce et al. (1977) found that exploitative depletion of soil moisture gave them a competitive advantage over other hardwoods. In addition to reduced tolerance of water stress, loblolly pine also has an increased capacity for water loss. While hardwoods have a higher rate of transpiration per unit leaf area (Teskey and Shrestha 1984), actual water loss on a stand basis is expected to be greater for pines due to a greater total leaf area and leaf area duration (Dougherty and Hennessey 1986). However, Zahner (1955) measured soil water depletion in 17-to-35-year-old pure pine and pure hardwood forests throughout a growing season and found little difference in evapotranspiration rates. While seemingly more prone to drought than hardwoods, loblolly pine typically outperforms hardwood trees on dry upland sites (Kellison 1985, Gjerstad and Barber 1987), perhaps because of greater internal water-use efficiency or because of reduced heat absorption due to self-shading of pine needles arranged in fascicles (Baker and Langdon 1990) which reduces water loss.

Generally, a tree's survival in a given environment will be dependent not only on whether its net production is higher than its competitors, but also on whether it can keep its rate of water loss during photosynthesis below that of its total supply (Wuenschel and Kozlowski 1971). Because of this relation to photosynthetic rate, a useful comparison of the competitive ability for moisture between pine and hardwood species could be based on water-use efficiency (WUE) (Kramer 1983), where:

$$\text{WUE} = \text{grams of CO}_2 \text{ fixed/unit of water loss}$$

In agronomic studies WUE is often expressed as:

$$\text{WUE} = \text{water used in evapotranspiration/crop yield}$$

While WUE may be important in droughty areas where plant density is low, DeLucia and Schlesinger (1991) found that high WUE for trees in some dry, but more densely vegetated, areas of the Western U.S. did not increase competitive success, perhaps because high WUE may have also imposed limitations on net photosynthesis that would have been advantageous in competition. There is also evidence for a trade-off between WUE and nutrient-use efficiency for competitive success.

As previously mentioned, herbaceous weeds have been implicated as important competitors for water in pine stands. Likewise, control of herbaceous vegetation in hardwood stands is essential for successful plantation establishment (Miller 1987). However, the negative effects of herbaceous competition may be compensated in some situations by their reduction of surface evaporation, which has shown to be an important mechanism of water loss in some plantations (Flint and Childs 1987).

Competition for Nutrients

While local deficiencies can occur for almost any nutrient, the most commonly limiting nutrients in southeastern forests are phosphorus and nitrogen. For loblolly pine, limitations of phosphorus are generally restricted to the Coastal Plain province, while nitrogen limitations occur both in the Piedmont and Coastal Plain (Burger and Kluender 1982, Allen et al. 1990).

Because hardwoods also require a greater amount of nutrient cations, such as calcium and magnesium, their growth may also be restricted by nitrogen and phosphorus.

Nitrogen is a crucial element in plant competition because growth rates for plants are typically proportional to plant nitrogen concentration (Axellson 1985, Hirose 1988) and leaf nitrogen is a major determinant of photosynthetic capacity (Field et al. 1983). Because diffusion and mass flow are the principal mechanisms of nutrient uptake, competition for nutrients is often closely tied with competition for moisture. Since phosphorus is relatively immobile in the soil matrix, its uptake is primarily influenced by root length and diffusion. Transfer of nitrogen is dependent on its inorganic form. Nitrate (NO_3^-) is supplied largely by mass flow, while the ammonium form (NH_4^+) is primarily supplied by diffusion (Carlyle 1986). However, diffusion is often the rate limiting step in the uptake of either form since transfer by mass flow cannot always meet the plants demands for nitrogen (Chapin 1980).

For nitrogen, organic forms are often present in sufficient quantities in the soil, but uptake is restricted by a low rate of conversion to usable forms. For example, in the Piedmont, large amounts of organic nitrogen (2000-4000 kg/ha) are present in the soil. However, only a small fraction of this nitrogen is mineralized as ammonium each year, much of which is taken up by microbial organisms (Vitousek and Matson 1985). Nitrate is not as prevalent in the soil as ammonium, except after disturbance, when there is an increase in bacterial nitrification rates.

According to Harper (1977), competition for any nutrient occurs when depletion contours (gradients) in the soil for that nutrient overlap between plants. The steepness of these depletion contours is often tied closely to the mobility of the nutrient. For example, nitrate contours are often less steep than ammonium because of its greater mobility. Competition due to overlap of depletion contours may be compensated by a greater rate of uptake by another area of the root system (Russel 1977). According to Tilman (1990), superior competitors for nitrogen have low maximum growth rates, long-lived roots and leaves, ability to maintain growth with a low tissue nutrient concentration, and a high resistance to herbivores. Many of these traits coincide with the definition of Grime (1979) for a stress-tolerant plant, but it is

important to recognize that plants may succeed in competition through rapid growth rates and preemptive exploitation of nutrients (Harper 1977, Grime 1979).

Measures of nutrient-use efficiency can be used to determine competitive abilities of plants and to predict competition outcomes. These measures have been based on respiration, photosynthesis, or net assimilation per gram of nutrient. Nutrient-use efficiency has often been calculated as dry matter production per gram of nutrient (simply the inverse of tissue concentration). However, this measure can be affected by other plant processes, such as luxury consumption and storage, which are not related to necessity uses (Chapin 1980). Rather than using yield/nutrient amount as a measure of nutrient-use efficiency, Siddiqi and Glass (1981) recommended using yield/tissue concentration of nutrient because it would be more closely related to nutrient utilization.

Nambiar (1985) suggested that nutrient-use efficiency has two components - uptake efficiency, which is related to geometrical or physiological properties of root systems and is related to growth rates (Miller 1984); and yield or productivity per unit nutrient absorbed. These two separate elements are difficult to partition, but with regards to the latter component, it has been suggested that conifers can produce as much as 50% more dry matter per unit nitrogen than deciduous trees, which makes them more adaptive to nitrogen-limited sites (Vitousek 1982). In their study of nitrogen availability and use efficiency in loblolly pine, Birk and Vitousek (1986) found that higher nitrogen-use efficiency on low-nitrogen sites was best explained by higher production per unit of nitrogen rather than by more efficient translocation or increased uptake efficiency.

Competition for Light

Competition for light is unique in that, unlike competition for moisture or nutrients, there is no reservoir of light available from which all competitors draw. Light energy must be intercepted or lost as it becomes available (Donald 1963). The ability of plants to compete for light is thus related to their physical position (stature), as well as their photosynthetic efficiency and capacity.

The importance of light competition is manifested in its direct relation to two of the three basic components of carbon gain in forests; leaf area and rate of net photosynthesis (Teskey et al. 1987). It is also indirectly related to the other component, rate of respiration, through its influence on temperature. As mentioned previously, leaf area is a good indicator of the intensity of light competition (as well as other factors) because it determines the amount of light interception and the capability for further foliage production. However, it is also important to consider the integrative effect of leaf area with photosynthetic efficiency in assessing light competition in forest stands.

Early studies with Piedmont hardwoods and loblolly pine have shown that pines are not as efficient photosynthetically under reduced light intensities as hardwoods (Kramer and Decker 1944, Kramer and Clark 1947, Kozlowski 1949). In loblolly pine, the whole-tree photosynthetic rate increases with light intensity up to full sun, while some hardwood species reach their maximum at 1/3 or less of full sunlight. Individual needles of pine and hardwoods both saturated at 1/3 full sun. Loblolly pine can compensate somewhat for this reduced efficiency because it carries higher total leaf areas and has a greater leaf area duration (Dougherty and Hennessey 1986).

Plasticity in crown morphology is an important determinant in light competition since small changes in morphology can result in large changes in photosynthesis and dry matter production (Ryel et al. 1990). Ford (1985) related competitive ability for light of temperate tree species to the possession of well-spaced and leafy branches, along with rapid foliage expansion in the spring. Cannell et al. (1984) also found that branch foliage density was important, as well as the ability to plastically adjust to competitors.

As with nutrient and moisture competition, the ultimate use of the light resource is for tree growth. Thus, the best measure of a species' competitive ability for light should be the efficiency of light use. In addition, measures of light use and photosynthesis should be taken throughout the growing season to account for changes in the intensity and duration of the supply of light energy (Ledig and Perry 1969). According to Ballare et al. (1987), light quality may be a trigger mechanism for the early detection of competition by plants. Plants

may perceive vegetation shade through the phytochrome system which records the balance between red and far red radiation. Low red to far red ratios increased shoot extension rates and apical dominance and decreased the leaf to stem weight ratio. There is also some evidence that plants can detect the difference between live and dead neighboring vegetation in this manner.

Avoidance and Tolerance Mechanisms

While much attention is placed on determining what occurs during the competition process, the growth and development patterns in species mixtures can often be explained by plant strategies which avoid or limit the effect of competitive interactions. Since plants must often invest a large portion of their net production in attaining and maintaining a competitive advantage over their neighbors (Mooney 1972), it is not surprising that many mechanisms of competition avoidance and tolerance have evolved in plants.

Avoidance mechanisms may be manifested in plastic responses, such as adjustments in canopy and root morphology; or inherent physiological or morphological species traits, such as seasonality of growth, canopy or root stratification, differential growth requirements, or differential resource uptake ability (Radosevich and Holt 1984). The dormancy of many southern pines during late summer droughts is one of many examples of such avoidance mechanisms in the forest environment.

Competition tolerance mechanisms also appear to be common in the forest environment. Examples include shade tolerance of many seedlings and mature understory trees, increased stomatal resistance in many xerophytic species (Wuenschel and Kozlowski 1971, Chabot and Bunce 1979), and the luxury consumption and storage of nutrients during periods of high availability by plants in nutrient-poor environments (Chapin 1980). While avoidance and tolerance mechanisms (ecological combining ability) are important in determining the outcomes of competition, it is possible that competitive exclusion can also be avoided if competitive abilities of species balance so that neither species can effectively displace the other (competitive combining ability) (Aarssen 1983).

Root Dynamics and Competition

Most of what is known about competition mechanisms comes from observations on the aboveground portion of plant communities. Aaltonen (1926) suggested that the spatial arrangement of stems was mostly decided by belowground competition. However, until recently, few studies have focused on belowground competition. Nedrow (1937) addressed root competition for grass species and Bilan (1960) studied rooting patterns of loblolly pine in relation to environmental factors. Although it is receiving increased emphasis, root system interactions and competition are not well understood and are known mostly by their manifestations than their mechanisms (Caldwell 1987). Even basic questions, such as those regarding root overlap, have yet to be answered (Caldwell 1987). Still root interactions are clearly an important element in competitive interactions and the cost of maintaining root activity is fairly high, accounting for 50-80% of annual production (Chapin et al. 1987). Root competition also tends to be more intense than shoot competition and effects the balance between components more than shoot competition (Wilson 1988).

Because of the difficulty associated with studying root systems, particularly tree root systems, researchers have generally assumed the existence of a functional equilibrium between root and shoot systems, where growth in one system essentially mirrors the other. However, while this functional equilibrium may exist under certain conditions, non-equilibrium conditions are quite common (Brouwer 1983), and the existence of an equilibrium may be an incorrect assumption in studies of competition. For example, it is thought that belowground competition usually takes place long before the aboveground portion of many plants is developed enough for the occurrence of competition for light (Radosevich and Holt 1984). In addition, the occurrence of root parasitism, root grafting, differential patterns of root distribution (Berendse 1979, 1981, 1982), and mycorrhizal associations or root microbial populations (Caldwell 1987, Christie et al. 1978) are potentially important factors in competition, but they would be unaccounted for if only aboveground observations were included for study.

Since rooting density for any plant is very low (only 2% of soil volume at its highest density), spatial limitations are relatively unimportant in root competition (Caldwell 1988). In-

stead roots interfere with each other through zones of influence (Harper 1977, Caldwell 1988). Root distribution tends to be clumped, according to soil resources, and competition is often preemptive. Competition is thus decided by the ability of a plant's root system to quickly exploit small fertile patches of soil resources (Caldwell 1988). Perhaps because of the patchy distribution of soil resources, root growth appears to be asynchronous, with pulses of growth occurring in different parts of the root system at different times (Caldwell 1979, Eis 1986). Besides this plasticity in activity within the root system, increased competition may also cause shifts in biomass allocation belowground. For example, Atkinson et al. (1976) found that orchard trees grew vertically rather than horizontally in response to increased root density. It is possible that superior competitors are those that are able to make rapid adjustments in root morphology and physiology (Caldwell 1987, Feldman 1988). Yet, Newton and Cole (1991) found no shift in belowground biomass allocation in young Douglas-fir seedlings under varying levels of competitive stress.

Another reason for increasing the study of belowground competition is the recent important findings in the study of fine root dynamics. Important in nutrient and water uptake, fine roots (typically classified as <5 mm in diameter) are often sinks for significant quantities of photosynthate in trees because of their rapid turnover (Fogel 1983). While representing only 1% of a tree's biomass, the production of fine roots can account for as much as 2/3 of the annual production of forest trees (Marshall 1986). Fine roots are also sinks for nutrients. Root nitrogen concentration is generally negatively correlated with root diameter (Nambiar 1987, Yin and Perry 1991). In addition, little nitrogen appears to retranslocate from senescing fine roots (Nambiar 1987). Fine roots are also thought to be critical in early site capture of resources in young stands. Nambiar (1983) found that in young radiata pine (*Pinus radiata* D. Don.) stands that roots less than 1 mm in diameter accounted for 87% of total root length in the stand after four years.

While some studies have reported an increase in fine root production on poor sites under conditions of limiting resources (Keyes and Grier 1981, Vogt et al. 1983), Nadelhoffer et al. (1985) found greater root production on better sites. However, the biomass was lower at

any point in time due to more rapid turnover. Because fine roots account for such a large share of photosynthetic allocation, and because this allocation is shifted with changes in resource availability, fine root dynamics should have an important relationship with competitive interactions. As yet, little is known about the role of fine root production and turnover in forest competition.

Root-Shoot Biomass Allocation

Another advantage of measuring both aboveground and belowground variables in competition studies is the ability to determine patterns of biomass allocation and their relation to the process and outcomes of competition. Root-shoot ratios and source-sink relationships have been studied for many tree species, including loblolly pine (Kaufmann 1968, Ledig et al. 1970); however, their relation to competition mechanisms remains unclear. Density has been shown to affect root-shoot allocation. For red alder, Bormann and Gordon (1984) found that high densities seemed to favor top growth at the expense of root growth. According to models of source-sink relationships (Cannell 1984, McMurtie and Wolf 1984), biomass allocation is determined by the source where resources are obtained (roots, leaves) and a sink, usually where the greatest meristematic activity is occurring. The location of the source is determined by the nutrient-carbohydrate balance within the tree (Mooney 1972, Drew and Ledig 1980). Hirose (1988) hypothesized that there exists an optimum root-shoot ratio, at which growth rates are maximized.

Ecological factors that affect plant growth and nutrition (such as competition) may have a large impact on root vs. shoot allocation (Ingestad and Agren 1991). According to Tilman (1988), source-sink relationships are related to an unavoidable trade-off plants face in allocation of soil and light resources during competition. To obtain a higher proportion of one resource, a plant must allocate more of its growth to the structure involved in capturing that resource, and thus less to the structure for obtaining the other resource. Each allocation pattern (trade-off between roots and shoots) will determine the amount of resources which a plant can obtain, and thus its competitive ability along a gradient of soil vs. light resource

availability. However, Thompson (1987) points out that, in some instances, good aboveground competitors may also be good belowground competitors. With experiments using shrub and grass species, Aerts et al. (1991) provide evidence that trade-offs between aboveground and belowground competitive ability can be overcome by plasticity in spatial arrangement of leaves and roots, as well as through adjustments in specific leaf area or specific root length.

While they may provide some insight into competition mechanisms, it is important to note that point estimates of root-shoot ratios for forest trees can be somewhat misleading. For instance, it has been observed that storage patterns for carbohydrates and nutrients may alternate between roots and shoots according to their episodic activity (Drew and Ledig 1980). Changes in root-shoot ratios often attributed to environmental factors may actually be due to changes in plant size which normally occur during plant ontogeny (Ledig and Perry 1966, Ledig et al. 1970). Also, rapid rate of turnover for the large nutrient pool associated with fine roots, may imply that these ratios seriously underestimate the amount of biomass allocated belowground (Caldwell 1979). Moreover, these estimates do not account for the fact that roots and shoots also serve as support and storage organs, in addition to resource acquisition apparatus (Tilman 1988).

Summary and Implications for Future Research

It has been well-established in the literature that competing vegetation can significantly detract from the yield of southern pines. While earlier studies focused on competition from hardwood trees, recent studies have collected data from the entire competing plant community. Soil moisture is cited most often as the object of resource competition, particularly with herbaceous weeds in young stands. Competition from woody plants for light and soil moisture tends to increase with age in young stands, and effects may persist throughout the rotation. Regional limitations of phosphorus and nitrogen in the South also lead to com-

petition for nutrients. Besides resource competition, other interference interactions, such as allelopathy and additions from nitrogen-fixing plants, have also been observed in southern pine forests.

While there is a large body of competition response data, the effect of competition in southern pine forests has yet to be fully quantified, and accurate estimates of tree crop yield lost to competing vegetation are still unavailable. Only recently has the detailed measurement of competing vegetation been a standard procedure in competition studies. Studies are currently underway to more precisely quantify competitive effects.

While the pattern of competition in the South is becoming clearer, much more investigation is needed regarding the physiological process of competition, especially with respect to belowground interactions. The current lack of understanding of competition mechanisms is largely due to the immense difficulty involved with studying the competition process without adversely disturbing the system. Researchers have traditionally tried to reduce this difficulty by adopting a single-factor ecology approach to competition study, such as limiting study only to competition for soil moisture. While some good information has been gained by this approach, it only provides a narrow perspective of the competition process, since it ignores the many multi-factor interactions which are thought to be operative in any competitive relationship. More effort is necessary to develop innovative sampling methods and to integrate measurements of all important competition parameters if the complex interactions of competition relationships are to be fully understood.

Another area of competition research which has received relatively little attention is the quantification of the competitive effects of individual species. Studies from physiological and community ecology have detected great variety in the life histories of plant species and it is likely that there are distinct differences in the competitive abilities of the weed species in southern forests. Information on species competitive abilities will allow for greater focus in weed control, expending a larger proportion of control efforts on critical competitors, while reducing the impact on beneficial species and insignificant competitors. This type of knowledge will also be essential for the successful management of even-aged mixed pine-

hardwood stands, which are currently of special interest to many silviculturalists and forest managers.

Optimizing Competition in Pine-Hardwood Mixtures on the Piedmont

Knowledge of the mechanisms of competition can be applied to the management of existing stands through silvicultural practices which optimize competitive relationships between forest tree species. Nowhere, perhaps, is there more potential for increasing yield through this optimization of competition than in the mixed pine-hardwood forests of the southeastern Piedmont.

The Piedmont Physiographic Province

The southeastern Piedmont is an extensive physiographic region encompassing 17.8 million hectares of land from Northern Virginia to West Central Georgia. Although 62% of the region is forested, the potential for wood production in the Piedmont is limited by an abundance of low quality stems and undesirable species. Poor stand conditions are largely the result of natural succession from farmland following abusive agricultural practices, periodic removal of high quality stems while leaving undesirable species, and wildfire (Oosting 1942, Boyce and Knight, 1980). According to recent forest surveys (Brown 1985, 1986), 13.3% of Piedmont timberland is less than 60% stocked, and an additional 46% is 60-90% stocked.

The Economic and Ecological Cost of Pine Monocultures

Because of price incentives and the availability of investment capital, forest industry has concentrated management effort on monocultural plantations of the more economically important southern pines. These plantations, however, comprise only 6.7% of commercial forest land in the Piedmont (Phillips 1983). Hardwood and mixed pine-hardwood stands are

more prevalent since the climax vegetation type in the area is oak-hickory (Braun 1950), or possibly beech-red maple on some sites (Bornkamm 1975). Hardwood encroachment into pine monocultures has been a perpetual concern to forest industry (Walstad 1976) and is likely to continue since the biological and social forces favoring hardwoods are greater than the cultural factors favoring pure pine stands (Boyce and Knight 1980, Cain and Yaussy 1984).

To maintain pine monocultures, intensive mechanical site preparation and/or chemical release have been necessary to control competing herbaceous and hardwood vegetation. However, the costs of these practices is considerable. For example, in the Piedmont, site preparation costs range from \$125-530 per hectare and post-planting vegetation control costs range from \$125-225 per hectare. Thus, including planting, it is not uncommon for plantation costs to range from \$375-955 per hectare (Hickman et al. 1987). In addition, these costs are usually not recoverable until the first crop is harvested some 20-40 years in the future.

Besides pure economic expense, concern has also been raised over the ecological consequences of some intensive silvicultural practices employed for pine monocultures. For example, the use of heavy machinery for slash disposal and competition control on the Piedmont has been implicated in site quality decline due to damage to physical and chemical soil properties (Gent et al. 1984, Pye and Vitousek 1985, Tew et al. 1986, Fox et al. 1986). Public concern has also been raised over the possible reduction of species diversity due to intensively managed pine monocultures, and since 1979, the Forest Resource Management and Planning Act mandates that foresters do not reduce species diversity with their silvicultural practices on public lands.

Considering the economic and ecological costs of maintaining pine monocultures, some researchers have advocated the development of even-aged pine-hardwood mixtures in the Piedmont (Boyce and Knight 1980, Sims et al. 1981, Zahner 1982, Phillips and Abercrombie 1987). Phillips (1983) summarized some of the benefits of these mixtures including reduced regeneration costs, better stocking, more flexibility in management objectives, reduced risk of disease and insect attack, and improved wildlife habitat and visual attractiveness. In addition, mixed stands provide greater market flexibility, which is of considerable importance

given the past history of market fluctuations for forest products (Smith 1988). Still, management of mixed stands could be difficult and costly without increased knowledge of the silvics of individual tree species and the mechanisms of interspecific competition (Auclair 1983).

Early Work in Even-aged Pine-Hardwood Mixtures

Research is just beginning into the development of silvicultural systems for the management of mixed pine-hardwood stands. Phillips and Abercrombie (1987) have developed a low-input system for the management of shortleaf pine (*Pinus echinata* Mill.) - hardwood stands in the South Carolina Piedmont, which includes felling of residuals, timed harvests, and controlled burns at optimum moisture contents. Loftis (1985) and Zedaker et al. (1987) have advocated pre-harvest or at-harvest elimination of undesirable hardwoods, which could be used to improve composition in these stands. An ongoing study in the Virginia Piedmont (Zedaker et al. 1987, Newcomer et al. 1988, Kays et al. 1988, Zedaker et al. 1989, Kreh et al. 1991) has shown that season of harvest, site selection, cut-stump herbicide application, and chemical release can be useful low-cost silvicultural tools for the management of pine and mixed pine-hardwood stands.

Still, some basic knowledge is required for further insight into establishing and maintaining even-aged pine-hardwood mixtures. More data is needed concerning the relative yields of pure vs. mixed stands in the southern Piedmont (Knight and Phillips 1987), as well as specific information on the compatibility of various hardwoods species for growth with southern pines. In addition, knowledge of the competitive process on a physiological scale will be necessary to determine the silvicultural practices required for optimizing competitive relationships in pine-hardwood mixtures in the Southeast. A recent symposium (Waldrop et al. 1989) on the ecology and management of pine-hardwood mixtures is symbolic of the perceived importance of this forest type in the Southeast.

A Short Summary of the Autecology of Species Involved in this Study

1. Loblolly Pine (*Pinus taeda* L.)

Loblolly pine is one of the most abundant and wide-ranging species in the South, as well as the leading commercial timber species. Because of its ecological and economic importance, a great deal of information exists concerning the autecology of this species, some of which has already been related in this review. A monograph on the species is available by Wahlenberg (1960).

A shade-intolerant species, loblolly pine often occurs in pure stands which regenerate by seed after fire, logging, or other disturbance. While pines achieve rapid growth and may dominate a site for 100-150 years, they eventually lose dominance to hardwood species due to the inability of their seedlings to germinate and survive in the shade of their own understory (Oosting 1942). Hardwoods usually have a competitive advantage over loblolly pine because they reach maximum leaf photosynthetic rates at 1/3 or less of full sunlight, while loblolly pine generally reaches its maximum at full sun levels (Kramer and Decker 1944, Kramer and Clark 1947, Kozlowski 1949, Wenger 1958). Pines also tend to have less extensive root systems than hardwoods (Duncan 1941, Wenger 1958). Thus, where low light and low moisture occur together simultaneously, pines are more adversely affected than hardwoods.

While best development occurs on somewhat poorly-drained soils of the Coastal Plain, loblolly pine also thrives in the Piedmont where its site index is related mostly to depth of soil surface horizon and soil subsurface texture (Coile and Schumacher 1953). Growth of loblolly pine is 80% complete by July 1 in all parts of its range. Roots grow at all times of the year, but peak in April and May and again in early Fall (Wenger 1958).

The most serious pests of loblolly pine include fusiform rust (*Cronartium fusiforme*) and the Southern pine beetle (*Dendroctonus frontalis*). The Nantucket pine tipmoth (*Rhyacionia frustrana*), which attacks young pine stands, may influence competition outcomes by preventing early canopy closure of pines over competing vegetation.

2. Red Maple (*Acer rubrum* L.)

Red maple has one of the widest ecological amplitudes of all North American forest tree species. It occurs from Canada to S. Florida, west to Texas and Minnesota and can tolerate almost the entire spectrum of soil moisture classes (Hutnik and Yawney 1961). Red maple is often referred to as a "xero-hydric" species because it often exhibits best growth on dry upland sites and wet sites. Root morphology is affected by soil moisture with deep taproots on dry sites and short taproots and well-developed laterals on wetter sites.

Red maple is becoming an increasingly common competitor with loblolly pine throughout the South largely due to its ability to sprout vigorously after fire and cutting, and because it was not cut during past high-grading practices (Christensen 1977). Because it is intermediate in shade tolerance, red maple is also able to colonize the understory in partially-cut and high-graded stands in the absence of fire. Yet, while abundant, red maple from sprout origin often has little timber value due to its susceptibility to butt-rot and a host of other diseases (Hutnik and Yawney 1961). Red maple stems within a sprout clump also exhibit an inability to express dominance. While natural regeneration from seedling origin has superior wood quality, little is known about the development of red maple in plantation culture.

Average mature red maples may reach 60-90 feet in height and 1.5-2.5 feet in diameter. Early growth can reach one foot in the first year and two feet for a few proceeding years. Taproot growth up to one foot is possible on upland sites during the first year (Hutnik and Yawney 1961). Red maple is known to be a good competitor for resources, especially soil moisture (Kozlowski 1949, Lewis 1974, Pham et al. 1978).

3. Black Locust (*Robinia pseudoacacia* L.)

Black locust is a shade-intolerant pioneer which colonizes sites following major disturbances. It grows naturally in the Appalachian Mountain region from Pennsylvania to Alabama, and separately in Missouri and Arkansas. While it reaches its best growth in regions with humid climate and on limestone soils, it is very adaptable and has been planted extensively outside its range, including Europe and the Middle East (Keresztesi 1981). It is

also renowned for its fuelwood potential (Stringer and Carpenter 1986), as well as for its ability to grow rapidly on strip mine spoils (Carpenter and Eigel 1979, Rowell and Carpenter 1983).

Although it is tolerant of many site conditions, black locust is not very tolerant of competition (Roach 1958). While it has a more extensive root system than loblolly pine (Kozlowski 1949), rooting is typically shallow and sensitive to both waterlogging and drought (Roach 1958). Late summer defoliation is a drought avoidance mechanism in this species (Dickman et al. 1985).

An attribute of special interest with regards to competition is the nitrogen-fixing ability of black locust. While variable, studies have shown that locust has some of the highest N-fixing rates (35-200 kg/ha/year) of any leguminous species (Ike and Stone 1958, Jencks et al. 1982, Boring and Swank 1984). Because of its biomass production and because nitrogen is a limiting nutrient in many forest stands, black locust has potential as a wood-producing species as well as a nurse crop. Finn (1953) found that other trees grown with locust had greater heights, diameters, and foliar nitrogen levels. In addition, black locust is also thought to be an accumulator of nutrients such as calcium and potassium, which may increase fertility of stands directly, as well as indirectly by accelerating litter decomposition and mineralization (Garman and Merkle 1938, Auten 1945, Keresztesi 1981). Turnover from black locust branches and leaves may provide 50 kg/ha/year of nitrogen, which is approximately two times the turnover of other forest trees (Ike and Stone 1958). Chapman (1935) found that the growth of many hardwood tree species increased when planted with black locust due to fertility amendment from nitrogen fixation and high quality litter additions of black locust.

Despite these positive benefits, other reports indicate some negative attributes of black locust in mixed stands. For example, the symbiotic nitrogen-fixing bacteria may often consume a large amount of photosynthate, at the expense of growth to the tree (Gibson 1966). Also, intense competition for other resources besides nitrogen, may counterbalance the positive gain in nitrogen availability (Binkley 1986). Other problems include an unfavorable canopy structure in mixed stands of black locust (Dickman et al. 1985) and the potential dis-

aster of locust borer (*Megacyllenne robiniae*) infestation (Berry 1945). Roach (1958) states that black locust may provide excellent cover for underplanted hardwoods, but not for pines.

4. Tall Fescue (*Festuca arundinacea* Schreb.)

Tall (Kentucky-31) fescue is a cool-season grass which has been used extensively on an international scale for pasture forage, agropastoral systems, and revegetation of mine spoils. The results of several studies indicate that tall fescue is also a potentially important competitor with both pine and hardwood forest tree species. While it may begin growth as early as late winter, it can maintain production well into late summer (Eck et al. 1981) when competition is most severe. In one competition study, Smith (1989) indicated that tall fescue decreased the height and diameter of loblolly pine seedlings more than broomsedge (*Andropogon virginicus*) or Bermuda grass (*Dactylis glomeratus*). There is also some evidence that foliage litter of tall fescue is allelopathic to black locust (Larson and Schwarz 1980). The competitive ability of tall fescue may be enhanced when infected by a fungal endophyte (*Acremonium coenophialum*) which increases tall fescue drought tolerance (Arachevaleta et al. 1989).

Chapter II

INTERFERENCE INTERACTIONS IN GREENHOUSE PINE-HARDWOOD STANDS

Introduction

Coniferous and hardwood tree species occur together in a variety of forest ecosystems. Interactions which take place between these tree species are important for predicting vegetation patterns during natural forest succession, as well as for managing forests for wood production. Interference interactions between plant species include both positive (mutualistic, commensalistic) and negative (amensalistic, competitive) interactions (Harper 1977). The nature of these interactions among tree species, however, is poorly understood due to the difficulty in determining the mechanisms of interference between large woody plants, much of whose activity occurs below ground.

Pioneering work on conifer-hardwood interference mechanisms was conducted by researchers in the first half of this century (Korstian and Coile 1938, Kozlowski 1949), but much of the emphasis of this research was concerned with separating the effects of factors in re-

source interference (light, nutrients, and water). Since trees grow by acquiring and utilizing these resources, it is logical that interference mechanisms should be, at least ultimately, resource-based (Zedaker 1983, Tilman 1987a, 1988). For example, these resources may be the objects of competition if they are limiting in supply, or one plant may interfere with the uptake or use of resources by another plant even though its resource supply is plentiful. However, it is difficult to separate interference effects and attribute them quantitatively or qualitatively to individual factors whose combined effects are rarely additive (de Wit 1960, Harper 1977). Moreover, resource factors which are the object of competitive interference are typically measured on different scales, making it difficult to compare their importance to interference.

The existence of non-additive effects requires that multiple environmental factors be integrated in explaining interference interactions (Chapin et al. 1987, Aldrich 1987). This integration should consider the broad spectrum of possible interference mechanisms including allocation and use of resources, aboveground and belowground competitive overlap, avoidance mechanisms, and plasticity in plant form and function. Scaling differences between resources can be alleviated, to some extent, by relating resource use to uptake or biomass production in the form of resource-use efficiencies. These efficiencies may take the form of uptake rates (resource uptake/unit of resource) or internal resource use (dry matter production or photosynthesis/unit of resource) (Nambiar 1985). Comparisons of the efficiency with which plants obtain and utilize resources may provide a scale-free measure of competitive ability for resources and help to explain interference mechanisms.

The objective of this study was to identify interference mechanisms between pine and hardwood tree species using a multi-resource factor approach, with particular regard to species resource-use efficiencies. Since the mechanisms of interference are most easily studied under controlled conditions, our approach utilized simulated seedling stands of pine and hardwood species grown at close spacing in a greenhouse environment. This small-scale model of field forest stands also decreases the time interval required for reaching the outcome of interference interactions.

Methods

The study utilized one conifer, loblolly pine (*Pinus taeda* L.), and two hardwood species, black locust (*Robinia pseudoacacia* L.) and red maple (*Acer rubrum* L.), which commonly occur together in the southeastern United States. 1-0 seedlings of black locust and loblolly pine were obtained from the Virginia Department of Forestry nursery at Crimora, VA. Red maple seedlings were also 1-0 stock obtained from Triangle Nursery, McMinnville TN. Seedlings used in the study were selected for uniformity within species. Pine seedlings were interplanted in a 50-50 mixture with each hardwood species in 2700 cm³ plywood boxes. Pure stands of each species were planted as controls. Boxes were painted with a non-toxic waterproofing compound and lined with an inert plastic to ensure durability during the course of the experiment. Holes in the bottoms of the boxes and plastic allowed for drainage. Each box was filled with a 50-50 mixture of sand and the surface horizon (0-10 cm) of an Altavista sandy loam soil (Fine-loamy, Mixed, Thermic Aquic Hapludult).

Each stand consisted of a 6 x 6 matrix of tree seedlings planted at 5 x 5 cm spacing. Mixed stands had an alternating arrangement of pine and hardwood seedlings. Stand types were randomly assigned to boxes. Boxes were randomly assigned to either a control (daily-watering) or water-stressed (watering to field capacity once every 10 days) treatment. This design created 10 stand x stress combinations which were replicated three times and blocked by bench location.

To ensure that all seedlings of each species began the experiment from a somewhat even starting point, all hardwood seedlings were clipped to the approximate average height of the pines (20 cm). For the most part, height reduction of hardwoods due to clipping was minor. The average height of black locust seedlings was close to the average height of pines. Heights of red maple seedlings from the nursery ranged from 30-45 cm before clipping, but selection for uniformity eliminated larger seedlings from the experiment. Cuts were positioned so that a viable bud was left at the 20 cm height. However, initial biomass after clipping, ob-

Table 2.1 Mean total, shoot, and root dry weights for seedlings of each species before planting. Column means with the same letter are not significantly different at $p = .05$.

Species	Total	Shoot	Root
	----- (g) -----		
Loblolly Pine	4.2 a	3.4 a	0.8 b
Red Maple	3.7 b	1.4 b	2.3 a
Black Locust	1.4 c	0.7 c	0.7 b

tained from a subsample of 25 randomly selected seedlings, was unequal both aboveground and belowground (Table 2.1).

Shading effects between stands were eliminated by spacing individual boxes 30 cm apart (one box length) on the bench. In addition, each stand was enclosed in a cylinder of standard gauge poultry mesh to prevent intermingling of seedling crowns between experimental stands. Nutrients were maintained above adequate levels for all species with a 200 ml aqueous solution containing 200 ppm N, 97 ppm P, and 166 ppm K in each box at planting and at thirty-day intervals thereafter.

Stands were planted in late January 1990 in the greenhouse and allowed to grow until the end of May 1990. Supplemental light was provided to all stands to simulate light conditions which would normally exist in the field. After planting, all stands were given two weeks of daily watering to field capacity to facilitate establishment and promote bud break before administering watering treatments. Bud break was fairly synchronous between species; however, red maple seedlings did not complete full leaf expansion until 10 days after pine and black locust seedlings. Seedling status in water-stressed treatments was monitored periodically by measuring leaf water potentials with a pressure chamber (PMS Instruments, Corvallis OR, USA). Occasional light watering of stress-treated stands was administered between ten-day intervals to prevent mortality.

For data collection, the inner 4 x 4 matrix of seedlings in each stand was designated for measurement, with the surrounding seedlings serving as a buffer with the environment outside the stand. Seedling heights were measured every 30 days. A final analysis of biomass yield was obtained by destructively harvesting all measurement seedlings in each stand and recording leaf, stem, lateral root, and taproot dry weight. Since initial biomass differed between species (Table 2.1), all measures of biomass were expressed as biomass increment (final stand biomass - initial stand biomass) or a relative growth rate (biomass increment/initial stand biomass).

Leaf and root surface area were measured to estimate resource uptake capacity. A linear regression equation to predict leaf area from leaf biomass was developed using twenty

seedlings of each species in both stressed and control stands. Leaf areas were measured with a Li-Cor 3000 (Li-Cor Inc., Lincoln NE, USA) photoelectric area meter. The resulting slope coefficients among watering treatments were not significantly different, so a single regression equation was used for each species. Root surface area under the watering treatments and stand combinations was estimated with a subsample of three root systems of each species randomly selected from each stand. Root systems were cleaned and photographed using high contrast film and scanned for projected surface area using a high-resolution scanner (Hewlett-Packard, Palo Alto CA, USA).

Photosynthetic and light measurements were collected simultaneously from leaves in the upper crown of one randomly selected seedling of each species in each stand on four separate occasions at three-week intervals during the experiment. Measurements were made with a Li-Cor 6200 portable photosynthetic system (Li-Cor, Lincoln, NE, USA). On each date, measures were taken in the morning and afternoon and averaged. Photosynthetic measurements were taken on intact leaves for hardwood species and on pine fascicles immediately after excision from the seedling using a .25 l cuvette. The area of all sample leaves was measured in order to express photosynthesis on a leaf area basis. Light readings were taken simultaneously with a quantum sensor mounted beside the cuvette. During measurements, the cuvette was situated in the stand so that light conditions were similar to those which the target leaf was receiving before measurement. Light-use efficiency was calculated as photosynthesis per unit of light received at the leaf surface.

An integrated measure of water-use efficiency for each stand, calculated as grams of biomass increment/kg of water lost in evapotranspiration, was obtained by averaging the amount of water lost over five separate occasions spaced evenly throughout the course of the experiment. Each box was weighed at dusk and dawn, the difference representing the water lost through evapotranspiration. Because measures were collected on a stand basis, water-use efficiency could not be obtained for individual species in mixed stands.

Measures of nutrient use were restricted to nitrogen because it is the most common limiting nutrient in the range of these species. Nitrogen-use efficiency was calculated as kg

of biomass increment/mg of nitrogen in seedling tissue. Nitrogen concentrations were determined from a composite sample of each species in each stand using a micro-Kjeldahl procedure and an autoanalyzer (Technicon Instruments, Tarrytown NY, USA).

All data analysis was performed using Statistical Analysis Systems procedures (Statistical Analysis Systems, Cary, NC). Mean separation procedures were performed using Duncan's Multiple Range Test.

Results

Differences in total, aboveground, and belowground increment and relative growth rates were highly significant between stand types and watering treatments (Table 2.2). A significant interaction between stand types and watering treatments for biomass increment and growth rates indicated that differences due to stand types should be interpreted separately for each watering treatment.

Red maple seedlings in both pure stands and mixtures had the greatest biomass increment, especially belowground, in both control and water-stressed stands. However, black locust seedlings exhibited the highest relative growth rates (Table 2.2). Pure pine stands had lower biomass increment and relative growth rates than pure hardwood stands, and pine also exhibited decreased biomass increment when grown in mixtures with hardwoods. Pine relative growth rates in mixtures varied depending on watering treatment and stand type. In terms of reduction in relative growth rate and yield increment for pines in mixtures compared to pure stands, interference with pines from black locust was greatest in control watering treatments, while red maple interference was greatest in water-stress stands. Although total biomass increment of hardwoods in mixed stands was lower than in pure hardwood stands due to fewer hardwood seedlings, mean biomass per hardwood tree increased in mixed stands compared to pure stands for both hardwoods in both watering treatments. Relative

Table 2.2 Total biomass increment (TBI), aboveground increment (AG), belowground increment (BG), and relative growth rate (RGR) of seedling stands in control and water stress treatments. Numbers within parentheses represent contributions of each species within mixed stands. Column means with the same letter within watering treatments are not significantly different at $p = .05$.

STAND/SPECIES	TBI		AG		BG		RGR	
<hr/>								
----- g -----								
<u>CONTROL TREATMENT</u>								
Loblolly Pine	11.3	b	6.8	b	4.5	b	0.2	c
Red Maple	68.9	a	40.4	a	28.5	a	1.2	b
Black Locust	55.3	a	46.7	a	8.6	b	2.5	a
Pine-Maple	49.2	a	24.9	ab	24.1	a	0.8	b
Pine	(4.1)		(2.7)		(1.3)		(0.1)	
Maple	(45.1)		(22.2)		(22.8)		(1.5)	
Pine-Locust	46.0	a	38.9	a	7.0	b	2.4	a
Pine	(-11.2)		(-11.2)		(-0.1)		(-0.3)	
Locust	(57.2)		(50.1)		(7.1)		(5.1)	
 <u>WATER STRESS TREATMENT</u>								
Loblolly Pine	3.6	b	-1.6	b	5.2	a	0.1	b
Red Maple	34.7	a	24.5	a	10.2	a	0.8	a
Black Locust	16.9	ab	13.0	ab	3.9	a	0.8	a
Pine-Maple	15.4	b	7.1	b	8.2	a	0.3	b
Pine	(-3.7)		(-4.1)		(0.4)		(-0.1)	
Maple	(19.1)		(11.2)		(7.8)		(0.6)	
Pine-Locust	7.3	b	0.8	b	6.4	a	0.6	a
Pine	(-8.5)		(-9.0)		(0.4)		(-0.2)	
Locust	(15.8)		(9.8)		(6.0)		(1.4)	
 <u>OVERALL SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS</u>								
<u>P VALUES</u>								
WATERING TRT	.0001		.0001		.0001		.0001	
STAND TYPE	.0001		.0001		.0001		.0001	
WATERING X STAND TYPE	.0357		.0378		.0008		.0006	

growth rates increased for black locust, but remained the same for red maple in mixed stands compared to pure stands.

Shifts in biomass allocation with stand type and watering treatment varied with species (Table 2.3). Allocation of biomass for pines did not change for any treatment combination. Black locust seedlings had relatively greater allocation of biomass to roots compared to shoots under water stress, but allocation increased to foliage in control treatment mixtures with pines. Red maple biomass allocation did not vary with watering treatment, but allocation to lateral roots appeared to increase slightly for seedlings planted with pines.

Resource-use efficiency changed significantly with stand type and watering treatment (Table 2.4). Light-use efficiency (LUE) was significantly greater for hardwood species than pine in control watering treatments, but there was no difference in LUE between water-stressed stands. Pine LUE did not appear to vary between mixed as compared to pure stands, but LUE differed for hardwood species in control treatments. Water-use efficiency (WUE) varied with stand type, but not with watering treatment (Table 2.4). Pure stands of red maple exhibited significantly higher WUE than any other stand, while pine had the lowest WUE. Nitrogen-use efficiency (NUE) differed for both watering treatment and stand type. Red maple and pine seedlings had the highest NUE, while black locust seedlings had the lowest NUE.

Leaf area index (LAI) varied with stand type and watering treatment, while mean seedling root area changed only with stand type (Table 2.5). Pure pine stands had the highest LAI in both watering treatments, although black locust pure stands and pine-black locust mixtures were similar to pure pine stands in control treatments. Mean pine LAI was greatly reduced in mixture with hardwoods, especially with black locust. Pines contributed the greatest amount of leaf area in all mixtures with hardwoods, except in pine-black locust stands in control watering treatments.

Water-stress treatments decreased height growth of live seedlings in all stands compared to control treatments (Table 2.6). Mean seedling height increased for all stands with time in control treatments. Mean seedling heights of some species in water-stressed stands decreased near the end of the experiment due to the death of some canopy parts caused by

Table 2.3 Mean biomass allocation for seedlings to stem, foliage, lateral root, and taproot tissue as a percentage of total final seedling biomass within stands for control and water stress treatments. The ratio of root-shoot biomass (RSR) is also presented. Means in parentheses indicate the biomass allocation of individual species within stands. Column means with the same letter are not significantly different from other stands within watering treatments at $p = .05$. Means with asterisks in control watering treatments are significantly different from corresponding stands or species in water stress treatments at $p = .05$.

STAND TYPE	STEM	FOLIAGE	LATERAL	TAPROOT	RSR
----- % of Total Biomass -----					
<u>CONTROL TREATMENT</u>					
Loblolly Pine	26 c	52 a	12	10 c	0.3 c
Red Maple	31 ab	18 d	16	35 a	1.0 a
Black Locust	31 ab	44 b *	11	14 c *	0.3 c *
Pine-Maple	28 bc	29 c	16	27 b	0.8 b
Pine	(29)	(50)	(11)	(10)	(0.3)
Maple	(27)	(18)	(20)	(35)	(1.2)
Pine-Locust	35 a	41 b *	13	11 c *	0.3 c *
Pine	(29)	(42)	(14)	(15)	(0.4)
Locust	(40)	(40) *	(12)	(8) *	(0.2) *

WATER STRESS TREATMENT

Loblolly Pine	28 a	46 a	14	12 c	0.4 c
Red Maple	34 a	18 c	14	36 a	1.0 a
Black Locust	33 a	31 b	15	21 b	0.6 b
Pine-Maple	32 a	26 b	15	27 b	0.7 ab
Pine	(31)	(45)	(12)	(12)	(0.3)
Maple	(33)	(13)	(18)	(36)	(1.2)
Pine-Locust	34 a	32 b	15	19 bc	0.5 bc
Pine	(29)	(43)	(14)	(14)	(0.4)
Locust	(38)	(20)	(20)	(22)	(0.7)

SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS

P Values

WATERING TRT	.0476	.0054	.1140	.0070	.0223
STAND TYPE	.0340	.0001	.6725	.0001	.0001
WATERING X STAND TYPE	.8891	.3138	.3257	.0835	.0658

Table 2.4 Light-use efficiency (LUE), water-use efficiency (WUE) and nitrogen-use efficiency (NUE). Biomass (B) values indicate biomass increment, not total biomass. Means in parentheses indicate the contribution of each species to the overall mean in each stand. Means with the same letter within watering treatments are not significantly different at $p = .05$.

STAND TYPE	LUE		WUE		NUE	
	(PS/uE/m ² /s)		(g B/kg H ₂ O)		(kg B/mg N)	
	g B					
<u>CONTROL TREATMENT</u>						
Loblolly Pine	.006	d	2.02	c	.151	b
Red Maple	.024	a	14.33	a	.134	c
Black Locust	.017	b	6.80	bc	.069	e
Pine-Maple	.011	c	8.72	b	.165	a
Pine	(.006)		---		(.170)	
Maple	(.016)		---		(.160)	
Pine-Locust	.017	b	5.82	c	.090	d
Pine	(.005)		---		(.119)	
Locust	(.027)		---		(.061)	
<u>WATER STRESS TREATMENT</u>						
Loblolly Pine	.005	a	1.29	b	.112	ab
Red Maple	.005	a	22.82	a	.115	ab
Black Locust	.008	a	8.00	b	.083	b
Pine-Maple	.008	a	8.14	b	.131	a
Pine	(.008)		---		(.118)	
Maple	(.008)		---		(.144)	
Pine-Locust	.007	a	3.74	b	.106	ab
Pine	(.005)		---		(.123)	
Locust	(.009)		---		(.089)	

SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS

	<u>P Values</u>		
WATERING TREATMENT	.0001	.4242	.0004
STAND TYPE	.0019	.0010	.0001
WATERING X STAND TYPE	.0020	.2710	.0953

Table 2.5 Stand leaf area index and mean root surface area of species within stands in control and water stress treatments. Numbers within parentheses represent contributions of each species within mixed stands. Means with the same letter within watering treatments are not significantly different at $p = .05$.

STAND TYPE	Projected Leaf Area Index	Projected Mean Root Area per Seedling
	(cm ² Foliage /cm ² Ground)	Surface Area (cm ²)
<u>CONTROL TREATMENT</u>		
Loblolly Pine	10.7 a	20.8 b
Red Maple	4.6 b	45.2 a
Black Locust	9.0 a	18.8 b
Pine-Maple	7.6 ab	
Pine	(5.0)	(19.2) b
Maple	(2.6)	(50.0) a
Pine-Locust	10.6 a	
Pine	(2.6)	(17.2) b
Locust	(8.0)	(25.6) b
<u>WATER STRESS TREATMENT</u>		
Loblolly Pine	8.6 a	22.4 b
Red Maple	2.9 b	23.6 b
Black Locust	3.2 b	14.4 b
Pine-Maple	4.9 b	
Pine	(3.6)	(19.6) b
Maple	(1.3)	(64.4) a
Pine-Locust	4.3 b	
Pine	(2.9)	(18.0) b
Locust	(1.4)	(23.6) b
<u>OVERALL SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS</u>		
	<u>P Values</u>	
WATERING TREATMENT	.0004	.6673
STAND TYPE	.0001	.0016
WATERING X STAND TYPE	.1002	.2769

Table 2.6 Mean height of live seedlings within stands throughout the experiment following completion of full leaf extension for each species. Percent mortality is listed in parentheses to the right of height means. Height means within parentheses are for individual species within mixed stands. The initial height of each species was 20 cm. Means of stands with the same letter are not significantly different from other stands within the same watering treatment at $p = .05$.

MEAN SEEDLING HEIGHT									
STAND TYPE	DAY 50			DAY 80			DAY 110		
----- cm -----									
<u>CONTROL TRT</u>									
Loblolly Pine	26.4	(0)	b	26.6	(0)	b	35.4	(0)	c
Red Maple	37.8	(0)	a	40.6	(0)	a	48.5	(2)	b
Black Locust	32.7	(0)	ab	36.2	(2)	a	59.0	(4)	a
Pine-Maple	32.4	(0)	ab	36.7	(0)	a	41.4	(4)	bc
Pine	(27.6)	(0)		(29.5)	(0)		(32.2)	(8)	
Maple	(37.2)	(0)		(43.8)	(0)		(50.5)	(0)	
Pine-Locust	30.0	(0)	b	36.0	(2)	a	56.7	(6)	a
Pine	(23.2)	(0)		(25.2)	(0)		(26.9)	(8)	
Locust	(37.2)	(0)		(46.8)	(4)		(84.4)	(4)	
<u>WATER STRESS TRT</u>									
Loblolly Pine	25.2	(0)	a	27.2	(2)	a	22.5	(16)	b
Red Maple	31.6	(0)	a	30.9	(4)	a	30.0	(4)	a
Black Locust	32.3	(0)	a	27.9	(8)	a	26.2	(15)	ab
Pine-Maple	31.0	(0)	a	34.1	(0)	a	32.8	(12)	a
Pine	(28.5)	(0)		(28.8)	(0)		(29.8)	(16)	
Maple	(34.0)	(0)		(39.1)	(0)		(39.0)	(8)	
Pine-Locust	28.7	(0)	a	30.9	(10)	a	32.8	(33)	a
Pine	(24.8)	(0)		(26.8)	(20)		(22.3)	(58)	
Locust	(32.5)	(0)		(34.9)	(0)		(43.3)	(8)	
<u>SIGNIFICANCE OF MAIN EFFECTS AND INTERACTIONS</u>									
<u>P Values</u>									
WATERING TRT	.1445			.0202			.0001		
STAND TYPE	.0118			.0045			.0012		
WATERING X	.3643			.2485			.0121		
STAND TYPE									

water stress. Some seedling mortality was evident in stands of both watering treatments near the end of the experiment, but was much greater in water-stress treatments. Mortality was exceptionally high for pines in mixtures with black locust under water stress, where more than half of the seedlings died. In control-watered stands, mixtures became progressively two-tiered, with hardwoods in the canopy and pines in the understory. Under water stress, the height differential was reduced and some pines remained as codominants.

Discussion

The greater biomass increment of pure hardwood stands compared to mixtures of pines and hardwoods supports the view that the differential niche utilization of mixed stands does not always translate into higher stand yields (Smith 1986). One-sided interference allowed hardwoods to establish early dominance over pines at close spacing. Some pines were able to remain in the upper canopy of red maple stands, but only under conditions of severe water stress. Pine growth was also decreased by this stress. Because of this one-sided exploitative interference, interspecific interference was more intense for pines than intraspecific interference, thus also lending support to assertions (Harper 1977, Huston and Smith 1987) that intraspecific interference is not necessarily more intense than interspecific interference.

The mechanisms by which hardwoods interfered with and suppressed pines included higher relative growth rates, increased allocation to roots and increased root surface area, effective positioning of foliage, and higher resource-use efficiencies. High resource uptake rates for hardwoods as observed in this study, have also been reported in other studies of pine-hardwood interference (Duncan 1941, Kozlowski 1949). High resource uptake rates have been shown in the past to be closely related to high relative growth rates (Miller 1984, Nambiar 1985, Grace et al. 1990). High uptake rates of black locust should have induced in-

tense intraspecific competition in pure stands and would explain the much smaller yield per seedling of this species in pure stands compared to mixed stands (Table 2.2) where this intraspecific competition was reduced. The greater uptake capacity and growth rates for hardwoods compared to pines appeared to be related more to belowground resource uptake than aboveground uptake, since hardwoods generally had greater root surface areas, but lower leaf areas, than pines.

While it may appear that belowground interactions controlled interference outcomes in this experiment, belowground and aboveground interference interactions are unlikely to be independent (Thompson 1987). For example, it was visually observed in this study that the horizontal leaf positioning of hardwood species effectively shaded much of the vertically-oriented fascicles in pine crowns. After establishing dominance aboveground, hardwood species should have had an increased ability to obtain light and, therefore, a greater ability to allocate photosynthate to belowground structures compared to pine. Loblolly pine growing with red maple in control stands may have attained greater yield than in mixture with black locust since the relatively lower leaf area of red maple (Table 2.5) allowed for greater light availability.

An additional set of mechanisms likely affecting the outcome of this study were species resource-use efficiencies. With the exception of lower NUE for black locust seedlings, hardwood species had equal or higher resource-use efficiencies than pines. The lack of difference in LUE in water-stressed stands may be due to reductions in canopy growth under water stress which lowered the level of interaction aboveground and/or reduced LUE of all species to a common low level. The lower NUE of black locust may be attributed to the nitrogen-fixing capacity of this species which likely resulted in luxury consumption of nitrogen. NUE typically decreases under conditions of higher nitrogen availability (Vitousek 1982).

Results in this study generally do not support past observations of increases in WUE under water stress (Kramer 1983, Chapin et al. 1987). In addition, the decrease of LUE under water stress indicates that resource-use efficiencies do not necessarily increase under general stress conditions. The very low WUE of pines in both watering treatments in this study

was unexpected. The greater WUE of hardwoods compared to pines under water stress conditions may be related to the greater ability of hardwood species to reduce leaf area under water stress through foliar abscission, thus reducing water loss. The relatively high NUE of loblolly pine compared to hardwood species was expected, since nutrient-use efficiencies tend to be greater for conifers than deciduous species (Waring and Schlesinger 1985). However, this study was completed during a single growing season, thus eliminating the effect of longer foliage retention of nitrogen by pines and reabsorption of nitrogen from senescing foliage. Although measures of resource-use efficiencies have been commonly employed in ecological and physiological research (e.g. Kozlowski 1949, Vitousek 1982, Kramer 1983), measures of light-, water-, and nutrient-use efficiency have not been commonly employed together. From the results of this study, it appears that this approach may provide useful information in the study of interference mechanisms.

In addition to general competition mechanisms, there is evidence in this study for the existence of differing interference strategies among hardwood species. Black locust appeared to be an uptake specialist, which depleted resources beyond that available for pine growth. This strategy is similar to both Grime's competitor strategy (Grime 1979) or Tilman's equilibrium resource competitor (Tilman 1988). The strategy of black locust differed, however, with watering treatment. In control stands, black locust possessed very rapid growth rates with high allocation to aboveground structures (stem and foliage), thus attaining great height, but also resulting in low root-shoot ratios. However, black locust was able to adjust to water stress by shifting a greater proportion of biomass belowground, particularly to lateral roots. Early rapid growth and the ability to plastically adjust to changing environments is typical of trees, like black locust, which occupy early successional environments (Roach 1958) and rely on preemptive interference. In contrast to black locust, red maple could be classified as an internal resource-use and/or belowground interference specialist. Red maple had significantly higher LUE and WUE and similar NUE compared with loblolly pine, and a high proportion of biomass allocated belowground. Unlike black locust, the strategy of red maple seedlings did not change under conditions of water stress. Additionally, in mixtures with

pinus, red maple allocated greater biomass to lateral roots than in maple seedlings in pure stands. These traits correspond well with an intermediate successional tree species, such as red maple (Hutnik and Yawney 1961). These species possess somewhat reduced growth rates and interfere with pines through efficient exploitation and use of resources, particularly belowground resources, rather than through preemptive interference.

The strategies of black locust and red maple lend some support to the hypotheses of both Mooney (1972) and Caldwell (1987) which suggest that plants will shift allocation of resources to achieve and maintain a competitive advantage. However, unlike hardwood species, pine did not display a high degree of morphological or physiological plasticity under water stress or interference from hardwood species. For example, pine leaf areas were not reduced in water-stressed stands, perhaps accounting for the very low WUE observed for pine. The differences in hardwood strategies also supports Chapin et al.'s (1987) hypothesis of trade-offs between strategies of resource-use efficiency vs. relative growth rates.

This study provides an example of a multi-resource factor approach to studying the mechanisms of pine-hardwood interference, as well as the employment of resource-use efficiencies for understanding interference mechanisms and predicting outcomes in interference interactions. The use of seedling stands as a small-scale model of field seedlings provided enhanced control of experimental conditions and rapid results. However, it is possible that the decreased time and spatial scales of these analog experiments may create artificial conditions and mechanisms that produce different outcomes than those which may occur under field conditions. For example, pines may have been able to overcome hardwoods if sufficient time and space was allowed for them to mobilize their greater leaf area to accelerate growth rates. Hardwood seedlings may have also been given a competitive advantage belowground, at least under conditions of water stress, by an increase in root-shoot ratios after top clipping.

The greater leaf area duration of pines, which also was not a factor in this experiment, may also increase pine competitive ability. In fact, it has been observed that planted loblolly pine generally outgrows natural hardwood seedlings during early succession in many areas of the Piedmont and Coastal Plain provinces of the southeastern United States except for

bottomland sites (Kellison 1985). In field plantings, however, there are often significant differences in the timing of establishment and initial seedling sizes. It should also be noted that the container culture used in this study forced seedlings to interfere with each other and eliminated potential avoidance of interference through such mechanisms as the exploitation of different soil depths by the root systems of each species (Harper 1977).

For this type of experiment, it would be beneficial to repeat the experiment at various densities. Other experiments could also manipulate light and nutrient environments in addition to moisture environments, or include some combinations of these resource factors, to provide completeness and better generality concerning their role in the mechanisms of interference. Multi-species tree stands could also be planted to examine the mechanisms which take place in interference hierarchies (Keddy and Shipley 1989).

Chapter III

POTENTIAL ALLELOPATHIC EFFECTS OF TALL FESCUE ON PINES AND HARDWOODS.

Introduction

Negative interference between plants is often attributed to competition for resources, such as nutrients, light, and soil moisture. In tree-herbaceous plant interference, competition for soil moisture has been cited repeatedly as the principal mechanism of interference (Nelson et al. 1981, Sands and Nambiar 1984, Zutter et al. 1986, Creighton et al. 1987). Elliot and White (1987) and Carter et al. (1984) found that herbaceous vegetation competed with pines for both soil moisture and nutrients. However, in addition to their role as resource competitors, many herbaceous species have also been implicated as potential allelopathic agents (Horsley 1977, Priester and Pennington 1978, Larson and Schwarz 1980, Hollis et al. 1982, Rice 1984), exuding substances which directly or indirectly reduce tree growth. Silviculturalists need to be aware of allelopathic plants which may inhibit the establishment of pine and hardwood tree plantations to a greater degree than expected given knowledge of their resource competitive ability.

Fredericksen (Chapter IV, this volume) established a field study examining interference outcomes and mechanisms between seedlings of loblolly pine (*Pinus taeda* L.), black locust (*Robinia pseudoacacia* L.), red maple (*Acer rubrum* L.), and herbaceous vegetation in the Virginia Piedmont. The principal component of the herbaceous vegetation was tall fescue (*Festuca arundinacea* Schreb.) which was established from seed. One obligation in documenting allelopathic effects is to exclude the effects of resource competition (Williamson 1990). Similarly, it has been suggested that researchers in resource competition should also be obliged to exclude allelochemic effects (Muller 1969). This paper describes a companion experiment to the above field study designed to determine the potential allelopathic effect of tall fescue on seedlings of loblolly pine, black locust, and red maple under controlled conditions in a greenhouse.

Past studies have indicated that tall fescue is a potential allelopathic agent to some species of tree seedlings. Walters and Gilmore (1976) found that leachates from live and dead tissue of tall fescue reduced the dry matter production of sweetgum (*Liquidambar styraciflua* L.) seedlings by as much as 60%. Larson and Schwarz (1980) demonstrated that foliage litter of tall fescue added to soil around seedlings of black locust reduced seedling growth compared to controls. Smith (1989) suggested that allelopathy was a potential mechanism of interference between some perennial grasses, such as tall fescue, and loblolly pine, although his study did not separate the effects of allelopathy from those of resource competition. No information is available concerning allelopathic effects of tall fescue on red maple seedlings.

Methods

The study was arranged as a donor-receiver bioassay with a completely randomized design. Twenty 1-0 seedlings of each tree species were planted in 2-liter pots containing a mixture of 50% sand, 25% peat, and 25% soil by volume from the surface horizon of an

Altavista sandy loam (Fine-loamy, Mixed, Thermic Aquic Hapludult). Black locust and loblolly pine seedlings were obtained from the Virginia Department of Forestry nursery in Crimora, VA. Red maple seedlings were obtained from Triangle Nursery in McMinnville, TN. Tree seedlings were selected for uniformity within species and randomly assigned to bench locations in a greenhouse.

Half of the seedlings of each species were randomly assigned to receive a treatment consisting of twice-weekly watering of 500 ml of leachate collected from pots containing tall fescue. The remaining seedlings of each species received a control treatment consisting of bi-weekly watering of 500 ml from leachate collected from similar pots not containing tall fescue. Three red maple seedlings assigned to the control leachate treatment died after planting and were deleted from the experiment. Between leachate waterings, pots received light supplemental waterings to prevent moisture stress. None of the treatment or intermediate waterings was administered in an amount which would cause gravitational drainage of soil water from the bottom of pots containing seedlings. All pots containing seedlings received 200 ml of an aqueous solution of fertilizer (200 ppm N, 97 ppm P, and 166 ppm K) every other week to offset any potential differences in leachate nutrient concentration. Leachate was collected and tested periodically throughout the experiment for ammonium and nitrate concentration and pH to determine if leachates from the two treatments altered soil fertility or acidity. No significant differences were detected in the composition of the two leachates for nitrogen in the ammonium form or for leachate acidity (Table 3.1). Control leachate did have significantly higher levels of nitrogen in the nitrate form than fescue leachates (Table 3.1). This difference can probably be attributed to higher nitrification rates in control leachate pots, which had exposed bare soil instead of grass. However, considering the surplus of nitrogen from bi-weekly fertilization of pots containing trees, the difference in nitrate nitrogen between treatments was unlikely to be biologically significant. Nitrate levels ranged from 4-16 ppm greater in control leachates than fescue leachates. This difference would amount to a maximum of 64 ppm of nitrogen added per two-week period, only 32% of nitrogen added during the same period from fertilization. The high rates of nitrogen applied during the course

Table 3.1 Nitrogen content (NH_4^+ and NO_3^-) and acidity of leachate collected at intervals from control and fescue pots throughout the course of the experiment.

Days From Start of Treatment	NO_3^-		NH_4^+		pH	
	Control	Fescue	Control	Fescue	Control	Fescue
	----- ppm -----		-----		1/(Log H^+) --	
0	74.09	55.80	22.1	28.1	6.0	5.9
0	64.48	54.87	23.9	24.8	6.0	6.0
7	27.80	16.10	12.6	14.2	6.1	6.1
14	20.50	8.54	8.4	8.5	6.2	6.2
30	17.70	4.40	6.5	4.8	6.2	6.3
45	18.30	2.92	1.9	1.0	6.3	6.2
70	4.72	0.97	0.4	0.1	6.6	6.6
Paired T-test Value	.0003		.4457		.3505	

of the experiment would likely make any additional nitrogen due to leachate treatments insignificant. Furthermore, since leaching of nitrogen from pots containing tree seedlings was not allowed, nitrogen limitation became increasingly unlikely as the experiment progressed.

Pots used for leachate collection had a similar potting mixture as those containing tree seedlings, except that the sand was refined and triple-washed and a sterilized top soil was used in place of the Altavista soil. Pots for leachate collection were assigned to bench locations and were also randomly assigned to receive 20 kg/ha of tall fescue seed or no fescue. In order to facilitate establishment, all pots (grass and controls) received 100 ml of fungicide (Banrot, Trademark - Sierra Crop Protection Corp., Milipitas, CA) and an application of a 100 ml aqueous solution of fertilizer (200 ppm N, 97 ppm P, and 166 ppm K) at the beginning of the experiment. After two weeks, pots were thoroughly leached to reduce any fertilizer remaining in solution in the pots. One-week later, leachate collection began two times a week from all pots and was composited for each treatment for application to the pots containing seedlings. Because allelochemicals may originate from either live or dead plant tissue (Rice 1984), tall fescue was clipped back to approximately 10 cm on a weekly basis and the clippings were deposited on the perimeter of the same pot.

After 80 days of leachate treatment, photosynthesis was measured on one leaf in the upper crown of each seedling using a Li-Cor 6200 (Li-Cor Inc., Lincoln NE) portable photosynthetic system. Measurements were made using a .25 liter cuvette. Light levels ranged from 900-1000 microeinsteins/m²/sec, temperatures from 29-31 C, and relative humidity from 35-48%. Measurements were expressed on a leaf area basis. Seedling heights were recorded monthly. After three months of treatment, seedlings were excavated and the soil was washed from the roots. Seedlings were separated into the following fractions: leaves, stems, fine roots (<2 mm), and large roots (>2 mm). All material was oven-dried to a constant weight.

Zero-intercept regressions of leaf surface area on leaf weight were obtained from the dry weight of individual leaves from each seedling and the corresponding leaf area. Leaf area was determined for broadleaf species with a photoelectric leaf area meter (LI-Cor Inc., Lincoln

NE). For loblolly pine, leaf area was determined on individual fascicles using the following equation: leaf area = $\pi d l + n d l$, where d = fascicle diameter, l = fascicle length, and n = number of needles per fascicle. For loblolly pine and red maple, specific leaf area (leaf area/leaf weight) was not different for seedlings receiving fescue or control leachates and all observations were pooled to obtain one slope coefficient. Specific leaf area differed significantly with treatment for black locust (Figure 3.1), and separate coefficients were used to estimate leaf area for each treatment.

Statistical analyses comparing controls and seedlings receiving grass leachate were performed separately for each species. T-tests were used to detect any differences in seedling heights, photosynthesis, leaf area, or in the dry weight fractions of seedlings.

Results

After three months of growth, no statistically significant differences between fescue and control leachate treatments were found for final total or component seedling weights of any tree species (Table 3.2). Root-shoot ratios were also not significantly different between treatments. There was a consistent trend, however, for numerically higher mean weights of loblolly pine and black locust seedlings receiving control leachate compared to those receiving fescue leachate for all biomass components except for large roots. Red maple trends were similar except that mean large root weight was lower and mean stem weight was higher for the fescue leachate treatment compared to the control leachate treatment. Some evidence for a reduction in red maple leaf biomass due to fescue leachates was observed ($p = .1322$). A trend of higher root-shoot ratios in fescue leachate treatments compared to control treatments was also evident (Table 3.2). Mean height growth of seedlings was not significantly different between leachate treatments for any tree species except for black locust at 90 days,

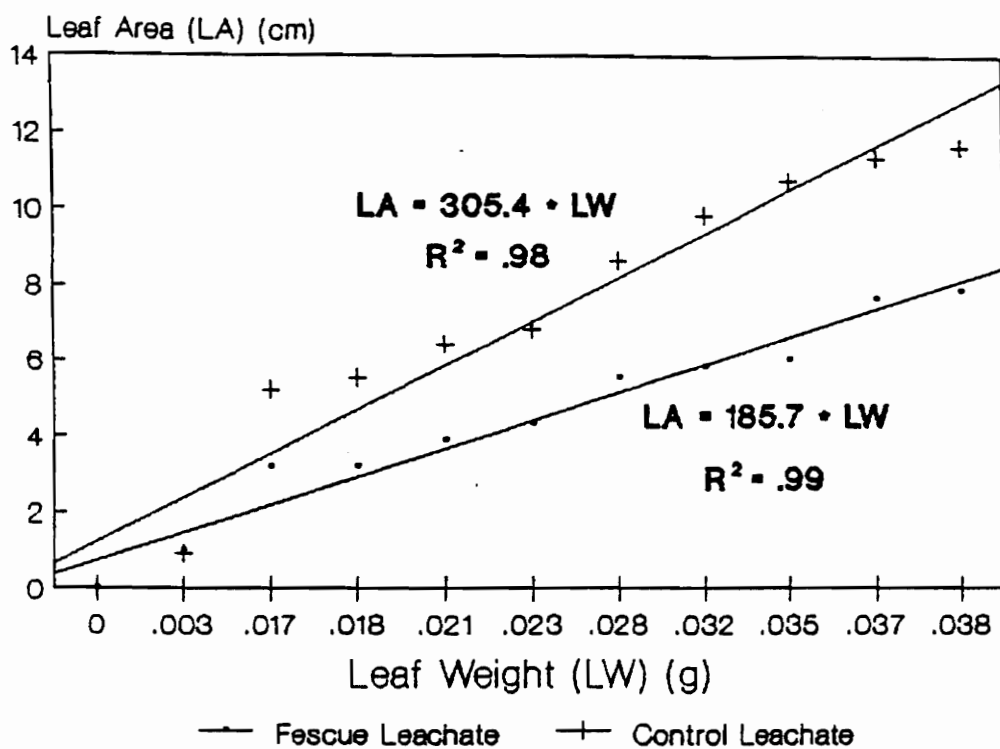


Figure 3.1 Leaf area - leaf weight regression relationships for black locust seedlings receiving fescue leachate or control leachate treatments. Regressions were formed with a zero intercept.

Table 3.2 Mean biomass and root:shoot ratio (RSR) at harvest for seedlings of each species receiving fescue and control leachate treatments.

Species / Trt	Total	Stem	Leaf	Fine Root	Large Root	RSR
----- g -----						
<u>LOBLOLLY PINE</u>						
Control leachate	15.90	3.24	8.60	2.91	1.15	0.34
Fescue leachate	14.55	2.72	7.70	2.63	1.50	0.41
T-test P Value	.5609	.3236	.4665	.6040	.2215	.1463
<u>BLACK LOCUST</u>						
Control leachate	33.67	9.34	9.86	8.39	6.08	0.82
Fescue leachate	32.11	8.64	8.67	8.27	6.53	0.93
T-test P Value	.2631	.4686	.5208	.9016	.5095	.4057
<u>RED MAPLE</u>						
Control leachate	27.20	6.81	11.67	3.36	5.36	0.54
Fescue leachate	21.99	6.90	6.96	3.17	4.96	0.62
T-test P Value	.3588	.9465	.1322	.7959	.6762	.3673

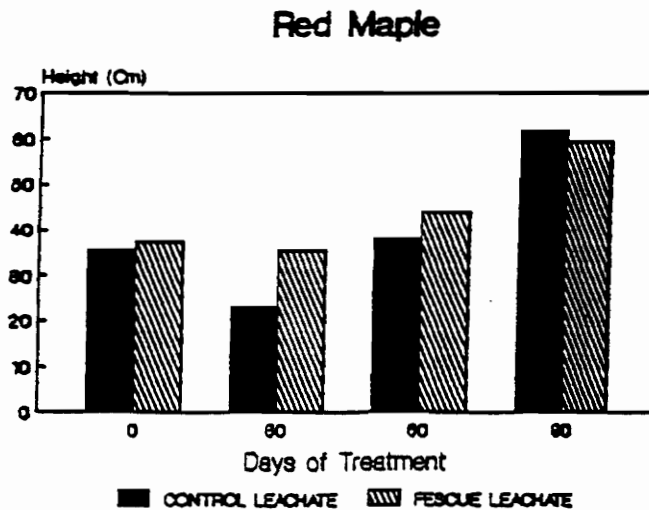
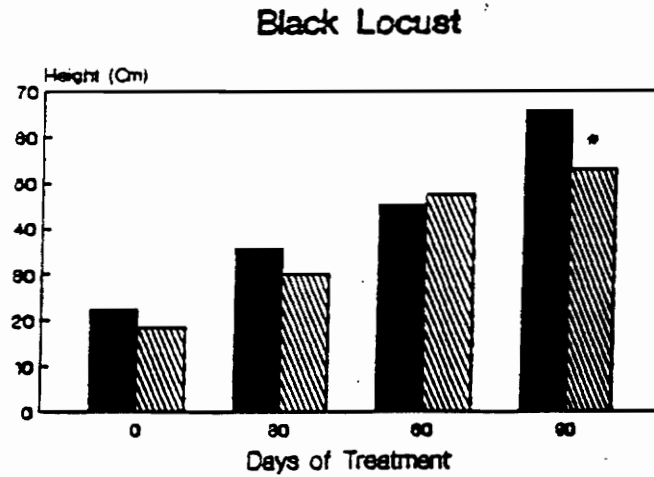
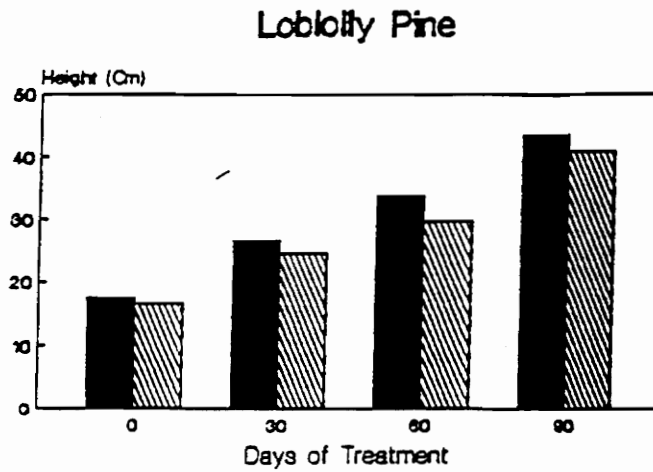


Figure 3.2 Mean height growth of seedlings receiving fescue or control leachate recorded at thirty-day intervals during the experiment. Asterisk indicates a statistically significant difference at $p = .07$.

where control leachate seedlings were taller ($p = .07$) than fescue leachate seedlings (Figure 3.2).

Mean seedling leaf area was significantly greater for black locust seedlings receiving control leachate than those receiving fescue leachate (Table 3.3). This same trend was also observed, with both loblolly pine and red maple although differences were not as great and not statistically significant. Pine seedlings receiving control leachate had significantly higher photosynthetic rates compared to those receiving fescue leachate. There is also some evidence that fescue leachates reduced the photosynthetic rates of black locust (Table 3.3). No significant differences in photosynthesis were found between leachate treatments for red maple.

Discussion

Three months of leachate applications from tall fescue did not appear to significantly alter the final total or component seedling weights for the tree species examined in this experiment. However, a trend in reduced weight of all components except for large roots for both loblolly pine and black locust seedlings may indicate that allelopathic effects were beginning to occur near the end of the experiment. A significant reduction in the height of black locust seedlings after 90 days is also supportive evidence for the onset of allelopathic effects on this species. This delayed onset of allelopathic effects indicates that relatively longer periods of treatment application should be allotted in allelochemic experiments. Treatment periods for allelopathic experiments which involved forest trees ranged from a few weeks to over a year (e.g. Walters and Gilmore 1976, Horesly 1977, Larson and Schwarz 1980, Norby and Kozlowski 1980, Hollis et al. 1982, Bhatt and Todaria 1990). However, most experiments were harvested in three months or less.

Table 3.3 Mean photosynthetic rate and leaf area of seedlings of each species receiving control and fescue leachate treatments.

Species / Treatment	Photosynthesis	Leaf Area
	(u Moles/M ² /Sec)	(Cm ²)
<u>LOBLOLLY PINE</u>		
Control leachate	4.74	1670.21
Fescue leachate	3.48	1494.45
T-test P Value	.0351	.4865
<u>BLACK LOCUST</u>		
Control leachate	15.02	3099.06
Fescue leachate	12.84	1618.27
T-test P Value	.1499	.0070
<u>RED MAPLE</u>		
Control leachate	6.81	2006.68
Fescue leachate	7.77	1195.98
T-test P Value	.5528	.1322

Some physiological and morphological variables, such as photosynthesis and leaf area, may be more instantaneously affected by allelochemic effects than dry weight production. The effects observed in this study of fescue leachate on the leaf area and specific leaf area of black locust seedlings indicate that tall fescue may reduce the photosynthetic capacity and/or efficiency of these species through chemical effects, in addition to any competitive effects for resources. Walters and Gilmore (1976) found that tall fescue interfered with the uptake and utilization of nitrogen and phosphorus by sweetgum seedlings. Reduced utilization of these elements may prevent full leaf expansion and also reduce photosynthesis (Field et al. 1983, Axellson 1985, Hirose 1988). Although not measured in this experiment, fescue may also inhibit nodulation and nitrogen fixation rates of black locust (Larson and Schwarz 1980) in addition to any effect of reduced nitrogen uptake by roots. While the leaf area and specific leaf area of loblolly pine seedlings appeared to be unaffected by leachate treatments, photosynthetic rates were significantly reduced by fescue leachate treatments, which may indicate the existence of a similar mechanism in this species as well.

Trends observed for red maple showed a greater weight of large roots and slightly lower stem weight for seedlings receiving control leachate compared to fescue leachate. Yet seedlings of all three species had higher root-shoot ratios with fescue leachate treatments compared to control treatments. Aside from an effect on leaf weight, red maple apparently was less affected by fescue leachate treatments than black locust or loblolly pine. Fisher (1980) lists phenolic compounds as allelopathic agents in tall fescue. However, without isolation of suspected allelochemicals, verification of their effects, and an understanding of the mechanism by which they operate on, one can only speculate on the attributes of this species which may increase its tolerance to allelopathy. However, it is plausible that a species, such as red maple, which is very tolerant of adverse physical conditions (Hutnik and Yawney 1961) may also be tolerant of negative chemical conditions in the rhizosphere.

Many problems exist with methodology in allelopathic experiments and the relevance of their results to natural conditions (Qasem and Hill 1989). In this study, leachate was collected under artificial conditions with regards to soil composition and water percolation. Yet,

collection of significant amounts of leachate requires these conditions. It is also possible that the peat or soil added to leachate and seedling pots in this experiment may have immobilized some chemicals in the leachate which could have had an allelochemic effect. However, on a weight basis, organic matter constituted only 2.7% of the potting mixture, which is similar to many natural soil conditions. A field experiment may have provided a better approximation of allelopathic effects under field conditions, but only at the expense of increased difficulty of experimental control and problems with separating allelochemic from competitive effects.

It should also be emphasized that this experiment was designed to detect potential allelopathic effects of fescue on tree seedlings under near ideal conditions of moisture, light, and nutrients. These conditions may reduce or eliminate allelopathic effects in which the mechanism only operates under resource-limited conditions. For example, one response to allelopathy observed in experiments is reduced nitrogen uptake (Hollis et al. 1982, Rice 1984). In such a case, the effect on growth of a target species under conditions of adequate nitrogen may be less than the effect observed under nitrogen limitation. A logical step following this study would be to repeat the experiment under various combinations of moisture, light, and nutrient stress. After allelochemic effects have been repeatedly demonstrated, it would then also be necessary to isolate the suspected allelochemicals and repeat experiments using extracts of these chemicals in place of leachates according to Koch's postulates (Williamson 1990).

In summary, while no significant effects of fescue leachates were observed on final biomass of the three seedlings in this experiment, some early indications of allelopathic effects were observed. Trends in component weights of all seedlings were fairly consistent, with some reduction in biomass and an increase in root-shoot ratios observed for seedlings in fescue leachate treatments. Black locust seedlings appeared to be most affected by fescue leachate treatments with significant reductions in leaf area, specific leaf area, and final seedling height. Photosynthesis was significantly reduced in loblolly pine by the fescue leachate with a similar trend evident for black locust. The results of this study indicate that the allelopathic potential of perennial grasses, such as tall fescue should be considered in

addition to their resource competitive effects. It should be emphasized, however, that this study displays only the potential for allelochemic effects on the seedlings examined and further testing will be required to provide more definitive evidence for the existence or intensity of effects, particularly under natural conditions.

Chapter IV

INTERFERENCE INTERACTIONS IN FIELD PINE-HARDWOOD STANDS

Introduction

Forests of the southeastern United States, which range from Virginia to Florida and west to Texas, are projected to supply an increasing share of world demand for wood resources in the next forty years (USDA 1988). Currently, this area contains 40% of the timberland in the United States. Southeastern forests are diverse, consisting of mixed stands of hardwood species, natural stands and intensively-managed plantations of pine species, and mixed pine-hardwood stands. In addition to limitations in site conditions and genetic composition, forest productivity in the Southeast is most limited biologically by the presence of non-crop vegetation which competes for resources or otherwise negatively interferes with the growth of crop tree species (Farnum et al. 1983, Boyce et al. 1986). The term "interference" is used to describe various interactions among plants. Interference interactions may have

negative effects on plants, as in resource competition or allelopathy; or they may have positive effects, as in beneficial microclimate modification or nitrogen fixation.

For the most part, studies of interference in forestry have been phenomenological in nature, usually measuring the response of crop trees to the reduction of weed species after site preparation, mechanical intermediate stand treatments, or chemical release (Stewart et al. 1984). Few studies employed controlled experiments specifically designed to study interference interactions. Recent studies have attempted to quantify interference interactions between loblolly pine (*Pinus taeda* L.) and woody and herbaceous competitors in the Southeast using more closely controlled experiments. Bacon and Zedaker (1987) employed an additive design and found that pine growth was maximized when two-thirds of surrounding woody vegetation was removed along with all herbaceous vegetation. In a region-wide study, Miller et al. (1991) quantified the response of crop pines to total removal of surrounding vegetation, removal of woody vegetation only, and removal of herbaceous vegetation only. After five growing seasons, pine stem volume yield was increased by 67%, 171%, and 424% over an untreated check for woody control, herbaceous control, and total vegetation control, respectively.

While these studies were important in helping to quantify the effects of interference on crop tree yield, they provide no insight into the mechanisms of tree and herbaceous interference. An understanding of the patterns caused by interference interactions and the development of silvicultural systems to manage interference is likely to come only from the study of these mechanisms of interference interactions (Radosevich 1987). Studies which have addressed interference mechanisms in the Southeast have been limited to the effect of one or two factors of interference, usually soil moisture (Nelson et al. 1981, Carter et al. 1984, Byrne et al. 1987). However, interference typically occurs under the influence of many resources and conditions interacting in the environment and in the different ways plants respond to them (Aldrich 1987, Chapin et al. 1987). Interference studies in the southeast are currently attempting to determine how a number of physiological and morphological mechanisms, oc-

curing aboveground and belowground, interact to explain interference outcomes between crop trees and interfering vegetation (Morris et al. 1991, Mitchell et al. 1991).

Better quantification of the effect of interference and an understanding of interference mechanisms is likely to lead to a greater ability to direct weed control treatments in southeastern pine stands. In addition, recent increases in the stumpage value of hardwoods, as well as an interest in maintaining forest diversity, has increased the attractiveness of managing pine-hardwood mixtures, particularly on the southeastern Piedmont (Waldrop et al. 1989). Knowledge of interference interactions will be essential for the development of silviculture systems to manage these mixtures.

In response to these needs, a replacement series field experiment was established on the Virginia Piedmont. The objectives of the study were 1) to estimate the relative yields and assess the compatibility of mixtures of loblolly pine and two hardwood species, black locust (*Robinia pseudoacacia* L.) and red maple (*Acer rubrum* L.), grown with and without the presence of herbaceous vegetation; 2) to determine biomass allocation patterns as affected by interference; and 3) to investigate the nature of competitive mechanisms and other interference interactions which determine the early growth and development of pure and mixed stands.

Methods

Study Site and Experimental Design

The study site is located at the Reynolds Homestead Agricultural Experiment Station in Patrick County, Virginia. A split-plot design was employed in five blocks, each approximately 0.2 hectares in size (Figure 4.1). Four blocks are located on gently-sloping upland terrain with eroded Cecil soils (Typic Hapludults, Clayey, Kaolinitic, Thermic). The other block is located on a level stream terrace with an Altavista sandy loam soil (Typic Hapludults,

EXPERIMENTAL DESIGN

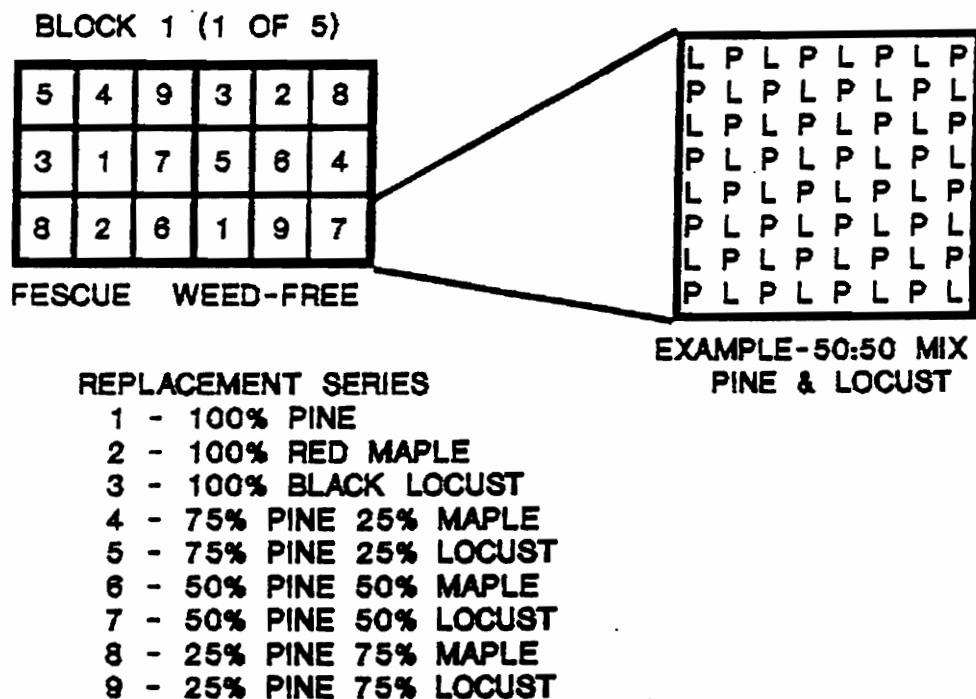


Figure 4.1 Experimental design of field study. The design is a split-plot replicated in five blocks, each approximately 0.2 hectares in size. Whole plots in each block were randomly assigned to a herbaceous control (weed free) or a herbaceous vegetation (planted tall fescue) treatment. Subplots consist of randomly assigned stands in a replacement series between loblolly pine and each hardwood species.

Fine-loamy, Mixed, Thermic) and a minor component of Chewacla silt loam soil (Fluvaquentic Dystrochrepts, Fine-loamy, Mixed, Thermic). All areas of the study were grass-dominated old fields and were treated in the fall of 1988 with glyphosate to remove existing vegetation.

Whole plots were randomly assigned to either an herbaceous vegetation treatment primarily consisting of seeded tall fescue (*Festuca arundinacea* Schreb.) or an herbaceous-free (control) treatment. Subplots were randomly assigned to one of nine replacement series combinations including pure stands of pine, red maple, and black locust; as well as 25-75, 50-50, and 75-25 percent mixtures of pine and each hardwood species, respectively. Loblolly pine and black locust seedlings were obtained from the Virginia Division of Forestry nursery in Crimora, VA. Red maple seedlings were obtained from Triangle Nursery, McMinnville, TN.

Planting of 1-0 loblolly pine and hardwood seedlings took place in March 1989. Each subplot contained a total of 48 measurement seedlings planted at 1 x 1 meter spacing. Mixtures (50:50 and 75:25 combinations) were planted in a systematic design to assure equality in the number of intraspecific and interspecific interactions within each of the subplot stands. The perimeter of each subplot was planted with one row of buffer seedlings equal in species proportion to that within the stand. Each whole plot was also enclosed by a single row of pines as an additional buffer between measurement trees and the exterior of the whole plot.

Tall fescue was not seeded in herbaceous plots until August 1989 to allow seedlings to become initially established. Grass seed was applied at a rate of 25 kg/hectare. Irrigation was also applied during the first growing season to facilitate seedling and grass establishment. Applications of glyphosate (Roundup - Trademark - Monsanto Corporation, St. Louis MO) using a shielded backpack sprayer were conducted as needed to control herbaceous vegetation on control plots. Some native forbs and grasses were allowed to invade plots planted with grass, but all of these plots continued to be dominated by tall fescue.

Seedling mortality of loblolly pine and red maple was low (< 3%) during the first growing season. Mortality of black locust, however, reached 45% during the first growing season due to consecutive late spring frosts which defoliated the seedlings. In order to maintain constant density in the experiment, seedlings of all species which died due to es-

establishment failure were replaced at the beginning of the second growing season with 2-0 stock from the same nursery source. Mortality at the end of the second growing season was less than 1% for loblolly pine and red maple and 14% for black locust. For measurement purposes, trees which died due to establishment failure were replaced by randomly selected live trees. Trees whose death could be attributed to interference remained in the data set.

Applications of lindane were necessary during the second and third growing seasons to prevent an outbreak of locust leafminer (*Xenochalepus dorsalis*) in pure locust stands and locust-pine mixtures. One application was conducted in July 1990, followed by two applications in June and July of 1991. A high incidence of locust borers (*Megacyllene robiniae*) and possibly (*Ecdytolopha insiticiiana*) was also noted during the second and third growing seasons.

Yield Response and Biomass Allocation

To assess aboveground yield response, groundline diameter, height, and live crown volume were measured using a 25% systematic sample of trees at the end of the each of the growing season to age three. Since it integrates two separate measures of yield, conical stem volume yield (calculated as $1/3 * \text{groundline dm}^2 * \text{height}$) was used as the principal aboveground yield indicator of stands. The effects of interference on stand yield was evaluated with the use of relative yield total (RYT) and relative crowding coefficient (RCC) indices (Harper 1977). RYT is a measure of the yield of mixed stands relative to pure stands and is calculated as the sum of the mean yield of each species in mixture divided by its yield in pure stands:

$$\text{RYT} = Y_{a(ab)}/Y_{a(aa)} + Y_{b(ab)}/Y_{b(bb)} \text{ where } Y = \text{mean yield of species a,b.}$$

RCC is a comparison of the competitive effect of each species on the other and is expressed as a ratio formed from the quotient of mixed stand yields and the quotient of pure stand yields:

$$\text{RCC} = (Y_{a(ab)}/Y_{b(ab)}) / (Y_{a(aa)}/Y_{b(bb)})$$

In addition, whole tree biomass was estimated by excavating one tree of each species in late July-August of the third growing season in pure stands and 50-50 mixtures in three

blocks. Trees selected for excavation were average in height and vigor for trees of that species in each stand. Tree biomass was estimated for each of the following components: total biomass, aboveground biomass, belowground biomass, leaf biomass, stem biomass, large (> 5 mm diameter) root biomass, medium (2-5 mm diameter) root biomass, and fine (< 2 mm diameter) root biomass. Since the clayey soils of study area made total recovery of fine roots from excavation difficult, a separate estimate of fine roots during this period was obtained from core samples for comparison.

Fine root biomass in pure stands and 50:50 mixtures of control treatments was estimated by monthly soil coring from March-September during the third growing season. During each sampling period, cores were extracted using a 8 cm diameter auger from three randomly-selected locations in each plot on four blocks. In order to obtain an unbiased estimate of rooting of tree species relative to each other, all cores were located at midpoints between two trees. Cores were sorted by three depth classes: 0-10 cm, 10-20 cm, and 20-30 cm; the soil depth where most fine roots in young pine and hardwood stands are located (McNeil and Sanford 1987). For each core, live and dead roots were separated from the soil, washed, and oven-dried, and sorted into size classes (< 2 mm, 2-5 mm, and > 5 mm), before weighing. Because of the difficulty involved with separating herbaceous roots from tree roots, sampling was restricted to herbaceous control treatment plots. Fine root (< 2 mm) turnover of trees in herbaceous control stands was also estimated by the method of balancing transfers between live and dead fine root pools (Fairley and Alexander 1983).

Leaf area of excavated seedlings was estimated during the third growing season for each species on pure stands and 50-50 mixtures using species and treatment-specific regression equations of leaf area on leaf weight developed from 15 measures of leaf weight and leaf area on individual needles or leaves. Leaf area was determined on a one-sided basis for hardwoods and on an all-sided basis for conifers according to the methods in Chapter III (this volume). Total leaf area for excavated seedlings was estimated by multiplying leaf biomass estimates by specific leaf area coefficients for each species and stand.

Resource Use and Resource Availability

Due to sampling constraints, physiological and morphological measures of tree response to herbaceous and stand composition treatments were generally restricted to pure stands and 50:50 mixtures. Sampling of resource use and availability was restricted to those resources considered to be most important on the study site: light, soil moisture, and soil nitrogen.

Photosynthesis and transpiration was measured on trees in three randomly selected blocks each month from May-August using a portable photosynthetic system (Li-Cor 6200, Li-Cor, Lincoln NE). Measures were obtained from leaves in the upper crown of three trees of each species in each stand at 1000 and 1400 hours on each sampling date, converted to a leaf-area basis, and averaged. From these measurements, estimates of instantaneous water-use efficiency (photosynthesis/unit transpiration) were also obtained. Measures of light availability in all stands of one block were conducted in May and July of the third growing season with a Li-Cor quantum sensor. Because canopy response to aboveground interference is best detected where tree size and light competition is greatest, the block selected for canopy morphology measurements had the highest site quality of all blocks in the experiment. Measures were obtained in the upper third of the crown of four seedlings of each species in each stand type at half-hour intervals from 0700-1800 hours on a cloudless day. Self-shading effects were removed by bending the upper crown of the measured seedling away from the quantum sensor. To determine the effect of light interference on crown morphology, the crowns of all trees in herbaceous control stands in this same block were measured for lateral spread in eight different directions, crown height, crown shape, and the height at which the crown attained maximum lateral spread. Tree leaf or needle water potentials were also obtained on two separate dates for three seedlings of each species per stand on three blocks at predawn (0400-0600 hours) and midday (1100-1300 hours) using a pressure chamber (PMS Instruments, Corvallis OR).

Foliar nitrogen levels were estimated by sampling three seedlings of each species in pure stands and 50:50 mixtures on two blocks of the study during the third growing season.

Samples were digested and analyzed for total Kjeldahl nitrogen using an autoanalyzer (Technicon Instruments, Tarrytown NY). Nitrogen-use efficiency was estimated in two different ways including photosynthetic nitrogen-use efficiency (calculated as photosynthesis per unit nitrogen in leaf tissue) and yield-based nitrogen-use efficiency (calculated as total tree biomass per unit of foliar nitrogen).

In order to determine the relative degree of influence that different morphological and physiological measures had on stand yield, stand stem volume yield was regressed on several of these variables to determine their relative ability to predict tree yield. These variables included photosynthesis, midday water potential, water-use efficiency, percent foliar nitrogen, photosynthetic nitrogen-use efficiency, yield-based nitrogen-use efficiency, growth efficiency (stem volume per unit leaf area), mean fine root biomass, root-shoot ratio, and leaf area. All variables were measured during the third growing season on trees in the same stands where stand stem volume was measured. Logarithmic transformation of the dependent variable was applied when data did not exhibit a linear structure. Forward stepwise regression was performed using all the variables listed above. A probability level of $p = .05$ was set for entry of variables into the model.

Statistical analyses were performed using analysis of variance (ANOVA) or regression analysis with the use of SAS (Statistical Analysis Systems, Cary NC). Analysis of covariance was also employed to separate treatments effects from size differences in biomass allocation data. For ANOVA, a logarithmic transformation was applied to the data in cases of heterogeneous variance between treatments.

Results

Stand Yield

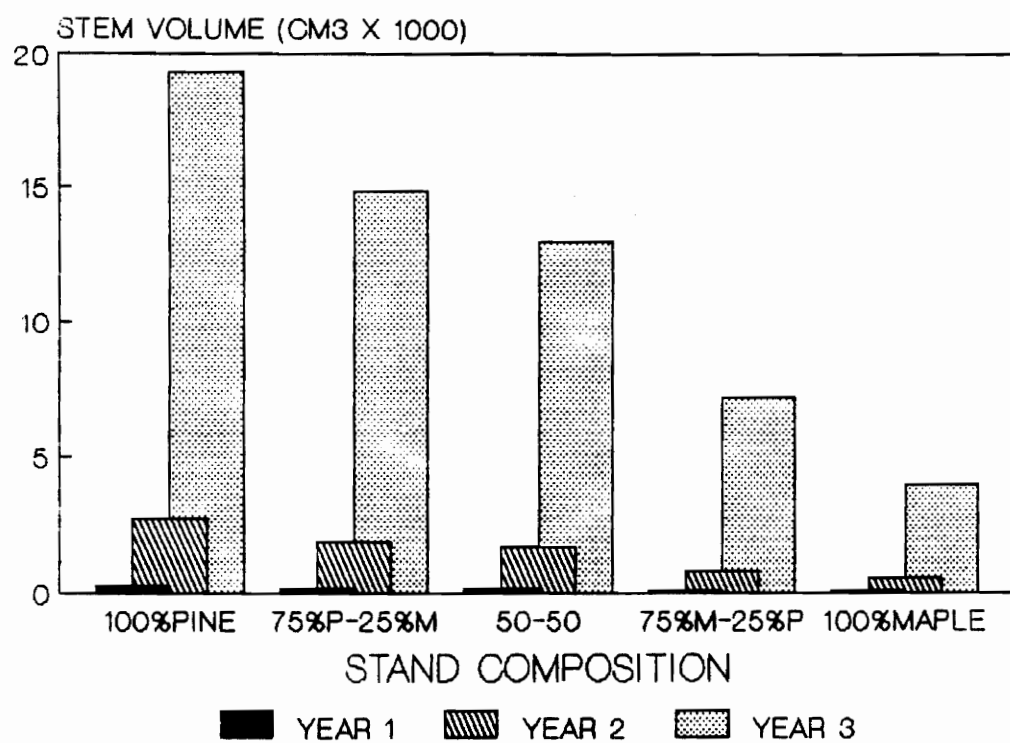
ANOVA indicated that herbaceous and stand combination treatments had significant effects on aboveground stand yield indicators during the first three growing seasons (Table 4.1). Stand composition significantly affected stand stem volume, mean tree canopy volume, and mean tree height for all three growing seasons. Herbaceous treatment effects only became statistically significant during the second and third growing seasons. An herbaceous treatment-stand composition interaction was evident only at the end of the third growing season. Mortality was mostly species-dependent, being much higher for locust than for maple or pine. Mortality was evenly-distributed between herbaceous control (1.9%) and herbaceous vegetation (2.3%) treatments.

For most stands, stem volume increased exponentially over the three growing seasons in all four replacement series (Figures 4.2-4.5). Exceptions to this trend were pure hardwood stands in herbaceous treatments, which increased very little in stem volume during the three growing seasons (Figures 4.3 and 4.5). During the second and third years, stand stem volume was dramatically lower in herbaceous vegetation compared to herbaceous control treatments, particularly in stands dominated by hardwood species. For all series, stand stem volume was positively correlated with the proportion of loblolly pine in the stand. This trend became evident in the second year of the study, but was more pronounced after the third growing season. Since interference was generally expected to increase with time and plant size in this study and because the order of stand stem volume as affected by the treatments does not change substantially for the three growing seasons, further results will focus mainly on the most recent (third) growing season.

Relative yield total (RYT) diagrams for stand stem volume yield at the end of the third year for the loblolly pine-red maple series with herbaceous control (Figure 4.6) and with

Table 4.1 Probability values for main effects (herbaceous treatment and stand composition) and interactions of Analysis of Variance for stand stem volume (SV), tree canopy volume (CV), and tree height (HT), for each growing season. Canopy volume was not measured in the first growing season.

Source	df	<u>Year 1</u>		<u>Year 2</u>			<u>Year 3</u>		
		SV	HT	SV	CV	HT	SV	CV	HT
Block	4	.001	.094	.286	.391	.502	.113	.004	.018
Herb.	1	.822	.263	.012	.082	.020	.001	.001	.001
Block x Herb. (Error a)	4	.438	.175	.018	.008	.003	.001	.057	.438
Stand	8	.001	.001	.001	.001	.001	.001	.001	.001
Herb. x Stand	8	.215	.529	.980	.929	.500	.001	.001	.121
Error b	64								
Total	89								



Figures 4.2 Mean stem volume of loblolly pine-red maple stands at the end of each growing season in the herbaceous control treatment.

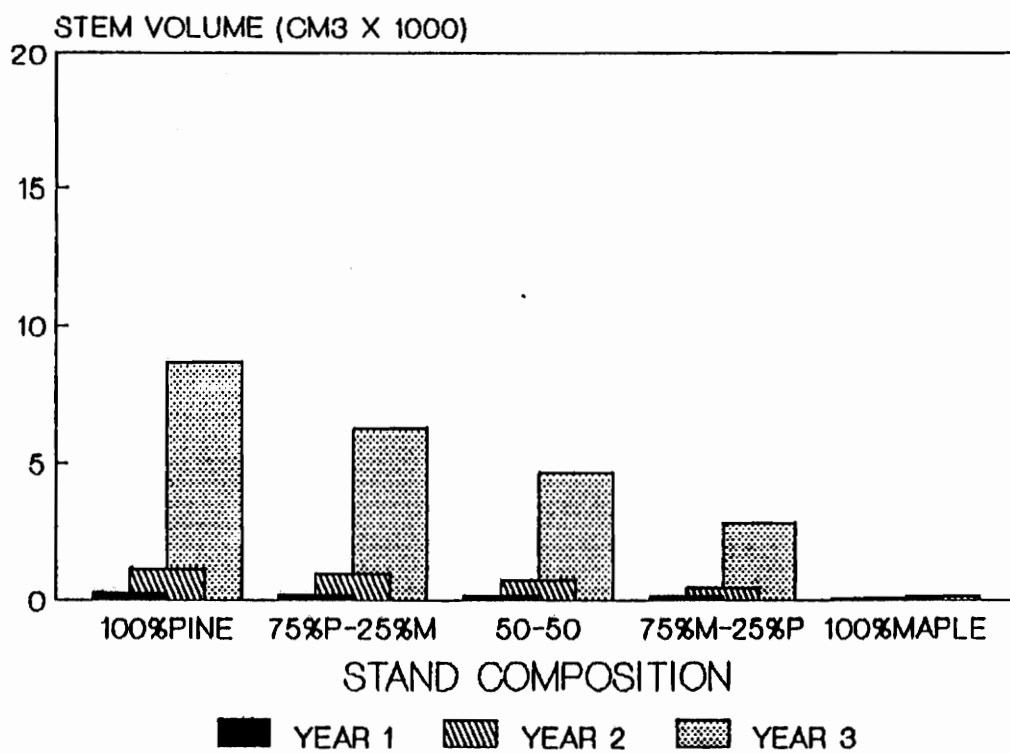


Figure 4.3 Mean stem volume of loblolly pine-red maple stands at the end of each growing season with herbaceous vegetation.

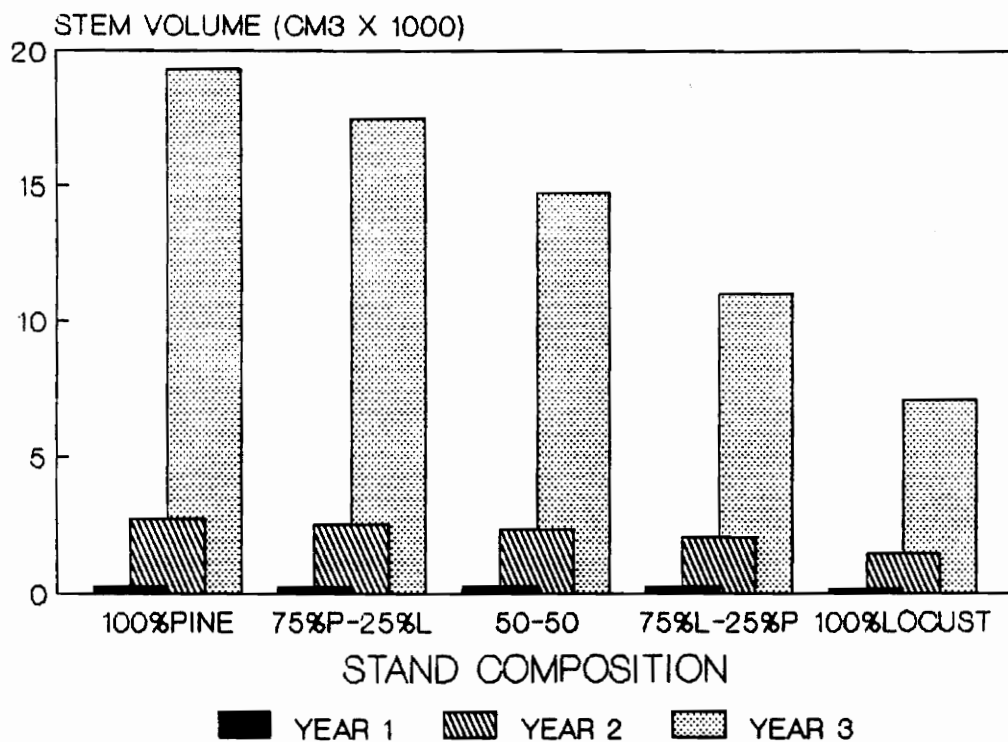


Figure 4.4 Mean stem volume of loblolly pine-black locust stands at the end of each growing season in the herbaceous control treatment.

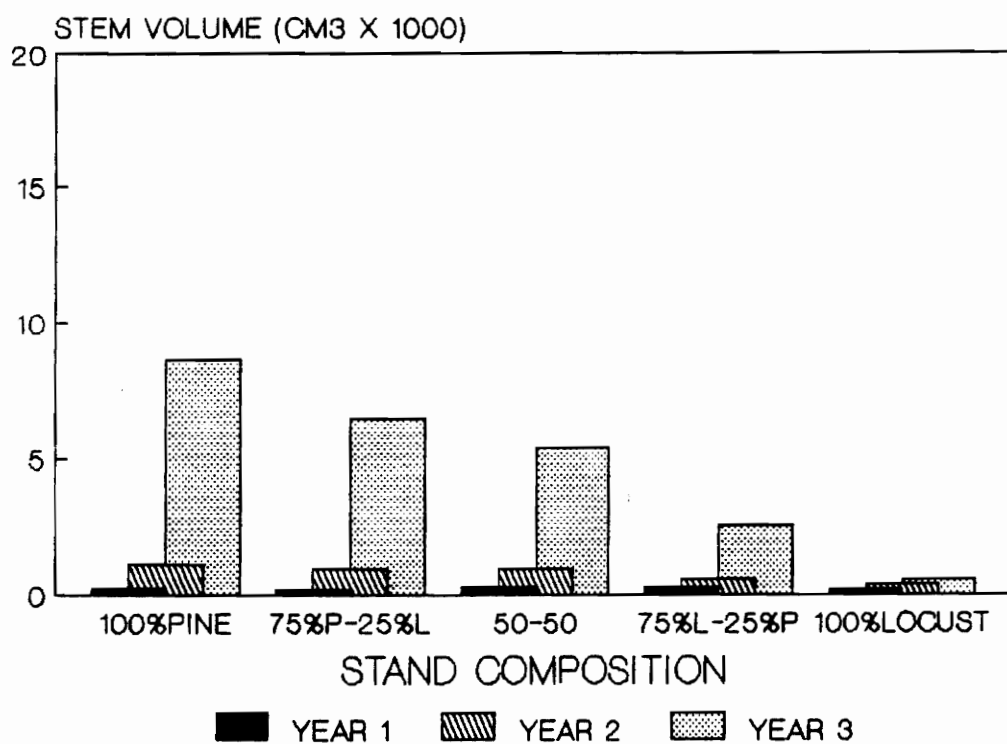


Figure 4.5 Mean stem volume of loblolly pine-black locust stands at the end of each growing season with herbaceous vegetation.

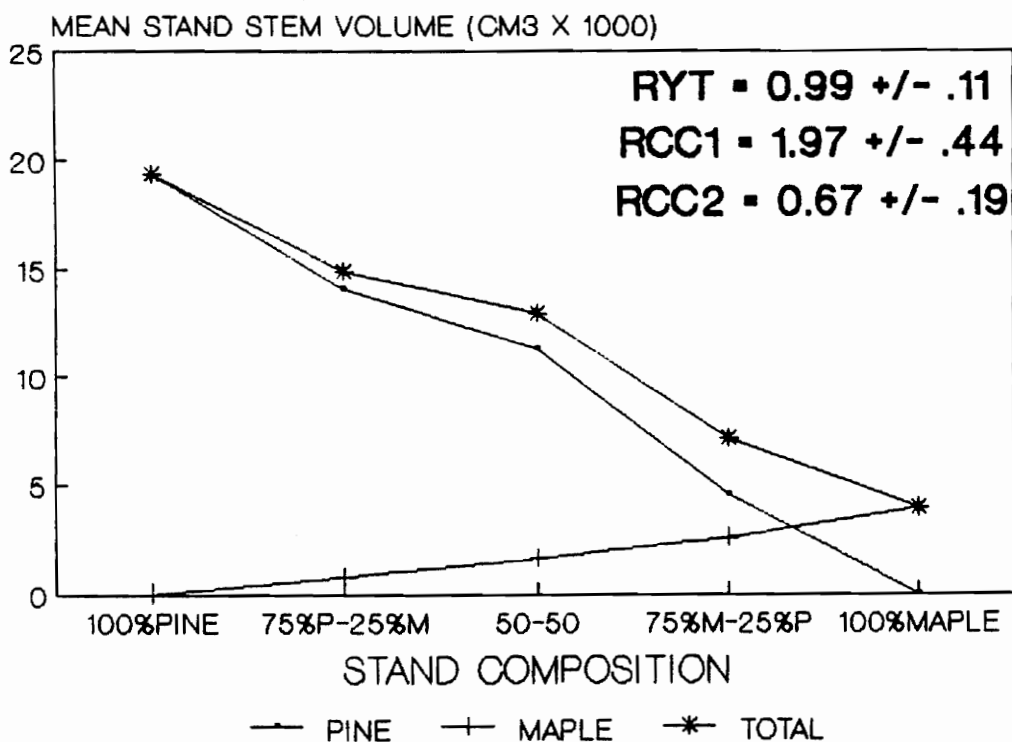


Figure 4.8 Relative yield total (RYT) of stem volume of loblolly pine-red maple stands after the third growing season in the herbaceous control treatment. RYT and the relative crowding coefficients (RCC1 and RCC2) are given with standard errors. RCC1 and RCC2 represent the interference effect of pine on maple and maple on pine, respectively.

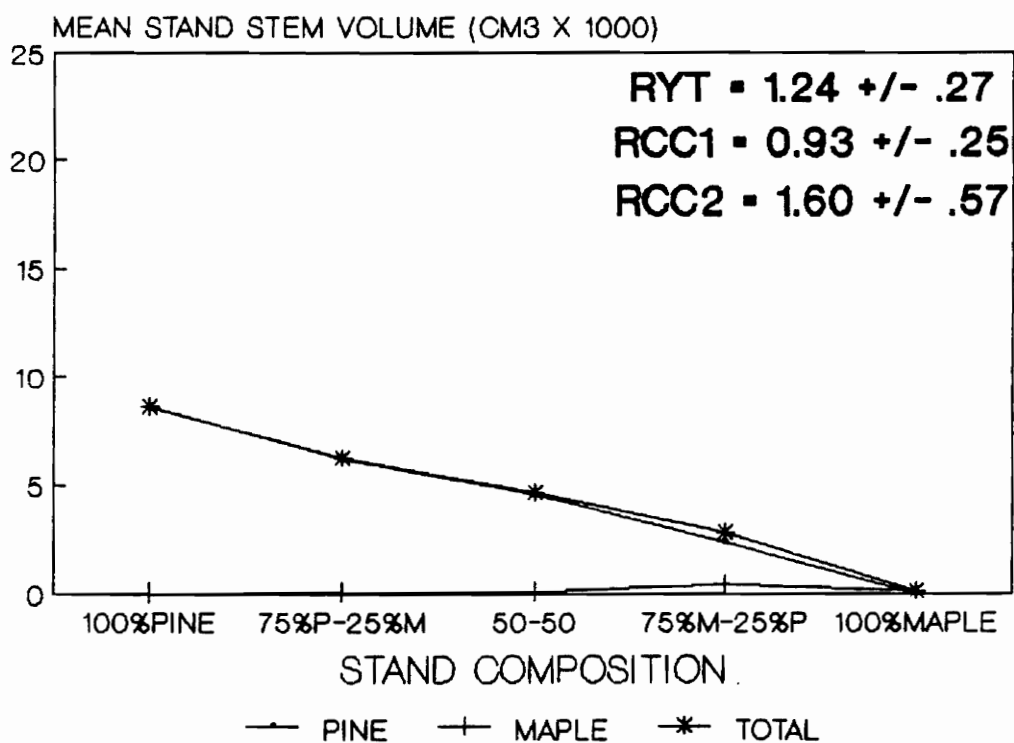


Figure 4.7 Relative yield total (RYT) of stem volume of loblolly pine-red maple stands after the third growing season with herbaceous vegetation. RYT and the relative crowding coefficients (RCC1 and RCC2) are given with standard errors. RCC1 and RCC2 represent the interference effect of pine on maple and maple on pine, respectively.

herbaceous vegetation (Figure 4.7) verify the greater yield contribution of loblolly pine compared to red maple. While pine stem volume is reduced by half when planted with herbaceous vegetation, the reduction of red maple yield is reduced approximately twenty-fold. Pine-maple RYT_s for both herbaceous control and herbaceous vegetation series are not significantly different from 1 (Figures 4.6 and 4.7), indicating that neither species is significantly affecting the yield of the other (Harper 1977). However, in the pine-maple-herbaceous control series, the relative crowding coefficient (RCC) of pine (RCC₁) is significantly greater than 1, while that of red maple (RCC₂) is less than 1, indicating that pine may have a somewhat greater effect on the yield of maple compared to the effect of maple on pine yield (Harper 1977). In the pine-maple-herbaceous vegetation series, neither RCC is significantly different from 1.

In the pine-black locust series, pine stem volume was reduced approximately by half with herbaceous vegetation compared to herbaceous control treatments and black locust stem volume was reduced, on average, by a factor of 10 (Figures 4.8 and 4.9). Yield analysis for stand stem volume in pine-locust series varied with herbaceous treatment. In herbaceous control treatments, RYT and RCC of black locust were not significantly different from 1 and the RCC for pine was not much greater than 1 (Figure 4.8). However, in herbaceous vegetation treatments, RYT had a large variance but was still much greater than 1 (Figure 4.9). The high variance in RYT was driven by a large site effect. RYT on blocks 4 and 5 (relatively good sites) was not significantly different from 1 (RYT = 1.16 +/- .17) and RCCs were close to 1 (RCC for pine 1.10 +/- .06, RCC for locust 0.91 +/- .05). On blocks 1-3 (relatively poor sites), RYT was much greater than 1 (RYT = 4.57 +/- 1.38) and the RCC was much greater for locust than pine (RCC for pine = .11 +/- .01, RCC for locust = 9.37 +/- 1.10).

Mean tree crown volume was generally greatest for loblolly pine in herbaceous control treatments with the exception of black locust trees in 75-25% pine-locust mixtures with herbaceous control (Figure 4.10). Pine crown volumes tended to increase in stands with increasing hardwood proportion, but this difference was not statistically significant. Red maple had the lowest crown volume of all species in herbaceous control treatments and did not change substantially with pine proportion. Crown volumes of all species were considerably

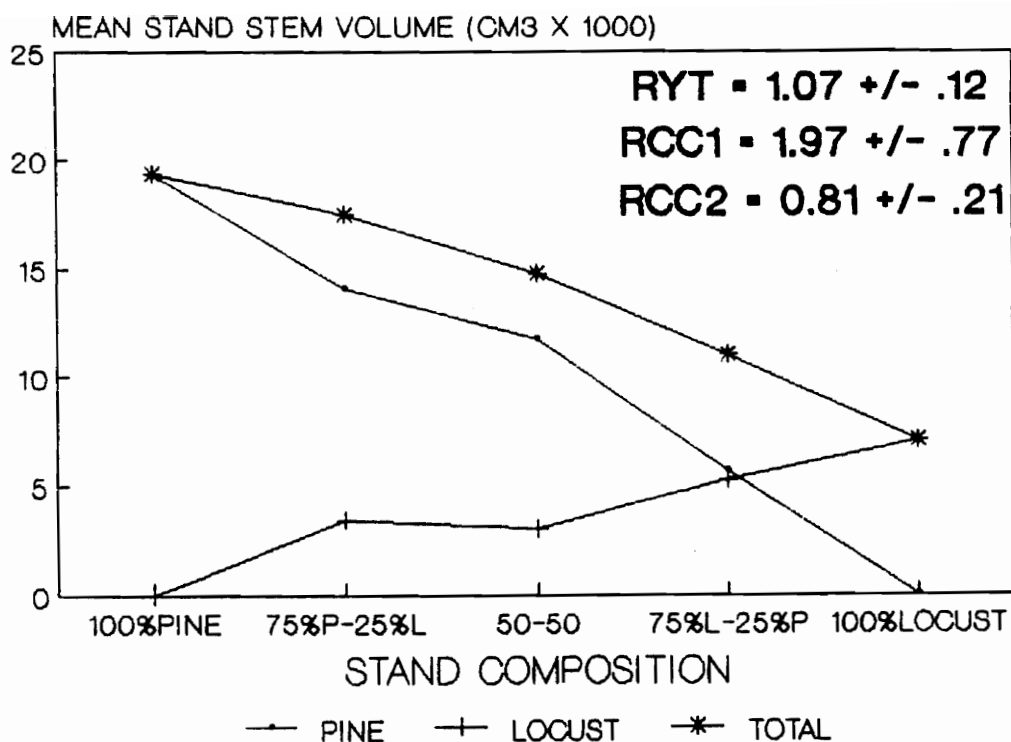


Figure 4.8 Relative yield total (RYT) of stem volume of loblolly pine-black locust stands after the third growing season in the herbaceous control treatment. RYT and the relative crowding coefficients (RCC1 and RCC2) are given with standard errors. RCC1 and RCC2 represent the interference effect of pine on locust and locust on pine, respectively.

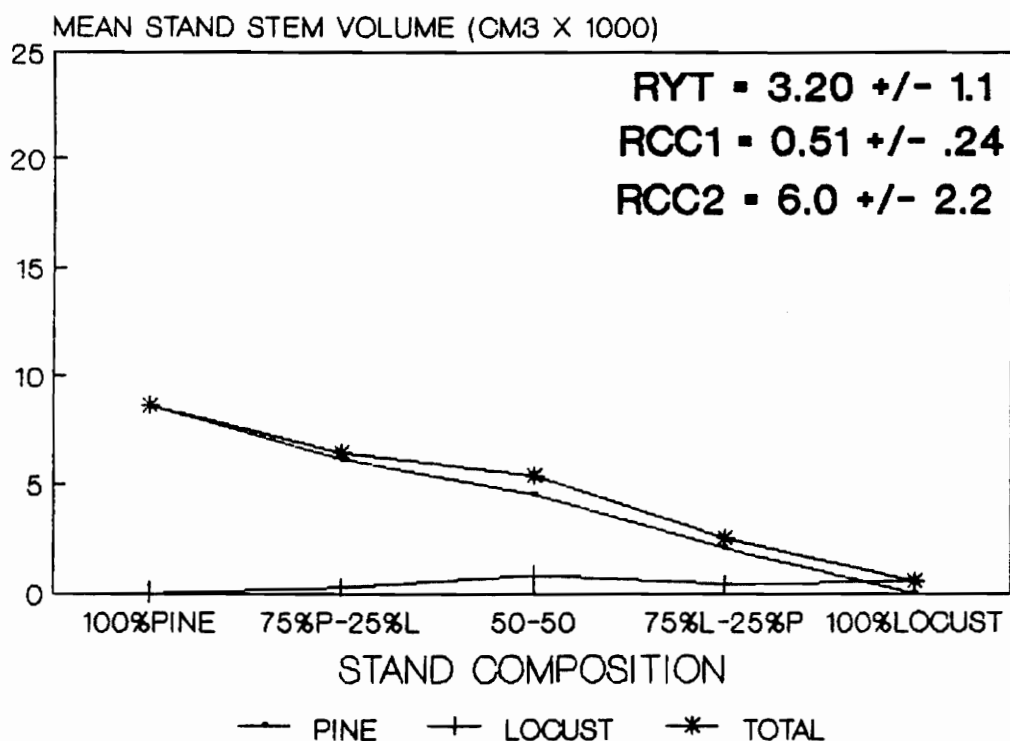


Figure 4.9 Relative yield total (RYT) of stem volume of loblolly pine-black locust stands after the third growing season with herbaceous vegetation. RYT and the relative crowding coefficients (RCC1 and RCC2) are given with standard errors. RCC1 and RCC2 represent the interference effect of pine on locust and locust on pine, respectively.

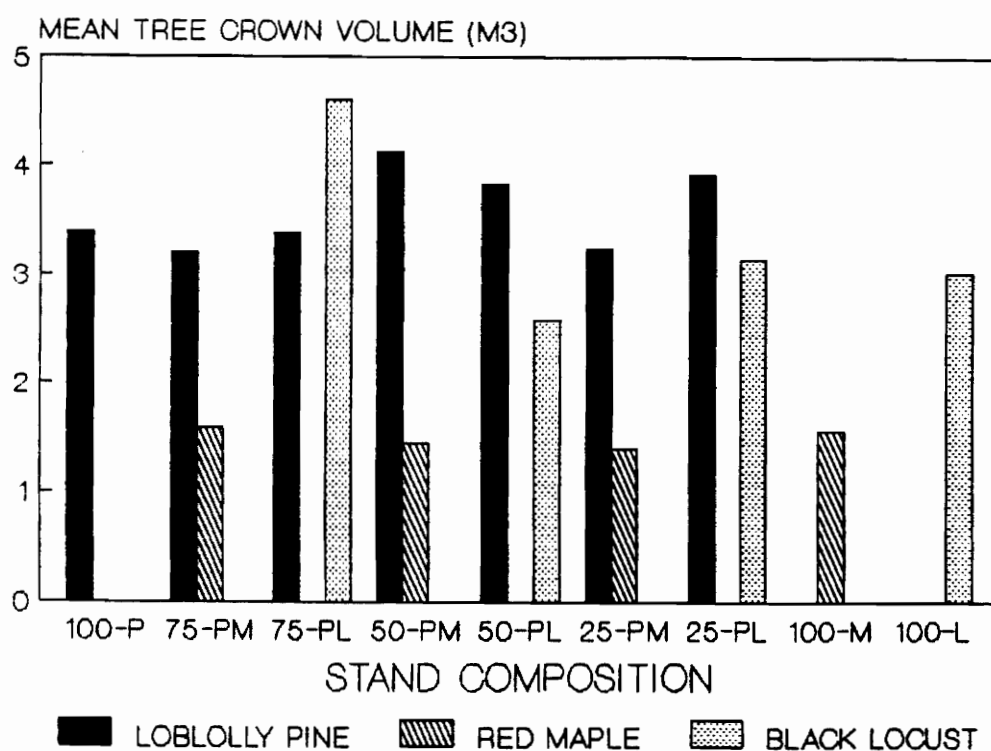


Figure 4.10 Mean tree crown volume of each species in herbaceous control treatment stands. Stand composition is indicated by percentage given with the first letter of the dominant and subdominant species in the stand (P = Pine, M = Maple, and L = Locust).

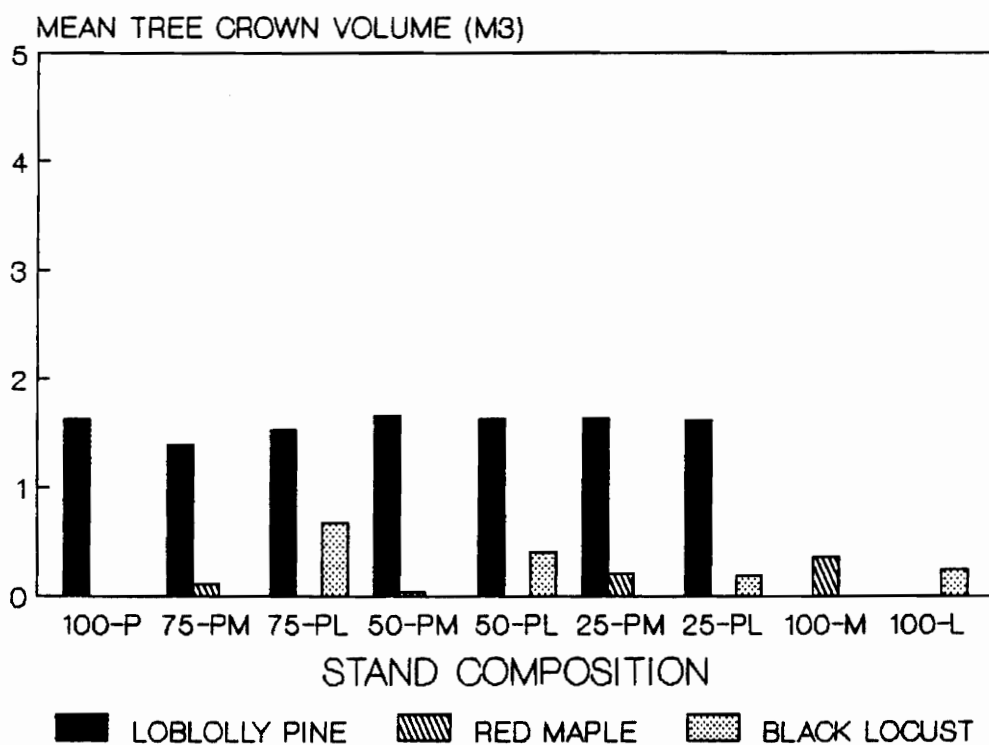


Figure 4.11 Mean tree crown volume of each species in stands with herbaceous vegetation. Stand composition is indicated by percentage given with the first letter of the dominant and subdominant species in the stand (P = Pine, M = Maple, and L = Locust).

reduced in herbaceous vegetation treatments compared to herbaceous control treatments, especially hardwood species (Figure 4.11). Mean locust crown volume tended to increase with increasing pine proportion in herbaceous vegetation treatments, while the opposite trend occurred for red maple.

Mean tree height of species was not greatly affected by stand composition in control or herbaceous vegetation treatments. In herbaceous control treatments (Figure 4.12), pine and locust had equal height (approximately 2.5 m), while red maple averaged 1.5 m in both pure and mixed stands. With herbaceous vegetation (Figure 4.13), however, pine had the greatest mean height in all stands because of the proportionately greater height reduction of hardwood species. Loblolly pine planted in stands with black locust had greater stem volume, height, and canopy volume than pine in stands with red maple after the second growing season, but there was no statistically significant difference after the third growing season (Figure 4.14). Whole-tree biomass estimates of species obtained from excavated trees closely paralleled trends in stem volume, canopy volume, and height. Trends for individual species did not differ considerably with stand composition, but varied greatly with herbaceous treatment (Table 4.2). Loblolly pine had the greatest biomass of all species, followed by black locust and red maple. Hardwood tree total biomass was reduced substantially more than pine in herbaceous vegetation compared to the herbaceous control treatment.

Biomass Allocation

Loblolly pine had the lowest root-shoot ratio of any species and it was not significantly affected by stand type or herbaceous treatment (Table 4.2). Red maple had the highest root-shoot ratio. Hardwood root-shoot ratios were not affected by stand composition in herbaceous control treatments, but root-shoot ratios of both hardwood species were greater in pure stands than in mixtures with pine and herbaceous vegetation. Hardwood root-shoot ratios were also greater in herbaceous vegetation than in herbaceous control treatments.

Loblolly pine and red maple had a similar percentage of biomass in foliage, as well as in branches and stems in herbaceous control treatments (Table 4.3). Black locust had a

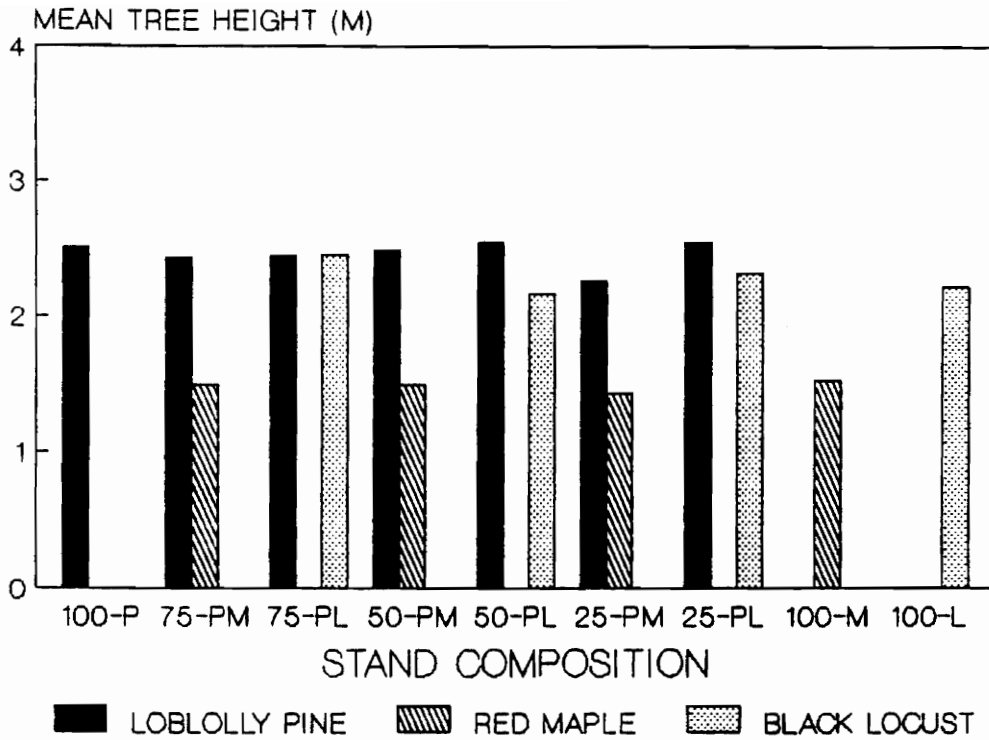


Figure 4.12 Mean tree height of each species in herbaceous control treatment stands. Stand composition is indicated by percentage given with the first letter of the dominant and subdominant species in the stand, respectively (P = Pine, M = Maple, and L = Locust).

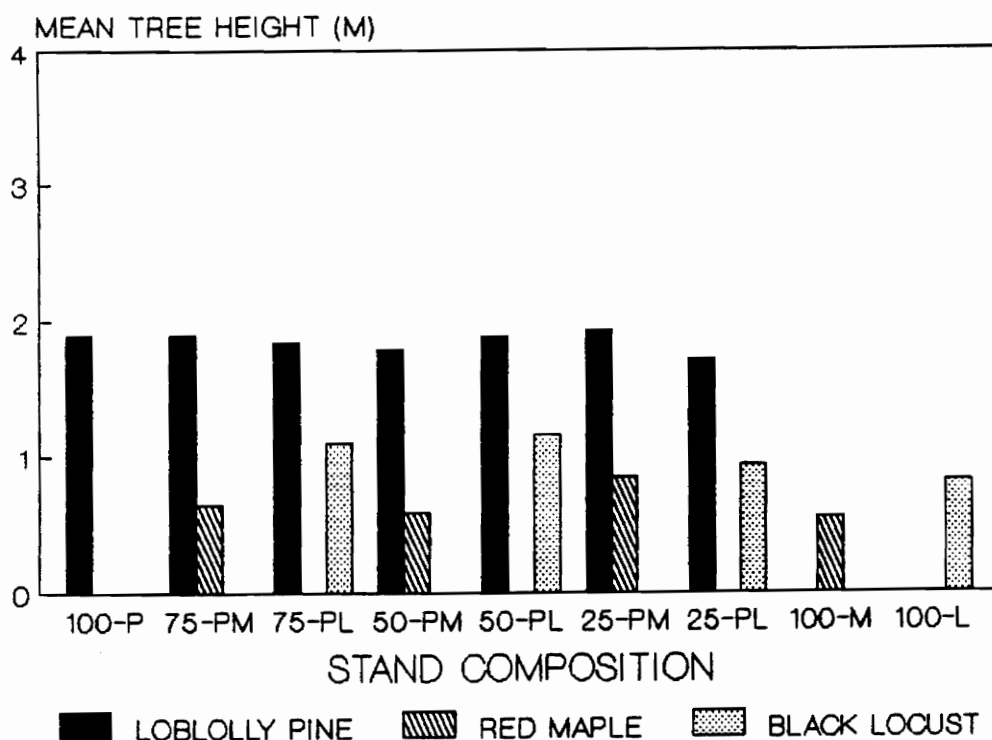


Figure 4.13 Mean tree height of each species in stands with herbaceous vegetation. Stand composition is indicated by percentage given with the first letter of the dominant and subdominant species in the stand, respectively (P = Pine, M = Maple, and L = Locust).

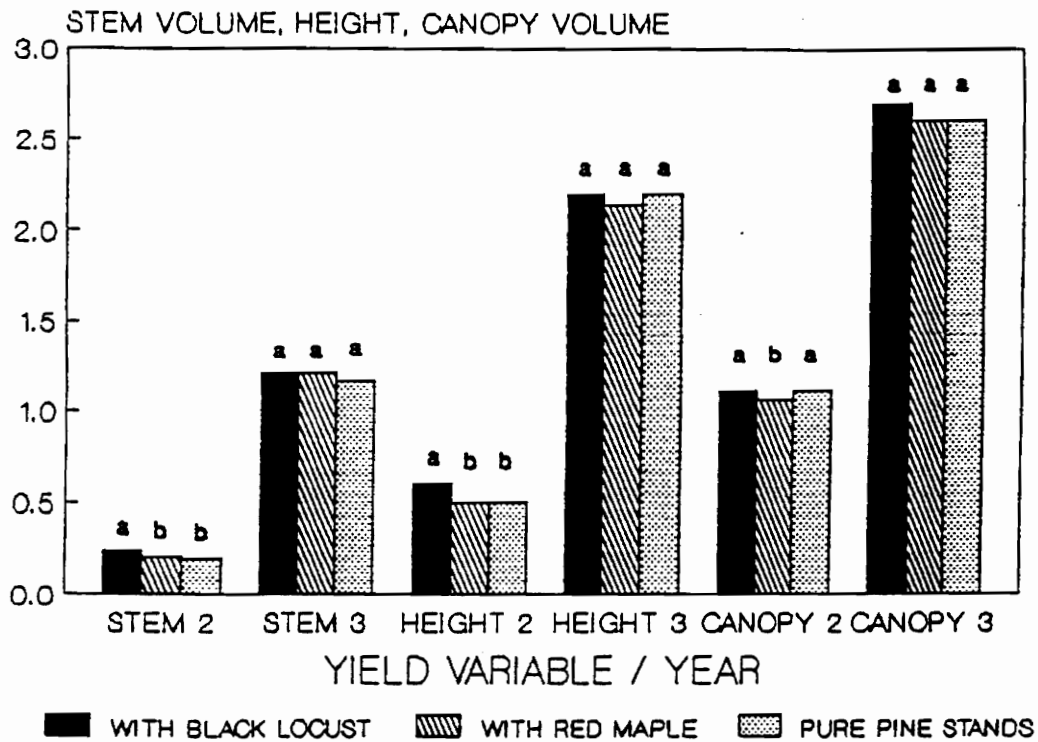


Figure 4.14 Mean tree stem volume ($\text{Cm}^3 \times 1000$), Height (M), and Canopy Volume (M^3) of loblolly pine trees with black locust, with red maple, or in pure stands at the end of the second and third growing seasons. Means with the same letter within bar clusters are not significantly different at $p = .10$.

Table 4.2 Mean yield in biomass and root:shoot ratio (RSR) of excavated trees in pure and mixed stands of control and herbaceous treatments. Standard errors are included in parentheses.

STAND/SPECIES	Total Biomass	Shoot Biomass	Root Biomass	RSR
----- Kg/Tree -----				
<u>CONTROL TREATMENT</u>				
Loblolly Pine	1.33 (.17)	1.10 (.14)	0.23 (.04)	.20 (.01)
Red Maple	0.44 (.15)	0.30 (.10)	0.14 (.05)	.47 (.01)
Black Locust	0.72 (.05)	0.52 (.04)	0.20 (.02)	.40 (.04)
Pine-Maple				
Loblolly Pine	1.27 (.19)	1.05 (.14)	0.23 (.05)	.21 (.02)
Red Maple	0.61 (.31)	0.44 (.25)	0.16 (.06)	.45 (.08)
Pine-Locust				
Loblolly Pine	1.18 (.16)	0.98 (.15)	0.20 (.01)	.21 (.02)
Black Locust	0.67 (.24)	0.49 (.19)	0.17 (.05)	.39 (.06)
<u>HERBACEOUS TREATMENT</u>				
Loblolly Pine	0.52 (.24)	0.44 (.19)	0.08 (.04)	.17 (.02)
Red Maple	0.02(.006)	0.01(.003)	0.01(.003)	1.1 (.03)
Black Locust	0.05 (.03)	0.03 (.01)	0.02 (.01)	.78 (.02)
Pine-Maple				
Loblolly Pine	0.48 (.15)	0.41 (.13)	0.07 (.02)	.18 (.02)
Red Maple	0.03(.006)	0.02(.004)	0.01(.002)	.93 (.02)
Pine-Locust				
Loblolly Pine	0.77 (.41)	0.63 (.33)	0.14 (.08)	.21 (.02)
Black Locust	0.08 (.03)	0.05 (.03)	0.02(.005)	.55 (.01)

Table 4.3 Percent allocation of biomass to foliage, stem, fine root (<2 mm diameter), medium root (2-5 mm in diameter), and large root (>5mm diameter) components of excavated trees in pure and mixed stands of control and herbaceous treatments. Standard errors are included in parentheses.

STAND/SPECIES	Foliage	Stem & Branch	Fine Roots	Medium Roots	Large Roots
----- % of Total Biomass -----					
<u>CONTROL TRT</u>					
Loblolly Pine	39 (3)	45 (3)	3 (1)	3 (.3)	11 (1)
Red Maple	35 (2)	33 (2)	7 (2)	5 (2)	19 (2)
Black Locust	11 (3)	61 (4)	5 (.2)	5 (1)	18 (1)
Pine-Maple					
Loblolly Pine	41 (1)	41 (1)	3 (.3)	2 (.1)	12 (1)
Red Maple	34 (1)	35 (3)	5 (2)	4 (.4)	21 (2)
Pine-Locust					
Loblolly Pine	41 (1)	42 (2)	4 (2)	3 (.5)	11 (1)
Black Locust	14 (3)	58 (1)	5 (.4)	4 (1)	18 (1)
<u>HERBACEOUS TRT</u>					
Loblolly Pine	44 (2)	41 (1)	3 (.3)	2 (.2)	9 (1)
Red Maple	20 (2)	28 (2)	11 (4)	9 (4)	32 (4)
Black Locust	17 (12)	41 (6)	10 (3)	5 (1)	28 (4)
Pine-Maple					
Loblolly Pine	43 (3)	42 (4)	4 (1)	2 (.4)	10 (1)
Red Maple	22 (4)	31 (3)	12 (2)	6 (1)	30 (2)
Pine-Locust					
Loblolly Pine	50 (4)	33 (2)	4 (1)	3 (1)	10 (2)
Black Locust	21 (6)	45 (3)	9 (3)	3 (1)	22 (4)

much smaller proportion of total biomass in foliage. However, by July and August when biomass estimates were obtained, black locust had lost a large percentage of its foliage, which is a reported response of this species to moisture deficits (Dickman et al. 1985). Estimates of leaf litter biomass in black locust stands averaged 229.6 g/m². The high nutrient quality of black locust leads to rapid decomposition (Auten 1945). Assuming, therefore, that this litter accumulated during the current growing season, relative biomass allocation to foliage would have ranged from 43-55% if measured earlier in the growing season; somewhat more than red maple or loblolly pine. The percentage of stem and branch biomass of black locust was greater than pine or maple in herbaceous control treatments and also greater than stem and branch allocation of black locust with herbaceous vegetation. Percentage of total biomass in foliage did not change for loblolly pine or black locust in herbaceous control compared to the herbaceous vegetation treatment, but decreased by almost half with herbaceous vegetation for red maple.

Recovery of medium and large roots during excavation was essentially complete. However, fine root biomass was probably underestimated due to breakage of fine roots into fragments in the clay soils on the study site. For all species, percentage allocation to the standing biomass of large roots was greater than medium and fine roots combined (Table 4.3). Red maple and black locust had a similar percentage of total biomass for both large and medium roots in herbaceous control treatments, while pine allocation to these root size categories was the lowest for all species. Large and fine root biomass percentage increased for black locust with herbaceous vegetation and increased for all root size categories for red maple. Percentage of pine root biomass did not change for any size category with herbaceous treatment.

Comparisons of fine root biomass from core samples with fine root biomass of species from excavations in similar stands varied (Table 4.4). Generally, estimates of pine fine root biomass from excavation were lower than those obtained from core samples. Conversely, hardwood fine root biomass estimates were higher for excavation than for core samples. On average, however, estimates from the two methods were similar. Generally, fine root biomass

Table 4.4 Estimates of fine root biomass from core samples in herbaceous control stands compared to estimates from whole tree excavation. Standard errors of means are given in parentheses. Percent difference of excavation compared to coring estimates are also presented.

FINE ROOT BIOMASS			
STAND/SPECIES	EXCAVATION	CORE SAMPLES	% DIFFERENCE
	----- g -----		
Loblolly Pine	39.8 (11.9)	70.8 (3.2)	42.8
Red Maple	21.9 (5.3)	20.6 (1.0)	5.8
Black Locust	33.6 (0.1)	29.4 (0.4)	14.3
Pine-Maple			
Loblolly Pine	26.2 (0.1)	23.8 (9.3)	29.6
Red Maple	21.5 (3.2)	16.7 (1.2)	30.7
Pine-Locust			
Loblolly Pine	24.2 (1.6)	39.5 (2.2)	28.2
Black Locust	25.1 (8.7)	24.3 (3.4)	4.8

Table 4.5 Fine Root (<2mm) biomass collected at monthly intervals during the third (1991) growing season for loblolly pine, red maple, and black locust in pure and mixed stands in herbaceous control treatments. Standard errors are included in parentheses.

STAND/SPECIES	MARCH	APRIL	MAY
----- Mg/Ha -----			
Pine	.440 (.235)	.539 (.161)	.634 (.108)
Maple	.052 (.021)	.121 (.064)	.069 (.045)
Locust	.242 (.116)	.160 (.030)	.208 (.061)
Pine-Maple	.351 (.095)	.442 (.115)	.353 (.110)
Pine	.175 (.060)	.337 (.090)	.320 (.115)
Maple	.176 (.155)	.105 (.050)	.033 (.011)
Pine-Locust	.846 (.050)	.341 (.057)	.847 (.205)
Pine	.499 (.052)	.196 (.027)	.403 (.115)
Locust	.147 (.002)	.145 (.047)	.244 (.096)
STAND/SPECIES	JUNE	JULY	AUGUST
Pine	.584 (.215)	.676 (.173)	.739 (.036)
Maple	.196 (.094)	.196 (.046)	.215 (.035)
Locust	.313 (.050)	.298 (.041)	.290 (.047)
Pine-Maple	.414 (.085)	.324 (.088)	.486 (.067)
Pine	.383 (.095)	.145 (.023)	.331 (.039)
Maple	.031 (.016)	.179 (.132)	.155 (.084)
Pine-Locust	.763 (.135)	.537 (.093)	.753 (.134)
Pine	.624 (.124)	.373 (.078)	.416 (.124)
Locust	.139 (.024)	.164 (.020)	.337 (.022)
STAND/SPECIES	SEPTEMBER		
Pine	.860 (.243)		
Maple	.577 (.310)		
Locust	.447 (.068)		
Pine-Maple	.541 (.168)		
Pine	.382 (.127)		
Maple	.158 (.053)		
Pine-Locust	1.01 (.249)		
Pine	.665 (.239)		
Locust	.349 (.126)		

from coring in herbaceous control stands was highest in pure pine stands and in pine-locust mixtures (Table 4.5). Pure maple stands had consistently lower fine root biomass, except in September. Red maple fine root biomass in pure stands generally increased during the growing season. Black locust fine root biomass was fairly constant in pure stands, but increased in mixed stands in August and September. No trends in fine root biomass of pine or red maple in mixture with pine were readily discernible. With few exceptions, all species had greater fine root biomass in mixed stands compared to pure stands when correcting for the 2x sampling dilution of fine root biomass of a single species in core samples from mixed vs. pure stands.

The distribution of fine roots between sampling dates with regards to depth was quite variable and trends for individual species were not easily distinguished (Table 4.6). Generally, however, 48.9 ± 2.0 , 28.9 ± 1.4 , and 22.2 ± 1.9 percent of fine roots of all species were found in the 0-10, 10-20, and 20-30 cm depth ranges, respectively. Fine root production tended to be higher for pine than for hardwood species (Table 4.7). However, estimates of fine root production and its distribution (Table 4.8) were highly variable and trends for individual stands were difficult to determine. Overall fine root production was more evenly distributed with depth than fine root biomass with 37.0 ± 3.3 , 35.1 ± 2.4 , and 27.9 ± 2.4 percent of fine root production located in the 0-10, 10-20, and 20-30 cm depth ranges, respectively.

Differences in root system morphology were noted during excavation. All root systems had short (approximately 20-50 cm) taproots, but lateral and fine root networks differed between species. Loblolly pine lateral roots often extended 1 m or more from the stem and were uniformly distributed with respect to direction and amount of fine roots. All pine fine roots sampled had mycorrhizal associates. Red maple lateral roots were generally short (.25-.75 m) and larger in diameter than pine roots. Near the horizontal ends of lateral roots, one or more sinker roots descended .5 m or more. Fine root biomass was distributed close to the stem associated with horizontal lateral roots. Black locust lateral roots were mostly thin and located close to the stem. However, black locust trees usually had 2-4 large lateral roots

Table 4.6 Fine Root (<2mm) biomass distribution collected at monthly intervals during the third (1991) growing season for loblolly pine, red maple, and black locust in pure and mixed stands in herb. control treatments. Letters correspond to depth increments: A = 0-10 cm, B = 10-20 cm, C = 20-30 cm.

STAND/SPECIES DEPTH	MARCH			APRIL			MAY		
	A	B	C	A	B	C	A	B	C
----- % -----									
Pine	55	40	5	58	21	21	54	27	19
Maple	89	6	5	71	21	8	20	40	40
Locust	43	28	29	55	18	29	39	43	18
Pine-Maple	27	18	55	59	22	19	35	35	30
Pine	37	33	29	61	29	18	35	35	30
Maple	17	2	80	54	25	21	38	30	32
Pine-Locust	53	32	15	50	42	8	46	32	22
Pine	55	32	13	56	38	6	55	24	21
Locust	44	34	22	42	47	11	32	44	24
STAND/SPECIES DEPTH	JUNE			JULY			AUGUST		
	A	B	C	A	B	C	A	B	C
Pine	48	25	27	60	30	10	59	24	17
Maple	24	45	31	60	16	24	45	32	23
Locust	63	23	14	47	41	12	45	35	20
Pine-Maple	49	39	12	49	29	22	44	24	32
Pine	46	30	24	37	38	25	48	33	19
Maple	84	16	0	59	21	20	36	6	58
Pine-Locust	49	29	22	55	30	15	57	22	21
Pine	51	27	22	67	26	7	67	19	14
Locust	41	38	21	28	39	33	45	25	30
STAND/SPECIES DEPTH	SEPTEMBER			SEPTEMBER (CONTINUED)					
	A	B	C	DEPTH	A	B	C		
Pine	65	23	12	Pine-Maple	48	29	23		
Maple	41	42	17	Pine	59	21	20		
Locust	34	50	16	Maple	22	49	29		
				Pine-Locust	55	23	22		
				Pine	66	23	11		
				Locust	35	23	42		

Table 4.7 Monthly fine root (<2mm) production estimated at monthly intervals from April-September during the third (1991) growing season for loblolly pine, red maple, and black locust in pure and mixed stands of herbaceous control treatments. Standard errors are included in parentheses.

STAND/SPECIES	APRIL-MAY	MAY-JUNE	JUNE-JULY
----- Mg/Ha -----			
Pine	.321 (.100)	.212 (.050)	.381 (.217)
Maple	.040 (.038)	.199 (.104)	.123 (.051)
Locust	.117 (.055)	.209 (.068)	.089 (.023)
Pine-Maple	.184 (.065)	.270 (.153)	.220 (.116)
Pine	.170 (.067)	.234 (.163)	.014 (.010)
Maple	.014 (.007)	.036 (.022)	.206 (.121)
Pine-Locust	.462 (.219)	.352 (.149)	.123 (.037)
Pine	.279 (.126)	.309 (.123)	.041 (.024)
Locust	.184 (.095)	.043 (.030)	.082 (.016)

STAND/SPECIES	JULY-AUGUST	AUGUST-SEPTEMBER	TOTAL
----- Mg/Ha -----			
Pine	.204 (.100)	.175 (.127)	1.293
Maple	.069 (.015)	.391 (.295)	0.822
Locust	.065 (.017)	.148 (.167)	0.628
Pine-Maple	.354 (.083)	.409 (.083)	1.437
Pine	.240 (.035)	.254 (.062)	0.912
Maple	.114 (.083)	.155 (.044)	0.525
Pine-Locust	.394 (.044)	.563 (.144)	1.894
Pine	.175 (.047)	.378 (.138)	1.182
Locust	.219 (.024)	.185 (.148)	0.713

Table 4.8 Distribution of fine root (<2mm) production collected at monthly intervals during the third (1991) growing season for loblolly pine, red maple, and black locust in pure and mixed stands in herbaceous control treatments. Letters correspond to depth increments: A = 0-10 cm, B = 10-20 cm, C = 20-30 cm.

STAND/SPECIES	APRIL-MAY			MAY-JUNE			JUNE-JULY		
DEPTH	A	B	C	A	B	C	A	B	C
	----- % -----								
Pine	51	36	13	44	33	23	65	29	6
Maple	8	42	50	30	40	30	77	12	11
Locust	15	62	23	71	21	8	10	71	19
Pine-Maple	5	51	44	60	28	12	44	33	23
Pine	4	52	44	58	28	14	29	44	27
Maple	11	37	52	72	28	0	45	33	22
Pine-Locust	45	23	32	44	27	29	25	45	30
Pine	48	19	33	47	28	25	45	49	6
Locust	29	41	30	26	20	54	15	43	42

STAND/SPECIES JULY-AUGUST AUGUST-SEPTEMBER

DEPTH	A	B	C	A	B	C
	----- % -----					
Pine	33	31	36	74	14	12
Maple	7	58	35	39	48	13
Locust	18	43	39	36	53	11
Pine-Maple	42	20	38	47	27	26
Pine	46	27	27	67	6	27
Maple	33	6	61	16	60	24
Pine-Locust	45	30	25	54	12	34
Pine	35	35	30	74	16	10
Locust	53	26	21	12	4	84

which reached 2 m or more from the stem. Most locust fine roots were sparsely-branched, had nodules of *Rhizobium* spp. bacteria, and were located near the stem.

Specific leaf area of loblolly pine and red maple was significantly greater with herbaceous vegetation compared to herbaceous control stands, but herbaceous vegetation did not appear to significantly affect the specific leaf area of black locust (Table 4.9). Specific leaf area of red maple also appeared to be greater in pure stands compared to foliage of red maple trees in mixtures with pine. Although not statistically significant at $p = .10$, there is some evidence that specific leaf area was lower for pines planted with black locust compared to those planted with red maple and also that black locust specific leaf area was greater in mixed stands compared to pure stands.

Leaf area per tree predicted from specific leaf area regressions and foliage biomass from excavated seedlings indicated that leaf area was reduced for all species by herbaceous vegetation, particularly hardwood species (Figure 4.15). Loblolly pine had the greatest leaf area of all species and was not generally affected by stand type. There was a trend for greater leaf area of red maple and black locust in mixtures with pine compared to pure stands, but it was not statistically significant.

Measures of efficiency in biomass allocation include stem growth efficiency which is calculated as mean tree stem volume per unit leaf area, and the efficiency of conversion to stem volume per total tree biomass (Table 4.10). As calculated here, growth efficiency is similar to the Growth Efficiency Index (GEI) of Waring (1983), which is stem biomass production per unit leaf area. The high growth efficiency of black locust is probably an artifact of the reduction in leaf area occurring through midsummer for this species. Pine growth efficiency was not affected by herbaceous vegetation, but increased slightly in mixed stands compared to pure stands. Red maple growth efficiency was not significantly affected statistically by herbaceous or tree stand composition treatments, but red maple growth efficiency appeared to be somewhat higher in herbaceous control compared to herbaceous vegetation. Loblolly pine had the greatest mean tree stem volume per mean total biomass of all species, which generally increased in herbaceous vegetation compared to control treatments (Table 4.10).

Table 4.9 Leaf area in cm predicted by zero-intercept regressions on leaf weight in g for loblolly pine, red maple, and black locust for various stand-herbaceous treatment combinations. Probability values indicate level of difference between slope coefficients (b) for the two treatments being compared.

Loblolly Pine

Treatment Combinations	b	R ²	P Value
With locust or with maple	95.03	.9663	
With locust	91.47	.9529	.1897
With maple	98.72	.9814	
In mixed stands or pure stands	93.53	.9688	
Mixed stands	95.02	.9633	.8151
Pure stands	90.98	.9747	
In control stands or herb. stands	93.53	.9688	
Control stands	90.71	.9678	.0560
Herbaceous stands	96.78	.9719	

Red Maple

Treatment Combinations	b	R ²	P Value
In mixed stands or pure stands	93.11	.9684	
Mixed stands	90.48	.9687	.0832
Pure stands	95.33	.9685	
In control stands or herb. stands	93.11	.9684	
Control stands	89.64	.9762	.0084
Herbaceous stands	121.75	.9945	

Black Locust

Treatment Combinations	b	R ²	P Value
In mixed stands or pure stands	119.80	.9714	
Mixed stands	126.50	.9806	.1463
Pure stands	113.68	.9669	
In control stands or herb. stands	119.80	.9714	
Control stands	126.88	.9786	.3439
Herbaceous stands	109.09	.9722	

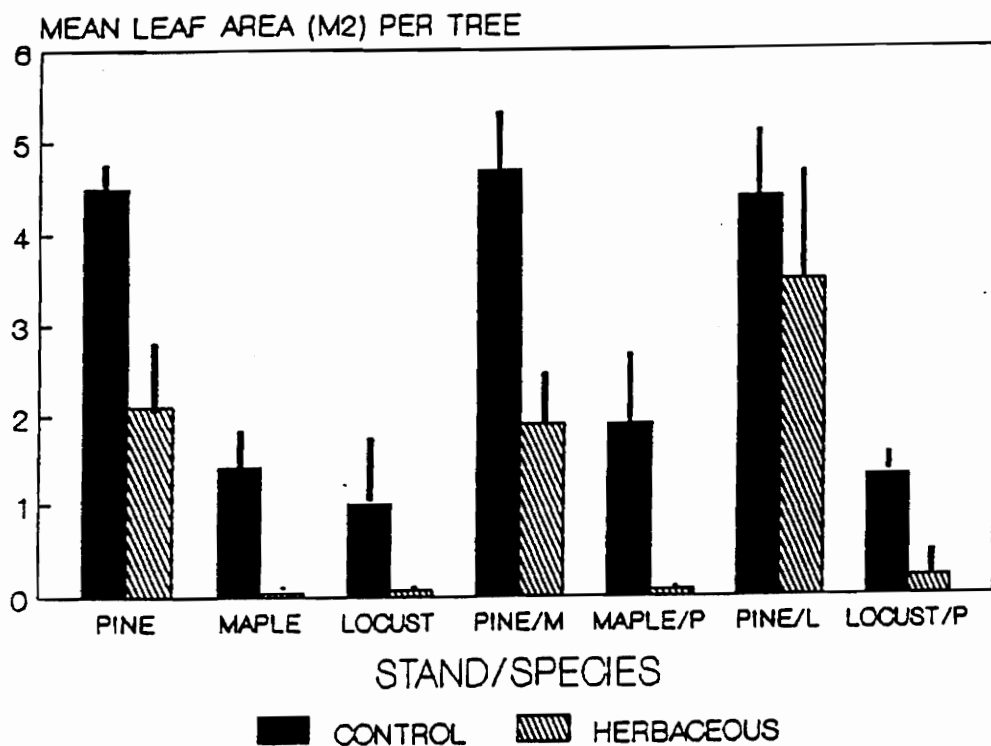


Figure 4.15 Mean leaf area and standard error per tree of species in pure stands and 50:50 mixtures in herbaceous control and herbaceous vegetation treatments. For mixed stands, species is indicated along with first letter of associate (P = Pine, M = Maple, and L = Locust).

Table 4.10 Growth Efficiency (Mean tree stem volume per unit leaf area) and mean stem volume per total biomass of tree species in pure and mixed stands in control and herbaceous treatments. Standard errors are included in parentheses.

STAND/SPECIES	Growth Efficiency	Stem volume/ Total biomass
	--- cm ³ /cm ² ---	----- cm ³ /g -----
<u>CONTROL TRT</u>		
Loblolly Pine	.034 (.006)	1.19 (.281)
Red Maple	.026 (.006)	0.85 (.175)
Black Locust	.073 (.018)	0.88 (.172)
Pine-Maple		
Loblolly Pine	.041 (.002)	1.52 (.110)
Red Maple	.029 (.017)	0.82 (.459)
Pine-Locust		
Loblolly Pine	.054 (.020)	2.02 (.729)
Black Locust	.093 (.042)	1.25 (.371)
<u>HERBACEOUS TRT</u>		
Loblolly Pine	.033 (.004)	1.41 (.146)
Red Maple	.021 (.004)	0.53 (.156)
Black Locust	.117 (.059)	1.08 (.292)
Pine-Maple		
Loblolly Pine	.040 (.017)	1.58 (.059)
Red Maple	.020 (.005)	0.49 (.063)
Pine-Locust		
Loblolly Pine	.020 (.003)	0.96 (.094)
Black Locust	.040 (.008)	0.86 (.106)

Red maple had the lowest stem volume-biomass ratio and it decreased due to herbaceous vegetation. No consistent trends in black locust stem volume-biomass ratios were apparent.

Resource Use and Resource Availability

Light availability in herbaceous control stands was greater in pure pine stands than in pure hardwood stands (Figure 4.16). Pines received less light in mixtures with black locust than in pure stands, particularly during midday and afternoon (Figures 4.16 and 4.17). In mixtures with red maple, however, light reception by pine was apparently not much different from pure pine stands. Light availability to hardwoods in mixture with pine was not greatly reduced in herbaceous control stands. In stands with herbaceous vegetation (Figures 4.18 and 4.19), shading by trees was reduced because the height and canopy dimensions of trees were smaller than in herbaceous control stands, although some minor reduction in light availability occurred to the smaller hardwood trees in herbaceous vegetation. Light levels were similar among pure stands (Figure 4.18), yet both red maple and black locust trees received shade from pines in mixed stands (Figure 4.19). Neither hardwood species reduced light availability to pine in herbaceous vegetation.

Crown morphology of tree species in herbaceous control stands appeared to be affected by stand composition which was measured on the best site of the study area. Generally, trees in the mixed stands had larger crown widths, crown heights, and total tree heights than trees in pure stands (Tables 4.11 and 4.12). Loblolly pine trees tended to have greater live crown ratios and reduced heights at largest canopy dimension in the pure stand and the mixtures with red maple than in mixtures with black locust (Table 4.11). Pines also had greater crown width and total height in mixtures with black locust compared to mixtures with red maple.

Black locust total tree height and crown height at largest dimension were not significantly affected by pine proportion (Table 4.12). However, there was a tendency for greater live crown ratios and greater crown widths for black locust trees in the plots with higher pine proportion. Red maple live crown ratios were not significantly affected by pine proportion

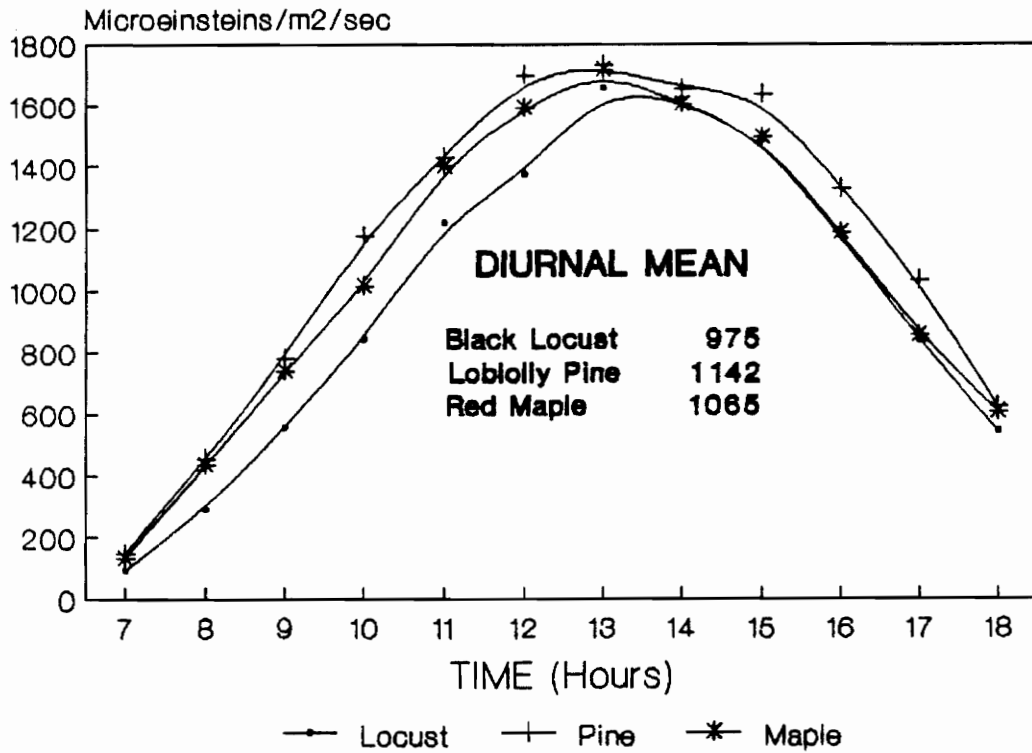


Figure 4.16 Mean light availability in pure stands in the herbaceous control treatment.

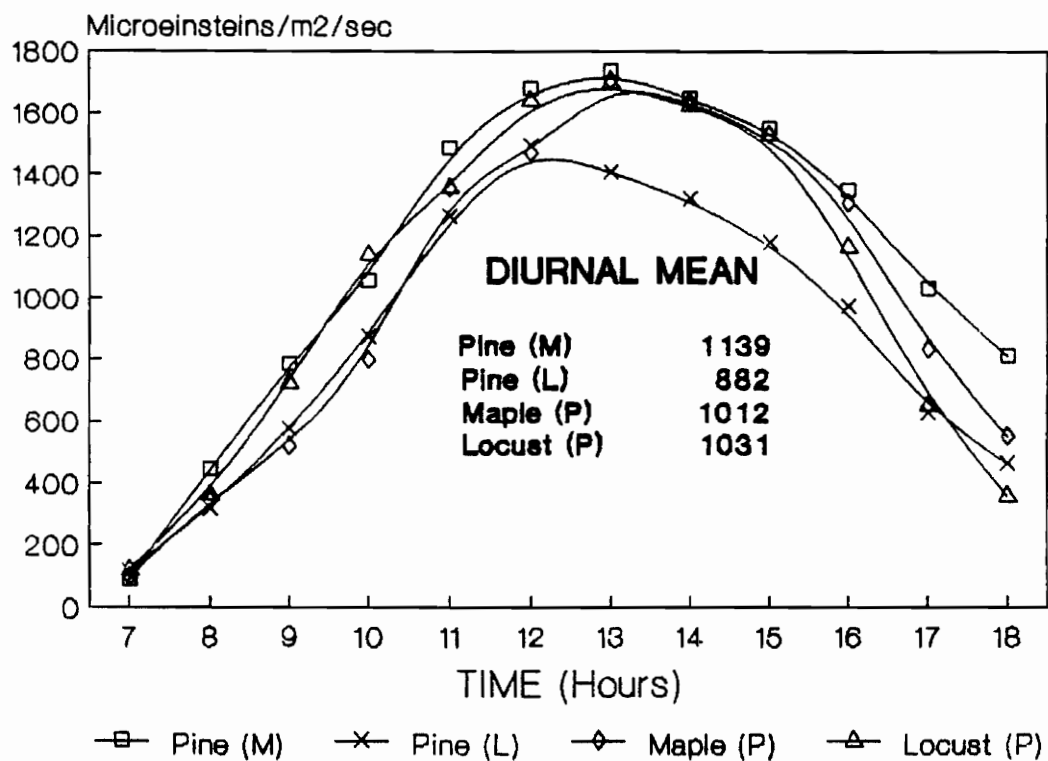


Figure 4.17 Mean light availability in mixed stands in the herbaceous control treatment. Associate species is indicated in parentheses.

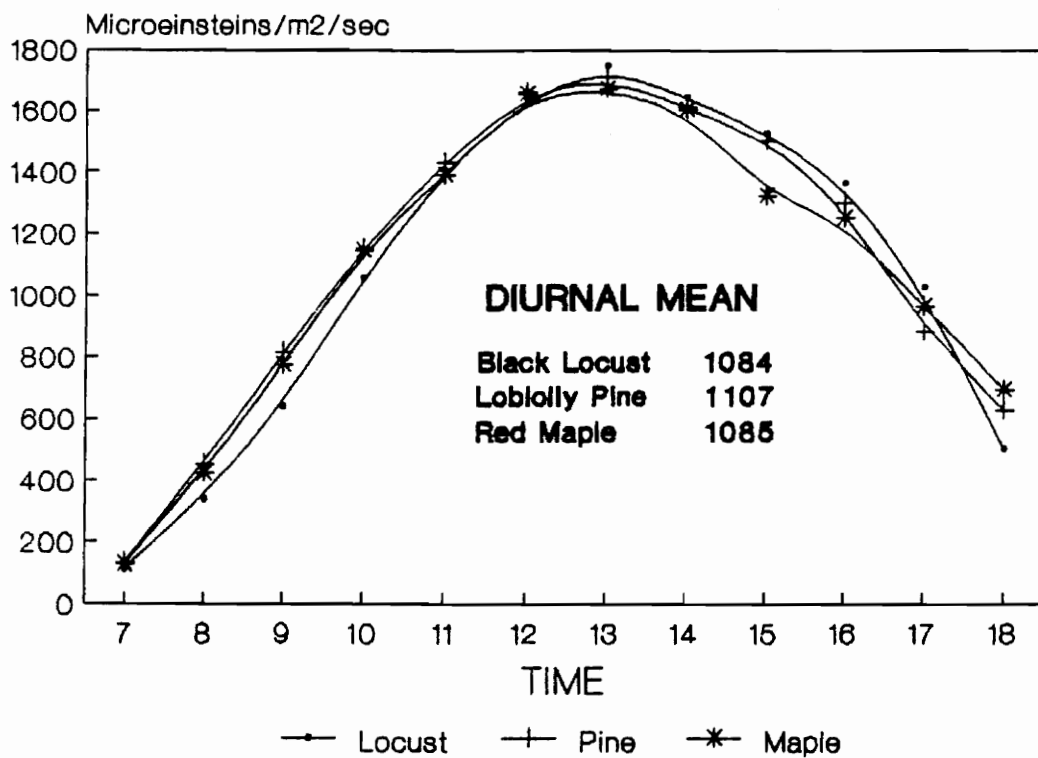


Figure 4.18 Mean light availability in pure stands with herbaceous vegetation.

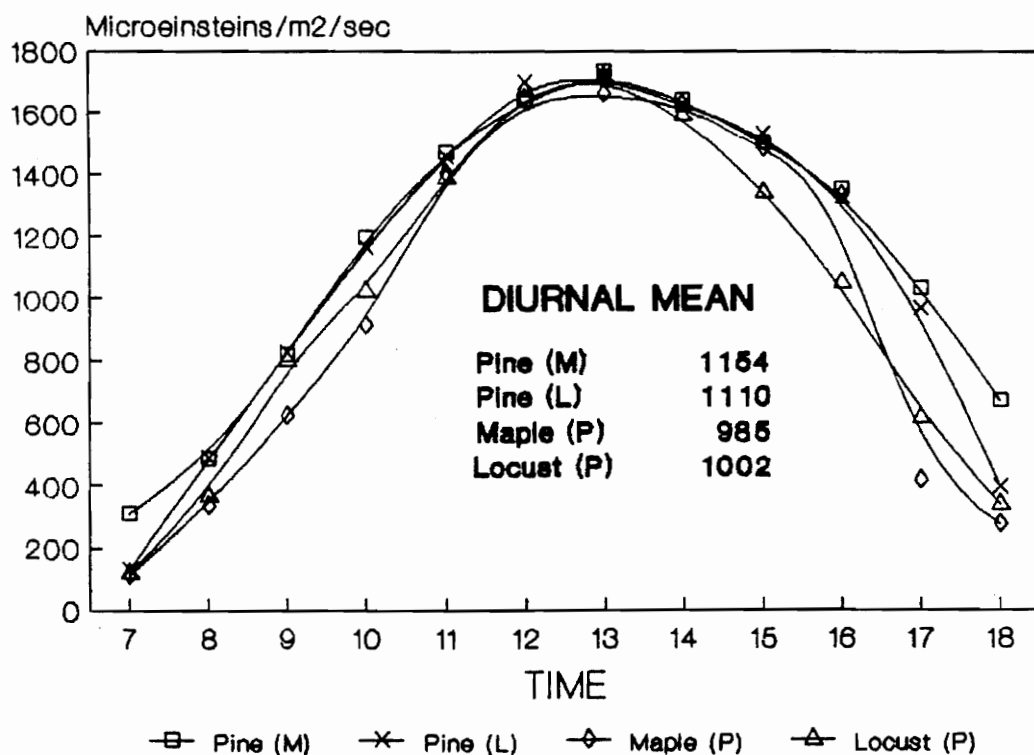


Figure 4.19 Mean light availability in mixed stands with herbaceous vegetation. Associate species is indicated in parentheses.

Table 4.11 Influence of type and proportion of hardwood associate on canopy morphology of individual pines on one block of the study. Measures include live crown ratio (LCR), height at largest diameter of crown (HLD), mean crown radius (MCR), and total tree height (TTH). Means with the same letter within the same column are not significantly different using Duncan's multiple range test.

Stand Composition	LCR	HLD	MCR	TTH
			----- m -----	
100% Pine	.886 ab	.388 bc	.496 b	2.055 b
75% Pine, 25% Maple	.878 ab	.374 c	.521 b	2.114 b
75% Pine, 25% Locust	.855 b	.511 a	.544 b	2.369 a
50% Pine, 50% Maple	.867 ab	.407 bc	.549 ab	2.100 b
50% Pine, 50% Locust	.858 b	.458 ab	.598 a	2.446 a
25% Pine, 75% Maple	.909 a	.400 bc	.495 b	2.046 b
25% Pine, 75% Locust	.853 b	.441 bc	.513 b	2.067 b

(Table 4.12), but there was a tendency for reduced crown height at largest dimension, increased crown width, and greater total tree height for maple in mixture with pine.

Pine crown shapes were not very different in mixtures with red maple compared to the pure stand, but pines mixed with black locust displayed more elliptical rather than conical crowns (Table 4.13). Inverse pyramidal shapes were generally more common for red maple with increasing pine proportion, but black locust crown shape was not affected by pine proportion in the stand.

Soil moisture conditions in May and July when photosynthetic measures were taken were different. In May, soil moisture was fairly high, while July readings were taken during a period of dry conditions. In the month preceding the May measurement, the site received 7.91 cm of rain, while in the month preceding the July measurement only 1.69 cm of rain was recorded. Despite the more favorable soil moisture conditions, photosynthetic rates were generally higher in July than in May (Table 4.14).

Significant differences in photosynthesis between stands during both measurement periods were detected between tree species type and herbaceous treatments, but photosynthetic rates for individual species did not differ significantly between pure and mixed stands (Table 4.14). The effect of herbaceous vegetation on tree photosynthesis was greatest for black locust. Overall, black locust averaged a 20% reduction in photosynthesis due to herbaceous vegetation, while pine and maple photosynthesis was reduced by an average of 2 and 10%, respectively. On both sample dates, a trend towards greater pine photosynthesis in pure stands compared to mixed stands on herbaceous control plots was observed. The opposite effect was observed on plots with herbaceous vegetation. Red maple had consistently higher photosynthetic rates in pure stands regardless of herbaceous treatment, although differences were not always statistically significant.

Midday water potentials in May were more negative for loblolly pine than for hardwoods in herbaceous control treatments, but were similar between species with herbaceous vegetation (Table 4.15). Herbaceous vegetation decreased the water potentials of hardwoods substantially, but did not significantly affect those of pines. In July, there was

Table 4.12 Influence of loblolly pine proportion on red maple and black locust canopy morphology including live crown ratio (LCR), height at largest diameter of crown (HLD), mean crown radius (MCR), and total tree height (TTH). Means with the same letter within the same column for each species are not significantly different using Duncan's multiple range test.

Stand Composition	LCR		HLD		MCR		TTH	
	----- m -----							
100% Red Maple	.889	a	.663	a	.420	b	1.226	b
75% Maple, 25% Pine	.877	a	.580	ab	.422	b	1.234	b
50% Maple, 50% Pine	.861	a	.499	b	.512	a	1.567	a
25% Maple, 75% Pine	.875	a	.537	b	.521	a	1.492	a
100% Black Locust	.681	ab	.653	a	.709	b	1.722	b
75% Locust, 25% Pine	.622	b	.608	a	.752	b	2.387	a
50% Locust, 50% Pine	.697	ab	.678	a	.759	b	2.511	a
25% Locust, 75% Pine	.727	a	.681	a	.930	a	2.708	a

Table 4.13 Subjectively estimated crown shape of tree species with differing stand composition.

Loblolly Pine		Crown Shape		
Stand Composition	Pyramid	Ellipse	Other	
	----- % -----			
Pure Pine	68	30	2	
With Maple	75	12	13	
With Locust	47	53	0	

Red Maple		Crown Shape		
Stand Composition	Inverse Pyramid	Other		
	----- % -----			
Pure Maple	53	47		
With 25% Pine	43	57		
With 50% Pine	58	42		
With 75% Pine	83	17		

Black Locust		Crown Shape		
Stand Composition	Inverse Pyramid	Other		
	----- % -----			
Pure Locust	100	0		
With 25% Pine	100	0		
With 50% Pine	90	10		
With 75% Pine	100	0		

Table 4.14 Mean tree photosynthetic rate measured on two dates during the third growing season for trees in pure and mixed stands in control and herbaceous treatments. Each measurement represents an average of two readings taken on three seedlings of each species at 1000 and 1400 hours on each sampling date. Standard errors are included in parentheses.

STAND/SPECIES	PHOTOSYNTHESIS	
	5/22/91	7/17/91
----- (uM/M ² /Sec) -----		
<u>CONTROL TREATMENT</u>		
Loblolly Pine	5.59 (.623)	8.42 (.235)
Red Maple	8.70 (1.848)	8.80 (1.313)
Black Locust	15.86 (.090)	16.82 (.797)
Pine-Maple		
Loblolly Pine	4.86 (.577)	8.12 (.981)
Red Maple	6.38 (.343)	8.15 (1.089)
Pine-Locust		
Loblolly Pine	4.92 (.433)	7.13 (.518)
Black Locust	10.02 (2.570)	20.17 (1.944)
<u>HERBACEOUS TREATMENT</u>		
Loblolly Pine	4.79 (.783)	5.41 (.546)
Red Maple	6.48 (.182)	9.17 (.182)
Black Locust	9.69 (3.182)	10.33 (2.766)
Pine-Maple		
Loblolly Pine	6.25 (1.167)	6.60 (.646)
Red Maple	5.87 (.336)	7.34 (.853)
Pine-Locust		
Loblolly Pine	5.34 (.370)	9.41 (3.622)
Black Locust	9.46 (1.679)	17.56 (.928)

a significant stand and herbaceous effect for predawn water potentials, but only the herbaceous effect was significant for midday water potentials. Black locust and pine predawn water potentials decreased in herbaceous stands, while those of red maple did not change. Midday water potentials decreased in herbaceous vegetation for all species in each stand.

Loblolly pine tended to have higher water-use efficiency than either hardwood species, except in herbaceous control treatment stands in July (Table 4.16). Black locust typically had higher water-use efficiency than red maple in all stands. No significant trends were observed for pine water-use efficiency in mixed stands compared to control treatments. On the other hand, hardwood species had higher water-use efficiencies in pure stands than in mixture with pine.

Nitrogen deficiencies were visually apparent in hardwood trees on herbaceous vegetation plots during the second and third growing seasons, especially during periods of drought. Foliage of red maple and black locust trees became light green to yellow in color, a symptom of nitrogen deficiency (Erdmann et al. 1979). Foliage of hardwood trees on herbaceous control plots had a much darker green color.

No significant differences were found in foliar nitrogen levels for a given species due to stand composition, except that pine growing with herbaceous vegetation had a greater level of foliar nitrogen in pure stands than pine in mixture with either hardwood species (Table 4.17). Pine in pure stands with herbaceous vegetation also had higher foliar nitrogen levels than pine in similar stands in herbaceous control treatments. Pine in mixed stands did not significantly differ in foliar nitrogen between herbaceous treatments. Foliar nitrogen of hardwood species, however, was substantially lower in all stands with herbaceous vegetation compared to herbaceous control treatments. Results were conflicting between the nitrogen-use efficiency measures calculated in this study (Table 4.17). If expressed as photosynthesis per unit of foliar nitrogen, pine tended to have higher nitrogen-use efficiency than hardwoods in herbaceous control treatments, but not in herbaceous vegetation treatments. However, if expressed as total biomass per unit of foliar nitrogen, pine had consistently higher nitrogen-use efficiency than hardwoods, especially in herbaceous vegetation treatments.

Table 4.15 Mean leaf water potentials measured on two dates during the third growing season for trees in pure and mixed stands in control and herbaceous treatments. Predawn measures were recorded between 0400 and 0600 hours. Midday measures were recorded between 1100 and 1300 hours. Each measurement represents an average of readings taken on three seedlings of each species, except for predawn readings taken on 5/22/91 which include only one measurement. Standard errors are included in parentheses.

STAND/SPECIES	LEAF WATER POTENTIALS			
	5/22/91		7/17/91	
	Predawn	Midday	Predawn	Midday
----- (-MPa) -----				
<u>CONTROL TRT</u>				
Loblolly Pine	.15	.73 (.07)	.30 (.10)	1.08 (.21)
Red Maple	.15	.50 (.01)	.23 (.03)	.85 (.12)
Black Locust	.20	.33 (.02)	.18 (.08)	.87 (.03)
Pine-Maple				
Loblolly Pine	.15	.98 (.09)	.18 (.08)	1.10 (.18)
Red Maple	.25	.70 (.15)	.23 (.03)	0.82 (.09)
Pine-Locust				
Loblolly Pine	.20	.78 (.09)	.28 (.08)	1.18 (.02)
Black Locust	.15	.42 (.04)	.13 (.03)	1.07 (.22)
 <u>HERBACEOUS TRT</u>				
Loblolly Pine	.25	.88 (.04)	.48 (.08)	1.32 (.19)
Red Maple	.20	.72 (.06)	.15 (.05)	1.80 (.46)
Black Locust	.15	.72 (.12)	.30 (.10)	1.78 (.27)
Pine-Maple				
Loblolly Pine	.25	.83 (.04)	.23 (.03)	1.42 (.28)
Red Maple	.10	.82 (.04)	.28 (.08)	2.03 (.37)
Pine-Locust				
Loblolly Pine	.15	.78 (.04)	.40 (.05)	1.53 (.17)
Black Locust	.10	.73 (.03)	.40 (.10)	1.58 (.09)

Table 4.16 Mean tree water-use efficiency measured on two dates during the third growing season for trees in pure and mixed stands in control and herbaceous treatments. Each measurement represents an average of two readings taken on three seedlings of each species at 1000 and 1400 hours on each sampling date. Standard errors are included in parentheses.

STAND/SPECIES	WATER-USE EFFICIENCY	
	5/22/91	7/17/91
	---(uM Photosynthesis/ Moles Transpiration)---	
<u>CONTROL TREATMENT</u>		
Loblolly Pine	.596 (.058)	.791 (.065)
Red Maple	.496 (.023)	.944 (.213)
Black Locust	.521 (.138)	.845 (.062)
Pine-Maple		
Loblolly Pine	.673 (.073)	.787 (.064)
Red Maple	.342 (.017)	.778 (.073)
Pine-Locust		
Loblolly Pine	.576 (.027)	.777 (.034)
Black Locust	.420 (.013)	.894 (.114)
<u>HERBACEOUS TREATMENT</u>		
Loblolly Pine	.601 (.083)	.681 (.100)
Red Maple	.249 (.039)	.566 (.108)
Black Locust	.298 (.106)	.617 (.210)
Pine-Maple		
Loblolly Pine	.565 (.180)	.756 (.132)
Red Maple	.224 (.038)	.556 (.068)
Pine-Locust		
Loblolly Pine	.592 (.126)	.798 (.109)
Black Locust	.353 (.048)	.571 (.106)

Table 4.17 Mean foliar nitrogen content, photosynthetic nitrogen-use efficiency, and yield-based nitrogen-use efficiency during the third growing season for trees in pure and mixed stands in control and herbaceous treatments. Standard errors are included in parentheses.

STAND/SPECIES	Foliar N content	Ps / Foliar N	Total Biomass / Foliar N
	% of Leaf Biomass	Ps / PPM N	Kg / PPM N
<u>CONTROL TREATMENT</u>			
Loblolly Pine	1.37 (.21)	2.75 (.57)	.473 (.155)
Red Maple	2.42 (.17)	1.54 (.60)	.088 (.053)
Black Locust	4.59 (.28)	1.54 (.04)	.063 (.010)
Pine-Maple			
Loblolly Pine	1.56 (.16)	1.96 (.27)	.220 (.161)
Red Maple	2.31 (.21)	1.56 (.44)	.198 (.019)
Pine-Locust			
Loblolly Pine	1.53 (.17)	2.05 (.15)	.361 (.057)
Black Locust	3.89 (.47)	2.20 (.29)	.047 (.004)
<u>HERBACEOUS TREATMENT</u>			
Loblolly Pine	2.06 (.18)	1.14 (.005)	.060 (.013)
Red Maple	1.48 (.11)	1.89 (.05)	.004 (.0003)
Black Locust	3.21 (.25)	1.07 (.33)	.002 (.0001)
Pine-Maple			
Loblolly Pine	1.44 (.19)	1.80 (.26)	.100 (.021)
Red Maple	1.25 (.18)	2.63 (.32)	.009 (.0002)
Pine-Locust			
Loblolly Pine	1.64 (.26)	1.63 (.46)	.094 (.008)
Black Locust	3.31 (.43)	2.34 (.39)	.005 (.0003)

Table 4.18 Strength of relationship between stand stem volume and physiological and morphological variables using regression analysis with all species, pines only, or hardwoods only for both pure stands and 50:50 mixtures of pine and hardwoods. Coefficients of determination (R^2) and probability values for regressions are presented. Asterisks indicate that a logarithmic transformation was applied to the dependent variable - stand stem volume.

VARIABLE	ALL STANDS		PINES ONLY		HARDWOODS ONLY	
	R^2	P	R^2	P	R^2	P
Photosynthesis	.31	.1915	.93	.1764	.98	.0079
Leaf Water Potential	.80	.0061	.19	.4395	.36	.4026
Water-use Efficiency*	.85	.0001	.01	.9955	.18	.5747
Foliar Nitrogen	.44	.1022	.88	.2283	.99	.0066
Photosynthetic N-use Efficiency	.35	.1635	.91	.2008	.12	.6540
Yield-based N-use Efficiency	.56	.0539	.48	.5116	.63	.2062
Growth Efficiency	.01	.8034	.78	.3081	.75	.1336
Fine Root Biomass	.84	.0039	.32	.6202	.33	.4299
Root:Shoot Ratio*	.96	.0001	.96	.1345	.97	.0001
Leaf Area	.90	.0001	.09	.8011	.85	.0762

Of all physiological and morphological variables used to predict stand stem volume yield, root-shoot ratio, leaf area, and water-use efficiency were the most closely-related to yield ($p=.0001$) (Table 4.18). Fine root biomass, leaf water potential, and yield-based nitrogen-use efficiency also showed a significant relation to stand stem volume yield at ($p=.10$). Stepwise regression of all variables indicated that root-shoot ratio alone explained 94% of the variation in stand stem volume yield. Other significant variables in the model were leaf area and water-use efficiency, but these variables only accounted for an additional 3% of the variation in the model.

Discussion

After three growing seasons, stand yield was largely a function of species-specific yield and interference from herbaceous vegetation. The impact of pine-hardwood interference interactions had a smaller influence on stand yield. The effect of stand composition was the greatest in duration of main effects for all yield measures (Table 4.1) and the magnitude of its effect can be attributed to the large difference between the species with the highest yield, loblolly pine, and the species with the lowest yield, red maple. Differences in aboveground stem volume yield were greater than yield in total biomass (Table 4.2) since loblolly pine had the lowest root-shoot ratio of all species, and also had greater stem volume per total tree biomass (Table 4.10). The yield of all stands was affected significantly by herbaceous vegetation, but not until the second growing season. This delayed onset of an herbaceous effect is most likely attributable to the delayed onset of herbaceous vegetation establishment.

An interactive effect of stand composition with herbaceous vegetation treatment was evident during the second and third growing seasons, which was driven by the proportionately greater effect of herbaceous vegetation on the yield of hardwood species compared to pine. Hardwood species are extremely sensitive to herbaceous interference until canopy closure

(Kellison 1985, Miller 1987). Interestingly, mortality was not significantly affected by herbaceous vegetation. These results are similar to those observed in a study by Bowersox and McCormick (1987) with white pine (*Pinus strobus* L.), hardwood seedlings, and herbaceous vegetation. In that study, fern and grass vegetation affected the growth of planted hardwoods to a much greater degree than planted white pine seedlings, yet mortality of all species was not influenced by herbaceous vegetation. Although herbaceous vegetation is cited as a cause of plantation failure (Gjerstad and Barber 1987), high seedling survival may allow for the salvage of plantations impacted by herbaceous vegetation by releasing them from herbaceous interference in subsequent growing seasons. The greater yield reduction of hardwood tree species compared to pines also implies that silviculturalists should increase the pine component in mixed stands unless silvicultural systems incorporate herbaceous vegetation control. The pine component should perhaps be increased in any case, since pine attains much higher yield than hardwood species on most sites in the Southeast, particularly on upland sites (Kellison 1985, Gjerstad and Barber 1987).

The high yield of stands composed largely of loblolly pine and/or black locust compared to stands with red maple is not surprising since these shade-intolerant, early successional species are typified by very rapid early growth (Baker and Langdon 1990, Huntley 1990), while red maple is a mid-successional, shade-tolerant species (Walters and Yawney 1990). Similar growth patterns and shade-tolerance for pine and locust, however, may ultimately lead to less compatible mixtures than with pine and red maple. Mixed stands are generally most compatible when species differ in height, with the understory species more tolerant of shade than the overstory species (Smith 1986). A greater degree of niche partitioning for light is achieved in these stands, resulting in reduced competition for light. Stratification of species may also allow for multiple harvests as each species reaches maturity in the overstory (Smith 1986, Oliver and Larson 1990).

While less efficient light partitioning and greater light competition would be expected in pine-locust mixtures due to the similar height of these species, a more efficient crown morphology appears to have resulted for pines with black locust. These changes in

morphology may influence competition for light in subsequent growing seasons. Changes in crown morphology observed for pine in mixture with black locust compared to pines with red maple or in pure pine stands indicate a reduction in live crown ratio, but larger crown heights and volumes due to increased total tree height and larger crown diameters (Table 4.11). Crown height appears to be closely related to efficiency in light collection (Jahnke and Lawrence 1965, Grace 1988). However, this increased light collecting efficiency may become unimportant if pine photosynthetic capacity is severely reduced due to shading from locust.

In the second growing season, pine grew better with locust than by itself or with red maple, possibly due to enhanced nutrition from nitrogen-fixation or accelerated nutrient cycling which has been attributed to black locust (Boring and Swank 1984, Huntley 1990). However, during the third growing season, black locust caused a great degree of light reduction to pine in mixed stands of herbaceous control treatments (Figure 4.17) which probably accounted for the disappearance of a positive effect on pine growth from black locust after the third year (Figure 4.14). The effect of locust shading on pine yield may have been more severe if not for a continual decrease in leaf area of locust beginning in June, which increased light availability to pines and may have allowed some recovery in yield.

Future yield of pine in black locust stands will likely be the result of the trade-off between nutrient addition vs. light reduction caused by black locust. Haines et al. (1978) and Dickman et al. (1985) found a similar cost-benefit situation in mixtures of sycamore (*Platanus occidentalis* L.) and black locust. In Oregon, Shainsky (1988) concluded that any benefits of nitrogen fixation from red alder for Douglas-fir were masked by competition for resources by red alder. The balance of the trade-off between enhanced nutrition and light competition for pines with black locust may be altered significantly by the proportion of locust in stands in upcoming growing seasons. A reduced locust proportion, such as 75% pine-25% locust mixtures, may decrease the amount of canopy overlap and light reduction to pine, while still maintaining some nutritional benefits. With increasing locust proportion, there is a greater possibility of pines being overtopped and suppressed by the joining of inversely-pyramidal black locust crowns. It is probable that the competitive impact of black locust will decline with

time due to damage from locust borer, which is evident in all stands in the field study. Borer infestation results in crown breakage and dieback due to interference with vascular transport (Craighead 1939, Hall 1942, Roach 1958). Borer damage may also contribute to the mid-summer defoliation in black locust observed in this study. Borer-induced decline may allow for the eventual release of overtopped pines in pine-locust mixtures. It is also probable that the interference effects of black locust on pine would have been substantially less if not for the control of locust leafminer, and possible reduction of locust borer populations, by lindane applications.

Loblolly pine appeared to ameliorate the negative effects of herbaceous interference on hardwood species in some situations. Black locust trees appeared to have increased stem volume yield with increasing pine proportion. Red maple stem volume and height increased with increasing pine proportion, but canopy volume was reduced. The taller height of pines in herbaceous vegetation may have increased shading of herbaceous vegetation, reducing its interference effect on hardwoods. In addition, partial shading of hardwood seedlings may have reduced respiration and transpiration rates of hardwoods, since these processes are temperature-dependent (Kramer 1983). Although not always statistically significant, air temperatures taken during July photosynthetic measurements were consistently lower near hardwood species in mixed stands compared to those in pure stands in herbaceous vegetation for both morning and afternoon measurements. Overall, mean cuvette air temperatures averaged approximately 1 degree C lower near hardwoods in mixed stands (34.96 C) compared to pure stands (35.95 C) in herbaceous vegetation. Pine and black locust stands had higher yield when planted together with herbaceous vegetation compared to pure stands of each species on poorer sites. Most of this increase is due to improved black locust yield. The reason for increased pine yield in pine-locust mixtures is unclear, since pine did not have greater foliar nitrogen levels in mixtures with black locust compared to those in pure stands in herbaceous treatments (Table 4.17). However, increased pine growth in mixtures with black locust may have reduced foliar nitrogen concentration back to levels comparable to those of pine in pure stands.

The increase in pine and maple specific leaf area in trees with herbaceous vegetation compared to control treatments (Table 4.9) is similar to results from other studies (Zutter et al. 1986a, Elliot and White 1991). Increases in specific leaf area may be due to reduced formation of structural tissue in favor of increased leaf area under conditions of nutrient and moisture limitation caused by competition with herbaceous vegetation. Brand (1986b) concluded that specific leaf area was a good indicator of competitive stress for Douglas-fir. For black locust, specific leaf area estimates were highly variable and not statistically significant. Yet, there was a trend observed for higher specific leaf area in herbaceous control treatments, the opposite of that observed for pine and maple. This trend is similar to that observed for black locust seedlings receiving control leachates compared to fescue leachates in an allelopathy experiment (Chapter III, this volume), indicating that black locust specific leaf area may be influenced more by allelopathy than resource competition from fescue. The relationship between locust specific leaf area and interference treatments is masked, however, by leaf drop of this species in the middle and late growing season. Less of an effect on specific leaf area was observed between tree species in pure vs. mixed stands. The greater specific leaf area of red maple trees in pure stands is counterintuitive since shading was greater for maple in mixtures with pine and a shift to greater specific leaf area would be expected under these conditions (Logon and Krotkov 1968, Kolb et al. 1990, Lei and Lechowicz 1991). In the reduced light environment of mixtures with locust in herbaceous control stands, pine had greater specific leaf area, but differences were not significant.

Changes in specific leaf area related to the light environment of mixed stands combined with changes in crown morphology can have a large influence on interference outcomes. The ability of trees to plastically change canopy morphology may determine competitive ability for light (Hutchings and Budd 1981, Grime et al. 1986). Greater light reduction caused by black locust compared to red maple or loblolly pine resulted in an upward shift in pine crowns. Binkley (1984) noted a similar shift in Douglas-fir seedlings planted with red alder compared to pure stands. Red maple crowns also plastically responded to changes in light in mixtures with pine compared to pure stands by an upward shift in the canopy and

also through a greater lateral extension of branches which would not be advantageous in competition with other similarly-formed red maple trees. Black locust crown morphology in herbaceous control stands did not adjust to interference from pine. However, the inversely-pyramidal crowns of locust were probably not influenced much by conically-shaped pines of similar height. Black locust trees may also plastically respond to interference by adjustment in leaf area. Compound leaves have been likened to cheap, disposable branches which are rapidly constructed to exploitatively capture light in rapidly changing light environments of forest canopies in early and mid-succession (Givnish 1978). After failing to provide a positive photosynthetic balance, they are rapidly discarded through foliar abscission.

Differences in photosynthetic rates were related more to inherent differences in species rather than to interference. Photosynthesis was generally reduced for species in herbaceous vegetation compared to control stands, particularly hardwoods in pure stands (Table 4.14), but, as is generally the case (Waring and Schlesinger 1985), decreased photosynthesis could not fully account for differences in yield. The lack of direct correlation between efficiency in carbon fixation and yield can be accounted for by differences in conversion efficiency due to factors such as respiration, temporal patterns in assimilation efficiency not reflected by photosynthetic measurements, the influence of total tree photosynthetic capacity (leaf area), and different structural costs of tissue production (Ledig and Perry 1969, Canham and Marks 1985, Waring and Schlesinger 1985, Teskey et al. 1987). The smaller reduction in hardwood tree photosynthesis caused by herbaceous vegetation in mixture with pine compared to pure stands may again reflect the influence of partial shading by pines which increased photosynthetic efficiency, conversion to biomass, and/or reduced water loss.

The impact of herbaceous competition on trees for belowground resources is undoubtedly increased by the high degree of overlap between tree and herbaceous fine root systems. In this study, the majority of herbaceous roots (59%) are located in the upper 10 cm of the soil, while nearly 50% of tree roots recovered in cores from herbaceous control stands were located there. Excavation of trees in herbaceous stands also indicated that most tree

fine roots were located in the upper soil layer. No quantification of shifts in tree fine root distribution was attempted in herbaceous stands, because of the difficulty in sorting hardwood fine roots from herbaceous roots in core samples. However, even if trees shift fine root distribution to lower depths in the soil to avoid intense competition from herbaceous roots, their growth will probably be reduced compared to that of herbaceous control plots because of the probable decrease in aeration and fertility encountered with increasing depth with the soils in this study.

In general, hardwoods had higher root-shoot ratios than pines and this trend was magnified in herbaceous treatments (Table 4.2). Pine tolerance to herbaceous vegetation compared to hardwoods in this study is exemplified by the lack of a large biomass reallocation. Pine allocated only a slightly greater percentage of biomass to foliage and fine roots in herbaceous vegetation compared to herbaceous control treatments. From analysis of covariance results, shifts in black locust root-shoot ratios in herbaceous vegetation appear to be largely related to size. It is common for root-shoot ratios to change with tree size (Ledig and Perry 1966, Ledig et al. 1970, Kozlowski et al. 1991) and hardwood seedlings in herbaceous vegetation treatments were smaller than those in herbaceous control treatments. However, differences in root-shoot ratios for red maple trees due to herbaceous treatment was still statistically significant after the effect of size was removed, indicating that a significant shift in biomass allocation was attributable to herbaceous vegetation. Both hardwood species had lower root-shoot ratios in mixture with pine compared to pure stands in herbaceous vegetation. These observed shifts in root-shoot ratios may reflect a response to competition (Caldwell 1987, Feldman 1988), where intense belowground competition with herbaceous vegetation causes a shift in biomass allocation belowground. This shift may be modified somewhat, however, when aboveground competition for light is present with loblolly pine.

Analysis of biomass partitioning in tree species in herbaceous control compared to herbaceous vegetation treatments generally support Waring's (1983) hypothesis of a hierarchy of carbon partitioning for trees under stress. According to the hypothesis, trees allocate more

biomass to foliage and fine roots under stress than branches or larger roots. The stem is lowest in the partitioning hierarchy. All tree species in this experiment had a greater percentage of biomass in foliage and fine roots in herbaceous vegetation compared to herbaceous control treatments (Table 4.2). Growth efficiency was higher for loblolly pine and red maple with herbaceous control than with herbaceous vegetation, but these differences were not significant at $p = .05$ (Table 4.10). Interestingly, pine growth efficiency was higher in mixed stands compared to pure pine stands. Differences in growth efficiency did not explain the much higher yield of pine compared to hardwoods, but the lower specific gravity of pine translated into higher stem volume yield per unit biomass than hardwood species (Table 4.10). Waring's (1983) proposal of growth efficiency as an indicator of tree vigor is not well-supported by the result of this study and its use has met with mixed results in other studies (Binkley 1984, Britt et al. 1990). These findings seem to indicate the importance of other factors, besides assimilation efficiency, which influence carbon gain, such as leaf area capacity (Canham and Marks 1985, Teskey et al. 1987).

Coring estimates indicate much higher fine root densities for pine on herbaceous control plots (Table 4.5). Estimates from excavation on all plots indicate greater evenness in total root density between species, but pine root biomass was still greater due to greater allocation of biomass for hardwoods to medium and large roots (Table 4.3). Differences in fine root estimates between methods (Table 4.4) may reflect distributional differences between tree species. Greater recovery of pine fine roots from coring at random midpoints between trees may relate to the more even spatial distribution of pine fine roots compared to hardwood species. Greater recovery of hardwood fine roots by excavation would be expected if fine roots are more concentrated near the stem, since coring at midpoint locations between trees would underestimate fine root biomass compared to the excavation method. Differences in fine root distribution between species may explain the greater fine root biomass of mixed stands compared to pure stands, because fine roots may proliferate more in areas where roots from other trees are not present (Berendse 1979, Feldman 1988). Although cited as

occurring commonly between trees of the same species (Perry 1982), root grafting was rarely observed during excavation of root systems in this study.

Estimates of root surface area and root length were not obtained in this study, but trends for these variables are unlikely to be different from fine root biomass estimates. Red maple and loblolly pine fine roots appeared to be similar with respect to weight per unit area and morphology with fine roots arranged in finely-branched fans originating from small- or medium-sized lateral roots. Black locust roots exhibited less branching, but roots were longer than red maple or pine. The results of fine root coring and excavation in this study do not concur with earlier comparisons of pine and hardwood fine root biomass and surface area on Piedmont soils. Duncan (1941) found that pine seedlings had shorter roots with less absorbing surface than red maple, tuliptree (*Liriodendron tulipifera*), or flowering dogwood (*Cornus florida*). Kozlowski (1949) also reported that oaks (*Quercus* spp.) had larger root systems than loblolly pine. However, these studies utilized 1 or 2 year-old seedlings grown from seed, whereas trees in this study were originally 1-0 transplants which were excavated near the end of the third growing season in the field. Rapid pine growth did not begin in this field study until the second growing season when seedlings were more than two years old.

Physiological root uptake capacity of the species in this experiment is unknown. However, greater fine root density of pines compared to hardwoods may indicate greater resource uptake by pines since morphological parameters, such as root density, are generally more important for resource uptake than physiological parameters (Caldwell 1987). Movement through soil of water and nutrients, especially in the clayey soils of this study, is often slow and uptake is best increased by higher root density or surface area. Estimates of fine root production were highly variable and may not be useful in explaining interference outcomes. The high variability involved with estimating fine root production may be a function of the young age of these stands, in which root closure may not be fully complete. In addition, estimates in any forest stand are likely to be highly variable since root growth is opportunistic according to soil conditions and is often asynchronous within the root system itself (Caldwell 1979). One possible conclusion from these data is that the higher fine root production esti-

mates for pine compared to hardwoods may indicate that more resources are allocated belowground for this species than root-shoot ratios of excavated seedlings suggest.

Competition for soil moisture has been assumed to be of critical importance in young forest stands in the Southeast (Korstian and Coile 1938, Shoulders and Tiarks 1980, Nelson et al. 1981, Byrne et al. 1987). Soil moisture does appear to be an important factor in this study even though annual rainfall was above average during the course of the experiment. The greater drop in water potential for hardwoods than pine in herbaceous vegetation compared to herbaceous control stands (Table 4.15), may explain the reduced yield of hardwoods compared to pines. Pine also used water more efficiently than hardwoods in herbaceous vegetation (Table 4.16).

Intense belowground competition from herbaceous vegetation with hardwood tree species was also evident from the dramatic drop in hardwood foliar nitrogen levels in herbaceous vegetation compared to herbaceous control treatments (Table 4.17). Levels of red maple foliar nitrogen in herbaceous treatments did not differ markedly from those of red maple seedlings in a greenhouse study (1.43%) supposedly receiving a complete nutrient solution (Erdmann et al. 1979). Black locust foliar nitrogen levels in herbaceous vegetation were also higher than those of four-year-old trees (3.16%) in North Carolina (Boring and Swank 1984). However, the field-grown hardwood trees in this study appeared to display nitrogen deficiency symptoms including yellowing of foliage and scorching of leaf tips (Erdmann et al. 1979). Surprisingly, pine foliar nitrogen levels did not consistently decrease in herbaceous vegetation compared to control treatments and nitrogen levels actually increased for pine in pure stands in herbaceous vegetation compared to control treatment pure stands. It is possible that increased yield of pine on control treatments may have led to an earlier onset of nitrogen deficiency than in herbaceous treatments. Since the density of pine in mixed stands is only half that of pure stands, and because pine yield was much greater than that of associated hardwoods, it is probable that nitrogen deficiencies would first become evident in stands of pure pine. Although no pine on any treatment are currently below critical levels for deficiency in loblolly pine (1.1%) (Allen 1987), it is possible that nitrogen may become the first

belowground limiting factor to pine on control treatments, while soil moisture is limiting pine growth with herbaceous vegetation.

Conflicting results were obtained from the two measures of nitrogen-use efficiency used in this study. Both measures revealed generally higher nitrogen-use efficiency of pine in herbaceous control treatments compared to hardwood species. Yet, pine had much higher yield-based nitrogen-use efficiency, but lower photosynthetic nitrogen-use efficiency, in herbaceous vegetation compared to hardwood species. In general, pine is expected to have higher nitrogen-use efficiency than hardwoods (Vitousek 1982). However, if moisture limited the growth of hardwoods in herbaceous vegetation more than nitrogen, it is possible that their photosynthesis per unit of nitrogen would not be greatly affected. Yet, reduced yield due to moisture limitation would result in a low nitrogen-use efficiency that is based on yield. In addition, the difference between nitrogen-use efficiency measures in this study may reflect a trade-off between factors which increase nitrogen retention and internal use (high yield-based nitrogen-use-efficiency) and those which increase photosynthetic nitrogen-use efficiency. Factors which promote efficient internal use of nitrogen and high nitrogen residence times in pine, such as high conversion efficiency to wood biomass and long periods for needle retention, may also lead to reduced photosynthesis per unit of leaf nitrogen (Berendse and Aerts 1987).

It is difficult, however, to identify any single factor in this study which is dominant in influencing interference interactions. Resource factors typically interact to influence interference outcomes (Glover 1982, Aldrich 1987), and examples of this interaction were numerous in this study. Competition for moisture and nitrogen by herbaceous vegetation dramatically reduced the height of hardwoods eliminating light competition for pine in these stands. Reduction in hardwood yield was more severe in pure stands compared to mixed stands in herbaceous vegetation because of partial shading from pine. Kolb et al. (1990) found similar effects on hardwood seedlings due to interactions between aboveground and belowground resources. The modification of the light environment by pine may have actually decreased the belowground competitive ability of hardwoods with herbaceous vegetation by reducing root-

shoot ratios. Conversely, reduced foliar nitrogen levels due to competition from herbaceous vegetation may have also constrained hardwood photosynthetic rates since photosynthesis is highly dependent on leaf nitrogen levels (Field et al. 1983). Photosynthetic capacity of all species was lowered by the reduction of leaf area in herbaceous plots, which is probably related to moisture and nutrient competition (Jarvis 1985, Allen et al. 1990). The interaction between moisture and light uptake in plants is different for each species. Pine foliage limits radiant heat absorption by its arrangement of needles in fascicles which increases self-shading and reduces evapotranspiration (Baker and Langdon 1990). Red maple has a great ability to decrease water loss through stomatal closure at low water potentials (Walters and Yawney 1990). Black locust responds to drought through abscission of foliage (Dickman et al. 1985). Given these different mechanisms of moisture-light adaptation, it is not surprising that hardwood yield is reduced more under conditions of drought and high light, while pines are reduced more when both water and light are limited (Wenger 1958). Interactions between soil resources were also evident. Foliage of hardwoods often became light green during dry periods reflecting a deficiency of chlorophyll, of which nitrogen is a primary constituent. Since nitrogen is made available to roots via mass flow and diffusion (Carlyle 1986), nitrogen deficiencies become more critical during drought periods.

While many interacting factors contribute to the results of interference outcomes in this experiment, regression analysis revealed the strong relation of stand stem volume yield with certain variables, specifically root-shoot ratio, leaf area, and water-use-efficiency. Fine root biomass and yield-based nitrogen-use efficiency were also somewhat important in explaining tree yield. These variables help explain the success of loblolly pine in this study compared to hardwood species, especially in herbaceous vegetation. Pine displayed a high capacity for resource uptake with its greater leaf area and fine root biomass compared to hardwood species. Greater efficiency in the use of water and nitrogen of pines allowed pine to more effectively compete for these resources with herbaceous vegetation and to allocate more biomass to aboveground yield, as exemplified by pine's lower root-shoot ratios com-

pared to hardwood species. Indeed, stepwise regression indicated that root-shoot ratio alone explained 94% of the variation in stand stem volume yield.

Changes in root-shoot ratios may indicate a balance between interacting resource factors. In order to maximize growth, plants allocate relatively more resources to tissues involved with absorbing the most limiting resources (Duncan 1941, Mooney 1972, Drew and Ledig 1980, Kramer 1983, Tilman 1988, Shipley and Peters 1990). Increases in root-shoot ratios of hardwood trees with herbaceous vegetation may indicate the importance of herbaceous competition for soil moisture and nitrogen resources. However, the greater allocation of biomass aboveground for hardwoods in mixtures with pine compared to pure stands in herbaceous vegetation plots may indicate an equilibration of biomass allocation by hardwoods in response to simultaneous belowground competition from herbaceous vegetation and aboveground competition from pines.

Chapter V

SYNTHESIS

The results of the field and greenhouse experiments of this study indicate that a variety of factors influenced the processes and outcomes of interference between loblolly pine and hardwood tree species. These factors include spatial scale, site quality, resource competition and allelopathic effects from herbaceous vegetation, species-specific patterns of growth and biomass allocation, synergistic interactions between pine and hardwood species, and shifts in allometric relationships within tree species due to changes in stand composition. The results of this study reemphasize the importance of the interaction between site resource factors which influence species competitive abilities and ultimately determine interference outcomes.

The results of interference in mixed stands of loblolly pine, red maple, and black locust differed between field and greenhouse studies. In the field, pine yield was greater than that of hardwoods in mixed stands. The higher yield of pine appeared to be related to a large allocation of biomass to resource-gathering tissues and a higher utilization efficiency of water and nitrogen than hardwoods. In more densely-planted greenhouse stands, however, the horizontal extension of foliage by hardwood species restricted light availability to pine. Because of the shade-intolerance of loblolly pine (Wenger 1958) and the interaction between

aboveground and belowground factors in interference (Harper 1977, Aldrich 1987, Chapin et al. 1987), it is not surprising that the resource-use efficiency and yield of pines was low under these conditions. While the results of interference outcomes between the field and greenhouse studies were conflicting, they illustrate the importance of density in the interspecific interference process. Since species differ with regards to the phenology in their development, it is probable that interference outcomes will depend on whether interference intensity is high or low during stages of critical development. Loblolly pine appeared to require a longer period of initial establishment than hardwoods and was very susceptible to hardwood competition in the greenhouse experiment, where interference interactions took place immediately after planting due to high planting density. However, in the field experiment, a reduced density allowed pine to become established before the onset of interference, which allowed pine to later compete effectively with hardwood and herbaceous vegetation.

Site quality differences also influenced interference outcomes in this study by altering the amount and balance of site resources. Higher aboveground yield, related to better site quality on the stream terrace block in the field study, led to increased competition for light on this site compared to upland sites. Although not yet apparent, differences in site quality may eventually lead to different interference outcomes between blocks of the field study. Increased availability of belowground resources may favor hardwoods over pine on the stream terrace compared to upland sites. Differences in site quality may also explain the greater yield of pine and black locust mixtures on certain blocks of the field study, because elevated yield in mixtures of these species was seen only on poorer sites. In the greenhouse interference study, interference outcomes between pine and hardwood species were altered by water availability, a major determinant of site quality. Severe water stress adversely affected both pine and hardwoods, but the reduction of hardwood height and leaf area in this treatment allowed pine to compete better with hardwoods than in control treatment stands.

Herbaceous vegetation severely affected the yield of all stands due to resource competition and chemical interference. Tree species in herbaceous vegetation stands generally had reduced photosynthesis, more negative leaf or needle water potentials, and reduced foliar

nitrogen content. Hardwood species were affected more than loblolly pine. Mortality was not significantly affected by herbaceous vegetation, but may have been more severe if establishment of herbaceous vegetation had not been delayed until late in the first growing season. The impact of herbaceous vegetation in the field can be mainly attributed to competition for belowground resources, although the severe reduction in hardwood tree height allowed some tall herbaceous plants to interfere with hardwoods aboveground as well. The large impact of herbaceous competition is not surprising given the large amount of overlap between tree fine roots and herbaceous roots in the upper 10 cm of soil. In addition to resource competition effects, evidence of allelopathic effects of tall fescue on all tree species was observed in a greenhouse experiment. All species appeared to have reduced total biomass, reduced leaf area, and increased root-shoot ratios with application of leachate from pots containing fescue compared to control pots. In addition, some species-specific effects were observed, including a reduction in specific leaf area and seedling height for black locust and reduced photosynthetic rates for loblolly pine by fescue leachates. Unfortunately, it is not possible to partition the effect of allelopathic interference from that of resource competition in this study. However, it would be difficult to partition these effects even with more controlled experiments since direct allelopathic effects should also produce secondary effects on competitive ability for resources (Harper 1977, Williamson 1990).

Species-specific patterns of growth and biomass allocation also accounted for large differences in yield in field and greenhouse stands. Loblolly pine attained the greatest aboveground yield in stem volume and the greatest total biomass of all species in the field and stand stem volume was positively related to the proportion of pine. The success of loblolly pine in the field study can be attributed to its large resource absorbing surfaces, including leaf area and fine root biomass, as well as its high conversion efficiency to stemwood. The efficient use by pine of nitrogen and water resources allowed for greater allocation of biomass aboveground. Black locust attained higher yields in both field and greenhouse studies than red maple. Like loblolly pine, black locust is a shade-intolerant, early successional species with an inherent high growth rate. Results from the greenhouse study

indicated that black locust is a resource-uptake specialist which succeeded by rapidly exploiting site resources. Red maple, on the other hand, is a more shade tolerant mid-successional species which also allocates a greater proportion of biomass to belowground structures. Given its higher internal resource-use efficiency, red maple should have an advantage in competition under conditions of reduced resource availability. Yet, the results of the field study demonstrate a high sensitivity of red maple to belowground competition from herbaceous vegetation. A similar high sensitivity to moisture and nitrogen limitation for red maple has been shown in a factorial resource addition experiment by Canham et al. (1991). It is apparent that resource-use efficiencies cannot totally explain interference outcomes because other factors, such as resource demand and uptake capacity (Canham and Marks 1985), are also important determinants of success under interference. A similar argument can be made for other growth efficiency measures, such as Waring's (1983) growth efficiency index.

Many benefits of mixed stands have been hypothesized, such as increased yield due to efficient resource partitioning between species, comensal or mutualistic nutrient amendment, and protection from pest outbreak (Auclair 1983). Yet, verification of benefits from field studies has been lacking. While the differences in yield due to synergistic interactions in mixed stands has generally not been great, some evidence of mixed stand synergism is offered by this study. The most definitive evidence is the increased yield of pine-black locust mixtures compared to pure stands on poor-site herbaceous plots. Black locust yield was enhanced by the presence of pine, possibly due to partial shading by pines which reduced respiration and/or evapotranspiration. However, the fact that the effect was only observed on poorer sites may indicate enhanced fertility from nitrogen fixation or increased nutrient cycling by black locust improving growth of both species. Since black locust appeared to be the main beneficiary of the mutualistic interaction, it is unclear how improved pine growth could have substantially improved the yield of locust. It is possible that some suppression of herbaceous vegetation competitive ability could have occurred from the larger pines which in turn benefitted black locust. Like black locust, red maple photosynthesis and leaf area was somewhat

higher with pine compared to pure stands, but these increases did not generally translate into higher yields for this species in mixture with pine.

Although evidence of mutualistic or antagonistic interactions were not prevalent in the field study, it is possible that more will develop as interference interactions increases in intensity in future growing seasons. Mutualistic relationships may arise from the observed changes in crown morphology or increases in root biomass seen in mixed stands compared to pure stands. Antagonistic relationships may also develop as resources become more limiting with full canopy closure, particularly with black locust and loblolly pine competition for light in herbaceous control stands. Mutualistic interactions were not apparent in the greenhouse interference study. Interference outcomes in the greenhouse experiment were highly one-sided, with hardwoods suppressing pine growth. There was an apparent release, however, of hardwoods from intense intraspecific interference in mixture with pine compared to pure stands which increased mean seedling biomass of hardwoods in mixtures.

Given that trees appear to invest a large amount of carbon in attaining and maintaining a competitive advantage (Mooney 1972), it is likely that interference regimes will impact allometric relationships (Shainsky 1988) and that these changes in allometry will influence future interference outcomes (Morris and Myerscough (1987). Changes in biomass allocation patterns due to interference were evident in both field and greenhouse experiments including hardwood root-shoot ratios, fine-large root ratios, and specific leaf area of both pine and hardwoods. These changes appear to indicate a response to competitive stress, most of which translated into reduced stem volume yield. Changes in root-shoot ratios may indicate a balancing between competition for aboveground (light) and belowground (water and nutrients) resources. Effects due to interference in one area may have cascading effects which alter interference in another area. For example, reduction in photosynthesis by pine due to light competition from hardwoods, reduced the belowground competitive ability of pine. Similarly, intense belowground interference from herbaceous vegetation on hardwoods may compromise their ability to compete aboveground with pine. Furthermore, soil moisture and nitrogen resources appear to be intimately associated with one another, as evidenced by the

increased appearance of leaf color nitrogen deficiency symptoms under conditions of water stress. Such interactions between resource factors reinforces the importance of integrating, multi-factor experimental approaches in the study of plant interference.

While emphasizing basic research, this study does have some implications for forest management and silviculture. Quantification of tree and herbaceous interference effects indicate the great degree of differences in yield which result from stand composition and herbaceous control. Stem yield can vary by as much as 5x with herbaceous vegetation control and 68x without herbaceous control. Herbaceous vegetation itself reduced stand yield by 2x, 10x, and 20x, for loblolly pine, black locust, and red maple, respectively, compared to stands receiving herbaceous control. Species-specific differences on pine stem volume yield were not observed after three growing seasons, but black locust did improve pine growth after the second growing season. By lowering the proportion of black locust or decreasing stand density, negative effects on pine yield due to shading from black locust may allow for continued benefits to pine growth from black locust. Although mutualistic increases in yield are not yet apparent, red maple-loblolly pine mixtures appear to be developing a desirable stratification of both above- and belowground structures which may improve the efficiency of resource utilization as these stands mature.

The results of this study indicate the importance of considering stand composition, herbaceous vegetation, stand density, stand proportion, and site quality in predicting the outcomes of interference interactions. Further research in the area of forest tree interference should focus on better quantification of the effects of stand density, resource availability, and resource-use on tree interference interactions. Greenhouse and field experiments which use controlled levels of many different resource factors in stands planted at different densities will be difficult to conduct, but would be invaluable in understanding the interaction of site resource factors in the interference process. More work is also needed to determine species-specific effects of different hardwood and herbaceous species on southern pines. Many differences in species-specific traits, such as plant growth rate, crown morphology, resource-use efficiencies, and allelopathic potential have demonstrated that species may differ greatly

in their interference capabilities. Once species-specific interference capabilities are determined, silviculturalists can move to improve vegetation management regimes by optimizing interference interactions.

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