Physiology

Moderator:

DONAL D. HOOK
Clemson University

COMPARATIVE PHYSIOLOGY OF LOBLOLLY PINE CLONES THAT HAVE EXHIBITED A WIDE RANGE IN GROWTH PERFORMANCE

Phil Dougherty and Andy Laviner[1]

Abstract—Net photosynthesis light response and foliage age response curves were developed for three rapid- and three slow-growing clones of loblolly pine. Maximum rates of net photosynthesis were the same for all clones. However, total tree leaf area on the three rapid-growing clones was much greater than that on the three slow-growth clones. Thus, whole tree carbon gain would be much greater for the rapid-growth clones because of their greater total tree leaf area. These results suggest that tree growth potential is more a function of leaf area than potential carbon fixation rates per unit leaf area.

Foliage age response curves were developed in September when multiple flushes were present and at different stages of development. Needles on the last flush were still extending in September and their lengths were less than 20 percent of the length of first flush needles. Net photosynthesis rates of needles with lengths less than 20 percent of maximum were about 50 to 55 percent of the rates observed for needles that had achieved 60 to 70 percent of their maximum size. The longest and oldest needles (usually first-growth flush) actually had lower net photosynthesis rates than second or third flush needles. All six clones exhibited the same net photosynthesis-age trends although actual rates were different for each growth flush. Stomatal conductance trends with age were similar to those observed for net photosynthesis with one exception: needles that were less than 20 percent of the maximum needle length had high stomatal conductance. This suggests that the low rate of net photosynthesis of young developing tissue is not due to stomatal limitations but instead due to lack of development of the photosynthetic system and/or high respiration cost.

INTRODUCTION

Large differences in growth performance of loblolly sources (Wells and Wakeley 1966) and source-families (McKeand and others 1989) have been reported. Similar differences in growth of loblolly pine clones are currently being observed in Westvaco's clonal test. Genetic progeny tests are designed such that growth differences are a reflection of true genetic differences in growth potential and not differences in growth environment. Thus, observed differences in growth potential have to be manifestations of genetic influences on plant phenology, physiology, and/or morphology. Increases in aboveground yield can theoretically result from improvement in many plant factors: increased net carbon gain, nutrient acquisition and utilization efficiency, or carbon allocation into stemwood. In the past, it has not been important to understand which tree morphological or physiological processes were responsible for rapid or slow tree growth rates. It has been sufficient to test for and select the best performing crosses and to enhance their growth by using silvicultural treatments that improve site resource availability. Now forest industry is interested in increasing productivity through application of forest biotechnology. Knowledge about which processes or morphological characteristics determine growth rates is needed to provide direction regarding which compliment of genes it is important to manipulate to further increase growth potential. The objective of this research was to determine if differences in the rates of net carbon gain of foliage might be responsible for observed differences in growth rates.

METHODS

Research Approach

Three good- and three poor-growing clones were selected for comparison of gas exchange rates. The three good-growth clones had attained a height of nearly twice the average height of the poor-growing clones over a 3-year period.

The study site is located in Berkeley County, SC. Soil on the study site is a Goldsboro series, which is moderately well drained. Prior to the establishment of the clonal test in the spring of 1994 the land was used for agricultural purposes. In the spring of 1994, 120 clones of loblolly pine were established on this site using rooted cuttings (Les Pearson and Farrell Wise, personal communication). Three of the best and three of the poorest performing clones after 2 years in the field were selected for comparison of gas exchange characteristics.

Measurements

Five individuals of each of the six clones were selected for measurement of gas exchange characteristics. All foliage gas exchange measurements were made in September of 1996 using a LI-6400 Portable Photosynthesis System.

Light response curves were developed over a 2-day period for all clones. Quantum efficiency was estimated as the slope of the response curve between a light intensity of zero and 250 micromoles per square meter per second. Maximum, light saturated, net photosynthesis was determined as the rate of net photosynthesis at a photosynthetically active radiation (PAR) of greater than 1600 umoles per square meter per second. All light response measures were made in the early morning hours. During each light response curve measurement, cuvette temperature was held at 27 °C, relative humidity at 70 percent, and CO_2 concentration at 350 parts per million.

[1] Ecophysiologist and Research Project Assistant, respectively, Westvaco Forest Science and Technology, Summerville, SC 29484.

The effects of needle age (development) on gas exchange was also made on five individuals of each of the six clones. Detached shoots were used to determine maximum net photosynthesis and stomatal conductance of each flush of needles present on the growing shoots in September. Ginn and others (1991) previously determined that stomatal conductance of detached loblolly pine shoots does not change over a 30-minute period. Gas exchange measurements in this study were completed within 3 to 5 minutes after removal from the tree. Most shoots had four age classes of foliage. Needles on the first flush were considered as 100 percent full development. Relative needle development of the remaining three flushes were expressed on a percentage basis by dividing their needle length by the needle length of the first flush and multiplying by 100.

Stem Gas Exchange

Net carbon exchange of developing stem material was determined on five individuals of a single clone in September. Relative stem development was based on the length of the needles on each flush relative to that on the first flush in the same manner as described above for foliage. Stem gas exchange was determined under light-saturated conditions (1,500 micromoles per square meter per second), constant cuvette temperature (27 °C) and constant relative humidity (70 percent).

RESULTS AND DISCUSSIONS

Light Response

None of the parameters (dark respiration, quantum efficiency, or maximum net photosynthesis) that were derived from the light response curves shown in figure 1 were significantly different (alpha=.1) between fast- and slow-growing clones. There was a tendency for light-

saturated net photosynthesis to be greater for slow-growing clones than for fast-growing clones (fig. 1). Stomatal conductances also tended to be higher for the poorer-growing clones than for the fast-growing clones (fig. 2) but were also not statistically significantly different. Maximum net photosynthesis and stomatal conductance rates observed in this study are lower than those previously reported for loblolly pine (Murthy and others 1996, Teskey and others 1987). At the time these measurements were made available, soil moisture in the upper 0-30 cm of the soil profile was low and partial stomatal closure was apparent (fig. 2). The tendency for lower stomatal conductance and light-saturated net photosynthesis rates in the fast-growing clones may be related to the fact that the fast-growing clones had much more leaf area than the slow-growing clones. Recent work by Laviner (personal communications) has shown that at a given soil moisture supply and moderate-to-high vapor pressure deficits that loblolly trees with large leaf area have lower stomatal conductance than smaller trees with lower leaf area. Based on our preliminary results, it would appear that differences in carbon gain capacity between fast- and slow-growing clones are likely to be dictated more by development of greater leaf area than by differences in the rate of gas exchange per unit leaf area.

Foliage Development and Gas Exchange

Net photosynthesis rates at each relative needle development stage, ranging from near 20 percent to 100 percent full development, were not significantly different between clones. All clones exhibited the same response in net photosynthesis as foliage approached 100 percent full development (fig. 3). At near 20 percent development, net photosynthesis was only 50 to 55 percent of the maximum net photosynthesis observed at later stages of development. Stomatal conductance (fig. 4) at a relative
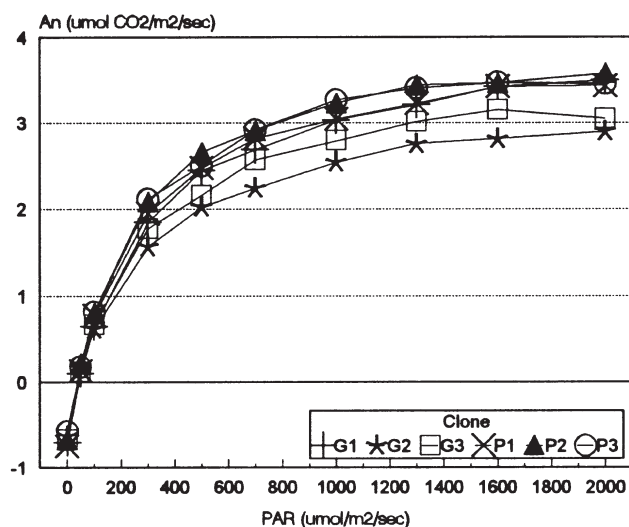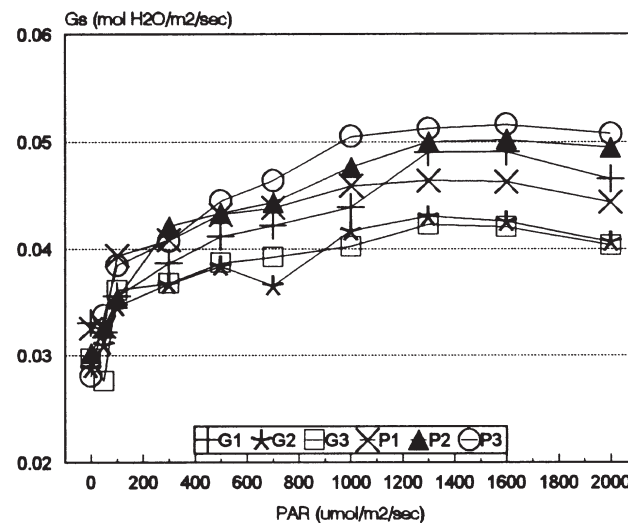

Figure 1—Average net photosynthesis (An) of three good-growing loblolly pine clones (G1, G2, G3) and three poor-growing clones (P1, P2, and P3) plotted as a function of photosynthetically active radiation (PAR). Each point is the average of five measurements.

Figure 2—Average stomatal conductance to water vapor (Gs) of three good-growing clones (G1, G2, and G3) and three poor-growing (P1, P2, P3) clones of loblolly pine plotted as a function of photosynthetically active radiation (PAR). Each point is the average of five observations.
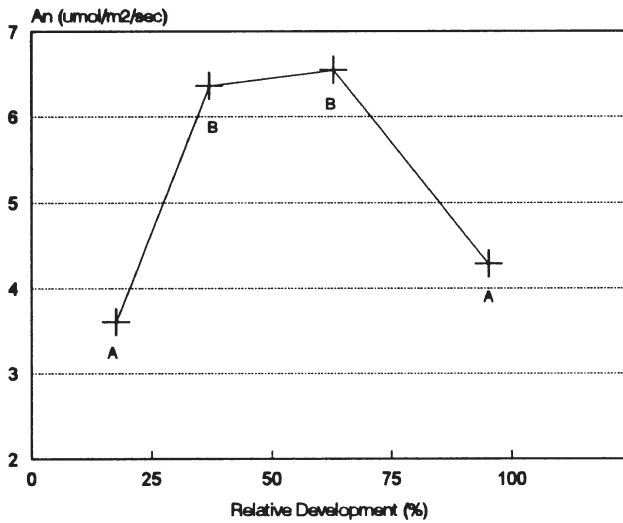
Figure 3—Average light saturated net photosynthesis (An) rates of six clones plotted as a function of relative foliage development. Relative foliage development was obtained by dividing the length of needles on each flush by the length of needles on the first flush and multiplying by 100.

Figure 4—Average light saturated stomatal conductance to water vapor (Gs) of six clones of loblolly pine plotted as a function of relative foliage development. Relative foliage development was obtained by dividing the length of needles on each flush by the length of needles on the first flush and multiplying by 100.
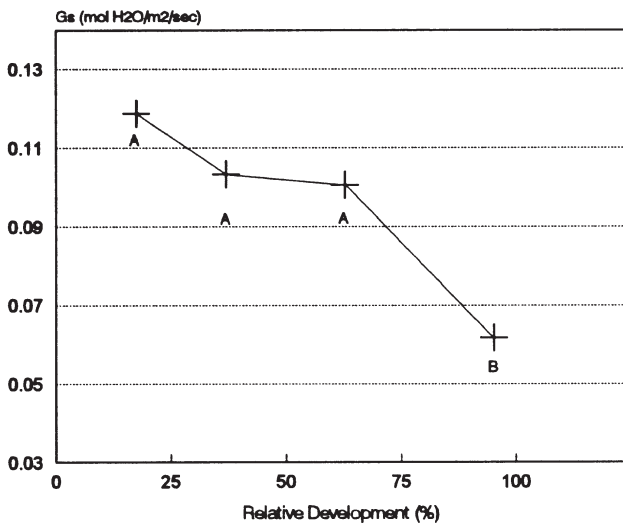
development stage near 20 percent was equal to or greater than that observed for more mature foliage. This suggests that low rates of net photosynthesis at this early stage of development were not due to stomatal limitations. Internal factors related to the development of the photosynthesis process, mesophyll resistance, or high respiration cost are all factors that could result in low net photosynthesis rates at this stage of development. By the time foliage had reached 35 to 40

percent full development, net photosynthesis rates were near maximum. Surprisingly, the rate of net photosynthesis of the most mature tissue was lower than that observed at midstages of development. Previous studies have shown light-saturated net photosynthesis rates tend to remain near their maximum in the year that they are formed (Murthy and others 1996) until environmental conditions result in a decline in net photosynthesis.

Stem Development and Gas Exchange

Stems of young shoots appear green and succulent and should have the capacity to photosynthesize. The observed trend in carbon dioxide exchange rates of developing shoots, which ranged from near 20 percent (needle development) to 100 percent development, from which all needles had been removed, is shown in figure 5. At the earliest stage of development, carbon exchange rates are positive, suggesting that stem photosynthesis may be completely offsetting maintenance and construction respiration cost under high light conditions. Stems which had foliage that had attained near 60 percent full expansion also appear to offset a considerable amount of respiration cost. Shoots with needles that are near 100 percent at their final size do not appear to be able to offset much growth and/or maintenance respiration cost.

CONCLUSIONS

Differences in rates of net photosynthesis per unit leaf area do not appear to be a major factor contributing to differences in the growth of loblolly pine clones. The role of other physiological processes, phenology, and crown morphological factors such as leaf area and distribution will be considered in future studies.
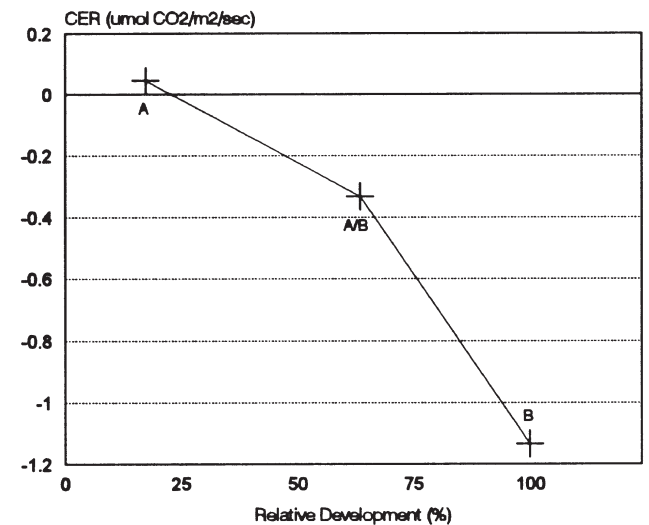

Figure 5—Average stem carbon dioxide exchange rates (CER) of a single clone of loblolly pine plotted against stem relative development. Relative development of each stem section (flush) was determined on the basis of the relative development of needles located on each flush. Each point is the average of five measurements.

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A CONCEPTUAL APPROACH TO STAND MANAGEMENT USING LEAF AREA INDEX AS THE INTEGRAL OF SITE STRUCTURE, PHYSIOLOGICAL FUNCTION, AND RESOURCE SUPPLY

D.A. Sampson, J.M. Vose, and H.L. Allen[1]

Abstract—Stand management involves manipulation of factors that are thought to control ecophysiological mechanisms determining forest growth and function. Stand leaf area index can be used to assess current growth, as well as site growth potential based on the perceived ability of the stand to respond to silvicultural manipulation (e.g., fertilization). We sampled the leaf area index (LAI) in 30 plots for each of six forest cover-types across the Southeast to examine natural variability in LAI. The mean index ranged from 3.5 to 5.1 m^2 m^{-2} (projected); spruce-fir had the lowest while maple-beech-birch had the highest. We present a conceptual model that relates LAI to site resources, occupancy, and shade tolerance to initiate discourse and development of diagnostic tools for evaluating site-specific determinants of forest growth. Simulations from a process model suggest that biologically achievable LAI may not be optimal LAI for maximum growth.

INTRODUCTION

Imposition of silvicultural treatments to improve forest productivity by increasing leaf area index (LAI) has only recently been considered in southern land management. Earlier work in southern pine stands demonstrated that site manipulation to improve soil water availability and fertility increased loblolly pine growth (Fisher and Garbett 1980, Pritchett and Cumerford 1982). Absent, however, has been the physiological basis for increased stem growth following improved resource availability. Managing LAI to increase yield in southern forest ecosystems is an idea long overdue.

Canopy leaf area intercepts photosynthetically active radiation (PAR) and, through photosynthesis, converts absorbed light energy into dry matter (Cannell 1989). The empirical relationship between intercepted PAR and dry matter production suggests that increased radiation absorbed, or increased efficiency of conversion of absorbed radiation to biomass, will increase dry matter produced (Cannell 1989). However, the relationship is curvilinear, with decreased fractional interceptance as LAI increases (Russell and others 1989), indicating decreased interception efficiency as LAI increases. Thus, a reduction in light capture efficiency as LAI increases suggests that a species optimum LAI for maximum productivity may exist. Increasing leaf area will increase PAR interception (Cannell 1989). Therefore, we can manipulate the stand to increase LAI and, subsequently, PAR absorbed. The PAR conversion efficiency is, more or less, species specific and constant (c.f., Cannel and others 1988).

The objectives of this paper are (1) to develop a conceptual approach for discussing the structural and physiological basis of stand LAI in determining productivity of southern pines and hardwoods, and (2) to examine how this approach may be used to design a tool that would aid in stand management decisions.

APPROACH

Our approach is to use a combination of concepts, published and unpublished data, and modeling to establish the foundation for analyses of LAI as the integration of site properties determining stemwood growth. We estimated LAI for six forest cover-types (cypress-water tupelo, blackgum-red maple, sweetgum-yellow-poplar, oak-hickory, maple-beech-birch, and spruce-fir) in North and South Carolina and Georgia. We sampled projected LAI at 25 systematic points in each of 30 stands for each forest type, using a LI-COR LAI-2000 Plant Canopy Analyzer and the 90-degree view cap. Estimates were taken under diffuse sky conditions, or in the dawn or predusk periods during sunny days in closed-canopy stands throughout the summers of 1994 and 1995. Simulation data were obtained from a series of sensitivity analyses conducted with the process model BIOMASS (McMurtrie 1991) that has been adapted for loblolly pine. We examined the interactions among LAI, climate, and gross and net canopy carbon assimilation for three regions across the Southeast (NCSFNC 1996).

RESULTS AND DISCUSSION

Southern Pines

Variability in LAI—The amount, pattern, and duration of southern pine LAI incorporate region-specific characteristics of growing season length and annual foliage cohort retention. Loblolly and slash pine carry an effective maximum of two annual foliage cohorts. As such, they exhibit a relatively stable yearly minimum leaf area in late winter and early spring after needlefall of the previous year's cohort has completed and prior to new foliage production for the current year begins (c.f., Vose and Swank 1990). Peak LAI is generally reached in late August or early September following completion of elongation of current year foliage. For southern pines, peak LAI varies considerably, with lower quality mid-rotation loblolly pine stands typically ranging from 0.8 to 2.2 (m^2 m^{-2}; one-half

total) (Sampson and Allen 1995). For those stands where fertilizer has been applied, LAI may exceed 4 (m^2 m^{-2}; projected) (Vose and Allen 1988). Silvicultural operations intended to manipulate site characteristics determining LAI must consider and incorporate principles regulating seasonal LAI dynamics to effectively administer and identify treatment responses.

LAI and resource supply and use—Inadequate soil N supply is the dominant limitation to foliage production in southern pine stands (Vose and Allen 1988, Colbert and others 1990). In addition to N, phosphorus (P) has also been identified as an important element controlling stand LAI (NCSFNC 1991), although the magnitude of response is generally lower than from N. Inadequate water availability has long been thought to limit leaf area production in southern pine stands. However, there are few data that support this hypothesis. Gholz and others (1991) found little interaction between water availability and LAI in slash pine stands. Similarly, a fertilization and irrigation experiment in a young loblolly pine stand growing on an excessively drained sandy soil in North Carolina suggests that water does not limit LAI (Albaugh and others, in review). Apparently, the amount and pattern of rainfall, along with soil water holding capacity, must be considered.

LAI and site occupancy—Stand density, the stage of stand development, and basal area (BA) all influence site occupancy and, therefore, crown closure and LAI. Southern pine plantations under nominal nutrient supply typically achieve canopy closure in 10 to 14 years (Vose and Swank 1990). LAI also increases with stand development, and reaches a maximum that coincides with crown closure and full site occupancy (Vose and others 1994). The amount of canopy in nonfoliated gaps can also be used as an indicator of site occupancy; LAI and canopy gap fraction are negatively correlated.

Loblolly pine LAI increases linearly with increased BA (vis a vis sapwood area support of canopy foliage) (Shinozaki and others 1964) up to approximately 30 to 35 m^2 ha^{-1} (Dougherty and others 1995), after which the relationship becomes asymptotic. Decoupling between basal area and LAI can occur for several reasons, and can include the development of heartwood and, thus, decreased sapwood area relative to basal area (c.f., Long and Smith 1988), a reduction in resource supply, or a reduction in basal area efficiency (basal area growth per unit LAI).

LAI and shade tolerance—Few studies have examined the relationship between shade tolerance and LAI for pine species. However, increased LAI with increased shade tolerance has been observed (Vose and others 1994). Assuming the branch autonomy model (e.g., Sprugel and others 1991), foliage longevity will be related to a time integral of incident PAR and net carbon balance. The ecophysiological mechanism determining the presence of foliage in lower crown positions is related to the activity of meristematic buds for the development of new foliage rather than influencing abscission of current foliage in southern pine species.

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We can conclude that inherently high resource supply, or improved soil nutrition (N and P amendments), will result in high LAI. In the Eastern United States, soil water supply appears considerably less important than soil nutrients. In addition, stand development, stand density, and the amount of canopy in gap will all influence LAI. An upper level of LAI will be reached at a basal area considerably less than maximum. Much more work is needed on the role of shade tolerance in determining LAI for southern pine stands. Empirical data suggest that an LAI of 4.0 (m^2 m^{-2}; projected) or more is possible in southern pine stands.

Hardwood Ecosystems

Natural variability in LAI—Leaf area development in deciduous hardwood ecosystems must, by definition, occur within one growing season. Foliage development occurs rapidly, with maximum LAI achieved usually within 4 to 9 weeks of bud break. Maximum LAI for the six forest cover-types studied varied considerably (table 1). Mean LAI ranged from 3.5 for spruce-fir stands to 5.1 for maple-beech-birch forest types (table 1). The low LAI found for spruce-fir was unexpected; shade tolerant conifers generally exhibit greater LAI than deciduous broad-leaf forests (Kira 1975). However, spruce-fir forests of the Southern Appalachian region are in decline, which may explain the low LAI's obtained. Vose and others (1995) examined LAI for five Appalachian hardwood ecosystems where LAI varied from 3.9 m^2 m^{-2} in a high elevation stand dominated by red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and birch (*Betula* spp.) to 7.3 m^2 m^{-2} in a lower elevation stand dominated by black oak (*Q. velutina* Lam.), chestnut oak (*Q. prinus* L.), and black tupelo (*Nyssa sylvatica*).

LAI and resource supply and use—To our knowledge, no experimental data are available to examine relationships between soil nutrition and LAI of southern hardwood ecosystems. Instead, only anecdotal evidence exists to

Table 1—Cover-types and leaf area index statistics for six forest cover-types of the Southeastern United States; data represent a five-State region from Virginia to Alabama

Cover-type	Mean and (range) of LAI (m^2 m^{-2}; projected)		Std. of LAI
Cypress-water tupelo	4.02	(2.68-5.44)	0.89
Blackgum-red maple	3.89	(2.73-5.20)	0.71
Maple-beech-birch	5.05	(2.74-6.30)	0.98
Oak-hickory	3.87	(2.78-5.95)	0.82
Sweetgum-yellow-poplar	4.18	(2.34-5.90)	0.81
Spruce-fir	3.46	(2.20-4.89)	0.68

Note: sample size of 30 for each cover-type.

support patterns similar to pines (i.e., lower LAI on resource-poor sites). For example, in the Southern Appalachians, LAI is lowest (~3) on dry and typically nutrient deficient ridge sites, and highest (~5 to 7) in more mesic midslope and cove sites (J.M. Vose, unpublished data). We hypothesize that LAI of hardwood ecosystems could be substantially increased with fertilization. Studies are underway by industry to examine nutrient and water availability on key hardwood species. These studies will provide important information on single-species versus resource availability relationships; however, responses in mixed species stands will remain unknown.

LAI and site occupancy—We found no relationship between stand basal area and LAI for the six forest cover-types, indicating that basal area may not be a good indicator of LAI in hardwood ecosystems. In addition, stand development for mixed-species forests is considerably more complex than single-species plantation derived forests. After disturbance, hardwood regeneration can come from three sources: seed germination, sprouting, and advanced regeneration. In the Southern Appalachians, the regeneration source depends on topographic position and stand age. For example, in coves, yellow- poplar (*Liriodendron tulipifera*) regenerates from seed in sufficient numbers (e.g., 18,000 seedlings ha^{-1}) to dominate the developing stand for several years (Boring and others 1988). In more midslope positions, sprouting is the primary regeneration method, and it increases in prevalence in younger stands (Boring and others 1988, Elliott and Swank 1994). Advanced regeneration occurs in all slope positions, but is less predictable than either seed or sprouting regeneration.

LAI and shade tolerance—The method of regeneration in mixed hardwood ecosystems influences the time trajectory of LAI, and the maximum LAI attainable. If regeneration occurs primarily from seed, then the stand will typically be comprised of light seeded, intolerant species which may dominate the stand for the first 100 years. Maximum LAI will be attained rapidly, but at a lower level than stands of mixed shade tolerance. If regeneration occurs primarily from sprouting, then species of mixed shade tolerance are present throughout the length of the rotation and the relative mixture of shade tolerant versus shade intolerant species changes throughout stand development. As pure stands get older (i.e., > 100 yrs), LAI increases from successful regeneration of more shade tolerant species beneath the predominately shade intolerant canopy. As the intolerant canopy declines, intermediate or shade tolerant species will replace them in the mid- and upper canopy. In mixed stands, increased LAI results from greater dominance of intermediate or shade tolerant species after canopy closure. The rate at which these shifts occur is a complex function of site resource availability, predisturbance species composition, and disturbance intensity and frequency in the developing stand. For example, on poor sites, site resources are inadequate to support resource-demanding and, typically, shade tolerant late successional species. Hence, it is biologically infeasible for a low resource site to support higher resource-demanding shade tolerant species.

LAI and forest productivity—Several common principles relating LAI and forest productivity in both southern pines and hardwoods can be observed. First, we can manage LAI by manipulating those factors thought to limit leaf area production. In some cases, low LAI may not be due to a resource limitation but, rather, stand structural characteristics associated with stand development (i.e., the mix of shade tolerant and intolerant species), natural disturbances, or past stand management practices. Second, for mixed species stands there exists a species mix that optimizes the existing site potential for fixing carbon. Although there are obvious limitations to species associations based on slope, aspect, elevation, etc., we can incorporate management strategies to manage stand LAI by knowing basic principles about species development, light tolerance, and competitive ability. Third, there is evidence to suggest that biologically maximum LAI may not be optimal LAI for maximum net primary production.

Simulations using BIOMASS version 13.0 for loblolly pine suggest decreased net production efficiency with increased LAI. Specifically, although net canopy assimilation (carbon available for partitioning to growth) increases with increased LAI, the relationship is curvilinear, with decreased net carbon per unit LAI as LAI increases (NCSFNC 1996). The concave functional form results in maximum net canopy assimilation at an LAI that is less than biologically attainable; there is less net carbon assimilation at LAI's greater than "optimal." A reduction in net assimilation efficiency is attributed to decreased light interception efficiency as LAI increases, and increased maintenance respiration (R_m) costs (relative to gross carbon fixed) of the canopy foliage (NCSFNC 1996). Climate determines the R_m/gross primary production ratio; warmer regions have higher respiratory demands and, thus, less carbon available for growth.

For mixed-species hardwood, relationships between stemwood NPP and LAI depend on the relative mixture of species and their contribution to total stand LAI. For example, species specific leaf photosynthesis (Pnet) (Sullivan and others 1996) and R_m rates indicate that stands with a greater proportion of intolerant species in the upper canopy (high light; > 1000μmol m^{-2} s^{-1}) will fix more canopy carbon than stands with a greater intermediate and shade tolerant species. Patterns at low light (<300μmol m^{-2} s^{-1}) are reversed, indicating that without major disturbance during stand development, shade tolerant species will eventually dominate the stand, LAI will increase due to multilayering, and NPP will be reduced. While more complex, the mixture of species may present more opportunities to increase NPP by altering the composition and structure of natural stands through selective thinning.

MANAGEMENT IMPLICATIONS

Conceptual Diagram
The relationships among resource supply, site occupancy, shade tolerance, and LAI can be examined in a conceptual diagram (fig. 1). Stand level shade tolerance can be defined as a "light compensation ratio" (the ratio of total LAI in
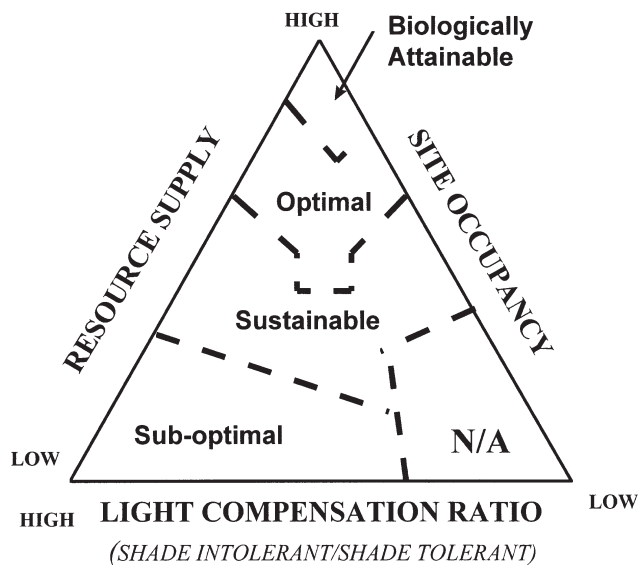
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Figure 1—A conceptual representation of the relationships among resource supply, site occupancy, light compensation ratio, and leaf area index (LAI) groupings. The light compensation ratio, as used here, incorporates stand-level shade tolerance described as the ratio of LAI in shade intolerant species to that of shade tolerant species. The category N/A represents not applicable.

intolerant species to LAI of tolerant species). The region formed by the intersection of lines drawn to opposite corners of the triad conveys a level of LAI (fig. 1). We classify these regions as: (1)suboptimal, (2) sustainable, (3) optimal, and (4) biologically attainable LAI. These will be discussed individually.

LAI Thresholds

Suboptimal LAI corresponds to stands exhibiting marginal growth. Intensive management intervention would likely be required to increase LAI to improve forest yield. Examples for southern pine would be low-site stands (low nutrient supplying soils), and/or intentionally or unintentionally low stocking (< 200 trees ha^{-1} at a basal area of 10 m^2 ha^{-1}). These stands would likely have much understory vegetation and poor crop tree basal area growth rates (< 2.3 m^2 ha^{-1} yr^{-1}). Examples of suboptimal LAI stands for southern hardwoods may correspond to recently thinned stands or stands on poor sites, such as xeric ridges or highly eroded soils with low nutrient supply.

Sustainable LAI infers natural conditions in the general absence of disturbance, but where poor site quality (low nutrient availability), or high competition from nontarget species, restricts leaf area production of desired species. Hardwoods, because of annual foliage production, would have a much more dynamic interaction between existing site resources, and yearly recycling of mineral nutrients.

Optimal LAI would be found on either high-quality sites due to naturally high nutrition, or where moderate nutrient inputs to the stand have occurred. For midrotation loblolly pine, this may correspond to nutrient amendments (200

kilograms nitrogen and 25 kilograms phosphorus ha^{-1} over a repeated cycle of 4 to 6 years). Simulations suggest that an LAI of 3.0 to 3.5 (projected) is optimal for loblolly pine over most of the Southeast. For mixed hardwood stands, optimal LAI may be that found in midsuccessional ecosystems with a mixture of shade-intolerant and shade tolerant species. This mixture may provide for optimal conditions of light use efficiency; i.e., high light-requiring (and productive) species in the upper canopy and lower light-requiring species in the mid- and lower canopy.

Biologically attainable LAI would be that theoretical LAI created from heavy nutrient inputs, either from fertilization or from atmospheric deposition. Biologically attainable LAI has been identified from simulations, or from theoretical relationships between LAI and light extinction (k). Assuming a k of 0.5 to 0.8, and an under-canopy PAR transmittance of 0.05, biologically attainable LAI could range from 3.6 to 6.0 (projected). Gholz (1986) suggests that LAI of slash pine stands could reach six m^2 m^{-2} projected. From simulations, we suggest that an LAI of 4.0 to 4.5 (projected) would be biologically attainable but not optimal for maximum NPP in southern pine stands.

Biologically attainable LAI for hardwood ecosystems has yet to be identified. However, LAI values > six are uncommon in hardwood ecosystems. Where they occur, the general stand conditions include a dense mid- and understory of shade tolerant species (J.M. Vose, unpublished data). While contributing substantially to total stand LAI, low light conditions in the mid- and understory result in only slight increases in NPP. What is not known is whether altering site resources (e.g., via fertilization) would increase LAI in the upper canopy and result in proportional increases in stemwood NPP.

The next step for this approach would be an attempt to quantify the levels of resources, site occupancy, and the canopy light compensation ratio to create a working diagram for use in stand management. The general principles that hold for broad comparisons may not hold for stand level management. As such, region-specific, or ecosystem-specific models may be required.

ACKNOWLEDGMENT

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STEM MECHANICS AS A BASIS FOR BIOMASS ALLOCATION IN SOUTHERN PINES

Thomas J. Dean[1]

Abstract—The opportunity may exist to increase forest yield beyond what may be possible through site amelioration through a better understanding of biomass allocation within trees. Two general principles currently exist that explain the response of allocation to environmental changes. The first is considered a "goal seeking" approach where the tree maintains a critical ratio between mineral nutrient and carbon concentration within its tissues. Biomass is allocated to the foliage and root system, according to this ratio. The other principal is a physiological approach that relates meristem activity to the combined local concentration of mineral nutrients and carbon. The principal difficulty of the goal seeking approach is that it does not apply well to trees. The principle deficiency of the physiological approach is that simplifying assumptions must be incorporated into the model since not all of the physiological processes involved in nutrient and carbon uptake and in carbohydrate allocation are completely understood. An alternative approach exists that accounts for the allocation between the main stem and fine-root system by treating the main stem as a structural member of the tree. According to this approach, carbohydrate is preempted by the stem in order to counter the increased mechanical stress created by crown growth or by changes in the exposure to lateral wind forces. This approach corresponds with the negative linear relationship between fine-root allocation and stem allocation observed in several coniferous species. It also agrees with differences in allocation patterns seen among genotypes. Possible experiments to test this approach involve manipulating the mechanical stress experienced by the stem. If the hypothesis is correct, fine-root allocation will decrease as greater stress is generated in the stem.

INTRODUCTION

The most common approach to increasing forest yield has been to ameliorate the abiotic limits to growth. In the Southeastern United States, many of the areas available for forest production are naturally low in fertility due to highly weathered soils or past agronomic practices. Thinning has long been used to make more site resources available to crop trees, and fertilization has recently become a standard practice in plantation management. In the near future, several forest industries expect to fertilize and irrigate plantations. Resource use efficiency varies with genotype, and yield can be further increased by carefully matching families with site conditions.

Forest yield is a function of both the total amount of biomass produced (net primary production) and the amount of that biomass allocated to the stem. Many environmental factors such as light availability and soil fertility have been found to influence biomass allocation within trees (Gower and others 1995). Allocation patterns also vary by family in southern pines (Li and others 1991). The interaction between environmental and genetic variation in biomass allocation produces a wide spectrum of allocation patterns and suggests that silvicultural treatments may have the potential of changing conventional site and family associations. Making precise matches between family, site, and silvicultural treatments can be achieved through conventional screening studies in the field, but this approach is slow and cannot include a large range of combinations. A better understanding of the mechanisms controlling allocation would aid in determining the correct combination of family and silvicultural prescription for a particular site.

Gower and others (1995) reviewed the factors that influence biomass allocation in evergreen conifers. However, despite extensive knowledge of factors affecting allocation, no consensus has been reached in the mechanisms responsible for allocation patterns. The purpose of this paper is to present a hypothesis that accounts for this tradeoff between stem and fine-root allocation. The hypothesis is based on the mechanical relationship between the crown and the stem and states that decreases in fine-root allocation result from the stem's preemption of carbohydrate to counteract mechanical loads generated by the crown. Since crown morphology differs among families, the hypothesis should also account for genetic differences in stem and root allocation. Several experimental approaches that could test the proposed hypothesis are also outlined in this paper.

BRIEF SUMMARY OF EXISTING HYPOTHESES

Carbon allocation in trees, and plants in general, exhibits considerable plasticity. This plasticity has been treated as either goal seeking or as a consequence of the principally opposite directions carbohydrate and nutrients move through trees (Cannell and Dewar 1994). From a goal seeking perspective, trees allocate carbon according to the relative supply of resources in order to maintain proper tissue balances of essential elements. From the physiological perspective, the different movement of carbohydrates and nutrients produces changes in the relative abundance of essential elements within the primary and secondary meristems, resulting in different growth and allocation patterns within the tree. Both views result in realistic allocation patterns. The main difference between the two views is that the physiological approach changes

[1] Associate Professor, School of Forestry, Wildlife and Fisheries, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA 70803.

allocation patterns much more quickly than the goal seeking approach (Thornley 1995).

Goal Seeking Hypotheses

For plants in general, the most common expression of treating allocation as a goal seeking process is the functional-balance equation. This equation combines two simple mass balance equations that state that the fraction of carbon in the plant is the product of shoot mass and the photosynthetic activity of the shoot, and that the fraction of a soil-mineral nutrient in the plant, most commonly nitrogen, is the product of root mass and the specific uptake rate of the root system for that particular nutrient. The ratio between the fractions of carbon and the soil-mineral nutrient is expressed as

$$fc/fn = (Ms\ Ps)/(Mr\ an), \qquad (1)$$

where

fc and fn = the tissue fractions of carbon and a mineral nutrient,

Ms and Mr = the mass of the shoot and root system, respectively,

Ps = photosynthetic rate, and

an = specific uptake rate of the root system for the mineral nutrient.

Equation (1) was first presented by Davidson (1969) for alfalfa and clearly indicates that when photosynthesis increases, more carbon is allocated to the root system, and when specific uptake rate of the root system increases, more carbon is allocated to the shoot. While the functional-balance equation has been the starting point for a number of analytical solutions for optimal allocation (e.g., Hilbert and Reynolds 1991), it does not apply directly to trees because the stem and branches are not photosynthetic, and the stem comprises the majority of the plant mass. Cannell (1985) has suggested that the functional-balance equation may apply to trees only if the foliage and fine roots are considered, but because nutrient concentrations vary by two orders of magnitude among the various tree structures (Switzer and others 1966), and nutrients are retranslocated from older foliage to new foliage (Birk and Vitousek 1986), much more information is needed to use the functional-balance equation to quantify carbon allocation in trees. The value of the functional-balance equation for carbon allocation in trees has been that it supports the reduction in relative allocation to the fine roots often observed when trees are fertilized or are growing on fertile soils.

Genetic differences in carbon allocation also support the goal seeking approach to allocation. Van Buijtenen and others (1976) noted a tendency for families of loblolly pine from the extreme western portion of the loblolly pine range to allocate greater amounts of carbon to the root system than families from the central portion of its range. Bongarten and Teskey (1987), working with loblolly pine seedlings, found that coastal families allocated less carbon to the root system than interior families when subjected to drought.

Another common variant of the goal seeking approach is the priority hypothesis of carbon allocation developed by Waring and Pitman (1985). According to this hypothesis, foliage allocation has the highest priority, the root system is second, and stemwood allocation is below both foliage and root allocation. This is a difficult hypothesis to test, partly because the hypothesis allows priorities to shift to maintain critical, physiological balances within the tree.

Physiological Hypotheses

The most comprehensive, physiological approach to carbon allocation is the transport-resistance model of Thornley (1991). In this model, carbon is fixed in the foliage and moves basipetally to the fine roots, and nitrogen is taken up by the fine roots and moves acropetally to the foliage. The intrinsic growth rate of the meristems along transport path is proportional to the concentrations of carbon and nitrogen within the meristematic region. A set of rules is defined to keep the structural growth of each component in balance with supporting structures. This model produces realistic results, but it does not include retranslocation of mineral nutrients within the crown.

While the transport-resistance model relates meristematic growth to the concentrations of carbon and nitrogen, the functions that maintain the proper balances among the various tree components are based on hydraulic relationships according to the pipe model of Shinozaki and others (1964). Use of the pipe model as a basis for either constraining allocation or determining allocation, as in the carbon-balance model of Valentine (1988), requires some questionable assumptions. Typically, these models assume that leaf area, sapwood cross-sectional area, and fine-root surface area are all linearly correlated. The relationship between leaf area and fine-root surface area is unsubstantiated, and the relationship between leaf area and sapwood cross-sectional area is curvilinear for several species (Baldwin 1989, Dean and Long 1986a). In addition, some sapwood loss rate must be assumed. If each new ring of sapwood corresponded to each year of foliage production, the loss of sapwood would correspond directly with litter fall. This is not the case, however. Albrektson (1984) has shown that the number of rings in sapwood do not correspond with the number of needle cohorts in Scots pine, and that the number of rings in sapwood changes with position on the stem. Sapwood also serves as a storage organ for carbohydrate, and the carbohydrate storage needs may also determine the quantity of sapwood (Bamber 1976). The majority of water transport occurs in the outer sapwood rings (Shelburne and others 1993) leaving the remainder for carbohydrate storage. This may be the reason why sapwood changes slowly after artificial removal of leaf area (Margolis and others 1988).

MECHANICAL SUPPORT HYPOTHESIS

The dominant shift in allocation in response to soil fertility occurs between the stem and the fine-root system (Beets and Whitehead 1996, Santantonio 1989) (fig. 1): allocation to branches and course roots is comparatively small and does not appear to influence the tradeoff between stem allocation and fine-root the production (Santantonio 1989).
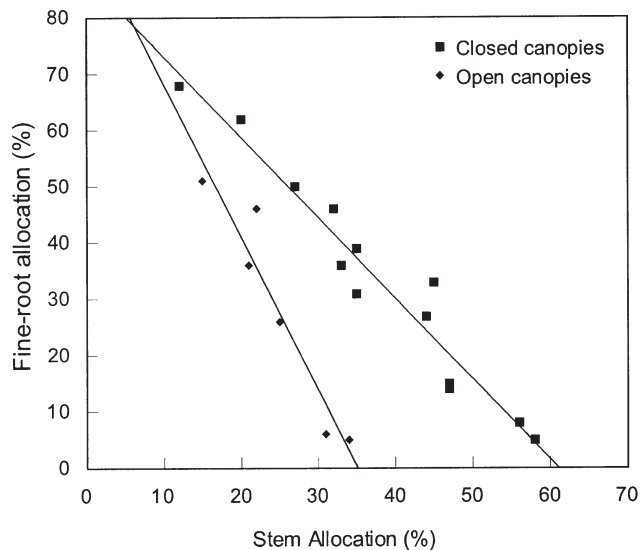
Figure 1—Fine-root allocation as a function of stem allocation for various northern coniferous species. Line is from linear regression. Data from Santantonio (1989).

Across a soil fertility gradient, increases in annual stem increment are associated with corresponding decreases in annual fine-root production. Tradeoffs between stem and root allocation can also be seen in loblolly pine seedlings representing a range of seed lots subjected to common moisture regimes (fig. 2). Each additional unit of carbon
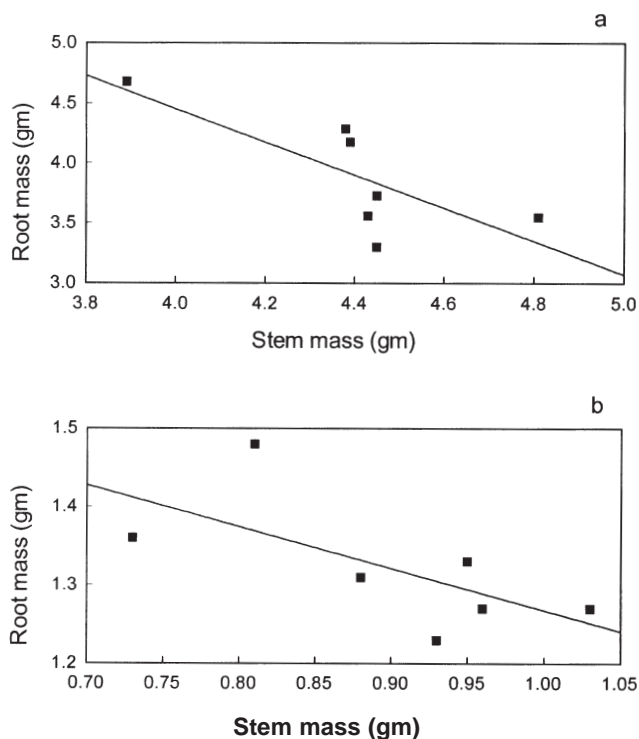

Figure 2—Root mass as a function stem mass for 1-year-old loblolly pine seedlings. Seedlings represent a range of families and were subjected to moist (a) and dry (b) soil conditions. Data from Bongarten and Teskey (1987).

required to counteract greater mechanical load on the stem may reduce allocation to the fine roots by a proportional amount (Santantonio 1989). The negative relationship between stem and fine-root allocation suggests that stem growth preempts carbohydrate from the root system and corresponds to studies showing that stem and fine-root growth are offset with cambial activity occurring during primary bud and leaf expansion and fine-root growth occurring during the interim, provided adequate soil moisture and temperatures (Reich and others 1980). Preemption of carbohydrate during cambial activity is supported by studies on source-sink relationships showing that sinks closest to the carbohydrate source are the strongest competitors for available supply (Wardlaw 1990).

The most common response to soil fertility or fertilization is increased foliage production (Brix 1983, Colbert and others 1990, Gholz and others 1991, Keyes and Grier 1981). The additional foliage increases the amount of stress generated in the stem by lateral wind pressure and increases the gravitational load on the stem. Since much of the new foliage under normal stand conditions is produced near the top of the crown (Borghetti and others 1986), the increased force is applied higher on the stem adding additional stress to the stem. Stem cross-sectional area increases to counteract this load (Niklas 1992) and may preempt carbohydrate that may otherwise be used for fine-root allocation.

Several lines of evidence indicate that mechanical support is the primary function of the main stem and that hydraulic support develops within the framework established by the mechanical relationships. Long and others (1981) found that stem taper in four Douglas-fir trees representing a range of canopy classes conformed with elementary structural beam theory, and that the amount of sapwood cross-sectional area appeared independent of the total cross-sectional area required for structural integrity. Dean and Long (1986b) found that both stem diameter and taper for lodgepole pine also conformed to structural beam theory. Dean (1991) found that saturated sapwood permeability is affected by the bending stress experienced by the cambium in slash pine seedlings where the entire basal area is needed for water conduction. When supplemented with water and nutrients and allowed to sway freely with the wind, these seedlings had significantly greater mean cross-sectional areas but lower saturated sapwood permeability than similarly treated seedlings that were prevented from swaying.

The effect of lateral and vertical forces on stem size can be described with tapered-beam mechanics and tapered-column mechanics, respectively. Mature trees appear to conform to both tapered-beam and tapered column mechanics; however, sapling stems, with relatively little crown weight, appear to conform only to tapered-beam mechanics (Dean and Long 1986b). For stems that are constructed with uniform material and experiencing a lateral force applied at the top of the stem, the most efficient geometry for the stem is a cubic parabloid where diameter cubed varies directly with height. This geometry

produces both equal bending stress and bending strain along the length of the stem. Increases in either height or the applied lateral force requires an increase in cross-sectional area to maintain a specified bending stress or strain.

While sophisticated applications of tapered-beam principles have been derived for trees (Morgan and Cannell 1994), a simplified equation derived by Dean and Long (1986b) provides a good approximation of the relationship between bending stress, stem diameter, and stem taper and clearly identifies canopy variables that influence bending stress. According to this equation, stem diameter at any cross section i (Di) is proportional to the product of the leaf area above i (Ai) and the distance from i to the center of leaf area above i (Si), i.e.,

$$Di = a \, (Ai \, Si)b, \qquad (2)$$

where

a = proportionality constant and

b = 0.33 for stems conforming perfectly with the constant-stress model.

Experimental values of b obtained through regression analysis range from 0.28 for lodgepole pine saplings (Dean and Long 1986b) to 0.33 for mature loblolly pine trees (Dean and Baldwin 1996).

Experimental manipulation of bending stress generally indicates increased stem allocation with increased loading (Kellogg and Steucek 1980, Larson 1965) and decreased stem allocation with decreased loading (Dean 1991). Moderate pruning of the lower crown increases the bending moment, represented by S_i in the constant-stress equation and can increase allocation to stem wood if the associated reduction in leaf area is not severe (Larson 1965). Wind exposure also increases the bending moment and may explain why light thinning increases total stand growth over an unthinned control (Lo-Cho and others 1991).

Data from various studies also support the idea that the reduction in relative allocation to the fine roots in response to improved soil fertility occurs by the stem preempting carbohydrate to counter the additional bending stress created by accelerated foliage growth. Data presented by Friend and others (1994) show that additional nitrogen beyond 25 milligrams per liter (mg/l) supplied to Douglas-fir seedlings results primarily in increased shoot growth with little or no increase in fine-root growth. In mature slash pine stands growing in northern Florida, fine-root allocation as determined by root respiration was not significantly different between fertilized and unfertilized stands (Cropper and Gholz 1994) even though fertilization significantly increased foliage biomass (Gholz and others 1991). Linder and Alexsson (1982) supplied a 14-year-old Scots pine plantation with a complete fertilizer solution for 6 years and saw no significant difference in the carbon allocated to fine-roots between the fertilized and unfertilized stands, despite a nearly threefold difference in allocation to the stems and

branches in the fertilized stand. Beets and Whitehead (1996), working with radiata pine plantations, saw significant fertilization effects on stem allocation but no significant effects on fine-root allocation.

In some cases, preemption of carbohydrate by the stem in response to soil fertility may result in reduced allocation to fine roots in absolute terms. Keyes and Grier (1981) compared the differences in biomass allocation in 40-year-old Douglas-fir stands growing on a poor site and a good site and on the good site, found a threefold decrease in the amount of biomass allocated to the fine-root system while stem allocation increased nearly twofold. Gower and others (1992) applied various treatments to a 50-year-old Douglas-fir stand including fertilization and found that fertilization reduced root allocation nearly 50 percent and increased stem allocation by 30 percent. Haynes and Gower (1995) compared fine-root production and mortality in fertilized and unfertilized plantations of red pine and found significant reductions in belowground carbon allocation in 2 of the 3 years they collected measurements. Ryan and others (1996) found that fertilization reduced fine-root production by 30 percent and nearly doubled stem production in radiata pine plantations.

POSSIBLE EXPERIMENTS
Several types of experiments could test this hypothesis. The basic premise of the hypothesis is that increased mechanical stress placed on the stem by an increase in crown size causes the stem to preempt carbohydrate that would otherwise be used to produce fine roots. Therefore, treatments that affect only the mechanical stress experienced by the cambium, but not the total amount of carbohydrate produced by the foliage, should result in significant changes in fine-root production. Mechanical stress experienced by the stem can be manipulated several ways. The classical way of minimizing mechanical stress is through tying the main stem to rigid stakes or by guying the main stem. Minimizing wind sway should result in significant increases in fine-root production compared to trees allowed to sway normally with the wind. The mechanical stress can be increased through artificial swaying. Stems can either be bent by hand or wrenched with a mechanical pulley. Increases in the amount of stress experienced by the stem should result in significant reductions in fine-root production.

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BRANCH AND FOLIAGE LEAF AREA OF LOBLOLLY PINE (*Pinus taeda* L.) 6 YEARS AFTER THINNING AND FERTILIZATION

S.F. Yu, J.L. Chambers, and J.P. Barnett[1]

Abstract—Branch and foliage biomass and leaf area were measured at two crown positions (upper and lower crown) of 48 trees that were harvested from a 14-year-old loblolly pine (*Pinus taeda* L.) plantation in conjunction with ongoing physiological studies. The collected data were used to evaluate the cultural treatment effects on foliage and branch characteristics, and will provide part of the information needed as a basis for scaling photosynthesis from the needle to the stand level. The study was conducted on the Palustris Experimental Forest, Rapides Parish, LA, during early spring 1995, six growing seasons after treatment. Thinning (thinned versus unthinned) and fertilization (fertilized versus unfertilized) were randomly assigned to 12 plots in a 2 by 2 factorial design with three replications at the site. Thinning significantly increased branch length, diameter, and foliage biomass and leaf area per branch. Effects of thinning at the branch level mainly occurred in the lower crown. The thinned treatment had twice as many shoots per branch as the unthinned treatment. The vertical distribution of leaf area per branch was positively related to branch size but negatively related to crown depth after midcrown. Fertilization had no significant residual effects on leaf area and branch size either in the upper crown branch or in the lower crown branch 6 years after treatment. The interaction of thinning and fertilization was not significant for branch and foliage leaf area.