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

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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 \( \text{m}^2 \text{m}^{-2} \) (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 interception 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., Cannell 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.

APPRAOCH

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, black gum-red maple, sweet gum-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 (NCFSC 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 \( \text{m}^2 \text{m}^{-2} \); one-half

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total) (Sampson and Allen 1995). For those stands where fertilizer has been applied, LAI may exceed 4 (m² 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 m² 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.

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 (m² 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 m² m⁻² in a high elevation stand dominated by red oak (*Quercus rubra*), sugar maple (*Acer saccharum*), and birch (*Betula* spp.) to 7.3 m² 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 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.

<table>
<thead>
<tr>
<th>Cover-type</th>
<th>Mean and (range) of LAI (m² m⁻²; projected)</th>
<th>Std. of LAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cypress-water tupelo</td>
<td>4.02 (2.68-5.44)</td>
<td>0.89</td>
</tr>
<tr>
<td>Blackgum-red maple</td>
<td>3.89 (2.73-5.20)</td>
<td>0.71</td>
</tr>
<tr>
<td>Maple-beech-birch</td>
<td>5.05 (2.74-6.30)</td>
<td>0.98</td>
</tr>
<tr>
<td>Oak-hickory</td>
<td>3.87 (2.78-5.95)</td>
<td>0.82</td>
</tr>
<tr>
<td>Sweetgum-yellow-poplar</td>
<td>4.18 (2.34-5.90)</td>
<td>0.81</td>
</tr>
<tr>
<td>Spruce-fir</td>
<td>3.46 (2.20-4.89)</td>
<td>0.68</td>
</tr>
</tbody>
</table>

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 (P\(_{net}\)) (Sullivan and others 1996) and R\(_m\) rates indicate that stands with a greater proportion of intolerant species in the upper canopy (high light; > 1000 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) will fix more canopy carbon than stands with a greater intermediate and shade tolerant species. Patterns at low light (<300 \(\mu\)mol 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
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 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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LITERATURE CITED


One hundred seventeen papers, 3 abstracts, 2 poster summaries, and 1 summary address a range of issues affecting southern forests. Papers are grouped in several categories including tree improvement and nursery technology, site preparation, vegetation management, site classification, longleaf pine silviculture, nutrient dynamics, silvicultural systems, intermediate management, hardwood regeneration, pine and pine-hardwood regeneration, impacts of harvesting and site preparation, pine nutrition management, physiology, plant and structural diversity, growth and yield, stand development and dynamics, and measurement and research methods.

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