CHAPTER 24

A CONCEPTUAL MODEL
OF FOREST GROWTH
EMPHASIZING STAND LEAF AREA

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Abstract. A conceptual model of forest stand growth based on radiation interception, conversion efficiency, respiration costs, and carbon allocation patterns is developed. A critical model component is leaf area index (LAI) which influences the amount of radiation interception, an important determinant of forest growth. Changes in resource availability (water, nutrients) influence the amount and vertical distribution of stand radiation interception. Conversion efficiency is modeled as a function of environmental conditions (photon flux density, water, nutrients, temperature). Little is known about the effects of resource supply on respiration, an important process influencing the availability of fixed carbon for stemwood growth. Carbon allocation is also partially regulated by stand environmental conditions (e.g., more carbon is allocated below-ground on dry and infertile sites). The proposed modeling approach has practical utility in that it can be easily understood, parameterized, and tested.

INTRODUCTION

Predicting changes in forest growth in response to altered environmental conditions requires process-based models. Top-down versus bottom-up process models are alternative approaches for simulating forest stand growth. Top-down models typically begin at the stand level and use empirical representations of physiological processes. Bottom-up models begin at the leaf level (or lower) and contain physiological functions scaled up to the stand. For example, Reynolds et al. (1980) used detailed physiological measurements to simulate seasonal net canopy photosynthesis in loblolly pine (*Pinus taeda* L.). At the other extreme, Vose and Allen (1988) and Teskey et al. (1987) demonstrated linear relationships between loblolly productivity and leaf area index (LAI) or foliar biomass, indicating that a single factor such as light interception may be an adequate predictor of growth in single-species stands. Extremes of both approaches have limited practical utility in predicting growth response to stress: Detailed bottom-up models are too data-intensive, and simplified top-down models are too empirical. Thus a merged approach is needed to develop useful predictive models of forest growth response to environmental stress. In this paper we propose such a conceptual framework for modeling growth responses to altered environmental conditions in pine plantations.

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THE MODEL

Similarly to the approach discussed in Landsberg (1986), growth of forest stands can be modeled as a function of four factors: (1) radiation interception (Q); (2) conversion efficiency (net carbon fixation/unit radiation interception) (E); (3) growth and maintenance respiration (R); and (4) carbon allocation to stemwood growth (A_{stem}). Functionally, these factors can be expressed as follows:

$$\text{stemwood production (kg/ha/t)} = \sum_{i=1}^{t} (Q_i \times E_i - \sum_{c=1}^{n} R_{i,c}) \times A_{stem} \qquad (1)$$

where the subscript $_c$ in $R_{i,c}$ is respiration rate for specific plant components (leaves, stem, roots, etc.). As shown, the model predicts total carbon gain, a proportion of which is then allocated to stemwood by the A_{stem} coefficient. The environment regulates productivity through the effects of resource availability and stress (e.g., nutrients, water, temperature, air pollution) on the four key factors. Among recent efforts to parameterize models similar to ours (e.g., Mohren et al., 1984; McMurtrie, 1985), only McMurtrie (1985) directly addressed the effects of altered environmental conditions on physiological processes.

Recent theoretical treatments of forest productivity (Jarvis and Leverenz, 1983) have emphasized that radiation interception (primarily a function of LAI) is the major determinant of growth. Existing data (Monteith, 1977; Linder, 1985) support this contention. Therefore, our approach concentrates on stand LAI development (annual and seasonal), canopy LAI distribution, and the effects of altered environmental conditions on LAI. We also discuss the importance of conversion efficiency, respiration, and carbon allocation in determining forest growth. Radiation interception and conversion efficiency are treated at two levels of resolution: (1) whole stand, and (2) within the canopy. The information discussed here provides the basis for the functional relationships upon which the proposed modeling approach depends.

LAI AND RADIATION INTERCEPTION

Whole Stand

The proposed modeling approach requires an understanding of changes in LAI with stand age. Data on leaf area development in pine plantations, particularly data from repeatedly measured stands, are limited. Repeated measurements from an eastern white pine (*Pinus strobus* L.) plantation in North Carolina, U.S.A. (Figure 1), showed that projected LAI reached a stable maximum value of about 5.5 by age 15 (Swank and Schreuder, 1973). Gholz and Fisher (1982) examined a chronosequence of slash pine (*Pinus elliotii* Engelm.) stands in Florida and found that LAI increased rapidly from 0–10 years, reached a maximum of 2.0 between 10–20 years, and then declined to about 1.5 in a 30-year-old stand.

Differences among species in stand LAI development are due to the physiological characteristics of each species and to environmental conditions that regulate leaf area. Fertilization studies have demonstrated that the maximum potential leaf area is limited by nutrient supply (Vose and Allen, 1988). Fertilization may also increase the rate at which this maximum is reached (Miller, 1984). The implications of altered nutrient relations on radiation interception are shown in Figure 2, where the highest nitrogen fertilization rate resulted in an increased interception of 65 MJ/m² above controls during August.

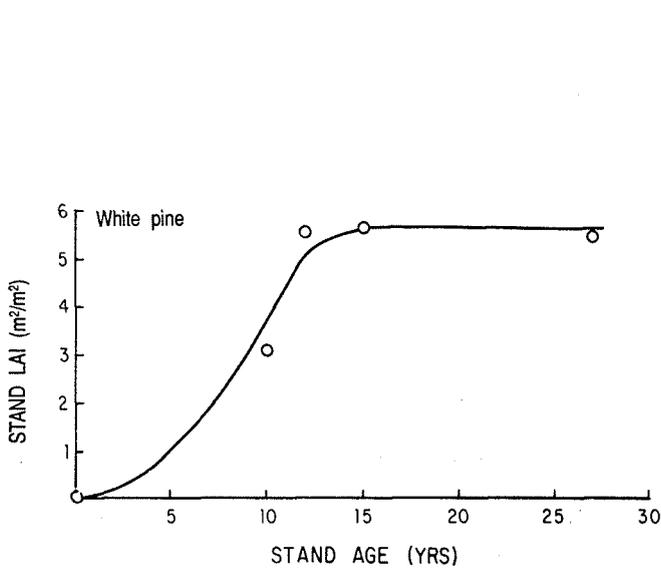Stand leaf area is also regulated by soil moisture, as demonstrated by strong relation-

Figure 1. Leaf area index development in eastern white pine (*Pinus strobus* L.). Data were obtained from repeated measurements and represent the growing season maximum LAI (projected).
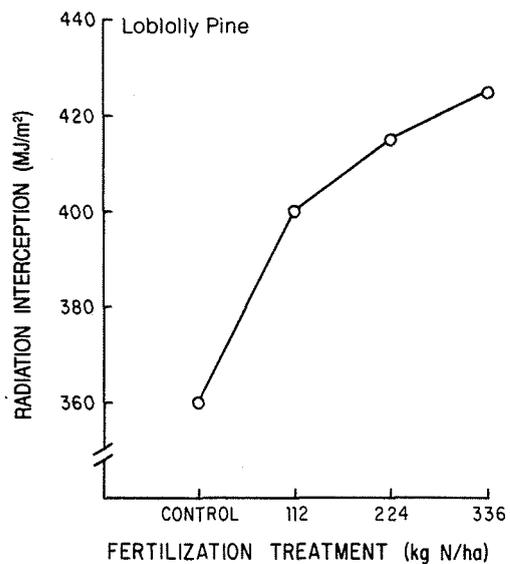

Figure 2. Effects of increased nitrogen supply on stand radiation interception in loblolly pine (*Pinus taeda* L.). Radiation interception data were estimated from stand LAI using the Lambert-Beers equation and an extinction coefficient of 0.46.
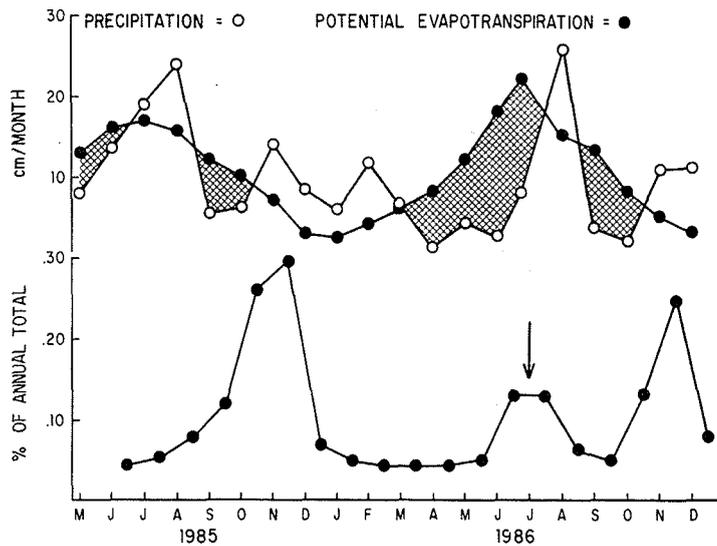

Figure 3. Effects of moisture stress on needlefall patterns in a loblolly pine plantation. Shaded areas on top graph represent periods of potentially high moisture stress. Arrow indicates peak in needlefall in response to droughty conditions.

ships between LAI and site water balance for many western conifers (Grier and Running, 1977). No studies have directly examined soil moisture effects on LAI in southern pine stands. However, in loblolly pine stands, needlefall patterns indicate that moisture stress reduces leaf area by accelerating needlefall (Figure 3). Additionally, drought limits needle elongation (Linder et al., 1987) and probably limits the maximum leaf area a stand is able to maintain. Temperature may also influence leaf area (Gholz, 1986). Respiration rates

depend on temperature, and needle respiration rates are higher than those for other tissues (Kinerson, 1975).

For fully stocked stands, it should be possible to model the relationships between stand age and LAI. However, model parameters are dependent upon site resources. One approach is to model the pattern of stand LAI development under optimal site conditions, and to make adjustments based on deviations of actual site conditions (e.g., based on soil type, site water balance, nitrogen availability indices) from the optimal. Region-wide fertilizer field trials provide an excellent data base for this approach.

Seasonal Patterns Within the Stand

In many pine species, stand LAI changes seasonally. Figure 4 summarizes data on seasonal solar radiation input and patterns of leaf area development (based on Kinerson et al., 1974) in a 13-year-old loblolly plantation and a 27-year-old white pine plantation. The fraction of solar radiation intercepted (at solar noon) was estimated using the Lambert-Beers equation and light extinction coefficients of 0.46 for loblolly (Sinclair and Knoerr, 1982) and 0.45 for white pine (Jarvis and Leverenz, 1983). The amount of solar radiation intercepted by the canopy varies seasonally in response to radiation input, development
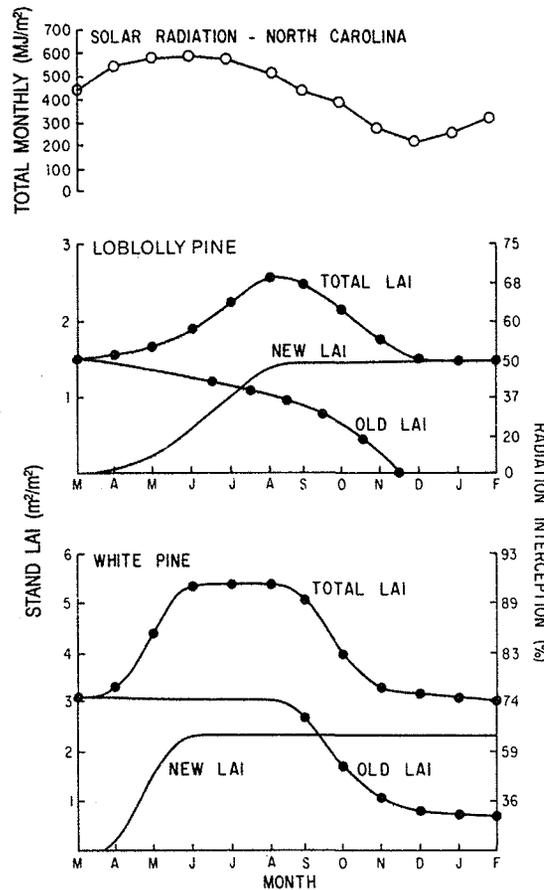
Figure 4.   Seasonal radiation input, radiation interception, and patterns of stand LAI development in loblolly and eastern white pine plantations. Changes in old foliage were determined from litterfall. Changes in new foliage were estimated from actual measures of total new LAI and typical flushing patterns. Total LAI = old LAI + new LAI. X-axis for the top graph is the same as for the bottom graphs.

of the current year's foliage, and loss of older foliage. Additionally, environmental conditions such as drought alter needlefall and LAI development patterns. Thus, process models with a resolution of less than one year must account for the dynamic nature of radiation interception.

Within the Canopy

At a finer resolution, radiation interception should be modeled by canopy depth because photosynthetic rates vary by canopy position (Higginbotham, 1974). Vertical distribution of leaf area changes with stand development because as the canopy closes, shading in the lower canopy causes branch mortality and restricts leaf growth. For example, the vertical leaf area distribution with stand development for a white pine plantation (Schreuder and Swank, 1974) showed a shift from a skewed to a normal LAI distribution as the canopy closed (Figure 5). Vertical leaf area distribution in both loblolly and white pine have been successfully modeled with the Weibull function (Vose, 1988; Schreuder and Swank, 1974). These studies have shown that the Weibull function can fit many of the potential foliage distribution patterns in forest canopies (i.e., negative skew, normal, positive skew).

In closed canopies with high leaf areas, increased nutrient supply may alter leaf area distribution and thus alter patterns of radiation interception (Ford, 1984) and photosynthate production (Linder and Axelsson, 1982). Similarly, stresses such as reduced nutrient supply, drought, or ozone damage may reduce canopy LAI sufficiently to stimulate branch retention and leaf growth in the lower crown. Figure 6 shows the LAI distribution (modeled with the Weibull) within the canopy and the amount of radiation intercepted in each 1 m layer for a 13-year-old loblolly pine stand during August. Based on crown development patterns, the theoretical amount of radiation intercepted by each foliage age class is indicated. Separation by foliage age class is important because conversion efficiency varies with foliage age (Higginbotham, 1974); however, phenological data on leaf area development are limited.
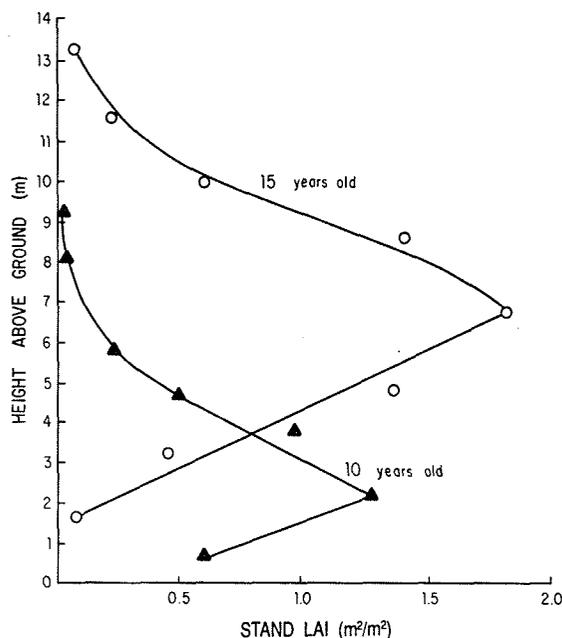

Figure 5.   Changes in vertical stand LAI distribution in white pine with stand age.
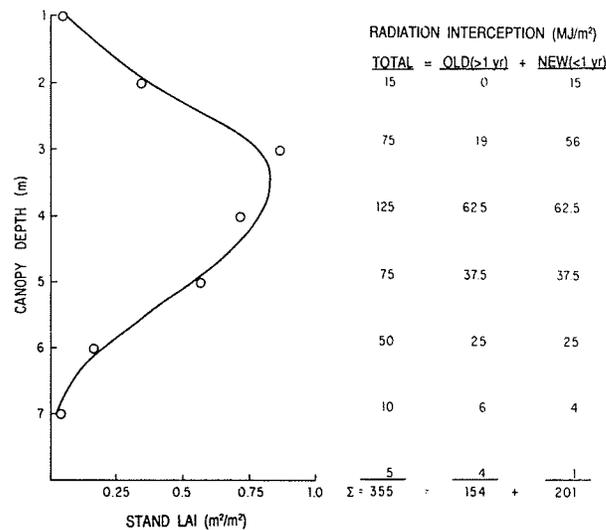
Figure 6.   Vertical stand LAI distribution and radiation interception (during August) in loblolly pine. LAI distribution curve was fitted with a Weibull function.

CONVERSION EFFICIENCY

At the stand level, Jarvis and Leverenz (1983) reported an average annual conversion efficiency (E) value of 1.42 g/MJ for a Scots pine (*Pinus sylvestris* L.) stand; the highest seasonal value occurred in August (E = 3.14 g/MJ). Seasonal variations in E reflect the importance of environmental conditions (i.e., light, temperature, water) and canopy characteristics in determining photosynthetic rate. As an example of nutrient and water limitations on E, an average annual value of E = 1.80 g/MJ was found on irrigated and fertilized plots from the same Scots pine study. Manogaran (1973) demonstrated a relationship between several measures of evapotranspiration and growth in loblolly pine, suggesting that evapotranspiration models may have some utility in predicting stand E. Growth efficiency (stemwood growth/unit LAI) has often been used as a measure of stand E (Brix, 1983) in fertilization studies. However, it is difficult to attribute changes in growth efficiency directly to changes in E because growth efficiency is also a function of carbon allocation patterns. Comeau and Kimmins (1986) used Ågren's (1983) concept of canopy nitrogen use efficiency (ANPP/kg canopy N) as an integrator of nitrogen availability and photosynthetic rate in lodgepole pine (*Pinus contorta* Dougl.). Similar approaches may permit incorporation of environmental conditions into canopy conversion efficiency models.

More detailed conversion efficiency models must account for the effects of canopy position, needle age, and environmental conditions. Linder and Axelsson (1982) found that photosynthate production in Scots pine varied by canopy position due both to patterns of vertical LAI distribution and to photosynthetic rate. Photosynthetic rate is a function of photon flux density in each whorl position, and photon flux density in each whorl may vary with environmental conditions. For example, Linder and Axelsson (1982) found that irrigation and fertilization increased photosynthetic rates and leaf production in the upper canopy. In the lower canopy, however, the same treatments increased shading and reduced photosynthetic rates. The net effect of irrigation and fertilization on canopy photosynthesis was only a 20% increase. The model of Reynolds et al. (1980) showed that

newly developing loblolly pine needles were sinks for fixed carbon until May for the first flush and July for the second flush, and that the major source of photosynthate in the course of the year was 2-year-old foliage. Thus, detailed canopy conversion models should account for differences in foliage age and radiation interception within the canopy. An approach to modeling canopy dynamics is to combine the data provided in Figure 1 (total LAI), Figure 4 (seasonal LAI patterns), and Figure 6 (vertical radiation interception) to estimate radiation interception by foliage age class, month, and canopy position. Combined with a model of Q (e.g., Q = f[photon flux density, environment, foliage age class]), canopy carbon gain can be simulated (Figure 7).

$$\text{Carbon gain}_1 = E_{1,1} \times Q_{1,1} - R_{1,1} + E_{2,1} \times Q_{2,1} - R_{2,1}$$

$$\text{canopy carbon gain} = \int_{i=1}^{6} \text{carbon gai}$$

$$\text{Carbon gain}_6 = E_{1,6} \times Q_{1,6} - R_{1,6} + E_{2,6} \times Q_{2,6} - R_{2,6}$$
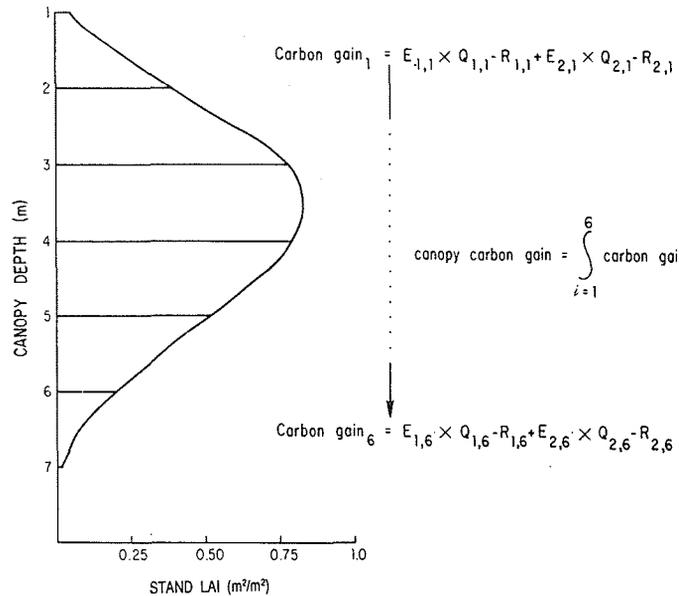
Figure 7.   Canopy carbon gain model, where E = radiation interception, Q = conversion efficiency, and R = respiration. Parameter subscripts represent foliage age class and canopy position, respectively.

RESPIRATION

Growth and maintenance respiration are major processes utilizing fixed carbon. Total respiratory carbon losses depend upon environmental conditions and upon the surface area, physiological activity, and growth of living tissue. Maintenance respiration rate is exponentially related to temperature, while growth respiration rate is less sensitive to environmental conditions (Linder and Rook, 1984). Kinerson (1975) estimated that about 60% of gross primary production in a loblolly pine plantation in North Carolina, U.S.A., was utilized in respiration. Highest respiration rates were observed in summer. Leaf tissue had the highest respiration rates (12.5 g CO_2/m^2 ground area/hr), followed by stems (0.95 g CO_2/m^2 ground area/hr), branches (0.2 g CO_2/m^2 ground area/hr), and roots (0.04 g CO_2/m^2 ground area/hr).

Respiration for each tissue type can be estimated by determining tissue surface area and calculating a temperature-dependent respiration rate per unit surface area. As a rough approximation of respiratory losses, Mohren et al. (1984) used constant annual maintenance respiration coefficients for needles, branches, stemwood, and root biomass and a single constant growth respiration coefficient for all plant components. In contrast,

Reynolds et al. (1980) used temperature-dependent respiration rate functions which accounded for shifts in Q_{10} before and after initiation of spring cambial activity.

More research is needed on the effects of other environmental parameters on respiration. For example, Lavigne (1987) found that respiration rates in balsam fir (*Abies balsamea* [L.] Mill.) depended upon stem water content and supplies of reducing sugars. Linder and Rook (1984) reported that nitrogen fertilization increases respiration in many species, and that there is a linear relationship between tissue nitrogen concentration and respiration. Stresses such as ozone damage may also increase respiration rates (Barnes, 1972).

CARBON ALLOCATION

Carbon allocation is strongly regulated by environmental variables (Linder and Rook, 1984; Cannell, 1985). The proportion of net primary productivity allocated belowground is highest on dry or infertile sites. Because stemwood growth has lower priority for fixed carbon than root growth (Waring and Schlesinger, 1984), less carbon is allocated to stemwood under dry and infertile conditions.

Data on belowground carbon allocation for southeastern pines are limited. In a 14-year-old loblolly plantation, carbon allocation ratios were 0.40 for stemwood (and bark), 0.05 for branches, 0.20 for foliage, and 0.35 for roots (Kinerson et al., 1977; Harris et al., 1977). In a 12-year-old plantation, allocation ratios were 0.64 for stemwood (and bark), 0.08 for branches, 0.14 for foliage, and 0.12 for roots (Nemeth, 1973). Differences between studies may be related to site quality and sampling methodology. Increased nutrient and water availability decreases the proportion of net primary production allocated belowground and increases the proportion allocated to foliage and stemwood (Linder and Rook,1984). Carbon allocation patterns also vary with stand age.

Approaches to modeling carbon allocation range from detailed sink-source models (Reynolds et al., 1980) to constant allocation ratios that allocate fixed carbon to various tissues (Mohren et al., 1984). It is clear from experiments and observations that fixed allocation ratios are inappropriate for modeling forest productivity under variable site or environmental conditions. We advocate allocation ratios for top-down approaches, but such ratios must account for changes in site water and nutrient status (cf. McMurtrie, 1985).

CONCLUSIONS

A conceptual approach for modeling forest growth is proposed. In contrast to traditional growth and yield models, this approach is based on functional relationships that regulate productivity. A simple, physiologically based model will have immediate practical utility because (1) it can be parameterized and tested; (2) it can be understood by the user (e.g., a forest manager); and (3) it can be adapted and modified for specific conditions. Leaf area is a critical component of the proposed approach because significant variation in forest growth can be explained by this single parameter. In addition to influencing radiation interception, LAI is a valuable parameter because of its interactions with respiration, photosynthesis, and carbon allocation patterns. These processes and interactions must be considered in physiologically based process models. Unfortunately, limited information is available on stand-level measures of respiration, photosynthesis, and carbon allocation. Including these parameters in stand-level models will require several assumptions, generalizations, and scaling-up procedures.

Models that do not consider the effects of "site quality" on physiological processes will

have limited practical utility in predicting forest growth response to altered environmental conditions. Traditional approaches, such as the use of a site index, are too general and lack a physiological base. As discussed in this paper, knowledge gained from fertilization and irrigation studies provides insight and data for incorporating environmental effects into process models.

Most growth and yield models cannot accommodate the impacts of air pollution, disease, and insect damage. The present model can incorporate the effects of mortality and foliage loss through reductions in LAI. Air pollution, disease, and insect damage may also be simulated via the impacts on carbon allocation, photosynthesis, and respiration.

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