Predicted leaf area growth and foliage efficiency of loblolly pine plantations

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Abstract

Foliage dynamics research is helpful for better understanding the process of forest production and improving silvicultural practice. However, the difficulty of measuring foliage amount has slowed down the research progress. Since leaf area of an individual tree can be reliably predicted from its diameter, growth and yield models that provide detailed information for each diameter class can be used to benefit foliage dynamics research. Simulation results from a growth and yield system for unthinned loblolly pine plantations indicated that foliage area increased with stand age, peaked between ages 36 and 51, and decreased after that. Volume growth increased with leaf area for young stands and decreased for older stands, whereas foliage efficiency consistently decreased with age. Better sites supported higher levels of leaf area index, volume growth, and foliage efficiency. Higher planting densities led to higher maximum leaf area indices and shorter time to reach that level. Initial density had no effect on foliage efficiency through time. © 1997 Elsevier Science B.V.

Keywords: Leaf area index; Foliage dynamics; Biomass; Diameter distribution models; Growth and yield models

1. Introduction

Foliage is a major factor in many biotic processes. The amount and efficiency of foliage in forest canopies have been related to stand production (Waring, 1983; Long, 1984; Smith and Long, 1989; Long and Smith, 1990) and tree vigor (Waring, 1983; Blanche et al., 1985). It has also been used as a measure of site occupancy (Waring et al., 1981; Long and Dean, 1986), light competition (Waring, 1983; Smith and Long, 1989; Long and Smith, 1990), and as a means to assess the effects of silvicultural

practices (Waring et al., 1981; Binkley and Reid, 1984). Studies on foliage dynamics are considered an efficient way to investigate mechanisms regulating forest production (Waring et al., 1981; Kuuluvainen, 1991).

However, the difficulty of measuring foliage amount directly has slowed down leaf area growth and foliage efficiency research progress. Grier and Waring (1974) suggested the use of sapwood area to estimate foliage mass. Their method transformed the difficult problem of measuring foliage amount directly into an easier one of measuring sapwood area. This was a milestone in estimating foliage amount, and the technique has since been widely used in

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foliage growth and efficiency research. However, there are problems in measuring sapwood area. For standing trees, sapwood area is usually determined from increment cores. Baldwin (1989) stated that the cross-sectional shape of loblolly pine heartwood was best depicted by an ellipse. Therefore, two increment cores should be extracted at right angles to obtain a reasonably good measure of the heartwood basal area. The measurements may vary, depending on the locations of the boring relative to the orientation of the elliptical shape. This is a potential problem for repeated measurements on the same tree.

A natural extension of the Grier and Waring (1974) method is to use stem diameter at breast height (or DBH, measured at 1.3 m above the ground) or stem cross-section area at breast height (called basal area) to predict foliage amount (Whittaker and Woodwell, 1968; Waring et al., 1978; Kuuluvainen, 1991). Shelburne et al. (1989) indicated a close relationship between leaf area and DBH with an R^2 of 0.88, which is only slightly lower than an R^2 of 0.89 between leaf area and sapwood area of loblolly pine plantations. Recalculating a linear regression using data from Dean and Long (1986) showed an R^2 of 0.92 between leaf area and basal area, and 0.96 between sapwood area and basal area for lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.). Baldwin (1989) concluded that diameter at breast height was at least as good as either sapwood area at breast height or sapwood area at the base of full live crown in predicting foliage weight for loblolly pine plantations. These results indicate that there is a close relationship between leaf area and DBH, and DBH could be used to estimate foliage amount.

Since leaf area of an individual tree can be successfully predicted from its diameter at breast height, forest remeasurement data and resulting growth and yield models can be used to benefit foliage dynamics research. Existing growth and yield models provide information on diameter growth, height growth, volume growth, and their relationship with site quality, stand density, and age. With the help of equations that relate individual tree leaf area or weight with stem diameter at breast height, foliage amount can be derived from growth and yield models for stands with different age, site quality, and density.

There are two obvious benefits in using forest growth and yield models in foliage dynamics re-

search. First, large amount of growth and yield data have been collected and various growth and yield models are readily available. By using the existing data and models, money and time for data collecting can be reduced. Second, because of the difficulty in measuring leaf area, data on foliage development are usually incomplete in terms of stand conditions (site quality, stand density, and age). On the other hand, existing growth and yield data and models cover a variety of tree species that grow at different conditions. For many important tree species, growth and yield data have been accumulated for a long period of time. This information can be used to provide a relatively more complete picture of foliage dynamics.

There are mainly three types of forest growth and yield models for even-aged stands: whole stand models, diameter distribution models, and individual tree models. They differ in detail of the outputs. Whole stand models provide prediction for overall stand attributes, e.g. tree volume per unit area, without breaking down the numbers into diameter classes. Diameter distribution models predict volume and number of trees per unit area for each diameter class. Individual tree models provide prediction based on simulation of individual trees.

Among the three types of growth and yield models, diameter distribution models have some advantages over the other two. They provide more detailed information than whole stand models and are easier to construct and use than individual tree models. The objective of this research is to demonstrate the use of a diameter distribution model in studying foliage dynamics of loblolly pine plantations.

2. Procedures

2.1. A growth and yield system for loblolly pine plantations

Baldwin and Feduccia (1987) developed a growth and yield system for loblolly pine (*Pinus taeda* L.) plantations. This diameter distribution model was based on data from 252 remeasurement plots. There were 527 measurements in stands having site indices from 12 to 24 m (based age 25 years), planting densities from 620 to 3700 trees ha^{-1}, and plantation

ages from 3 to 45 years. More detailed information can be found in the Baldwin and Feduccia (1987) paper.

Outputs from this system included volume, basal area, and number of surviving trees per unit area in each diameter class. The following inputs were needed:

1. stand age,
2. site index or average height of dominant and codominant trees, and
3. number of surviving trees, or basal area, or trees planted per unit area.

2.2. Leaf area estimation

Baldwin (1989) experimented with different models to predict individual tree foliage dry weight and found that diameter at breast height was as good an independent variable as diameter at base of the full live crown, or sapwood basal area at breast height or at base of the full live crown. Baldwin (1989) developed the following regression model using biomass data from 112 planted loblolly pine trees:

$$\ln(FW) = -4.5716 + 2.1741 \ln(D)$$

where FW = individual tree dry foliage weight (kg), D = diameter at breast height (cm), and $\ln(x)$ = natural logarithm of x.

The fit index (analogous to coefficient of determination) of the above model was 0.86.

In our research, foliage dry weight was converted into leaf area using a constant specific leaf area (leaf area per unit of leaf weight) of 112.53 cm^2 g^{-1}. This number was the average of specific leaf area values reported by Shelton and Switzer (1984) for loblolly pine.

2.3. Simulations

The growth and yield model by Baldwin and Feduccia (1987) was used to simulate unthinned loblolly pine plantations from age 3 to 45 years, for three levels of site index (12, 18, and 24 m at base age 25), and five levels of planting density (1200, 1800, 2400, 3000, and 3600 trees ha^{-1}). For each simulated stand, number of trees per hectare for each diameter class provided by the growth and yield model was used to compute the foliage dry weight

for each diameter class. These numbers were then summed to give total foliage dry weight per hectare and finally converted to leaf area per hectare.

Outputs for each combination of stand age, site index, and planting density were total stem volume per hectare and leaf area index (ratio of total leaf area to land area).

3. Results and discussion

3.1. Foliage growth

The change of leaf area index (LAI) over time was plotted in Fig. 1 for all combinations of site index and planting density simulated. Because the data used to develop the growth and yield model were collected from forest stands up to 45 years old, results for stands 45 to 99 years old shown on the chart were based on extrapolation from the model.

The overall pattern of LAI growth for different site indices and planting densities is approximately the same. Stand leaf area increased at early ages, reached a maximum, and then decreased with age. This result agrees with reports by many researchers (Ford, 1982, 1985; Gholz, 1986; Kuuluvainen, 1991).
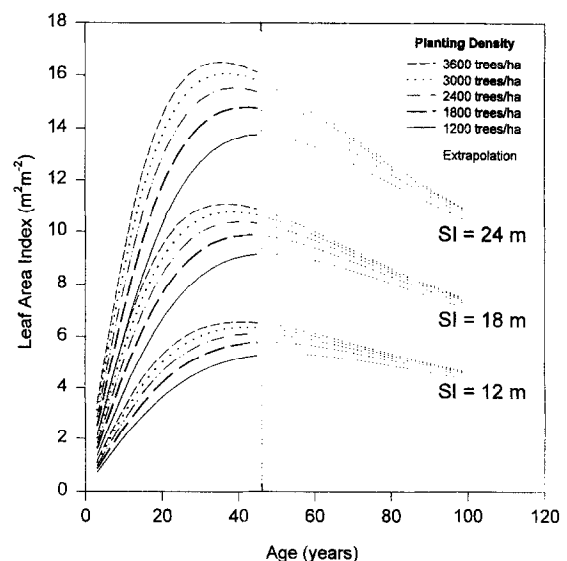

Fig. 1. Relationship between leaf area index and stand age for different combinations of site index (SI) and planting density.

Table 1
Maximum leaf area index (m^2 m^{-2}), by site index and planting density

Site index (m)	Planting density (trees ha^{-1})				
	1200	1800	2400	3000	3600
12	5.35	5.80	6.12	6.36	6.56
18	9.16	9.87	10.37	10.76	11.07
24	13.76	14.79	15.52	16.07	16.52

Other reports stated that foliage amount increases to a maximum and then settles down to maintain fairly stable foliage amount over time (Switzer et al., 1966; Marks and Bormann, 1972; Tadaki, 1977; Grier and Running, 1977; Pook, 1984). Fig. 1 shows that the decline of leaf area index was gradual after the peak for medium and poor sites (site indices 12 and 18 m at base age 25), especially for site index 12 m. If the focus was on a short period of time after the peak, leaf area index could be assumed to remain stable at an equilibrium level. Also the rate of decline of LAI after reaching its maximum amount slowed down over time for all site indices and planting densities. As this trend continues, leaf area index might eventually reach an equilibrium level.

The maximum level of LAI that a stand could reach was greatly affected by site quality and planting density (Table 1). Higher LAI levels occurred on better sites. For the same site index, leaf area index was higher for stands with high planting density. Extrapolation to age 99 showed that differences in LAI due to different stand densities got smaller with increasing age. This pattern for older ages agreed with findings from Jarvis (1975), Turner and Long (1975), and Long and Smith (1990), who reported that the equilibrium level is independent of past density.

Table 2
Age (years) at maximum leaf area index, by site index and planting density

Site index (m)	Planting density (trees ha^{-1})				
	1200	1800	2400	3000	3600
12	51	48	45	42	39
18	48	42	39	39	36
24	45	42	39	36	36

The rate at which a stand accrued leaf area and approached a maximum depended on the initial density. Stands at high densities reached maximum LAI sooner than stands at low densities (Table 2). This result agreed with findings by Tadaki (1970), Turner and Long (1975), and Long and Smith (1984). Furthermore, Table 2 also shows that stands at better sites reached maximum LAI earlier than those on poorer sites.

3.2. Net volume growth

Fig. 2(a) presents a nonlinear relationship between net volume growth of loblolly pine plantations and leaf area index for different combinations of site quality and planting density. Curves depicting the response of volume growth with respect to LAI had similar shapes for different site indices and initial planting densities. The better the site or the higher the stand density, the higher the volume growth for stands with the same age and leaf area index. For stands with relatively low LAI, volume growth increased with leaf area. This agrees with findings reported by Madgwick and Olson (1974), Miller and Miller (1976), Boyer (1968), Albrektson et al. (1977), Oren et al. (1987), Smith and Long (1989), Long and Smith (1990), Binkley and Reid (1984), Magnussen et al. (1986), and Dean and Baldwin (1996). As leaf area index grew, volume growth reached a maximum amount, and decreased thereafter. The same trend was observed by Waring et al. (1981) and Kuuluvainen (1991).

Researchers generally agreed that net stand productivity is related to total stand leaf area, but differed in opinion as to how they are related. Waring (1983) proposed that the two different theories in literature, i.e. volume growth increased with LAI vs volume growth increased with LAI first and decreased later, were based on data of different ranges of leaf area. He stated that stands with relatively low leaf area (LAI less than 6 m^2 m^{-2}) demonstrated a positive relationship between stand productivity and leaf area. When a stand developed a higher canopy leaf area, its productivity began to decrease. Waring's explanation was supported by Fig. 2(a) and especially by Table 3, which shows the peak occurring at an average leaf area index ranging from 3.34 (for site index 12 m) to 8.11 (site index 24 m), and from 4.79
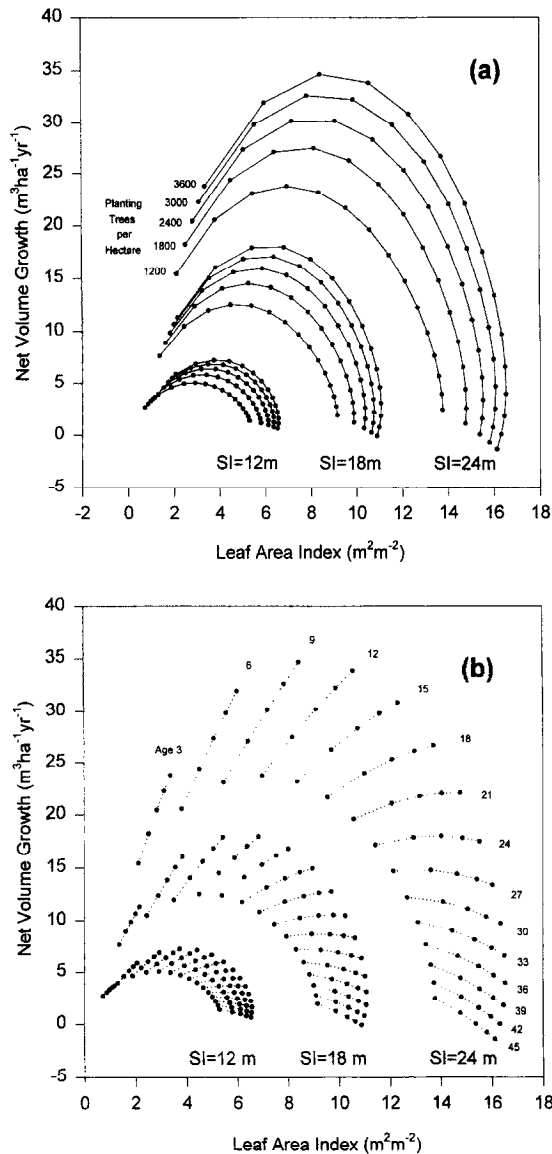
Fig. 2. Relationship between net volume growth and leaf area index for different combinations of site index (SI) and planting density. In (a), points of the same planting density and site index were connected, whereas points of the same age and site index were connected in (b).

(for a planting density of 1200 trees ha^{-1}) to 6.33 (3600 trees ha^{-1}). These results indicated that the level of LAI where volume growth peaked depended on site quality and stand density.

The ratio of LAI_v (LAI at maximum volume growth) to LAI_m (maximum LAI) ranged from 49 to

Table 3
Leaf area index (m^2 m^{-2}) at maximum volume growth, by site index and planting density

Site index (m)	Planting density (trees ha^{-1})				
	1200	1800	2400	3000	3600
12	2.91	3.41	3.18	3.47	3.72
18	4.49	5.27	5.88	6.39	6.84
24	6.98	8.17	9.11	7.86	8.44

62% (Table 4), depending on site quality and stand density. The results agreed with reports from Waring et al. (1981) and Kuuluvainen (1991) that stand productivity peaked at approximately half to two thirds of the maximum leaf area.

Fig. 2(b) is similar to Fig. 2(a), except that points of the same age and site index were connected to reveal the effect of stand age on the relationship between volume growth and LAI. For age 24 and below, volume growth increased with leaf area index. The rate (slopes of the lines) decreased with age. By age 27, volume growth ceased to increase with LAI. After that, net volume growth decreased as leaf area increased and reached zero about 5 to 9 years after the stand reached its maximum LAI level. The pattern was true for all three site indices.

3.3. Foliage efficiency

Foliage efficiency or growth efficiency is the annual volume growth per unit of leaf area. Fig. 3 shows that foliage efficiency of loblolly pine plantations decreased with LAI for all site indices and planting densities. The same trend was observed by Waring et al. (1981) and Oren et al. (1987). Low growth efficiency at high leaf area index may be a result of increased shading, higher respiration, or increased moisture stress (Vose and Allen, 1988).

Table 4
Ratio of LAI_v (leaf area index at maximum volume growth) to LAI_m (maximum leaf area index), by site index and planting density

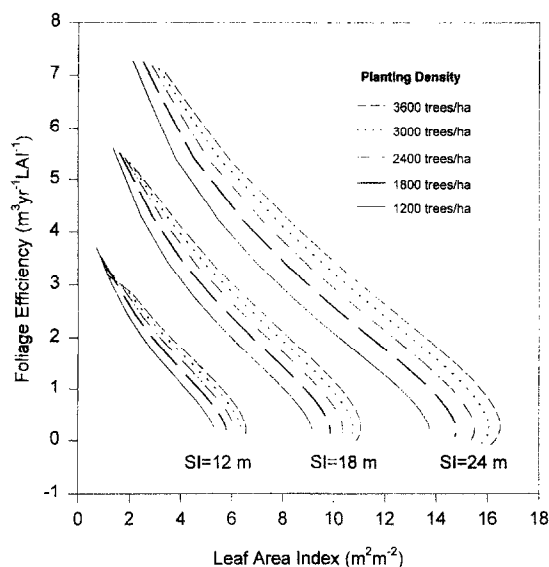| Site index (m)	Planting density (trees ha^{-1})				
	1200	1800	2400	3000	3600
12	0.54	0.59	0.52	0.55	0.57
18	0.49	0.53	0.57	0.59	0.62
24	0.51	0.55	0.59	0.49	0.51

Fig. 3. Relationship between foliage efficiency and leaf area index for different combinations of site index (SI) and planting density.

Stand density and site index appeared to affect growth efficiency. Better sites and higher planting densities resulted in higher foliage efficiency (Fig. 3). Colbert et al. (1991) and Brix (1983) reported that fertilizer application increased both stand leaf area and foliage efficiency. Miller and Miller (1976) found that higher nitrogen application levels led to higher LAIs, and that growth efficiency stayed constant for different levels of fertilizer, but was still higher than that of control plots. Mixed results from fertilization were reported by Vose and Allen (1988). They found no significant difference among growth efficiencies of control and fertilized plots in two stands. In the third stand, fertilizer application increased LAI but decreased foliage efficiency.

4. Conclusion

Simulation results for unthinned loblolly pine plantations indicated that stand leaf area increased at early ages, reached a maximum and then decreased with age. The maximum level is affected by site quality and the differences among initial densities declined with age. Volume growth increased with leaf area for young stands and the rate of increase declined with stand age. After age 27, volume growth started to decrease with leaf area. Foliage efficiency

decreased with LAI and was affected by site index and planting density.

Forest growth and yield models could be used to benefit foliage dynamics research. Large amount of growth and yield data have been collected and diameter distribution models are readily available for many tree species at different regions. With the help of an equation that relates leaf area or weight of an individual tree to its diameter at breast height and/or total height, simulations could be conducted on an existing growth and yield model to answer various questions that are often asked in foliage dynamics research, such as how stand leaf area changes with stand age, the effects of site quality and stand density on the change, the relationship between volume growth and leaf area, how stand age and site index affect the relationship, etc. One advantage of the above approach is to save time and money by making use of the vast existing growth and yield data and models. A second advantage is that it is possible to simulate what happens in stands of many tree species, covering a wide range of stand variables (site quality, age, and density). The difficulty in collecting data in past leaf area research has led to apparently contradicting theories based on data of narrow ranges. These theories might all be reasonable in their respective data range because they explained only fragments of the processes. The approach introduced in this paper is useful in its capability to provide a relatively more complete picture of foliage growth and efficiency, and to help in derivation of a comprehensive model of leaf area dynamics.

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