

Monthly leaf area index estimates from point-in-time measurements and needle phenology for *Pinus taeda*

D.A. Sampson, T.J. Albaugh, K.H. Johnsen, H.L. Allen, and S.J. Zarnoch

Abstract: Leaf area index (LAI) of loblolly pine (*Pinus taeda* L.) trees of the southern United States varies almost twofold interannually; loblolly pine, essentially, carries two foliage cohorts at peak LAI (September) and one at minimum (March–April). Herein, we present an approach that may be site invariant to estimate monthly LAI for loblolly pine using point-in-time measurements from a LI-COR LAI-2000 plant canopy analyzer (PCA). Our analyses used needle accretion and abscission data from monthly needle counts and destructive harvest data from a replicated 2 × 2 factorial experiment of water and nutrition amendments. No significant treatment effects on relative needle accretion or abscission were observed. Cohort (interannual) differences in needle accretion were found but appeared trivial. Cohort year had variable effects on needle abscission. Abscission of current-year foliage began in July and continued through November of the third year; however, only 7%–9% remained 23 months following bud initiation. A treatment-invariable regression of PCA measurements on cohort foliage biomass ($r^2 \approx 0.98$) was used to estimate annual cohort LAI. We derived monthly estimates of LAI from cohort accretion and abscission and cohort LAI. Monthly estimates of LAI for loblolly pine, using point-in-time measurements from the PCA, appear possible, although further testing is required.

Résumé : L'indice de surface foliaire (LAI) du pin à encens (*Pinus taeda* L.) du sud des États-Unis varie du simple au double au cours d'une année; essentiellement, le pin à encens porte deux cohortes de feuillage au moment du pic de LAI (septembre) et une seule lors de son minimum (mars–avril). Nous présentons ici une approche indépendante du site pour estimer le LAI mensuel du pin à encens à l'aide de mesures ponctuelles avec le LI-COR LAI-2000 « plant canopy analyzer » (PCA). Nos analyses ont utilisé des données de croissance et d'abscission issues de comptages mensuels d'aiguilles et des données provenant de récoltes destructives faites dans une expérience factorielle comportant deux facteurs (irrigation et fertilisation) avec deux niveaux chacun. Aucun effet significatif des traitements n'a été observé sur la croissance relative ou l'abscission des aiguilles. Des différences entre les cohortes (interannuelles) ont été observées pour la croissance des aiguilles mais sont insignifiantes. L'année des cohortes avait des effets variables sur l'abscission des aiguilles. L'abscission du feuillage de l'année commence en juillet et se poursuit au-delà de novembre de la troisième année, avec par contre seulement 7 à 9 % des aiguilles qui restent 23 mois après l'initiation des bourgeons. Une régression ne tenant pas compte des traitements et liant les mesures faites avec le PCA et la biomasse foliaire des cohortes ($r^2 \approx 0,98$) a été utilisée pour estimer le LAI des cohortes annuelles. Nous avons dérivé des estimations mensuelles de LAI à partir de la croissance et de l'abscission des cohortes et de LAI des cohortes. Les estimations mensuelles de LAI pour le pin à encens à l'aide de mesures ponctuelles effectuées avec le PCA semblent possibles même si des tests supplémentaires sont requis.

[Traduit par la Rédaction]

Introduction

Leaf area index (LAI) of loblolly pine (*Pinus taeda* L.) stands of the southern United States varies almost twofold interannually because, in general, loblolly pine carries two

foliage cohorts at peak LAI (September) and one at minimum (March–April). Canopy LAI largely determines the amount of incident photosynthetically active radiation intercepted by a forest and, therefore, photosynthesis and net canopy carbon gain (Landsberg and Gower 1997). Empirical

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and simulation investigations that seek to describe, or predict, relevant inquiry (such as carbon sequestration, net primary productivity, or net ecosystem exchange) depend on accurate, continuous estimates of LAI (e.g., McCrady and Jokela 1998; Sampson and Allen 1995; Jokela and Martin 2000; Luo et al. 2001; Sampson et al. 2001). However, estimating the temporal pattern in LAI can be problematic, particularly for loblolly pine. Loblolly pine exhibits tremendous variation in canopy architecture because of, in large measure, indeterminate growth (multiple flushes) and high plasticity in foliage production and abscission in response to site fertility and drought (e.g., Hennessey et al. 1992; Dougherty et al. 1995; Herbert and Jack 1998; Vose 1988; Vose and Allen 1988).

There are three common approaches to estimate LAI in forest stands. These include destructive biomass harvesting, litterfall collections, and techniques that employ measures of relative light flux density. Of these, instantaneous methods, such as the LI-COR LAI-2000 plant canopy analyzer (PCA) (LI-COR Inc., Lincoln, Nebr.), should be best suited to estimate seasonal patterns in LAI when LAI varies continuously over the course of the year. The PCA measurements are rapid and inexpensive, while destructive harvesting is expensive, time-consuming, and site specific. Estimating LAI from litter-trap data requires a waiting period, depending on both the number and the longevity of individual annual foliage cohorts. While the apparent utility of the PCA seems promising, it often performs poorly when used in coniferous forest applications; the PCA may underestimate LAI by 23% or more when used in pine stands (Gower and Norman 1991; Smith et al. 1993; Sampson and Allen 1994; Stenberg et al. 1994; Stenberg 1996). Underestimation of LAI by the PCA can, in large measure, be attributed to self-shading of foliage elements within shoots (shoot silhouette area less than projected area of the needles within a shoot) (Stenberg 1996) and the effects of stem and branch biomass on the PCA estimates (Smolander and Stenberg 1996). Species and site-specific correction factors have been used to adjust the instrument outputs to improve the LAI correspondence to more direct methods (Fassnacht et al. 1994; Stenberg 1996). However, uncertainty remains as to whether the PCA more closely estimates LAI or vegetation area index (VAI) (the projected area of all phytoelements) when used in coniferous forests. In addition, if one assumed that the PCA best approximated LAI, then questions remain whether the PCA estimates LAI on a one-half total or a projected area basis. Because of these uncertainties, outputs from the PCA must be interpreted with caution; monthly estimates of loblolly pine LAI may require an empirical modeling approach.

We had two objectives. First, we quantified treatment and cohort year (calendar year in which a foliage cohort is produced) effects on loblolly pine needle accretion and abscission at the Southeast Tree Research and Education Site (SETRES). Second, we sought to develop a generalized equation to estimate monthly LAI from single estimates of LAI (or foliage biomass) obtained from destructive harvests or from measures of VAI from the LI-COR PCA. Site specificity of a generalized equation may depend on whether or not treatment and cohort year influenced monthly needle accretion and abscission in these trees and stands. This ap-

proach, if successful, would reduce the cost, and possibly increase the accuracy, of estimating the temporal pattern in loblolly pine LAI.

Materials and methods

Study site

The study was conducted at SETRES, an intensive eco-physiological study of loblolly pine trees and stands located in the Sandhills of Scotland County, North Carolina (34°55'N, 79°30'W). The SETRES study is located on an infertile, well-drained site and was hand-planted on a 2 m × 3 m spacing in 1985 using a mix of 10 open-pollinated families originating from the North Carolina Piedmont. The SETRES study is a factorial experiment with two fertilization and two irrigation treatments replicated in four blocks. Fertilization was applied to achieve "optimum" foliar nutrition. The irrigation treatments were no irrigation and irrigation (supplemental with precipitation) to meet a target soil water content. For the optimum nutrition treatment, nitrogen was applied annually in attempt to achieve a foliar nitrogen concentration of 1.3% with other macro- and micronutrients in balance. Control foliar nitrogen was approximately 0.9% (in 1992). Fertilization treatment goals have been achieved (Albaugh et al. 1998). More details on the site, stands, and treatments can be found in Albaugh et al. (1998). Stand characteristics during the study period may be found in Table 1.

Annual precipitation averages 1210 mm (30-year average), but extended droughts are possible during the growing season. Average annual temperature is 17 °C (30-year average). Monthly climatic conditions during the 5-year study are provided in Table 2.

Approach

A test of treatment and cohort year effects on monthly needle accretion and abscission required a split-plot design and several steps. The whole-plot treatments were the 2 × 2 factorial combinations of fertilization and irrigation. Within each treatment plot, the four foliage cohort classes were the split-plot factor (blocks served as replication). The analyses required three components. First, field measurements of needle elongation and mortality, by flush, were collected (repeated measurements). Second, we used nonlinear regression procedures in SAS (SAS Institute Inc. 1999) to model treatment- and cohort-specific needle accretion and abscission using biologically relevant equations. Finally, we used the split-plot design (in analysis of variance (ANOVA)) to test the significance of the model parameters between the fertilization and irrigation treatments and cohort classes.

Our generalized equation to estimate monthly LAI of loblolly pine depended on (i) treatment and cohort year effects on needle phenology, (ii) estimates of foliage biomass at the stand scale, and (iii) point-in-time measurements of VAI that were obtained from the LI-COR LAI-2000 PCA. Details regarding the equation and the elements necessary to develop it, along with the field methodology and the statistical analyses, are provided below.

Table 1. Mean (and 1 SE) of descriptive stand characteristics at the research site SETRES, Scotland County, North Carolina, during the study period.

| Year | Treatment | Stand basal area (m ² ·ha ⁻¹) | Tree height (m) | Live crown length (m) | Crown foliage density (g·m ⁻¹) |
|------|--------------------------|--|-----------------|-----------------------|--|
| 1992 | Control | 4.2 (0.27) | 4.2 (0.10) | 3.73 (0.1) | 239 (2.1) |
| | Irrigated | 3.9 (0.29) | 4.1 (0.10) | 3.64 (0.01) | 224 (5.1) |
| | Fertilized | 5.1 (0.15) | 4.3 (0.09) | 3.79 (0.09) | 282 (2.7) |
| | Irrigated and fertilized | 4.9 (0.45) | 4.2 (0.11) | 3.79 (0.11) | 283 (20.9) |
| 1993 | Control | 6.1 (0.38) | 4.8 (0.13) | 3.99 (0.13) | 303 (2.5) |
| | Irrigated | 6.1 (0.30) | 4.9 (0.08) | 4.10 (0.08) | 299 (6.9) |
| | Fertilized | 8.7 (0.20) | 5.1 (0.11) | 4.42 (0.11) | 401 (6.5) |
| | Irrigated and fertilized | 9.3 (0.86) | 5.5 (0.14) | 4.82 (0.14) | 421 (29.2) |
| 1994 | Control | 8.2 (0.56) | 5.6 (0.17) | 4.39 (0.17) | 356 (1.6) |
| | Irrigated | 8.5 (0.34) | 5.7 (0.09) | 4.43 (0.09) | 356 (10.1) |
| | Fertilized | 13.1 (0.28) | 6.3 (0.14) | 5.12 (0.14) | 500 (7.9) |
| | Irrigated and fertilized | 13.9 (1.10) | 6.6 (0.14) | 5.32 (0.14) | 523 (30.7) |
| 1995 | Control | 10.1 (0.68) | 6.2 (0.22) | 4.58 (0.22) | 394 (2.5) |
| | Irrigated | 11.0 (0.42) | 6.6 (0.08) | 4.92 (0.08) | 398 (11.3) |
| | Fertilized | 17.1 (0.39) | 7.6 (0.16) | 5.87 (0.16) | 532 (6.7) |
| | Irrigated and fertilized | 18.3 (1.46) | 8.1 (0.16) | 6.19 (0.16) | 560 (30.0) |
| 1996 | Control | 11.6 (0.90) | 6.8 (0.24) | 4.90 (0.24) | 415 (3.1) |
| | Irrigated | 12.8 (0.49) | 7.4 (0.07) | 5.25 (0.07) | 422 (12.0) |
| | Fertilized | 20.3 (0.56) | 8.6 (0.15) | 6.36 (0.15) | 559 (10.8) |
| | Irrigated and fertilized | 21.5 (1.84) | 9.2 (0.18) | 6.68 (0.18) | 585 (28.8) |

Table 2. Monthly and yearly variation in climate at the research site SETRES during the study period.

| Year | Month | | | | | | | | | | | | Total |
|--|-------|-----|------|------|------|------|------|------|------|------|------|-----|-------|
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| Precipitation (mm) | | | | | | | | | | | | | |
| 1992 | 49 | 66 | 83 | 40 | 45 | 206 | 151 | 251 | 15 | 80 | 159 | 59 | 1204 |
| 1993 | 177 | 47 | 137 | 101 | 58 | 34 | 127 | 75 | 68 | 135 | 48 | 83 | 1090 |
| 1994 | 107 | 78 | 108 | 19 | 70 | 198 | 209 | 120 | 0 | T | 76 | 99 | 1084 |
| 1995 | 155 | 155 | 53 | 20 | 69 | 293 | 142 | 121 | 88 | 190 | 71 | 39 | 1396 |
| 1996 | 82 | 57 | 122 | 81 | 119 | 32 | 132 | 75 | 250 | 109 | 102 | 73 | 1234 |
| Mean daily shortwave radiation (MJ·m⁻²·day⁻¹) | | | | | | | | | | | | | |
| 1992 | 8 | 11 | 14 | 19 | 20 | 21 | 23 | 17 | 17 | 15 | 9 | 7 | — |
| 1993 | 8 | 12 | 14 | 21 | 21 | 23 | 21 | 19 | 17 | 12 | 10 | 9 | — |
| 1994 | 8 | 11 | 16 | 22 | 22 | 21 | 20 | 19 | 16 | 12 | 10 | 8 | — |
| 1995 | 9 | 10 | 17 | 21 | 21 | 19 | 22 | 20 | 14 | 13 | 10 | 9 | — |
| 1996 | 8 | 11 | 16 | 20 | 22 | 25 | 21 | 18 | 16 | 15 | 10 | 9 | — |
| Mean daily air temperature (°C) | | | | | | | | | | | | | |
| 1992 | 6.4 | 8.0 | 10.5 | 14.7 | 16.8 | 21.1 | 25.1 | 23.8 | 22.3 | 13.4 | 11.7 | 5.8 | — |
| 1993 | 6.0 | 3.7 | 8.0 | 11.9 | 19.5 | 24.1 | 27.5 | 24.4 | 21.8 | 14.1 | 9.3 | 3.4 | — |
| 1994 | 1.9 | 5.4 | 10.0 | 15.8 | 17.5 | 25.4 | 26.6 | 24.0 | 19.3 | 13.7 | 9.7 | 4.6 | — |
| 1995 | 4.3 | 4.2 | 10.8 | 16.2 | 21.0 | 24.3 | 28.6 | 28.1 | 21.7 | 16.9 | 8.0 | 3.0 | — |
| 1996 | 3.8 | 5.9 | 7.7 | 14.5 | 21.2 | 26.9 | 27.8 | 24.7 | 21.4 | 15.6 | 7.9 | 7.1 | — |

Note: T denotes trace.

Needle accretion

Field measurements

Fascicle development was measured from 1992 to 1995 (four individual cohorts) on one branch from the upper crown of five trees in each of the 16 plots (total of 80 branches each year) following Stow et al. (1992). Spe-

cifically, current-year fascicles were measured in 1992 and 1994 on the previous year first flush branch and in 1993 and 1995 on the 2-year previous first flush branch. For example, in 1992, we measured the 1992 foliage cohorts produced on a branch initiated in the first flush of 1991, while in 1993, we measured 1993 foliage cohorts on a branch initiated in the first flush of 1991. We assessed fascicle development by

averaging the measured length of three undamaged fascicles from the middle of each flush on a sample branch bimonthly from March to October and monthly the remainder of the year. The number of needles produced on each flush was recorded in the late summer (August and September) of the year the foliage was produced.

Relative flush contribution to the total annual foliage produced was calculated as the ratio of the total needle count for each flush and the total count for all flushes produced in that year for the branch for each tree by measurement date. Relative needle accretion for each flush was estimated as the ratio of the current length achieved to the maximum length achieved for the year for each flush. The product of the relative flush contribution and relative flush accretion provided a flush-level estimate of needle accretion. Relative needle accretion for the tree was then calculated as the sum of all flushes for the branch sample by measurement date. For each plot, average relative needle accretion for all measured trees in the plot was estimated for each date; needle accretion for these trees was assumed to be representative of the plot.

Regression

We used a reduced Chapman–Richards equation to model relative needle accretion as

$$[1] \quad N_A = (1 - e^{-Z_0 \times \text{month}})^{Z_1}$$

where N_A is relative needle extension as a proportion of the total needle length achieved, Z_0 is a shape parameter, month is calendar month (3–12), and Z_1 is the inflection parameter. We fitted eq. 1 to the plot-level accretion data for each fertilization–irrigation–cohort treatment combination from each block, resulting in 64 sets of model parameters. The parameter estimates for each regression resulted in a data reduction from many repeated measures to only two parameters that represent the response surface for the specific accretion relationship. These parameters were then examined in the GLM analyses that follow.

General linear models

We used two approaches to examine the effects of treatment and cohort year on needle accretion. We used a multivariate analysis of variance (MANOVA) (SAS Institute Inc. 1999) to test the hypothesis that treatment, cohort year, and their interaction had no influence on the Z_0 or Z_1 parameter estimates jointly. This is equivalent to testing for general differences in the entire model. We used the Wilks' lambda statistic to test this hypothesis. In addition, univariate ANOVAs were performed on the parameters individually and also on the instantaneous rates of needle accretion change (slopes of eq. 1 with respect to month). The whole-plot effects were tested against the block \times treatment error term, while the split-plot factor and all interactions were tested with the typical mean square residual error. We used the 0.05 significance level for all hypothesis testing. Least squares means were used for specific treatment effects in all pairwise comparisons using an adjusted Bonferroni type I error rate of 0.05.

Over the 60-month sampling period, there was one month (August 1995) where needle accretion was not measured. For graphical purposes only, we estimated missing values for

August, following the GLM analyses, using estimated best linear unbiased predictors (eBLUPs) (Littell et al. 1996). We used a “no-profile” residual variance method with a scoring equal to 5 in the model, and to check for goodness of fit, the eBLUPs were compared with the measured data. These eBLUPs were not used in the statistical analyses; they simply aided in graphing outputs.

Needle abscission

Field measurements

We measured needle abscission by counting surviving needles monthly (January through August) and bimonthly (September through December) on branch samples as described above. Relative needle abscission was estimated as the ratio of the missing needles for each flush to the total number of needles produced for the flush for each sample date. The relative contribution of each flush to the total needle pool was determined by the ratio of the total number of needles produced by a flush to the sum of all flushes produced in a year. Because foliage abscission occurs over multiple years, a running, consecutive-month variable (1–36 months) was ascribed to each cohort to permit tracking foliage loss over the duration (3 years) of individual cohorts.

Regression

A scatterplot of relative needle abscission over time indicated, essentially, two phases; we observed an exponential phase that was associated with rapid needle fall during autumn and a dampened, curvilinear phase that extended from autumn until complete cohort loss. To maintain biological relevance in the regression parameter estimates, we used a segmented modeling approach (SAS Institute Inc. 1999). Segmented modeling permits multiple functional forms within a single regression, thereby maintaining continuity in the resulting fit statistics (i.e., coefficient of determination and the F value); we used two equations to model needle abscission.

For the first phase (phase I) of needle abscission, we used the exponential model

$$[2] \quad \text{abscission}_{\text{EXP}} = \beta_0 e^{\beta_1 \times \text{month}}$$

where $\text{abscission}_{\text{EXP}}$ is the initial exponential phase in relative needle abscission expressed as a proportion of the total cohort lost, β_0 is a scaling parameter, β_1 is a shape (rate) parameter, and month is the calendar month interval (1–22).

The second phase (phase II) of needle abscission was fit using a power function of the form

$$[3] \quad \text{abscission}_{\text{POW}} = \beta_2 \times \text{month}^{\beta_3}$$

where $\text{abscission}_{\text{POW}}$ is the second, curvilinear phase in relative needle abscission expressed as a proportion of the total cohort lost, β_2 is a scaling parameter, month is the calendar month (23–36), and β_3 is a shape parameter.

We fitted eqs. 2 and 3 to the plot-level abscission data for each fertilization–irrigation–cohort treatment combination from each block, again resulting in 64 sets of model parameters. And, similar to the needle accretion data, these parameters were evaluated with GLM procedures as mentioned above and, for these models, with slight modification as described below. The month designating whether eq. 2 or eq. 3

was used was determined by sequentially changing the curve intersection month (starting at 21 and ending at 24) one month at a time and choosing the lowest sums of squares error.

General linear models

A similar approach as that described above for needle accretion was used to test the effects of treatment, cohort year, and their interaction on the needle abscission parameter estimates, slopes chosen, and tests of the overall model. Because the regression to model needle abscission required two equations, an additional MANOVA was used to examine the joint, exponential parameter estimates (β_0 and β_1) for phase I and then the joint, curvilinear estimates (β_2 and β_3) for phase II.

As with needle accretion, needle abscission data were also missing for various months for the 1993–1995 foliage cohorts. Data gaps included 3 months in 1995, 1 month in 1996, and 3 months in 1997. However, linear predictors were not estimated for needle abscission because their absence, from the figures, was not deemed obstructive to the visual display of the data.

Estimating foliage biomass

We used 4 years of destructive harvest data (1992, 1994, 1996, and 1998) and 7 years of stand inventory data (1992–1998) to estimate dormant season (January estimate) foliage biomass (grams dry mass of foliage per square metre of ground) for control and fertilized plots at SETRES. Albaugh et al. (1998) described in detail the sampling protocol and measurement procedures for the destructive harvests. These total tree harvests provided an estimate of total foliage on each of the harvested trees as well as an estimate of the most recent foliage cohort. For these analyses, we used 16 trees (one from each block and plot) sampled in each of the harvests.

Influential statistics

Influential statistics, diagnostic statistics that measure the influence of each observation on regression model estimates (SAS) (SAS Institute Inc. 1999), were conducted on the individual tree foliage biomass data. Namely, we used the Cook's *D* diagnostic statistic, a variant of the studentized residual test (SAS Institute Inc. 1999), in a regression to predict current-year foliage biomass (treatment combined) from diameter at breast height (DBH). We defined 0.2 as the critical level based on ocular analysis. One datum was dropped as a result of this procedure.

Individual tree foliage biomass regressions for both the most recent foliage cohort (hereafter referred to as "current-year cohort") and total foliage biomass were developed using nonlinear regression procedures in SAS (SAS Institute Inc. 1999). First, we regressed individual tree foliage biomass (current-year cohort and total foliage) using DBH in a power function (Sit and Poulin-Costello 1994). The residuals of this model were then plotted against stand basal area, stocking, crown length, and crown ratio (the ratio of live crown length to total tree height). There was a strong, consistent, and curvilinear residual bias with crown ratio. This variable was included in the regressions, yielding a final model:

$$[4] \quad \text{foliage}_{\text{BIO}} = \eta_0 \times \text{DBH}^{\eta_1} \times \text{crown}_{\text{RATIO}}^{\eta_2}$$

where foliage_{BIO} is foliage biomass (kilograms of foliage per tree), η_0 is a scaling parameter, DBH is tree diameter at breast height (centimetres), η_1 is a shape parameter for tree diameter, crown_{RATIO} is crown ratio (proportional), and η_2 is a shape parameter for crown ratio.

We applied eq. 4, for both the current-year foliage cohort and total tree foliage, to every tree in each block and plot in the study using the inventory data for each year examined. We did this using treatment-combined data over the entire study as well as for every treatment separately to determine generality of the regression. To evaluate if separate equations were required for each treatment, we compared the parameter estimates, between the treatment-combined model and the individual treatment regressions, with respect to the 95% confidence intervals (CIs) for each comparison (e.g., η_0 from the regression for pooled data was evaluated with respect to the 95% CI for η_0 obtained for the control plot regression). Individual tree foliage biomass estimates were summed over the blocks and plots and divided by plot area (900 m²) to obtain an estimate of stand-level foliage biomass per square metre.

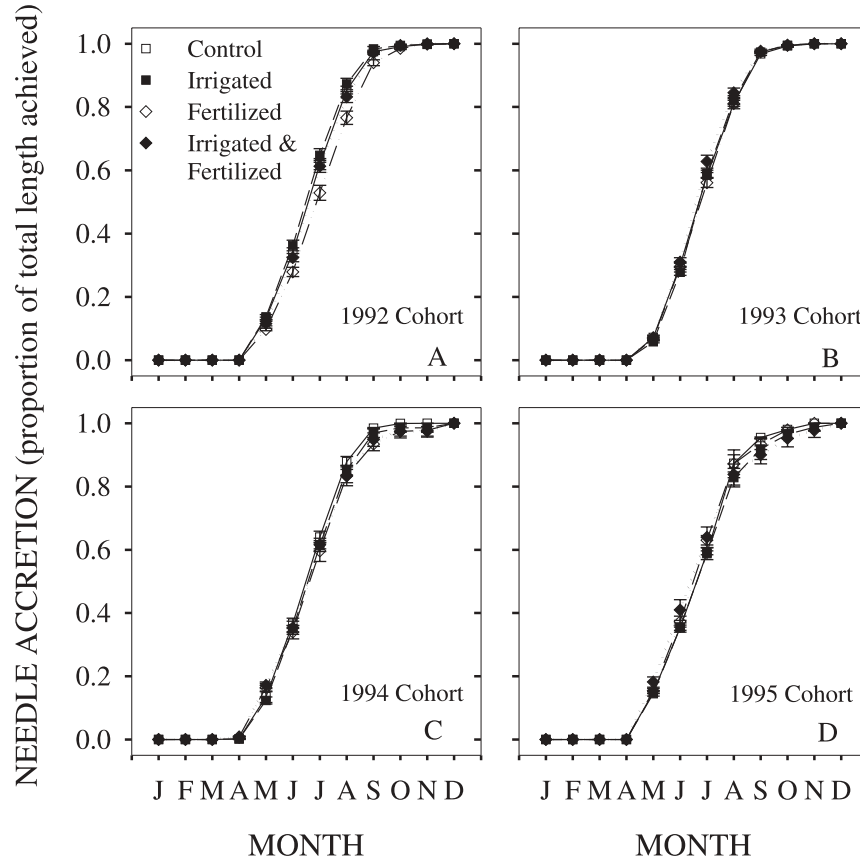
Total foliage biomass (for December) was used to estimate LAI to compare with the modeled estimates. For these analyses, we separated the empirical estimates of foliage biomass into three fractions (control plots: top = 0.18, middle = 0.41, bottom = 0.41; fertilized plus irrigated plots: top = 0.13, middle = 0.57, bottom = 0.30) (Maier et al. 2002). For each fraction, we multiplied foliage biomass by the corresponding treatment-invariant specific leaf area (SLA) (square centimetres per gram) (top = 30.47, middle = 32.49, bottom = 36.65) (Maier et al. 2002) to convert foliage mass on an area basis into LAI units (projected area basis).

LI-COR LAI-2000 VAI

Plot estimates of VAI from the PCA consisted of simultaneous readings of diffuse light levels (one above the canopy and one below) taken at roughly monthly intervals from March 1992 through December 1996. Twenty samples per plot, a systematic random sample along a transect, were taken under diffuse sky conditions (or early morning when necessary) using the 90° view cap for 1992 through 1996. The remote unit, located on a 3-m ladder, recorded above-canopy diffuse light from a central location. Plot estimates of VAI were calculated using the software provided by LI-COR (LI-COR Inc.). While we recognize that most studies that use the PCA in coniferous forest applications derive species and site adjustment factors to "correct" the VAI estimates, for the purposes of this study, we used uncorrected PCA outputs. Uncorrected outputs were thought to increase the potential utility of this model for off-site loblolly pine stands.

We used the nonlinear regression procedure in SAS (SAS Institute Inc. 1999) to examine the relationship between the September estimates of VAI from the PCA and December estimates of foliage biomass of the current-year foliage cohort. Foliage biomass (instead of LAI) was used in the comparison (regression) to, again, increase the transportability of

Fig. 1. Average monthly relative needle accretion in loblolly pine trees for the four treatments and four cohorts examined at SETRES, Scotland County, North Carolina. Needle accretion was expressed as the summation of the proportion of maximum needle length achieved, for each flush, weighted by the number of individual needles per flush. Error bars are 1 SE.



the model for off-site analyses; we wanted to eliminate errors caused by potential differences in SLA.

We also used nonlinear regression procedures to evaluate the regression to predict foliage biomass from the PCA estimates of VAI. The intercept was examined to test for significance from 0 (using the 95% CIs), while the slope was evaluated with respect to 0 and to 1 to evaluate the validity of the regression equation.

Results

Foliage development

Three distinct periods in foliage development were observed: (i) the first 4 months of the year when no measurable needle growth was detected, (ii) a period of rapid development and needle expansion, and (iii) reduced growth to final asymptotic length (Fig. 1). The MANOVA tests found no overall treatment effect on relative needle accretion ($p = 0.1036$). There were, however, cohort year ($p < 0.0001$) and treatment by cohort year interactions ($p = 0.0021$). When the parameter estimates (Z_0 and Z_1) were examined individually, the hypothesis tests from the univariate ANOVA yielded similar conclusions (Table 3). Moreover, the instantaneous rates of change for relative needle accretion for selected months yielded little additional insight; however, there was a

Table 3. Results (p values) from the univariate ANOVA associated with the individual tests of significance for the parameter estimates (Z_0 and Z_1) of the Chapman–Richards equation and for the instantaneous rates of change (slopes) for relative needle accretion (N_A) for loblolly pine trees at the research site SETRES.

| Test (month) | Source | | |
|-----------------|-----------|---------|--------------------------------|
| | Treatment | Cohort | Treatment × cohort interaction |
| Z_0 | 0.2828 | <0.0001 | 0.0084 |
| Z_1 | 0.0601 | <0.0001 | 0.0011 |
| Slope (April) | 0.0145 | <0.0001 | 0.0029 |
| Slope (May) | 0.4355 | <0.0001 | 0.0202 |
| Slope (August) | 0.2236 | <0.0001 | 0.0098 |
| Slope (October) | 0.4204 | 0.0027 | 0.0225 |

Note: The regression model $N_A = (1 - e^{Z_0 \times \text{month}})^{Z_1}$ was fitted to the plot-level accretion data for each fertilization–irrigation–cohort treatment combination from each block, resulting in 64 sets of model parameters.

significant treatment effect ($p = 0.0145$) but only for April (Table 3).

Although treatment was nonsignificant (for Z_0 and Z_1), the highly significant interactions warranted further tests on the specific effects of treatment at each level of the cohort factor. Thus, all six pairwise comparisons between the four

Table 4. Least squares means for the Z_0 and Z_1 parameters of the Chapman–Richards accretion model.

| Cohort | Parameter | Control | Fertilized | Irrigated | Fertilized and irrigated |
|--------|-----------|---------|------------|-----------|--------------------------|
| 1992 | Z_0 | 0.87a | 0.82a | 0.90a | 0.88a |
| 1993 | Z_0 | 0.91a | 0.91a | 0.97a | 0.97a |
| 1994 | Z_0 | 0.90a | 0.78b | 0.86ab | 0.77b |
| 1995 | Z_0 | 0.78a | 0.78a | 0.74a | 0.71a |
| 1992 | Z_1 | 194a | 179a | 214a | 215a |
| 1993 | Z_1 | 283a | 300a | 435b | 415b |
| 1994 | Z_1 | 217a | 116b | 203ab | 105b |
| 1995 | Z_1 | 107a | 104a | 89a | 69a |

Note: Least squares means in a row followed by the same letter are not significantly different based on an adjusted Bonferroni type I error rate of 0.05.

treatments were tested at each year. Closer inspection of the Z_0 and Z_1 estimates indicated that there were treatment differences in only a few of the comparisons. The shape parameter Z_0 for fertilized and irrigated plus fertilized plots was significantly smaller than for control plots in 1994 (Table 4). Delayed development in these plots was visibly apparent (Fig. 1C) but was not observed in the other years examined. The inflection parameter Z_1 for fertilized and irrigated plus fertilized plots was also significantly different from that of the control in 1994, while the irrigated and irrigated plus fertilized Z_1 values were different from that of the control in 1993 (Table 4). However, these significant differences were hardly noticeable (Fig. 1B). We did not conduct pairwise comparisons among cohorts; the MANOVA tests and the parameter estimates among cohorts demonstrate the cohort differences (Table 4), which can readily be observed in the gradual approach to final asymptotic needle length in 1995 (Fig. 1D). Favorable moisture (Table 2) throughout the summer and into the autumn of 1995 may have slowed relative needle accretion; dampened development may be the result of a longer-needled final flush or perhaps an additional flush.

Foliage abscission

Relative foliage abscission was more variable than needle accretion. The MANOVA analysis did not find any overall treatment effects on the combined phase I and phase II parameter estimates in the regression model of relative needle abscission ($p = 0.5050$). But we observed a significant cohort year effect ($p = 0.0306$) and a treatment by cohort year interaction effect ($p = 0.0388$) on the regression model parameters. Isolating the phase I parameter estimates, MANOVA showed that treatment was still not significant ($p = 0.3985$), but, unlike the combined model, cohort year ($p = 0.0659$) and the interaction between treatment and cohort year ($p = 0.1410$) were both not significant. The phase II estimates, in isolation, were also not significant for treatment ($p = 0.5715$). However, the cohort year ($p = 0.0079$) and the treatment by cohort year interaction (0.0414) were significant. Thus, it appears that cohort year differences in needle abscission, and its interaction with treatment, are manifested in the later stages of needle fall during early win-

ter of the second year of the cohort life through complete cohort abscission (Fig. 2) and are likely attributed to climate (discussed below).

Unlike needle accretion, the univariate ANOVA on the individual parameter estimates ($\beta_0, \beta_1, \beta_2, \beta_3$) of needle abscission yielded variable results. Similar to needle accretion, no significant treatment effects on the parameter estimates for needle abscission were found (Table 5). We also observed cohort year influences on needle retention. But, unlike needle accretion, and as supported by the MANOVA tests mentioned above, significant differences were only observed for the second phase in needle litterfall associated with the β_2 and β_3 parameter estimates (Table 5). These differences are readily apparent (Fig. 2). And although there were no significant treatment effects, control plots appeared to retain their needles longer than the other treatments for the 1992 cohort in 1994 (Fig. 2A). Late retention was repeated for the 1994 cohort in 1996 for the unfertilized treatments (Fig. 2C). All treatments exhibited a similar pattern to the control plots during 1993 for phase II abscission (Fig. 2B). And no consistent pattern in needle abscission during phase II was seen for the 1995 foliage cohort (Fig. 2D).

For the months examined, tests from the univariate ANOVA for differences in slope were variable. There were only two months, June and July of the second year, where a significant treatment effect could be detected (Table 5). Cohort year effects on relative needle abscission were found for all months examined except June and July (Table 5). We found no significant treatment by cohort interactions, which resulted in simpler interpretation of the main effects, and thus, some interesting trends were observed. For example, for phase I (June through October), the treatment slopes were marginally significant (June and July), but no significant pairwise comparisons could be found (data not shown). In general, the irrigated plus fertilized treatment had slopes that were approximately 50% greater than the control and irrigated treatments through phase I. This was somewhat apparent for the 1994 cohort in 1995 (Fig. 2C) and even more apparent for the 1995 cohort in 1996 (Fig. 2D); accelerated needle abscission for the 1995 foliage cohort in 1996 may be attributed to low rainfall during the summer of 1996 (Table 2). In phase II, no significant treatment effects were

Fig. 2. Average monthly relative needle abscission in loblolly pine trees for the four treatments and four cohorts examined at SETRES. Needle abscission was expressed as the summation of the proportion of needles lost, for each flush, weighted by the number of individual needles per flush initially produced. Error bars are 1 SE.

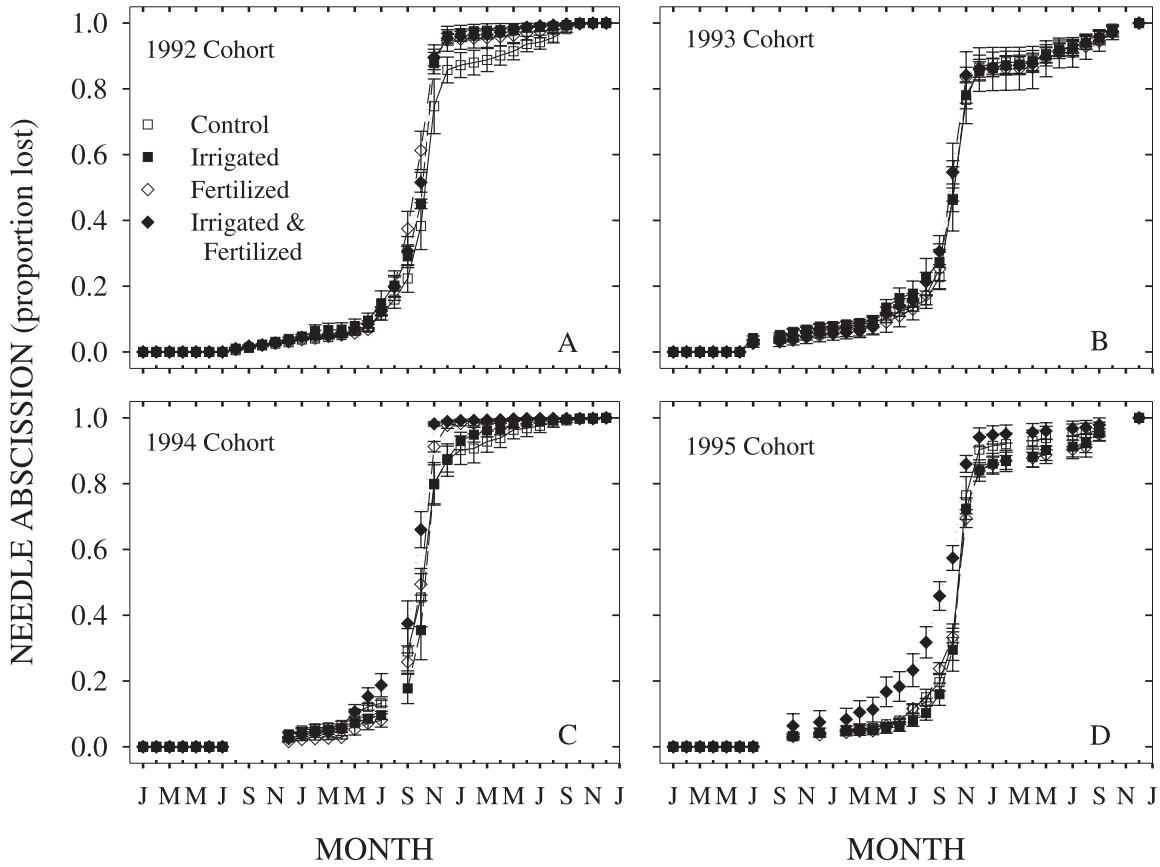


Table 5. Results (*p* values) from the univariate ANOVA associated with the individual tests of significance for the parameter estimates (β_0 , β_1 , β_2 , and β_3) of the two equations used in the segmented modeling of relative needle abscission (N_S) and for the instantaneous rates of change (slopes) for loblolly pine trees at the research site SETRES.

| Test | Phase | Month | Year | Source | | |
|-----------|-------|----------|--------|-----------|--------|--------------------------------|
| | | | | Treatment | Cohort | Treatment × cohort interaction |
| β_0 | I | | | 0.4563 | 0.0327 | 0.1487 |
| β_1 | I | | | 0.1049 | 0.0851 | 0.3685 |
| β_2 | II | | | 0.3042 | 0.0012 | 0.0558 |
| β_3 | II | | | 0.2988 | 0.0076 | 0.1041 |
| Slope | I | June | Second | 0.0291 | 0.6113 | 0.1465 |
| Slope | I | July | Second | 0.0423 | 0.1072 | 0.1422 |
| Slope | I | August | Second | 0.0535 | 0.0071 | 0.1804 |
| Slope | I | October | Second | 0.0610 | 0.0100 | 0.4748 |
| Slope | II | November | Second | 0.2738 | 0.0077 | 0.0743 |
| Slope | II | December | Second | 0.2739 | 0.0080 | 0.0755 |
| Slope | II | January | Third | 0.2741 | 0.0084 | 0.0766 |

Note: An exponential function, $N_S = \beta_0 \times e^{\beta_1 \times \text{month}}$ (phase I, prior to the intersection month), and a power function, $N_S = \beta_2 \times \text{month}^{\beta_3}$ (phase II, following the intersection month), were used in a segmented modeling approach, fitted to each fertilization–irrigation–cohort treatment combination from each block, resulting in 64 sets of model parameters. The intersection month was 23 in all cases.

found. However, the irrigated plus fertilized treatment's slope was generally two thirds that of the other treatments in phase II (data not shown). This decreased rate of abscission reflects that irrigated plus fertilized plots dropped most of their needles during phase I as compared with the other treatments. The cohort effect was not significant until the latter part of phase I and the entire duration of phase II, but few differences could be found with pairwise comparisons (data not shown).

Individual tree foliage biomass, stand characteristics, and regressions

Individual tree foliage biomass of the current-year foliage cohort ranged from 0.197 to 10.33 kg dry mass-tree⁻¹ and averaged 2.670 kg dry mass-tree⁻¹ for the 1992, 1994, 1996, and 1998 harvested trees examined in this study ($n = 64$). Total tree foliage biomass for these same trees ranged from 0.211 to 11.062 kg dry mass-tree⁻¹, averaging 2.983 kg dry mass-tree⁻¹. The corresponding DBH ranged from 1.0 to 20.6 cm and averaged 10.3 cm, while the crown ratio for these trees varied from 47% to 99%.

The regressions to predict individual tree foliage biomass (current-year foliage cohort and the total tree foliage biomass) from DBH and crown ratio (eq. 4) explained about 90% of the variation in foliage biomass. The treatment-combined parameter estimates (i.e., lower 95% CI, estimate, upper 95% CI) for the current-year foliage cohort were all significant: $\eta_0 = 0.0297$ ($0.0132 < \eta_0 < 0.0463$), $\eta_1 = 2.0532$ ($1.8270 < \eta_1 < 2.2795$), and $\eta_2 = 1.7990$ ($1.4224 < \eta_2 < 2.1756$) ($n = 62$). Similarly, the parameter estimates in the regression to estimate total tree foliage biomass (all treatments) were also significant: $\eta_0 = 0.0493$ ($0.0241 < \eta_0 < 0.0745$), $\eta_1 = 1.9057$ ($1.6974 < \eta_1 < 2.1140$), and $\eta_2 = 1.9413$ ($1.5893 < \eta_2 < 2.2932$) ($n = 61$, $r^2 \approx 0.90$).

When individual treatments were regressed separately using eq. 4, no consistent trends in the parameter estimate comparisons were observed. For example, when the slope parameter for tree diameter, η_1 , for control plots fell outside the 95% CI for the treatment-combined model, the slope parameter for crown ratio, η_2 , did not. Thus, a treatment-combined model for use in eq. 1 was appropriate in these analyses. The combined model was fairly robust considering the dramatic differences in stand structure and crown characteristics apparent over the course of this study (Table 1).

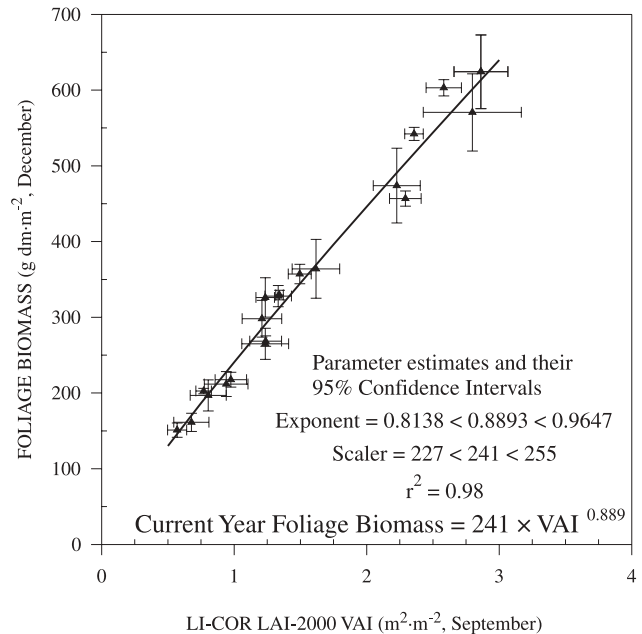
Foliage biomass and PCA VAI

Treatment average foliage biomass (grams dry mass of foliage per square metre of ground) of the current-year cohort (December estimate) ranged from 151 to 624 g·m⁻², averaging 346 g·m⁻² throughout the study period. Total foliage biomass for the same period ranged from 185 to 657 g·m⁻² and averaged 388 g·m⁻² over all treatments. The September PCA estimates of VAI ranged from 0.57 to 2.68 m²·m⁻² during the study.

We found a significant (curvilinear) relationship between foliage biomass of the current-year foliage cohort (December estimate) and the September estimate of VAI from the LI-COR PCA (Fig. 3). The regression model was

$$[5] \quad C_{\text{BIO}} = \alpha \times \text{VAI}^P$$

Fig. 3. Relationship between LI-COR LAI-2000 estimates of vegetation area index (VAI) and the empirical estimates of foliage biomass. A treatment-invariant allometric equation to estimate individual tree foliage biomass was derived from destructive harvest data for 1992, 1994, 1996, and 1998. Using yearly plot inventory data (1992–1996), foliage biomass was estimated as the ratio of the summation of individual tree foliage biomass to plot area. Error bars are 1 SE of the treatment mean.



where C_{BIO} is the foliage biomass of the current-year foliage cohort (grams per square metre of ground), α is a scaling parameter, and P is a shape parameter. The parameter estimates of this model were significant: $\alpha = 244.3$ ($226.7 < \alpha < 254.9$) and $P = 0.889$ ($0.8138 < P < 0.9647$). The regression accounted for roughly 98% of the variation in foliage biomass ($n = 20$).

A generalized equation to estimate monthly LAI

We pooled our needle accretion data and our needle mortality data to develop a generalized equation to estimate monthly LAI. Although cohort year influences on needle abscission were found, they were typically associated with the phase II abscission when senescent foliage peaks (Table 5; see Fig. 2). Notwithstanding, a test of the biological implication of pooling the phenology data is presented below. We used nonlinear regression procedures for the pooled data to obtain the study average parameter estimates (Table 6).

We used September estimates from the PCA measurements of VAI for 1994–1996 and eq. 5 to estimate foliage produced (i.e., the foliage cohort) in 1994, 1995, and 1996:

$$[6] \quad C_{\text{BIO}} = 241 \times \text{VAI}^{0.889}$$

where C_{BIO} is as before and VAI is the vegetation area index from the LI-COR LAI-2000 PCA.

We then estimated cohort LAI for 1994 ($C_{\text{LAI}_{C-2}}$), 1995 ($C_{\text{LAI}_{C-1}}$), and 1996 (C_{LAI_C}) from the estimate of foliage cohort biomass and crown-specific estimates of SLA and

Table 6. Parameter estimates of the pooled data, the lower and upper 95% CIs, and the mean square error for relative needle accretion (N_A) and relative needle abscission (N_S) for loblolly pine trees at the research site SETRES.

| | Phase | Estimate | Lower 95% CI | Upper 95% CI | MSE |
|------------|-------|-----------|--------------|--------------|-----------|
| Accretion | | | | | 0.001 43 |
| | | Z_0 | 0.837 3 | 0.818 8 | 0.855 9 |
| | | Z_1 | 159.5 | 140.4 | 178.5 |
| Abscission | | | | | 0.003 63 |
| | I | β_0 | 0.000 224 | 0.000 130 | 0.000 318 |
| | I | β_1 | 0.344 0 | 0.324 1 | 0.363 9 |
| | II | β_2 | 0.300 4 | 0.268 1 | 0.332 7 |
| | II | β_3 | 0.339 4 | 0.307 6 | 0.371 2 |

Note: The regression model for needle accretion was $N_A = (1 - e^{-Z_0 \times \text{month}})^{Z_1}$. An exponential function, $N_S = \beta_0 \times e^{\beta_1 \times \text{month}}$ (phase I, prior to the intersection month), and a power function, $N_S = \beta_2 \times \text{month}^{\beta_3}$ (phase II, following the intersection month), were used to fit the needle abscission data. The approximate coefficient of determination was >0.99 for needle accretion and 0.98 for needle abscission. The intersection month for needle abscission was 23.

relative foliage distribution (data mentioned above). A generalized form would be

$$[7] \quad C_{LAI} = C_{BIO} \times SLA$$

where C_{LAI} is LAI for any given cohort and C_{BIO} and SLA are as before. Monthly LAI for 1996 was estimated as

$$[8] \quad AI_n = C_{LAI_c}(A_{C_n} - A_{B_n}) + C_{LAI_{c-1}}(1 - A_{B_{n+12}}) + C_{LAI_{c-2}}(1 - A_{B_{n+24}})$$

where LAI_n is stand leaf area index (square metres per square metre) for month n (1–12), C_{LAI_c} , $C_{LAI_{c-1}}$, and $C_{LAI_{c-2}}$ are as before, A_{C_n} is relative needle accretion (from eq. 1) for month n , and A_{B_n} is relative needle abscission (from eq. 2 and eq. 3) for month n .

In this schema, we may evaluate overall variability in our LAI estimates attributed to (i) cohort phenology, (ii) the VAI estimates, and (iii) deviations in C_{BIO} and thus our C_{LAI} estimates. To confirm our decision to pool our phenology data, we conducted a test of the relative contribution of each of these factors as used in eq. 8 by modifying the parameter estimates (or, in the test of VAI, the sample estimate itself) of one factor while holding the estimates for the other two factors constant. We used simple contrasts of the percent change in monthly LAI associated with each factor for 1996 control plots using

$$[9] \quad \Delta LAI = \frac{LAI_{UPPER} - LAI_{LOWER}}{LAI_{LOWER}} \times 100$$

ΔLAI represents the percent change in LAI attributed to each factor examined, while the variables LAI_{UPPER} and LAI_{LOWER} are the LAI estimates from eq. 8 for each contrast. To examine the effect of cohort phenology on our monthly LAI estimates, we choose two extremes in observed cohort abscission from Fig. 2. Namely, to estimate LAI_{UPPER} , we fitted eqs. 1–3 to the 1992 cohort accretion and abscission data for control plots. Parameter estimates from these regressions were then used in eqs. 1–3 to derive

Table 7. Average monthly difference (%) in leaf area index (LAI) estimates for control plots for 1996 at SETRES attributed to cohort influences on phenology versus differences in cohort LAI estimates obtained from eqs. 6 and 7 ($n = 12$ for each comparison).

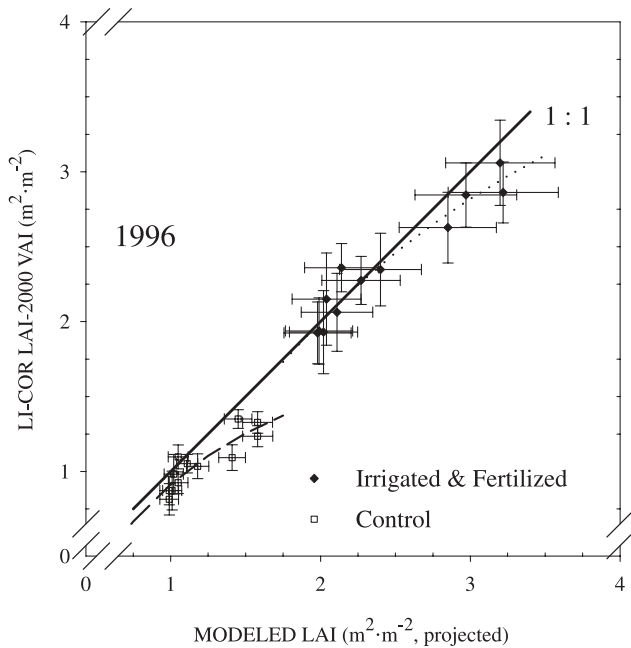
| Statistic | Variation in LAI attributed to: | | |
|-----------|---|--|----------------------|
| | Phenology, ΔN_A and ΔN_S (eqs. 1–3) | Foliage cohort biomass $\Delta\alpha$ and ΔP (eq. 5) | ΔVAI (eq. 6) |
| Mean | 12.97 | 14.14 | 19.3 |
| SD | 3.58 | 0.05 | 4.81 |
| Maximum | 19.39 | 14.23 | 24.3 |
| Minimum | 6.91 | 14.09 | 11.51 |

Note: The phenology contrasts used needle accretion (N_A) and abscission (N_S) data from the 1992 and 1995 cohorts for control and irrigated plus fertilized plots, respectively. Refer to the text for details. VAI, vegetation area index from the LI-COR LAI 2000 plant canopy analyzer. The symbols α and P are parameter estimates from eq. 5. The LAI response was generated using eq. 9 as discussed in the text.

the A_{C_n} and A_{B_n} estimates that, along with C_{LAI} estimates from eq. 7, were used in eq. 8 to estimate monthly LAI. In a similar manner, and to maximize our contrast, we fitted eqs. 1–3 to the 1995 cohort phenology data for irrigated plus fertilized plots. Again, these regression parameter estimates were used in eqs. 1–3 to generate the A_{C_n} and A_{B_n} estimates that were used in eq. 8. This LAI estimate provided the LAI_{LOWER} as used in eq. 9.

To examine the effect of sample variability in VAI on our LAI estimates, we used the pooled phenology parameter estimates (Table 6) in eqs. 1–3 to derive estimates of A_{C_n} and A_{B_n} . We then estimated C_{BIO} using the mean VAI plus 1 SE of the mean in eq. 6 and then eqs. 7 and 8 to estimate monthly LAI. This provided the LAI_{UPPER} for eq. 9. Likewise, we used the mean minus 1 SE of the mean in eq. 6 and eqs. 7 and 8 to estimate LAI_{LOWER} . Finally, we used the parameter estimates from the pooled phenology data to exam-

Fig. 4. Relationship between modeled estimates of monthly leaf area index (LAI) for control and irrigated plus fertilized plots and the uncorrected estimates of vegetation area index (VAI) obtained from the LI-COR LAI-2000 plant canopy analyzer. The solid line represents a 1:1 line. Individual treatment regressions were fit using a type three exponential model (Sit and Poulin-Costello 1994) using nonlinear regression procedures in SAS. Error bars for the modeled LAI are the LI-COR VAI September estimate ± 1 SE in eq. 5. Error bars for the LI-COR VAI are 1 SE of the treatment mean.

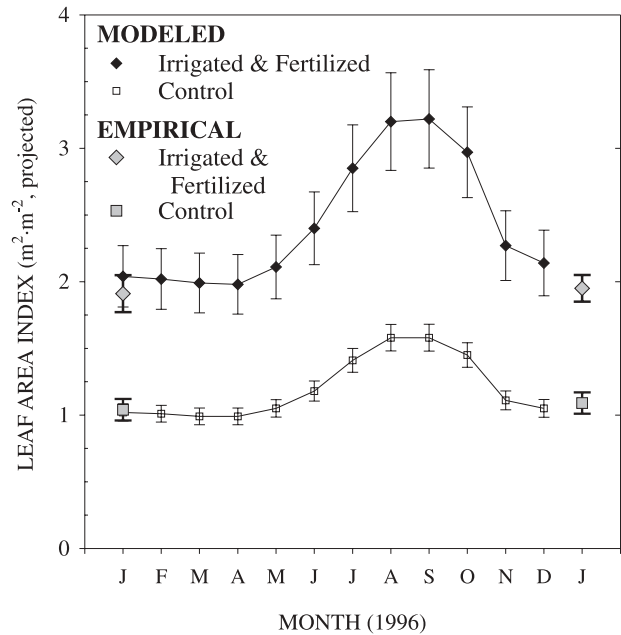


ine the effect of deviations in our estimates of cohort LAI. We estimated C_{BIO} using the parameter estimates from the upper and lower 95% CIs from eq. 5 in eq. 6 and contrasted them in a similar manner as the test of VAI. We used PROC MEANS in SAS (SAS Institute Inc. 1999) to evaluate average monthly variability in LAI for each factor.

Factor sensitivity in our generalized equation indicated that sampling variability in VAI had the greatest impact on our LAI estimates with variation in C_{LAI} second (Table 7). Cohort and cohort by treatment influences on needle phenology, although significant in the analyses, had the least impact on the final monthly LAI estimates (Table 7). We concluded that pooling the needle accretion data and pooling the needle abscission data would not unduly influence our LAI estimates.

There was bias in the comparison between the 1996 estimates of modeled LAI and the VAI estimates from the PCA for control and irrigated plus fertilized treatments (Fig. 4). We observed increased underestimation in the VAI estimates as modeled LAI increased. Control plots exhibited many months where VAI was lower than the modeled LAI estimates (Fig. 4). Higher variability in the irrigated plus fertilized plots resulted in closer unity of the VAI-LAI comparisons. Although not demarcated within the figure, there were monthly patterns in the relationship between the modeled LAI versus the PCA estimates of VAI. Winter esti-

Fig. 5. Yearly trends in modeled leaf area index for control and irrigated plus fertilized plots at SETRES for 1996. Empirical estimates of leaf area index for January serve as a reference. A treatment-invariant allometric equation to estimate individual tree foliage biomass, for current-year foliage, was derived from destructive harvest data for 1992, 1994, 1996, and 1998. Using yearly plot inventory data, foliage biomass was estimated as the ratio of the summation of individual tree foliage biomass to plot area. Foliage biomass was converted to leaf area index using treatment-specific estimates of specific leaf area and foliage distribution. Error bars are 1 SE.



mates of LAI were lower than the VAI estimates, while summer estimates were always higher. The September estimates of VAI were 14% and 30% lower than the modeled estimates for irrigated plus fertilized and control plots, respectively.

There was good correspondence between the modeled LAI estimates and the empirical estimates of LAI (derived from stand survey data and destructive harvest regressions) (Fig. 5). In 1996, the control plots had only one half the LAI of the irrigated plus fertilized plots. The temporal changes in LAI resulted in a 67% increase in LAI during 1996 in the irrigated plus fertilized plots, while LAI estimates in control plots increased by 63% between March and September (Fig. 5).

Discussion

LAI is a major determinant of stand productivity and, thus, is an important functional attribute of stand structure and canopy architecture. Loblolly pine exhibits broad intra-annual variation in LAI that must be accurately quantified for descriptive and predictive modeling purposes. Modeling LAI, however, is problematic. Although interannual patterns in loblolly pine LAI have been described (e.g., Dalla-Tea and Jokela 1991; Gholz et al. 1991), and a few studies have modeled annual variation in needle accretion (e.g., Kinerson

et al. 1974; Dougherty et al. 1995) and foliage abscission (Hennessey et al. 1992; Dougherty et al. 1995), none have sought general, site-invariant combined models of needle accretion and abscission to model LAI. When yearly trends are estimated, a proxy for LAI is typically used (i.e., estimates of VAI from the LI-COR LAI-2000 PCA). And while species- and site-specific corrections to PCA estimates are available, and typically necessary, it has not been demonstrated whether these corrections are preserved when yearly trends in LAI are examined; certainly, they may not apply across stands of varying stand structure (i.e., basal area and crown closure) (e.g., Smolander et al. 1996) and site fertility (e.g., Sampson and Allen 1995; Vose and Allen 1988). The generic approach described herein represents one attempt to estimate the seasonal pattern in loblolly pine LAI using needle accretion and abscission data and a single, point-in-time estimate of VAI from the PCA (eqs. 6–8). Although not examined in this study, cohort LAI estimates from needle litterfall could also be used in this model. These results suggest that this model can be applied across years for stands that vary markedly in their stand structure, canopy architecture, and LAI (interpreted from foliage biomass). Some caution may be warranted in the generalized use of this schema because cohort differences in both accretion and abscission were found. However, the sensitivity analysis of the three major sources of variability inherent in this approach indicated that other factors may have more influence on our LAI estimates.

Needle accretion (for similar months across multiple years) was relatively consistent, especially considering that climate (Table 2), stand structure (Table 1), and site fertility varied greatly during the study period. Dougherty et al. (1995) also observed little effect of monthly and yearly variation in climate on relative monthly needle accretion in an Okalahoma loblolly pine plantation. Needle accretion in loblolly pine has been previously described using a logistic functional form (Kinerson et al. 1974; Dalla-Tea and Jokela 1991; Dougherty et al. 1995). A Chapman–Richards equation provided a very good fit for relative needle accretion in this study; the Chapman–Richards equation is flexible because it permits asymmetry in the inflection point of growth. The generally smooth (uninterrupted) response in relative needle accretion suggests a decoupling between needle elongation timing and rate with current-year site conditions and weather patterns. Of course, the absolute production of foliage would depend on site fertility (Albaugh et al. 1998; Vose and Allen 1988) and, to a lesser extent, soil available water (Albaugh et al. 1998).

We observed two phases in foliage abscission. Segmented modeling in SAS enabled good fit to needle fall using two biological models. Kinerson et al. (1974) observed a similar trend for needle litterfall for loblolly pine. A single biological function to model loblolly pine needle mortality has not been found. As single functions, the Weibull equation, a combined power and exponential function, and polynomial regressions conducted in PROC LOESS (SAS Institute Inc. 1999) were examined, but none of these models provided a satisfactory fit to the data. Others have modeled foliage abscission using various polynomial equations (Hennessey et al. 1992; Dougherty et al. 1995). We observed treatment and

cohort year effects on foliage abscission. Foliage abscission in this study was accelerated in the irrigated plus fertilized treatments, principally in the second year (first year following development), and may be linked to low rainfall, especially for the 1995 cohort in 1996 (Fig. 2D). However, we have not examined the correlation between premature senescence and climate as did Hennessey et al. (1992) or Dougherty et al. (1995); incorporating the effects of climate on needle abscission was not an objective.

Although a site correction to the PCA estimates would be possible, the utility of using uncorrected PCA estimates is readily apparent. Uncorrected outputs from the PCA potentially extend the transportability of using this approach to other stands and other sites. Of course, it is not yet known whether these equations are transportable, as is, to loblolly pine stands growing under markedly different stand structures, climatic regimes, or site conditions (i.e., soil water-holding capacity, harvesting effects on soil physical properties, and age). Moreover, populations that have a different genetic or environmental response in needle phenology, or some other aspect associated with the factors used in this schema, may not be well suited to this approach. In this instance, further parameterization or equation modification may be necessary. The utility of this approach to cross-site applications still needs to be examined.

These results indicate that the LI-COR LAI-2000 may inadequately estimate the temporal pattern in LAI when used in loblolly pine stands. There was increased underestimation in the VAI estimates as modeled LAI increased (Fig. 4). This result was not surprising because many have already observed similar trends (e.g., Gower and Norman 1991; Stenberg et al. 1994; Sampson and Allen 1995; Stenberg 1996). Indeed, some have observed no correlation between estimates of LAI and VAI measures (Hebert and Jack 1998). Regardless, studies that use the PCA typically pursue species- or site-specific correction factors to improve the LAI–VAI correspondence. Results presented here suggest that generic correction factors may not be appropriate.

We observed asymmetric bias in the functional relationship between LAI and VAI estimates; unit changes in LAI, across the LAI modeled, do not necessarily correspond to unit changes in VAI. Apparent dissimilarity in the degree of correspondence for control plots versus irrigated plus fertilized plots may be related to plot differences in stand structure and canopy architecture (Table 1). The control plots have more intracrown gaps than the irrigated plus fertilized plots. Parameter estimates for the curves defining the LAI–VAI relationships for each treatment indicate that control plots have a steeper descent in the approach to a horizontal asymptote (data not shown). This may be due to treatment effects on standing branch and stem biomass, canopy gap fraction, and LAI. Although the influence of several attributes of stand structure on VAI estimates has been examined (e.g., Smolander and Stenberg 1996), this clearly needs further investigation. And although we have reasonable confidence in our modeled LAI estimates, we cannot confirm the accuracy of these estimates beyond the dormant season.

We recognize that variation in SLA can, and often does, vary as trees age and at a finer resolution than used here.

Nonoffsetting differences in SLA would adversely affect our results. The use of three values for SLA, one for each crown third, as used here greatly simplified our approach. The model, however, could be used with a finer resolution in SLA and relative foliage distribution. Notwithstanding, sampling variation in the destructive harvest data and in the VAI measurements may supercede slight differences in SLA that may be found in closed-canopy, mature pine stands. We feel that our general approach is still valid for stand-level analyses.

As process and process-based models become useful to policy and management decisions, estimates of LAI will be needed across numerous sites, an expensive proposition even using the PCA. Here, we have demonstrated that the PCA estimates are representative of “true” LAI, when examined as a surrogate for foliage mass of the current-year foliage cohort. While our approach represents a departure from traditional studies using the PCA, it demonstrates the potential utility of the PCA as a generic tool for loblolly pine. Even more significantly, modeled LAI was shown to be resolvable using point-in-time PCA estimates. Moreover, the model may be site invariant; this study was conducted across 5 years under broad differences in environmental conditions (climate, site fertility) in developing stands that vary greatly in their productivity. The potential to extend this approach to other loblolly pine stands and sites will be addressed in a subsequent paper.

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References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., and King, J.S. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* **44**: 317–328.
- Dalla-Tea, F., and Jokela, E.J. 1991. Needlefall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. *For. Sci.* **37**: 1298–1313.
- Dougherty, P.M., Hennessey, T.C., Zarnoch, S.J., Stenberg, P.T., Holeman, R.T., and Wittwer, R.F. 1995. Effects of stand development and weather on monthly leaf biomass dynamics of a loblolly pine (*Pinus taeda* L.) stand. *For. Ecol. Manage.* **72**: 213–227.
- Fassnacht, K.S., Gower, S.T., Norman, J.M., and McMurtrie, R.E. 1994. A comparison of optical and direct methods for estimating foliage surface area index in forests. *Agric. For. Meteorol.* **71**: 183–207.
- Gholz, H.L., Vogel, S.A., Cropper, W.P., Jr., McKelvey, K., Ewel, K.C., Teskey, R.O., and Curran, P.J. 1991. Dynamics of canopy structure and light interception in *Pinus elliottii* stands, North Florida. *Ecol. Monogr.* **61**: 33–51.
- Gower, S.T., and Norman, J.M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology*, **72**: 1896–1900.
- Hebert, M.T., and Jack, S.B. 1998. Leaf area index and site water balance of loblolly pine (*Pinus taeda* L.) across a precipitation gradient in East Texas. *For. Ecol. Manage.* **105**: 273–282.
- Hennessey, T.C., Dougherty, P.M., Cregg, B.M., and Wittwer, R.F. 1992. Annual variation in needle fall of a loblolly pine stand in relation to climate and stand density. *For. Ecol. Manage.* **51**: 329–338.
- Jokela, E., and Martin, T. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* **30**: 1511–1524.
- Kinerson, R.S., Higginbottom, K.O., and Chapman, R.F. 1974. The dynamics of foliage distribution within a forest canopy. *J. Appl. Ecol.* **11**: 347–353.
- Landsberg, J.J., and Gower, S.T. 1997. Applications of physiological ecology to forest management. Academic Press, New York.
- LI-COR Inc. 1992. Operating manual. LAI-2000 plant canopy analyzer. LI-COR Inc., Lincoln, Nebr.
- Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute Inc., Cary, N.C.
- Lou, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., and Katul, G. 2001. Gross primary productivity in Duke Forest: modeling synthesis of CO₂ experiment and eddy-flux data. *Ecol. Appl.* **11**: 239–252.
- Maier, C.A., Johnsen, K.H., Butnor, J.R., Kress, L.W., and Anderson, P. 2002. Branch growth and gas exchange in 13 year-old loblolly pine (*Pinus taeda* L.) trees in response to elevated CO₂ and fertilization. *Tree Physiol.* **22**: 1093–1106.
- McCrary, R.L., and Jokela, E.J. 1998. Canopy dynamics, light interception, and radiation use efficiency of selected loblolly pine families. *For. Sci.* **44**: 64–72.
- Sampson, D.A., and Allen, H.L. 1995. Direct and indirect estimates of leaf area index (LAI) for lodgepole and loblolly pine stands. *Trees*, **9**: 119–122.
- Sampson, D.A., Johnson, K.H., Ludovici, K.H., Albaugh, T.J., and Maier, C. 2001. Stand scale correspondence in empirical and simulated labile carbohydrates in loblolly pine. *For. Sci.* **47**: 60–68.
- SAS Institute Inc. 1999. SAS/STAT® user’s guide, version 8. SAS Institute Inc., Cary, N.C.
- Sit, V., and Poulin-Costello, M. 1994. Catalog of curves for curve fitting. Ministry of Forests Research Program, Crown Publications, Victoria, B.C. Biometrics Inf. Handb. 4.
- Smith, N.J., Chen, J.M., and Black, T.A. 1993. Effects of clumping on estimates of stand leaf area index using the LI-COR LAI-2000. *Can. J. For. Res.* **23**: 1940–1943.
- Smolander, H., and Stenberg, P. 1996. Response of LAI-2000 estimates to changes in plant surface area index in a Scots pine stand. *Tree Physiol.* **16**: 345–349.
- Stenberg, P. 1996. Correcting LAI-2000 estimates for the clumping of needles in shoots of conifers. *Agric. For. Meteorol.* **79**: 1–8.
- Stenberg, P., Linder, S., Smolander, H., and Flower-Ellis, J. 1994. Performance of the LAI-2000 plant canopy analyzer in estimat-

- ing leaf area index of some Scots pine stands. *Tree Physiol.* **14**: 981–995.
- Stow, T.K., Allen, H.L., and Kress, L.W. 1992. Ozone impacts on seasonal foliage dynamics of young loblolly pine. *For. Sci.* **38**: 102–119.
- Vose, J.M. 1988. Patterns of leaf area distribution within crowns of nitrogen- and phosphorus-fertilized loblolly pine trees. *For. Sci.* **34**: 564–573.
- Vose, J., and Allen, H.L. 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *For. Sci.* **34**: 547–563.