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Effects of stand development and weather on monthly leaf biomass dynamics of a loblolly pine (*Pinus taeda* L.) stand

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Abstract

Annual leaf biomass production, monthly needle accretion and monthly needlefall were measured in an 11- to 17-year-old thinned stand of loblolly pine. Initial thinning levels were 7.8 m^2 ha^{-1}, 12.6 m^2 ha^{-1}, and 25.5 m^2 ha^{-1} (unthinned). A light thinning was done again at Age 14.

Annual variations in annual leaf biomass production and monthly variations in monthly needle accretion and needlefall were related to measured stand and weather variables. Age variations in annual leaf biomass production occurred over the 6 year study period. The variation in annual leaf biomass production was best quantified as a quadratic function of stand basal area and average weighted temperature for the months of June, July, August and September. Although stand basal area was the major determinant of annual leaf biomass production, an increase in average temperature from 24.5 to 26.5°C resulted in a 27% reduction in annual leaf biomass production. This was translated to an approximate reduction of 7.3 m^2 ha^{-1} $year^{-1}$ of stemwood. Monthly needle accretion varied little between years or with stand density. Thus, a single normalized logistic function was suitable for describing monthly needle accretion for all 6 years. Monthly needlefall was variable from year to year. Variation in needlefall was low for a period of 7 months (January 16–August 15). During this period monthly needlefall averaged from 3 to 8% of the previous year's annual leaf biomass production at the beginning of the phenological year. Variation in this 7 month period was not consistently related to stand density or any of the weather variables considered in this study. Monthly needlefall from August 16 to January 15 was extremely variable. This variability was not related to stand density. The weather variable that explained most of the monthly variation in needlefall during this period was the average rain–potential evapotranspiration determined for the 2 months preceding a monthly needlefall event. Peak needlefall was found to occur 2 months earlier in a drought year than in a year when rain–potential evapotranspiration was high.

Keywords: Potential evapotranspiration; Monthly temperature; Needlefall; Needle production; Phenology; Rainfall

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1. Introduction

Leaf biomass is an important driving variable in ecophysiology process models because it reflects a tree or stand's capacity to intercept radiation, reduce carbon dioxide, store carbohydrates, intercept rainfall, transpire water, and, to some extent, accumulate and store nutrients. Since loblolly pine (*Pinus taeda* L.) produces a new age class of needles each year while retaining the previous age class until the fall of the year, phenology alone can result in annual variations in leaf biomass of nearly 100%. Weather can also significantly affect leaf biomass dynamics because both needle accretion and needlefall can be altered by annual weather conditions (Dougherty et al., 1990). Hennessey et al. (1992) have demonstrated that weather (temperature, rain, and potential evapotranspiration) can alter annual leaf biomass production of a loblolly pine stand by 29% and accelerate needlefall by 2 months. In addition, site variables, such as nitrogen availability, and stand density can also have large influences on annual leaf biomass production. Vose and Allen (1988) have reported that alterations in nutrition can cause leaf area to vary by 60% for loblolly pine stands that have similar basal areas. Gresham (1982) showed that needlefall increased with basal area until stand closure occurred at about 26 m^2 ha^{-1}, after which it remained constant. Thus, from previous studies it is clear that leaf biomass dynamics of loblolly pine are dependent on stand density, phenology, site factors (i.e. nutrition), and weather.

Kinerson et al. (1974) used normalized logistic functions to describe needle accretion and needlefall but did not consider stand density, nutrition, or weather effects. Dougherty et al. (1990) used the same approach as Kinerson et al. (1974) for quantifying leaf biomass dynamics of loblolly pine but the parameters of the needlefall function were predicted from stand density and weather variables. The approach taken by Dougherty et al. (1990) predicted annual leaf biomass production and the cumulative monthly needlefall; however, it did not permit good predictions of individual monthly needle accretion and monthly needlefall. Predictions of leaf biomass dynamics at the monthly level are needed for most ecophysiology process models.

The objective of this study was to determine if monthly leaf biomass dynamics of a young loblolly pine stand was related to stand density and monthly variations in weather. Our approach developed relationships for annual leaf biomass production, monthly needle accretion and monthly needlefall. Weather variables considered in these relationships were monthly rainfall, mean temperature, potential evapotranspiration (PET), and rain minus potential evapotranspiration (RMP).

2. Materials and methods

2.1. Site description

The study site was located in southeastern Oklahoma on a soil which is mapped as Cahaba soil series (US Dep. Agric., 1974). The soil is a Cahaba fine sandy loam (Typic Hapludult, fine-loamy, siliceous, thermic) which has 22 cm of available water holding storage capacity in the upper 122 cm and is quite fertile with foliar nitrogen levels of about 1.2% in the fall. Average annual rainfall is 125 cm, average temperature is 17°C and length of the frost-free season is 240 days (Oklahoma Water Resources Board, 1984). A more detailed description of the study site can be found in Cregg et al. (1988).

2.2. Study design

This study was derived from a thinning study which was established in an 11-year-old loblolly pine stand. The three thinning levels initiated in March 1984 were 7.8 m^2 ha^{-1}, 12.6 m^2 ha^{-1} and 25.5 m^2 ha^{-1} (unthinned). The experiment was a randomized block design. In each of the three blocks, each thinning level was applied to a 0.1 ha plot which contained a 0.04 ha measurement plot. In the spring of 1987 the originally thinned plots were rethinned to a target level of 11.3–13.2 m^2 ha^{-1} while the unthinned plots were left unthinned. Fig. 1 illustrates these basal area relationships during the study.

2.3. Stand measurements

Loblolly pine initiates growth each year around mid-March; therefore, this was assumed to be the beginning of the phenological year. April is referred to as Phenological Month 1 (PM = 1) and goes from March 16 to April 15. The other phenological months are defined in a similar, consecutive manner. At Age 17 (1990) an irrigation treatment was applied to the heavily thinned plot in Block 1 and all biological responses initiated thereafter were deleted from the analysis.

Stand basal area ($m^2\ ha^{-1}$) was computed for each measurement plot from tree diameters at breast height taken with a diameter tape at the beginning of each growing season. This was initiated at Age 11 (spring 1984) and continued to the end of Age 17 (spring 1991). The average basal area for each thinning treatment throughout the study period is shown in Fig. 1.

Monthly needlefall was measured beginning in October at Age 11 (1984), with five 0.49 m^2 litter traps which were randomly placed in each measurement plot. Monthly collection continued through the end of Age 17 (March 1991) except when the plots were rethinned during Age 14 (April–June 1987) and at Age 17 (1990) when needlefall for 2 or more months were combined. Only needles were collected and they were placed in paper bags and dried at 68 °C to a constant weight. No corrections were made for weight loss that may have occurred during the period when the needles began the senescence phase on the tree to when they were collected and dried. Annual leaf biomass production was calculated for a phenological year beginning March 16 by summing monthly needlefall collections from April of the subsequent year through the following March.

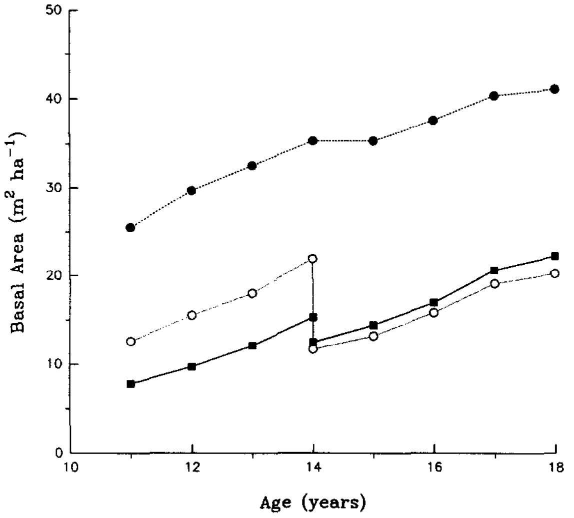

Fig. 1. Annual stand basal area for thinning treatment 7.8 $m^2\ ha^{-1}$ (■), 12.6 $m^2\ ha^{-1}$ (○), and 25.5 $m^2\ ha^{-1}$ (●), averaged over the three blocks (except for 7.8 $m^2\ ha^{-1}$ at ages 17 and 18 where only two blocks were used since Block 1 was irrigated). The average basal area before study installation was 27 $m^2\ ha^{-1}$.

Monthly needle accretion was obtained by periodically measuring shoot and needle elongation throughout the growing season on all plots at Ages 13 (1986) and 15 (1988). Several auxiliary plots were measured for shoot and needle elongation in 1988 and 1989. Thus, the monthly needle accretion data came from a total of 23 plot-years and consisted of 261 observations. Four mid-crown branches were selected for sampling shoot and needle elongation at 2- to 4-week intervals from each measurement plot. Three fascicles per flush were measured to the nearest 0.1 cm on current and expanding flushes. Monthly leaf biomass was calculated for each branch by the method described by Harms (1971) and converted to a proportion of the annual total. Using the mid-crown position assumes that the relative rate of leaf biomass production is similar throughout the crown. This assumption should be reasonable since most of loblolly pine leaf biomass is located in the middle third of the crown.

2.4. Environmental measurements

The weather data consisted of monthly measurements from Age 11 (1984) to the end of Age 17 (spring 1991). Monthly rainfall was measured on the study site with standard rain gauges. Daily air temperature was obtained from a NOAA weather station located 27 km from the

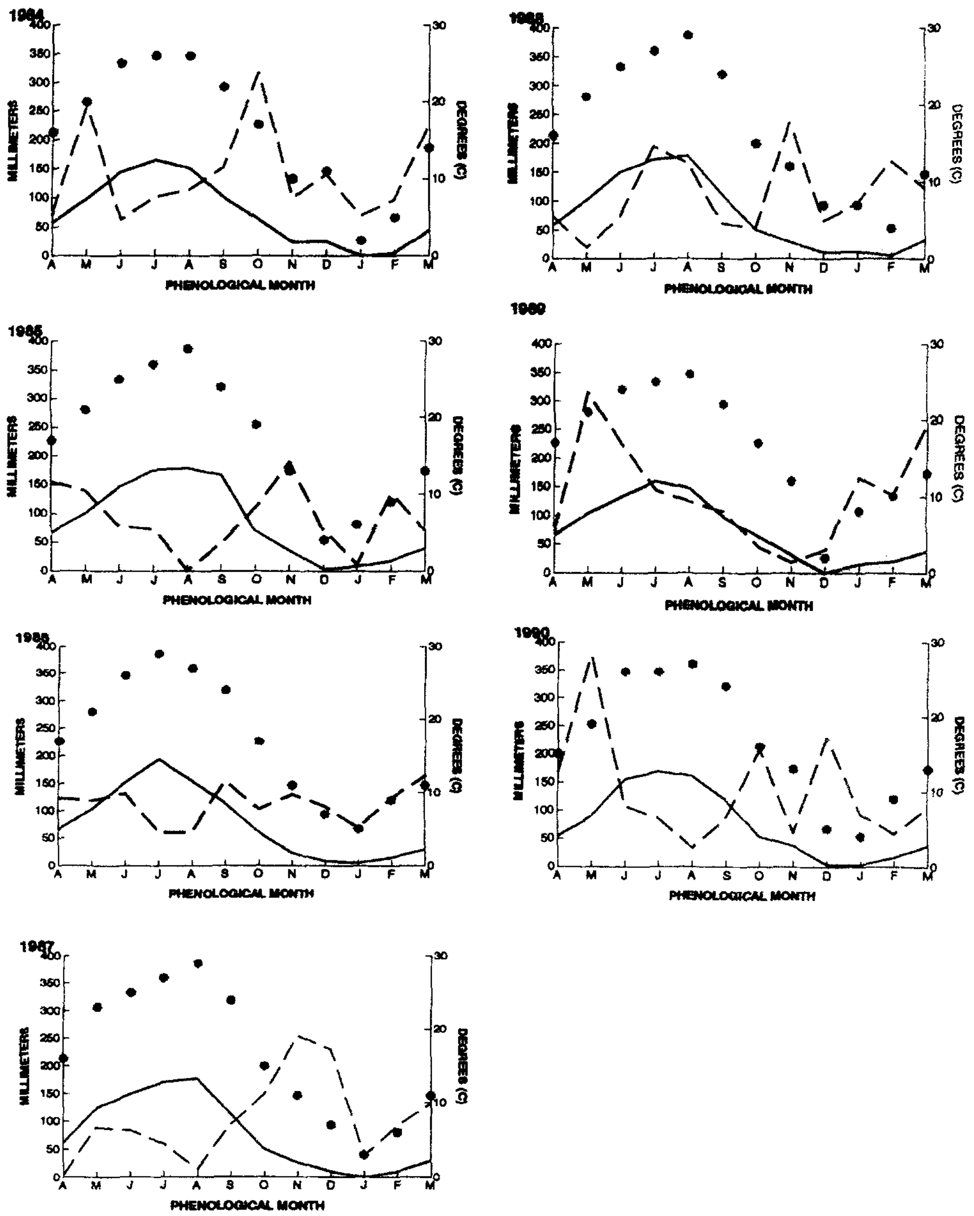

Fig. 2. Trends in the monthly weather data during the study; rain (- -), temperature (●), and potential evapotranspiration (—).

study site and converted to a monthly mean. PET was calculated on a monthly basis using the Thornthwaite and Mather (1957) method. This method of estimating PET was utilized because only temperature and rainfall were available. RMP was computed. The monthly and annual trends in rain, potential evapotranspiration and temperature, which indicate the magnitude of drought stress, are illustrated (Fig. 2).

3. Leaf biomass dynamics relationships

Relationships were developed to quantitatively describe annual leaf biomass production, monthly needle accretion and monthly needlefall for a 6 year period. The objective was to develop these relationships based on stand basal area and monthly weather variables which could biologically explain (1) the monthly phenological pattern of leaf biomass of new and 1-year-old foliage classes on the tree and (2) the monthly phenological pattern of needlefall available for decomposition and nutrient recycling. These components will now be explained.

3.1. Annual leaf biomass production

The annual leaf biomass production relationship consisted of a weather effect added to the quadratic annual leaf biomass production–basal area relationship (Gresham, 1982; Hennessey et al., 1992). The general form is

$$L_i = b_0 + b_1 B_i + b_2 B_i^2 + \sum_{j=1}^{k} b_{j+2} X_{ij}$$

where L_i is annual leaf biomass (kg ha^{-1}) production during Age i, B_i is stand basal area (m^2 ha^{-1}) at the beginning of Age i, X_{ij} denotes weather variable j during Age i, and b_0, b_1, b_2, ... are parameters to be estimated.

Effects of weather factors on annual leaf biomass production are dependent not only on the magnitude of weather factors but also on timing of weather events during the year. For instance, a favourable temperature and moisture regime will have little effect if it occurs when a tree is not producing needles. The months of June through September were considered to be the primary growing season since they are the most influential leaf biomass production months and, thus, the weather variables were restricted to this interval. Monthly weights were applied to each weather factor to reflect its importance within specific months with respect to potential leaf biomass production. These weights were based on the average relative monthly needle accretion observed for these months.

Candidate variables were the four weather variables which have been reported to affect annual leaf biomass production and various stand and weather interactions. Stepwise regression procedures were used to select the variables which influenced annual leaf biomass production.

3.2. Monthly needle accretion

Kinerson et al. (1974) used a logistic equation to describe monthly needle accretion, defined as

$$\mathrm{NA}_{ij} = \frac{1}{1 + e^{r(t - \mathrm{NDATE}_j)}}$$

where NA_{ij} is the normalized cumulative needle accretion in Month j of Age i, NDATE_j is the normalized phenological date (March 16 = 0.00) for Phenological Month j, r is the parameter related to the intensity of needle accretion, and t is the parameter related to the normalized date of peak needle accretion. In this analysis we also fitted logistic equations to each set of observations on a plot-year basis and then related the two parameters (r and t) to stand and weather variables.

3.3. Monthly needlefall

For predicting monthly needlefall, a system of equations to describe the proportion of the previous year's annual leaf biomass production which falls each month of the current year was utilized. The approach taken was to develop a system of equations as functions of stand basal area and weather variables and to consider the dependencies of the 12 monthly proportions since they must sum to 1. In addition, the proportions must have logical bounds of 0 and 1. Thus, the system of equations is defined as

$$P^f_{ij} = \begin{cases} \left(1 + e^{c_0 + c_1 B_i + \sum_{k=1}^{m} C_{k+1} X_{ijk}}\right)^{-1} & j = 1 \\ \left(1 - \sum_{l=1}^{j-1} P^f_{il}\right)\left(1 + e^{c_0 + c_1 B_i + \sum_{k=1}^{m} C_{k+1} X_{ijk}}\right)^{-1} & j = 2,3,\ldots,11 \\ 1 - \sum_{l=1}^{11} P^f_{il} & j = 12 \end{cases}$$

where P^f_{ij} is the proportion of Age i needlefall which occurs in Month j, B_i is stand basal area at Age i, X_{ijk} denotes the weather variable k for Month j and Age i, and c_0, c_1, c_2, ... are parameters to be estimated.

Thus, for describing monthly needlefall in Age i, there are 12 equations, each predicting a monthly needlefall. Stepwise regression procedures were used to determine which weather variables were significantly related to monthly needlefall. Candidate weather variables were mean monthly temperature, rain, PET, and RMP. These variables were also lagged 1 and 2 months and interactions were considered.

3.4. *Evaluation of regression relationships*

The relationships were evaluated by means of several criteria. In the initial stage, each candidate variable's merit was judged by the traditional t-statistics and its contribution to explaining variance in the data (R^2). In addition, it was desired to have equations which were biologically reasonable with parameters that reflect the correct sign and magnitude for the known biological relationship. Plots of the residuals versus independent and predicted variables were also performed. A variable was interpreted as significant if it was significantly different from zero at the $P \leq 0.05$ level.

After construction of an equation by the above procedures its significance was determined by a set of fit statistics. One of these fit statistics was the bias which evaluates how far the predicted value is from the observed and is defined as

$$\text{Bias} = \frac{1}{n} \sum_{i=1}^{n} (\hat{y}_i - y_i)$$

where y_i is the observed value for observation i, $\hat{y}_i$ is the predicted value for observation i and n is the number of observations.

Although bias is a very important property, it could be misleading since it doesn't consider variation of the predictions. For instance, bias could be zero even if predictions fluctuate wildly between large over-estimates and large under-estimates because they tend to cancel each other out. Hence, another fit statistic that was calculated was the absolute bias defined as

$$\text{Absolute bias} = \frac{1}{n} \sum_{i=1}^{n} |\hat{y}_i - y_i|$$

This statistic can be interpreted as the average absolute amount which a prediction varies from observed value in either a positive or negative direction and is a reflection of variation in the predicted values.

The bias and absolute bias may be difficult to interpret when the scale among observed variables changes or when the variables are very large or small. Hence, relative criteria are often used. Two used in this research were the percent bias and the absolute percent bias defined, respectively, as

$$\text{Percent bias} = \frac{100}{n} \sum_{i=1}^{n} \left(\frac{\hat{y}_i - y_i}{y_i} \right)$$

and

$$\text{Absolute percent bias} = \frac{100}{n} \sum_{i=1}^{n} \left| \frac{\hat{y}_i - y_i}{y_i} \right|$$

Another fit statistic which was found useful was the correlation coefficient for predicted and observed. This statistic is useful for non-linear models where correlation may be considered analogous to the square root of the R^2 statistic for linear models.

4. Results

4.1. *Annual leaf biomass production*

Annual leaf biomass production was considered a function of stand basal area (B_i) and four weather variables. All four weather variables were very strongly correlated, which resulted in difficulties in fitting various models, possibly due to a high degree of multicollinearity. To alleviate this problem, only temperature and rain, the variables which had the lowest pairwise correlation, were used. These weather variables were taken from June, July, August and September (PM = 3–6) which constituted the part of the growing season during which leaf biomass growth may be limited by moisture due to effects of rainfall and temperature. Average weighted growing season temperature ($\bar{T}_i$) and rain ($\bar{R}_i$) were calculated as:

$$\bar{T}_i = \sum_{j=3}^{6} W_j T_{ij}$$

denoting weighted average growing season temperature during Age i and

$$\bar{R}_i = \sum_{j=3}^{6} W_j R_{ij}$$

denoting weighted average growing season rainfall during Age i where T_{ij} is mean temperature in Month j during Age i, R_{ij} is rainfall in Month j during Age i, $W_3=0.38169$, $W_4=0.35901$, $W_5=0.19048$ and $W_6=0.06882$. The weights W_j, $j=1,...,4$, are based on the relative amount of needle accretion expected to occur each month of the growing season and are defined as

$$W_j = (\mathrm{NA}_{ij} - \mathrm{NA}_{ij-1}) / (\mathrm{NA}_{i6} - \mathrm{NA}_{i2})$$

The relationship developed for annual leaf biomass production (L_i) using the above weather variables and stand basal area (B_i) as independent variables was

$$L_i = 13163 + 271.6B_i - 3.676B_i^2 - 501.1\bar{T}_i$$

The ranges of these variables are given in Table 1. This equation had the following fit statistics; correlation coefficient of 0.85 with bias 0.00, absolute bias 600, percent bias 6.47, and absolute percent bias 20.8 (Table 2). Plots of the residuals versus independent and predicted variables revealed horizontal bands of points which indicate no need for transformations or other remedial measures. The parameters were all significantly different from zero at the $P \leq 0.05$ level. The trends in annual leaf biomass production predicted by this equation are shown in Fig. 3 for the range of basal areas and temperatures observed in this study.

4.2. Monthly needle accretion

The logistic equation was fitted individually to each set of monthly observations on a plot-year basis. Parameter estimates of t and r were consistent and not significantly related to any measured weather variables. Thus, the logistic equation was fitted to the pooled data, resulting in the following equation,

$$\mathrm{NA}_{ij} = \frac{1}{1 + e^{14.4099(0.2469 - \mathrm{NDATE}_j)}}$$

which had a correlation coefficient of 0.99, bias of 0.01, absolute bias of 0.03, percent bias of 11.6, and absolute percent bias of 16.2 (Table 2). The ranges of the variables in this equation are shown in Table 1. Plots of the residuals versus independent and predicted variables revealed appropriate horizontal bands of points. The parameters were all significantly different from zero at the $P \leq 0.05$ level. However, caution must be used in interpretation of these statistics due to a high degree of autocorrelation which was present between observations with a plot-year. The trend

Table 1
Summary statistics on the variables used in the annual leaf biomass production and monthly needle accretion relationships

Variable	Minimum	Maximum	Mean	Standard deviation
Annual leaf biomass production ($n=45$)				
B_i (m^2 ha^{-1})	6.8	40.0	19.2	9.9
$\bar{T}_i$ (°C)	24.5	26.8	25.9	0.86
L_i (kg ha^{-1})	1247	6405	3700	1391
Monthly needle accretion ($n=261$)				
NDATE$_j$ (proportion)	0.068	0.753	0.380	0.200
NA$_{ij}$ (proportion)	0.02	1.02	0.68	0.347

Table 2
Evaluation criteria for the strength of the leaf biomass dynamics relationships

Dependent variable	Bias	Absolute bias	Percent bias	Absolute percent bias	Correlation predicted observed
Annual leaf biomass production					
L_i	0.00	600	6.47	20.8	0.85
Monthly needle accretion					
NA_{ij}	0.01	0.03	11.6	16.2	0.99
Monthly needlefall					
P_{i1}	0.000	0.018	43	67	0.51
P_{i2}	0.000	0.012	23	42	0.32
P_{i3}	0.000	0.016	80	109	0.44
P_{i4}	−0.002	0.034	104	138	0.41
P_{i5}	−0.001	0.025	44	68	0.55
P_{i6}	−0.007	0.038	−10	30	0.87
P_{i7}	−0.002	0.021	2	17	0.38
P_{i8}	−0.008	0.052	7	41	0.89
P_{i9}	−0.006	0.018	−5	32	0.86
P_{i10}	0.000	0.012	2	17	0.96
P_{i11}	−0.002	0.008	−3	31	0.90
P_{i12}	–	–	–	–	–

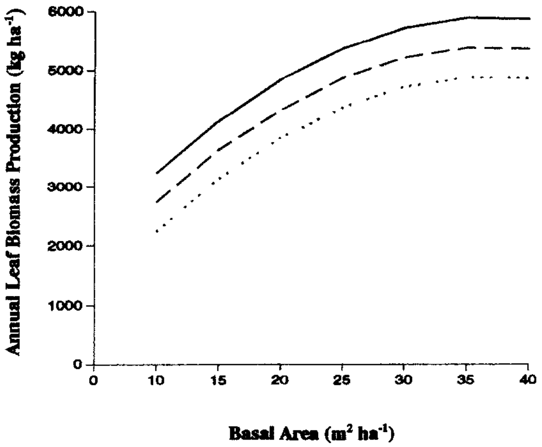

Fig. 3. Predicted annual leaf biomass production–basal area relationship for a range of weighted mean growing season temperatures $\overline{T}_i=24.5°C$ (—), $\overline{T}_i=25.5°C$ (– –), and $\overline{T}_i=26.5°C$ (●●●●).

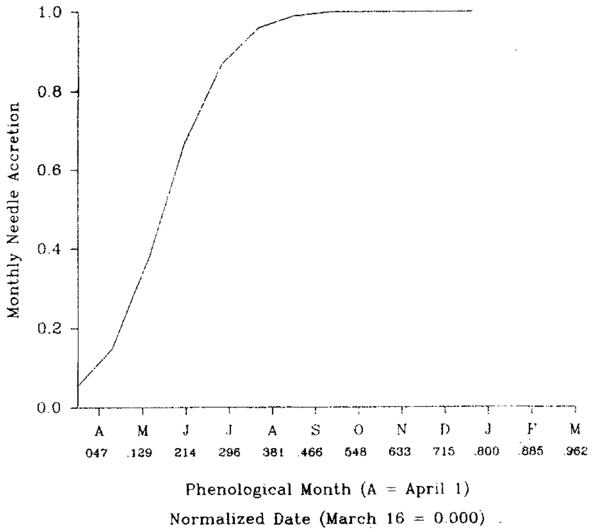

Fig. 4. Average trend in monthly needle accretion observed for the 23 plot-years.

in monthly needle accretion predicted by the final logistic equation is presented (Fig. 4).

4.3. Monthly needlefall

Previous studies have used the logistic equation for describing monthly needlefall (Kinerson et al., 1974; Dougherty et al., 1990). While this appropriately describes the general pattern of needlefall, the logistic equation cannot account for monthly oscillations in the data since one set of parameters can only represent a smooth function over an entire year. Oscillation in monthly needlefall is shown for one of our plots together with monthly predictions using both a logistic equation and the system of equations for estimating monthly needlefall (P^f_{ij}) developed in this research (Fig. 5). It is obvious that the logistic equation cannot mimic the monthly trend since it tends to give smooth, general trends over the year. The P^f_{ij} equations do remarkably well since they consider the fundamental dependency among the months. The logistic equation does not consider this time series relationship which is inherent over the months.

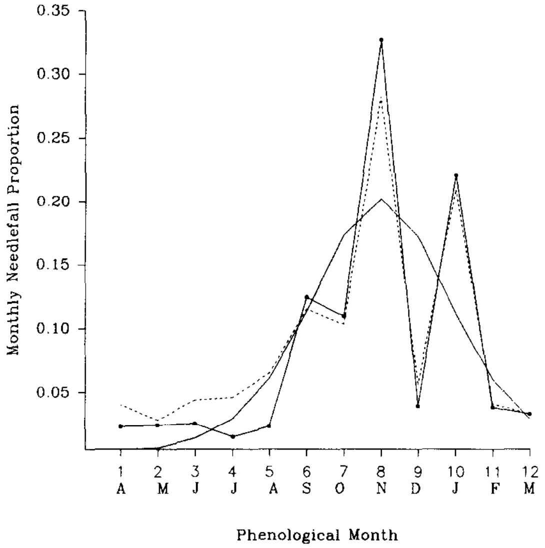

Fig. 5. Comparison of the monthly needlefall system of equations P^f_{ij} (- -) to the logistic equation (—) fitted to the observed (●) monthly needlefall in Block 2, treatment 12.6 m^2 ha^{-1}, and Phenological Year 1984.

Stand basal area was not a significant variable in the final system of equations for predicting monthly needlefall, hence, this variable was not included. Numerous combinations of weather variables were evaluated by lagging the basic weather variables for up to 2 months. Generally, the best fit was obtained by using weather variables defined as the average for the previous 2 months. For consistency, all monthly equations contained the same variables even if statistical significance for the parameters was not achieved at $P \leq 0.05$ level. It was desirable for the coefficients of the independent variables to have the appropriate positive or negative sign depending on their biological relationship to the dependent variable. However, this was relaxed to some event to ensure one consistent set of parameters for all equations. Using the above philosophy, the final system of equations is

$$P^f_{ij} = \begin{cases} (1+e^{c_0+c_i\overline{\mathrm{RMP}}_{ij}+c_2\bar{T}_{ij}})^{-1} & j=1 \\ (1-\sum_{k=0}^{j-1} P^f_{ik})(1+e^{c_0+c_1\overline{\mathrm{RMP}}_{ij}+c_2\bar{T}_{ij}})^{-1} & j=2,3,\ldots,11 \\ 1-\sum_{k=1}^{11} P^f_{ik} & j=12 \end{cases}$$

where $\bar{T}_{ij}=1/2(T_{ij-1}+T_{ij-2})$ denotes average monthly lagged temperature for Month j during Age i, $\overline{\mathrm{RMP}}_{ij}=1/2(\mathrm{RMP}_{ij-1}+\mathrm{RMP}_{ij-2})$ denotes average monthly lagged RMP for Month j during Age i,

$$T_{ij-k}=$$

$$\begin{cases} \text{mean temperature in Phenological Month } j-k \text{ during Age } i \text{ if } j-k>0 \\ \text{mean temperature in Phenological Month 12 during Age } i-1 \text{ if } j-k=0 \\ \text{mean temperature in Phenological Month 11 during Age } i-1 \text{ if } j-k=-1 \end{cases}$$

$$\mathrm{RMP}_{ij-k}=$$

$$\begin{cases} \text{rain minus PET in Phenological Month } j-k \text{ during Age } i \text{ if } j-k>0 \\ \text{rain minus PET in Phenological Month 12 during Age } i-1 \text{ if } j-k=0 \\ \text{rain minus PET in Phenological Month 11 during Age } i-1 \text{ if } j-k=-1. \end{cases}$$

Table 3 gives the ranges of the variables utilized in these equations. Estimates of parameters for each monthly equation are in Table 4. The fit statistics are not as good as was achieved for annual leaf biomass production and monthly needle accretion. However, they are reasonably good for

Table 3
Summary statistics on the variables used in the monthly needlefall system of equation

Phenological Month j	n	$\sum_{k=1}^{j-1} P^f_{ik}$ (proportion)				$\overline{\mathrm{RMP}}_{ij}$ (mm)				$\bar{T}_{ij}$ (°C)				P^f_{ij} (Proportion)			
		Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	Min	Max	Mean	S.D.	Min	Max	Mean	S.D.
1	53	0.00	0.00	0.00	0.00	74	168	124	33	8.8	11.4	10.0	1.01	0.01	0.10	0.04	0.026
2	53	0.01	0.10	0.04	0.026	38	168	91	48	13.1	15.7	14.2	0.95	0.01	0.09	0.03	0.018
3	53	0.02	0.16	0.07	0.039	−47	201	49	81	17.2	19.9	18.5	0.87	0.00	0.07	0.04	0.021
4	53	0.03	0.20	0.11	0.051	−79	120	0	63	22.4	24.4	23.1	0.66	0.00	0.16	0.06	0.045
5	45	0.04	0.36	0.17	0.082	−88	−27	−70	22	25.4	27.2	26.1	0.59	0.01	0.16	0.08	0.038
6	45	0.05	0.41	0.25	0.092	−140	4	−88	56	26.1	27.8	27.4	0.63	0.03	0.38	0.17	0.097
7	53	0.15	0.67	0.43	0.146	−123	6	−57	45	24.2	26.4	25.7	0.77	0.08	0.22	0.13	0.029
8	53	0.25	0.81	0.55	0.153	−25	152	42	59	19.5	21.4	20.2	0.69	0.07	0.54	0.22	0.136
9	45	0.49	0.93	0.79	0.123	75	165	121	37	13.3	16.0	14.1	0.96	0.02	0.25	0.07	0.046
10	45	0.62	0.96	0.85	0.102	96	223	133	47	8.7	10.5	9.3	0.66	0.01	0.32	0.08	0.076
11	53	0.79	0.98	0.92	0.052	35	157	93	39	4.5	6.9	5.6	0.83	0.01	0.11	0.03	0.024
12	53	0.81	1.00	0.95	0.046	60	124	80	23	3.4	7.9	5.8	1.54	0.00	0.19	0.05	0.046

Table 4
Parameter estimates for the monthly needlefall system of equations

Equation	c_0 (Intercept)	c_1 ($\overline{\mathrm{RMP}}_{ij}$)	c_2 ($\bar{T}_{ij}$)
$\hat{P}_{i1}$	5.96644*	−0.00654*	−0.19627*
$\hat{P}_{i2}$	5.69001*	−0.00365*	−0.13582
$\hat{P}_{i3}$	−1.39030	−0 00111	0.25362
$\hat{P}_{i4}$	5.27102	0.00566*	−0.11374
$\hat{P}_{i5}$	13.14259*	−0.00276	−0.42432*
$\hat{P}_{i6}$	−9.84627	0.02550*	0.50062
$\hat{P}_{i7}$	3.91468	0.00759*	−0.08676
$\hat{P}_{i8}$	−31.19118*	0.00486*	1.55013*
$\hat{P}_{i9}$	0.41741	0.01286*	−0.06755
$\hat{P}_{i10}$	6.63239*	0.00340	−0.75004*
$\hat{P}_{i11}$	7.11356*	0.00250	−1.22586*
$\hat{P}_{i12}$	–	–	–

*Denotes that a parameter is significantly different from zero at the 0.05 level.

Phenological Month 5 and above (except Phenological Month 7, October) which are the months where the biological importance of needlefall is focused (Table 2). Predicted monthly needlefall averaged over the three 25.5 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ treatment plots reflected the oscillations in observed monthly needlefall (Fig. 6). An example of the monthly needlefall equation for September for a fixed temperature ($\bar{T}_{i6}=27.5$°C) and varying cumulative monthly needlefall levels and varying rain minus potential evapotranspiration is shown (Fig 7).

4.4. Combined equation for estimating leaf biomass dynamics

Equations for annual leaf biomass production, monthly needle accretion, and monthly needlefall were combined to estimate canopy leaf biomass of a stand for each month of a year as

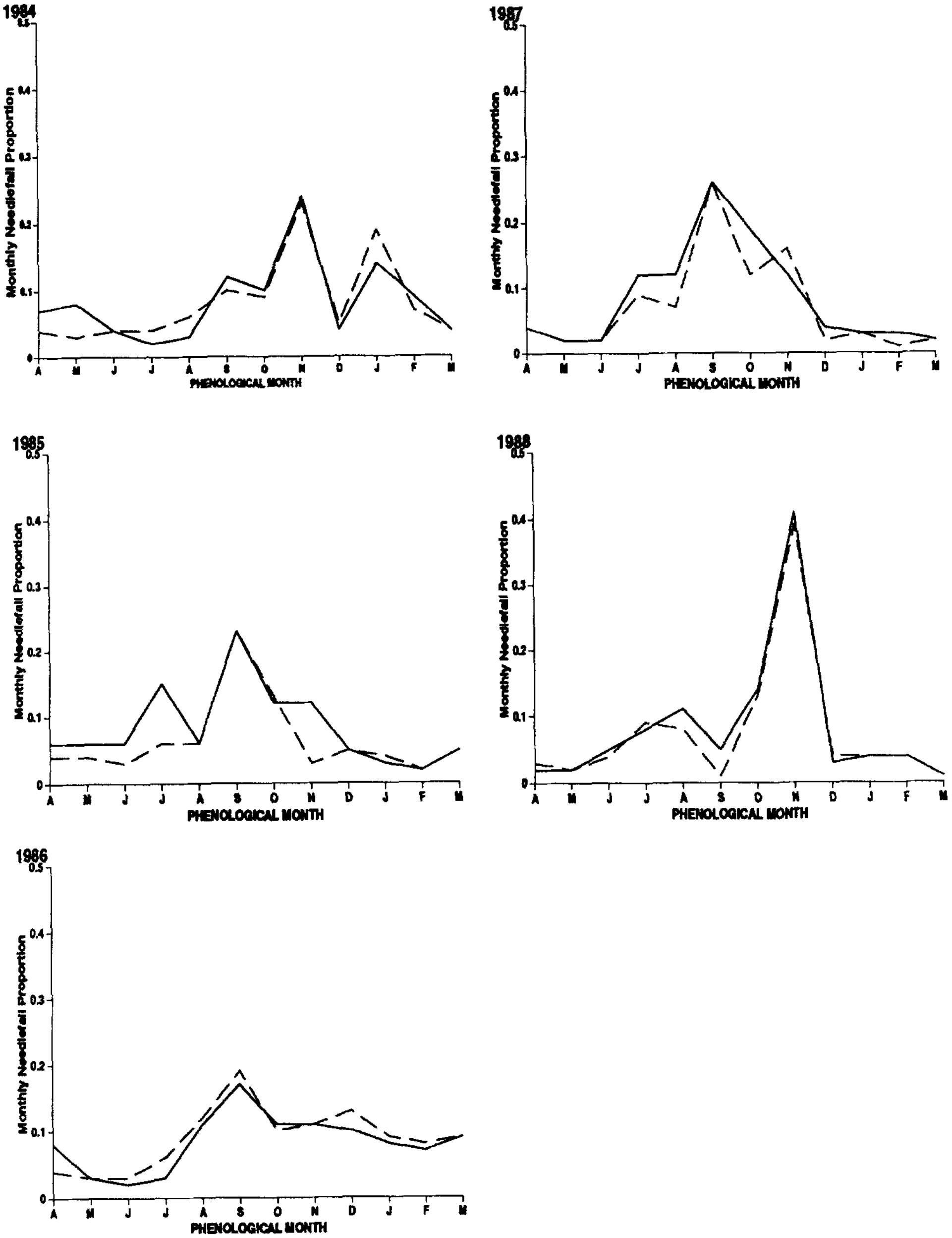

Fig. 6. The observed (—) and predicted (– –) monthly needlefall averaged over the three 25.5 m^2 ha^{-1} treatment plots.

$$\mathrm{TOTAL}_{ij} = \left(1 - \sum_{k=1}^{j-1} P^{f}_{ik}\right) L_{i-1} + \mathrm{NA}_{ij} L_i$$

where TOTAL_{ij} denotes leaf biomass present in the canopy in Month j of Age i. Note that the first term on the right of the equals sign is the amount of 1-year-old leaf biomass still on the tree while the second term is the amount of new leaf biomass being formed in the current year.

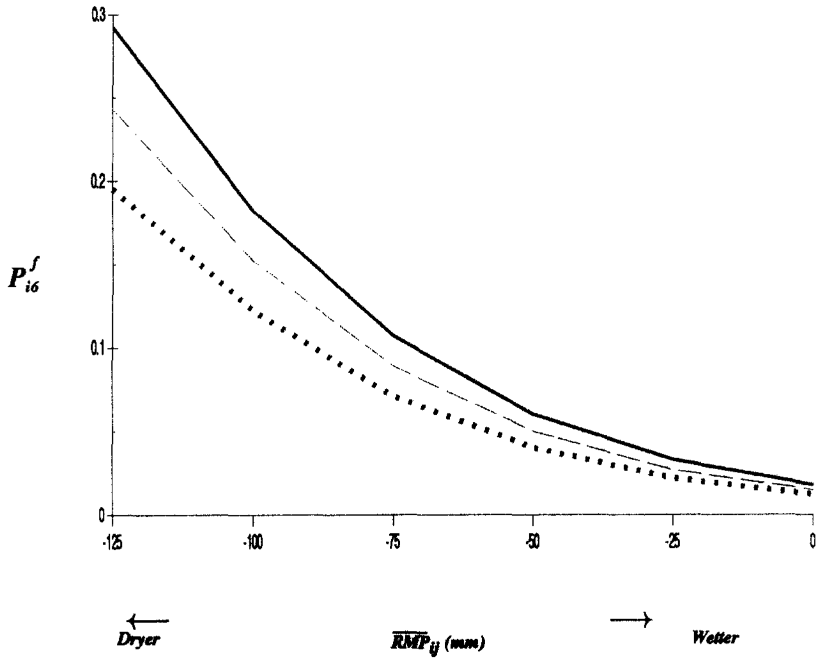

Fig. 7. Predicted proportions of the annual needlefall that occurs in September (P^f_{i6}) at a fixed temperature ($\bar{T}_{i6}=27.5°C$), previous cumulative monthly needlefall levels of $\sum_{k=1}^{5} P^f_{ik}=0.10$ (—), $\sum_{k=1}^{5} P^f_{ik}=0.25$ (- -), and $\sum_{k=1}^{5} P^f_{ik}=0.40$ (●●●●), and varying rain minus potential evapotranspiration levels ($\overline{\mathrm{RMP}}_{ij}$).

5. Discussion

Leaf biomass dynamics of an 11- to 17-year-old loblolly pine stand that had been thinned at Age 11 was described with: (1) an equation which related annual leaf biomass production to stand basal area and a weather variable, (2) an equation which described monthly needle accretion, and (3) a system of equations which predicts monthly needlefall as a function of the proportion of the previous year's annual leaf biomass production present and lagged weather variables.

5.1. Annual leaf biomass production

Annual leaf biomass production on the study site was best predicted ($r=0.85$) by an equation which accounted for stand density and temperature. Annual leaf biomass production increased as a quadratic function of stand basal area. Similar relationships have been reported by Gresham (1982), Dalla-Tea and Jokela (1991), and Hennessey et al. (1992) for loblolly pine. In this study the stand was thinned and this could have influenced the annual leaf biomass production–basal area relationship. Although the initial thinning at Age 11 was heavy (Fig. 1), the before-thinning stand density was not high (25.5 m^2 ha^{-1}). The second thinning at Age 14 was very light (Fig. 1) and the thinned plots had low stand densities prior to thinning. Thus, it is unlikely that a thinning effect, other than that associated with changes in basal area, resulted from the second thinning. However, due to the design of the study, the effects of thinning could not be quantified.

In addition to stand basal area, average mean temperature for June, July, August, and September, weighted by their average relative monthly contribution to annual biomass production, was important in predicting annual leaf biomass production. No interaction effect of stand basal area and temperature on annual leaf biomass production was detected. An increase in average temperature for the 4 month period (June–September) from 24.5 to 26.5 °C would cause annual leaf biomass production to be reduced by about 1000 kg ha^{-1} (Fig. 3). This is a 27% reduction in annual leaf biomass production for the average stand in our study. Hennessey et al. (1992) reported that annual needlefall varied by as much as 29% for high density unthinned plots. Our results suggest that only a 2°C change in average temperature would have significant effects on annual leaf biomass production and subsequently on loblolly pine yield in this region. Both Vose and Allen (1988) and Dalla-Tea and Jokela (1991) demonstrated a linear relationship between aboveground yield and indices of foliage biomass. Using a projected specific leaf area of 50 cm^2 g^{-1} and the leaf area–stemwood relationship of Vose and Allen (1988), we estimate that the 27% reduction in annual leaf biomass production would translate to a 7.3 m^3 ha^{-1} year^{-1} reduction in stemwood production.

5.2. Monthly needle accretion

A logistic function was used to describe monthly needle accretion. Kinerson et al. (1974) and Dalla-Tea and Jokela (1991) have previously utilized the logistic function for predicting needle accretion of loblolly pine. The logistic function was adequate for describing monthly needle accretion because cumulative needle biomass increased in a continuous manner and the relative monthly contributions did not vary from year to year. The correlation coefficient between observed and predicted needle accretion was 0.99 for data collected over 3 years for the basal area treatments. Thus, even though annual leaf biomass production varied widely from year to year and was related to the average temperature during the 4 months when needle expansion occurred most rapidly, the relative pattern of needle accretion did not change. This is the same type of response that was reported for *Pinus radiata* (D.Don) by Raison et al. (1992a).

5.3. Monthly needlefall

Monthly needlefall of loblolly pine can be divided into two phases. Phase 1 consists of the last 2 months of the previous phenological year, (16 January–15 March) and the first 5 phenological months of the current phenological year (16 March–15 August). In Phase 1, monthly needlefall was observed to average from 3 to 8% of the previous year's annual leaf biomass production. In Phase 2 (16 August–15 January), needlefall varied widely between months and years (Fig. 6). A system of 12 non-linear equations was developed to describe monthly needlefall. Each equation expressed monthly needlefall as a function of the amount of the previous year's annual leaf biomass production that remains in the canopy, the average RMP and average temperature determined for the 2 previous months. The correlation of predicted monthly needlefall with observed needlefall did not exceed 0.55 for the phenological months from 16 March to 15 August and was not related to either RMP or temperature. Needlefall during Phase 1 is probably not due to weather stimulating the senescence process but rather to a host of unpredictable variables such as wind thrashing, insects and diseases, and hail, all of which may cause early needlefall. However, this was not assessed in this study. For this phase of needlefall, assigning an average of 4–5% needlefall per month would seem appropriate (Table 3).

In Phase 2 (16 August–15 January) reasonable predictions of monthly needlefall were obtained for all months except Phenological Month 7 (October). In this phase, the RMP variable was much more important in predicting monthly needlefall than temperature, suggesting that drought stress may be the major factor that triggers early needlefall. A similar conclusion was reached for *P. radiata* by Raison et al. (1992b) who reported that water stress could accelerate needlefall by 3–4 months in dry years if irrigation was not applied. Peak monthly needlefall for loblolly pine normally occurs in November (PM = 8) but Hennessey et al. (1992) reported that summer water deficits could shift this by 2 months in years with extremely dry summers. The effect of drought (RMP) on the amount of needlefall that would be expected to fall 2 months earlier than the average peak needlefall month (November) is illustrated (Fig. 7). If rainfall and potential evapotranspiration are equal (RMP=0) in the 2 months previous to September, then only about 2% of the previous year's annual leaf biomass production would fall in September. This represents the conditions that would exist in a wet year such as occurred in 1988 (Figs. 2 and 6). However, if it is droughty for the 2 months prior to September, as much as 30% could fall in September. An RMP such as −125 mm occurred in 1985 and 1987 and shifts in peak needlefall did occur (Figs. 2 and 6). Results from this study suggest that a shift to hotter and drier summers in this region would result in a substantial reduction in leaf area duration on similar sites as ours and, thus, probably lead to reductions in yield.

5.4. Monthly total leaf biomass

To determine the amount of monthly total leaf biomass remaining in the canopy requires that monthly needle accretion and monthly needlefall are known. Trends in the amount of leaf biomass remaining in the canopy can be described by coupling annual leaf biomass production and monthly needle accretion equations with the system of monthly needlefall equations as discussed previously. It is the amount of leaf biomass left in the canopy that is important for evaluating effects of alterations in temperature and rain due to climate change on annual water and carbon balance of loblolly pine forests. For loblolly pine, which carries only two age classes of foliage, good estimates of monthly canopy leaf biomass will be required to model carbon and water fluxes. Although limited in scope, the approach utilized in this article represents a framework that should be suitable for describing the monthly leaf biomass dynamics of loblolly pine stands.

5.5. Conclusion

Loblolly pine stands carry only two age classes of foliage in a phenological year. About one-half of the leaf biomass develops (accretion) and one-half dies each phenological year. Thus, leaf biomass changes throughout the year are large. In addition, as shown in this study and others, annual leaf biomass production and monthly needlefall also vary annually depending on weather conditions (Hennessey et al., 1992) and resource availability (Vose and Allen, 1988). To develop process models which predict annual carbon and water balance will require that effects of normal phenology, weather and resource availability on leaf biomass dynamics be quantified. This study has demonstrated an approach for relating leaf biomass dynamics to stand development and to annual variation in weather. Further studies are needed to cover a wider range of stand basal areas, soils and weather conditions before models can be developed. Additional needs include incorporation of nutrient effects on annual leaf biomass dynamics.

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