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Growth in loblolly pine plantations as a function of stand density and canopy properties ¹

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Abstract

Interrelationships between forest-canopy properties, stand growth, and Reineke's stand density index (SDI) were investigated for unthinned plots of a loblolly pine, growth-and-yield study. Gross, periodic-annual increment (I_{y}) and mean-tree, gross, periodic-annual increment (I_{mv}) were calculated for the intervals between 17, 22, 27, 32, and 37 years of age. Data to calculate canopy variables were available only after age 22. Regression analysis indicates that a second-degree polynomial of SDI is statistically related to both growth variables during the first two measurement intervals but not the last two. The shape of the significant equations generally agreed with conventional growth-growing stock relationships, and $I_{\rm v}$, adjusted for SDI, decreased significantly with age. Leaf area index (L) and foliage density (F) were linearly related to SDI for each measurement period. While the equations relating F and SDI were not significantly different between measurement periods, the intercepts of the fitted equations for L and SDI generally decreased with plantation age. Mean-live-crown ratio (C_r) was significantly related to SDI for all measurement periods, with the exception of age 32, and canopy depth (C_d) was statistically related to SDI only at age 22. Significant multiple-linear regression models were found between the growth variables and canopy properties with one exception. With that one exception, I_v was significantly related to L during each measurement interval and to F and C, during the first two intervals. Mean, gross, periodic-annual increment was statistically related only to those canopy variables that described canopy structure. With the exception of F, the overall average value of the canopy variables decreased with age in these loblolly pine plantations, probably leading to the systematic reduction in $I_{\rm o}$ with age. Although growth-growing stock relations were not significant in these plantations after age 27, the relationships between canopy variables and canopy variables emphasize the importance of early density management to maintain vigorous crowns and growth rates as plantations age.

Keywords: Productivity; Stand density; Loblolly pine; Leaf-area index; Live-crown ratio; Canopy depth

1. Introduction

Field trials are the best method for developing density management plans; however, the range of planting density, soils, and the timing and intensity of thinning available for loblolly pine create more

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combinations than can be tested on a uniform site. Growth-growing stock relationships provide a means for developing density management plans until field trials can be completed as they describe the total amount of growth (gross) as a function of growing stock for a particular combination of species, age, and site (Daniel et al., 1979). Growth-growing stock relationships for loblolly pine exist (Nelson and Brender, 1963; Allen and Duzan, 1981), but recent advancements in forest production ecology indicate that these existing relationships may need reexamination.

Growing stock is typically measured with an index of stand density, and the growth-growing stock relationships that exist for loblolly pine are based on total basal area per unit ground area (BA). Nelson and Brender (1963) chose BA because it is easy to measure and produced results similar to other density indexes; however, they developed their relationships with net increment instead of gross increment. Allen and Duzan (1981) chose BA based on dimensional analysis between crown area and diameter at breast height and a relationship between crown area and growth. Leaf area is a more direct measure of growing space than crown area because leaf area correlates well with stand increment (Long and Smith, 1984; Oren et al., 1987; Vose and Allen, 1988; Dean et al., 1988; Long and Smith, 1990a; Dalla-Tea and Jokela, 1991). Long and Smith (1990a) have shown a good relationship between canopy leaf area and stand increment, suggesting that Reineke's stand

Table 1

Average characteristics of unthinned plots in a loblolly pine, growth-and-yield study located near Merryville, LA, USA. Data were averaged across all measurement periods (n = 64, 16 plots measured at 17, 22, 27, 32, and 37 years of age)

Variable	Mean	SD	Minimum	Maximum
Frees per hectare	900	420	430	2440
Site index (m) ^a	20	l	16	22
Basal area (m ² ha ⁻¹)	31	6	17	41
Quadratic mean diameter (cm)	21.9	4.0	12.7	31.4
Height (m)	18	4	11	27
Reineke's stand density index	660	130	390	920
Gross periodic-annual increment $(m^3 ha^{-1} year^{-1})$	7.1	2.1	2.2	11.6
Mean-tree gross periodic-annual increment (m ³ year ⁻¹)	8.7	3.5	3.4	18.3
Leaf area index $(m^2 m^{-2})$	3.2	0.6	1.8	4.6
Foliage density $(m^2 m^{-3})$	0.5	0.1	0.3	0.9
Canopy depth (m)	6	1	4	9
_ive-crown ratio	0.31	0.07	0.17	0.47

^a Base age 25 years.

density index (SDI) may be a more suitable measure of growing stock than *BA*. In addition, a growthgrowing stock relationship based on SDI would complement existing density-management diagrams for loblolly pine (Dean and Baldwin, 1993; Williams. 1994).

This study had two objectives: (1) to analyze growth-growing stock relationships for loblolly pine, and (2) to analyze the interrelationships between growth, SDI, canopy leaf area, and canopy structure. Data to accomplished these objectives were provided by the USDA Forest Service from a long-term, loblolly pine, growth-and-yield study. The data from this study allowed the calculation of gross, periodicannual increment and various canopy variables. Investigation of growth-growing stock relationships and canopy properties simultaneously gives us an insight into how stand density influences growth.

2. Methods

2.1. Data

The loblolly pine, growth-and-yield study used for these analyses is located near Merryville, LA, USA. The study was established on cutover longleaf pine land by machine planting 1-year-old, bare-root seedlings of unknown geographic seed source in January 1952. Seedlings were planted at five planting spacings (1.8 m \times 1.8 m, 2.4 m \times 2.4 m, 2.7 $m \times 2.7$ m, 3.0 m \times 3.0 m, and 3.7 m \times 3.7 m) in a randomized, complete-block design. In 1969, 88 plots of approximately 0.16 ha were established (0.04 ha measurement plots), and five thinning treatments applied (residual basal areas of 27.5, 23.0, 18.4, 13.8 m², and no thinning) in each of the spacings. Data from the 16 unthinned plots (three replications minimum from each planting spacing) were used for this analysis. Overall means for the standard mensurational data for these plots and for the variables calculated for this study are shown in Table 1.

At ages 17, 22, 27, 32, and 37 years, diameter at breast height (*DBH*, 1.37 m) was recorded for each tree by tree number. Starting at age 22, total tree height and height to the base of the live crown were recorded in addition to *DBH*. Data recorded by tree number allowed the calculation of gross-volume increment between measurement periods. Individual, whole-tree volume (m^3) was calculated from DBH (cm) using the regression equation

$$\ln(V) = \exp(2.593\ln(\text{DBH}) - 8.991) \ R^2 = 0.92$$

where V is outside bark stem volume from the stump to the top of the stem. This equation was developed from 139 trees destructively sampled from unthinned, loblolly pine plantations in central Louisiana. Trees were sampled across a range of ages (9-55 years), DBH (8-53 cm), and height (9-27 m) as described by Baldwin and Feduccia (1991). Although heights were recorded after age 22, these data were not available by tree number; consequently, tree height could not be included in the equation for stem volume. Standing volume is the plot total of all individual tree volumes. Gross, periodic-annual increment (I_y) was calculated as the difference in standing volumes between measurement periods plus one-half of the volume lost from mortality during the period. This figure was then converted to annual, per hectare values. Mean-tree, gross, periodic-annual increment (I_{mv}) is I_v divided by the average number of trees per hectare surviving during the period.

Leaf area index (leaf area per unit ground area) $(L, m^2 m^{-2})$ for each measurement period is the plot total of individual tree leaf area divided by the area of the measurement plot. Leaf mass per tree $(M_{\rm L}, \rm kg)$ was calculated with DBH (cm) and height

to the middle of the crown (S_c, m) using the equation from Baldwin (1989)

$$M_{\rm L} = \exp(2.795 \ln(\text{DBH}) - 1.095 \ln(S_{\rm c}) - 3.579)$$

and converting it to projected leaf area using the factor 4.737 m² kg⁻¹ (T.J. Dean, unpublished data, 1994). Canopy depth (C_d , m) is the average length of individual live crowns per plot, and mean-live-crown ratio (C_r) is the average ratio of crown length and total tree height per plot. Foliage density (F, m² m⁻³) is L divided by C_d (Smith and Long, 1989). Reineke's stand density index is calculated with the standard equation

$$\text{SDI} = \text{TPH}(D_o/25)^{1.6}$$

where D_q is quadratic mean diameter (cm) and TPH is the number of trees per hectare (Daniel and Sterba, 1980).

2.2. Analysis

While stand density at the beginning of the growth period has been used in relating growth to growing stock (e.g. Allen and Duzan, 1981), for this analysis, growth-growing stock relationships were analyzed using the average value of SDI during the growth period. Large changes can occur during 5 years in a loblolly pine plantation, and the average value of SDI should be more sensitive to these changes than the value at the beginning of the measurement interval. With the exception of the first measurement interval, average values of the canopy variables during the measurement intervals were also used in investigating the relationship between canopy properties and growth. Since the variables necessary to calculate the canopy variables were not measured at age 17, canopy properties at the end of the first measurement period were used for the analyses.

Stepwise linear regression analysis was conducted between the growth variables and the canopy properties that could be calculated from this data to determine which canopy variables influence stand-level and mean-tree growth; not to construct predictive equations. Therefore, nonlinear canopy effects were represented by squared transformations of the variables. Each step of the procedure determined the combination of variables that maximized the coefficient of determination, selecting from the linear and square transformations of L, F, C_d , and C_r . Models presented were the most parsimonious models that exhibited the largest coefficient of determination with all independent variables statistically significant at $\alpha = 0.10$.

3. Results

3.1. Growth-growing stock relationships

A second degree polynomial of SDI significantly covaried with both I_v and I_{mv} (Table 2). Across all growth intervals, however, SDI explained only 16% and 20% of the variation in I_v and I_{mv} , respectively. The amount of variation in I_v and I_{mv} explained by SDI depended on the specific measurement intervals analyzed. For growth between ages 17 and 22, SDI explained 54% and 41% of the variation in I_v and I_{mv} , respectively, and between ages 22 and 27, SDH explained 30% of the variation in both growth variables. After age 27, neither growth variable significantly covaried with SDI, explaining the low coefficient of determination when analyzed across all growth intervals.

Gross, periodic-annual increment decreased with age. For the two measurement intervals that showed significant relationships between I_v and SDI, the regression line for the earliest measurement interval lies above the regression line for the next measurement interval (Fig. 1(a)). Analysis of covariance using growth interval as a fixed effect and SDI and SDI² as covariates indicates that I_v decreases significantly with each successive measurement interval (P < 0.01), from a high of 8.7 m³ ha⁻¹ year⁻¹ between ages 17 and 22 to a low of 5.7 m³ ha⁻¹

Table 2

Multiple regression statistics for the model $Y = \beta_0 + \beta_1 X + \beta_2 X^2$, where Y is gross, periodic-annual increment $(I_v, m^3 ha^{-1} year^{-1})$ or mean-tree, gross, period-annual increment $(I_{mv}, m^3 year^{-1})$ and X is Reineke's stand density index. The model was fitted separately and across all measurement intervals with data from the unthinned plots in a loblolly pine growth-and-yield study located near Merryville, LÅ, USA

Measurement interval *	β_0	β ₁	β_2	R*	<i>P</i> -value
$Y = I_{\rm v}$					
17–22	- 19.23	0.075	-4.8×10^{-5}	0.54	< 0.01
	(8.70)	(0.026)	(1.8×10^{-5})		
22–27	- 11.65	0.047	-2.8×10^{-5}	0.30	0.04
	(11.32)	(0.033)	(2.3×10^{-5})		
27-32	1.77	0.008	6.2×10^{-7}	-0.02	0.46
	(15.63)	(0.047)	(3.6×10^{-5})		
32-37	- 4.67	0.026	-1.7×10^{-5}	0.01	0.43
	(14.99)	(0.048)	(3.8×10^{-5})		
Overall	5.88	0.0055	1.0×10^{-6}	0.23	< 0.01
	(2.22)	(0.0060)	(4.3×10^{-6})		
$Y = I_{my}$					
17-22	-0.014	8.3×10^{-5}	-6.9×10^{-8}	0.41	0.01
	(0.019)	(5.5×10^{-5})	(4.0×10^{-8})		
22-27	-0.031	1.3×10^{-4}	-9.8×10^{-8}	0.30	0.04
	(0.022)	(6.4×10^{-5})	(4.0×10^{-8})		
27–32	-0.004	5.5×10^{-5}	-4.9×10^{-8}	-0.05	0.54
	(0.029)	(9.1×10^{-5})	(7.0×10^{-8})		
32-37	0.017	8.9×10^{-5}	-7.5×10^{-8}	-0.06	0.57
	(0.032)	(1.0×10^{-5})	(8.0×10^{-8})		
Overall	0.016	1.0×10^{-5}	-6.4×10^{-10}	0.10	0.01
	(0.004)	(1.0×10^{-5})	(1.0×10^{-8})		

^a Age in years at the beginning and end of the measurement interval.

Standard errors are given in parentheses.

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Mean-tree, gross, periodic-annual increment for a given value of SDI does not appear to change with measurement interval (Fig. 1(b)). While the average tree in these stands had a growth rate of 9.3×10^{-3} m³ year⁻¹ between ages 17 and 22 compared with 8.1×10^{-3} m³ year⁻¹ between ages 32 and 37, analysis of covariance using growth interval as a fixed effect and SDI and SDI₂ as covariates indicates that age has no significant effect on I_{mv} in these loblolly pine plantations (P = 0.90).

3.2. Relationship between growth variables and canopy properties

For all measurement intervals, stepwise linear regression produced significant models for both I_v and I_{mv} , with the exception of I_v between ages 32 and 37 (Table 3). The amount of variation in I_v explained with these canopy variables systematically decreased with plantation age from a maximum of 81% to a minimum of 21%. The canopy variables identified as significant for two earliest measurement intervals were F, C_r , and L. During the last measurement interval, only L was significantly related to I_v . None of the squared canopy variables were significantly related to I_v during any measurement interval. The resulting equations indicate that I_v is positively related to L and negatively related to both F and C_r . When significant, the fitted coefficients

for L, F and C_r decrease with each successive measurement interval.

A significant regression model between I_{mv} and the canopy variables was found for each measurement interval. The amount of variation in I_{mv} explained with the regression models did not exhibit the same systematic decrease with age as found in the regression analysis for I_{v} , though the coefficients of determination for the first two measurement intervals were greater than the coefficients of determination for the last two measurement intervals (Table 3). For all measurement intervals, the only canopy variables that were significantly related to I_{mv} were those that described canopy structure. Leaf area index was not a significant variable in any of the equations. The coefficient for C_d is nearly the same for each measurement interval and indicates that in these loblolly pine plantations, the same amount of $I_{\rm mv}$ can be expected per unit $C_{\rm d}$, at least until age 37. Mean-live-crown ratio is significantly related to I_{mv} during three of the four measurement intervals; however, its relationship to I_{mv} is complex: both linear and quadratic transformations of C_r are significant in all but one equation. For the last measurement interval, only $C_{\rm d}$ was significantly related to $I_{\rm mv}$.

3.3. Relationship between SDI and canopy properties

Linear regression between L and SDI was significant for each age, and while the slopes of the lines

Table 3

Results of stepwise regression of plantation growth as a function of various canopy variables by measurement interval for the unthinned plots in a loblolly pine growth-and-yield study located near Merryville, LA, USA. Growth is represented in terms of either gross, periodic-annual increment $(I_v, m^3 ha^{-1} year^{-1})$ or mean-tree, gross, periodic-annual increment $(I_{mv}, m^3 year^{-1})$. Independent variables were selected from leaf area index $(L, m^2 m^{-2})$, foliage density $(F, m^2 m^{-3})$, canopy depth (C_d, m) , mean-live-crown ratio (C_r) , and their square transformations. The number of observations for each measurement interval is 16

		D ²		
Measurement interval *	Equation	<u></u>	P-value	
$\overline{Y = I_v}$				
17-22	$Y = 20.98 - 24.95F - 48.46C_{\rm r} + 5.66L$	0.81	< 0.01	
22-27	$Y = 23.51 - 26.14F - 55.04C_{\rm r} + 5.08L$	0.74	< 0.01	
27-32	no significant model			
32–37	Y = 2.14L - 0.46	0.21	0.07	
$Y = I_{mv}$				
17-22	$Y = 0.004C_{\rm d} - 0.053C_{\rm r}^2 - 0.012$	0.80	< 0.01	
22-27	$Y = 0.004C_{\rm d} - 0.047C_{\rm r} - 0.004$	0.84	< 0.01	
27-32	$Y = 0.003C_{\rm d} + 3.23C_{\rm r}^2 - 2.00C_{\rm r} - 0.30$	0.51	0.03	
32-38	$Y = 0.004 C_{\rm d} - 0.014$	0.59	< 0.01	

^a Plantation age in years at the beginning and end of the measurement interval.

were not significantly different between ages (P = 0.62), the intercepts systematically and significantly decreased with age (P < 0.01), with the exception of age 27 (Fig. 2(a)). Foliage density was also significantly related to SDI for each measurement period (Fig. 2(b)); however, neither the slopes nor the intercepts were significantly affected by age (P = 0.15 and P = 0.13, respectively).

Linear regression between C_d and SDI was significant only for the earliest measurement period (Fig. 2(c)). Analysis of covariance using SDI as a covariable indicated that C_d decreased significantly from 7.0 to 5.2 with each successive measurement period (P < 0.01). Linear regression between C_i and SDI was statistically significant for each measurement period, with the exception of age 32 (Fig. 2(d)).



Fig. 1. Relationship between gross, periodic-annual increment (I_v) and Reineke's stand density index (SDI) (a) and between mean-tree, gross, periodic-annual increment (I_{mv}) and SDI (b) by measurement period for the unthinned plots in a loblolly pine, growth-and-yield study at Merryville, LA, USA. Lines drawn when statistically significant fits exist ($\alpha = 0.1$) for the model $Y = \beta_0 + \beta_1 X + \beta X^2$, where $Y = I_v$ or I_{mv} and X = SDI. Data fit by intervals between measurements: ages 17-22 years (solid line); ages 22-27 years (dashed line).



Fig. 2. Relationships of leaf area index (a), foliage density (b), canopy depth (c), and mean-live-crown ratio (d) with Reineke's stand density index (SDI) for the unthinned plots in a loblolly pine, growth-and-yield study located near Merryville, LA, USA. Data are denoted by years of age when measured, and lines are drawn when significant linear relationships exist for a measurement period ($\alpha = 0.1$): 22 years (\bullet , solid line); 27 years (\bigcirc , coarse dashed line); 32 years (\blacktriangledown , fine dashed line); and 32 (\bigtriangledown , dotted line).



Fig. 3. Growth-growing stock relationships as hypothesized by Langsaeter (1941) (a) and Long (1985) (b). Roman numerals mark the stages of increasing intraspecific competition from none (I) to strong (III), and severe (V).

However, after age 22, the linear regressions are extremely weak. While SDI explains 74% of the variation in C_r at age 22, it explains only 18% and 12% of the variation in C_r at ages 27 and 37, respectively.

4. Discussion

4.1. Growth-growing stock relations

The relationship between I_v and SDI tends to support the original hypothesis of Langsaeter (1941) (Fig. 3(a)), especially for growth between ages 17 and 22. Gross, periodic-annual increment increases rapidly up to about the self-thinning threshold, peaks at around 70% of maximum SDI, and begins to drop with further increases in SDI. The self-thinning threshold for loblolly pine occurs at approximately 55% of maximum SDI or SDI = 630 (Dean and Baldwin, 1993). Langsaeter's hypothesis and other investigators state that stand-level increment remains relatively constant across a broad range of densities after canopy closure (Mar:Möller, 1947; Allen and Duzan, 1981; Nebeker et al., 1985). While fitting a second-degree polynomial precludes detecting a plateau, analysis of the residuals indicate that a growth plateau with respect to SDI does not exist for these loblolly pine plantations between 17 and 22 years.

Long (1985) has argued against a decline in stand-level, gross-volume increment at high densities. He reasoned that if the gross-volume increment was predominantly a function of L and if L increases monotonically with SDI, stand-level growth should approach a maximum asymptotically with increasing density (Fig. 3(b)). Gross, periodic-annual increment between ages 22 and 27 in these loblolly pine plantations tend to support the growth-growing stock relationships described by Long (1985). Growth during this interval increases at a decelerating rate and appears to level off at some point after the self-thinning threshold (Fig. 1(a)). Again, a second degree polynomial will force the curve downwards at higher values of SDI, but within the range of data for this growth interval, $I_{\rm v}$ does appear to slowly reach a maximum.

Long (1985) also hypothesized that the volume growth of the mean tree should be independent of stand density prior to canopy closure and thereafter decrease at an accelerating rate (Fig. 3(b), bottom). Langsaeter (1941) illustrates this same hypothesis in terms of percent increase in stand increment (Fig. 3(a), bottom). Gross, periodic-annual increment of the mean-tree during the first two measurement intervals in these loblolly pine plantations decreases at an accelerating rate within the self-thinning stage. but between canopy closure and the self-thinning threshold, I_{mv} increases with SDI, in contrast to the hypothesized pattern. While increases in $I_{\rm nw}$ prior to the self-thinning threshold may be an artifact of fitting a second-degree polynomial to the data, residuals of the fitted equation indicate that the increase exists in the data.

4.2. Relationship to canopy properties

The 35% reduction in I_v between the first and last measurement intervals may be related to the systematic reduction of L associated with a given value of SDI as the plantations age. According to the stepwise regression results, the increase in stand productivity per unit L is approximately same during the first two measurement intervals. Consequently, for given values of F and C_r , the decrease in L with age would translate into lower values of I_v . During the last measurement interval, I_v per unit L is less than half the amount that occurs during the first two measurement intervals. Lower efficiencies combined with lower values of L during the last measurement interval reduce stand productivity even further.

The reduction in C_r with age does not appear to contribute much to the decrease in I_v with age. Although C_r decreases by 18% from the first to the second measurement periods, according to the stepwise regression, the effect on I_v of this reduction in C_r is negligible because the difference in coefficients for C_r between the first and second measurement intervals nearly offsets this change (Table 3). Foliage density does not appear to contribute to the reduction in I_v with age since no significant age differences were detected in the relationships between F and SDI.

The positive relationship between L and I_v found with the stepwise regression agrees with results from other studies (Oren et al., 1987; Smith and Long, 1989; Long and Smith, 1990a; Dalla-Tea and Jokela, 1991), and the negative relationship between C_r and $I_{\rm v}$ can be explained on the basis of increasing respiratory tissue relative to photosynthetic tissue (Kira and Shidei, 1967; Sprugel, 1990; Long and Smith, 1990b) (Table 3). The negative relationship between F and I_v , however, contradicts the results of Smith and Long (1989) who found a positive relationship between I_v and F. When I_v is related singularly to F, F appears to represent additional effects such as L. In fact, when I_{ν} in these loblolly pine plantations is plotted against F, the scattergram shows a positive relationship between the two variables. However, regression analysis indicates that when L and C_r are included in the equation, I_v decreases with F. Such multifactor analysis apparently separates the positive effect of L from F, allowing F to represent a negative effect of canopy structure on total stand productivity.

Linear regression shows that the covariance between I_{v} and SDI weakens with age. Stand density index accounts for 54% and 30% of the variation in I_{v} during the first two measurement intervals, respectively, and none of the variation in I_v during the last two measurement intervals. The deterioration in the relationship between I_v and SDI corresponds to deteriorating relationships between SDI and canopy structure as the plantations age. The strongest relation between I_{v} and SDI occurred between age 17 and 22 when both C_{d} and C_{r} were strongly correlated with SDI. However, after age 27, SDI accounted for none of the variance in C_d and less than 20% of the variation in C_r . These results support previous research showing the influence of canopy structure on stand growth (Ford, 1982; Dean et al., 1988; Smith and Long, 1989); however, they also suggest that as plantations age, canopy structure and thus, stand productivity, becomes more sensitive to factors other than stand density, e.g. weather.

As with stand-level productivity, I_{mv} is significantly related to SDI only for the first two measurement periods before age 27 (Table 2). However, in contrast to total stand productivity, I_{mv} is only related to variables describing canopy structure, C_d and C_r . L is not significant in any of the regression equations (Table 3). The regression coefficient for C_d is nearly constant for each measurement period. Since C_d adjusted for SDI significantly decreases with age, this would indicate that I_{mv} also decreases with age; however, there were no statistical difference in I_{mv} adjusted for SDI between measurement periods in these loblolly pine plantations. The effect of the systematic decrease in C_d is apparently offset by a complex relationship between I_{mv} and C_r that changes with age. Different combinations of linear and squared transformations of C_r are significant at each measurement period (Table 3). Mean-live-crown ratio embodies several effects, including competition for light and the average balance between carbon uptake and loss. As stand density changes and the plantations age, how C_r represents these effects apparently also changes, resulting in complex relationships between $I_{\rm mv}$ and $C_{\rm r}$.

5. Conclusions

These results show that for these loblolly pine plantations, I_v and I_{mv} are significantly related to stand density until the plantations are 27 years old; after this age, predictable changes in stand growth cannot be affected by manipulating stand density. The pattern of the statistically significantly relationships generally concurs with the accepted, conceptual relationships.

Various combinations of average L, F, C_r , and C_d are significantly related to I_v and I_{mv} for each growth period, with the exception of total-volume increment between ages 27 and 32. Although canopy properties are significantly related to growth, the reason that density management is not possible after age 27 in these loblolly pine plantations is that canopy structure loses its sensitivity to stand density as the plantations age. Eventually, canopy structure and consequently, growth, become independent of stand density.

For a large number of industrial plantations of loblolly pine, prudent density management is required for most of the rotation. However, density management is also necessary in production plantations managed on long rotations. A common strategy in managing the density of loblolly pine plantations is to maintain acceptable rates of average tree growth while sacrificing some total stand productivity. In order to maintain acceptable average growth rates, density must be maintained at levels that promote deep canopies and large, mean-live-crown ratios. According to these results, if the canopy possesses these properties at the stage when growth becomes independent of stand density, the high growth rates associated with these properties will be maintained. However, if stands are allowed to become too dense, canopies will have shallow depths and small livecrown ratios when growth becomes independent of density and will exhibit slow growth despite the crown being independent of density.

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References

- Allen, H.L. and Duzan, H.W., 1981. What measure of stand density is best for growth predictions in loblolly pine plantations. In: J.P. Barnett (Editor), Proc. of the 1st Biennial Southern Silvicultural Research Conf., 6 November 1980, Altanta, GA. Gen. Tech. Rep. SO-34, USDA Forest Service, New Orleans, LA, pp. 175-178.
- Baldwin, V.C., Jr., 1989. Is sapwood area a better predictor of loblolly pine crown biomass than bole diameter. Biomass, 20: 177-185.
- Baldwin, V.C., Jr. and Feduccia, D.P., 1991. Compatible treevolume and upper-stem diameter equations for plantations loblolly pine in the West Gulf Region. South. J. Appl. For., 15: 92-97.
- 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.
- Daniel, T.W. and Sterba, H., 1980. Zur Ansprache der Bestandesdechte. Allg. Forstztg., 91: 155–157.
- Daniel, T.W., Helms, J.A. and Baker, F.S., 1979. Principles of Silviculture. McGraw-Hill, New York, 500 pp.
- Dean, T.J. and Baldwin, V.C., Jr., 1993. Using a density-management diagram to develop thinning schedules for loblolly pine plantations. Res. Pap. SO-275, USDA Forest Service Southern Forest Experiment Station, 7 pp.

- Dean, T.J., Long, J.N. and Smith, F.W., 1988. Bias in leaf area—sapwood area ratios and its impact on growth analysis in *Pinus contorta*. Trees Struct. Funct., 2: 104-109.
- Ford, E.D., 1982. High productivity in a polestage sitka spruce stand and its relation to canopy structure. Forestry, 55: 1-17.
- Kira, T. and Shidei, T., 1967. Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. Jpn. J. Ecol., 17: 70–87.
- Langsaeter, A., 1941, Om tynning i enaldret gran-og furuskog (About thinning in even-aged stands of spruce, fir, and pine). Medd. Nor. Skogforsoksves., 8: 131-216.
- Long, J.N., 1985. A practical approach to density management. For. Chron., 61: 23-27.
- Long, J.N. and Smith, F.W., 1984 Relation between size and density in developing stands: a description and possible mechanism. For. Ecol. Manage., 7: 191-206.
- Long, J.N. and Smith, F.W., 1990a. Canopy development and leaf area efficiency: links between production ecology and density management. In: R.N. James and G.L. Tarlton (Editors), New Approaches to Spacing and Thinning in Plantation Forestry, Rotorua, New Zealand, 10 April 1989, International Union of Forestry Research Organizations and Forest Research Institute, Ministry of Forestry, New Zealand, pp. 260–266.
- Long, J.N. and Smith, F.W., 1990b. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. J. Appl. Ecol., 27: 847-856.
- Mar:Möller, C., 1947. The effects of thinning, age, and site on foliage, increment, and loss of dry matter. J. For., 45: 393–404.
- Nebeker, T.E., Hodges, J.D., Karr, B.K. and Moehring, D.M., 1985. Thinning practices in southern pines---with pest management recommendations. Tech. Bull. 1703, USDA Forest Service, 36 pp.
- Nelson, T.C. and Brender, E.V., 1963. Comparison of stand density measures for loblolly pine cubic-foot growth prediction. For. Sci., 9: 8-14.
- Oren, R., Waring, R.H., Stafford, S.G. and Barrett, J.W., 1987. Twenty-four years of ponderosa pine growth in relation to canopy leaf areas and understory competition. For. Sci., 33: 538-547.
- Smith, F.W. and Long, J.N., 1989. The influence of canopy architecture on stemwood production and growth efficiency in *Pinus contorta* var. *latifolia*. J. Appl. Ecol., 26: 681–692.
- Sprugel, D.G., 1990. Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. Trees Struct. Funct., 4: 88–98.
- Vose, J.M. and Allen, H.L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. For. Sci., 34: 547-563.
- Williams, R.A., 1994. Stand density management for loblolly pine plantations in north Louisiana. South. J. Appl. For., 18: 40–45.