

# Size–density metrics, leaf area, and productivity in eastern white pine

J.C. Innes, M.J. Ducey, J.H. Gove, W.B. Leak, and J.P. Barrett

**Abstract:** Size–density metrics are used extensively for silvicultural planning; however, they operate on biological assumptions that remain relatively untested. Using data from 12 even-aged stands of eastern white pine (*Pinus strobus* L.) growing in southern New Hampshire, we compared size–density metrics with stand productivity and its biological components, including leaf area index (LAI) and measures of crown morphology. Density indices included Reineke's stand density index (SDI), a  $-3/2$  relative density law, and trees per hectare. We examined models with and without site index and stand age as components, to predict total stand accretion (PAI), LAI, and growth efficiency (GE). LAI was a strong linear predictor of PAI ( $R^2 = 0.89$ ). However, of the indices tested only SDI was a significant predictor of accretion, and none were significantly related to LAI or GE. Site index was not a significant predictor of any variable when used alone, but in combination with SDI and stand age did lead to significant relationships with PAI ( $R^2 = 0.84$ ), LAI ( $R^2 = 0.67$ ), and GE ( $R^2 = 0.92$ ). Of the density indices tested only trees per hectare was strongly correlated with crown attributes. These results demonstrate that size–density metrics combined with other stand attributes are reasonably correlated with biological measures of stand growth.

**Résumé :** Les relations allométriques entre la taille des arbres et la densité des peuplements sont abondamment utilisées pour la planification sylvicole. Toutefois, ces relations sont basées sur des hypothèses biologiques qui demeurent relativement peu testées. Avec des données récoltées dans 12 peuplements équiennes de pin blanc (*Pinus strobus* L.) croissant dans le sud du New Hampshire, ces relations allométriques ont été reliées à la productivité du peuplement et à ses composantes biologiques, ce qui inclut l'indice de surface foliaire et des mesures de morphologie de la cime. Les indices de densité testés étaient l'indice de densité de Reineke, la densité relative basée sur la relation à la puissance  $-3/2$  et le nombre d'arbres à l'hectare. Les auteurs ont testé des modèles avec et sans indice de qualité de station et âge du peuplement comme variable explicative dans le but de prédire l'accroissement total des peuplements, l'indice de surface foliaire et l'efficacité de croissance. L'indice de surface foliaire était fortement et linéairement relié à l'accroissement total des peuplements ( $R^2 = 0,89$ ). Cependant, parmi les indices testés, seul l'indice de densité de Reineke était significatif pour prédire l'accroissement, et aucun n'était significativement relié à l'indice de surface foliaire ou à l'efficacité de croissance. Utilisé seul, l'indice de qualité de station n'était significativement relié à aucune variable, mais en combinaison avec l'indice de densité de Reineke et l'âge du peuplement, il a contribué à l'établissement de relations significatives avec l'accroissement total des peuplements ( $R^2 = 0,84$ ), l'indice de surface foliaire ( $R^2 = 0,67$ ) et l'efficacité de croissance ( $R^2 = 0,92$ ). Parmi les indices de densité testés, seul le nombre d'arbres à l'hectare était fortement corrélé aux caractéristiques de la cime. Ces résultats démontrent que les relations allométriques entre la taille des arbres et la densité du peuplement, combinées à d'autres caractéristiques du peuplement, sont raisonnablement corrélées aux mesures biologiques de la croissance du peuplement.

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## Introduction

Currently, the use of size–density metrics for silvicultural planning is extensive. Indices combining tree size and number provide silvicultural guidelines for manipulating stand productivity and predicting future tree size, stand yield, and mortality (Drew and Flewelling 1977, 1979; Long 1985; Jack and Long 1996; Newton 1997). Graphical forms, in-

cluding stocking guides and density management diagrams (e.g., Gingrich 1967, Drew and Flewelling 1979), are commonly employed by field foresters. Size–density metrics and relationships are also implicit in many models and decision tools (e.g., Simpson et al. 1995; Doruska and Nolan 1999; O'Hara and Valappil 1999).

Size–density metrics operate on a set of assumptions that remain relatively untested. Jack and Long (1996) recently re-

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viewed the existing literature and identified the following assumptions of density management models using size–density metrics:

- (1) Maximum size–density relationships and the onset of self-thinning are independent of site and age;
- (2) Allometric relationships are independent of site, age, and the effects of previous management;
- (3) Relative density effectively predicts size–density combinations at which self-thinning and maximum productivity occur.

Jack and Long (1996, p. 271) concluded that although there may be some weaknesses in the assumptions of density management models, overall they are useful reliable tools that "...integrate relationships between density, stand structure, canopy dynamics and production efficiency, and link quantitative silviculture to population ecology, production ecology and biometrics". In contrast, other studies have presented data that suggest the density management models are not calibrated for general applicability. For example, Leak (1981) found that recommended size–density combinations for peak growth were inaccurate when compared with long-term growth data for eastern white pine (*Pinus strobus* L.) and hardwoods in the northeastern United States. The recommended stocking guide thinning levels were below the empirical optimum for eastern white pine and above that for hardwoods. Cameron (1988) found that the density management diagram of Drew and Flewelling (1979), based on the  $-3/2$  law of plant self-thinning, can substantially overestimate volume and diameter predictions in coastal Douglas-fir. Experimentally, the manipulation of site quality has been shown to have a dramatic effect on productivity in plantation stands (Vose and Allen 1988; Colbert et al. 1990; Dalla-Tea and Jokela 1991; Jokela and Martin 2000). After manipulating site quality, Vose and Allen (1988) concluded that leaf area was a superior predictor of stand productivity and stocking relative to traditional size–density metrics.

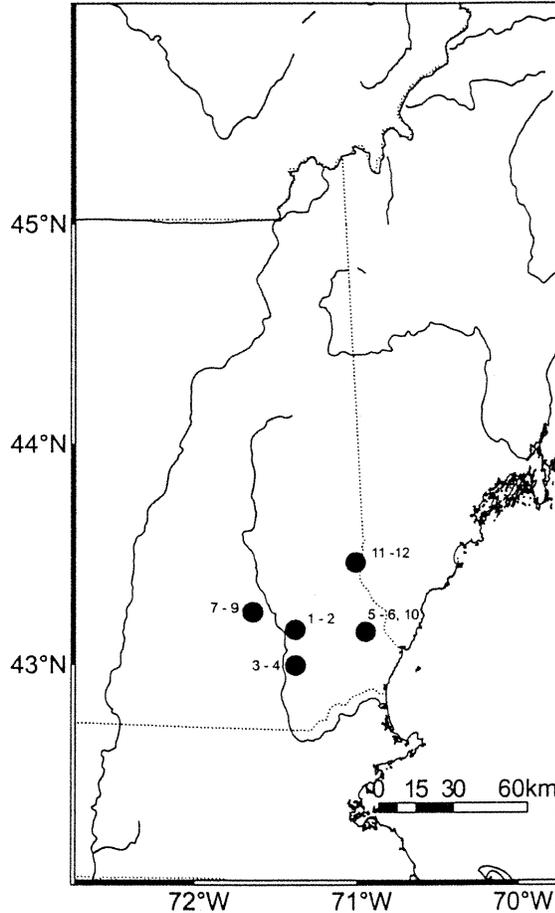
Despite the strong predictive power of leaf area it remains very difficult to measure, making size–density metrics appear relatively attractive for management purposes. However, the question of how well size–density metrics compare with biologically based components of stand growth still remains unclear. The objectives of this study were to test how well commonly used density management metrics predict total stand productivity and related biological variables in a chronosequence of eastern white pine stands varying in structure and site quality. We do not address relationships between stand density, self-thinning, and other sources of mortality in this study. We will address stand age as a predictor in the tests, but recognize the assumption that those allometrics relevant to stand production are assumed to be independent of site and age (Jack and Long 1996). To examine relationships between size–density metrics and gross production, we tested the following hypotheses:

- (1) Size–density metrics, site index (SI), and leaf area are correlated with gross stand-level periodic annual increment (PAI). Curtis (1970, p. 403) stated that if the measurable characteristics of a stand (e.g., size–density metrics) are to be used to reflect growth they should be independent of site quality, stand age, and "capable of visualization and interpretation in biologically meaningful terms". One interpretation is that a biologically meaningful density

index should provide a direct prediction of growth. Alternatively, one might suppose that the information provided by a density index is indirect and that prediction of growth is only relative; prediction of absolute growth rate is contingent on other factors such as age and site quality. The assertion that density management models reflect productivity and can index stand growth across a range of densities (see the Forest Production Theory of Langsaeter (1941) as outlined by Long (1985) and Newton (1997)) suggests that they reflect a primary component of productivity at the stand level and are biologically based (Long 1985). Reviews of stand density approaches do not always distinguish these two interpretations, and there have been relatively few direct tests of either interpretation. Under the indirect interpretation, one might view a size–density metric as indexing relative site occupation and therefore relative productivity of a stand, with absolute maximum or potential productivity strongly controlled by site factors that are independent of maximum density levels. In that case, a multiplicative model including both a size–density metric and a measure of site quality, such as SI, would be required to predict production.

- (2) Density indices and (or) SI are positively correlated with leaf area. We suggest, as have others (Seymour and Smith 1987; Dean and Baldwin 1996a), that if size–density metrics are biologically correlated with productivity then they should also be correlated with leaf area index (LAI). The interception of photons is largely controlled by leaf area and canopy architecture and is very closely correlated with the accumulation of biomass (Monteith 1972; Cannell 1989; Russell et al. 1989). The relationship between leaf area and productivity has been demonstrated for many species (Waring et al. 1981; Schroeder et al. 1982; Oren et al. 1987; Vose and Allen 1988; Colbert et al. 1990). Furthermore, a straightforward definition of site quality is that stands on good sites will be more productive than stands with the same structure on poor sites. In understanding whether density indices have a biological basis, it is important to understand how relationships with leaf area are partitioned between measures of density, stand age, and site quality.
- (3) Size–density metrics are correlated with foliar growth efficiency (GE), or volume growth per unit leaf area (Waring 1983). An alternative view of the biological basis of variability in production between stands states that the primary driver of differences in production is not differences in leaf area, but differences in the efficiency of foliage. Such differences may be correlated with either density or site quality. For example, Vose and Allen (1988) suggest SI may be correlated with GE, because relative allocation to fine roots may be less on high-quality sites, allowing greater allocation to stem growth. Since size–density relationships are used to target optimum densities where site resources are used effectively (Drew and Flewelling 1979), we should expect GE to relate to stand density measures (Burns and Irwin 1942; Waring et al. 1981; Smith and Long 1989).
- (4) Size–density metrics are correlated with stand canopy properties. Dean and Baldwin (1996a, 1996b) show relationships between size–density metrics and the dis-

**Fig. 1.** Locations of the sample stands in New Hampshire and their associated stand numbers (see Table 1 for stand number reference).



tribution of foliage within the tree crown. Many arguments in favor of density metric – GE relationships are based on relating crown size and foliar density to GE and (or) volume growth (Smith and Long 1989; Long and Smith 1990; Long and Smith 1992; Dean and Baldwin 1996a, 1996b; Burkes et al. 2003). Testing for the presence of these relationships will elucidate the biological basis for the relationships examined in hypothesis 3.

**Methods**

**Site description**

A total of 12 even-aged pure or nearly pure stands of eastern white pine were chosen for the study. The study sites are second-growth stands, both natural and planted in origin, chosen to represent a range of age, structure, management, and site quality (Fig. 1; Table 1). Land use in the previous rotation involved cultivation and (or) grazing. The most recent silvicultural treatments occurred in 1996 on plots 3 and 4, where whole-tree volume removals were estimated at 33 and 44 m<sup>3</sup>·ha<sup>-1</sup>, respectively. The other plots received no silvicultural treatments within the last 10 years. No fertilizer, herbicide, or pesticide use has been recorded on the study

**Table 1.** Characteristics of the 12 study stands.

Stand	Stand age (2000)	Avg. height (m)	SI (m)	BA (m <sup>2</sup> ·ha <sup>-1</sup> )	N (trees·ha <sup>-1</sup> )	QMD (cm)	% BA in white pine	LAI (m <sup>2</sup> ·m <sup>-2</sup> )	PAI (m <sup>3</sup> ·ha <sup>-1</sup> ·year <sup>-1</sup> )	Most recent silvicultural activity
1	94	24.99	15.9	31.53	469	29	88	1.0	4.8	TSI – light girdling, 1966
2	107	28.06	18.6	34.33	358	35	89	2.0	9.3	Moderate thinning, 1984
3	80	27.52	21.0	34.13	297	38	92	1.5	8.4	Moderate thinning, 1996
4	80	27.67	21.0	26.24	208	40	89	1.1	6.0	Moderate thinning, 1996
5	127	27.98	16.5	51.36	185	59	80	1.5	7.0	Unmanaged
6	121	29.87	20.7	82.08	445	48	82	2.4	16.6	Unmanaged
7	39	17.09	22.3	44.70	1124	22	94	2.4	18.1	Unthinned plantation
8	81	26.03	18.0	46.26	692	29	74	1.4	7.7	Light thinning, 1963
9	47	21.57	22.6	18.20	173	37	100	1.7	9.7	Heavy thinning, 1991
10	34	13.83	20.7	36.54	581	28	100	2.3	15.3	Unthinned plantation
11	54	16.28	15.2	45.22	1754	18	95	1.6	11.4	TSI – light girdling, 1985
12	54	15.44	15.2	39.77	1359	19	94	1.5	9.1	TSI – light girdling, 1986

**Note:** Site index (SI, m) is from Frothingham (1914). BA, basal area; QMD, quadratic mean diameter; LAI, leaf area index; PAI, periodic annual increment; TSI, timber stand improvement.

plots. The plots were located in New Hampshire in the towns of Hopkinton, Milton, Madbury, Auburn, and Durham. Nine of the plots represent a subset of a permanent plot growth and yield study initiated in 1957 (Leak et al. 1970; Barrett et al. 1976) with remeasurements. The remaining three plots came from two separate long-term thinning trials initiated by state and county foresters. The elevation of the plots ranged from 18 to 167 m a.s.l. Annual precipitation ranged from 95 to 129 cm, evenly distributed throughout the year (<http://cdo.ncdc.noaa.gov>). Minimum and maximum annual temperatures ranged from 14 to 20 °C and from 31 to 32 °C, respectively (<http://cdo.ncdc.noaa.gov>).

### Sampling and measurements

Each stand was measured using a single plot ranging in size from 0.04 to 0.10 ha, depending on density. In 2000, diameter measurements were taken on all live trees with DBH (at 1.37 m) greater than 5 cm on the tree bole. Seven to 10 trees per plot were randomly chosen, with the probability of selection proportional to individual tree basal area. On each of these trees total height and height to the base of the live crown were recorded.

In stands 1, 2, 5, 6, 8, and 9, tree diameters had been measured in a consistent fashion in 1993. For the remaining stands, diameter measurements from 1993 were not available. For these plots the 1993–2000 diameter increment was estimated using increment cores collected from each height-measurement tree. Within each plot, a linear regression was fit to predict the 1993 basal area from the 2000 basal area of each tree. On all plots, the 1993–2000 height increment was estimated by counting back the whorls from the leader to the 1993 measurement period and measuring height increment using a laser (Laser Tech Impulse 2000). For each plot and year, unmeasured tree heights were estimated using height-diameter regressions following the form

$$\ln H = \frac{b_0 + b_1 D}{D}$$

Diameters and heights for 1993 and 2000 were used to calculate total cubic volume using Honer's (1967) volume equation. PAI ( $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ ) was calculated over the 7-year period from 1993 to 2000, based on the volume growth of the trees still present in 2000. This total cubic growth rate served as the basis for the hypothesis tests in this study.

Since stands 3 and 4 were thinned early in the measurement period of the study, we examined the increment cores of these stands to check the growth response since the thinning. Core data indicated that the growth response to the thinning had occurred slowly on the survivor trees, increasing only within the last 2 years. Additionally, visual inspection of the canopy did not reveal substantial canopy response leading to crown closure. These observations suggest that the thinning of these stands has not substantially altered the growth trajectory and allometry of the survivor trees during the measurement period of this study.

### Leaf area

LAI was determined directly using litterfall traps (Sato 1982, Vose and Allen 1988). On 9 of the 12 plots, six 1 m<sup>2</sup> × 5 cm high litter traps were used; on the remaining three plots, six 0.5 m<sup>2</sup> × 5 cm high traps were used. Litter traps

were randomly placed within each plot in early April 2000 prior to spring needle drop, and collections made once every 2 months in the spring and summer and at least monthly during peak leaf fall until late December 2000. Litterfall from December 2000 through April 2001 was negligible on those plots where it could be collected; however, a severe snowstorm in early spring 2001 prevented litterfall collection on some plots. Consequently, litterfall between December 2000 and April 2001 has been omitted from this analysis. Collected foliage was dried at 65 °C for 72 h, sorted by species, and weighed to the nearest 0.1 g.

Conversion of litterfall to projected leaf area requires knowledge of specific leaf area and foliar longevity. These attributes were estimated from branch samples taken on eight of the plots using a shotgun or pole pruners. Three sample trees were located adjacent to the plot approximately 120° apart relative to the plot center. For most trees, foliage samples were extracted from upper and lower canopy positions. In sample trees with short crown lengths only one sample was taken. All foliage samples were taken from the side of the tree facing the plot center to avoid a directional bias. On four plots, canopies were too high to permit sampling with a pole pruner, and safety considerations or landowner restrictions prevented sampling with a shotgun.

Specific leaf area was estimated for litter using needles subsampled from the litter basket collections. A composite sample of 40 needles was collected from each plot, weighed to the nearest 0.01 g, and the projected area estimated using a LI-COR area meter (LI-COR, Lincoln, Nebraska). The estimates of projected area were divided by their dry mass to estimate a specific leaf area of 48.32 cm<sup>2</sup>·g<sup>-1</sup> (SD = 4.4 cm<sup>2</sup>·g<sup>-1</sup>,  $n = 12$ ).

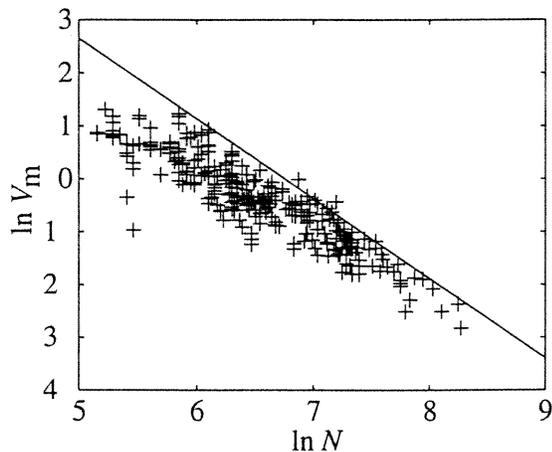
To estimate foliar retention, one upper-canopy and one lower-canopy sample were randomly selected from each plot. Foliar retention was calculated for each foliage cohort as the ratio of the number of fascicles retained over the number of potential fascicles for that year identified as leaf scars. The ratio of actual fascicles / potential fascicles retained was then summed across the sample shoot and the retention time obtained. Estimates of foliar retention ranged from 2.0 to 2.8 years; plot-specific values were used where possible in estimates of foliar biomass. On those plots where branch samples could not be obtained, the average foliar retention time of 2.32 years was used. Other reported values of foliar retention for eastern white pine have been 3 years for a plantation in Wisconsin (Gower et al. 1993), 2.2 years for the Harvard Forest in Petersham, Massachusetts, and 2.0 in the White Mountain National Forest, New Hampshire (Mary Martin, personal communication, 2001).

The product of foliar retention and annual needle fall provides an estimate of the total peak foliar biomass of each stand. LAI (m<sup>2</sup>·m<sup>-2</sup>) was calculated as foliar biomass multiplied by specific leaf area. GE (m<sup>3</sup>·m<sup>-2</sup>) was calculated as stemwood accretion per unit leaf area (Waring 1983).

### Density indices and canopy properties

We examined two density management models: (1) Reineke's (1933) stand density index (SDI), which models density as a function of trees per hectare and quadratic mean diameter, and (2) a  $-3/2$  law relative density index (RD) modeled after

**Fig. 2.** Derivation of the  $-3/2$  maximum density relationship for eastern white pine.



Drew and Flewelling (1979), which models density as a function of trees per hectare and mean tree volume.

Despite slight differences in construction, both density management approaches share similarities in their stated purpose, implementation, and assumptions. We also examined trees per hectare ( $N$ ) directly, as it represents a simple alternative to more complex density measures (Spurr 1952).

To calculate the relative density of each stand we first had to construct a maximum size–density relationship following the  $-3/2$  law of plant self-thinning (Drew and Flewelling 1977; Westoby 1984). We used data from 62 plots from a long-term eastern white pine growth and yield study (Leak et al. 1970), including remeasurements and additional plots established through 2000. The plots in the data set have been remeasured 1–12 times from 1957 to 2000, yielding 282 pairs of mean tree volume ( $V_m$ ) and density ( $N$ ) values. The variables were log-transformed, and the plots that defined the upper bound of the maximum size–density relationship were identified. Using simple linear regression, the slope and intercept of the maximum stocking line were determined (Fig. 2), resulting in the following equation:

$$\ln V_m = 10.2 - 1.51 \ln N$$

The slope of the regression line is very close to  $-3/2$ , consistent with expectations (Drew and Flewelling 1977; Westoby 1984). We note that other methods have been suggested to fit the line, including reduced major axis regression (Solomon and Zhang 1998) and principal components analysis (Bi and Turvey 1997). For the purposes of this investigation, the slope is the most important parameter, since changing the intercept of the maximum density line changes the relative density of individual stands by an equal multiplier. The relative density of a stand can be calculated as the ratio of actual  $N$  over the predicted maximum  $N$  in a stand of the same  $V_m$  (Drew and Flewelling 1979).

Canopy variables were calculated from measurements made on the height-measurement trees within each stand of the 12 study plots. Canopy depth (CD) is defined as the average length of the live crown. Percent live crown is the average ratio of the live crown to total tree length. Foliar density (FD) ( $\text{m}^2 \cdot \text{m}^{-3}$ ) is calculated as LAI per unit crown length

and is an indicator of the distribution of the foliage (Smith and Long 1989; Dean and Baldwin 1996a).

SI was calculated from average stand height and average tree age taken at the root collar. However, the plots used from the long-term growth and yield study (Leak et al. 1970) were aged from cores taken at breast height (1.37 m) and adjusted using the age corrections of Marty (1965). To test the effect of differences in site, Frothingham's (1914) SI curve for New Hampshire was used.

The effect of stand age was also considered in analysis. Although the size–density metrics used are sometimes assumed to be free of the effects of site and age, the effect is an important variable to be considered. However, our small sample size and unbalanced distribution of age does not allow the proper nonlinear fit and therefore only linear fits were considered; we focused on testing for relationships, rather than estimating a robust predictor based on those relationships.

### Statistical analysis

Both simple linear regression (to test for linear trends) and Spearman's rank correlation test (to identify possible nonlinear but monotonic trends) were used to test for relationships between density indices and volume accretion, LAI, GE, and canopy properties. Multiple linear regression was used to test for combinations and interactions of SI, age, and size–density metrics that gave improved predictions of PAI, LAI, and GE. All statistical relationships were considered significant at  $\alpha = 0.05$ .

## Results

### Predicting volume growth

The first hypothesis tests the assumption that size–density metrics, SI and leaf area are correlated with periodic volume accretion (PAI) and that the residual variation in PAI not explained by the density management model would be accounted for by SI.

The only density measure significantly related to PAI was Reineke's SDI (Spearman rank correlation  $r = 0.53$ ,  $P = 0.073$ ), but the relationship was fairly weak. Neither the  $-3/2$  law for relative density nor SI were significant predictors of PAI (Table 2). We did find LAI to be a strong, significant linear predictor of PAI, confirming that there is a biological connection between growth and leaf area in the 12 stands of eastern white pine studied (Fig. 3).

The incorporation of SI and age with SDI and RD improved estimates of PAI produced by these two variables considerably (Table 3). The best estimates of PAI were produced by incorporating SDI with SI and stand age. This result correlates with our alternative version of the first hypothesis, suggesting that size–density metrics represent an indirect measure of stand productivity.

### Predicting leaf area

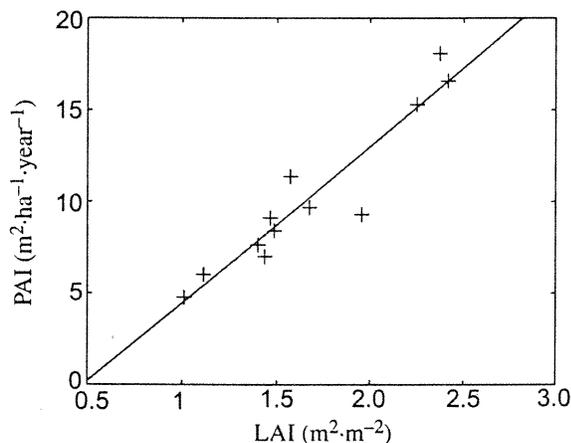
Our second hypothesis states that density management models and SI should be linearly correlated with LAI and that SI should account for any residual variation not explained by the size–density metric. The importance of this hypothesis is reinforced by the strong linear relationship between LAI and

**Table 2.** Predicting periodic annual increment (PAI), leaf area index (LAI), and GE (growth efficiency) using density indices and site index in a linear regression model.

Predicted variable	Predictor variable	Slope	Intercept	R <sup>2</sup>	P
PAI (m <sup>3</sup> ·ha <sup>-1</sup> ·year <sup>-1</sup> )	SI (m)	0.707	-3.147	0.21	0.134
	SDI	0.0093	3.359	0.34	0.048
	RD	9.905	5.079	0.22	0.123
LAI (m <sup>2</sup> ·m <sup>-2</sup> )	SI (m)	0.084	0.077	0.24	0.102
	SDI	0.0008	1.039	0.24	0.109
	RD	0.9448	1.184	0.16	0.190
GE (m <sup>3</sup> ·m <sup>-2</sup> )	SI (m)	0.093	4.185	0.07	0.414
	SDI	0.002	4.289	0.36	0.039
	RD	2.255	4.768	0.21	0.131
	N (trees·ha <sup>-1</sup> )	0.00125	5.149	0.42	0.022

Note: Site index (SI) is from Frothingham (1914), stand density index (SDI) is Reineke's (1933), and RD is relative density. P, probability; significance cutoff at  $\alpha = 0.05$ .

**Fig. 3.** Relationships between gross periodic volume increment (PAI) and leaf area index (LAI) ( $R^2 = 0.89$ ,  $p < 0.0001$ ).



growth in Fig. 3. However, none of the density indices tested were significantly correlated with LAI, nor was SI (Table 2).

The multiple regression model using SDI and SI was the best linear predictor of LAI (Table 3). In both of the multiple regression models, SI explained slightly more of the model sum of squares than did the density indices. These results suggest that a model employing both size–density measures and site quality measures may be a better predictor of LAI than size–density metrics alone.

#### Predicting GE

Our third hypothesis states that the density indices and SI should be correlated with GE (Table 2). Of the size–density metrics, SDI was once again the only significant predictor. Interestingly, number of trees per hectare ( $N$ ) was a positive linear predictor of GE and a better predictor of GE than SDI.

SI was not significantly related to GE, but multiple regression models incorporating SDI or RD with SI and age did lead to significant regressions (Table 3). When predicting GE the density indices and age tended to explain a larger amount of the model sum of squares than did the SI curves.

#### Predicting canopy properties

Our fourth hypothesis states there should be a relationship

between size–density metrics and stand canopy properties (Table 4). The only significant predictor of any canopy properties was trees per hectare ( $N$ ). Foliar density, canopy depth, and percent live crown were all influenced by  $N$ , although the relationship between  $N$  and percent live crown is somewhat weaker.

#### Discussion

The strong, positive linear relationship between LAI and PAI in eastern white pine is similar to that found in other conifer species, including loblolly pine (Vose and Allen 1988; Jokela and Martin 2000), slash pine (Jokela and Martin 2000), Douglas-fir (Waring et al. 1981), ponderosa pine (Oren et al. 1987), and lodgepole pine (Long and Smith 1992). The biological relationship between LAI and PAI supports the use of leaf area as a metric of stand-level productivity for management (Vose and Allen 1988). Additionally, the relationship between LAI and PAI appears to be consistent across the range of site types, ages, and management histories of our study stands. For example, stands 3 and 4, which had been thinned early in the 7-year measurement period, nonetheless showed an LAI to PAI relationship consistent with that of the other stands. The proportion of variance in PAI explained by LAI is much higher than that reported by Dean (2004), despite the range of age and past management history in the study stands. Size–density relationships, however, can suffer after thinnings from what is referred to as the “memory problem” (Drew and Flewelling 1979; Cameron 1988; Jack and Long 1996). Following thinning, the growth of the stand temporarily falls below the potential productivity indicated by its size–density combination, but this “memory problem” is expected to be short-lived (Drew and Flewelling 1979).

The roughly linear relationship between density and PAI observed in our study is unusual, since theory and experimental evidence support a nonlinear form. The positive relationship between Reineke's (1933) SDI and PAI is consistent with the theory of Langsaeter (as outlined by Long 1985 and Newton 1997). However, Langsaeter theorized a nonlinear relationship and limited the applicability of his theory to even-aged stands of the same age growing on the same site. The linear relationship we observed may be a characteristic

**Table 3.** Predicting periodic annual increment (PAI), leaf area index (LAI), and GE (growth efficiency, wood production per unit LAI) using density indices, stand age, and site index in a multiple regression model.

Predictor variables			PAI (m <sup>3</sup> ·ha <sup>-1</sup> ·year <sup>-1</sup> )				LAI (m <sup>2</sup> ·m <sup>-2</sup> )				GE (m <sup>3</sup> ·m <sup>-2</sup> )			
Density index	Stand age	Site index (m)	R <sup>2</sup>	R <sup>2</sup> <sub>adj</sub>	RMSE	P	R <sup>2</sup>	R <sup>2</sup> <sub>adj</sub>	RMSE	P	R <sup>2</sup>	R <sup>2</sup> <sub>adj</sub>	RMSE	P
SDI	Yes	No	0.53	0.43	3.20	0.0025	0.29	0.14	0.43	0.200	0.83	0.79	0.44	0.0003
SDI	No	Yes	0.75	0.70	2.32	0.0018	0.66	0.59	0.30	0.007	0.56	0.46	0.72	0.0240
SDI	Yes	Yes	0.84	0.79	1.93	0.0051	0.67	0.55	0.31	0.022	0.92	0.89	0.31	0.0001
RD	Yes	No	0.49	0.37	3.35	0.0164	0.26	0.09	0.44	0.254	0.80	0.75	0.48	0.0007
RD	No	Yes	0.58	0.49	3.03	0.0194	0.55	0.45	0.34	0.027	0.36	0.80	0.86	0.1200
RD	Yes	Yes	0.75	0.66	2.47	0.0081	0.59	0.43	0.35	0.056	0.86	0.81	0.42	0.0008

Note: Site index is from Frothingham (1914), stand density index (SDI) is Rienekes's (1933), RD is relative density. "Yes" or "no" indicates whether stand age or site index was included in the model. The statistics presented here are for linear models employing main effects only. *P*, probability; significance cutoff at  $\alpha = 0.05$ .

**Table 4.** Linear regressions for predicting crown attributes from site quality and density measures.

Predicted variable	Predictor variable	Slope	Intercept	R <sup>2</sup>	P
Foliar density (m <sup>2</sup> ·m <sup>-3</sup> )	Site index (m)	-0.0089	0.3761	0.03	0.5641
	Reineke's SDI	0.0002	0.0504	0.25	0.0971
	-3/2 relative density	0.1708	0.1015	0.12	0.2736
	Stand density (trees·ha <sup>-1</sup> )	0.0002	0.0759	0.85	<0.0001
Canopy depth (m)	Site index (m)	0.2454	5.9052	0.02	0.6450
	Reineke's SDI	-0.0025	12.4356	0.02	0.6485
	-3/2 relative density	-1.2402	11.2118	0.00	0.8652
	Stand density (trees·ha <sup>-1</sup> )	-0.0067	14.8509	0.57	0.0044
Percent live crown	Site index (m)	1.6806	15.5568	0.13	0.2542
	Reineke's SDI	-0.0101	52.6649	0.04	0.5463
	-3/2 relative density	-16.3679	53.7712	0.06	0.4526
	Stand density (trees·ha <sup>-1</sup> )	-0.0162	55.5021	0.36	0.0388

Note: Site index (m) is Frothingham (1914). Foliar density is leaf area (m<sup>2</sup>) per unit crown volume (m<sup>3</sup>). Canopy depth is the length of the live crown. Percent live crown is the percentage of the total tree length that is live crown. SDI, stand density index. *P*, probability; significance cutoff at  $\alpha = 0.05$ .

specific to eastern white pine or a result of the variation in age and site quality of our study stands or our small sample size. In contrast, Dean and Baldwin (1996b) used a loblolly pine stand that strictly satisfied the assumptions of Langsaeter's theory. They found that SDI had a nonlinear relationship with PAI, but the fits were weak when examined across all age-classes and weak or even nonexistent within age-classes. Despite the sample-size differences between our small study and the study by Dean and Baldwin (1996b), neither supports SDI alone as a useful variable for predicting PAI, particularly when it is compared with a predictor as strong as LAI, even though LAI is difficult to measure.

The lack of a significant relationship between RD and any of the variables tested was surprising, since the -3/2 law is often viewed as a fundamental biological relationship underlying the success of measures such as SDI (Long 1985). This occurs despite the apparent agreement of our data with a maximum size-density line having a slope very close to -3/2 and a correlation between stand values of SDI and RD. However, Larson and Cameron (1986) emphasized that similar density measures may not show similar performance in the field. The poor performance of RD could be due to inadequacies of the -3/2 law of self-thinning, which is controversial (Westoby 1984; Smith 1986; Weller 1987, 1990; Osawa and Sugita 1989). However, White (1981), Smith and Hann (1984), and Smith (1986) suggest that the -3/2 maximum

density line is primarily concerned with final stand conditions and not the trajectories or rates of development of stands leading up to that line.

SI performed poorly in this study as a predictor of PAI and other attributes whenever it was used alone, even though the stands in this study were mostly closed-canopy stands. In contrast, Schroeder et al. (1982) found SI to be a reasonably good predictor of PAI in Douglas-fir ( $R^2 = 0.73$ ); however, they ultimately concluded that LAI was a superior predictor ( $R^2 = 0.97$ ). We might expect PAI and SI to be strongly correlated on the premise that height growth reflects the carbon metabolism of a tree (Valentine 1997) and SI is based on height growth. At the same time, it is recognized that leaf biomass is positively correlated with increasing site quality (Satoo 1982). Leaf area has been found to vary across gradients of site including water balance (Grier and Running 1977; Jose and Gillespie 1997) and induced fertility gradients (Vose and Allen 1988). Our results are similar to those of other studies, where SI and LAI were unrelated (Satoo 1982) or weakly related (Long and Smith 1990).

The improved predictive power of SDI and RD with the addition of SI and age supports the approach to density management incorporated in many density management diagrams (Jack and Long 1996). Incorporating site quality and stand age into density assessment appears to be important in achieving meaningful predictions, particularly for SDI. RD did not

benefit from the addition of age as much, but this may be due to fitting it to a linear model. These results are encouraging, and as outlined as the alternate version of the first hypothesis, suggest that density management models may predict PAI as long as the proper SI curves are used and stand age is known. The increased predictive power with the addition of site quality suggests that the position of the maximum line shifts with site quality and age and predictions made with a size–density metric alone are not accurate. Research by Jokela and Martin (2000) illustrates the effect of site quality and age on growth allocation patterns, supporting the use of these additional stand attributes in estimating growth.

Given the relatively weak relationship between density measures and LAI, and between SI and LAI, the relationship between density and GE becomes important for understanding how growth might respond to stand density. GE has been suggested to be both a site property and a transient property of current stand conditions. GE has been suggested to be analogous to SI (Vose and Allen 1988), based on the premise that as site quality increases carbon allocation shifts from root to stem-wood production (Keyes and Grier 1981; Albaugh et al. 1998; King et al. 1999). However, stand density and canopy properties may also influence GE (Smith and Long 1989), as may age (Jokela and Martin 2000). Experimental site quality manipulation has produced variable results in conifers (Albaugh et al. 1998; Vose and Allen 1988; Dalla-Tea and Jokela 1991; Valinger 1993; Jokela and Martin 2000), and correlations between LAI and GE have also been variable (Waring 1983; Axelsson and Axelsson 1986; Smith and Long 1989; Jose and Gillespie 1997). In our multiple-regression models, density was a more important determinant of GE than was SI or age.

A principal effect of density on GE is believed to arise from its influence on crown size. While larger crowns may carry more leaf area per tree, they are not necessarily more efficient (Waring 1983). We found that the GE of white pine stands increased with density ( $N$ ), suggesting that smaller crowns are in fact more efficient. This relationship is consistent with those of previous studies (Burns and Irwin 1942; Schroeder et al. 1982; Makela 1986; Smith and Long 1989; Long and Smith 1990; Jack and Long 1992). However, the problem remains of how best to predict GE and how best to analyze the density effect. In this study, surprisingly neither of the size–density metrics (SDI or RD) effectively predicted foliar density, crown depth, or percent live crown. In contrast, Dean and Baldwin (1996a) found that SDI was a significant predictor of foliar density in loblolly pine, and Curtis and Marshall (2002) found that crown depth had a negative linear relationship with RD in Douglas-fir stands. Our results suggest that, for eastern white pine, simpler models based directly on number of trees per hectare may be more effective at predicting crown attributes related to GE.

## Summary and conclusions

The purpose of this study was to examine a series of hypotheses that test underlying biological relationships between size–density metrics and stand growth. We found the most striking result to be the relationship between LAI and volume growth. Surprisingly, this relationship is very clear and strong despite the small sample size and mixed attributes of

the study stands. Therefore, across the same stands we would expect size–density metrics and their components to have a similar relationship with gross PAI, leaf area, and GE, but individually these metrics were not direct predictors. When the size–density metrics were combined with SI and stand age in the predictive model, estimates of production, leaf area, and GE were improved significantly. While these results raise questions about the broad applicability of some assumptions underlying size–density metrics, they also demonstrate their predictive ability when used with additional stand attributes, such as site quality.

The purpose of density management is to find the optimal combination of tree size and density that maximizes the site without wasting growing space. However, thinning decisions are ultimately influenced by final product and desired species from a given stand, particularly in natural stands. All these factors play into the practice of density management and the final outcome of any thinning. The ease of calculating stand attributes for estimating growth using size–density metrics is simple when compared with estimating leaf area. While it may not be cost effective to accurately measure LAI, the use of LAI, or a surrogate measure of LAI, as a tool for better understanding growth and stocking relationships is an important area of research.

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