Influence of age on growth efficiency of *Tsuga canadensis* and *Picea rubens* trees in mixed-species, multiaged northern conifer stands[1]

Robert S. Seymour and Laura S. Kenefic

Abstract: Well-known patterns in the fundamental relationship between tree-level stemwood volume increment (VINC) and projected leaf area (PLA) are examined and quantified for *Tsuga canadensis* (L.) Carrière (eastern hemlock) and *Picea rubens* Sarg. (red spruce) growing in managed, mixed-species, multiaged stands in east-central Maine, U.S.A. Both species follow a sigmoid pattern, suggesting a peak growth efficiency (GE, stemwood volume growth per unit of PLA) in mid- to upper-canopy trees with PLAs of less than half that of the largest trees sampled. Tree age negatively influenced the VINC–PLA relationship in the expected manner: at a given PLA, older trees produce less stemwood than younger ones. The combined effect of leaf area and age is accurately modeled with a Weibull-like function in which the asymptote is an index of tree maturity defined as tree age relative to an estimated maximum for the species. Although previous studies have independently documented both the sigmoid relationship between VINC and PLA and the negative effect of age, their conclusions have been confounded by the strong correlation between age and mean tree PLA. This study addresses both issues simultaneously, and is the first to demonstrate a decline in GE with age independent from the effect of increasing PLA.

Résumé : Les formes bien connues de la relation de base qui existe entre l'accroissement en volume ligneux de la tige d'un arbre (AV) et la projection de la surface foliaire (PSF) ont été étudiées et quantifiées chez *Tsuga canadensis* (L.) Carrière (pruche du Canada) et *Picea rubens* Sarg. (épinette rouge) croissant dans des peuplements inéquiennes mélangés sous aménagement dans le Centre-Est de l'État du Maine, aux États-Unis. Les deux espèces suivent une courbe sigmoïde; ce qui suggère que l'efficacité de croissance (EC : accroissement en volume ligneux de la tige par unité de PSF) est optimale chez les arbres dominants et codominants dont la valeur de PSF est inférieure à la moitié de celle des plus gros arbres échantillonnés. Tel que prévu l'âge des arbres influence négativement la relation entre AV et PSF : pour une valeur donnée de PSF, les plus vieux arbres produisent moins de bois que les plus jeunes. L'effet combiné de la surface foliaire et de l'âge peut être modélisé adéquatement avec une fonction de type Weibull dans laquelle l'asymptote est un indice de la maturité de l'arbre défini comme étant l'âge de l'arbre relativement à un maximum estimé pour l'espèce. Bien que des études antérieures aient documenté indépendamment la relation sigmoïde entre AC et PSF et l'effet négatif de l'âge, leurs conclusions étaient affaiblies par la forte corrélation entre l'âge et la valeur moyenne de PSF de l'arbre. Cette étude examine les deux éléments simultanément et est la première à démontrer une diminution de la valeur de EC avec l'âge indépendamment de l'effet dû à l'augmentation de la valeur de PSF.

[Traduit par la Rédaction]

Introduction

When silviculturists design stand structures to meet production objectives, it is not tree growth per se that matters but growth per unit of occupied growing space (O'Hara 1988, 1996). The concept of tree growth efficiency (GE), defined originally by Waring et al. (1980) as the volume (or biomass) of stemwood increment per unit of foliage, has seen increasing application in studies that attempt to understand and quantify the relationship between tree and stand growth, stand structure (e.g., Smith and Long 1989; Long and Smith 1990; Roberts and Long 1992; O'Hara 1996), and site resource availability (e.g., Binkley and Reid 1984; Kaufmann and Ryan 1986; Vose and Allen 1988; Velazquez-Martinez et al. 1992; McCrady and Jokela 1998). For conifers, the widespread development of allometric equations that predict tree leaf area (LA) from sapwood basal area (e.g., Long and Smith 1989; Gilmore et al. 1996; O'Hara and Valappil 1995) or a modified live crown ratio (Valentine et al. 1994) has facilitated the estimation of tree leaf areas, and thus GE, from simple non-destructive procedures.

A critical issue in the application of GE studies to stand density management is the fundamental relationship between tree growth and crown size. Obviously trees will produce more stemwood per tree if they develop large crowns for

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their height, but do they do so more or less efficiently than a higher density of smaller trees? Three distinct patterns relating volume increment (VINC) to LA can be postulated (Fig. 1). Much of the empirical evidence (Table 1) tends to support a monotonically decreasing pattern with increasing LA (Fig. 1*b*, pattern A), which corresponds to a continual, nonlinear declining GE as crown size increases (Fig. 1*a*). This pattern has a logical and well-established mechanistic explanation: as crowns increase in size, an increasingly higher proportion of their leaf area is displayed on relatively large, long, and old branches in the lower crown, which presumably are sustained physiologically at the expense of stemwood production (Assmann 1970; Long and Smith 1989; Jack and Long 1992). This pattern is most applicable to shade-intolerant trees in the upper strata of closed-canopied stands at the same age or height. Because crown size also increases with stand development (i.e., with height or age), such inferences about the GE–LA relationship do not necessarily apply to a chronosequence owing to the negative influences of aging or maturation on growth (Ryan et al. 1997; Day et al. 2001; Smith and Long 2001).

In single-age stands of shade-tolerant species, GE of the lower crown classes (intermediate and overtopped trees) is typically lower than that of trees in the main canopy. Presumably, this is because the negative effect of low light availability overrides the positive effect of having crowns that are smaller and architecturally more efficient in displaying LA than those of the larger codominants. Such lower GEs in both the largest and smallest crowned trees within the stand produces a peak in the GE–LA relationship; this corresponds to a sigmoid, rather than monotonically decreasing, pattern in the relationship between VINC and LA (Fig. 1, pattern B; Roberts and Long 1992). Indeed, pattern A may simply be a truncated pattern B, because intolerants do not survive long once they lapse into the lower crown classes (Roberts et al. 1993; Gilmore and Seymour 1996).

Multiaged stands with irregular canopies can also follow pattern B, but the underlying cause is different than in single-aged stands. In multiaged stands managed under single-tree selection with small canopy openings, trees with small LAs are, by silvicultural design, young and shaded; as they age and grow in height, their increasing LAs exist in more favorable light environments and, thus, exhibit higher GEs. If the study population is limited to the lower strata or young cohorts, then one may see only the lower end of pattern B (Fig. 1, pattern C). This corresponds to a monotonically increasing relationship between VINC and LA, as found by Kollenberg and O'Hara (1999) for three-cohort stands of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). Once trees reach the upper strata, the GE pattern changes to a declining one, as they become light saturated and the same architectural limitations causing pattern A assume more importance. Of course, trees in the upper strata of multiaged stands are normally older, so age-related phenomena can also come into play, likely in a negative sense. The fact that LA and age are inevitably confounded in multiaged stands thus produces a more dynamic and complex rationale for the sigmoid pattern B than the static relationship among crown classes in single-aged stands described by Roberts et al. (1993).

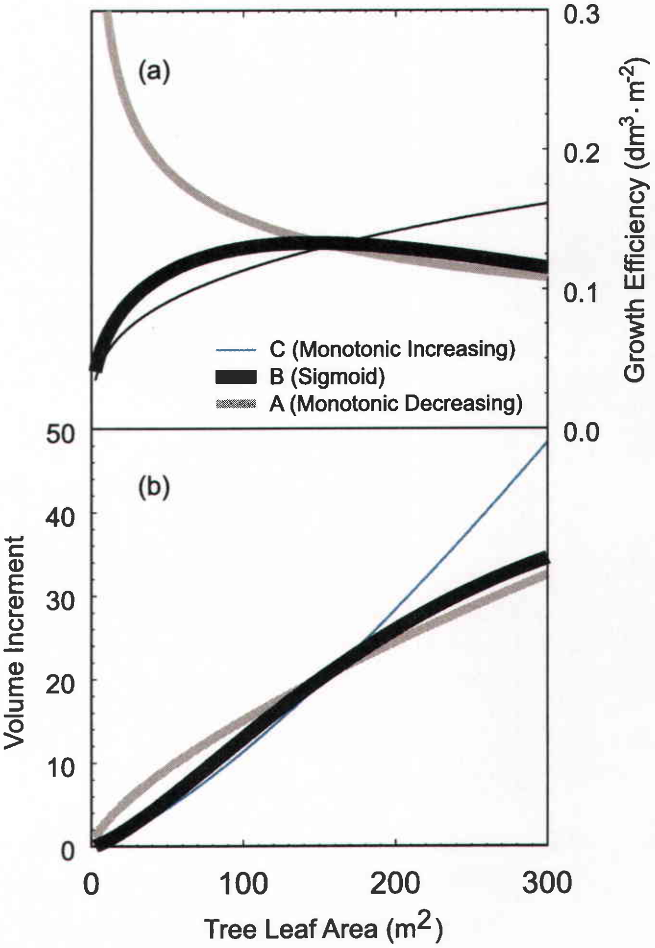


Fig. 1. Patterns of tree growth efficiency (*a*) and their corresponding pattern of stemwood volume increment (*b*) as influenced by tree leaf area, as documented in previous studies.

Few studies have explored the GE–LA relationship in multiaged stands. In a comprehensive study of multicohort ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands in the Intermountain West, O'Hara (1996) generally found no relationship between GE and LA (corresponding to a simple linear relationship between VINC and LA), although cohorts differed in their overall GEs. The oldest cohort in O'Hara's (1996) western Montana sites exhibited a continually increasing GE with LA (pattern C), an unexpected result that was not repeated in a subsequent study of *Pinus contorta* in which the oldest cohorts followed pattern A. The only study to examine explicitly the possibility of a sigmoid pattern in multiaged stands was conducted by Maguire et al. (1998), using 65 red spruce (*Picea rubens* Sarg.) trees from five multiaged stands in east-central Maine. They fit a sigmoid curve form to the VINC–LA relationship, divided the predicted VINCs by the LA, and examined the resulting GE patterns. Contrary to expectations, Maguire et al. found no inflection point within the data but the monotonically declining pattern A characteristic of single-aged stands. Indices of past suppression and relative canopy position were also significant predictors of VINC, but produced the seemingly illogical result that GE became negative (a declining VINC–LA curve) for the largest LA trees measured.

Table 1. Published growth efficiency (GE) patterns describing the relationship between projected leaf area (PLA) and stemwood volume increment (AVINC) of individual trees.

GE pattern, with possible algebraic formulation	Selected references with species	Stand age structure
Decreasing GE with increasing PLA	Assmann (1970, p. 121), *Quercus petraea*	Single-aged
[1] $\mathrm{VINC} = \beta_1 \mathrm{PLA}^{\beta_2}, \quad \beta_2 < 1$	Long and Smith (1990), *Pinus contorta*	Single-aged
	Roberts et al. (1993), *Pinus contorta*	Single-aged
	Velazquez-Martinez et al. (1992; implied by Fig. 3), *Pseudotsuga menziesii*	Single-aged
	Gilmore and Seymour (1996), *Abies balsamea*	Single-aged
	Maguire et al. (1998), *Picea rubens*	Multiaged
	Sterba and Amateis (1998), *Pinus taeda*	Single-aged
	Kollenberg and O'Hara (1999), *Pinus contorta*	Multiaged (cohort 1, overstory)
	Brunner and Nigh (2000), *Pseudotsuga menziesii*	Single-aged
Constant GE with increasing PLA	O'Hara (1996), *Pinus ponderosa*	Mutliaged (cohorts 2–4 in Montana, all cohorts in eastern Oregon)
[1] $\mathrm{VINC} = \beta_1 \mathrm{PLA}^{\beta_2}, \quad \beta_2 = 1$		
	Kollenberg and O'Hara (1999), *Pinus contorta*	Multiaged (cohort 2, understory)
Increasing GE with increasing PLA	O'Hara (1996), *Pinus ponderosa*	Multiaged (cohort 1, Montana)
[1] $\mathrm{VINC} = \beta_1 \mathrm{PLA}^{\beta_2}, \quad \beta_2 > 1$	Kollenberg and O'Hara (1999), *Pinus contorta*	Multiaged (cohort 3)
Increasing, then decreasing GE (sigmoid)	O'Hara (1988; implied by Fig. 3*b*), *Pseudotsuga mensiezii*	Single-aged
[2] $\mathrm{VINC} = \beta_1 \left(1 - \exp\left[-\left(\dfrac{\mathrm{PLA}}{\beta_2}\right)^{\beta_3}\right]\right),$	Roberts and Long (1992), *Abies lasiocarpa*	Single-aged
	Gilmore and Seymour (1996), *Abies balsamea*	Single-aged
(cumulative Weibull distribution; many other forms possible)		

Based on the studies reviewed above, we hypothesize that the GE–LA relationship in multiaged stands of tolerant conifers includes two potentially opposing patterns: increasing GE with LA as trees grow from lower to upper strata and experience more favorable illumination, and declining GE with advancing tree age. In this paper, we test this hypothesis for two shade-tolerant species, *P. rubens* and *Tsuga canadensis* (L.) Carrière (eastern hemlock) growing in diverse multiaged stands with a wider range of ages and more irregular structures than those studied by Maguire et al. (1998). First, within-stand differences in GE are established using ANOVA to compare crown strata. Using the postulated curve forms in Table 1, we then fit weighted nonlinear regression models to the VINC–LA relationship to quantify the basic GE–LA patterns, then tested whether tree age contributed significantly to these models. Finally, polynomial linear regressions were fit directly to the resulting GE–LA data to reinforce the peaking pattern and further support the effect of age on GE.

Methods

Study site

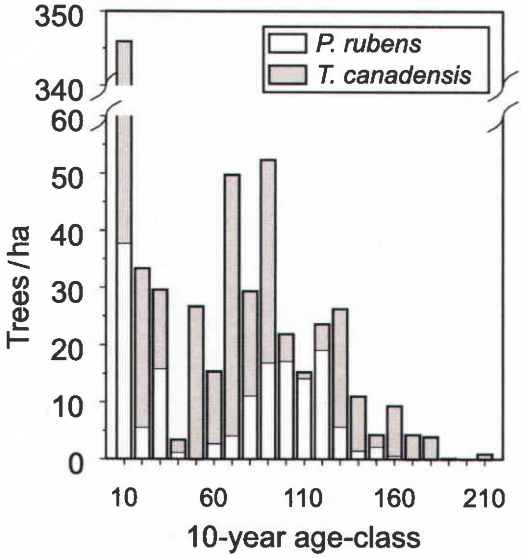
The two stands sampled in this study, C9 and C16, are part of a long-term silvicultural experiment on the 1540-ha Penobscot Experimental Forest (PEF) in east-central Maine, located at approximately 44°02′N, 68°38′W. Research began on the PEF in 1950 when the USDA Forest Service initiated an experiment to study even-aged and multiaged silvicultural systems. Treatments and remeasurements have continued to the present and follow a long-term study plan that ensures consistency in management over time. The two stands used for this research are replicates of selection cutting on a 5-year cycle, with nine (C9) and eight (C16) selection cuttings prior to our research. Stands C9 (11.0 ha) and C16 (6.6 ha) both have a structural goal defined using the BD*q* method (Guldin 1991), with a *q* factor of 1.96 on 5-cm classes, a residual maximum diameter goal of 48 cm, and a target residual BA of 26 $\mathrm{m}^2\cdot\mathrm{ha}^{-1}$. Both stands have irregular diameter and age distributions (Fig. 2; Kenefic and Seymour 1997, 2000; Seymour and Kenefic 1998). Relative density (Wilson et al. 1999) in the study stands is low (0.30 in C9, 0.31 in C16).

Within- and between-stand species compositions are highly variable because of small-scale differences in soil drainage and stand structural condition. The dominant species are *T. canadensis*, *P. rubens*, and *Abies balsamea* (L.) Mill (balsam fir). Other species include *Pinus strobus* L. (eastern white pine), *Thuja occidentalis* L. (northern white-cedar), *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), *Picea glauca* (Moench.) Voss (white spruce), and other hardwoods (Kenefic and Seymour 1997). Species composition goals based on their relative desirability are used to prioritize removals. Treatments to date have emphasized removal of *T. canadensis* and *A. balsamea* and retention and release of *P. rubens*.

Field and laboratory procedures

A 25-m systematic grid was established in the study stands in 1995. A random sample of 100 *T. canadensis* and 100 *P. rubens*, stratified by 5 cm diameter at breast height (DBH, 1.3 m) classes, was taken from 12.5 m radius plots centered on the grid points in July and August of 1995 (C16) and 1997 (C9). The sample included trees at least 1.3 m in

Fig. 2. Age structure of *P. rubens* and *T. canadensis* trees in the two study compartments combined.



height, up to a maximum of 50.0 cm DBH. Sampling was restricted to somewhat poorly, moderately well, and well drained soils. Diameter at breast height, bark thickness, total height, height to live crown, crown radii in four cardinal directions, and canopy stratum (Table 2; Oliver and Larson 1996, p. 154; Smith et al. 1997, p. 33) were recorded for each sample tree. To be consistent with measurements taken for development of published non-sapwood-based PLA prediction equations, height to live crown was defined as height to lowest living branch for *T. canadensis* (Kenefic and Seymour 1999) and *P. rubens* (Maguire et al. 1998). Two increment cores were removed at breast height for determination of tree age, annual radial increment, and sapwood radius. Ages at breast height of trees smaller than 5.0 cm were determined by counting internodes on the main stem. Height and DBH were remeasured in July 2000.

Sapwood–heartwood boundaries were identified on each increment core in the field and verified for *T. canadensis* by application of a 0.1 M solution of ferrous ammonium sulfate ($(Fe(NH_4)_2(SO_4)_2.6H_2O)$) (Kenefic and Seymour 1999). Increment cores were hand polished with fine grit sandpaper, and radial increments and width of the sapwood were measured to 0.01 mm with a Velmex measuring system (Velmex, Inc.). Sapwood area at breast height (SA_{bh}) was determined for each tree as a function of diameter, mean sapwood radius, and mean bark thickness at breast height. Ring-width series were cross-dated using COFECHA (Holmes 1983), and missing rings accounted for when possible. Ages at breast height of trees with incomplete cores (28 trees (25%) in C9, 42 trees (38%) in C16) were estimated using pith locators, i.e., transparencies with concentric circles equal in width and curvature to the last measured increment (Applequist 1958).

Projected leaf area

PLA, defined in the usual way as the one-sided shadow pattern of individual needles, was determined for each sample tree using published equations (Maguire et al. 1998; Kenefic and Seymour 1999) or leaf biomass (Young et al. 1980) multiplied by locally derived specific leaf areas (SLAs). Saplings <2.5 cm DBH were excluded from analysis, because there are no published PLA or biomass equations for trees of this size; thus, sample sizes of *T. canadensis* and *P. rubens* were reduced by 8 and 6, respectively.

In general, PLA was predicted for *T. canadensis* with DBH >6.8 cm (the smallest DBH used for PLA model development) using the equation $\mathrm{PLA} = \beta_0 + \beta_1(\mathrm{BA}_{\mathrm{bh}} \times \mathrm{mLCR})$ (Valentine et al. 1994), where $\beta_0 = 8.9221$, $\beta_1 = 0.1789$, and $r^2 = 0.95$ (Kenefic and Seymour 1999). $\mathrm{BA}_{\mathrm{bh}}$ is stem cross-sectional area at breast height (cm^2) outside bark and mLCR (modified live crown ratio) = CL/(HT – 1.3), where CL is crown length (m) and HT is height (m). Four trees had stem and (or) crown parameters slightly exceeding those used for PLA non-sapwood-based model development, but sapwood areas fell within the range used for development of the sapwood-based model (Kenefic and Seymour 1999). PLAs of these four trees were predicted with the equation $\mathrm{PLA} = \beta_0 + \beta_1(\mathrm{SA}_{\mathrm{bh}})$, where $\beta_0 = 7.5432$ and $\beta_1 = 0.3659$. Leaf biomass equations ($r^2 = 0.88$; Young et al. 1980) were used to predict dry leaf mass of trees 2.5–6.8 cm DBH, which was then multiplied by mean SLA ($58.43\ \mathrm{cm}^2\cdot\mathrm{g}^{-1}$; Kenefic and Seymour 1999) to determine PLA.

The equation $\mathrm{PLA} = \beta_1 \mathrm{SA}_{\mathrm{bh}}^{\beta_2}$, where $\beta_1 = 0.595\,009$, $\beta_2 = 0.987\,084$, and $r^2 = 0.89$ (Maguire et al. 1998) was applied to *P. rubens* with DBH >11.0 cm (the smallest tree used for model development in that study). The data used by Maguire et al. (1998) were also collected on the PEF, allowing PLA estimation without concern for regional variation in model form and parameter estimates (O'Hara and Valappil 1995). The PLA values of trees 2.5–11.0 cm DBH were determined using a *P. rubens* leaf biomass equation ($r^2 = 0.86$; Young et al. 1980) and mean SLA for this species ($43.51\ \mathrm{cm}^2\cdot\mathrm{g}^{-1}$; Maguire et al. 1998).

Volume increment

Total stemwood volume (*V*) inside bark was determined in cubic feet ($1\ \mathrm{ft}^3 = 0.02832\ \mathrm{m}^3$) for each sample tree at the initial sampling date *t* (1995 in C16 and 1997 in C9) using Honer's (1967) volume equations and converted to cubic metres. Mean annual radial increment (ARINC) for the 5-year period prior to sampling was determined for each tree using the mean of radial increments from the two breast height cores. Radial increments from the two cores were first averaged to determine a mean value for each year, then ARINC was calculated by averaging the mean annual values across a 5-year period. Radial increments of trees too small to core, and annual height increments (AHINC, m) of all trees, were determined by remeasuring DBH and height in 2000, subtracting the earlier (1995 or 1997) measurement and dividing by the number of intervening years. Trees that were cut or damaged were excluded from analysis (*T. canadensis*, $n = 16$; *P. rubens*, $n = 18$), with the exception of 15 *T. canadensis* for which height increment had been measured after felling for the PLA study (Kenefic and Seymour 1999). VINC was calculated by subtracting ARINC × 2 and AHINC from DBH at time *t* and HT at time *t*, respectively. The new DBH and HT (at time $t - 1$, 1994 in C16 and 1996 in C9) were entered into Honer's (1967) total

Table 2. Characteristics of the canopy strata for *Tsuga canadensis* and *Picea rubens* in the study stands.

Species and stratum	No. sampled	Age at breast height (years)	Height (m)	Crown length (m)	Crown projection area (m^2)
Tsuga canadensis					
B	57	118.6 (5.4)	18.66 (0.38)	14.52 (0.44)	41.55 (2.85)
C	14	77.3 (5.8)	12.42 (0.36)	9.66 (0.47)	34.80 (7.4)
D	20	52.8 (8.1)	6.85 (0.56)	4.75 (0.44)	9.78 (1.42)
E	9	14.4 (8.1)	2.61 (0.56)	1.95 (0.33)	2.35 (0.94)
Picea rubens					
B	65	107.6 (2.5)	19.30 (0.35)	11.36 (0.41)	32.31 (2.18)
C	14	83.4 (5.7)	11.73 (0.50)	6.69 (0.55)	7.96 (0.85)
D	12	76.5 (11.4)	6.78 (0.72)	3.68 (0.25)	6.10 (1.20)
E	9	8.9 (2.1)	2.31 (0.18)	1.72 (0.15)	1.62 (0.14)

Note: Values are means with SEs given in parentheses.

stemwood volume equations to calculate volume at $t - 1$ (V_{t-1}). Finally, VINC = $V_t - V_{t-1}$.

Analysis

Equations of the form $y_i = f(\beta|x_i + \varepsilon_i$, where $\varepsilon_i^{\text{iid}}\text{N}(0,\ x_i^n\sigma^2)$ were fit to the postulated VINC–PLA relationships (Table 1) using the least-squares nonlinear regression procedure in SYSTAT version 10. Equations were weighted by PLA$_i^n$ where $n = 0, -1$, or -2 to identify the optimal weighting factor to correct for heteroscedasticity. Furnival's (1961) index of fit (FI), a modified maximum likelihood criterion that allows concurrent evaluation of root mean square error, normality, and homoscedasticity, was used to identify optimal weights. Several distributionlike functions were explored before settling on the Weibull to model the sigmoid form (eq. 2; Table 1). The widely used Weibull has few parameters yet is flexible (Yang et al. 1978); it had among the lowest FIs of any model tested and converged readily in nonlinear fitting algorithms. The four-parameter Richards function used by Roberts and Long (1992) was explored but was impossible to fit over the entire range of the data without bias and had a higher FI than simpler models.

To examine possible age effects on the GE patterns, a simple multiplicative term of tree age at breast height (A) was added to eq. 1 (see Table 1) as follows:

$$[1a]\qquad \text{VINC} = \beta_1\text{PLA}^{\beta_2}A^{\beta_3}$$

When adding age to eq. 2, we tested both additive and multiplicative terms:

$$[2.1]\qquad \text{VINC} = \left(1 - \exp\left[-\left(\frac{\text{PLA}}{\beta_2}\right)^{\beta_3}\right]\right)(A^{\beta_4})$$

$$[2.2]\qquad \text{VINC} = \left(1 - \exp\left[-\left(\frac{\text{PLA}}{\beta_2}\right)^{\beta_3}\right]\right) + (\beta_4 A)$$

In all cases, β_4 was significant at $\alpha = 0.05$; in eq. 2.1, β_4 was 0.405 for *T. canadensis* and 0.497 for *P. rubens*; in eq. 2.2, β_4 was negative for both species. Both results justify statistically the inclusion of age as a negative influence into the volume prediction equation, but neither model form was ideal in terms of its biological properties. After further exploration of model forms, we settled on the following:

$$[2a]\qquad \text{VINC} = (A_{\max} - A)^{\beta_1}\left(1 - \exp\left[-\left(\frac{\text{PLA}}{\beta_2}\right)^{\beta_3}\right]\right)$$

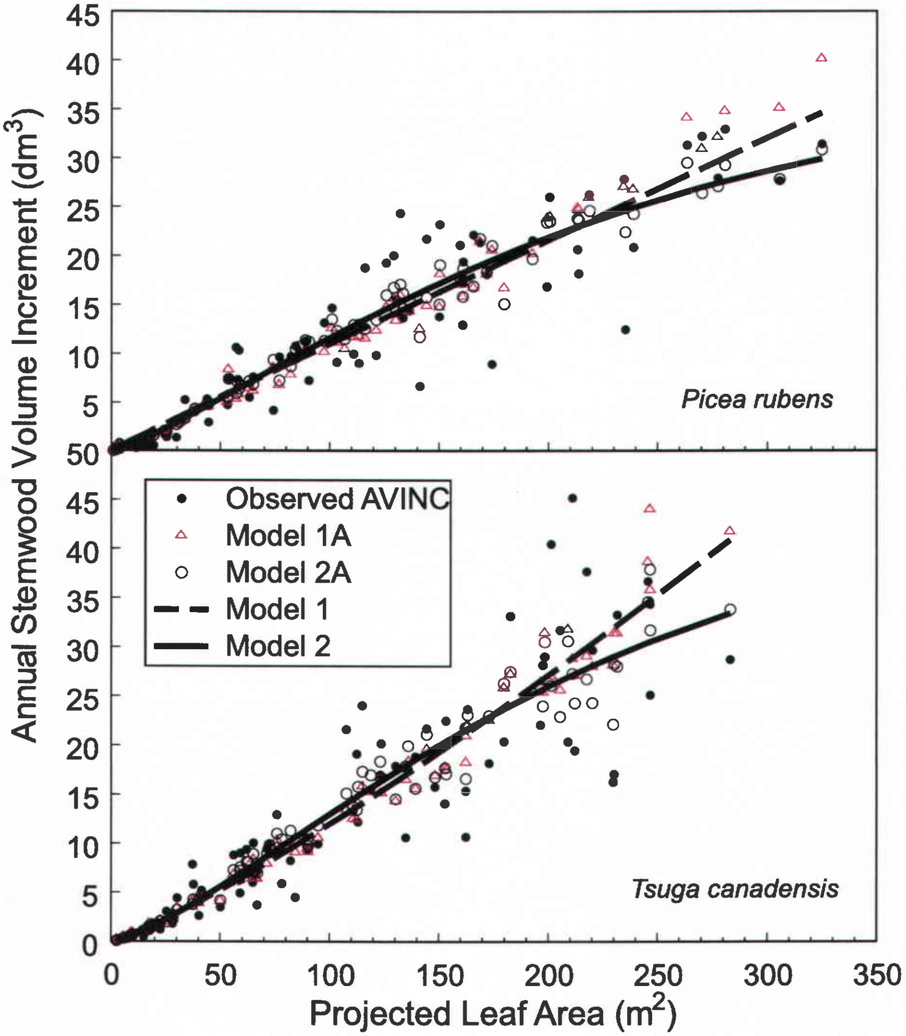
where $A_{\max}$ is an estimate of the maximum age for the species being analyzed, which must be greater than the oldest tree in the data set. Equation 2*a* essentially transforms the Weibull asymptote (parameter β_1 in eq. 2) into a negative index of tree maturity: the older the tree, the lower the first term, and thus, the lower the predicted VINC of the tree for a given PLA. $A_{\max}$ could simply be fixed based on published values; we chose to estimate it from the data. The exponent β_1 allows the effect of this maturity index to become relatively more or less severe as age increases. Equation 2*a* also has the logical property that VINC approaches zero as the tree age approaches $A_{\max}$.

To reinforce the evidence of a peaking pattern in the GE–LA relationship and to further examine the possible effect of tree age on this model, GEs (in dm^3·m^{-2}) were calculated by dividing VINC by PLA and fitting a linear second-degree polynomial of PLA with and added age term using SYSTAT's general linear models (GLM) procedure:

$$[3]\qquad \text{GE} = \beta_0 + \beta_1(\text{PLA}) + \beta_2(\text{PLA})^2 + \beta_3(A)$$

Analysis of variance (ANOVA, PROC GLM; SAS Institute Inc. 1990) was applied to test the effects of canopy position on mean GE and PLA ($\alpha = 0.05$). Bonferroni pairwise comparisons, which control experimentwise type I error rate but are conservative (i.e., higher type II error rate for pairwise comparisons) (Schlotzhauer and Littel 1997), were used to explore the differences in mean GE by species and stratum ($\alpha = 0.05$). ANOVA assumptions of normality and equal variance were assessed using the Shapiro–Wilk test (SAS Institute Inc. 1990, PROC UNIVARIATE) and Levene's test (SAS Institute Inc. 1990, PROC ANOVA).

Fig. 3. Comparison of monotonic and sigmoid regression models relating stemwood volume increment to projected leaf area for *P. rubens* and *T. canadensis*, with and without the inclusion of tree age.



Results

ANOVA indicated that both mean PLA and mean GE differ significantly by stratum for both species ($p = 0.0001$). Trees in the B stratum have significantly more PLA than the lower strata, which do not differ from each other ($\alpha = 0.05$; Table 3). In general, stratum B is more growth efficient than stratum D, as expected, although high within-stratum variation in GE precludes a strong overall inference. The conservative Bonferroni mean separation detected a difference only for *T. canadensis* but not for *P. rubens* at $\alpha = 0.05$.

Equations 1 and 2 (the monotonic and sigmoid forms, respectively; Table 1) both fit the data well, explaining about 78% of the variation in VINC for *T. canadensis* and about 84% for *P. rubens*. Indeed, there is essentially no difference between models in the predicted VINC between PLAs of 50–200 m^2 for both species; departures are subtle and occur at the extremes of the data (Fig. 3). Close inspection of residuals revealed a clear bias in eq. 1 for PLAs < 50, especially for *P. rubens*, which was not as evident for eq. 2. The slightly better FI of the sigmoid form for both species (Table 4) results from its ability to capture an inflection in the lower range of the data (at PLA = 59 for *P. rubens* and 79 for *T. canadensis*) as well as a slightly declining, potentially asymptotic pattern in the largest trees, especially for *P. rubens*. However, note that although the weighted models better meet the assumption of uniform variance, they empha-

Table 3. Comparisons of projected leaf area (PLA, m^2) and growth efficiency (GE, dm^3·m^{-2}) by stratum for *Tsuga canadensis* and *Picea rubens.*

Species and stratum	PLA	GE
Tsuga canadensis		
B	160.97 (10.18)*a*	0.127 (0.0063)*a*
C	60.07 (8.34)*b*	0.147 (0.0120)*a*
D	18.92 (3.340)*b*	0.096 (0.0091)*b*
Picea rubens		
B	151.37 (9.57)*a*	0.113 (0.0043)
C	34.11 (4.72)*b*	0.085 (0.0138)
D	15.98 (3.48)*b*	0.087 (0.0241)

Note: Values are means with SEs given in parentheses. Within each species, values with different letters are significantly different ($\alpha = 0.05$) according to Bonferroni multiple comparisons.

Table 4. Parameters and fit statistics of the weighted nonlinear regressions of VINC on PLA.

Equation	Species	FI	rMSE	β_1	β_2	β_3	$A_{\max}$
1	*Tsuga canadensis*	2.975	5.174	0.051 908 (0.011 11)	1.181 05 (0.045 47)		
	Picea rubens	2.900	3.735	0.121 05 (0.033 37)	0.978 10 (0.054 53)		
1*a*	*Tsuga canadensis*	2.841	5.034	0.151 11 (0.062 09)	1.279 77 (0.055 83)	–0.329 20 (0.115 59)	
	Picea rubens	2.778	3.541	0.548 23 (0.181 84)	1.139 30 (0.051 72)	–0.495 15 (0.113 39)	
2	*Tsuga canadensis*	2.896	5.131	43.684 (14.423)	215.80 (78.933)	1.358 7 (0.097 989)	
	Picea rubens	2.833	3.736	37.166 (10.471)	219.78 (82.060)	1.250 9 (0.142 02)	
2*a*	*Tsuga canadensis*	2.719	4.918	0.719 81 (0.061 79)	220.26 (69.405)	1.435 4 (0.133 64)	324.96 (54.183)
	Picea rubens	2.674	3.483	0.723 03 (0.053 49)	206.11 (59.915)	1.327 4 (0.136 18)	248.97 (38.997)

Note: Values are estimates with asymptotic SEs given in parentheses. Model forms are defined in Table 1 and the text. Weights are PLA^{-1} for spruce, PLA^{-2} for hemlock. FI, Furnival's index; rMSE, root mean square error of the unweighted model.

size the fit at the lower end of the data and may not extrapolate as well at the largest PLAs.

When age terms are added to these models, the exponents β_3 for eq. 1*a* or β_1 for eq. 2*a* are highly significant in all cases (Table 4). In eq. 1*a* the sign is negative, as expected if VINC and age are negatively related for a given PLA. The fit of eq. 1*a* is essentially the same as eq. 2 but appears to exhibit a bias for trees with large PLAs > 250 m^2 that would be troublesome if extrapolated beyond the range of the data (Fig. 3). The estimates of $A_{\max}$ for eq. 2*a* were reasonable for both species (Table 4); the fact that β_1 is significantly less than 1.0 indicates that the negative effect of age becomes more severe as tree age approaches the maximum. The sigmoid form with age (eq. 2*a*) performs much better than eq. 1*a* for the largest trees (Fig. 3), despite the weighting in favor of low PLAs. It also has the lowest FIs of all models tested.

If the VINC–LA pattern is indeed sigmoid and affected by age, then these effects should be apparent in a peaking GE–LA relationship (Fig. 1*a*, pattern B) with a statistically significant age term. Equation 3, a simple second-degree polynomial of LA with an additive age term, provides a straightforward way to confirm these patterns. The very high significance levels of β_2, a test for curvature (Table 5), leaves little doubt about the validity of the peaking pattern. The age coefficient β_3 is also highly significant (Table 5) and contributes materially to explaining variation in GE for a given LA, especially for *P. rubens* (Fig. 4). Interestingly, without age in the model, neither LA coefficient in the *P. rubens* eq. 3 is significant, even at $\alpha = 0.20$. Furthermore, tree height, an often-used surrogate for age in single-aged stands, was not significant ($\alpha = 0.10$) for either species when added in place of age.

Taken together, these regression analyses provide convincing support for a sigmoid VINC–LA pattern (Fig. 1, pattern B), along with a significantly negative effect of tree age on growth at a given LA, for these managed multiaged stands.

Discussion

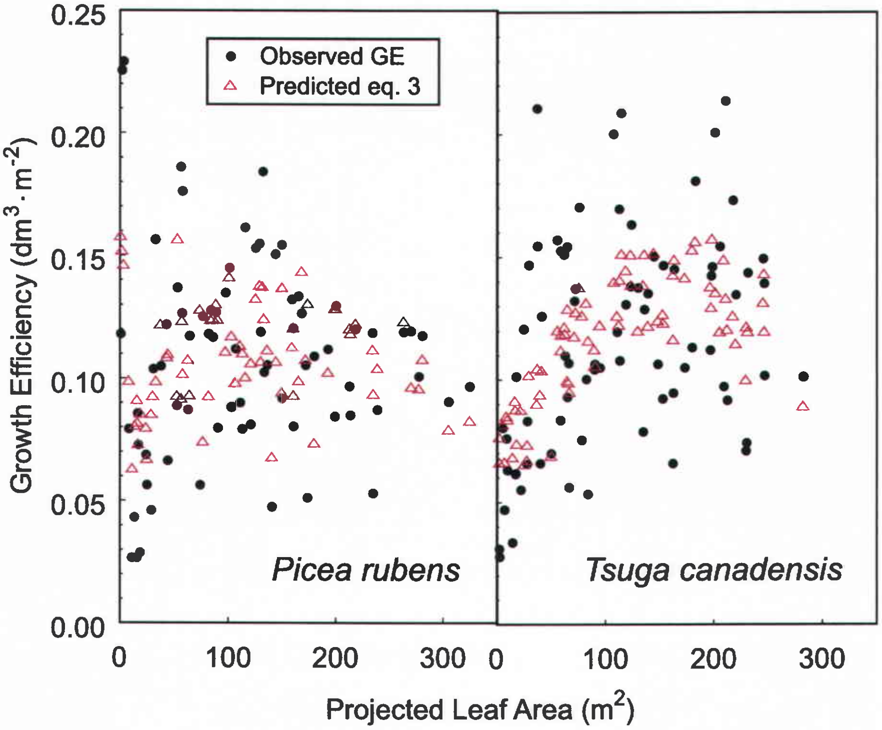
This is the first study to establish that tree growth in multiaged stands is negatively associated with advancing age, independent of possible confounding effects of increasing crown size with age. The nature of this effect can be illustrated by plotting predicted VINC over age, holding PLA constant in 50-m^2 classes over the age range in the data for each class (Fig. 5). This nonlinear declining pattern is not a new finding (Kaufman and Ryan 1986); furthermore, it is consistent with a rapidly growing body of evidence that points to reduced photosynthetic capacity with advancing tree age as an important cause (Yoder et al. 1994; Ryan and Yoder 1997; Ryan et al. 1997; Bond 2000). Virtually all of the published research has been conducted in chronosequences of single-aged stands, however, where the effects of increasing LA and advancing age are often confounded. Working in the same stands sampled in this study, Day et al. (2001) found a biomass-based measure of GE to be negatively associated with age for codominant *P. rubens* ranging from 25 to 145 years old. Day et al. also found significant differences in foliar morphology and reduced photosynthesis in old trees measured in situ as well as in 3-year-old scions

Table 5. Parameters and fit statistics of the linear polynomial eq. 3 that predicts GE from PLA and age.

Species	rMSE	β_0	β_1	β_2 (test for curvature)	β_3 (test for age)
Tsuga canadensis	0.036 92	0.084 43	0.001 278 6	–0.000 003 79	–0.000 408 95
		(0.012 51)	(0.000 239 31)	(0.000 000 86)	(0.000 134 21)
Probability $\beta_i = 0$		< 0.000 01	< 0.000 01	0.000 04	0.003 22
Picea rubens	0.035 48	0.164 28	0.000632 54	–0.000 001 80	–0.000 946 34
		(0.016 62)	(0.000 182 73)	(0.000 000 59)	(0.000 186 56)
Probability $\beta_i = 0$		< 0.000 01	0.000 93	0.003 50	< 0.000 01

Note: Values are estimates with asymptotic SEs given in parentheses. Equations are unweighted. rMSE, regression root mean square error.

Fig. 4. Observed tree growth efficiencies for *P. rubens* and *T. canadensis* compared with predictions from eq. 3, a linear regression model based on tree age and a second-degree polynomial of leaf area.



from old trees grafted onto a common juvenile rootstock, suggesting a fundamental maturational cause independent of crown size or stand structure (sensu Greenwood and Hutchinson 1993). In our study the fact that age, a direct index of maturation, was negatively associated with GE, but tree height, an often-used physical surrogate for age, was not, seems to lend empirical support to the maturation hypothesis.

Our results differ from Kollenberg and O'Hara (1999) who reported no relationship between tree age and GE of multiaged *P. contorta* stands. Their conclusion apparently was based on inspection of a scatterplot of GE versus age (Kollenberg and O'Hara 1999, Fig. 4); no analysis of model forms was presented. Although they found significant curvature in the GE–LA relationship (both positive and negative) based on the within-stand cohort ranking, this dependence of GE on LA and its possible confounding with age was not analyzed and evidently not considered in their conclusion of no age effect. Indeed, we would have reached the same conclusion from inspection of scatterplots alone. The simple relationship between GE and age, unadjusted for LA effects (Fig. 6), has an $r^2 = 0.01$, and neither species nor age approach significance at $\alpha = 0.20$.

The GE of the largest trees in multiaged stands holds particular silvicultural importance, because these trees account for a significant proportion of the growth and value of the overall structure. If clear declines in GE could be documented above a particular leaf area or age, then the traditional use of a maximum DBH for setting the upper size limit (Nyland 1996) could be replaced by a more biologically defensible criterion. Our best model (eq. 2*a*; Table 4, Fig. 3) suggests a very gradual decline in GE above a PLA ~100 m^2, but the reduction is subtle; no threshold is suggested. Trees that reach the upper strata and maintain a constant crown size will decline as they age (Fig. 5), but again, this decline is gradual. Even very old trees may produce additional stemwood if their crowns continue to expand more rapidly than they age; this can be represented by a trajectory upward and to the right in Fig. 5. Importantly, we have no evidence of the negative GEs predicted by Maguire et al.

Fig. 5. Predicted relationship between stemwood volume increment and tree age, holding leaf area constant in 50-m^2 classes, plotted over the range of ages in each leaf area class. Numbers are the class midpoints in square metres preceded by the species code (H, *T. canadensis*; S, *P. rubens*).

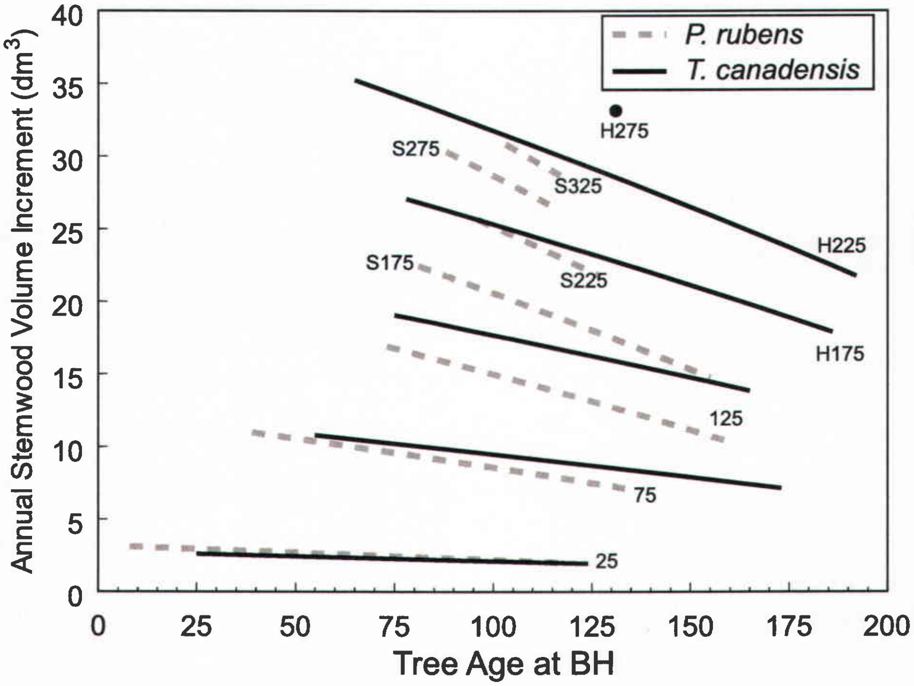
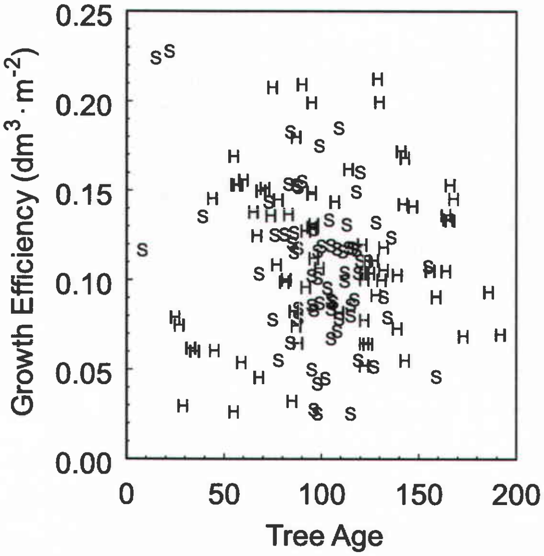


Fig. 6. Scatterplot of tree growth efficiency over age (H, *T. canadensis*; S, *P. rubens*).



(1998, Fig. 1) based on a fitted regression model that appears to be more asymptotic than their data warrant.

The gradual decline in GE with increasing LA predicted by eq. 2*a* agrees with Kollenberg and O'Hara's (1999) results for the oldest of their three cohorts but is at odds with O'Hara's (1996) analysis that suggests very large *P. ponderosa* in western Montana follow our pattern C (Fig. 1). Inspection of O'Hara's Fig. 11 shows this conclusion depends on about 20 trees with PLAs between 500 and 1000 m^2; however, the sapwood-based PLA prediction equations used by O'Hara were based on trees <400 m^2 (O'Hara and Valappil 1995). If O'Hara's (1996) data are restricted to leaf area <375 m^2, it appears that a differently shaped VINC–LA relationship, and thus GE–LA relationship, may be appropriate. Even with this possible extrapolation bias discounted, however, O'Hara clearly documents a general pattern of increasing GE with more dominant canopy position, following the model postulated by Oliver and Larson (1996, Fig. 13.4). The possible dependence of GE on tree age within cohorts or leaf-area classes was not analyzed.

The lower GEs of the lower strata in this study (Table 3) agrees with other studies of both single-aged and multiaged stands cited above, but this is of little practical consequence in terms of overall production in multiaged stands. Using O'Hara's (1996, 1998) approach to developing stand structures by allocating leaf area to cohorts, it becomes obvious that the lower strata, although numerous as individuals, account for relatively little of the stand leaf area. The key question of management importance is how rapidly these small trees are recruited into the upper strata. Here, silviculturists face a difficult tradeoff between maintaining high leaf areas in the productive, well illuminated upper strata, versus creating sufficient vacant growing space to regenerate new cohorts and avert their suppression. This issue is further complicated by the fact that shade-tolerant species managed under the single-tree selection system commonly share the same horizontal growing space, where young cohorts grow wholly within the crown projection area of older trees in response to diffuse light from nearby small gaps (Seymour and Kenefic 1998). To our knowledge, no one has comprehensively analyzed these important tradeoffs. O'Hara's (1996) MASAM model potentially incorporates these dynamics but requires the user to make assumptions about regeneration and development of the younger cohorts. A robust means of predicting leaf-area expansion, as influenced by within- and between-cohort competition as trees move upward through the canopy structure, would certainly be an important contribution to this field. This study contributes to an overall model of multiaged stand dynamics by documenting that the longer one waits to release lower stratum trees, the less efficient they will be at a given leaf area once they reach the upper strata. In this sense, we support Assmann's (1970, pp. 134–136) synthesis of the European literature on multiaged *Picea* and *Abies* forests, which concludes that large trees in selection forests never reach the efficiency of their counterparts in single-aged stands, because they experience a "period of much-impeded development" before entering the main canopy and are too large and old to grow efficiently once they get there.

We should emphasize the our results describe only tree-level phenomena, in stands of shade-tolerant species with very irregular, fairly open canopies resulting from a 50-year history of light selection cuttings at 5-year intervals. Our research does not address the much-discussed phenomenon of stand-level growth decline with age in single-aged stands caused by declining leaf area index from crown abrasion and perhaps other factors (Long and Smith 1992; Ryan et al. 1997) that cannot be quantified at the tree level (Smith and Long 2001). Neither does this address the causality of these age-related phenomena; further studies comparing the ecophysiology and crown architecture of different-aged trees with similar leaf areas would be valuable here. Finally, it is worth noting that such relationships may be more difficult to elucidate in multiaged stands of shade-intolerant species, owing to the fact that the inability of such species to persist in lower canopy strata limits the range of ages available within a given leaf-area size class.

To predict VINC for *P. rubens* or *T. canadensis* in managed multiaged stands, one must first estimate tree PLAs from suitable equations (Maguire et al. 1998; Kenefic and Seymour 1999). If age data are not available, then we recommend eq. 2 over eq. 1, because eq. 2 appears to less biased for both small and large PLAs. VINC estimates can be improved somewhat using eq. 2*a* if age data are available; note in Fig. 5 that for hemlock, the difference in predicted VINC between the youngest and oldest trees (ca. 100 years) at a given PLA is well over 30%.

Conclusions

Our analysis demonstrates that the relationship between stemwood volume increment and tree leaf area in multiaged stands of tolerant conifer stands is sigmoid, rather than monotonic as found by Maguire et al. (1998). The phase of development during which GE increases, as lower stratum reach the midstory and receive more light, appears to end at leaf areas well below 100 m^2. Above this point, GE gradually declines with increasing leaf area, a negative trend that is magnified as trees age in the upper strata without expanding their crowns.

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