

Height development of shade-tolerant conifer saplings in multiaged Acadian forest stands¹

Andrew R. Moores, Robert S. Seymour, and Laura S. Kenefic

Abstract: Understory growth dynamics of northern conifer species were studied in four stands managed under multiaged silvicultural systems in eastern Maine. Height growth of *Picea rubens* Sarg., *Abies balsamea* (L.) Mill., and *Tsuga canadensis* (L.) Carr. saplings between 0.5 and 6.0 m in height was related to the proportion open sky (POS), using sapling height as a covariate. Height growth of *T. canadensis* equaled *A. balsamea* and exceeded *P. rubens* under very low light levels (POS < 0.1) but is much less responsive to both increasing POS and taller heights, reaching 50% of its maximum height growth at a POS of only 0.09. *Abies balsamea* outgrew *P. rubens* under similar dark conditions; at higher light levels (POS > 0.10), both species grew similarly. Evidently, no feasible overstory manipulation of light alone can promote more rapid height development of *P. rubens* saplings over *A. balsamea*. A nonlinear light-prediction model using stand basal area is linked with height-growth prediction equations to quantify sapling development from 0.5 to 6 m. Depending on overstory density, *P. rubens* requires a height advantage of 0.14–0.33 m over a 0.5 m tall *A. balsamea* to reach a height of 6 m over the same time period.

Résumé : La dynamique de la croissance en sous-étage des conifères nordiques a été étudiée dans quatre peuplements soumis à un régime sylvicole multi-âge dans l'est de l'État du Maine. Avec la hauteur des gaules comme covariable, la croissance en hauteur des gaules d'épinette rouge (*Picea rubens* Sarg.), de sapin baumier (*Abies balsamea* (L.) Mill.) et de la pruche du Canada (*Tsuga canadensis* (L.) Carr.) entre 0,5 et 6,0 m de haut est reliée au pourcentage d'ouverture du couvert (POC). La croissance en hauteur de *T. canadensis* égale celle de *A. balsamea* et dépasse celle de *P. rubens* dans des conditions de très faible luminosité (POC < 0,1). Mais la croissance en hauteur de *T. canadensis* est très peu sensible à l'augmentation du POC et à une hauteur initiale plus élevée, atteignant 50 % de sa croissance maximale en hauteur à une valeur de POC de seulement 0,09. *Abies balsamea* dépasse *P. rubens* dans des conditions similaires de luminosité; dans des conditions de plus forte luminosité (POC > 0,10), les deux essences croissent de façon similaire. Évidemment, en pratique aucune manipulation de l'étage dominant pour augmenter la luminosité ne peut favoriser une croissance en hauteur des gaules de *P. rubens* plus rapide que celle de *A. balsamea*. Un modèle non linéaire de prédiction de la luminosité basé sur la surface terrière est relié aux équations de prédiction de la croissance en hauteur pour quantifier le développement des gaules de 0,5 à 6 m. Dépendamment de la densité de l'étage dominant, une tige d'épinette rouge doit avoir 0,14 à 0,33 m de plus qu'une tige de sapin de 0,5 m de haut pour atteindre une hauteur de 6 m au cours de la même période de temps.

[Traduit par la Rédaction]

Introduction

A natural disturbance regime dominated by gap dynamics and a long history of partial cutting have made multiaged, mixed-species forest structures common in the Acadian Forest of northeastern North America (Seymour et al. 2002). However, the dynamics of multiaged stands are complicated and poorly understood despite a century of research in the region. Forest managers commonly eschew multiaged sys-

tems for several reasons: greater challenges exist to maintaining high stemwood productivity, yields are more difficult to predict, and prescriptions are more complex relative to single-cohort systems. Three principal challenges exist to maintaining maximum productivity in these stands. First, overstory leaf area, which is the strongest predictor of stand stemwood productivity (O'Hara 1996; Ryan et al. 1997), must be kept well below the site potential to promote adequate development of regeneration. Secondly, more of the stand leaf area tends to be found on large-crowned, old trees, which can be less growth efficient than younger overstory trees with moderate crowns (Assmann 1970; Roberts et al. 1993; Seymour and Kenefic 2002). Finally, at least in Acadian mixed-conifer forests, long periods of suppression in the understory may reduce growth efficiency once trees reach the main canopy, independent of crown size or canopy stratum (Maguire et al. 1998; Seymour and Kenefic 2002). Thus, skillful management of multiaged structures involves allocating leaf area to overstory trees in a way that optimizes overstory growth and growth efficiency without delaying the timely advancement of seedlings and saplings from the understory into taller strata.

Previous studies of understory growth dynamics have con-

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sistently shown that light availability is the primary driver of understory seedling and sapling growth, whereas soil nutrient status and soil moisture availability play less important roles (Pacala et al. 1994; Finzi and Canham 2000; Mitchell 2001; Kranabetter and Coates 2004). In turn, quality and quantity of light reaching the understory is primarily determined by overstory leaf area and canopy openness (Chason et al. 1991; Sampson and Smith 1993; Baldocchi and Collineau 1994). In such cases, it is the interspecific competitive dynamics in the understory, as determined by the light environment, that ultimately drives the community and successional dynamics of the stand (Klinka et al. 1992; Claveau et al. 2002; Gratzner et al. 2004). Although we know that *Abies balsamea* (L.) Mill. (balsam fir), *Picea rubens* Sarg. (red spruce), and *Tsuga canadensis* (L.) Carr. (eastern hemlock) are all very shade tolerant and capable of responding to release after prolonged periods of suppression in the understory (Blum 1990; Frank 1990; Godman and Lancaster 1990; Seymour 1992), the relative development of these species under common understory conditions in multiaged stands has not been studied. Thus, a greater understanding of these species' responses to varying levels of canopy openness is critical to predicting and managing the developmental trajectories of these stands.

The purpose of this study was to better understand and quantify the relative growth dynamics of understory *A. balsamea*, *P. rubens*, and *T. canadensis* trees in multiaged, mixed-species Acadian conifer stands. Specifically, the objectives were to (i) rigorously compare the height growth of these species in different understory environments, (ii) model these height-growth patterns in response to changes in overstory canopy openness and tree size, and (iii) relate overhead canopy openness to stand density (basal area) and, thus, facilitate application under multiaged silvicultural systems.

Methods

Study site

Field data were obtained from four mixed-species, multiaged stands located on the 1540 ha Penobscot Experimental Forest (PEF) in Bradley, Maine. The PEF lies within the Acadian Forest Region, a transitional forest between the broadleaf forest to the south and the boreal forest to the north (Loo and Ives 2003). The natural disturbance regime is dominated by sporadic partial disturbances, such as insect epidemics and windstorms. Species composition is mixed and highly variable because of small-scale edaphic and topographic heterogeneity. Dominant conifers on the PEF include *P. rubens*, *A. balsamea*, *T. canadensis*, *Thuja occidentalis* L. (northern white-cedar), *Pinus strobus* L. (eastern white pine), and *Picea glauca* (Moench) Voss (white spruce). The more common hardwoods are *Acer rubrum* L. (red maple), *Betula papyrifera* Marsh. (paper birch), and *Betula alleghaniensis* Britt. (yellow birch). Glacial till is the principal soil parent material with soil types ranging from well-drained loams and sandy loams on low-profile ridges to poorly drained and very poorly drained loams and silt loams in flat areas between the ridges (Brissette et al. 1999; Brissette and Kenefic 1999).

The PEF, located at approximately 44°52'N and 68°38'W,

is the site of long-term silvicultural experiments established by the USDA Forest Service in the 1950s, which include both even-aged and multiaged silvicultural treatments (Sendak et al. 2003; Seymour et al. 2006). Two of the stands in the present study (C9 and C16) are replicates of selection cutting on a 5 year cycle, whereas the other two (C12 and C20) are replicates of selection cutting on a 10 year cutting cycle; each treatment unit is approximately 10 ha. The structural goal is defined by the BDq method (Guldin 1991): the 5 year cutting cycle uses a target residual basal area (BA) of 26 m²·ha⁻¹ and a maximum residual diameter at breast height (DBH) goal of 48 cm, whereas the 10 year treatment uses a target residual basal area of 23 m²·ha⁻¹ and a maximum residual DBH goal of 46 cm. The *q* factor for both treatments is 1.96, based on 5 cm DBH classes (Seymour and Kenefic 1998). Because these selection-cutting treatments contain no truly open conditions, archived measurements of saplings in young even-aged stands (the untreated control plots of a nearby precommercial thinning study established in 1976; Brissette et al. 1999) were used to establish benchmark height-growth rates without overstory competition.

Sampling scheme

Samples were obtained from points located on 25 m systematic grids established in each study stand. To reduce the influence of localized site variability on height growth, potential sample locations avoided poorly drained soils; sample points were limited to well drained, moderately well drained, or somewhat poorly drained conditions. Locations with evidence of harvesting during the past 5 years (e.g., recent stumps) within a 0.1 ha circular plot were excluded, as were points that included at least one hardwood tree greater than 10 cm DBH within the 0.1 ha zone. At all remaining grid points, all *A. balsamea*, *P. rubens*, and *T. canadensis* saplings between 0.5 and 6.0 m in height were tallied by 2 m height classes on 0.05 ha circular plots to provide a basis for designing a sample balanced by species, height, and canopy openness.

Canopy openness (after Machado and Reich 1999) was assessed on these preliminary grid points during July 2002 using a LAI-2000 plant canopy analyzer (LI-COR 1992) at a height of 1.6 m above the ground. To avoid bias from direct-beam sunlight, readings were taken without a viewcap within an hour of sunrise or sunset, or on uniformly overcast days. The LAI-2000 records the diffuse nonintercepted light (DIFN) penetrating the canopy (Chason et al. 1991; Lieffers et al. 1999); values are normalized between zero and unity using a second sensor placed above the canopy or in the open. In this study, the unobstructed sensor was in an open field located 1–2.2 km from the sample sites. Hereafter, we refer to a specific value of canopy openness using the abbreviation POS (for proportion open sky). Each grid point was assigned to a POS bin of 0.1 (0–0.09, 0.10–0.19, 0.20–0.29, ..., 0.90–1.00).

The target sample in the multiaged stands was 180 saplings consisting of 20 trees per species per height class distributed over the acceptable grid points. Using the results from the preliminary POS survey to establish approximate light strata, 20 suitable grid points were chosen for each species and height class as potential sample-tree locations. Effort was made to equally represent open conditions, intermediate conditions, and closed conditions regardless of their fre-

quency. However, because of the consistently dense overstories in these stands, there were not enough suitable grid points in the more open POS bins to accomplish this perfectly. Each chosen grid point was revisited, and a sapling of the appropriate height class and species was randomly chosen within a 4 m radius of the grid point. No more than one tree per species was sampled at each grid point.

Open-grown trees were selected from the archived data by randomly choosing 10 trees per height class per species, if available. These open-grown samples were drawn from an identical range of initial heights as in the multiaged stands. To ensure comparability to the relatively high sapling densities in the multiaged stands, archived data were further restricted to dominant or codominant trees on untreated control plots only based on earlier work that suggested thinning affected height growth of *A. balsamea* (Brissette et al. 1999). No *T. canadensis* met these selection criteria, so data on open-grown trees were limited to only 30 *A. balsamea* trees and 26 *P. rubens* trees.

Data collection

POS and basal area measurements

Canopy openness was measured at the top of the terminal leader for each sample tree between mid-August to mid-September 2002 using the LAI-2000. The below-canopy sensor was mounted to a telescoping height pole and leveled to the greatest extent possible with an attached carpenter's level. Four POS readings were taken above each sapling by rotating the height pole 90° between readings and then averaged. POS values for all trees in the archived open-grown data set were simply assigned a value of 1.0. On a subsample of grid points distributed proportionately over the entire POS range found in the preliminary survey, BA ($\text{m}^2\text{-ha}^{-1}$) of trees >2.5 cm DBH was measured using a 2 m^2 BAF prism sweep with the sample tree as plot center.

Height growth

Height growth measurements in the multiaged compartments were taken between mid-August and late September in 2002. The distances from the ground to the tip of the terminal shoot and from the ground to the base of the most recent two internodes were measured using a telescoping pole or measuring tape. The dependent variable in the multiaged sample is annual height increment (AHINC, in $\text{m}\cdot\text{year}^{-1}$), the total internodal distance measured on the terminal shoot divided by two. Height increments in the archived open-grown data set were obtained by subtracting successive height measurements made at 3 or 4 year intervals during the period 1976–1983 and dividing by the length of the measurement period. Because tree height itself has been shown to significantly affect tree height growth (Duchesneau et al. 2001; Uzoh 2001; Claveau et al. 2002; Boisvenue et al. 2004), height at the beginning of the growth period (initial height; IH) was included as a covariate in models relating height growth to canopy openness.

Data analysis

Quantifying canopy openness

The POS estimates from the LAI-2000 are derived from

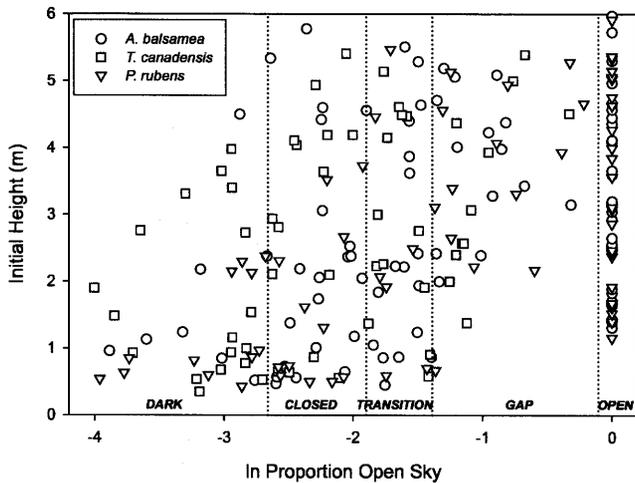
one to five successive circumferential rings of the light sensor. Varying the number of rings changes the size of the cone emanating from the LAI-2000 within which overhead vegetation intercepts light to the sensor below. Using only the innermost ring produces a cone with a zenith angle of 18°, whereas using the two, three, four, or five innermost rings produces cones with zenith angles of 28.6°, 43.4°, 58.1°, and 74.1°, respectively (LI-COR 1992). Because wider angles integrate canopy openness over a much larger area, trees on the periphery may be included in the estimate of POS when using all five rings, even though they may not influence the growth of the sapling in question (Bunnell and Vales 1989). Other scientists (Biging and Dobbertin 1992; Puettmann and D'Amato 2002) have reported that using angles of view greater than a zenith angle of 30° in the selection of competitors does not improve height and diameter growth models. We tested that assumption by running regressions on AHINC using POS estimates based on the innermost ring; the innermost two, three, four rings; and all five rings. Although the difference in model performance between using three, four, or five rings was negligible, using four rings produced the lowest MSE and, along with three rings, tied for the highest R^2 value. Models in all subsequent analyses were therefore based on the four inner rings (a zenith angle of 58.1°).

Height growth models

To test the hypothesis that species differ in their response to canopy openness, we first conducted an analysis of covariance in which trees were assigned to one of five POS zones, labeled as follows: dark, closed, transition, gap, and open. The first four zones encompass the gradient in canopy openness of the multiaged stands and include all three species, whereas the open zone is represented by the archived data of *A. balsamea* and *P. rubens* only. To create roughly equal sample sizes within POS categories, POS values in the multiaged stands were distributed into quartiles. The lower quartile POS value, median POS value, and upper quartile POS values were 0.073, 0.136, and 0.248, respectively, roughly proportional to the distribution of overstory canopy openness in the study stands that are dominated by relatively closed-canopy conditions interspersed with occasional small gaps. For simplicity, we rounded the upper boundaries of these zones to 0.07, 0.15, and 0.25, respectively. The gap zone contained all saplings growing in conditions of POS greater than 0.25 and less than 0.73 (fir), 0.80 (spruce), or 0.86 (hemlock). The resulting distribution of samples (Fig. 1) offers precision where it is most valuable, viz., at levels of canopy openness below 25%–30%, the zone within which height growth of shade-tolerant conifers is most responsive (Carter and Klinka 1992; Klinka et al. 1992; Parent and Messier 1995; Duchesneau et al. 2001; Grassi and Bagnaresi 2001).

Analysis of covariance was done using Systat's (version 11) general linear model procedure (SYSTAT, Inc., San Diego, California). The dependent variable was AHINC; independent variables were species and POS zone (both categorical variables), and the species \times POS interaction; the covariate was the sapling's height at the beginning of the 2 year growth period. Both continuous variables were natural-log transformed to counteract increasing variance. Because

Fig. 1. Joint distribution of sample trees by species, POS and initial height, showing quartile divisions (based on the untransformed data) used to form POS categories within the multiaged stand data.



T. canadensis trees were not represented in the open-grown data set, the comparison among the three species was limited to the multiaged stands only. A separate analysis excluding *T. canadensis* was run to compare *A. balsamea* and *P. rubens* in the open zone. Within each canopy openness zone, pairwise comparisons were made between predicted log-transformed AHINC values for each species, using Fisher's least significant difference (LSD) to suggest differences among species. Because specific contrasts were carried out only among species within POS zones, not among all possible 12 POS × species categories, more conservative mean separation was deemed unnecessary.

Because all effects proved to be highly significant (see Results section), we elected to formulate a continuous height-growth response function to facilitate modeling applications. The significance of species and its interaction with POS strongly suggested separate models for each species; further, the lack of any apparent optimum light zone suggested an asymptotic rather than a peaking function. The Michaelis-Menten curve (Wright et al. 1998, York et al. 2004), with IH as a nonlinear modifier, was used to enforce such asymptotic behavior:

$$[1] \quad \text{AHINC} = \left(\frac{\text{POS } a}{\text{POS} + b} \right) \text{IH}^c$$

where *a*, *b*, and *c* are parameters fitted using Systat's (version 11) nonlinear regression algorithm.

Gap fraction prediction

To further facilitate modeling applications in the typical situation where POS is not measured, we explored various model forms to predict POS from the commonly available stand BA. The following nonlinear model proved to be the most precise and unbiased:

$$[2] \quad \text{POS} = 1 - \left(\frac{\text{BA}}{\text{BA}_{\text{max}}} \right)^{b\text{HT}}$$

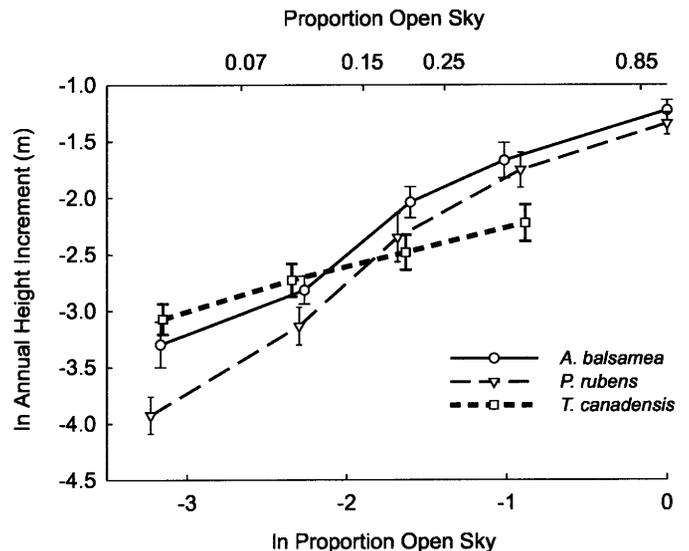
where HT is the height at which the POS measurement was

Table 1. Analysis of covariance comparing the natural-log transformed annual height increment (m) among species and POS zones, with the log-transformed initial height of the sample tree (IH, m) as the covariate (multiaged stands only; excludes *Abies balsamea* and *Picea rubens* in the open zone).

Source	SS	df	MS	F	p
Species	2.644	2	1.322	4.099	0.018
POS zone	40.599	3	13.533	41.96	<0.001
Species × POS zone	7.673	6	1.279	3.966	0.001
ln(IH)	12.179	1	12.179	37.77	<0.001
Error	49.338	153	0.322		

Note: SS, sum of squares; MS, mean square.

Fig. 2. Least-squares means of mean annual 2 year height increment (natural-log transformed, m) by species and POS zone, based on the analysis of covariance in Table 1. Means plotted at the overall mean log initial height of the multiaged stands = 0.695 (antilog = 2.59 m). The boundaries of the POS zones are marked on the upper horizontal axis. Error bars are SEs.



taken (height of subsample tree at time of measurement) and BA_{max} and *b* are fitted parameters. This equation has three desirable properties: POS approaches full sunlight (1.0) as BA approaches zero for all values of HT > zero; POS approaches zero as the stand BA approaches the site maximum; and POS can increase with increasing HT holding BA constant. Three different basal areas (all centered at the location of the POS reading) were tested: total plot-level BA (BA_1), BA of all trees greater than 6.0 m tall (middle- and upper-story trees; BA_2), and BA of all trees greater in height than the subject sample tree (BA_3).

Results

Height growth

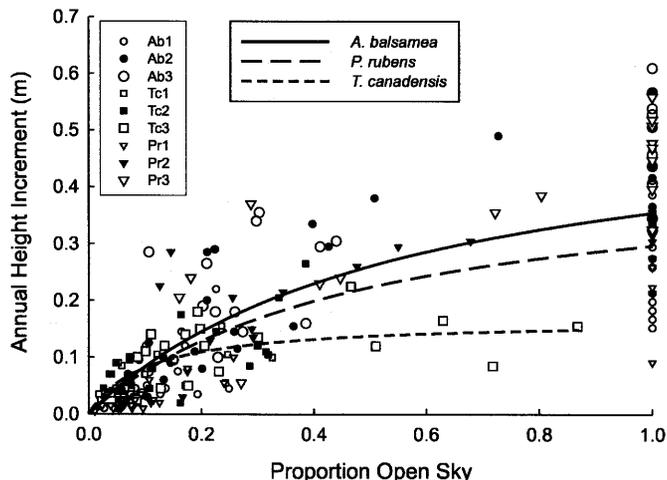
All terms in the analysis of covariance were highly significant (Table 1), with the full model explaining 70% of the variation in the log-transformed values of AHINC. Clearly, all species respond to increasing canopy openness, albeit to different degrees (Fig. 2), as reflected in the high significance of the POS term. The significant species × POS interaction is best illustrated by the relatively “flat” response of

Table 2. Probabilities of differences in annual height growth (natural-log transformed) among species within POS zones, based on the ANOVA in Table 1 (for all but the open zone) using Fisher's least significant differences among the least-squares means from Fig. 2.

Contrast	POS zone				
	Dark (n = 39)	Closed (n = 48)	Transition (n = 38)	Gap (n = 41)	Open (n = 56)
<i>A. balsamea</i> vs. <i>Tsuga canadensis</i>	0.351	0.648	0.033	0.012	—
<i>A. balsamea</i> vs. <i>P. rubens</i>	0.015	0.127	0.223	0.689	0.363
<i>T. canadensis</i> vs. <i>P. rubens</i>	<0.001	0.072	0.621	0.034	—
Means					
Proportion open sky	0.045	0.103	0.198	0.418	1.00
Initial height (m)	1.55	2.33	2.77	3.74	3.29

Note: The contrast between *A. balsamea* and *P. rubens* in the open zone is from a separate ANOVA excluding *T. canadensis* over all light zones (not shown). Corresponding mean POS and initial heights by zone are also shown.

Fig. 3. Scatterplot of 2 year mean height growth over POS, showing fitted Michaelis–Menten height-growth response models (eq. 1, Table 3) plotted at the overall mean initial height of 2.77 m. Letters are species abbreviations, and the associated values are height classes (1, 0.5–1.99 m; 2, 2.0–3.99 m; 3, 4.0–6.0 m).



T. canadensis relative to the other species. *T. canadensis* significantly outgrows *P. rubens* in the dark zone, equals the others in the closed zone, but is significantly less than *A. balsamea* in the transition zone and less than both species in the gap zone (Fig. 2, Table 2). *Abies balsamea* outgrows *P. rubens* only in the dark zone; these two species do not differ under better illuminated conditions. Importantly, there are no conditions under which height growth of *A. balsamea* does not at least equal or exceed that of the other species.

The Michaelis–Menten models (Fig. 3; Table 3) help to quantify and generalize the patterns suggested by the comparisons among least-squares means above. With IH held constant, *A. balsamea* and *P. rubens* exhibit similar responses to increasing canopy openness, with little evidence of a saturating pattern. In contrast, height growth of *T. canadensis* appears to saturate at or below POS = 0.5 at an asymptotic upper limit that is 38%–53% that of the other species.

Gap fraction prediction

Formulated as eq. 2, BA explained 65% of the variation in POS at various understory heights with the following parameters: BA_{max} = 58.959 and b = 0.1387. Differences in R²

among BA₁, BA₂, and BA₃ were negligible, so BA₁ (the total stand BA, all trees included) was used for simplicity. HT⁻¹ was the optimum weight to stabilize the variance. Note that the fitted value for BA_{max}, which is intended to represent the biological maximum density, is nearly 60 m², a reasonable value for fully stocked stands in this forest type (Wilson et al. 1999). This model (Fig. 4) behaves as expected: in these multiaged stands with irregular canopies, a tree's light environment becomes increasingly favorable as it grows taller, presumably because the crowns of neighboring trees intercept relatively less light in the inverted conical zone above the tree's terminal shoot. As BA decreases, this effect becomes more pronounced. For example, the light environment of a tree with a surrounding BA of 10 m² (the lowest density observed) improves from a POS of 0.22 to 0.77 as it grows from 1 to 6 m tall; comparable values for a BA of 30 m² (the mean stand density) range from 0.09 to 0.43 (Fig. 4).

Discussion and silvicultural implications

Our results support a key finding of previous studies on shade-tolerant conifers which demonstrate that such species are most responsive to increases in canopy openness under very shaded environments (Carter and Klinka 1992; Klinka et al. 1992; Parent and Messier 1995; Duchesneau et al. 2001; Finzi and Canham 2000). *Tsuga canadensis* is most remarkable in this respect; based on the equations in Table 3, it reaches 50% of its maximum height growth at a POS of only 0.09, compared with 0.25–0.27 for *P. rubens* and *A. balsamea*, respectively. Gratzner et al. (2004) found essentially the same pattern for *Tsuga dumosa* (D. Don) Eichler. Both *A. balsamea* and *P. rubens* show more sustained responses to increased canopy openness, reaching 75% of their maximum height growth at a POS = 0.50–0.52; in contrast, *T. canadensis* reaches this value at a POS of only 0.22. Clearly, *T. canadensis* is competitive in height growth only under very shaded conditions where POS < 0.15, but even in this zone, it does not outgrow *A. balsamea*. Most importantly, there appear to be no understory light conditions that favor either *P. rubens* or *T. canadensis* over *A. balsamea* of the same height.

The lack of a distinct optimum level of canopy openness below fully open conditions (i.e., that would be evident as a peaking pattern in Fig. 2) is consistent with other studies involving established natural regeneration of

Table 3. Parameter estimates \pm SEs and nonlinear regression statistics for the asymptotic Michaelis–Menten models (eq. 1) plotted in Figure 3.

Species	<i>n</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>R</i> ²
<i>Abies balsamea</i>	90	0.3758 \pm 0.053	0.5623 \pm 0.133	0.4294 \pm 0.075	0.77
<i>Picea rubens</i>	72	0.2655 \pm 0.040	0.4849 \pm 0.125	0.5607 \pm 0.072	0.87
<i>Tsuga canadensis</i>	60	0.1416 \pm 0.029	0.1041 \pm 0.040	0.1755 \pm 0.097	0.49

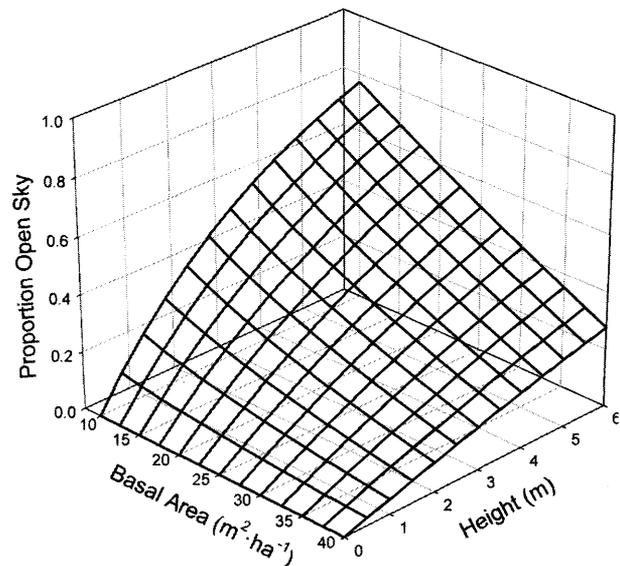
similar shade-tolerant species. Nonpeaking patterns have been found for *A. balsamea* (Parent and Messier 1995; Duchesneau et al. 2001) and *T. canadensis* (Finzi and Canham 2000) as well as in studies looking at other *Abies*, *Picea*, and *Tsuga* species associations in mixed-conifer stands of other geographic regions (Coates and Burton 1999; Gratzner et al. 2004).

Some comparative studies of the genera *Picea* and *Abies* report comparable growth rates but a delayed response for *Picea* spp. compared with *Abies* spp. after the canopy is opened (McCaughey and Schmidt 1982; Davis 1991; Messier et al. 1999; Doucet and Blais 2000), suggesting that the slower growth of *P. rubens* in our study could be an artifact of measuring too soon after canopy disturbance. Although we limited samples to locations that had not been disturbed within 5 years, we did not attempt to reconstruct exact dates of disturbances prior to this nor capture detailed, temporal trends in height-growth response beyond simple 2 year means. However, the difference between *P. rubens* and other species is most pronounced at very low light levels (Fig. 2), conditions which obviously have not experienced any recent disturbance or growth releases.

Studies that relate sapling height growth to light commonly incorporate initial tree size into their growth models either directly (Claveau et al. 2002; Boisvenue et al. 2004) or through the use of relative height growth as a dependent variable (Finzi and Canham 2000; Duchesneau et al. 2001; Fownes and Harrington 2004). In this study, POS was by far the most important predictor of height growth for a given species, but sapling height did explain an additional 6%–8% of the variation in the covariance analysis (Table 1) and nonlinear models (Table 3). The differing magnitudes of the *c* parameter in eq. 1 among species (Table 3) suggest that height growth of *P. rubens* increases more rapidly than the other species as saplings achieve a taller stature. For example, at a height of 0.5 m where *P. rubens* is predicted to grow 0.12 m·year⁻¹, predicted height growth of *A. balsamea* is 0.18 m·year⁻¹, which is a 47% advantage. However, at 6 m tall, *P. rubens* growth of 0.49 m·year⁻¹ is only 6% less than *A. balsamea*.

Other studies relating stand BA to canopy openness have been met with variable success. Although she did not fit a regression equation, Hale's (2001) data for *Picea sitchensis* (Bong.) Carr. (Sitka spruce) plantations in Britain agree with our model (Fig. 4) quite closely, with POS values <0.10 at BAs above 30 m²·ha⁻¹. Although Vales and Bunnell (1988) found BA to be weak in predicting direct and diffuse light penetration through western conifer stands, Kuusipalo (1985) achieved *R*² values of 0.63 predicting canopy openness based on stand-level BA alone and was able to achieve final *R*² values of 0.85 by adding a modifier to account for species composition, stand age, and stems per unit area.

Fig. 4. Relationship of stand basal area (m²·ha⁻¹, all trees >2.5 cm DBH) and POS at various heights in the understory of multiaged Acadian conifer stands.



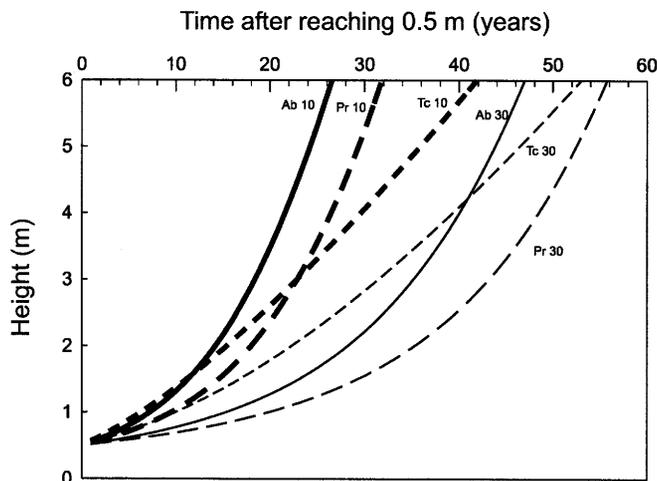
Although we did not test for species effects in eq. 2, we expect they would be minor, as we deliberately excluded plots with deciduous species in the main canopy.

Managing height development

Relative to *A. balsamea*, *P. rubens* has greater resistance to spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation and heart-rot fungi; *T. canadensis* is relatively long lived and pest resistant but much less valuable economically. Thus, management of Acadian conifers has attempted to favor *Picea* over other genera, with mixed success. Decades of observation and research demonstrate that *A. balsamea* regenerates more readily and prolifically and tends to outgrow *P. rubens* during the seedling and sapling stages, especially under open conditions on the more productive, well-drained soils (Seymour 1992). However, the question remains whether overstory manipulations that maintain relatively closed canopies, as in this study, could be designed to favor *Picea* spp. over other conifer species.

By linking the height increment equations (Fig. 3, Table 3) with the POS prediction model (Fig. 4), we can portray typical height development patterns under various levels of overstory cover and examine how overstory density might be manipulated to favor a given species. Because height growth and POS are both height dependent, equations must be solved recursively. First, POS is predicted from a fixed overstory BA at an arbitrary beginning height, say 0.5 m, using eq. 2. Next, eq. 1 is solved at the calculated POS to obtain height increment for a 0.5 m tall sapling. Height in-

Fig. 5. Estimated times required to grow from a height of 0.5–6.0 m, under overstory basal areas of 10 and 30 m²·ha⁻¹, by species. Letters are used to abbreviate species, and the associated values are basal areas.



crement is added to height, eq. 2 is solved again to obtain a new POS value (which will be slightly greater), and eq. 1 is solved again to predict the next height increment. Figure 5 illustrates the resulting height development for BAs of 10 and 30 m²·ha⁻¹ as each species grows from 0.5 to 6.0 m tall. In all cases, the curves increase exponentially, a direct result of the fact that height increment improves as trees grow taller and experience a more favorable light environment. The total time required to grow from 0.5 to 6 m, at which point the tree can be considered established in the midstory, was calculated under various overstory densities, and related to the time required if the tree were growing in the open (Table 4).

Study of Fig. 5 and Table 4 reveals that, under any overstory density up to ca. 30 m² (slightly greater than the target BA used to manage the multiaged stands), *A. balsamea* is the most competitive species. At a BA of 30 m²·ha⁻¹, at which POS increases from 0.05 to 0.43 as height increases from 0.5 to 6 m (Fig. 4), *T. canadensis* appears to have an early advantage at shorter heights; however, the much stronger response of *A. balsamea* as it gains stature results in *A. balsamea* surpassing *T. canadensis* at a height of 4 m and reaching 6 m 6 years sooner (Fig. 5). Thus, favoring *T. canadensis* would require keeping the BA at 40 m²·ha⁻¹ or higher; at that density, *T. canadensis* would reach 6 m in 66 years, 5 years sooner than *A. balsamea* and 18 years sooner than *P. rubens* (Table 4). As overstory BA is reduced, *P. rubens* becomes relatively more competitive, equaling *T. canadensis* at a BA of about 25 m²·ha⁻¹; under a BA of 10 m²·ha⁻¹, *P. rubens* reaches 6 m 10 years sooner than *T. canadensis* and only 5 years later than *A. balsamea* (Fig. 5). No feasible manipulation of overstory BA alone can favor *P. rubens* over *A. balsamea*. For *P. rubens* to reach 6 m during the time required by *A. balsamea*, *P. rubens* saplings require a “head start” of 3 years growing in the open to 13 years under a dense canopy of 40 m²·ha⁻¹ (Table 4, differences between species). These times correspond to *P. rubens* sapling heights ranging from 0.83 (in the open) to 0.64 m (BA = 40), equal to a height advan-

Table 4. Predicted times (years) required for saplings to grow from 0.5 to 6 m tall under a range of constant overstory basal areas in multiaged Acadian conifer stands (calculated recursively from eqs. 1 and 2).

Species	Overstory basal area (m ² ·ha ⁻¹)					
	0	5	10	20	30	40
<i>Abies balsamea</i>	17	23	27	35	47	71
<i>Picea rubens</i>	20	28	32	41	56	84
<i>Tsuga canadensis</i>	37	40	42	46	53	66

age of 0.14–0.33 m over a 0.5 m tall *A. balsamea*. Such an understory structure could be created by developing a healthy population of *P. rubens* saplings at least 1 m tall, then removing any competing *A. balsamea* and *T. canadensis* taller than 0.5 m in a cleaning treatment. Interestingly, this recommendation agrees with Westveld (1931) and Davis (1991), who both found that such *Picea* saplings compete successfully with shorter *A. balsamea*.

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