

Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine

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Abstract: Several hypotheses about the relationships among individual tree growth, tree leaf area, and relative tree size or position were tested with red spruce (*Picea rubens* Sarg.) growing in uneven-aged, mixed-species forests of south-central Maine, U.S.A. Based on data from 65 sample trees, predictive models were developed to (i) estimate the amount of foliage held by individual trees from sapwood cross-sectional area and (ii) define the relationship between stem volume growth and three variables: total foliage area, relative position in the stand, and the degree of past suppression. A model that included variables representing tree size (or relative social position) and degree of past suppression (live branch whorls per unit crown length) indicated that stem volume growth first increased but later decreased over leaf area when other variables were held constant. Growth efficiency declined with increasing tree leaf area, although greater height and diameter enhanced growth efficiency and greater past suppression diminished growth efficiency. The decline in growth efficiency with greater leaf area likely is attributable to one or several of the factors previously identified as contributing to growth declines in mature, even-aged stands.

Résumé : Plusieurs hypothèses concernant les relations entre la croissance d'un arbre individuel, sa surface foliaire et l'étage qu'il occupe, ou sa dimension relative, ont été testées chez des épinettes rouges (*Picea rubens* Sarg.) croissant dans les forêts mélangées et inéquiennes du Centre-Sud du Maine, aux États-Unis. Des modèles de prédiction ont été développés à partir de données provenant de 65 arbres-échantillons dans le but : 1) d'estimer la quantité de feuillage dans un arbre à partir de la surface de bois d'aubier dans une section radiale; et 2) de définir la relation entre la croissance en volume de la tige et trois variables : la surface totale du feuillage, la position relative dans le peuplement et le degré de suppression antérieure. Un modèle qui comporte des variables relatives à la dimension d'un arbre (ou sa position sociale relative) et au degré de suppression antérieure (nombre de verticilles avec des branches vivantes par unité de longueur du houppier) indique que la croissance en volume de la tige augmente et plus tard diminue par rapport à la surface foliaire lorsque les autres variables sont gardées constantes. L'efficacité de la croissance diminue avec l'augmentation de la surface foliaire, malgré le fait qu'une hauteur et un diamètre plus grands augmentent l'efficacité de la croissance et une plus forte suppression antérieure diminue l'efficacité de la croissance. La diminution de l'efficacité de la croissance avec l'augmentation de la surface foliaire est probablement due à un ou plusieurs des facteurs déjà identifiés pour leur contribution à la diminution de la croissance dans les peuplements équiennes matures.

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Introduction

Stem volume growth per unit leaf area has been applied to assess vigor of individual trees and to investigate the relationship between tree growth and stand structure (Waring et al. 1980; Smith and Long 1989; Long and Smith 1990). The variation in this index, commonly referred to as growth efficiency (GE), is relatively well understood in even-aged stands of a single species. Briefly stated, GE in these simple

stand structures follows a decreasing trend with increasing size, typically measured by total tree leaf area (Kaufmann and Ryan 1986; Smith and Long 1989). In relatively shade-tolerant species, this trend is modified slightly by the persistence of suppressed stems that are growing more poorly (lower GE) than trees of greater relative height within the stand (Roberts and Long 1992, Roberts et al. 1993).

In uneven-aged stands the expected general trends in growth efficiency are complicated by at least two factors: (i) the stands consist of two or more cohorts that typically form relatively distinct strata (for example, the A-B-C-D strata originally devised for tropical forests (Richards 1952) and suggested for uneven-aged temperate forests by Oliver and Larson (1990)); and (ii) relative size or height in the stand is generally correlated with both tree age and tree leaf area. In uneven-aged ponderosa pine stands (*Pinus ponderosa* Dougl. ex Laws.), O'Hara (1996) reported an accelerating rise in stem volume growth with increasing tree leaf area, implying an increase in GE with increasing tree size. However, GE is normally expected to decline with increasing size because of one or several contributing factors

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Table 1. Sample stand attributes based on nested 0.08- and 0.02-ha plots associated with sample trees.

Attribute	Minimum	Mean	SD	Maximum
Basal area (m ² /ha)	3.12	15.51	6.83	34.00
Trees/ha	234	3437	2917	15326
Quadratic mean DBH (cm)				
All species	3.94	9.39	4.05	21.13
<i>Picea rubens</i>	2.03	22.32	10.65	43.53
<i>Tsuga canadensis</i>	1.75	10.78	9.06	42.67
<i>Abies balsamea</i>	1.52	4.99	2.05	13.29
<i>Acer rubrum</i>	2.30	9.16	5.57	25.81
<i>Betula papyrifera</i>	1.27	14.28	11.22	38.10
Species composition by basal area				
<i>Picea rubens</i>	0	27.3	20.6	72.4
<i>Tsuga canadensis</i>	0	30.6	25.0	83.7
<i>Abies balsamea</i>	0	17.6	13.9	60.5
<i>Pinus strobus</i>	0	6.4	15.5	88.2
<i>Thuja occidentalis</i>	0	5.2	8.9	50.2
<i>Acer rubrum</i>	0	7.6	7.6	32.2
<i>Betula papyrifera</i>	0	2.4	3.3	13.3

including: increasing respiration load associated with live cells in the sapwood of stems or branches (Ryan 1989; Ryan and Waring 1992; Roberts and Long 1992), relative allocation to stemwood production (Kuuluvainen 1988), plant water relations (Ryan and Yoder 1997), and tissue maturation (Greenwood and Hutchinson 1993). The increase in GE reported by O'Hara for ponderosa pine stands may be attributable to a combination of factors that are unique to uneven-aged stands or to this particular species: relative shade intolerance; longevity and large attainable size; and correlations among total leaf area, vertical position in the stand, and intensity of intercepted light.

Roberts et al. (1993) have suggested a model that reconciles the difference in GE behavior between shade-intolerant species (lodgepole pine) and shade-tolerant species (subalpine fir, *Abies lasiocarpa* (Hook.) Nutt.) growing in even-aged stands. The peaking behavior of GE in the latter species is attributed to the tendency of this shade-tolerant species to develop greater vertical stratification. Greater leaf area of individual fir trees is initially associated with improved vertical position in the stand and, hence, with interception of more intense solar radiation (Roberts and Long 1992). For trees within the main canopy, however, greater leaf area is associated less with improved light interception per unit of foliage and more with the above-mentioned factors leading to the decline in stemwood growth per unit leaf.

Because uneven-aged stands are likewise characterized by extreme vertical stratification relative to even-aged stands, it stands to reason that an increase in tree leaf area would be associated with a superior social position and improved light environment. In fact, it is quite possible that the increase in GE associated with increase in tree size over the small end of the size range would extend over an even greater range in tree leaf area for uneven-aged stands; that is, the peak would be shifted to the right or to larger leaf areas. Although not indicated by O'Hara's (1996) ponderosa pine data, the GE of ponderosa pine in any given stand presumably would have to reach a peak and begin declining (Yoder et al. 1994;

Kaufmann 1996); in fact, there is some evidence in O'Hara's (1996) data that a different model form for describing the increase in tree increment with increasing leaf area would have detected the beginning of an apparent slow-down in growth for ponderosa pine trees with larger leaf areas. Regardless, the data for ponderosa pine suggest that a considerable range of increasing GE prevails as smaller trees emerge from lower canopy levels; hence, the presumed eventual decline in GE is delayed until surprisingly large leaf areas are attained.

A question arises as to the generality of increasing GE with increasing tree size for uneven-aged stands. Would the same trends be observed for more shade-tolerant and (or) more mesic species? If so, would these trends be enhanced or dampened? Can the positive influence of improved social position on stem volume growth be separated from the negative effects normally associated with greater tree size? Does the degree of past suppression affect GE, all else being equal? The objective of the present study was to test the following hypotheses for red spruce (*Picea rubens* Sarg.) growing in uneven-aged, mixed-species stands in the northeastern United States:

- (1) GE peaks over the range of observed tree leaf area;
- (2) for a tree of given leaf area, GE increases with relative height in the stand; and
- (3) for a tree of given leaf area and relative height, GE decreases with increasing past suppression (measured by number of branch whorls per unit crown length).

Methods

Study site

The study site is part of a silvicultural experiment within the Penobscot Experimental Forest (PEF), located in the towns of Bradley and Eddington, in southern Penobscot County, Maine, U.S.A. (approximately 44°52'N, 68°38'W). Under a recent ecological land classification, the PEF is located in the Central Maine Coastal and Interior Section of the Laurentian Mixed Forest Province (McNab and Avers 1994). Forest composition is consistent with Rowe's (1972) Acadian Forest Region. The 30-year (1951–1980) normal (i.e., mean annual) temperature for nearby Bangor, Maine, is 6.6°C. The warmest month is July with a normal temperature of 20.0°C; this is higher than the 18°C mean July isotherm that Kuusela (1990) used to define the southern boundary of the boreal coniferous forest. The coldest month in Bangor is January with a normal temperature of –7.7°C. Normal precipitation is 1060 mm per year, with 48% falling from May through October.

Glacial till is the principal soil parent material on the PEF. Soil types vary from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams and silt loams in flat areas between these low-profile ridges. In general, the northern conifer sites from which many of the trees were sampled in this study are underlain by poorly to very poorly drained loams and silt loams.

The forest canopy within the silviculture experiment is dominated by a mixture of species, primarily red spruce, balsam fir (*Abies balsamea* (L.) Mill), and eastern hemlock (*Tsuga canadensis* (L.) Carr.), with lesser amounts of white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), eastern white cedar (*Thuja occidentalis* L.), white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), and gray birch (*Betula populifolia* Marsh.) (Table 1). Red spruce, white spruce, and balsam fir dominate the

relatively low-lying sites of poorer drainage, but the proportion of eastern hemlock and white pine increases as drainage improves.

Field procedures

The long-term silviculture experiment was implemented on the PEF by the USDA Forest Service between 1952 and 1957, primarily to investigate the effect of silvicultural treatment on growth, yield, and regeneration (Frank and Blum 1978, Brissette 1996). The 10-ha selection system units forming the basis of this study have been managed with goals defined by species composition, density, and diameter-class distribution. Maximum diameter at breast height (DBH) was set at 51 cm, the post-harvest basal area goal was 23 m²/ha, the target diminution quotient (see Nyland 1996) for 2.54-cm DBH classes was 1.4, and *Picea* species were to be favored over all other trees. In practice, cutting has emphasized capturing mortality and improving stand quality and species composition over strict adherence to residual basal area, maximum DBH, and diminution quotient goals.

Sixty-five red spruce trees were sampled in July 1994 from units 6, 10, 12, 13, and 25, all of which were scheduled for some type of partial harvesting. Sample trees were selected uniformly across the diameter range (11–48 cm) and in association with nested permanent plots (0.08 ha and 0.02 acre (1 acre = 0.405 ha)) that are located in each unit on an approximate 100-m spacing. The following measurements were taken on the standing sample tree: DBH (nearest 0.1 cm); total height (nearest 0.1 m); height to crown base (nearest 0.1 m), and crown radii in the four cardinal directions (nearest 0.1 m).

Each sample tree was then felled at a 0.15-m stump and disks were cut at breast height (1.37 m), at the crown base, and at approximately 2.5-m intervals to the tip of the tree, but avoiding stem swellings associated with large branches and branch whorls. On the stump cut and on disks from the upper stem, two axes were marked with a pen: (i) the longest axis; and (ii) the axis perpendicular to the longest. Diameter inside bark (DIB) and diameter outside bark (DOB) were recorded (nearest 1 mm) on each axis, and all disks were then transported to the laboratory for further analysis.

On 40 of the 65 sample trees, a green branch was randomly sampled by selecting the branch nearest to a random height on the bole between crown base and tree tip. This branch was cut flush with the bole, and its height on the bole at point of insertion was recorded (nearest 0.01 m). Diameter of the branch (nearest 1 mm) was measured just above any basal swelling. A subsample of fresh foliage was picked from each sample branch by selecting age classes in approximate proportion to their representation on the whole branch. This fresh sample was then immediately placed in a cooler and transported to the laboratory for freezing at the end of the day. The remainder of the branch was clipped and packed into a large paper bag for drying.

Sixteen of the 65 sample trees were also measured for their primary branching structure. This process involved measuring height (nearest 0.01 m) and basal diameter (nearest 1 mm) of each live branch on the tree.

Laboratory procedures

Two radial growth rates (nearest 0.5 mm) were measured on each axis of each disk for the 5-year growth period ending in 1993 (that is, the current growing season was disregarded). In addition, breast height and crown base disks were analyzed for cross-sectional sapwood area by staining with methyl orange, delineating the transition between sapwood and heartwood, and determining areas with a Java image analysis system.

Full branch samples were dried at 70°C for at least 1 month, after which the foliage and wood + bark fractions were hand sepa-

rated. The sample was then redried at 70°C for at least another 24 h and the foliage was weighed to the nearest 0.01 g.

A subsample of 100 needles was randomly drawn from the frozen fresh sample collected on each branch, and total projected leaf area was determined with an AgVision image processing system. These 100 needles were then placed in a small envelope, dried at 70°C for at least 24 h, and weighed to the nearest 0.0001 g. Specific leaf area was computed as the ratio of projected foliage area (cm²) to dry weight (g). The needles remaining from the frozen fresh sample were dried and their weight was combined with the rest of the full branch sample.

Analysis

Total projected foliage area for each of the 40 sample branches was estimated by multiplying its foliage dry weight by its specific leaf area. The following linear regression model, selected on the basis of Furnival's (1961) index of fit, was fitted to the data to facilitate estimation of branch foliage area from branch diameter and position in the crown:

$$[1] \quad \ln(BLA) = a_0 + a_1 \ln(BD) + a_2 \ln(RDINC) + a_3 RDINC$$

where BLA is branch projected leaf area (cm²), BD is branch basal diameter (mm), and RDINC is relative depth into crown (RDINC = (tree height – branch height)/crown length). The branch-level foliage area equation was applied to each of the 16 crown-sample trees on which all primary branches were measured, allowing an estimate of the total foliage area for each tree. The following models were then developed for estimating tree-level foliage area from sapwood cross-sectional area at either crown base or breast height:

$$[2] \quad TLA = c_1 SACB^{b_2}$$

$$[3] \quad TLA = c_1 SABH^{c_2}$$

where TLA is predicted tree leaf area (m²), SABH is sapwood area at breast height (cm²), and SACB is sapwood area at crown base (cm²). Stem volume growth for each sample tree was computed as the difference between the initial and ending stem volumes for the 5-year growth period ending in late summer 1993. Each stem section was assumed to conform to the frustum of a paraboloid as implied in Smalian's formula for log volumes, except for the tip of the tree, which was assumed to be a cone. The past 5-year height growth of the conical tip section was assumed to maintain the same base-to-height proportion in the previous conical tip section as was observed in the current tip section.

Leaf area of the remaining 49 sample trees was estimated from eq. 2, and GE was computed as the ratio of periodic stem volume growth (m³) to current total foliage area (m²) for the tree. To allow comparison of the growth relationships for red spruce to results documented by Roberts and Long (1992) for subalpine fir and Gilmore and Seymour (1996) for balsam fir, the following regression model was fitted to the data:

$$[4] \quad dV = d_1 TLA^{d_3-1} \exp[-(d_2 TLA)^{d_3}]$$

where dV is 5-year stem volume growth (m³) and TLA is total projected leaf area for the tree (m²). This model had the flexibility to accommodate both the exponential growth potential of small trees (that is, trees with low leaf area) and the later deceleration and possible decline of stem volume growth with increasing leaf area. This basic model was then analyzed for two aspects of red spruce growth behavior: (i) GE, computed as the ratio of predicted stem volume growth to total tree leaf area; and (ii) marginal growth efficiency, MGE, computed as the predicted marginal change in stemwood volume growth per unit increase in leaf area (that is, the first derivative of eq. 4 with respect to TLA).

Table 2. Attributes of sample trees ($n = 65$) and sample branches ($n = 40$).

Attribute	Minimum	Mean	SD	Maximum
Sample trees				
DBH (cm)	11.0	28.0	9.8	48.3
Height (m)	9.45	17.91	3.39	23.68
Crown length (m)	3.12	9.60	3.30	17.24
Crown ratio	0.23	0.53	0.14	0.80
Crown diameter (m)	1.98	4.57	1.65	8.34
Crown projection area (m ²)	3.08	18.49	12.74	54.71
Crown volume (m ³)	3.7	69.0	63.3	273.0
Sapwood area at crown base (cm ²)	25.2	139.1	99.5	410.0
Leaf area (m ²)	23.8	133.6	85.7	401.7
Stem volume growth (m ³)	0.004	0.052	0.035	0.168
Sample branches				
Diameter (mm)	5	31	13	53
Depth into crown (m)	0.25	5.16	4.01	14.49
Relative depth into crown	0.02	0.54	0.32	1.00
Leaf mass (g)	7.7	345.7	272.1	1161.0
Projected leaf area (cm ²)	357	15 532	13 175	65 814

Table 3. Parameter estimates and standard errors for branch, crown, and tree growth models.

Parameter estimate	Estimated value	Standard error
Model (eq. 1) for estimating branch leaf area from branch diameter and depth into crown		
a_0	4.452 9	0.766 8
a_1	1.740 6	0.168 7
a_2	0.532 03	0.188 8
a_3	-1.024 1	0.549 3
Model (eq. 2) for estimating tree leaf area from sapwood area at crown base		
b_1	0.524 46	0.277 97
b_2	1.088 4	0.050 97
Model (eq. 3) for estimating tree leaf area from sapwood area at breast height		
c_1	0.595 01	0.215 15
c_2	0.987 08	0.069 58
Model (eq. 4) for predicting stem volume growth from tree leaf area		
d_1	0.000 592 20	0.000 194 06
d_2	0.001 667 0	0.000 520 0
d_3	1.970 0	0.074 4
Model (eq. 5) for estimating stem volume growth from tree leaf area, size, and past suppression		
g_1	0.000 790 76	0.000 323 25
g_2	0.001 967 5	0.000 506 0
g_3	1.820 66	0.094 2
g_4	0.010 750	0.002 976
g_5	-0.037 426	0.017 396

Because TLA was expected to be correlated with other influential variables such as relative height or size of the tree, eq. 1 was expanded to distinguish the effects of increasing leaf area from the effects of increasing relative position, yielding the following model:

$$[5] \quad dV = g_1 TLA^{g_3-1} \exp[-(g_2 TLA)^{g_3}] D^{g_4 H} (SUPP^{g_5})$$

where D is the tree diameter at breast height (cm), H is the total tree height (m), SUPP is the index of past suppression (number of live branch whorls/crown length), and dV and TLA are as defined above.

Analysis of this model as described above for eq. 4 provided insight into the behavior of GE and MGE relative to TLA, and relative to social position of the tree and degree of past suppression.

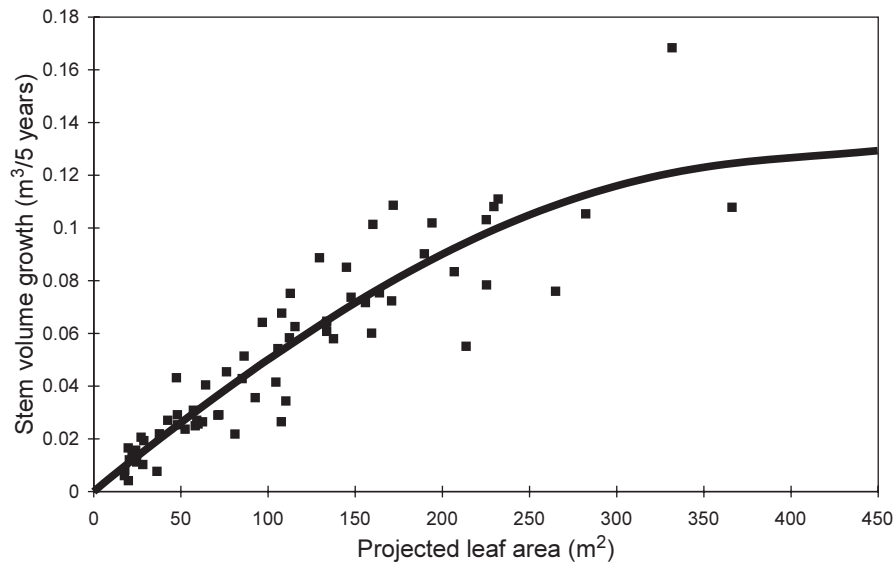
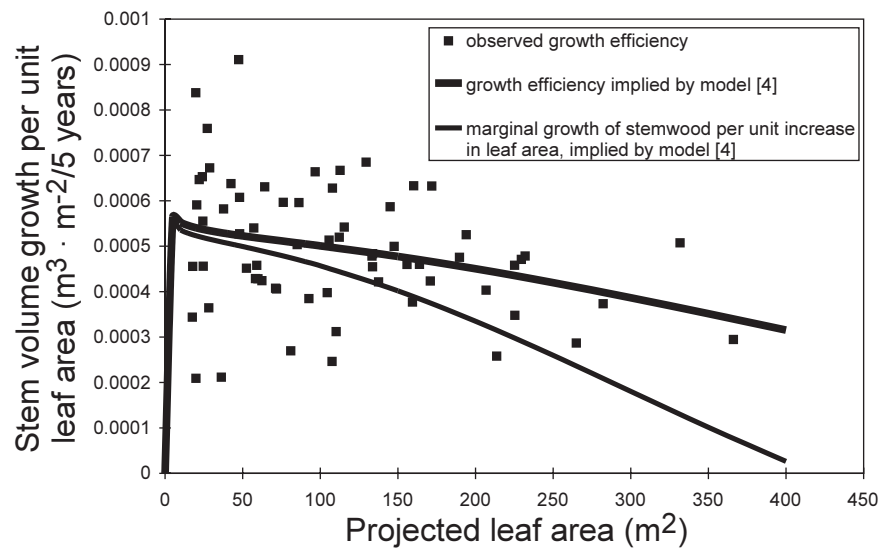
Results

Despite the fact that the five units were all similarly managed under a selection system, stand structure varied considerably among the plots with which the sample trees were associated (Table 1). By basal area, species composition varied from 0 to 72% red spruce, from 0 to 84% eastern hemlock, and from 0 to 32% red maple (Table 1). Individual sample trees ranged from 11 to 48 cm in DBH and from 9.5 to 23.7 m in height (Table 2). This size range corresponded to an age range of approximately 55–160 years at breast height. Crown ratios averaged 53%, but variation in this attribute (23–80%) can be considered a result of both variation in local stand density and irregularity in past harvesting intensity. Sample branches also covered a wide size interval because of the represented range in crown size and relative position in the crown (Table 2).

Parameter estimates for eqs. 1–5 were all significant at $\alpha = 0.05$, with the exception of a_3 , which had a p value of 0.07. The branch-level foliage area equation (eq. 1) explained 87% of the variation in branch leaf area and yielded an MSE of 0.0048. After including a simple log bias correction (Flewelling and Pienaar 1981), the implied prediction equation can be expressed as

$$[6] \quad BLA = 86.0862 BD^{1.740\ 607} \times RDINC^{0.532\ 027} \times \exp(-1.024\ 050\ RDINC)$$

Estimated leaf areas of the 16 individual crown trees ranged from 26 to 378 m², and these trees covered the

Fig. 1. Regression relationship between stem volume growth and total tree leaf area (eq. 4).**Fig. 2.** Growth efficiencies (GE) implied by eq. 4 (heavy line) superimposed on observed growth efficiencies. Light line shows the marginal growth in stem volume per unit increase in leaf area (MGE), as implied by eq. 4.

conditions represented by the full set of 65 sample trees (see Table 2 for the latter).

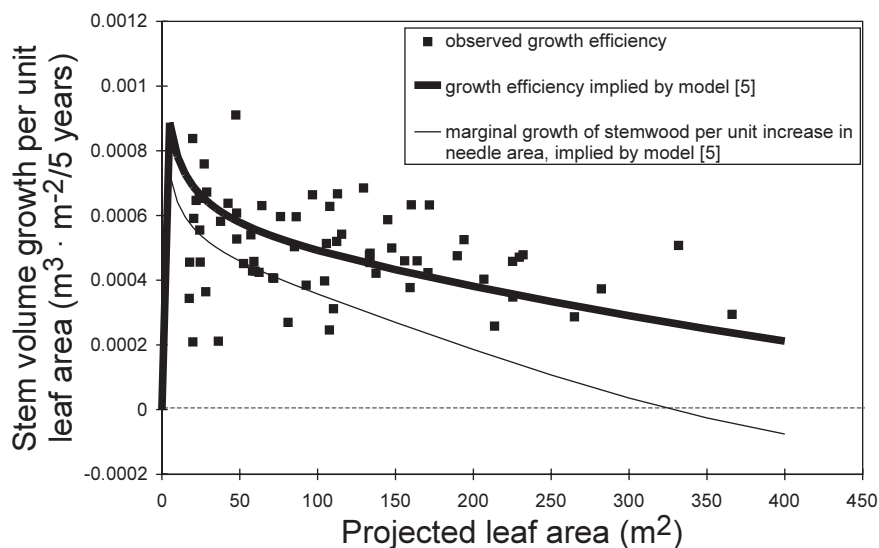
To correct for increasing variance, eq. 2 was weighted by $SACB^{-3}$. This nonlinear model accounted for 92% of the variation in weighted total leaf area for the 16 crown trees and yielded a weighted MSE of 0.000 162 3. The implied range in estimated leaf area for the full set of 65 sample trees was 24–402 m². The model for estimating tree leaf area from sapwood area at breast height accounted for 89% of the variation in weighted total leaf area and yielded a weighted MSE of 0.01849. Because eq. 3 was weighted by $SABH^{-2}$ rather than by $SACB^{-3}$ as in eq. 2, the MSEs are not directly comparable; however, Furnival's (1961) index was 15.9 and 23.3 for eq. 2 and 3, respectively, indicating that eq. 2 was superior. Although both eqs. 2 and 3 yielded much higher leaf area/sapwood area ratios than those reported by

Marchand (1984), a similar degree of departure from the latter was found for balsam fir in Maine (Gilmore et al. 1996).

The inference drawn from eq. 4 was that stem volume growth tended to increase with increasing leaf area but at a decreasing rate across the full range of observed total leaf areas (Table 3, Fig. 1). Analysis of the relationship described by eq. 4 revealed that average GE decreased monotonically over the range of the observed data (Fig. 2). Likewise, the instantaneous rate of change in stemwood growth per unit increase in leaf area, or MGE, decreased monotonically over the same range, but did not drop below zero (Fig. 2). In short, neither GE nor MGE exhibited the hypothesized early increase and later decrease over increasing leaf area.

In contrast to the results from eq. 4, the expanded model (eq. 5) contained effects of both tree size and degree of past suppression (Table 3). Stem volume growth continued to

Fig. 3. Growth efficiencies (GE) implied by eq. 5 (heavy line) superimposed on observed growth efficiencies. Light line shows the marginal growth in stem volume per unit increase in leaf area (MGE), as implied by eq. 5.



increase with increasing leaf area up to 328 m² and then began to decline. Consistent with expectations, as tree size, and hence, social position, in the stand increased, volume growth tended to increase (Table 3). In contrast, volume growth declined with an increasing number of branch whorls per unit of crown length (Table 3). The net result of accounting for the effect of relative tree position and degree of past suppression was that, in addition to the monotonic decline in both GE and MGE that was observed in eq. 4 across leaf area, MGE dropped below zero (Fig. 3). This latter result reflected the peak in volume growth observed at a leaf areas of approximately 328 m².

Discussion

The trend in GE over total tree leaf area observed for these uneven-aged stands of red spruce departed from the behavior that would be predicted from previous results in both even-aged stands of stratified shade tolerants (Roberts et al. 1993; Gilmore and Seymour 1996) and in uneven-aged stands of stratified shade intolerants (O'Hara 1996). Rather than exhibiting a peak over leaf area, GE declined monotonically, as has been observed in even-aged stands of lodgepole pine (Roberts et al. 1993). As discussed previously, an increase in tree leaf area is accompanied by a gain in relative height and, hence, by improved light conditions. For individual tree crowns, greater availability of light generally results in a greater net photosynthetic rate (Fuchs et al. 1977) and greater tree growth (Chen et al. 1996). This trend is supported by the strong performance of variables representing relative tree position in growth models; for example, tree growth is negatively correlated with the amount of stand basal area in trees that are larger than the subject tree (Wyckoff 1990). In the PEF red spruce stands, there does not seem to be a sufficient improvement in light or other conditions associated with increasing leaf area for the stemwood production per unit leaf area to be enhanced. Rather, other factors that contribute to growth decline with advancing age apparently offset the benefits of improved light environment.

It should also be noted that the expected increase in GE with increasing leaf area as documented for well-stratified shade-tolerant species (Roberts and Long 1992) and as might be expected for uneven-aged stands relies on the strong correlation between total leaf area and relative height in a stand; if this correlation is weak or nonexistent, then GE would be expected to increase with relative height but not necessarily with total leaf area.

It is important to consider the possibility that the increase in leaf area at the low end of the diameter distribution observed by Roberts et al. (1993) and Gilmore and Seymour (1996) may have been missed because of the 11-cm minimum DBH in the red spruce analysis. However, it was also expected that the peak in GE would be shifted to larger trees in these highly stratified uneven-aged stands. One alternative explanation for the lack of a GE peak may be the effects of past suppression on the smaller red spruce trees. The relatively advanced ages of even the smallest trees (≥ 55 years) suggests that they must have been suppressed understory trees at time of treatment initiation (ca. 1952). It remains to be seen whether younger cohorts representing seedlings established since 1952, or advance regeneration released relatively soon after establishment, will lead to structures and growth dynamics that are more consistent with past observations in highly stratified stands. It is conceivable that these more recent cohorts growing in the lower layers of stands undergoing conversion to an uneven-aged condition would be more vigorous and more capable of response to improved light conditions. On the other hand, red spruce is well known for its remarkable ability to release after years of persistence in the seedling pool as advance regeneration (Seymour 1994), and the index of suppression introduced into the full model should have accounted for the effect of past suppression. This index could be interpreted in a number of different ways, however, so it is plausible that several causal mechanisms were in operation. For example, since red spruce forms annual whorls of branches, the number of whorls per unit crown length is essentially the reciprocal of height growth averaged over a varying number of years prior

to 1994. Hence, as an index of past height growth and, to a certain extent, of past stemwood growth, it is logical to expect this measure to be correlated with stemwood growth during the previous 5-year growth period. Alternatively, Kuuluvainen (1988) has hypothesized that trees of given leaf area, diameter, and height have a poorer growth rate if the foliage is packed into a smaller vertical distance, because of less favorable within-crown light distribution, impeded gas exchange, or both.

The units sampled at the PEF were similar in overall structure, so despite some local variation in stand density and canopy height, trees of given size (diameter, height, and crown size) occupied, on average, similar social positions within these stands. Where a wider range in stand conditions is characteristic, the relationship between tree leaf area alone and stemwood growth would be more difficult to establish. For example, in the case of two stands having drastically different canopy heights or B-layer density, two trees with the same leaf area may be growing in entirely different light environments. Likewise, these two trees of similar leaf area could be very different in height and diameter if their respective stands differ dramatically in total stand density or within-in layer density. Hence, the introduction of variables that account for these differences in the statistical models (for example, eq. 5) becomes particularly important in highly variable stands. Under the condition of widely varying canopy heights, tree height alone is an insufficient surrogate for relative height or relative depth in the canopy; rather, a variable representing the ratio of the subject tree height to local canopy height would be necessary. In this regard, crown ratio offers strong potential as a surrogate for local stand density or general stand structure, although neither crown ratio nor crown length were marginally significant in the final volume growth model for red spruce. The combination of leaf area, DBH, and height almost certainly served as a comparable surrogate in these PEF units.

In summary, the results for red spruce suggested that a different relationship between tree growth and leaf area emerges depending on whether the statistical model is corrected for the influence of other factors such as relative social position of the tree. When the relationship between stem growth and leaf area alone was explored, growth continued to increase with leaf area even in the largest trees, apparently because tree leaf area is positively correlated with relative vertical position in the stand. In contrast, it became evident in the full model that, at large tree sizes, an increase in leaf area with no or little corresponding increase in tree height led to a decline in stemwood growth, yet an increase in tree height with no corresponding increase in leaf area led to an improvement in growth. In other words, interpretation of the relationship between tree growth and leaf area is complicated by the fact that leaf area is correlated with other determinants of tree growth, especially within a stand. In these uneven-aged, mixed-species stands, no evidence was found for an increase in red spruce growth efficiency with increasing leaf area, either with or without a correction for size or vertical position of the tree. More intricate variables representing local stand structure were not introduced into the models, but it is not likely that the general relationship between tree leaf area and GE would change even though some of the residual variation may be explained by these

variables. The general behavior of GE in uneven-aged stands does not appear to follow a general and consistent pattern but rather may depend on the silvics of the species involved and the specific stand structures and stand histories sampled. In many respects, this apparent inconsistency would be expected in light of the wide variety of stand structures described as uneven aged.

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