Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York

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This paper describes relationships between tree growth indices based on ring width measurements at 1.4 m aboveground and indices derived from whole-stem analysis for red spruce (*Picea rubens* Sarg.) in a high-elevation spruce-fir forest on Whiteface Mountain, New York. Coefficients of determination for linear regressions between mean, standardized chronologies for breast-height ring width versus whole-stem ring width and basal area increment versus annual volume increment are 0.89 and 0.93, respectively. However, substantial variability is apparent in breast-height versus whole-stem relationships for individual trees, particularly for unstandardized growth indices. Also, relationships between unstandardized growth indices exhibit temporal instability associated with individual tree maturation and stand dynamics. Nonetheless, strong relationships between mean standardized chronologies of breast-height and whole-stem growth indices validate the use of breast-height growth indices to represent year-to-year variation in mean growth performance of red spruce. A volume-equation-based procedure is described that provides better dendrochronological estimates of annual volume increment than estimates based on basal area increment alone.

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Ce texte décrit les relations entre les indices de croissance de l'arbre basés sur les mesures des cernes de croissance à 1,4 m au-dessus du sol et les indices obtenus de l'analyse de la tige entière d'épinette rouge (*Picea rubens* Sarg.) dans une forêt épinette-sapin de haute altitude de Whiteface Mountain, New York. Les coefficients de détermination pour les régressions linéaires, entre la moyenne standarisée des largeurs de cernes chronologiques à hauteur de poitrine versus les largeurs de cernes de la tige entière et l'accroissement en surface terrière versus l'accroissement annuel en volume sont 0,80 et 0,93, respectivement. Toutefois, une variabilité substantielle est apparente à hauteur de poitrine versus les relations de tiges entières pour des arbres individuels particulièrement pour des indices de croissance non standardisés. Aussi les relations entre les indices de croissance non standardisés indiquent une instabilité temporaire associée à la maturation individuelle de l'arbre et la dynamique du peuplement. Néanmoins, de fortes relations entre la moyenne standardisée des indices de croissance chronologiques à hauteur de poitrine et pour la tige entière valident l'utilisation des indices de croissance à hauteur de poitrine pour représenter la variation année par année de la performance de la croissance moyenne de l'épinette rouge. Une procédure de base d'équation de volume est décrite et elle fournit de meilleures estimations dendrochronologiques de l'accroissement du volume annuel que les estimations basées seulement sur l'accroissement en surface terrière.

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Introduction

Radial growth at breast height (1.4 m aboveground) is a widely used expression of forest productivity in forestry, dendroclimatology, and ecology. Conceptual models of carbon allocation in trees suggest that stem wood production is a sensitive index for overall growth performance (Waring and Schlesinger 1985). Most commonly, growth indices are based on measurements of tree ring width or ring area on samples of wood extracted from the stem with an increment borer. Alternatively, detailed stem analysis involves measurement of tree ring width at many points along the length of the stem, thus providing information on the exact dimensions of the annual xylem layer. However, because stem analysis requires destructive harvesting and is resource intensive, this procedure is rarely used. This paper compares tree stem wood growth indices derived from simple breast-height ring width measurements with indices derived by detailed whole-stem analysis.

Most historical growth data documenting red spruce (*Picea rubens* Sarg.) decline in the northeastern United States are derived from ring width measurements on increment cores taken at breast height (Adams *et al.* 1985; Cook *et al.* 1987; Hornbeck and Smith 1985; Hornbeck *et al.* 1986; Johnson and Siccama 1983; Johnson and McLaughlin 1986;

Johnson *et al.* 1988; McLaughlin *et al.* 1987; Van Deusen 1987). Standardized ring width (i.e., detrended; *sensu* Fritts 1976) is the most commonly used radial growth index in these studies. However, Hornbeck and others (1985, 1986) use unstandardized annual ring area (basal area increment) as an index of tree growth responses. These studies assume a close (i.e., linear and temporally stable) relationship between breast-height (BH) and whole-stem (WS) growth indices, but this has not been validated.

The complex stand dynamics and high wind speeds in uneven-aged, high elevation spruce-fir forests suggest *a priori* that relationships between breast-height and whole-stem radial growth indices may deviate from a temporally stable simple linear model. Red spruce grows more slowly than balsam fir (*Abies balsamea* (L.) Mill.) but is considerably longer living (Fowells 1965). Therefore, in high elevation spruce-fir forests, young red spruce are often suppressed by balsam fir competitors and then subsequently released when the fir overstory dies. Mature red spruce may have experienced temporal variations in competition associated with one to three generations of balsam fir. Effects of fir stand dynamics on red spruce radial growth may be complicated by the effects of high wind speeds at higher elevations on allocation patterns of radial growth

along the length of the stem. Removal of neighboring trees and consequent increased wind sway in the stem have been shown to increase radial growth at the base of the stem at the expense of growth along the upper stem (Larson 1963, 1965; Myers 1963; Thomson and Barclay 1984). Significant variation in allocation patterns of radial growth along the stem would degrade the presumed close relationship between radial growth at breast height and whole-stem growth performance.

The objectives of this study are (1) to characterize the relationships between breast-height and whole-stem radial growth indices for montane red spruce, and (2) to evaluate the effects of factors that cause BH-WS relationships to vary.

Methods

As part of a study of red spruce decline, 46 dominant and codominant red spruce trees were sampled from sites at 900- and 1100-m elevation on Whiteface Mountain, New York. Both sites are virgin spruce-fir forest with ca. 70% mortality of overstory red spruce (LeBlanc *et al.* 1987a). Ranges for some sample tree characteristics are as follows: total age, 62–320 years; age since release, 39–290 years; diameter at breast height, 21–52 cm; and height, 13–22 m. Sample trees were felled and cross sections (disks) were cut at 15-cm intervals acropetally until bud scale scars were visible on the bark, and thereafter in the center of each internode to the apex. This switch from fixed-interval to internode-based sampling provided detailed data on apical and radial growth near the apex for the 1960–1985 period, used in collateral analyses of recent red spruce decline (LeBlanc and Raynal 1990). Cross-dated ring counts (based on within-tree patterns of large and small rings) were made on each disk and used to reconstruct tree height for each year.

Ring widths were measured to ±0.01 mm along four radii on the cardinal compass bearings on disks at 45-cm intervals for that portion of the stem sectioned at 15-cm intervals, and on all disks cut from anatomically defined internodes. Growth indices were calculated from ring width and area measurements and "internode lengths" (i.e., the length of the stem represented by a disk). For that portion of the stem sectioned at 15-cm intervals, "internode length" was calculated as the sum of half the distances between a disk on which ring widths were measured and adjacent disks above and below on which ring widths were also measured. Where sections were cut from the center of anatomically defined internodes, internode length equaled the actual apical growth increment. Breast-height ring width (BHRW) is the arithmetic mean of four ring width measurements for each annual ring, made on the disk cut at 1.4 m aboveground. Annual ring area at breast height (basal area increment or BAI) was calculated from mean radius estimates derived by a running sum of mean ring width from the pith outward; area calculations used the formula for the area of a circle. Whole-stem ring width (WSRW) integrates the multiple ring width measurements made on each annual xylem layer at different positions along the stem. This integration was accomplished using a weighted average of mean ring widths measured along the entire length of the stem. The weight assigned to mean annual ring widths from any one disk is the proportion of total stem length represented by the internode length for that disk, recalculated for each year. This is equivalent to "specific volume increment" of Duff and Nolan (1957) and "growth layer average" of Fayle and Bentley (1989). Annual volume increment (AVI) was calculated as the summation of the product of ring area and internode length over the total length of the stem.

Simple linear regression was used to evaluate relationships between BH and WS growth indices. While this is not necessarily the best model, it is the implicit model in dendrochronological analyses that use BH growth indices to infer WS growth performance. In the absence of any information relating BH and WS growth

indices, the presumed linear regression model would have a slope of 1.0 and pass through the origin. Thus, the presumed ratio of appropriately scaled BH:WS growth indices is 1.0 and deviations from this would reflect the action of the various factors that influence growth allocation along the stem.

Because correlational relationships between time series of tree growth indices are usually influenced by both high- and low-frequency variation, regression analyses are performed for both unstandardized and standardized indices. Substantial long-term temporal trends in tree growth indices are often associated with tree maturation and stand dynamics. The strength of correlations among unstandardized growth indices can be determined in large part by the juxtaposition of such trends. While it is important in this analysis to determine if trends for different growth indices are correlated, it is also important to evaluate between-index correlations for high-frequency, interannual growth fluctuations associated with factors such as climate. Also, most dendrochronological analyses of red spruce decline are based on standardized BH radial growth indices. The detrending procedure used in this analysis is the ln 1st difference procedure of Van Deusen (1987). This procedure removes virtually all trend from growth index time series and also stabilizes the variance over time.

Regression models were derived using both the combined growth data for 46 individual trees and mean (averaged across trees by year) standardized chronologies. The former includes variance associated with individual tree variation in BH-WS relationships, while the latter is used to evaluate BH-WS relationships for a commonly expressed form of dendrochronological data.

A minimum diameter at breast height (dbh) limit of 2 cm was set to exclude highly variable ring widths near the pith. Inclusion of data for periods when tree dbh was less than 2 cm sometimes resulted in extreme outliers that reduced model r^2. Therefore, results of this analysis apply only for trees with dbh ≥2 cm.

In this analysis, temporal variation in BH-WS relationships is related to tree age since release. For the purposes of this paper, the identification of release was based on the following criteria: (1) an abrupt increase (50–100% increase over 1–3 years) in mean whole-stem ring width; (2) an abrupt increase in height growth; (3) altered distribution of radial growth along the stem, indicating either increased ring widths in the upper crown (for small saplings) or increased radial growth along the lower stem (for subcanopy trees; associated with increased wind sway); and (4) duration of these alterations in growth greater than 10 years. While the first three criteria usually occur more or less simultaneously, some trees exhibited arrested height growth (probably owing to damage to the terminal leader) during radial growth release. Because active height growth plays an important role in maturation related trends in radial growth indices, the year of release for this subset of trees was set at the year of height growth release.

Results

Overall breast-height versus whole-stem relationships

Breast-height growth indices account for 75–93% of the variance in whole-stem growth performance (Table 1), but relationships for unstandardized indices deviate from the presumed temporally stable linear model (Fig. 1). Relationships between mean standardized growth indices have high r^2s and are linear and temporally stable (Table 1 and Fig. 1). While relationships for unstandardized growth indices have high r^2 statistics (Table 1), residuals analysis indicates a systematic lack-of-fit in the assumed linear relationship (Fig. 1). The mean residuals curves in Fig. 1 were calculated using the regression models for the combined individual tree data (Table 1) to estimate WS growth indices and residuals chronologies for each of the 46 trees; the arithmetic mean residuals were then calculated by age since release. Averaging by age emphasizes age-related trends and tends to cancel

TABLE 1. Linear regressions of whole-stem growth indices on breast-height growth indices

Y	X	N	$\bar{Y}$	$\bar{X}$	B_0	B_1 (SE)	r^2	SE of estimate
			Combined data for individual trees					
$WSRW_s$	$BHRW_s$	7134	−0.006	−0.008	0	0.73 (0.005)	0.75	0.08
$WSRW_u$	$BHRW_u$		0.90	0.83	0.15	0.90 (0.005)	0.84	0.22
AVI_s	BAI_s		0.008	0.000	0.008	0.72 (0.004)	0.82	0.09
AVI_u	BAI_u		3.69	4.30	−0.11	0.88 (0.004)	0.89	1.20
AVI_u	AVI_A		3.69	2.64	0.33	1.26 (0.004)	0.93	1.00
AVI_u	AVI_B		3.69	3.63	0.52	0.87 (0.002)	0.93	0.97
			Mean standardized chronologies					
$WSRW_s$	$BHRW_s$	306	−0.004	−0.008	0	0.79 (0.016)	0.89	0.036
AVI_s	BAI_s		0.013	0.005	0.009	0.76 (0.012)	0.93	0.034

NOTE: Subscripts indicate if growth data are standardized (s) or unstandardized (u). AVI_A and AVI_B are estimators of AVI_u derived by entering tree-ring-based estimates of historical dbh into two different volume equations (see text for complete description). Mean chronologies were truncated when the number of trees available to calculate the mean was less than 5.
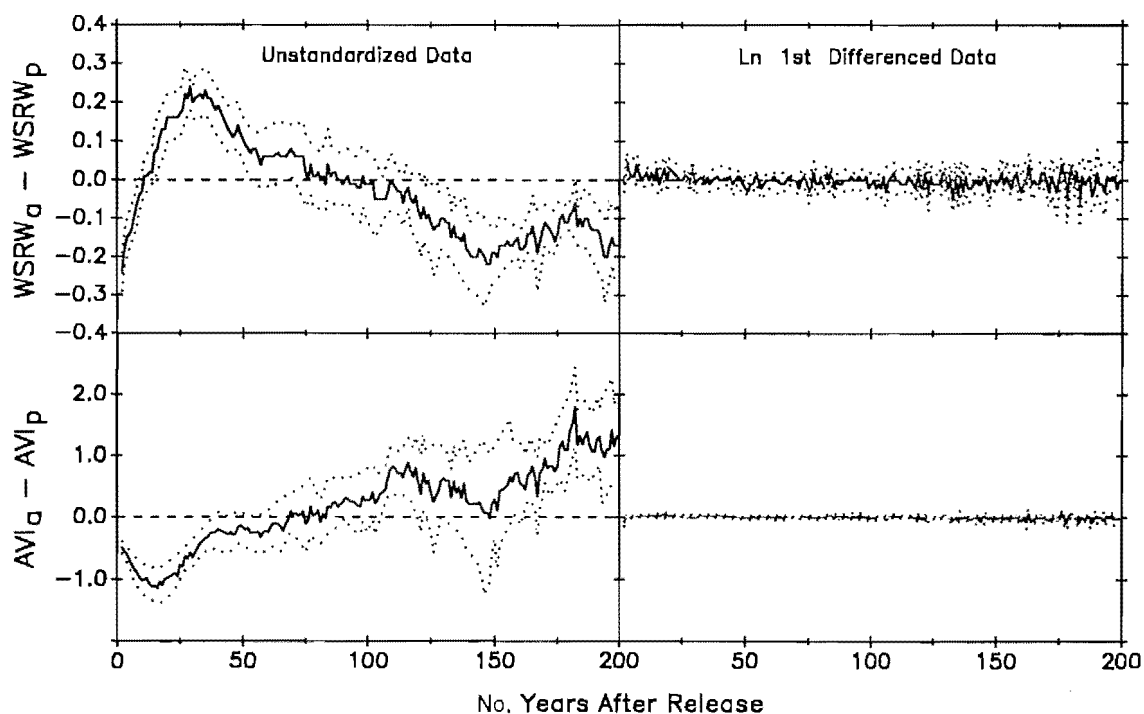
FIG. 1. Mean BH–WS regression residuals (±2 SE) versus age since release.

year-specific or tree-specific variations. Age-related trends in residuals are obvious for unstandardized growth indices, but are completely removed by standardization (Fig. 1). Residuals from BH–WS regression models for standardized indices indicate a temporally stable linear relationship.

The trend in unstandardized WSRW residuals (Fig. 1) is probably associated with differences in maturation-related trends between BHRW and WSRW. When the crown is near breast height, often during the years immediately after release, WSRW is less than BHRW (Fig. 2). As height growth continues, the stem around breast height becomes shaded and BHRW decreases earlier and more rapidly than WSRW (Fig. 2, 20–75 years after release). Once the period of rapid height growth ends, variation in ring width along the stem is reduced and BHRW is similar to WSRW (Fig. 2, 75–120 years after release). The sharp decrease in WSRW

residuals 120 years after release toward a negative long-term mean (Fig. 1) indicates a shift in allocation of radial growth to the lower stem. This may be due to mature trees attaining a canopy-emergent position, with consequent increases in wind sway and allocation of radial growth to the lower stem.

The more or less monotonic trend in residuals from regressions predicting AVI from BAI (Fig. 1) is consistent with the effect of increasing height on this BH–WS relationship. The age-related trends in BAI and AVI are generally similar, but BAI increases more rapidly than AVI immediately after release (Fig. 2), probably owing to the effect of limited stem length on AVI. Consequently, BAI overestimates AVI during the years immediately following release (Fig. 1). The flattened slope of the BAI curve from 25–50 years after release (Fig. 2) is probably due to competition and reduced
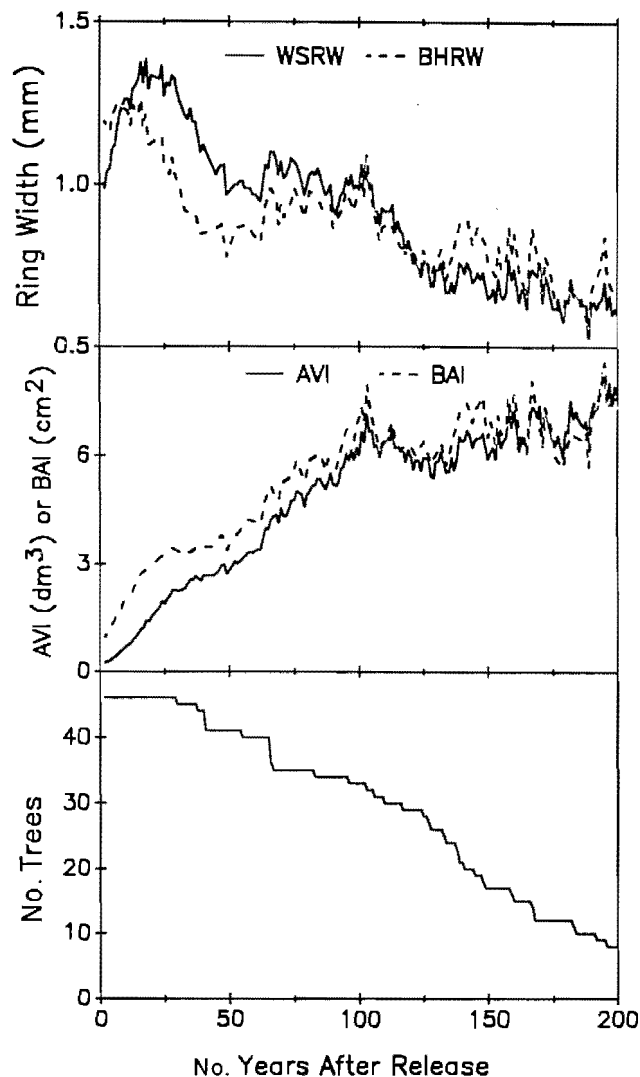
FIG. 2. Mean growth versus age (since release) curves based on data for all 46 trees. Growth versus age curves were truncated when less than 10 trees were available to calculate an average value. The bottom panel displays the number of trees used to calculate mean growth by age and represents the temporal variation in sample size for all age-based analyses in this paper.

FIG. 3. Mean AVI regression residuals (±2 SE) from volume-equation-based models. (A) AVI predicted by AVI estimates obtained by entering tree-ring-based dbh into the allometric volume equation for red spruce from Whittaker *et al.* (1974). (B) AVI predicted by AVI estimates from a paraboloid volume equation using a dbh–height regression model developed from this sample of trees.

stem sway associated with stand closure. Annual volume increment continues to increase during this period (Fig. 2), indicating that stand dynamics affect radial growth at breast height more than overall growth. While this reduces the initial difference between BAI and AVI curves, the trend in AVI residuals continues and the linear BAI–AVI regression model consistently underestimates AVI 100–200 years after release (Fig. 1). The generally linear trend in AVI residuals from 25–200 years after release (Fig. 1) is likely the result of the linear least-squares BAI–AVI regression line passing through the point of mean BAI and mean AVI. Mean AVI would occur at a time when tree height was approximately half total height at time of harvest. Because AVI is determined in large part by tree height, this would cause a linear model relating BAI and AVI to overestimate AVI immediately after release, and to underestimate AVI when tree height exceeded half of total height at the time of sampling.
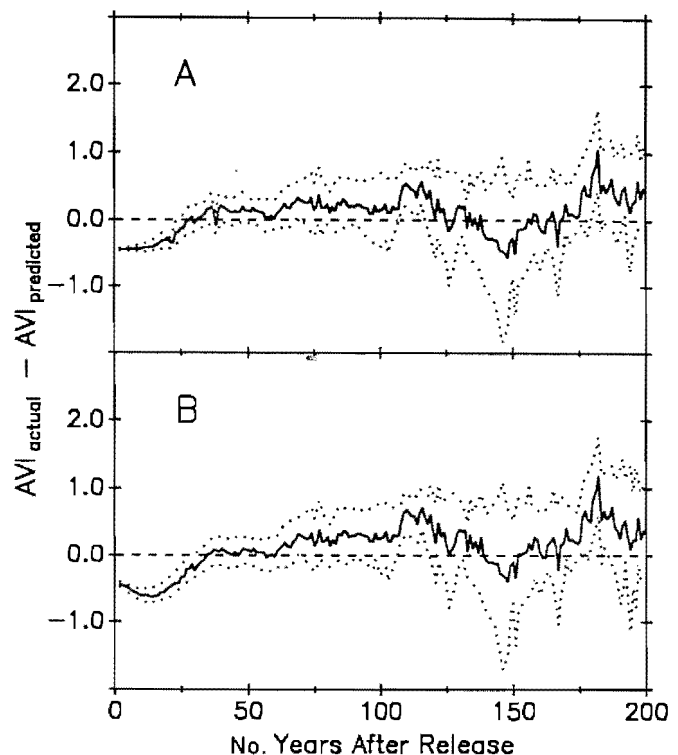
A volume-equation-based procedure

Most of the trend in AVI residuals can be removed by using volume-equation-based estimates of AVI instead of BAI. Tree-ring data can be used to reconstruct historical dbh (inside bark) and the annual dbh values entered into volume equations to estimate total stem wood volume (SWV) for each year. Subtracting SWV of the previous year from current year SWV provides an estimate of AVI. Because volume-equation-based estimates of AVI account for the influence of height on AVI, this procedure should provide better indices of whole-stem growth than BAI.

Because most dendrochronological studies cannot derive site-specific volume equations, results for two alternative procedures are presented. (*a*) Dendrochronologically reconstructed dbh was entered into a published dbh-based volume equation for red spruce to estimate SWV. (*b*) A site-specific dbh–height regression model was derived and used to estimate height, which was then entered along with reconstructed dbh in a paraboloid (Husch *et al.* 1982) stem-wood-volume equation (SWV = height × basal area ÷ 2).

The dbh–height equation used in this analysis ($HT_{cm} = 98.8 + 75.5(dbh_{cm}) - 0.78(dbh^2)$, $p \le 0.0001$; $r^2 = 0.96$; SE estimate, 117 cm) was derived from stem analysis data. However, such an equation could be derived from dbh and height measurements over a wide range of tree sizes (saplings to dominants). The necessary data could be collected as part of the increment core sampling process. The published volume equation for red spruce used in this analysis [log_{10}
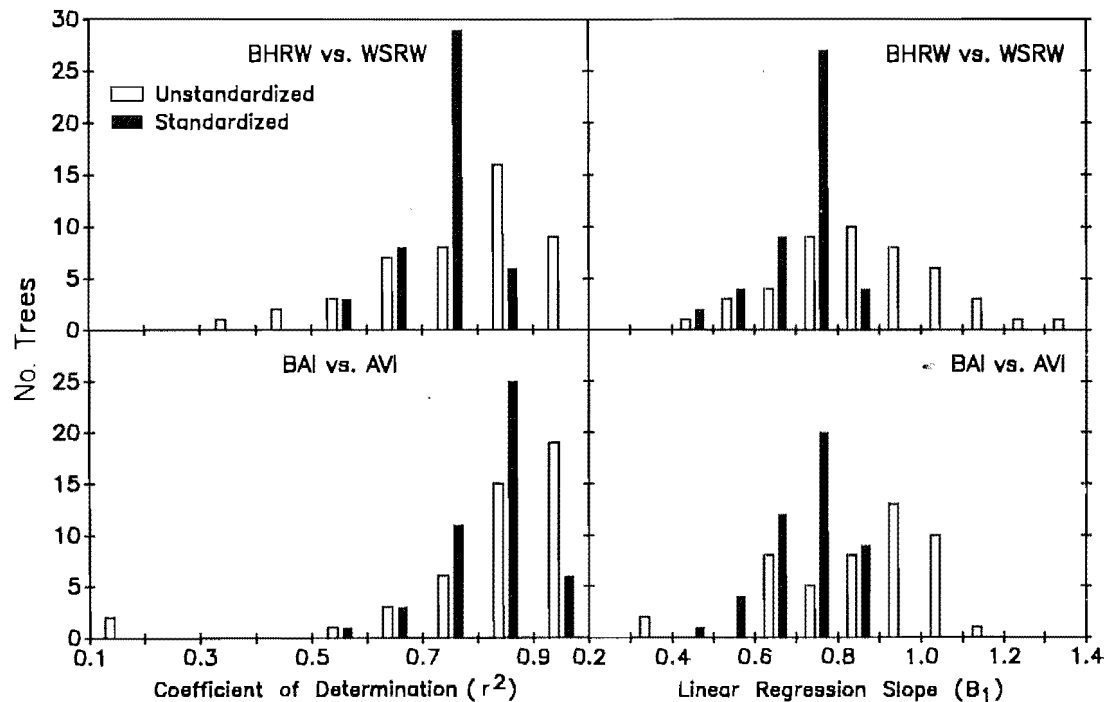
FIG. 4. Distribution of regression statistics (r^2 and slope) from individual tree BH–WS linear regression models.

SWV = 2.1212 + 2.3732($\log_{10}$ dbh)] was derived for red spruce from a northern hardwoods forest at Hubbard Brook, New Hampshire (Whittaker et al. 1974). The paraboloid volume equation was selected because of its simplicity (requires only basal area and total height) and because stem profile plots indicated this simple geometric shape most closely approximates actual red spruce stem shape. More complex volume equations (Husch et al. 1982) may provide better estimates of stem volume, but require stem measurements beyond the scope of most dendrochronological studies. Both volume equations had $r^2 = 0.98$ when applied to the stem-analysis-based estimates of SWV for this sample of 46 red spruce.

Regression statistics and residuals analysis indicate that both volume-equation-based estimates of AVI are superior to BAI as indices of whole-stem growth (Table 1, Figs. 1 and 3). Age-related trends in AVI residuals from the volume-equation-based analyses are greatly reduced compared with residuals from the AVI–BAI regression (Figs. 1 and 3). Volume-equation-based BH–WS regression models have higher r^2 values and lower standard errors of the estimate compared with those from the AVI–BAI regression (Table 1). The site-specific volume equation provided somewhat better estimates of AVI than those from the Hubbard Brook volume equation, particularly during the first 30–50 years after release (Fig. 3). Also, the difference in mean predicted AVI derived from the two volume equations (Table 1, $\bar{x}$) indicates that the Hubbard Brook equation may underestimate SWV.

Individual-tree variation in BH–WS relationships

Separate regression models for individual trees indicate substantial between-tree variability in BH–WS growth index relationships (Fig. 4). Regression statistics (r^2 and slope) for most individual tree BH–WS regressions are similar to those described for the combined-data models (Table 1), but

BH–WS relationships are weak for some trees. The range of variability in individual tree BH–WS relationships is greater for unstandardized growth indices than for standardized indices. This is particularly obvious in the slopes from individual tree BHRW–WSRW regressions, which range from 0.4 to 1.32. Except for a few outliers, r^2 values tend to be higher for unstandardized growth indices than for standardized indices, probably owing to generally similar long-term trends in unstandardized BH and WS indices (Fig. 2).

Plots of BHRW:WSRW and BAI:AVI ratios for four randomly selected trees indicate that temporal instability associated with tree age and stand dynamics is the probable cause of wide between-tree variability in BH–WS relationships (Fig. 5). While there is little evidence of temporally synchronized variation, ratios for all four trees exhibit similar patterns of variation. Both BHRW:WSRW and BAI:AVI ratios for all four trees decrease substantially during the first 25–50 years after release, suggesting a tree and stand maturation-mediated process. However, variation of these ratios is quite individualistic after the first 50–75 years subsequent to release, and is probably associated with localized stand dynamics. Thus, differences in tree age and stand dynamics are the probable causes of wide between-tree variation in BH–WS relationships (Fig. 5). Because this is an uneven-aged population, the variations in BH–WS relationships of individual trees should tend to cancel each other when growth index time series are averaged by year to produce a mean chronology. This is probably the basis for stronger BH–WS relationships for mean chronologies (Table 1).

A detailed analysis of growth indices for an individual red spruce (Fig. 6) provides insight into the processes that affect BH–WS relationships. This tree was released in 1725 and grew vigorously until ca. 1775, when height growth essentially ceased at 7 m and did not resume until 1845 (this is a common phenomenon in this population of red spruce).
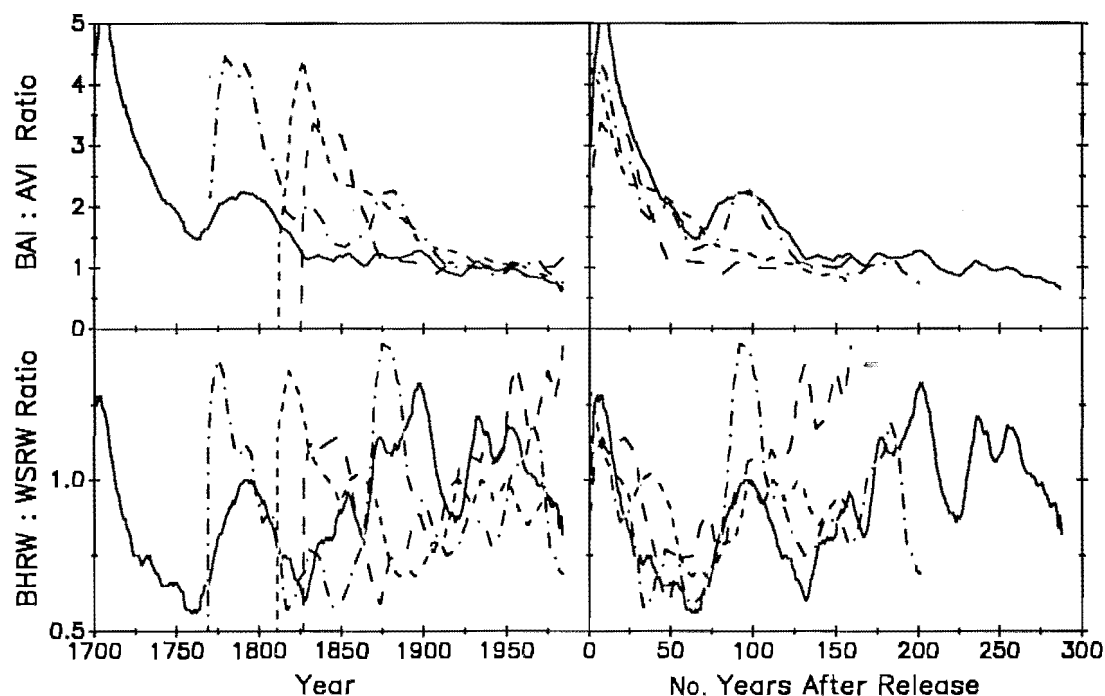
FIG. 5. BH:WS growth index ratios for four randomly selected sample trees plotted by chronological year and by age since release.

Height growth continued until 1915, when it began to gradually diminish until the time of harvest in 1985. The interruption of height growth from 1775 to 1845 appears to have arrested the decrease in BAI:AVI ratio during this period. This is consistent with the interpretation that early decreases in BAI:AVI ratio are due to progressively greater increases in AVI than BAI as the length of stem on which wood is deposited increases. Immediately after height growth resumed, the decrease of the BAI:AVI ratio toward a value ca. 1.0 resumed. While tree height has no direct influence on ring width growth indices, substantial variation in the BHRW:WSRW ratio is apparent during the period of arrested height growth. Initially, radial growth at breast height was more adversely affected than the WSRW, but radial growth along the entire stem was suppressed for the latter part of the 1775–1845 period. Immediately after height growth resumed, WSRW increased substantially relative to BHWS. This was due to the production of large ring widths along the upper stem within the expanding crown while radial growth on the lower stem was limited, probably by competition. The lack of growth response along the lower stem indicates that resumption of height growth after 1845 was not due to competitive release, but rather to recovery of apical growth after some injury. Diminished height growth after 1915, probably owing to maturation, is associated with increased correspondence between BH and WS growth indices, and indicates the influence of crown development on BH–WS relationships.

Discussion

A substantial body of literature describes temporal and spatial variation in radial growth along the stems of trees associated with tree allometry and maturation (Duff and Nolan 1953, 1957), stand dynamics (Farrar 1961), and other environmental stimuli such as defoliation (Mott et al. 1957), wind (Larson 1963, 1965), silvicultural thinning (Myers 1963; Thomson and Barclay 1984), and fertilization (Comerford

et al. 1980; Mitchell and Kellogg 1972). All of these studies provide evidence of differential growth responses between radial growth at breast height and whole-stem growth. Much of the difference between BH and WS growth responses is attributable to effects of shading and stem sway on allocation of radial growth to the lower stem. Also, for stimuli that act directly on the crown (e.g., defoliators and drought), the cambium closest to the point of injury may be more sensitive than the cambium at breast height (Mott et al. 1957; LeBlanc et al. 1987b).

Tree- and stand-maturation-related variation in relationships between BH and WS growth indices are gradual and progressive (Duff and Nolan 1953), while stand dynamics and silvicultural treatments cause abrupt changes in BH–WS relationships (Figs. 5 and 6). Tree maturation results in a progressive increase in the size of the crown to an asymptote, increased stem size, and an increasing proportion of the stem that is shaded or has no live branches (Duff and Nolan 1953; Farrar 1961). These structural changes cause progressive trends in radial growth indices until height growth is complete. These maturation-related trends are generally well defined and amenable to analysis and modeling. However, sudden alterations in growing conditions (e.g., neighbor mortality, fertilization) cause abrupt shifts in radial growth that may or may not be equivalent for BH and WS growth indices (Comerford et al. 1980; Myers 1963; Thomson and Barclay 1984). In silvicultural studies, the nature and timing of treatments are known and multiple measures of growth (e.g., breast-height radial growth, height growth, whole-stem volume increment) are often used to characterize responses. The effort required to obtain multiple measures of growth is warranted because growth response to altered stand conditions is the phenomenon of interest. However, dendrochonological reconstructions of historical tree growth in natural forests usually have little or no stand history information to use in interpreting past growth responses and almost universally rely solely on breast-height

ring width growth indices. Most dendrochronological studies attempt to remove both maturation- and stand-dynamics-related trends from the growth index time series. The maturation-related trends are often explicitly accounted for by growth models (Fritts 1976), and the stand dynamics effects are reduced by averaging growth responses of many trees. The latter procedure is based on the premise that most stand dynamics phenomena in natural forests are localized and not synchronous across the sample tree population (Cook 1987). This premise is supported by the individual tree growth analyses presented here. Also, the analysis of BH–WS relationships presented here indicates that a large part of the breast-height growth response to stand dynamics phenomena may be due to altered radial growth allocation patterns rather than altered overall growth performance. Thus, the common dendrochronological practice of removing nonreplicated, abrupt alterations of growth trends in breast-height ring width series may serve to strengthen the relationship between growth indices and actual growth performance.

This analysis of BH–WS relationships validates the common use of standardized BH indices in tree growth – climate studies to represent year-to-year variations in WS growth responses. This analysis employed the ln 1st difference standardization procedure, which removed virtually all trend from the radial growth series. Other standardization procedures, e.g., cubic splines, polynomials, negative exponential curve (Fritts 1976), may not remove all multiyear trends from the data. To the extent these remaining trends are due to maturation or stand dynamics effects, BH radial growth indices may not provide completely accurate indices of whole-stem growth performance at the individual-tree level.

Because their height, crown position, and competitive status have stabilized, older trees (> 100 years since release) exhibit substantially less temporal instability of BH–WS relationships than younger trees. Trees of long-lived species may produce at least 100 years of annual growth rings after attaining mature crown status but before senescence-related radial growth decline. Radial growth data from such trees may provide the best opportunity to assess effects of subtle environmental influences (e.g., regional air pollution or climate change) on tree growth in unmanaged, uneven-aged forests. Further research is needed to define the limits of this mature, pre-senescence phase for various long-living tree species across a spectrum of site types.

Age- and stand-dynamics effects warrant careful consideration in any interpretations of unstandardized BH growth indices. The systematic lack-of-fit apparent in residuals from BHRW–WSRW and BAI–AVI regression models during the first 50–100 years after release is likely due to both tree maturation and stand closure. Age-related trends in AVI residuals are reduced if a volume equation approach is used, but are still apparent for trees <30 years old. These trends in residuals indicate that unstandardized, BH-based growth indices of young trees confound responses to environmental factors with maturation-related changes in growth allocation patterns along the stem. However, high r^2 statistics and broadly similar growth curves for AVI and BAI (Fig. 2) indicate that BAI is a useful, though somewhat flawed, representation of whole-stem growth. Nonetheless, detailed studies of growth responses of young trees (<30–50 years since release) should be based on whole-stem analysis rather than on increment cores taken at breast
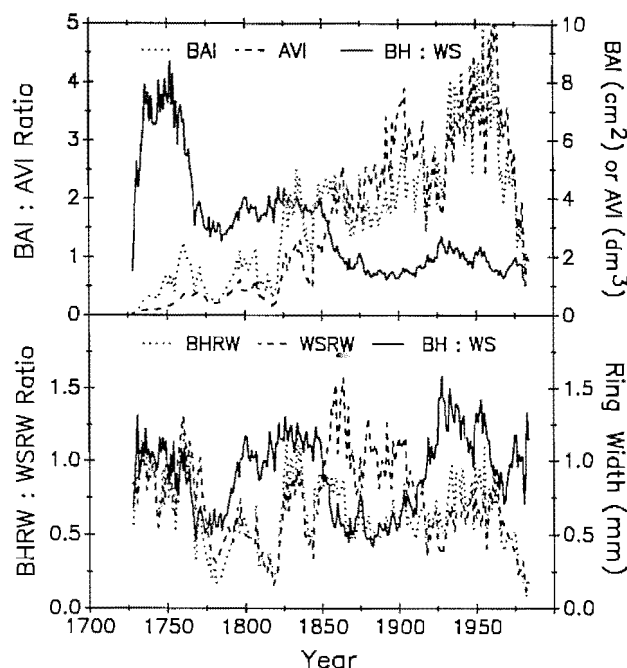

FIG. 6. Breast-height and whole-stem growth indices and their ratios for a single red spruce tree.

height. Detailed stem analysis is particularly appropriate for analyses of effects of environmental influences on tree growth in managed forests and plantations.

While standardization of radial ring width sequences prior to analysis is widely recognized as necessary within the dendrochronological community, unstandardized BHRW and BAI data have been used in many studies of atmospheric deposition effects on tree growth (e.g., Bondietti et al. 1989; Baes and McLaughlin 1984; Frelich et al. 1989; Hornbeck and Smith 1985; Hornbeck et al. 1986; Johnson et al. 1981; Sheffield and Cost 1987). Because tree and stand maturation cause long-term, progressive decline in annual ring widths at breast height (Fig. 2), the use of unstandardized BHRW data for young trees in forest decline studies is particularly problematic. The long-term decrease in unstandardized BHRW does not reflect actual whole-stem growth performance (as expressed by AVI), and the potential is great for spurious correlations with long-term trends in air pollution. This age-related decrease in unstandardized ring width data appears to continue until height growth is more or less complete (ca. 100 years after release for this sample of red spruce). However, the occurrence of significant, abrupt decreases in BHRW of older trees (>125 years old), particularly if the decrease is synchronous across a large segment of the population (e.g., Johnson et al. 1988), is not a normal, age-related phenomenon for red spruce (Fig. 2) and may be a strong indication of decline. Age-related trends in unstandardized BAI are generally positive during the period of early growth, culminating at an asymptotic level that can be maintained for many decades by red spruce (Fig. 2; also see Phipps and Whiton 1988 for Quercus alba L. BAI curves). There is little indication of a tree- or stand-maturation-related decrease in BAI of this sample of red spruce up to 200 years after release. Thus, a negative trend in BAI is a strong indication of true growth decline. However, a reduced rate of increase or flattening of the BAI

curve, particularly if it is associated with stand closure in young, developing stands, might be considered normal.

Hornbeck *et al.* (1986) are probably correct in proposing maturation and stand dynamics as major factors affecting BAI trends for their sample of predominantly young, low elevation red spruce. The comparison of BAI and AVI curves in Fig. 2 suggests that a BAI-based analysis would overestimate the degree of growth reduction associated with stand closure 25–50 years after release. Also, the comparison in Fig. 2 indicates that BAI consistently overestimates actual growth performance (i.e., AVI) for the first 30–50 years after release (Fig. 1). Thus, the rapid increase in BAI of red spruce from 1920 to 1960 reported by Hornbeck and others (1985, 1986) may overestimate actual growth and enhance the appearance of reduced growth during the post-1960 period, attributed to maturation by Hornbeck *et al.* (1986). The 20-year period of post-1960 BAI data presented in Hornbeck *et al.* (1986) is insufficient to determine if the "flattened" BAI curves reflect normal stand closure effects or the beginning of actual growth decline.

The volume-equation-based procedure described in this paper can provide estimates of growth performance that are less affected by age-related variation in BH–WS relationships than BAI. Estimates of AVI based on a site-specific dbh–height regression model are somewhat better than those derived from the allometric volume equation developed at Hubbard Brook (Whittaker *et al.* 1974), but the difference is small. Extrapolation of volume equations beyond the site from which they were developed can result in biased estimates of stem wood volume. However, most studies of red spruce decline focus more on temporal growth trends than on actual values of growth increments. For this purpose, the volume-equation-based procedure described here can provide better indices of growth performance than BAI, even if an off-site volume equation is used. This procedure should facilitate interpretation of growth responses with regard to environmental influences.

Acknowledgements

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