USING SPECIFIC VOLUME INCREMENT (SVI) FOR QUANTIFYING GROWTH RESPONSES IN TREES—THEORETICAL AND PRACTICAL CONSIDERATIONS

Eddie Bevilacqua[1]

ABSTRACT.—Comparative analysis of growth responses among trees following natural or anthropogenic disturbances is often confounded when comparing trees of different size because of the high correlation between growth and initial tree size: large trees tend to have higher absolute grow rates. Relative growth rate (RGR) may not be the most suitable size-dependent measure of growth when studying larger trees since RGR is also highly correlated with tree size: larger trees tend to have lower RGR. This article demonstrates that specific volume increment is a more appropriate size-dependent measure of growth based on theoretical considerations and on empirical evidence with competition indices.

In research investigations based on observational studies, the investigator is forced to deal with the constraint of limited local control of experimental units relative to comparative experiments. This is particularly true in forest growth studies that are designed to investigate the growth response of trees following disturbance or changing levels of resource availability. The lack of experimental control is often the consequence of dealing with trees of different size. The difficulty generally arises from the tendency of larger trees to accumulate more bole growth than smaller trees.

Possible solutions to these experimental problems are to incorporate a covariate, such as initial tree size, into the analysis, or to redefine the response variable to a measure of relative growth, that is, measure new growth relative to initial size, such as relative growth rate.

Relative growth rate (RGR) is a term originating from early studies in whole plant growth analysis (Blackman 1919; Briggs and others 1920a,b). The original premise of RGR was based on the assumption that the initial size of plant (W) has some physiological contribution or link to any new biomass produced. Therefore, when plants had ample resources needed for growth, they would grow at a constant exponential rate, implying a constant RGR. This facilitated the comparison of plant growth for plants of different initial sizes. When resource levels change or become limiting, the RGR of a plant should decrease.

Comparisons between plants having different RGR could then be assessed by decomposing RGR into two physiological components, the photosynthetic efficiency (PE) and photosynthetic capacity (PC) (see equation 1). Photosynthetic efficiency represents the amount of plant growth per unit leaf area, whereas photosynthetic capacity represents the relative amount of photosynthetic material per unit of plant weight.

RGR	=	PE	*	PC	(1)
[(dW/dt) / W]	=	[(dW/dt) / A]	*	[A / W]	

where W = total initial weight of plant, A = total leaf area of plant, and t = time

Schwinning (1996) further extended the concept of whole plant growth analysis and the decomposition of relative growth rates (i.e., equation 1) to examine the mode of competition, size dependence of growth, and their interdependence on resource uptake.

The forestry research community adopted the whole plant growth analysis to assess how silvicultural activities and environmental stresses influence tree growth. However, early researchers had difficulty measuring W (total weight of a tree, including roots) and would often substitute other measures of

[1] Assistant Professor, State University of New York, College of Environmental Science and Forestry, One Forestry Drive, Syracuse, NY 13210. Phone: (315) 470-6697; fax: (315) 470-6535; e-mail: ebevilacqua@esf.edu

tree size, such as aboveground weight, bole volume, or d.b.h. for W. Within this context, Waring and others (1980), when substituting bole volume for plant weight, considered the PE term—stem growth per unit leaf area—as a measure of tree vigor.

The limitation of using RGR in forestry growth studies, particularly in studies focusing on the bole growth in a tree, is the predictable change in RGR with tree age (fig. 1). This minimizes the utility of using RGR for comparing the effects of silvicultural activities or environmental influences over extended periods of time on trees of different sizes. Larger trees generally accumulate more new bole growth in absolute amounts. As trees age, the quantity of new bole growth becomes a smaller fraction of the underlying initial bole volume—i.e., decreasing RGR. The volume of the bole is the cumulative growth of the tree stem over its entire life, and as a tree ages, the volume of the bole has a decreasing physiological function with respect to any new bole growth. As trees become larger, the function of the main bole shifts from being an assemblage of pipes conducting water from the roots to the foliage to providing the mechanical support allowing the tree to reach greater heights. Only a portion of the bole volume, which is defined as sapwood, is used to conduct water. Morataya and others (1999) considered sapwood volume as a linkage between initial bole size and new bole growth. However, measuring or estimating sapwood volume in a standing tree can be quite difficult because of its very dynamic nature.

In their detailed analysis of stem growth, Duff and Nolan (1957) proposed a relative measure of internodal growth they termed Specific Increment in Volume (SIV), which measured the amount of new volume growth per unit of cambial surface area. They reasoned that the cambial surface contained all the new xylem cells that would eventually form the bole of a tree, as well as the respiratory surface for all new bole growth. They demonstrated mathematically that the SIV could be estimated as the average width of an annual ring within an internode. The use of volume growth per unit cambial surface area was later extended from its measurement within a single internode to a look at the whole bole of a tree. The volume of new bole growth is expressed relative to the bole surface area, which is used to estimate the total amount of cambial surface area over the entire bole. This measurement of size-dependent growth at the tree level was termed the Specific Volume Increment (SVI).

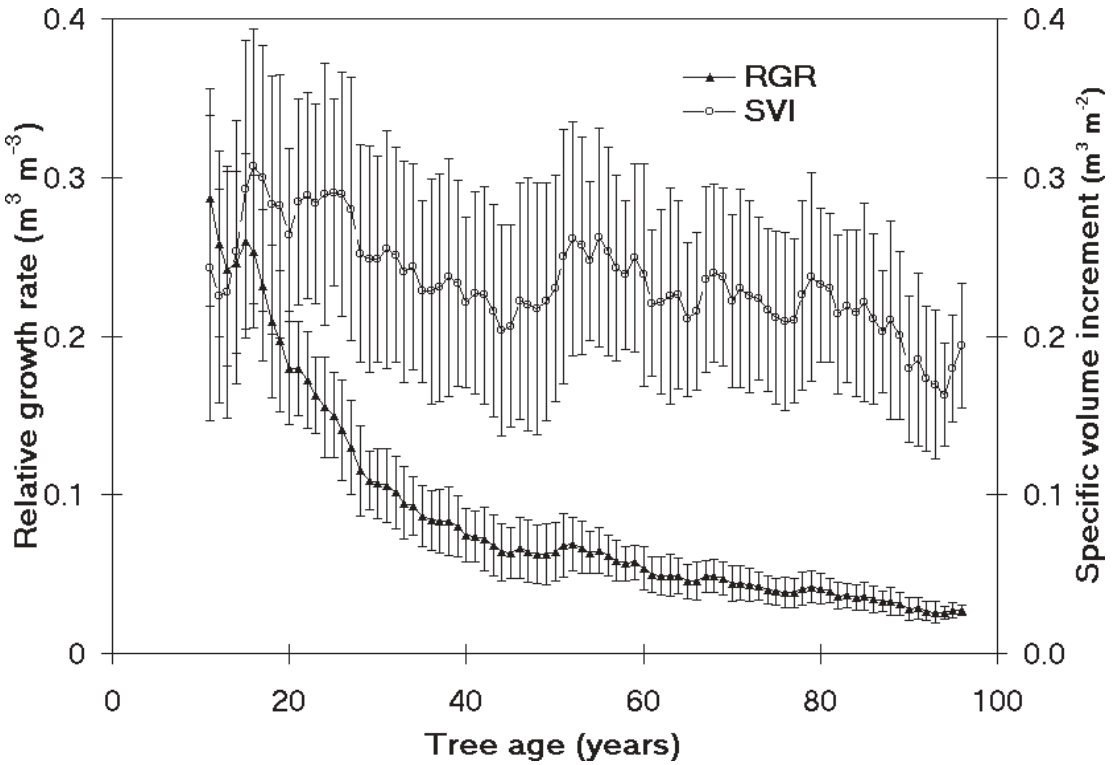

Figure 1—*Age-related variation in relative growth rate (RGR) and specific volume increment (SVI) of the main stem for 38 emergent and dominant white pine trees calculated on a yearly basis. The data were taken from the control group only, so as to not confound the age-related trend with the release treatment effect. Vertical bars represent one unit of standard deviation about the mean.*

Unlike RGR, which decreases with tree age, SVI remains relatively constant for an extended period of time as trees age. Figure 1 illustrates that early in a tree's life, RGR and SVI of the main stem have relatively similar mean values and levels of variation. However, as trees age, there is a rapid decline in both the mean and variance of RGR. This observation supports the hypothesis that the increasing size of the non-productive inner bole in large trees has a greater influence on RGR than differences in annual increment.

The use of RGR as a measure of tree vigor would suggest that all trees rapidly lose vigor with age, regardless of their immediate environment or canopy position. In contrast to this, the mean value of SVI displays a much more gradual decline with age, albeit with a large degree of variability among trees. The large variability in SVI would suggest that it might be more sensitive to changes in the growth response of trees to environmental stimuli and that it might better reflect the relative growth variation among trees that are the result of differences in the local level of resource availability immediately surrounding them.

Based on these theoretical considerations, there are three benefits of using SVI over RGR in studies designed to compare the effects of natural or anthropogenic disturbances on the growth of trees of varying size:

1. Using initial bole surface area to represent the amount of cambial tissue implies a physiological link to new bole growth, whereas initial bole volume does not.
2. SVI is less correlated with tree age, allowing for a more valid comparison in relative growth for trees of different ages.
3. SVI is more variable than RGR across a greater range of ages, suggesting it may be easier to identify the influence of natural or anthropogenetic disturbances on tree growth.

To confirm the benefit of using SVI over RGR, empirical evidence was collected from a study designed to investigate the effects of competition release on the growth of mature eastern white pine (*Pinus strobus* L.) trees.

METHODS AND MATERIALS

Field Site

Trees selected from within the Cartier Lake Silvicultural Area within the Petawawa Research Forest (PRF), Chalk River, Ontario were used in this study. The PRF is located on the eastern boundary of Algonquin Provincial Park, Renfrew County, Ontario (45º59'N 77º26'W). The climate is characterized by short warm summers and cold winters, with an average annual temperature of 4.3 ºC. The average length of the growing season is 116 frost-free days. Precipitation averages 832.1 mm per year, with 55 percent falling between April and September.

This study area had been cut in 1971 to varying levels of residual basal area. The aim of that earlier study was to improve the growth and yield of white pine for saw log production and "at providing the option of long-term uniform shelterwood management" (Stiell 1984). The cutting treatments consisted of the removal of all species of pulpwood size (9 cm d.b.h.) and larger, except for the understory pine and spruce. The main species removed were trembling and largetooth aspen and white birch. Thus, the residual stands in the treated areas were mainly composed of white pine, with a minor component of red pine and white spruce. The intensity of the cutting treatment varied depending on the pre-treatment level of white pine in the stand. Part of the area was left as an uncut control. Initial cutting treatments are described in more detail by Stiell (1984). Because of the ongoing study, restrictions were placed on which trees could be selected for this research; namely, trees were selected from a distance of at least two-tree lengths from existing permanent sample plots.

Tree Selection and Stem Analysis

Trees selected for detailed stem analysis were chosen from within the six treatments outlined in Stiell's (1984) experiment. To analyze the variation in tree response due to canopy position, trees were further stratified into three dominance classes: emergent (greater than 3 m above average canopy height), dominant/co-dominant (within +/- 3 m of average canopy height), and intermediate (greater than 3 m below

Table 1.—*Number of sample trees selected based on cutting treatment, pine density before cutting, and dominance class*

Cutting treatment	Pine density	Dominance class			TOTAL
		Emergent	Dominant	Intermediate	
Control	Low	2	2	2	6
Control	Medium	9	11	4	24
Control	High	4	10	1	15
Released	Low	4	10	2	16
Released	Medium	5	7	1	13
Released	High	4	8	2	14
TOTAL		28	48	12	88

average canopy height). A total of 88 trees were selected. Table 1 shows the distribution of selected trees based on cutting treatment, pine density, and tree dominance class.

The main stem of each tree was then divided into 20 sections, with the base of each section taken at the following heights: 0.15 m (stump), 1.37 m (d.b.h.), and at 5-percent intervals from 10 to 95 percent of total tree height. A disk was removed from the base of each section to conduct detailed stem analysis on each subject tree back in the lab.

Stem disks were stored in cold rooms at 5 °C for up to 8 months at the Petawawa Research Forest and the Faculty of Forestry, University of Toronto. They were then allowed to air dry for a minimum of 2 months before being prepared for tree-ring measurements. Disk preparation involved sanding the bottom surface of each disk, first with 60- to 80-grit sand paper, followed by light sanding with 100-grit sand paper.

On each disk, tree ring widths were measured along four radii taken at 90° angles from each other using the Tree Ring Increment Measurement (TRIM) system initially developed by Fayle and McIver (1986). The TRIM system was updated by interfacing the SONY electronic ruler in an IBM compatible PC using a LOTUS 1-2-3™ spreadsheet developed by the Miller (unpublished 1990). The average of the four ring widths was used to reconstruct the yearly cumulative diameter growth of each stem section and then compute the yearly volume and surface area for the entire tree bole using techniques described in Avery and Burkhart (1994).

Growth Estimation

Using the same principles as outlined in Causton and Venus (1981) and Hunt (1982), continuous functions—i.e., polynomial equations—of the bole surface area (SA, equation 2) and volume (V, equation 3) for each tree over time since treatment. Third-order polynomial equations were selected based on their better overall goodness of fit (i.e., higher coefficient of determination and lower root mean squared error) with the data.

$$SA = f(t) = a_o + a_1 \cdot t + a_2 \cdot t^2 + a_3 \cdot t^3 \quad (2)$$

$$V = g(t) = b_o + b_1 \cdot t + b_2 \cdot t^2 + b_3 \cdot t^3 \quad (3)$$

where SA = bole surface area, V = bole volume, t = time, a_0, .. ,a_3, b_0, .. , b_3 = parameters to be estimated

RGR and SVI can be calculated at any point in time using equations 4 and 5, respectively,

$$RGR = (dV/dt) / V = g'(t) / g(t) \quad (4)$$

$$SVI = (dV/dt) / SA = g'(t) / f(t) \quad (5)$$

Size-related Growth and Competition

Once the subject trees were identified, the size and location of potential competitors were determined using a BAF=2 (metric) prism, using each subject tree as the center point of prism sweep, following the procedures outlined by Spurr (1962). For each competitor, its azimuth and distance from the subject tree was recorded, as well as its species, diameter at breast height (d.b.h.) and height class relative to the subject tree's height (-1 = more than 3 m shorter than the subject tree, 0 = within +/- 3 m of subject tree, and +1 = more than 3 m taller than the subject tree).

Three distance-independent and eight distance-dependent competition indices were calculated for each subject tree for each year from 1971 to 1994 and correlated with the SVI. The distance-independent (DI) indices included number of competitors (CI01), cumulative squared relative diameter of competitors, and cumulative diameter of competitors (CI03). Distance-dependent indices included Weiner's (1984) neighbourhood interference (CI04), Spurr's (1962) point density index (CI05), cumulative horizontal angle (Rouvinen and Kuuluvainen 1997) (CI06), and Hegyi's (1974) size-distance ratio (CI07). Two of the indices included variations of the crown overlap (CO) index type. Since there is no available information on open growth crown width for white pine of different sizes, the radius of the influence zone for each tree was directly related to the tree's diameter using the same approach as Tome and Burkhart (1989). The radius of zone of influence was expressed as a linear function of tree d.b.h. from 0.1 to 1.0 times d.b.h. in steps of 0.1. The function that produced the best empirical correlation between size-related growth and competition was selected. One index was based on the cumulative overlap between zones of influences (CI08), while the other weighted the overlap by the relative size of the competitor to the subject tree (CI09).

The final two indices tested were based on area potential available (APA). Since APA increases with decreasing competition, the inverse of APA was used to be consistent with the other competition indices. One of the APA indices tested was Brown's (1965) original calculation, bisecting the distance between subject and each competitor at right angles and forming a polygon around the subject tree (CI10). The other applied Moore and others' (1973) weighted division of distance between trees based on relative tree size (CI11).

RGR and SVI were regressed against the 11 competition indices using equation 6 and employing data from the last 5 years of measurement (1990-94). Relationships between the two size-dependent measures of growth (i.e., RGR and SVI) and the competition indices were tested using the following model

$$\ln(Y) = \beta_0 + \beta_1 \cdot CI \qquad (6)$$

where Y is either RGR or SVI, CI is one of the competition indices, and b_0 and b_1 are parameters to be estimated.

RESULTS

The results from the regression equations in table 2 demonstrate that all competition indices explain a larger proportion of the variation in ln(SVI) (i.e., higher R^2) as compared to ln(RGR). R^2 values for ln(RGR) are comparable to the level of correlation Peterson and Squiers (1995) obtained when they

Table 2.—*Parameter estimates and regression statistics from regression analysis relating two size-dependent stem growth measurements, (i) relative growth rate (RGR) and (ii) specific volume increment (SVI) of white pine trees to competition indices*

Competition	Y = RGR[a]				Y = SVI			
Index[b]	β_0	β_1	RMSE[c]	R^2 [d]	β_0	β_1	RMSE	R^2
CI01	-3.111	-0.0287	0.3365	0.1250	-0.973	-0.0494	0.4333	0.2040
CI02	-3.381	-0.0084	0.3337	0.1394	-1.288	-0.0217	0.3376	0.5169
CI03	-3.094	-0.0010	0.3346	0.1349	-1.062	-0.0014	0.4454	0.1590
CI04	-3.138	-0.0054	0.3326	0.1450	-0.973	-0.0098	0.4155	0.2681
CI05	-3.310	-0.0002	0.3282	0.1678	-1.329	-0.0003	0.4189	0.2561
CI06	-3.241	-0.0143	0.3293	0.1619	-0.982	-0.0345	0.3373	0.5178
CI07	-3.380	-0.0054	0.3253	0.1824	-1.320	-0.0129	0.3165	0.5753
CI08	-3.105	-0.1009	0.3216	0.2009	-0.867	-0.1953	0.3722	0.4129
CI09	-3.316	-0.0461	0.3258	0.1800	-1.196	-0.1050	0.3398	0.5104
CI10	-3.494	-0.8585	0.3570	0.0153	-1.562	-2.5281	0.4677	0.0727
CI11	-3.469	-0.8699	0.3365	0.1251	-1.530	-2.1197	0.3738	0.4076

[a] Model: $\ln(Y) = \beta_0 + \beta_1(CI)$.
[b] see Methods and Materials for definitions of competition indices.
[c] RMSE = Root mean squared error.
[d] R^2 =Coefficient of determination.

analyzed the relationship between relative diameter growth rate and competitive interference in white pine. This strong correlation between ln(SVI) and competitive interference supports the hypothesis that SVI is a more appropriate measure of size-dependent growth compared to RGR when investigating the influence of competitive interference on the growth of older trees.

SVI is negatively correlated with the level of cumulative competitive interference of all species of competitors, and more than half of the variation in SVI could be accounted for by competitive interference alone (table 2). A comparison of the efficacy of the competition indices shows that the regression models from this study have comparable levels of correlation to that found in the literature.

PRACTICAL IMPLICATIONS

The estimation of SVI at the individual tree level does not require additional data collection procedures, such as complete stem analysis. Given simple allometric relationships for both bole volume and surface area as functions of tree d.b.h., height, and form, SVI can be estimated over time through simple differentiation over time.

$$V = FD^2H \quad (7)$$

$$SA = kDH \quad (8)$$

$$SVI = (D/k)*(dF/dt) + (2F/k)*(dD/dt) + FD/(Hk)*(dH/dt) \quad (9)$$

where V = bole volume, SA = bole surface area, D = tree d.b.h., H = tree height, F = tree form, t = time, k = constant, SVI = specific volume increment.

Can we extend the use of SVI as a size-dependent measurement of growth from the individual tree to the stand level? At the stand level, stand growth is already qualified using some measure of stand occupancy or density, such as variable density yield curves. The density variable is one method of quantifying the initial growing stock in a stand. In most of these growth models, density is expressed as either the number of trees or basal area per unit area. These measures are often used because of their simplicity in calculation rather than their direct biological compatibility with growth. The total bole surface area of all trees per unit area (stand bole area) should provide a more biologically meaningful measure of stand occupancy based on the premise that it quantifies the amount of cambial tissue from which new wood material initiates.

Lexen (1943) originally proposed using stand bole area as a measure of stand density when studying ponderosa pine stands. Mulloy (1944) later investigated the differences between using stand bole area and Reineke's (1933) Stand Density Index in red (*Pinus resinosa* Ait.) and white pine (*P. strobus* L.) stands, finding both measures of density to be similar. This would suggest that stand bole area might be the more appropriate measure of stand occupancy, particularly in process-based models of forest growth, based on the physiological link between cambial surface area and new xylem growth.

An additional benefit of using stand bole area is that the calculation of this variable will not require the collection of any additional forest inventory data. A simple allometric relationship predicting tree bole area using d.b.h. and height can be employed with a stand table to estimate stand bole area. Further research into the use of bole area as a measure of stand occupancy is needed.

CONCLUSIONS

To conduct valid comparisons between present and past growth rates in trees or stands, there is a need to express periodic growth relative to the initial size of a tree or growing stock in a stand (i.e., size-dependent growth). Using initial bole volume or stand yield may be inadequate because of the lack of a physiological link between any new growth and these initial size variables. It is being recommended the initial bole surface area (either at the tree or stand level) again be studied as possible measures of initial tree or stand size, particularly because of the strong physiological link between the amount of cambial material and periodic bole growth.

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