

Ideas and perspectives: use of tree-ring width as an indicator of tree growth

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Abstract

By taking core samples, dendroecological studies can reconstruct radial growth over the lifespan of a tree, providing a valuable way to estimate the sensitivity of tree productivity to environmental change. With increasing prevalence of such studies in global change science, it is worth cautioning that the incremental growth rate of a sub-dimension of a tree organ, such as annual ring width (w), does not respond to extrinsic perturbations with the same relative magnitude as the primary production of that organ. For example, if an extrinsic force causes a two-fold increase in the absolute growth rate of stemwood biomass (AGR), it should only theoretically translate into a 1.3-fold increase in w , or a 1.7-fold increase in basal area increment (BAI), when a 2 : 1 ratio in resource allocation to lateral and apical meristems is assumed. Expressing the magnitude of a response in relative terms does not, therefore, provide a valid means of comparing estimates of relative growth derived from measurement of different dimensional traits of the tree. From our perspective, enough conformity to facilitate comparison of environmental sensitivity across studies of tree growth is warranted so we emphasize the benefit of dimension analysis to transform measurements of w and BAI into the AGR. Although conversion to AGR introduces an error from the use of allometric equations, the approach is widely accepted in mainstream ecology and global change science at least partially because it avoids discrepancies in response magnitude owing to differences in dimension. Studies of organ elongation have historically provided invaluable information, yet it must be recognized that they systematically underestimate the response magnitude of primary production, and confound comparisons of growth sensitivity between many dendroecological studies that focus on w and studies of primary production.

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1 Introduction

Tree-ring measurements provide a cost-effective way to study historical variability in the growth rate of trees. They complement forest inventories by expanding the temporal viewing angle (Metsaranta and Lieffers, 2009; Bowman et al., 2013; Babst et al., 2014), providing the ability to study inter-annual variability in climate. Research typically focuses on one of three response variables: annual ring width (w), basal area increment (BAI), or the absolute growth rate of biomass (AGR). Most studies analyze variability in w , while fewer studies transform observations of w into BAI, and very few studies transform it into AGR. Greater attention to w most likely reflects cases where the pith goes undetected, prohibiting direct estimation of inside-bark diameter (D_{ib}) or basal area (BA) of the tree without extrapolation techniques (Duncan, 1989; Voelker, 2011). Studies that focus on w or BAI often report findings in relative terms so that the sensitivity of growth can be compared with other types of observation, such as ecophysiological model predictions, vegetation greenness indices, or stable isotope ratios. The practise of analyzing relationships between climate and standardized w or BAI is problematic, however, because relative changes in w or BAI are not directly comparable with relative changes in AGR. Here, we describe the problem in more detail and document some brief examples.

2 Dependence of forcing on dimension

Even when expressed in relative terms, the derivatives of D_{ib} and BA are systematically less than that of stemwood biomass (B), or stemwood volume (V). To understand this, consider the growth of a generic three-dimensional system with $V = \text{length } (l) \times \text{width } (w) \times \text{height } (h)$. In its initial state, the system has $V = 2.0 \text{ m}^3$ and subsequently increases at a relative growth rate of $2.0 \% \text{ yr}^{-1}$. After 100 years, the system grows to be 14.5 m^3 , constituting a 7.2-fold increase in V . If we assume equidimensional growth, initial and final values of l , w , and h are each 1.2 and 2.4 m, re-

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spectively, which constitute just 1.9-fold increases in each dimension. As the example demonstrates, derivatives of each dimension of a state variable with n dimensions, and undergoing equidimensional growth, are defined by the n th root of the state variable's derivative. So for a system volume, with $n = 3$ and sensitivity, λ , the expected forcing for each dimension is $\lambda^{1/3}$.

3 Examples

As an example with context, we measured a Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) tree growing near Campbell River, Canada that exhibited $D_{ib} = 12.6$ cm in 1970 and increased to 40.0 cm in 2010. From these measurements, we calculate 3.2- and 10.0-fold increases in D_{ib} and BA, respectively, over the forty year measurement period. Using locally-calibrated equations to derive h from D_{ib} , we estimate a 2.3-fold increase in h . Based on allometric functions of height and diameter for Douglas-fir from Canada's National Biomass Equations database (Ung et al., 2008), we estimate a 16.0-fold increase in B , while using the standard taper equation for Douglas-fir in British Columbia (Kozak, 1988), we estimate a 19.0-fold increase in V .

The dependence of forcing on dimension has important implications for the interpretation of studies that report temporal trends in tree growth based on observations of w , or BAI. If a perturbation in growth due to a combination of increasing atmospheric carbon dioxide and warming, for example, were to cause a two-fold increase (doubling) in biomass at the age of merchantability, then we would expect enhancements in D_{ib} and BA of just 19.0 and 60.0%, respectively. Likewise, if an extreme drought event reduced biomass by 100.0%, we should only expect decreases in D_{ib} and BA of just 9.5 and 30.0%. Taking a real example, the British Columbia Ministry of Forests Lands and Natural Resource Operations collected tree rings from a subsample of Douglas-fir trees at 35 permanent sample plots in coastal British Columbia, Canada. The stands were fully stocked and dominated by Douglas-fir. The plots were evenly distributed between maritime and sub-maritime regions within the natural range of coastal Douglas-

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5 fir. Date of establishment of the stands ranged from the 1860's to the 1960's. Temporal trends in tree growth were inferred using the “cohort comparison” approach (Lopatin et al., 2008), gauging trend from change in specific yield between stands of different date of establishment. Here, we arbitrarily chose a reference ring age of 75 years. Fitting Monod functions to D_{ib} , or Chapman–Richards functions to BA and B indicated positive temporal trends between discrete classes in date of establishment (Fig. 1), which may be the result of natural stand dynamics, extrinsic processes like climate change in increasing atmospheric carbon dioxide concentration, and sampling biases (Briffa and Melvin, 2011; Brienen et al., 2012). Regardless of the cause, differences in the relative magnitude of the enhancement – with trends in D_{ib} and BA being substantially less than that of B – are consistent with the above examples.

10 Lastly, the relative sensitivity of standardized w to extrinsic factors may vary with age or size in ways that are not consistent across dimensions. Consider a hypothetical simulation where annual growth of stemwood biomass is characterized by prescribed limitations of heat and water:

$$15 \text{ AGR} = G_{10} \left(Q_{10}^{\left(\frac{T-10}{10} \right)} \right) \left(\frac{1}{1 + \exp(\tau(ET_p - ET_{p,th}))} \right) \quad (1)$$

20 where the sensitivity to air temperature (T) is prescribed as $Q_{10} = 6$, the growth at $T = 10^\circ\text{C}$ (G_{10}) is set to 3.5 kg C yr^{-1} , and the sensitivity to potential evapotranspiration (ET_p , mm d^{-1}) is defined by the shape parameter, $\tau = 4.0$, and threshold, $ET_{p,th} = 2.1 \text{ mm d}^{-1}$. In a hypothetical scenario, the tree grows for 200 years under simulated inter-annual climate variability, defined by a normal distribution of air temperature ($\mu = 10.0$, $\sigma = 2.0^\circ\text{C}$) and ET_p that varies with T according to $ET_p = 0.17T + 0.1 + \varepsilon$, where ε adds a normally-distributed random component of variation ($\mu = 0$, $\sigma = 0.15 \text{ mm d}^{-1}$). The scenario is intended to simulate a tree that operates on the upper cusp of the transpiration stress function (i.e., lower cusp of the corresponding “vulnerability” curve), and thus commonly experiences moderate levels of hydraulic dysfunction. Ontogenetic

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variation is intentionally stationary (i.e., AGR is independent of B and age). The resulting case leads to a temperature sensitivity that is significantly different from zero ($\lambda_{\text{AGR}} = 0.15 \pm 0.01 \text{ kg C } ^\circ\text{C}^{-1}$). The relative sensitivity to T can be calculated as the slope of the AGR vs. T regression relationship, divided by the mean of AGR (for all ages), times 100 to convert it to a percent. If the relative sensitivity is subsampled from the first or second halves of the tree's existence (i.e., young and old treatments), the sensitivities are estimated to be $\lambda_{\text{AGR}} = 5.4$ and $5.3 \text{ \% } ^\circ\text{C}^{-1}$, respectively, which are not statistically different ($P < 0.001$). To compare this with estimates based on the more commonly analyzed ring width, we re-calculate the relative temperature sensitivity, only using w (λ_w), for each age treatment. In this case, w was derived from inverting the allometric equation for AGR assuming the relationship, $B = 0.018D^{2.05}$. As in standard dendroecological procedures, values of w were then standardized to remove the variance explained by ring age:

$$f(A) = b_1 \left(\frac{1}{1 + (b_2 A)} \right) \quad (2)$$

where b_1 and b_2 are fitted parameters, and A is age. In the absence of stand dynamics and a biological signal, the fitted age response function is an unbiased estimator of w and effectively removes the geometric effect. If the standardization is based on the ratio, $w/f(A)$, then the relative temperature sensitivity for the young and old age treatments are $\lambda_w = 7.7$ and $11.6 \text{ \% } ^\circ\text{C}^{-1}$, respectively. If the standardization is based on residuals, $w - f(A)$, then the relative temperature sensitivity for the young and old age treatments are $\lambda_w = 7.3$ and $3.4 \text{ \% } ^\circ\text{C}^{-1}$, respectively. The hypothetical scenario demonstrates that interaction between ontogeny and extrinsic factors can be specific to the dimension being measured due to different ontogenetic patterns of each dimension (Bowman et al., 2013). Although discrepancies in the sensitivities in the example are relatively small, they are strongly influenced by the relatively high level of prescribed water stress and are expected to be far greater in cases where temperature sensitivity is not as strongly counteracted by water stress.

4 Summary

Problems associated with the dimension and standardization of ring-width measurements indicate a bias in the sensitivity of tree growth inferred from w , or BAI. Several studies recognize the ineffective standardization of w and work instead with BAI because it is more closely related to AGR (e.g., Smith et al., 1989; Becker et al., 1994; Bert et al., 1997; Silva et al., 2010; Lapointe-Garant et al., 2010; Gómez-Guerrero et al., 2013). Despite the extent of valuable forest science that has reported findings based on analysis of BAI, we advocate use of AGR (e.g., Graumlich et al., 1989; Bascietto et al., 2004; Hogg et al., 2005; Metsaranta and Kurz, 2012) because it also resolves the problem of state variable-specific forcing. We are careful to note, however, that working with AGR does not dismiss the need to distinguish between intrinsic and extrinsic forcings through a combination of careful experimental design and statistical modelling (e.g., Girardin et al., 2008; Lapointe-Garant et al., 2010; Girardin et al., 2012; Hember et al., 2012). By working with absolute growth rate of stemwood biomass, studies can circumvent difficulties interpreting trends and environmental sensitivity of w that arise from geometric distortion and dimension-dependent sensitivity to extrinsic forcing and conform with the universally-accepted definition of primary production, as a flux density of mass or energy. Dendroclimatologists have compiled extensive databases of tree ring chronologies, yet they have limited capacity to clearly inform on the environmental sensitivity of tree growth without accurate reconstruction of tree size and transformation of dimensional measurements into AGR. Although use of allometric equations to convert tree ring measurements into gravimetric or volumetric units introduces additional uncertainty, we consider this source of error to be less confounding than the problems that currently arise from use of w or BAI. Hence, although there is a strong scientific need to use tree-level measurements to estimate the sensitivity of growth to environmental factors (Moore et al., 2006), or to compare tree-ring measurements with other data sources, such as model predictions (Girardin et al., 2011; Rammig et al., 2014), remote sensing (Andreu-Hayles et al., 2011; Beck et al., 2011;

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Williams et al., 2011), or stable isotopes (Bert et al., 1997; Sleen et al., 2014), it is important to recognize that sensitivity of primary production indirectly inferred from analysis of w or BAI is significantly underestimated.

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Table 1. List of variable symbols and description.

Symbol	Description
B	Biomass of stemwood (kg C tree^{-1})
AGR	Absolute growth rate of stemwood biomass, $\text{AGR} = \Delta B / \Delta t$ ($\text{kg C tree}^{-1} \text{ yr}^{-1}$)
D_{ib}	Inside-bark diameter of stemwood (cm)
D_{ob}	Outside-bark diameter of stemwood (cm)
w	ring width, or $\Delta(D_{\text{ib}}/2) / \Delta t$ (mm yr^{-1})
BA	Basal area of stemwood (cm^2)
BAI	Annual incremental growth of stemwood basal area ($\text{cm}^2 \text{ yr}^{-1}$)

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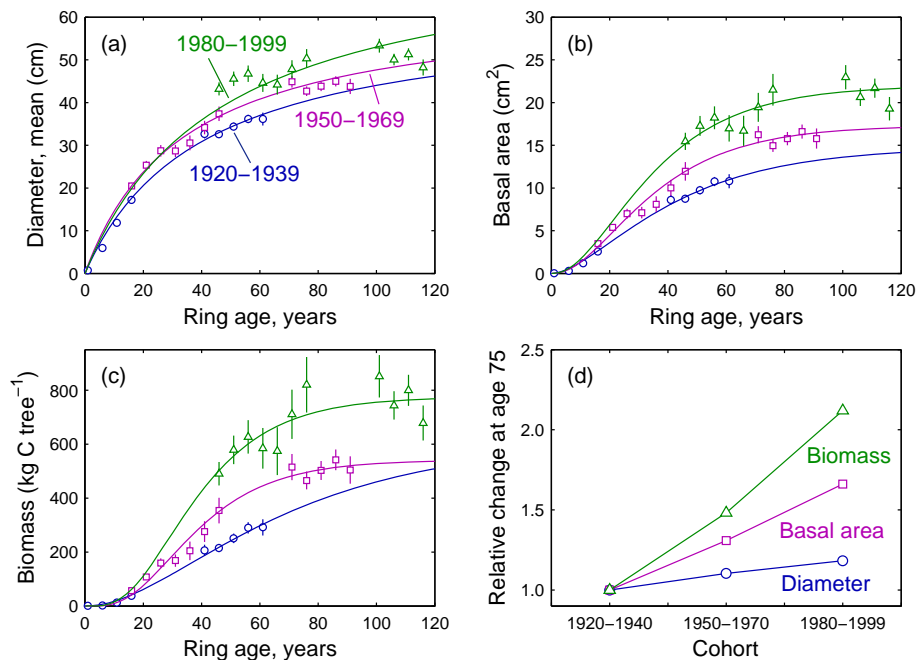


Figure 1. Analysis of age-class yield curves for discrete classes in calendar year ranging from 1920–1939, 1950–1969, and 1980–1999 **(a)** diameter **(b)** basal area **(c)** stemwood biomass **(d)** summary of the change in specific yield at ring age 75 years relative to the first class.