

An evaluation of boundary-line release criteria for eleven North American tree species

B.A. Black¹ & M.D. Abrams²

¹ Hatfield Marine Science Center, Newport, OR 97365, Email: Bryan.Black@oregonstate.edu

² Corresponding author, 4 Ferguson Building, Penn State University, University Park, PA 16802
Email: agl@psu.edu

Introduction

One of the most fundamental dendroecological techniques for identifying disturbance events in tree ring time series is the analysis of releases (Lorimer and Frelich 1989). Traditionally, a release has been defined as an event where the percent growth change in radial growth exceeds a given minimum threshold, such as 50 or 100 percent, which in some criteria must be maintained for a certain length of time such as five or ten years (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Thus, releases rely on the assumption that the magnitude of percent-growth change corresponds to the magnitude of a canopy disturbance. However, the relationship between percent-growth change and canopy disturbance is complicated by a number of interrelated and confounding variables such as crown size and position; gap proximity, size, and duration; prior growth rate; age and diameter; species, and climate (Nowacki and Abrams 1997).

To better describe the effects of and interactions among variables that could potentially affect the magnitude of a growth pulse following the release of a tree's canopy, Black and Abrams (2003) quantified relationships among tree age, size, canopy class, radial growth rate, and percent growth-change in eastern hemlock (*Tsuga canadensis* L.). A new set of release criteria were developed based on the finding that growth rate prior to a growth pulse was the most fundamental predictor of the maximum possible magnitude of the change pulse, when expressed in terms of percent growth change. In summary, young, small, and suppressed trees were found to be capable of extremely large pulses in percent-growth change in comparison to their older, larger, dominant counterparts. In addition, smaller, younger, and suppressed trees also showed slower radial growth rates. Radial growth rate appeared to be closely related to the magnitude of percent-growth change pulses. Indeed, when percent-growth change is graphed against average radial growth over the past ten years, percent growth-change values extend to a well-defined boundary that declines exponentially across increasing rates of prior growth (Black and Abrams 2003). An important aspect is that eastern hemlock of almost any age, size, and canopy class demonstrates percent growth-change pulses that reach this upper boundary. Slow-growing trees, which tend to be small understory individuals, reach the boundary with large pulses in percent-growth change. Fast-growing trees, which tend to be large dominant individuals, can reach the boundary with only modest pulses in percent-growth change. To incorporate the effects of prior growth into release criteria, each percent growth-change pulse is scaled in terms of its maximum possible value, as predicted by level of prior radial growth. This should better compensate for

differences among age, size, and canopy classes and allow for more direct comparisons of release events across all phases of a tree's lifespan.

In this study, the interactions among prior growth, age, and size are explored in eleven tree species representing a wide variety of ecological strategies and forest types throughout North America. We show that prior growth strongly influences maximum percent-growth change in all eleven species, and that the consistent relationships between prior growth and percent growth change suggest that boundary-line release criteria may be developed in all species. Releases could be better standardized by uniformly expressing them as a percentage of their maximum value predicted by species and prior growth rate. Such standardized releases would facilitate comparisons of disturbance history among species and among stands, increasing the power of release criteria to establish landscape-level patterns of disturbance.

Methods

Species were selected to represent a diversity of habitats in North America, ranging from the boreal forests of Canada to the mountains of the Desert Southwest. In total, nearly 1.3 million growth increments were included from 258 stands from the NOAA International Tree Ring Data Bank (Tab. 1). Eastern species include *Tsuga Canadensis* (hemlock), *Picea glauca* (white spruce), *Picea mariana* (black spruce), *Quercus alba* (white oak), *Quercus prinus* (chestnut oak), *Pinus strobes* (white pine), *Quercus macrocarpa* (bur oak), *Quercus stellata* (post oak), and *Pinus echinata* (shortleaf pine), while western species include *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas fir). Percent growth change was calculated for each series of tree ring measurements following the technique of Nowacki and Abrams (1997) in which percent growth change for a year is equal to $(M_2 - M_1) / M_1$ where M_1 equals average growth over the prior 10 years and M_2 equals average growth over the subsequent 10 years. The effects of growth history on maximum percent growth change were better quantified for each species by plotting percent growth change against prior growth. Prior growth was defined as the average raw growth over the ten years prior to a given growth increment. Thus, the prior growth value for the 1990 growth increment of a given tree would be the tree's average raw growth between 1980 and 1989. The relationship between prior growth and percent growth change was plotted for every growth increment of every tree, with the exception of the first and last ten years of growth in which percent growth change could not be calculated. The upper threshold of the relationship between prior growth and percent growth change was then quantified by calculating a boundary line. For each species, a boundary line was constructed by first dividing the data set into 0.5 mm segments of prior growth. Then within each segment, the percent growth-change values of the top ten points were averaged. The top ten points in each section ensured an equal sample size across all prior growth classes, and limited the analysis to the few points that represented true maximal releases. To quantify the boundary line linear, power, logarithmic, and exponential curves were fitted to all positive segment averages, and the function that yielded the highest R^2 value was selected (Black and Abrams 2003).

Table 1. Number of sites and total number of growth increments for each species. % of max sites refers to the percentage of sites in which percent growth change values come within at least 90% of the value of the boundary line. Max age indicates the approximate age at which trees consistently fail to reach the boundary line.

Species	N sites	N growth increments	boundary line equation	% of max sites	max age
<i>Pinus echinata</i>	22	74,925	$y = 998.65 e^{-1.0237x}$	33	150
<i>Pinus strobus</i>	12	72,714	$y = 501.96 e^{-0.664x}$	47	250
<i>Pinus ponderosa</i>	23	157,243	$y = 665.97 e^{-0.9354x}$	43	250
<i>Picea glauca</i>	32	102,306	$y = 649.97 e^{-1.0798x}$	17	200
<i>Picea mariana</i>	26	49,007	$y = 407.92 e^{-1.4679x}$	19	250
<i>Tsuga canadensis</i>	25	180,708	$y = 974.54 e^{-1.1202x}$	30	400
<i>Pseudotsuga menziesii</i>	25	172,372	$y = 569.80 e^{-0.928x}$	36	300
<i>Quercus macrocarpa</i>	38	92,092	$y = 511.27 e^{-0.7018x}$	34	50
<i>Quercus stellata</i>	23	169,333	$y = 948.45 e^{-1.6188x}$	39	150
<i>Quercus prinus</i>	8	35,337	$y = 742.83 e^{-0.9445x}$	29	200
<i>Quercus alba</i>	24	164,876	$y = 527.22 e^{-0.787x}$	38	200

Age and size-specific variations in growth rate and percent growth change were explored for each species as a way to validate whether the prior-growth boundary line applies to all phases of a tree's development. Age of each growth increment was estimated by counting all preceding growth rings, while radius was estimated by summing the widths of all preceding growth rings. Growth increments were assigned radius classes in 50 mm increments (0-49.9 mm, 50-99.9 mm, etc.) and age classes in 50 year increments (0-49 years, 50-99 years, etc.). All growth increments were plotted with respect to age or radius class, prior growth, and percent growth change. If all age and radius classes approach the upper threshold of percent growth change values, all classes are capable of maximum percent-growth change as predicted by prior growth. If any age and radius classes fall short of the threshold, the effects of prior growth on maximum percent-growth change do not adequately explain percent growth change differences among age or radius classes.

Results and Discussion

Prior growth is an important determinant of maximum percent-growth change for all surveyed species. In all eleven species, maximum percent-growth change diminishes at a negative

exponential rate with increasing levels of prior growth (Fig. 1). Negative exponential boundary lines appear to be a good fit to the data and all have high R^2 values, ranging from 0.92 to 0.99 (Fig. 1, Tab. 1).

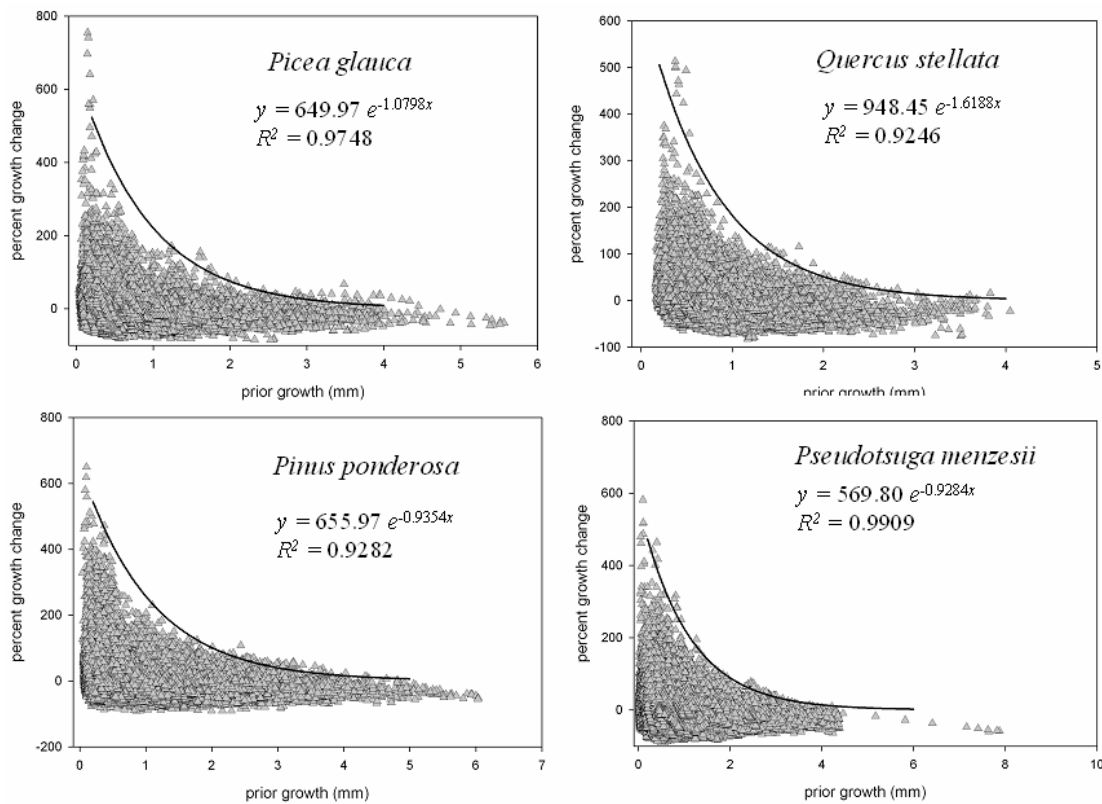


Figure 1: Relationship between percent growth change and prior growth for four North American tree species. A boundary line summarizing maximum values of percent-growth change is also shown.

The only potential exception is shortleaf pine in which a power function of $y = 242.21 x^{-1.2434}$ had an R^2 of 0.97. This is negligibly better than the fit of a negative exponential function ($R^2 = 0.96$), so for consistency the negative exponential function was chosen to represent the boundary line. Overall, the boundary lines closely follow the upper threshold of maximum percent-growth change for all species (Fig. 1). In each case, data from several sites approach the boundary line of each species, ranging from a minimum of 17% of all sites in black spruce to 47% of all sites in white pine (Tab. 1). Furthermore, sites that approach the boundary line occur across very broad geographic regions for many species. For the ponderosa pine these include sites from New Mexico to South Dakota to Oregon and California. Representative trees for Douglas-fir were sampled in New Mexico, Arizona, Wyoming, and Washington. Sites that approach the white oak boundary line are located in Kentucky, Illinois, Pennsylvania, and Minnesota while sites that approach the post oak boundary line are located in Texas, Oklahoma, and Kansas. In a more detailed evaluation, white oak sites from the eastern portion of its range (Pennsylvania, New Jersey, Ohio, and Virginia) approach the boundary line (Fig. 2 A) as do sites from the western portion of its range (Missouri, Iowa, and Minnesota) (Fig. 2 B). Also, Douglas-fir sites from the Cascade Mountains of the Pacific Northwest (Oregon, Washington, and Canada) approach the

boundary line (Fig. 2 C) as do sites from the mountains of Arizona, New Mexico, and Mexico (Fig. 2 D). Site-specific differences may exist, yet on a broad scale, a single boundary line appears to apply to a wide region. More detailed studies in which specific site conditions are known will be required to test whether certain site conditions correspond with failure of trees to attain the boundary line. If indeed site-specific differences are detected, these findings will have implicating for all release criteria, not just the boundary-line approach.

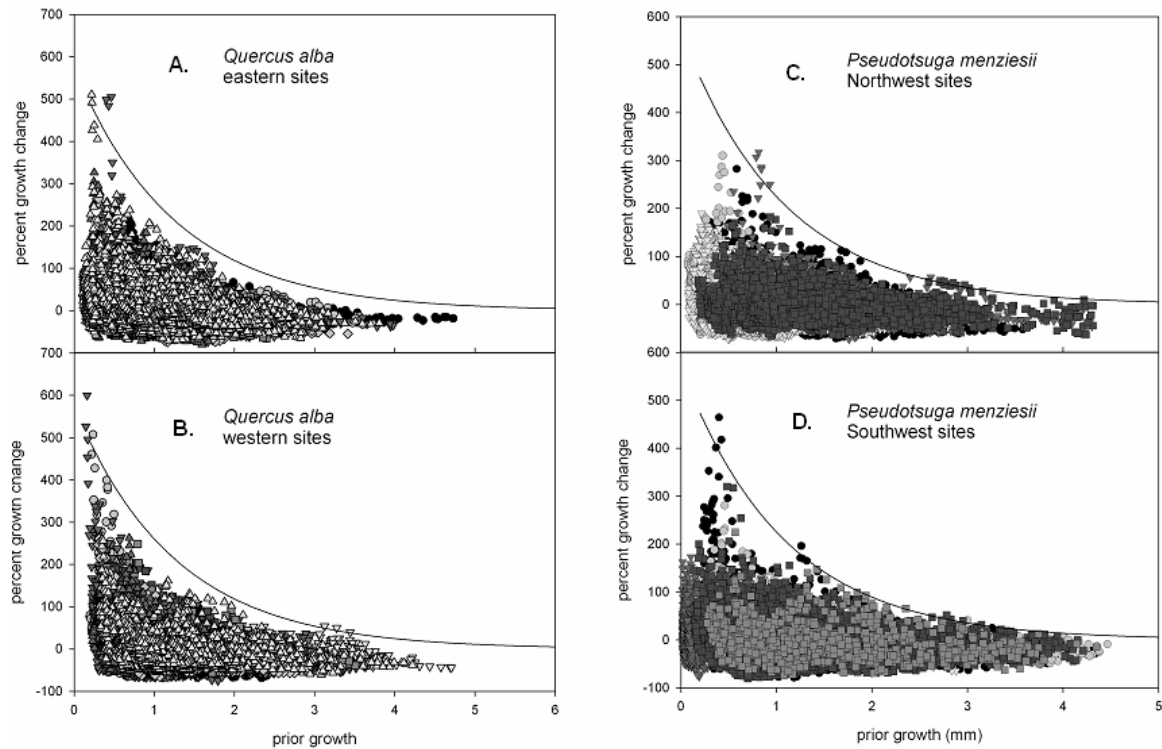


Figure 2: Relationship between prior growth and percent growth change for Douglas-fir and white oak sites. A) Eastern portion of white oak's range include Ohio, Pennsylvania, and Virginia. B) Western white oak sites include Minnesota, Iowa, and Missouri. C) Northwest Douglas-fir sites are located in the Cascade Mountains or Washington, Oregon, and Canada. D) Southwestern Douglas-fir sites are located in Arizona, New Mexico, and Mexico. The species-specific boundary line is shown for both species.

In many species, declines in raw growth and percent growth change result in the failure of large or old trees to reach the prior-growth boundary line (Tab. 1, Fig. 3). Perhaps the only true exception is eastern hemlock in which almost all age and radius classes approach the upper threshold of maximum percent-growth change as predicted by prior growth. Even trees as large as 80 cm in radius and as old as 400 years can approach this upper boundary of maximum percent-growth change (Tab. 1) (Black and Abrams 2003). Thus eastern hemlock trees of almost any age are capable of showing full releases, and the entire series of tree-ring measurements for each tree may be included in analyses of disturbance history using the boundary-line approach. All other species, however, consistently fail to reach the boundary line after a given age (Tab. 1, Fig. 3). This phenomenon is clearly shown when percent-growth change values of older trees are plotted with respect to the boundary line (Fig. 3). Failure to reach the boundary line often becomes increasingly severe with increasing age, as shown here for shortleaf pine, post oak, eastern white pine, and white spruce (Fig.

3). Overall, approximate age at which trees begin to consistently fail to reach the boundary line varies considerably among species (Tab. 1). Douglas-fir fails to reach the boundary line at the comparatively old age of 300 years. Yet considering the large maximum ages of this species, a substantial proportion of an old-growth tree would not be showing full release. The most extreme example of all species is bur oak, which consistently fails to reach the boundary line by as early as 50 years in age (Tab. 1).

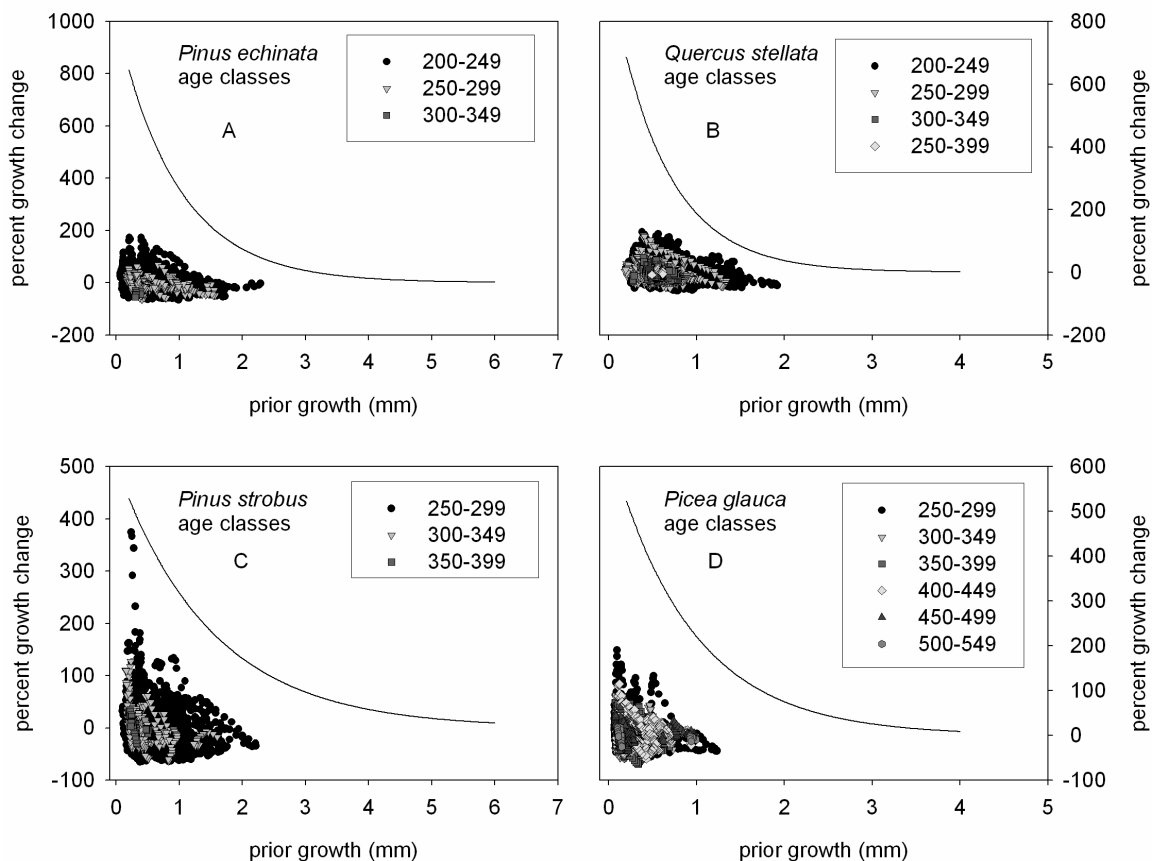


Figure 3: Relationship between prior growth and percent growth change in the oldest 50-year age classes of four species. Each species' boundary line is shown.

The reason as to why older trees fail to reach the boundary line is not immediately clear. These failures could be the result of physiological or morphological factors in which the tree is no longer able to vigorously exploit resources freed by disturbance. Or these older trees simply do not experience such a large increase in resources as compared to their younger counterparts. A disturbance may increase light levels by a factor of ten for a suppressed understory tree, but only expose a relatively small portion of the crown to light in a mature overstory tree. No matter the exact reason for these age-related failures, caution must be used when using older, larger trees. At this time, age or size limits may be necessary for reconstructing disturbance history. In the future, age-specific boundary lines may be developed after more experimental work has been conducted. But for now, growth increments formed after a certain age (or size) should be dropped from analysis. These age restrictions would apply not only to boundary line release criteria, but any release criteria

developed to date. The strength of the boundary-line release criteria is that they can help compensate for many age-related differences in release response, as is shown the most dramatically in eastern hemlock. Before trees reach the age at which they no longer reach the boundary line, releases may be expressed as a fraction of maximum potential value, as predicted by the boundary line. Thus boundary line release criteria will better standardize all releases within and among species and sites.

In conclusion, prior growth is clearly an important factor in determining the potential maximum percent-growth change and should therefore be included in release criteria. The prior-growth boundary-line provides a novel technique that can be applied to a wide range of species, as indicated by the diversity of species in this study. Not only could this provide more accurate estimates of the number and magnitudes of disturbance a tree experienced, but it also serves as a standardized framework of release criteria that can be applied to a wide range of species and forest types. All releases are expressed in terms of maximum potential as predicted by species and level of prior growth. So doing would reduce differences in maximum percent-growth change among individuals growing at different levels of prior growth, and would also standardize among species with different levels of maximum percent-growth change. This standardization would allow for better direct comparisons of disturbance histories among stands, and even for fine-scale studies of disturbance history in multi-species stands. Age and size may still influence maximum percent-growth change in that intolerant species are most likely to have severe reductions while tolerant species may show little or no change. For the present, older and larger trees may have to be eliminated from samples until the mechanisms behind these reductions are experimentally verified. Yet despite these complications, incorporation of prior growth into the release criteria will improve the accuracy of identifying disturbance events and estimating the magnitude of those events. For these reasons we believe the boundary-line technique will serve as a valuable tool for release calculations.

References

- Black, B.A., Abrams, M.D. (2003): A boundary-line approach to establishing release criteria in old-growth hemlock. *Ecological Applications* 13: 1733-1749.
- Black, B.A., Abrams, M.D. (2004): Development and application of boundary-line release criteria. *Dendrochronologia*. 22: 31-42.
- Lorimer, C.G., Frelich, L.E. (1989): A method for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* 19: 651-663.
- Nowacki, G.J., Abrams, M.D. (1997): Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* 67: 225-249.