

USE OF BOUNDARY-LINE GROWTH PATTERNS AS A BASIS FOR DENDROECOLOGICAL RELEASE CRITERIA

BRYAN A. BLACK¹ AND MARC D. ABRAMS

203 Forest Resources Lab, Penn State University, University Park, Pennsylvania 16802 USA

Abstract. Identifying releases from suppression represents one of the most fundamental dendroecological procedures for quantifying forest disturbance histories. In tree-ring series, releases are typically defined as pulses in percent growth change that exceed a minimum threshold. Past methodologies have applied fixed growth-change thresholds that may overly generalize the ability of a tree to respond to a disturbance event. In this study, we develop a more precise method that scales each release by its maximum release potential as defined by prior growth rates, using an old growth hemlock (*Tsuga canadensis* L.) forest in central Pennsylvania as an example. On average, tree age, diameter, and crown class appear to influence the magnitude of release response. However, differences in release response between age, diameter, and crown classes are largely an artifact of the more fundamental relationship between release response and growth immediately prior to release. Specifically, maximum percent growth change declines at a steep, negative exponential rate as prior growth levels increase. Slow-growing hemlocks can exceed 800% growth increases while fast-growing hemlocks do not exceed growth increases of 20%. This negative exponential threshold, or boundary line, represents the maximum percent growth change that is physiologically possible at a given level of prior growth. Thus, release potential is relative to prior growth rate. This relationship between prior growth and release potential is species specific and is demonstrated in 24 additional hemlock stands. We propose new criteria based on prior growth in which moderate and major releases are those falling within 20–49.9%, and 50–100% of the boundary line, respectively. Effects of short, moderate, and long-term climate events are mitigated by the percent-growth-change calculation and the high growth-change threshold applied to slow-growing trees. In addition, we demonstrate that similar boundary lines occur in *Pinus strobus* L. and *Quercus prinus* L., and interspecific variations in boundary line configuration reflect differences in understory tolerance. Overall, this approach provides a more theoretically sound and flexible approach to developing disturbance histories, and we believe it will ultimately have broad applications in a variety of forest types.

Key words: boundary line; disturbance; eastern hemlock; old-growth forest; release criteria; tree-ring data.

INTRODUCTION

Forest structure, growth, and composition are greatly influenced by edaphic factors, the autecological characteristics of individual species, and long- and short-term climate patterns. However, complete interpretation of forest stand development and current condition also requires consideration of disturbance history, including stand-wide and localized disturbance events. Both can profoundly alter stand structure and composition and maintain diversity on landscape and stand-level scales (Loucks 1970, Heinzelman 1973, Bormann and Likens 1979, Hibbs 1982, Foster and Boose 1992, Orwig and Abrams 1994, Frelich 2002). Recognizing the importance of disturbance, researchers have employed a number of techniques to quantify disturbance

history, including analysis of stand age structure (Heinzelman 1973, Foster 1988), identification of fire scars in bole cross sections (Buell et al. 1954), stratigraphic analysis of sediment cores (Clark and Royall 1995, Delcourt et al. 1998), historical accounts (Russell 1983, Foster 1988), and data recorded in original land surveys (Grimm 1984, Seischab and Orwig 1991, Black and Abrams 2001). In addition, dendroecological approaches have proven extremely useful in identifying the magnitude and frequency of disturbances over time, especially when coupled with stand-age structure and land-use information (Abrams and Nowacki 1992, Orwig and Abrams 1994, 1999).

One of the most fundamental dendroecological approaches for evaluating the disturbance history of a stand is identification of releases (Lorimer and Frelich 1989, Frelich 2002). Calculation of releases is a powerful and unique tool that reflects both localized and stand-wide disturbances at a high temporal resolution. Releases depend on the assumption that the magnitude of a disturbance corresponds to the magnitude of the

Manuscript received 11 April 2002; revised 25 October 2002; accepted 22 January 2003; final version received 18 April 2003.
Corresponding Editor: G. M. MacDonald.

¹ Present address: Hatfield Marine Science Center, Oregon State University, Newport, Oregon 97365 USA.
E-mail: bryan.black@oregonstate.edu

subsequent pulse in percent growth change. Mathematically, a release is typically defined as an event when the percent growth change of a tree's chronology exceeds a given minimum threshold, such as 50% or 100%, for a certain duration. Exact components of release criteria vary widely in the literature and depend in part on the specific goals of the study, which may be oriented to detecting only large-magnitude disturbances or disturbances of all sizes. For example, Lorimer and Frelich's (1989) release criteria were developed to determine rates of canopy turnover by estimating the date at which each tree accessed the canopy. The decadal proportion of trees with canopy accession dates is used to estimate the amount of canopy loss, and therefore disturbance intensity, in each 10-yr period (Lorimer and Frelich 1989). In order to eliminate the effects of climate and thinning events in which no understory trees were truly released to the canopy, very stringent release criteria are applied. In contrast, other release criteria are less strict and reveal a wider spectrum of disturbance events. Nowacki and Abrams (1997) set release criteria at levels just above maximal response to climate, allowing for the detection of small, local disturbances in addition to those of a broader scale.

Beyond the goals of the analysis, a number of biological variables affect the release response of a tree and must be considered in the formulation of release criteria. One of the most important of these is differences in release potential among species. Shade tolerant species such as black gum (*Nyssa sylvatica* Marsh.) and sugar maple (*Acer saccharum* L.) typically release with more vigor than less tolerant species such as red oak (*Quercus rubra* L.) and yellow poplar (*Liriodendron tulipifera* L.) (Lorimer and Frelich 1989, Orwig and Abrams 1994, Nowacki and Abrams 1997). To account for interspecies differences, threshold levels must vary in accordance with the release characteristics of each species. For example, a relatively low growth-change threshold of 25% has been established for overstory oak, a moderately intolerant and only somewhat responsive species (Nowacki and Abrams 1997). On the other extreme, much more conservative criteria of 100% increases in growth have been employed for the plastic, shade tolerant, eastern hemlock (*Tsuga canadensis* L.) (Lorimer and Frelich 1989).

In addition to interspecific variations in release response, individual trees within a species may be more or less sensitive to disturbance events. Factors that may cause such intraspecific variations include age and diameter, in that young or small trees are believed to be more responsive to disturbance events than older trees (Lorimer and Frelich 1989). Another widely cited variable is the canopy position of the tree (Lorimer and Frelich 1989, Nowacki and Abrams 1997, Ruffner and Abrams 1998). Understory individuals typically exhibit substantially larger percent growth increases

following a disturbance than their overstory counterparts. One explanation for this is that overstory trees generally receive adequate light and are growing almost as rapidly as possible. Additional resources of light, nutrients, or space beyond this saturation level cannot induce a substantial growth increase. By contrast, trees limited by the low light conditions of the understory will exhibit a sudden and dramatic increase to their full growth potential in response to improved conditions (Lorimer and Frelich 1989).

Although age, diameter, and canopy position may affect the sensitivity of trees to release response, release criteria to date have not fully accounted for these variables. Several methods implement a diameter limit on trees, yet this approach can be somewhat arbitrary and does not fully account for the developmental history of the tree as it ascends through various canopy positions (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Other methods partition the understory and overstory phases of the tree by identifying the canopy accession date, and then apply conservative criteria to the understory segment and less strict criteria to the overstory segment (Ruffner and Abrams 1998, Abrams et al. 1999). This type of approach attempts to eliminate the effects of canopy position and possibly age; yet the differences in release response between understory and overstory trees have not been thoroughly evaluated. Ideally, the differences between understory and overstory responses would be quantified and those values integrated into an even more relevant set of release criteria. Furthermore, the criteria would compensate for any other factor beyond crown class, diameter, and age that affects a tree's potential for growth increase.

In this study, we attempt to redefine release criteria by quantifying the exact effects of age, diameter, and canopy position on release response in an old-growth hemlock forest located in Schall's Gap, central Pennsylvania. Hemlock is of particular interest to dendroecologists because of its longevity and the relatively large number of old-growth remnants that persist throughout its range. Average longevity of old-growth hemlock reaches 300 years, providing rare opportunities to evaluate pre-European settlement disturbance regimes (Lorimer et al. 2001). In Schall's Gap, we describe differences in release potential across age, diameter, and crown classes, and then extend the analysis to include the effects of growth history immediately prior to a release. We show that slow growing trees intrinsically release more vigorously than fast growing trees, and the relationship between prior growth and release response is largely independent of age, diameter, and crown class. For verification of this phenomenon, consistent relationships between prior growth and release response are demonstrated in 24 additional chronologies located throughout hemlock's range. We then revise release criteria to include the effects of prior growth. As a final step, we show

that prior growth strongly influences release response in white pine (*Pinus strobus* L.) and chestnut oak (*Quercus prinus* L.), suggesting that these criteria will have broad applications to many other species and forest types.

STUDY AREA

This study was conducted within an old-growth hemlock forest in Schall's Gap, ~10 miles (~17 km) south-east of State College in Centre County, Pennsylvania. The region lies within the Ridge and Valley physiographic province, characterized by long, level, parallel ridges of sandstone and shale rising ~500 feet (~154 m) above broad, limestone-derived valleys (Braker 1981). Schall's Gap is indented within the north slope of Tussey Ridge and is surrounded by steep slopes of sandstone talus that are largely devoid of vegetation. Hemlocks persist mainly in the narrow (30–50 m wide), gently sloping floor of the gap, with some trees extending into the lower slopes of the talus fields. Soils of the gap floor are Andover, a deep, poorly drained loam of low permeability derived from sandstone and shale colluvium (Braker 1981). Consistent with the low permeability and typically high water table in these soils, a stream divides the floor of Schall's Gap. The forest exhibits several old-growth characteristics including diverse structure, large amounts of coarse woody debris, and dead-standing trees. Fire scars are evident on a few hemlocks growing on the upper slopes of the gap, but there is no indication of fire on the lower elevation sites. Deer droppings are common and intense browsing occurs on hemlock seedlings and saplings throughout the stand. Elevation of the stand ranges from 450 to 490 m above sea level.

The climate of Centre County is mainly dry continental with some humid, maritime influence. Winters are typically cold and dry with mean monthly minimum temperatures ranging from -5° to -7°C (December through March). Summers are warm and humid with mean maximum temperatures ranging from 26° to 28°C (June through August). Mean monthly precipitation ranges from 6.7 to 9.7 cm and total annual precipitation averages 93.4 cm. The average frost-free season is 170 d (14 April to 14 October; Braker 1981).

METHODS

In the summer of 2000, 20 fixed-area plots were established at 20-m intervals along two parallel transects. Plot centers were located on the gap floor between the stream and talus slopes. The species, diameter, and crown class were recorded for all trees >8.0 cm in diameter within 0.02-ha circular plots at each plot center. Crowns were assigned one of four classes (dominant, codominant, intermediate, overtopped) based on the amount and direction of incident light (Smith 1986). Each species' relative density (number of trees), relative frequency (presence or absence in plots), and relative dominance (basal area) was calculated and averaged into

an importance value. At each plot, two to four trees were cored at 0.5 m, or higher (e.g., 1.5 m) if rot or buttressing was encountered, for age determination and radial growth analysis. We randomly selected trees within each plot, including a variety of size classes and some recently dead individuals.

Hemlock cores were dried, mounted, and sanded with increasingly fine sandpaper to reveal the cellular structure (Phipps 1985). Any cores with rotten or excessively fragmented segments were discarded from further analysis. The remaining hemlock cores ($N = 47$) were then cross-dated using the signature-year technique to identify any partial, missing, or false rings (Yamaguchi 1991). Each series was then measured to the nearest 0.002 mm using a Unislide "TA" tree-ring measuring system (Velmex, Bloomfield, New York, USA). Once the cores were measured, cross-dating was verified using the program COFECHA version 2.1 (Cook et al. 1997).

To analyze the frequency and intensity of disturbances, disturbance histories were calculated for the 47 raw ring-width series using several different methods. The first of these were the conservative and moderate analyses proposed by Lorimer and Frelich (1989). In this approach, canopy accession dates are used as evidence of disturbance and are identified as recruitment years of gap-origin trees or sustained releases in tree-ring series. In the conservative version of the analysis, releases are events in tree-ring series where there is a 100% growth increase and a rapid acceleration of growth within 6 yr. Releases are only counted for trees <26.0 cm in diameter (Lorimer and Frelich 1989). The moderate version of the analysis is similar to the conservative analysis except that the diameter limit is 45.9 cm and releases also include less punctuated and temporary growth pulses between 50% and 99% (Lorimer and Frelich 1989). In a different technique, Nowacki and Abrams (1997) rely exclusively on releases to estimate disturbance history. Running comparisons are made of sequential 10-yr ring-width means and any event in which a 25% increase in growth occurs is defined as a release. Finally, Abrams et al. (1999) determine the canopy accession date for each tree using the methods of Lorimer and Frelich (1989). However, release criteria are different for overstory and understory trees, and releases are subdivided into major and moderate categories. In the years before the canopy accession date, a major understory release is defined as a greater than 100% mean growth increase lasting at least 15 yr. A moderate understory release is defined as a greater than 50% increase sustained for at least 10 yr (Abrams et al. 1999). In the years after the canopy accession date, a modified version of Nowacki and Abrams (1997) technique is applied in which a growth increase greater than 50% sustained for 10 yr is identified as a major overstory release, while a moderate overstory release is identified as a growth increase $>25\%$ sustained for 10 yr.

TABLE 1. Frequency, density, and dominance data for tree species in Schall's Gap, central Pennsylvania, USA.

Species	Relative frequency	Density (stems/ha)	Dominance (m ² /ha)	Relative frequency	Relative density	Relative dominance	Importance value
<i>Betula alleghaniensis</i>	6	28	1.3	15.4	6.3	2.5	8.0
<i>Betula lenta</i>	12	55	4	30.8	12.5	8.0	17.1
<i>Pinus strobus</i>	1	8	1.9	2.6	1.7	3.8	2.7
<i>Tsuga canadensis</i>	20	350	43.3	51.3	79.5	85.7	72.2
Totals	39	441	50.5	100.0	100.0	100.0	100.0

We first quantified differences in release response among crown classes by comparing the mean percent growth change among the understory (overtopped and intermediate), codominant, and dominant individuals. Percent growth change follows that of Nowacki and Abrams (1997) in which percent growth change for a year is equal to $(M_2 - M_1)/M_1$, in which M_1 equals mean growth over the prior 10 yr and M_2 equals mean growth over the subsequent 10 yr. First, percent growth change was averaged over the entire life span of understory trees and over the past 50 yr for dominant and codominant trees, unless there was a clear canopy accession event. Mean raw growth was calculated for each crown class across the same time intervals. Next, radius was estimated by summing total prior growth for each year in each tree-ring series. Then, mean percent growth change and raw growth was calculated within each of six diameter classes (expressed in this study as radius classes of 0–49.9, 50–99.9, 100–149.9, 150–199.9, 200–249.9, and ≥ 250 mm). Finally, age was determined for each year in each tree-ring series, and mean percent growth change and raw growth was calculated within each of the six classes of 0–49.9, 50–99.9, 100–149.9, 150–199.9, 200–249.9, and ≥ 250 yr.

The effect of prior growth on release response was evaluated by plotting prior growth against percent growth change. Calculation of percent growth change follows the method of Nowacki and Abrams (1997), while prior growth was defined as mean raw growth over the 10 yr prior to each tree ring. Prior growth and percent growth change were calculated for each year of each series. However, the first and last 10 yr of each series were excluded because at least that many years are required in the percent-growth-change formula. To evaluate the consistency of the relationship between percent growth change and prior growth, these variables were graphed in 24 additional hemlock chronologies. Furthermore, we plotted percent growth change and prior growth in eight chestnut oak chronologies and 12 white pine chronologies (Appendix).

RESULTS AND DISCUSSION

Existing release criteria

Hemlock heavily dominated Schall's Gap with a relative importance value of 72.2%. Black birch (*Betula lenta* L.), yellow birch (*Betula alleghaniensis* Britton), and white pine only composed a fraction of the forest

composition (Table 1). Thus, hemlock should capture most disturbances in the stand. To resolve the relative impacts of small-scale and stand-wide disturbances, disturbance histories were estimated for Schall's Gap using a variety of established methods (Fig. 1). Results are summarized as decadal tallies of trees that indicate a disturbance event. This includes releases or releases and recruitment of gap-origin trees, depending on technique. One common event to all techniques is the large response that occurred in the 1850s following major windstorms in 1846 and 1850 (Ludlum 1963) (Fig. 1). Not only was this disturbance widespread throughout the stand, affecting a large proportion of trees, but also was of large magnitude. The technique of Abrams et al. (1999) shows a large proportion of major understory releases following this event (Fig. 1D). Indeed, hemlock stands are moderately susceptible to the effects of catastrophic wind in comparison to the highly susceptible white pine stands and resistant hardwood stands (Foster and Boose 1992). Another commonality is the frequency of small magnitude disturbances throughout the 20th century with a consistently moderate pulse of releases in the 1930s (Fig. 1). Small gaps are typically the most common form of disturbance in temperate old-growth forests as reflected by this baseline level of releases and recruitment events (Dahir and Lorimer 1996).

Differences in results among disturbance histories largely depend on how strictly releases are defined. The Nowacki and Abrams (1997) criteria are the most liberal and allow the largest number of growth pulses to qualify as releases (Fig. 1A). A high frequency of releases occurs throughout the 19th and 20th centuries, portraying a somewhat different disturbance history than the other techniques. The more stringent criteria of the Lorimer and Frelich (1989) technique substantially reduce the number of releases, with the fewest occurring in the conservative approach (Fig. 1B). Another notable difference is that Lorimer and Frelich (1989) include the recruitment dates of gap-origin trees in the disturbance history (Fig. 1B). The reason for the persistence of the effects of the 1846 and 1850 windstorms is that the Lorimer and Frelich (1989) method captures a lengthy period of regeneration of gap-origin trees (Fig. 1D). In the Abrams et al. (1999) combination of the Nowacki and Abrams (1997) criteria and the Lorimer and Frelich (1989) criteria, the persistence of

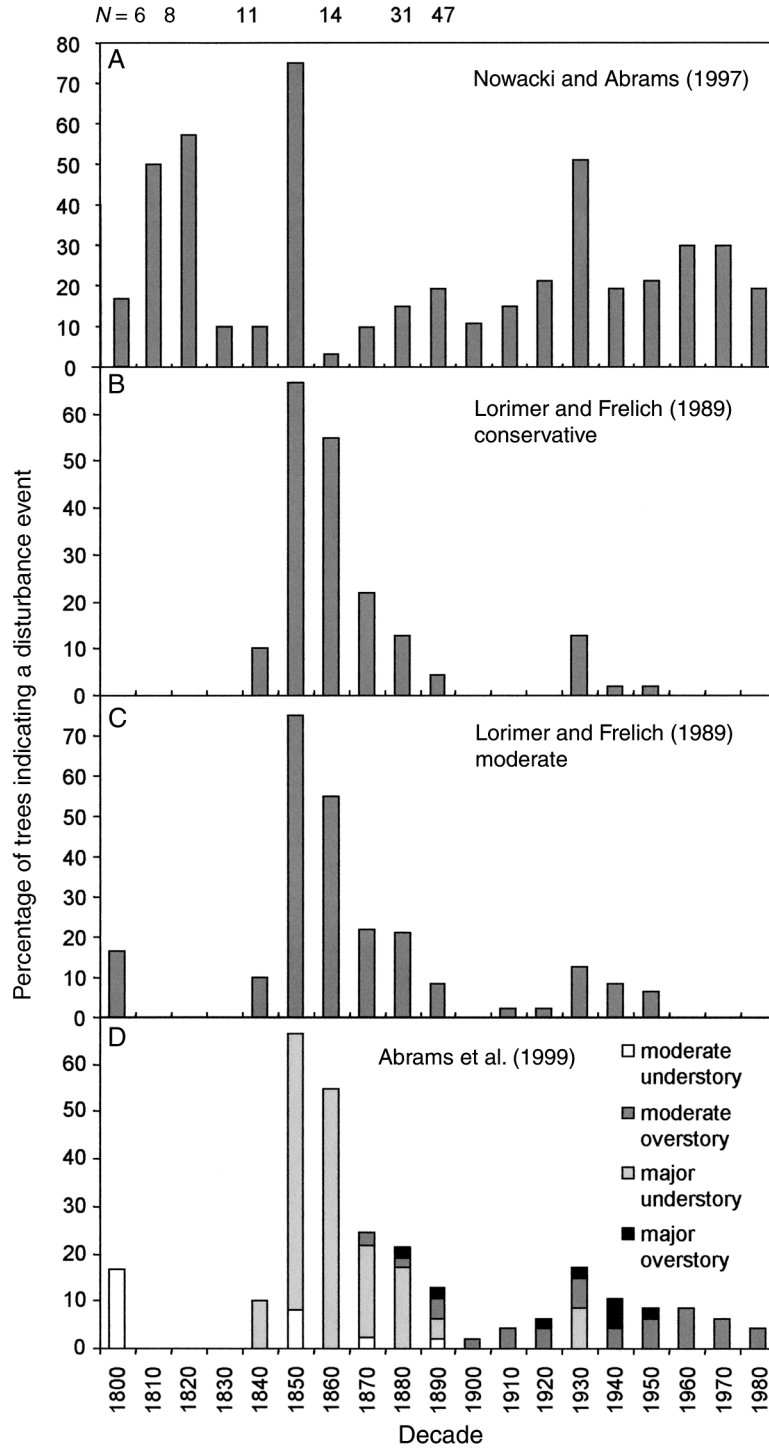


FIG. 1. Decadal percentages of *Tsuga canadensis* trees that indicate a disturbance event in Schall's Gap as estimated using the criteria of (A) Nowacki and Abrams (1997), (B, C) Lorimer and Frelich (1989), and (D) Abrams et al. 1999.

the windstorm effects is evident as well as a high release frequency in the 20th century (Fig. 1D). Also, understory releases are most common early in the disturbance history, with overstory releases increasing

through the 20th century (Fig. 1D). However, shifts from understory to overstory releases are due to the fact that most trees in the sample were a part of the understory in the first decades of the 19th century.

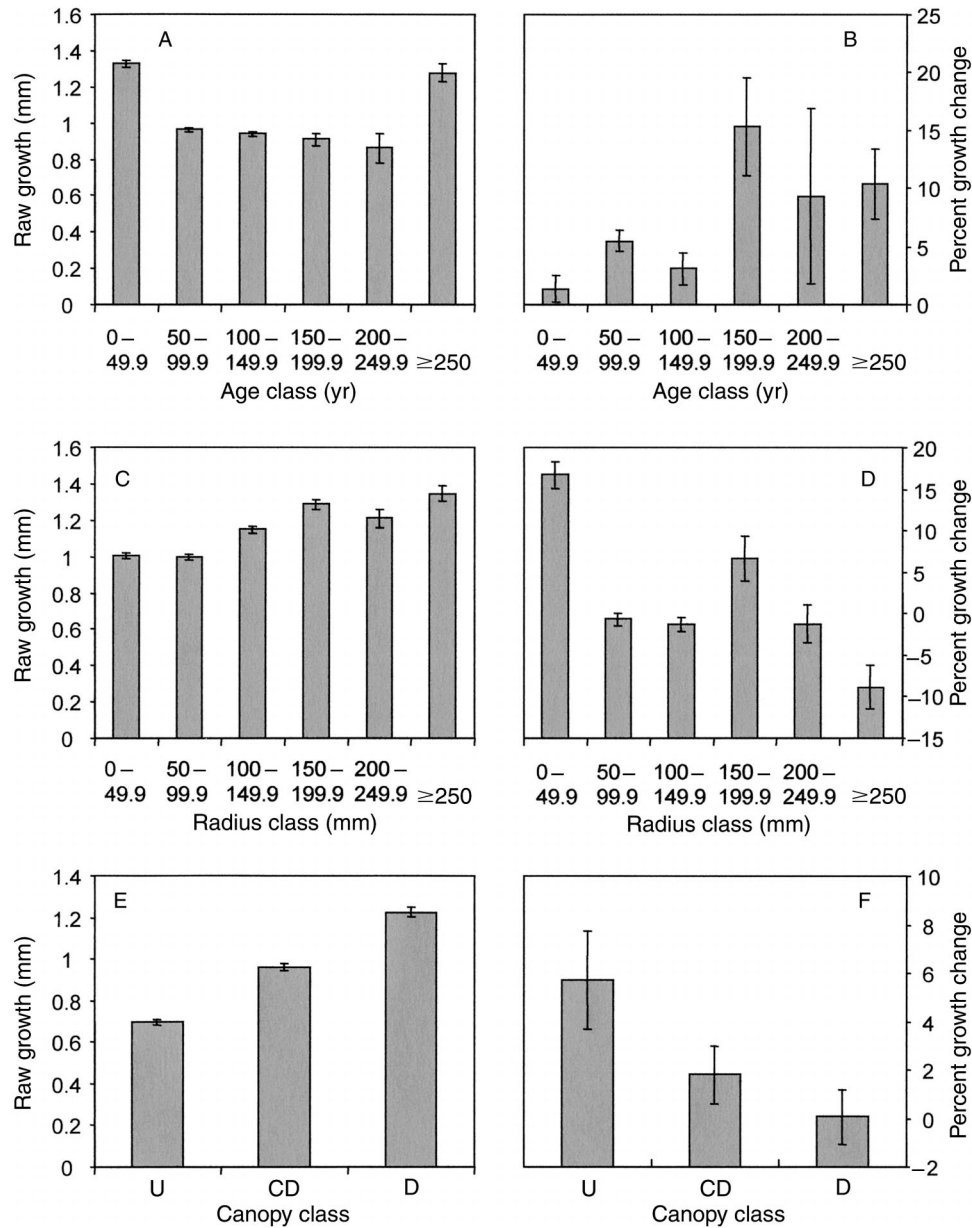


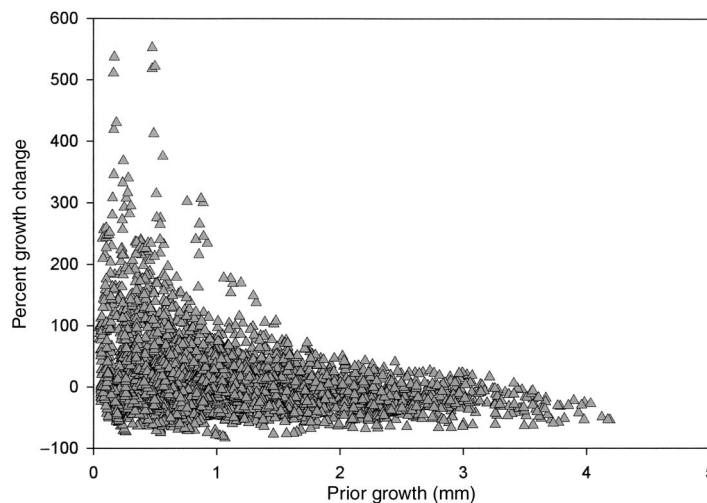
FIG. 2. Mean raw growth of *Tsuga canadensis* among (A) age classes, (C) radius classes, and (E) crown classes (abbreviations: D, dominant; CD, codominant; U, understory). Mean percent growth change among (B) age classes, (D) radius classes, and (F) crown classes. Error bars represent ± 1 SE.

*Influence of age, diameter, canopy position,
and prior growth*

The true nature of the disturbance history may be better described by analyzing the relationship between release response and variables pertaining to the development and physiological condition of the tree, such as tree age, diameter, canopy position, and history of suppression. The first of these, tree age, does not appear to have a strong impact on magnitude of release for the hemlock at Schall's Gap (Fig. 2A, B). Significant differences ($\alpha = 0.05$) in mean raw growth rate and

percent growth change do occur among age classes, but there are no consistent trends. A somewhat more regular pattern is apparent among radius classes, in which raw growth steadily increases and percent growth change decreases with increasing diameter (Fig. 2C, D). Also, dominant trees attain the fastest raw growth rates followed by codominant and understory trees while the understory trees exhibit the greatest potential for relative changes in growth rate (Fig. 2E, F). On average, smaller understory trees have the slowest growth rates and greatest release potential while larger

FIG. 3. Plot of percent growth change with respect to prior growth for all *Tsuga canadensis* tree rings measured in Schall's Gap.



overstory trees have the fastest growth rates and least release potential. However, there is considerable variability in this trend, as indicated by high standard errors in the means of percent growth change (Fig. 2D, F).

This variability within and among age, radius, and crown classes suggests that more factors could be involved in release response. The fact that crown class exhibits the strongest and most consistent differences in release response led us to investigate the role of growth history. We believed that crown class was closely linked to growth rate because understory trees typically spend a large proportion of their lives growing slowly under suppressed conditions, while overstory individuals can grow rapidly in the high-light conditions of the upper canopy (Fig. 2C). Therefore, to initially assess the effects of growth-rate history on release potential, we calculated mean radial growth between tree establishment (the first year of growth) and each year of the tree-ring series. Mean percent growth change generally declines as levels of prior growth increases. In a second analysis, we explored the relationship in a narrower interval using mean growth over the prior 10 years. When using only the prior 10 years of growth, a much more clearly defined relationship emerged between prior growth and percent growth change, indicating that a finer scale of growth history is a more accurate predictor of release response. A graph of this relationship illustrates that percent-growth-change values extend to a well-defined, upper threshold (Fig. 3). Maximal threshold responses form a negative exponential trend across increasing levels of prior growth, revealing a profound difference in maximum release potential between fast and slow-growing trees (Fig. 3). A hemlock in Schall's Gap with prior 10-yr growth of 0.5 mm could release with a 550% increase, while a tree with growth in excess of 4.0 mm did not even attain a positive percent growth increase (Fig. 3).

Although some differences in release potential seem to be due to age, radius, or crown class, the apparent effects of these variables can be explained in the context of prior growth. When age, radius, and crown classes are subdivided within a graph of prior growth and percent growth change, all classes approach the upper threshold and are thus capable of maximal release responses (Fig. 4A, B, C). In the case of age and radius classes, even the oldest and largest trees approach the threshold (Fig. 4A, B). Overall, differences in average release responses among age and radius classes (Fig. 2) are due to correlations of these classes with levels of prior growth. For example, trees with a small radius have the largest percent growth changes, but these trees also have the lowest radial growth rates (Fig. 2C), making them most prone to large growth pulses. The same is true to an even greater degree among crown classes. Large understory release responses are due to the fact that these individuals have by far the slowest mean growth rates and are predisposed to having larger percent growth increases (Fig. 2F, 4C). Dominant and codominant trees maintain higher mean growth rates and are consequently less capable of such large percent growth changes (Fig. 2). They still approach the upper threshold, but at faster prior growth values where maximal percent-growth-change values are relatively low (Fig. 4C). Therefore, differences in mean release response among crown classes, age, and radius are probably an artifact of the more fundamental relationship between release response and prior growth. Prior growth rate appears to be the most influential of these variables in determining release response.

Development of a boundary line

Given its importance, the relationship between growth immediately prior to release and release response should be incorporated into release criteria. The first step is to quantify as a boundary line the upper

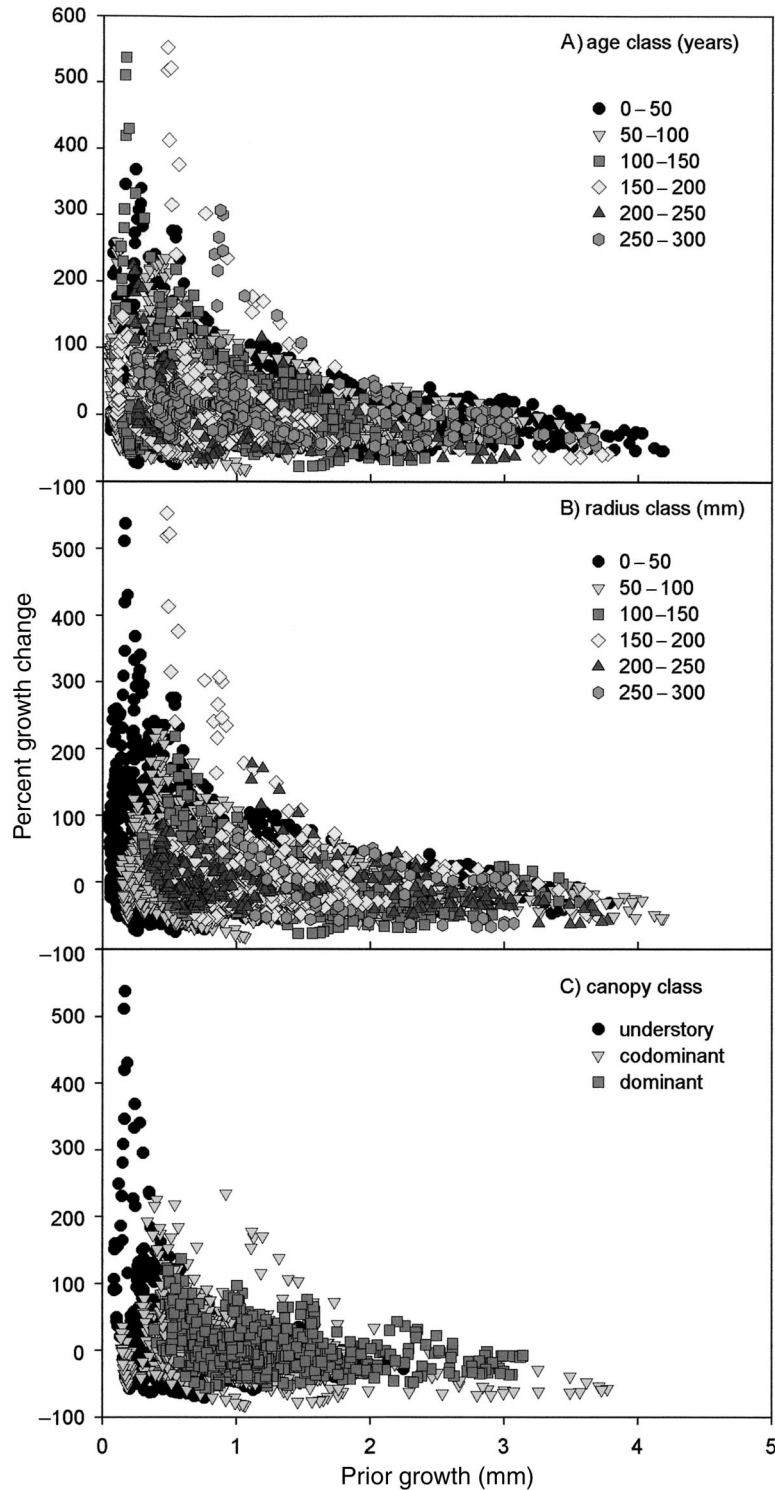


FIG. 4. Plot of percent growth change with respect to prior growth for all *Tsuga canadensis* tree rings measured in Schall's Gap. Data are subdivided into (A) age classes, (B) radius classes, and (C) crown classes. All years in the 47 *Tsuga canadensis* tree-ring series are included in age classes and radius classes. The entire life span of understory trees and the most recent 50 years of growth in codominant and dominant trees are used for crown-class data.

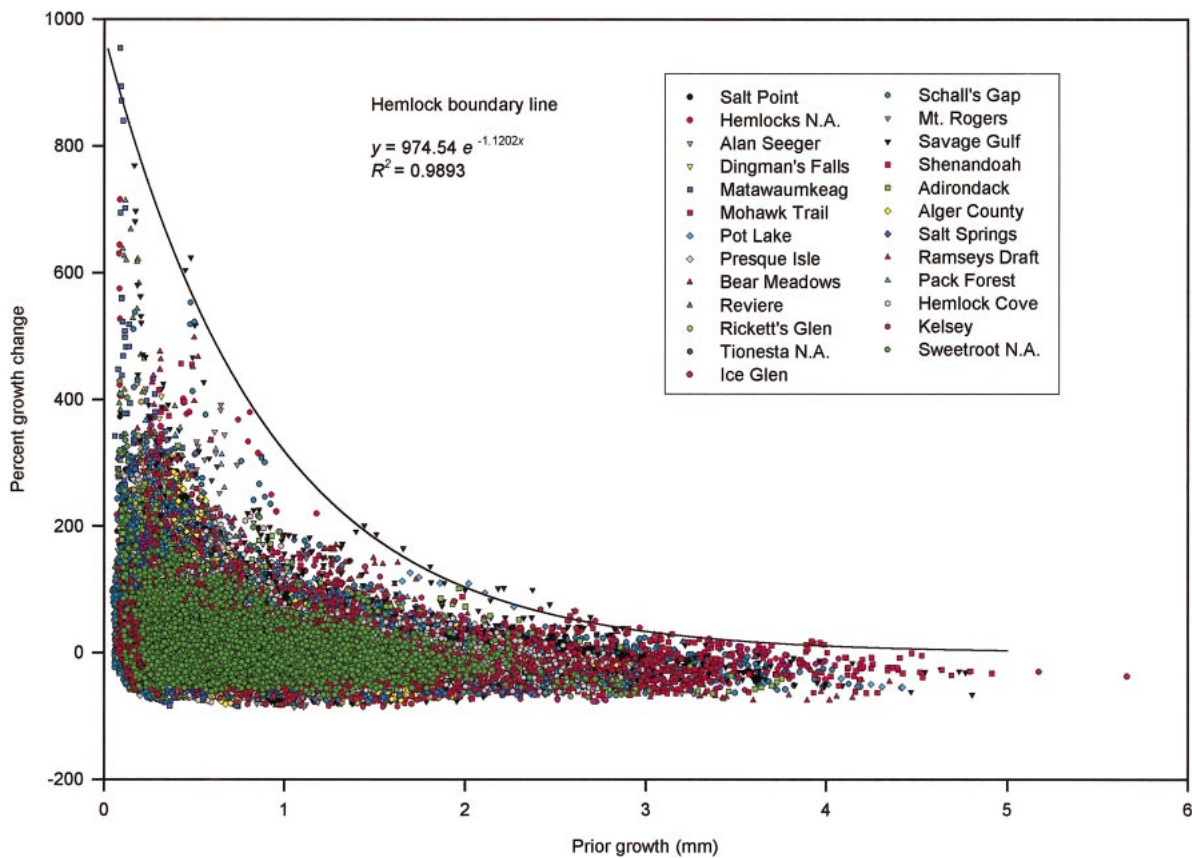


FIG. 5. Plot of percent growth change with respect to prior growth for all *Tsuga canadensis* tree rings measured in 25 stands. Data are subdivided by site, and the *Tsuga canadensis* boundary line is shown.

threshold of release response across the range of prior growth values. To more accurately describe this upper threshold of release response and evaluate its consistency, prior growth and percent growth change were plotted for hemlock in 24 additional sites, collectively containing 180 708 yr of growth (Appendix and Fig. 5). These sites are located throughout the range of eastern hemlock, occurring on a wide variety of edaphic and topographic conditions. Many stands are old growth with some trees in excess of 500 yr in age. But despite the diversity of site characteristics, maximal growth-change values are remarkably constant for a given level of prior growth (Fig. 5). Thus, the prior-growth thresholds appear to apply across the range of hemlock, and should allow for the construction of a single boundary line for the entire species.

Various approaches have been used to construct boundary lines, many of which are arbitrary and may only consist of drawing a line by hand (Chambers et al. 1985, Schmidt et al. 2000). No standardized approach yet exists for the development of boundary lines, but most quantitative techniques begin by subdividing the data into segments and averaging the top data points within each segment (Schmidt et al. 2000). A line or curve is then fit to the means of these top

points using regression. In this study, the boundary line was constructed by first dividing the data set into 0.5-mm segments of prior growth. Then, within each segment, we averaged the percent-growth-change values of the top 10 points. We chose not to use an upper percentile of points, or a multiple of standard deviation because of extreme differences in sample size across the levels of prior growth. If the upper 99th percentile had been used to compute the boundary line, 656 points would have been averaged in the 0.0–<0.5 mm segment and only one would have been used in the 4.5–<5.0 mm segment. The top ten points in each section ensured an equal sample size, and limited the analysis to the few points that represented true maximal releases. Finally, to determine the boundary line we fit linear, power, logarithmic, and exponential curves to all positive segment averages and selected the function that yielded the highest R^2 value. A negative exponential function with the equation $y = 974.54 e^{-1.1202x}$ had the highest R^2 of 0.9893 (Fig. 5).

Although trees from the majority of sites approach the boundary line, some sites do so more frequently than others (Fig. 5). Potential reasons for variability in release response could include genotype, site conditions, position in range, and disturbance regime. Ge-

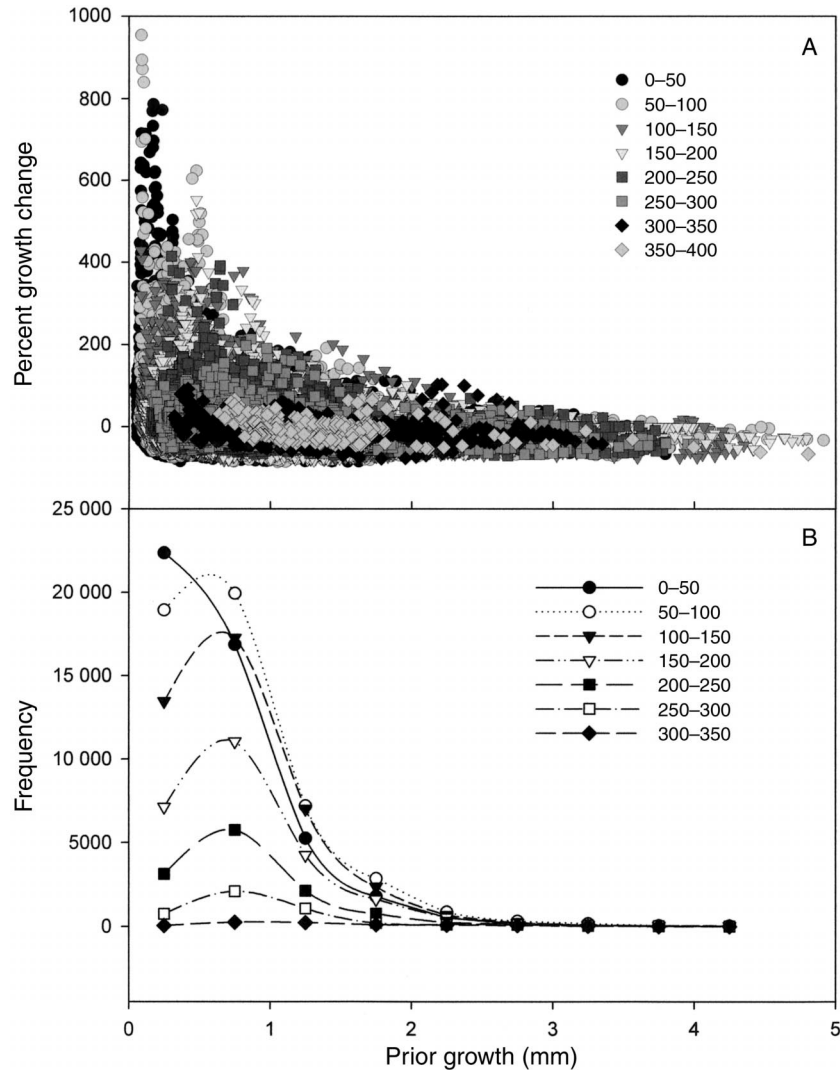


FIG. 6. (A) Plot of percent growth change with respect to prior growth for all *Tsuga canadensis* tree rings measured in 25 stands. Data are subdivided into radius classes (mm). (B) Frequencies of *Tsuga canadensis* tree rings in each radius class.

notype and position in range are unlikely significant factors because representative sites from the south and north of hemlock's range approach the boundary line with approximately equal frequencies. Also, old-growth stands from the contrasting site conditions of a protected, moist cove forest, a bog forest (Abrams et al. 1999), and forest located on steep talus (Abrams et al. 2000) all approach the boundary line, suggesting that site factors are not a significant influence. Instead, we believe that intensity of disturbance history is likely the most influential factor. Stands in which disturbance is rare or not intense would not often approach the boundary line, while those with a more intense disturbance history would frequently approach the boundary line. Indeed, tree rings from Schall's Gap and Bear Meadows bog forest frequently approach the boundary line, and both have a documented history of at least one major disturbance event (Abrams et al. 2001).

A final possibility that should be thoroughly addressed is the potential effect of diameter on release response. Diameter is frequently cited as a factor affecting release response, and many release criteria impose diameter limits (Lorimer and Frelich 1989, Nowacki and Abrams 1997). To verify that differences in release potential among diameter classes are indeed an artifact of prior growth, we graph percent growth change against prior growth for all hemlock stands and check to make sure that all radius classes approach the boundary line. In this larger sample, all radius classes do indeed approach the boundary line (Fig. 6A). Even the largest radius class approaches the boundary line at ~ 1.75 mm prior growth and again at ~ 2.75 mm (Fig. 6A). As in Schall's Gap, the absolute magnitude of releases in large radius classes is much less than those in small radius classes due to the fact that prior growth rates are, on average, much higher for large

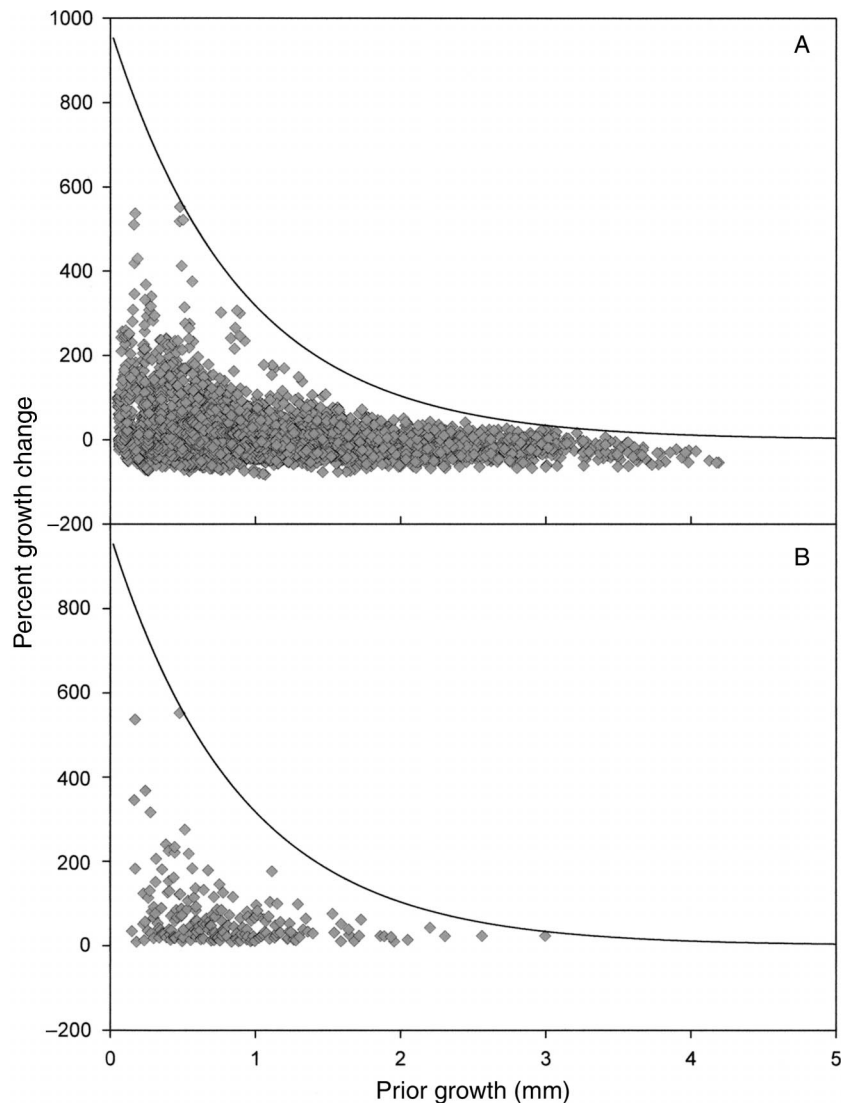


FIG. 7. (A) *Tsuga canadensis* boundary line and plot of percent-growth-change values with respect to prior growth for all tree rings measured in Schall's Gap. (B) *Tsuga canadensis* boundary line and maximum percent-growth-change values of growth pulses $>10\%$.

radius trees. For example, no growth occurs below ~ 0.5 and 0.75 mm in the largest two radius classes, respectively (Fig. 6A). This trend of increasing prior growth rates with increasing radius is clarified by a graph of prior growth frequencies across radius classes. As radius increases, the frequency histogram becomes more right skewed (Fig. 6B). These frequency histograms also show that sample sizes are much smaller for larger radius classes, which explains why few pulses from these radius classes approach the boundary line.

Boundary-line release criteria

In our proposed method, the boundary line is used to describe each percent-growth-change value as a fraction of its maximal potential, given its level of prior

growth. However, only those percent-growth-change values that represent positive pulses in growth are relevant in release criteria. To identify these pulses, we followed a procedure similar to Nowacki and Abrams (1997) in which only those percent-growth-change values greater than 10% were retained (in contrast to their 25% threshold). Every time growth change exceeded this value, only the maximum percent growth change was recorded so that each pulse would be considered just once as a potential release. This thereby excludes the years aggrading to and declining from the year of peak percent growth change. Of the 6300 growth rings measured in Schalls' Gap (Fig. 7A), a subset of 198 growth-change values qualified as pulse maxima (Fig. 7B). From there, each pulse maximum was then scaled as a fraction of its maximum potential using the prior-

growth boundary line. Pulse maxima falling above a minimum fraction of the boundary line are considered true releases while those falling below are considered insignificant.

The main factor we considered for establishing the lower boundaries of the release criteria is climate. If the criteria are not stringent enough, pulses due only to climate could be falsely counted as true ecological releases (Abrams and Orwig 1995). Indeed, hemlock in Schall's Gap responded strongly to high frequency and low frequency climate fluctuations (B. Black and M. Abrams, *unpublished data*). However, the effects of very high- and low-frequency fluctuations were substantially reduced or eliminated by using a 10-yr running mean of percent growth change (Nowacki and Abrams 1997). Yet medium-length climatic events (~5 yr in duration) could potentially cause pulses in the 10-yr running mean, yielding false releases if criteria thresholds were too low. Thus, we chose to evaluate the effects of the most significant known medium-length climate event, the 1960s drought, as an example. During this time, Palmer Drought Index values dropped to sustained levels of -2.5 to -3.0 for 5 yr (National Oceanic and Atmospheric Administration [NOAA] 2002). The prolonged drought provided an opportunity to test whether the proposed release criteria could filter climate signals and retain only the more sustained and pronounced effects of true ecological disturbance.

Comparisons of growth before, during, and after the drought with respect to canopy position indicated that substantial growth variations occurred in response to climate (Fig. 8A). Increases in growth from mid-drought to postdrought were greatest for overstory trees, followed by codominant trees (Fig. 8A). These increases appear to be climate effects rather than any true disturbance events due to the fact that the rebound of postdrought growth rates did not exceed predrought levels (Fig. 8A). To better analyze release patterns in the latter 1960s, percent-growth-change values corresponding with the drought rebounds were plotted with respect to prior growth and the hemlock boundary line (Fig. 8B). At 20% of the value of the boundary line, the majority of growth pulses were filtered by the release criteria, particularly among trees with a recent history of suppression. Some true releases likely occurred during that time and are represented by those few pulses that occur above the 20% threshold, but most true releases in the 1960s date from the early part of the decade. Thus, the proposed methodology employs stringent enough release criteria to block the effects of even the most extreme moderate-length climate event in the 20th century. However, one additional factor we were unable to test is the potential of insect defoliations to cause false ecological releases (Speer et al. 2001). We found no record of widespread hemlock defoliations in our study area, and could therefore not evaluate the effects of partial or complete defoliation. Given their potential impacts on radial growth patterns,

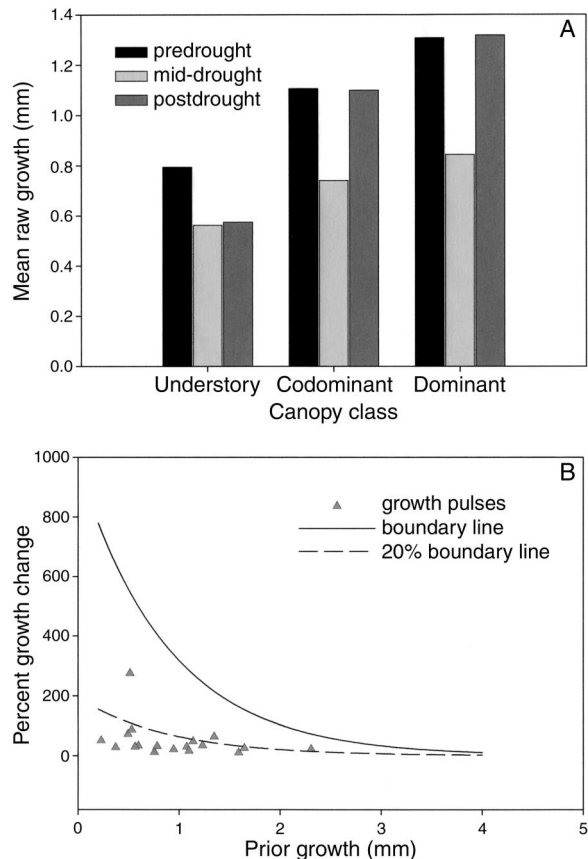


FIG. 8. Response of understory, codominant, and dominant *Tsuga canadensis* trees to the 1960s drought. (A) Mean raw growth rate before, during, and after the drought. (B) Maximum percent-growth-change values for growth pulses in the latter 1960s. The *Tsuga canadensis* boundary line is shown, as is 20% of its value. Pulses falling above the 20% threshold are considered true ecological releases.

the effects of insects should be considered in species or regions that are prone to outbreaks.

To better distinguish severe disturbance events from mild events, we subdivided releases into "moderate" and "major" categories based on percent distance to the boundary line. Major releases would lie closest to the boundary line and represent those events intense enough to elicit the largest possible growth pulses. For this study, we identified growth-change values between 50% and 100% of the boundary line as major releases and those between 20% and 49.9% as moderate releases. In Schall's Gap, a total of 57 releases were identified: 50 moderate and seven major (Fig. 9). In comparison to other methods, our technique reveals a pattern of disturbance most similar to that of Nowacki and Abrams (1997), but with fewer total release events (Figs. 1A, 10). Our release thresholds are much higher for trees with a history of slow growth. However, our technique still reveals the widespread effects of the Great Hurricane of 1846 and July Storm of 1850 as

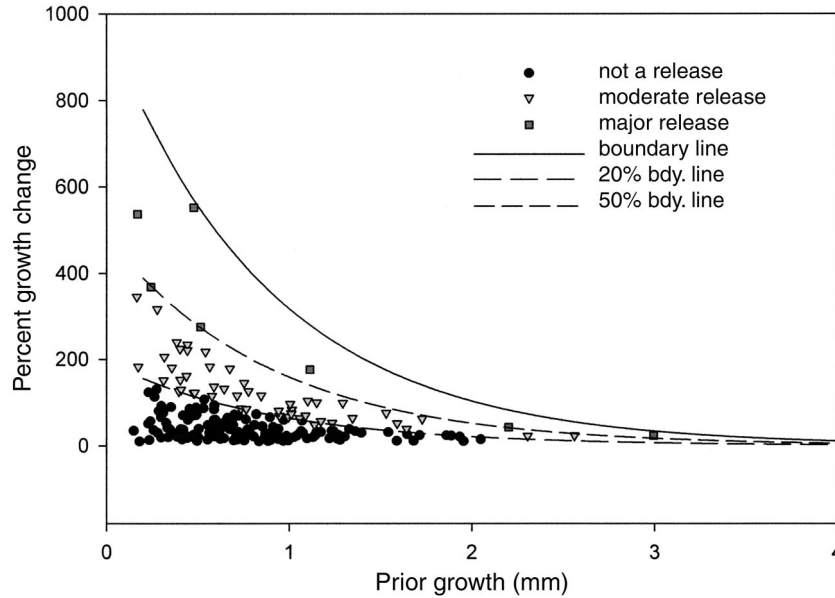


FIG. 9. Maximum percent-growth-change values in radial growth pulses that exceeded 10%. Data are shown for *Tsuga canadensis* in Schall's Gap. Pulses 50% or greater than the value of the boundary line are major releases. Pulses between 20% and 49.9% are moderate releases, while pulses less than 20% are not considered true releases.

well as smaller-scale disturbance events of the 20th century (Fig. 10). Also, due to our exclusion of recruitment events, the signal of these storms is very punctuated and does not extend beyond the 1850s (Fig. 10). Finally, our technique does not require the subdivision of moderate and major releases into understory and overstory phases of growth. This allows for a more direct comparison between the early portion of the dis-

turbance history, which is dominated by understory releases, and the recent portion of the history, which is dominated by overstory releases (Figs. 1D, 10). In our technique, the magnitude of all releases is scaled according to prior growth, which is a more fundamental predictor of release potential and should provide a more flexible and theoretically sound approach for developing disturbance histories.

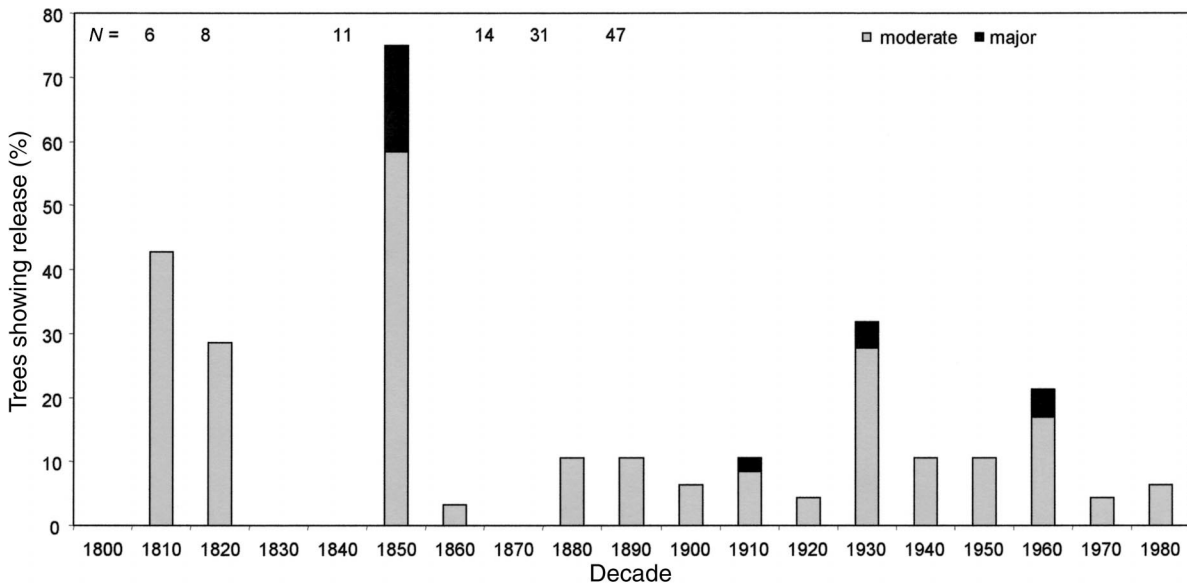


FIG. 10. Decadal distribution of *Tsuga canadensis* releases in Schall's Gap according to the boundary-line release criteria. Major releases are between 50% and 100% of the value of the boundary line, while moderate releases are between 20% and 49.9%.

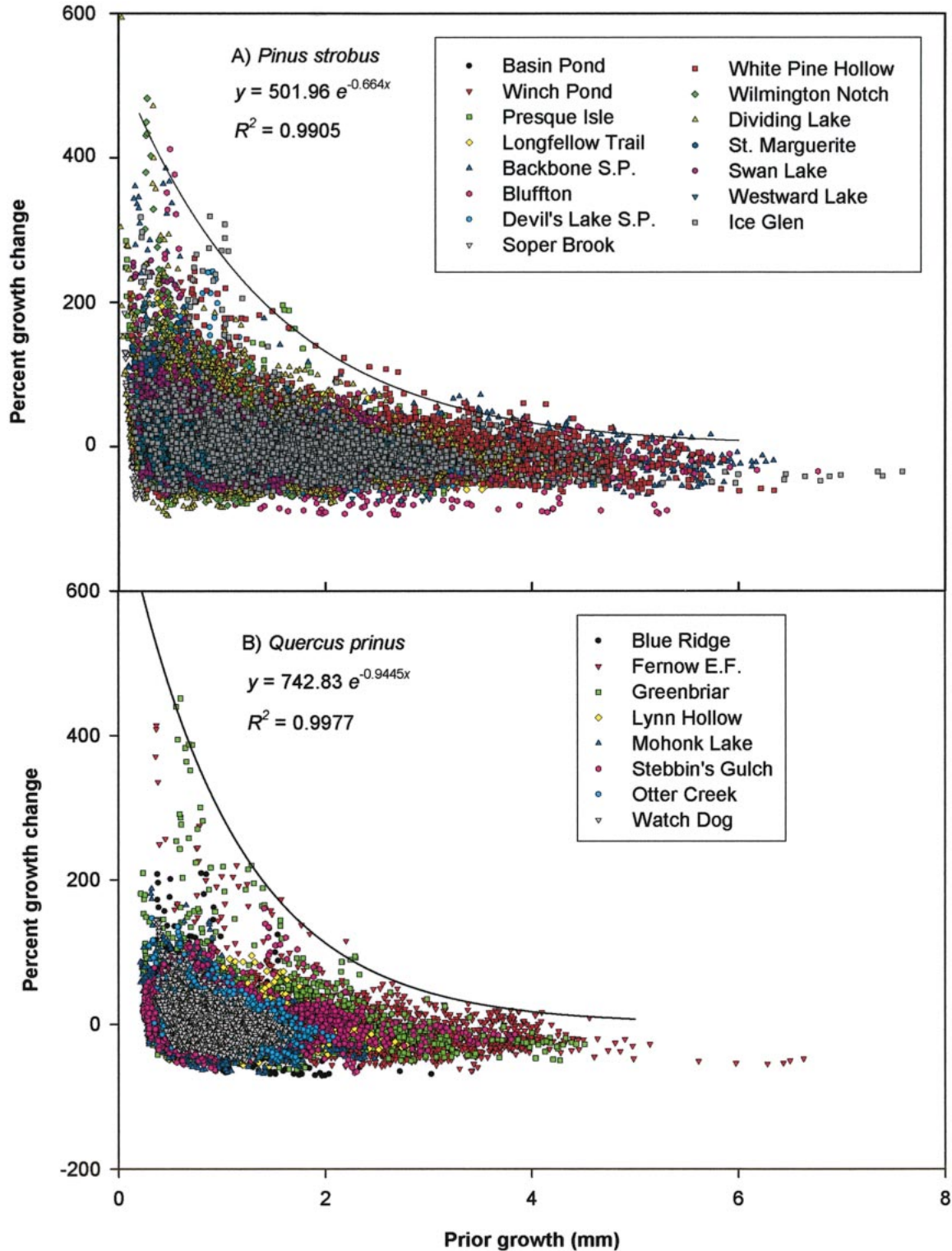


FIG. 11. (A) Plot of percent growth change with respect to prior growth for all *Pinus strobus* tree rings measured in 12 stands. Data are subdivided by site, and the *Pinus strobus* boundary line is shown. (B) Plot of percent growth change with respect to prior growth for all *Quercus prinus* tree rings measured in eight stands. Data are subdivided by site, and the *Quercus prinus* boundary line is shown.

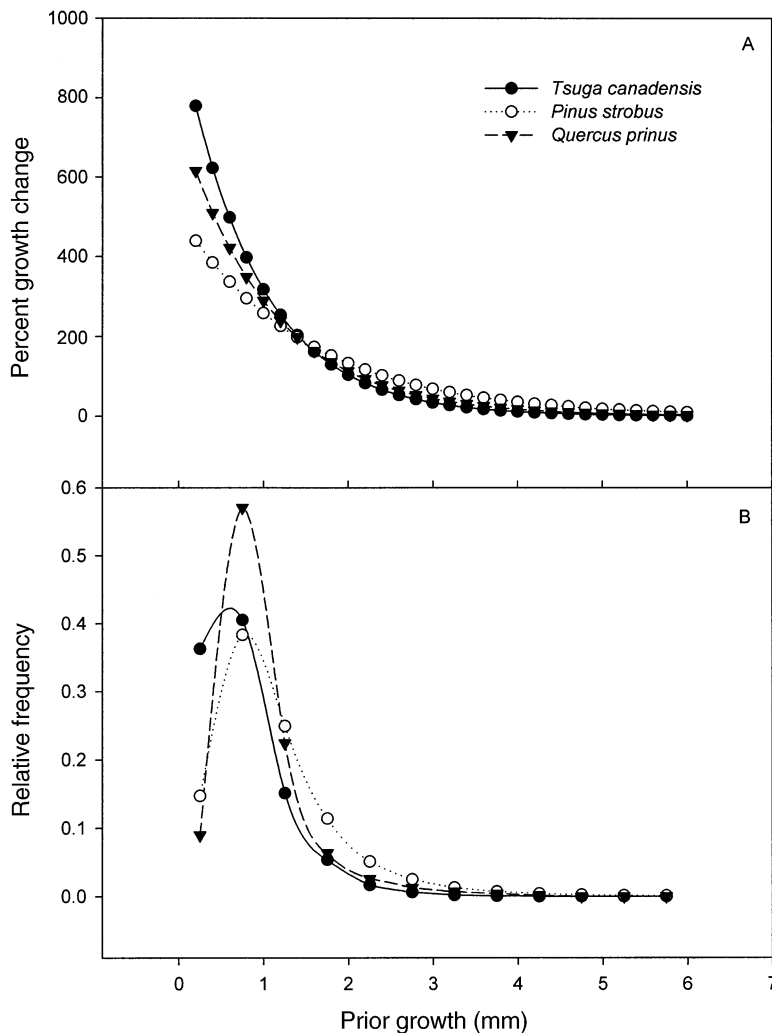


FIG. 12. (A) Boundary lines of *Tsuga Canadensis*, *Quercus prinus*, and *Pinus strobus*. (B) Relative frequency of *Tsuga Canadensis*, *Quercus prinus*, and *Pinus strobus* growth rings in each 0.5-mm prior-growth class.

White pine and chestnut oak

Applicability of the boundary-line technique for calculating releases extends beyond eastern hemlock. A graph of 12 white pine chronologies representing 72 714 yr of growth reveals a negative exponential trend of release potential, similar to that of hemlock (Fig. 11A, Appendix). As in hemlock, most sites approach the boundary line despite the fact that they occur throughout the range of white pine. When the boundary line is computed using the top 10 points in each 0.5-mm prior-growth class, the R^2 of fitted negative exponential curve ($y = 501.96e^{-0.664x}$) is 0.991. In eight chronologies of chestnut oak from across the eastern USA, the fitted boundary line is $y = 742.83e^{-0.9445x}$ with an R^2 of 0.998 (Fig. 11B, Appendix 1). Some chestnut oak chronologies appear to come from stands with low disturbance histories, as indicated by the fact that two sites do not approach the boundary line. These sites have low prior growth levels as well

as low percent growth changes, suggesting conditions of suppression and low disturbance frequency (Fig. 11B).

Interspecific differences among boundary lines and patterns of prior growth reflect differences in levels of understory tolerance (Fig. 12). Of the three species, hemlock is the most tolerant followed by the moderately intolerant chestnut oak and intolerant white pine (Burns and Honkala 1990). Thus, hemlock should have a relatively large proportion of slow prior growth, chestnut oak should have a relatively large proportion of moderate prior growth, and white pine should have a relatively large proportion of rapid prior growth. Indeed, among the three species, hemlock has the greatest proportion of prior growth values in the 0–0.5 mm class, chestnut oak has the greatest frequency of prior growth in the 0.5–<1.5 mm prior growth classes, and white pine has the greatest frequency of prior growth in the 1.5–<3.0 mm prior growth classes (Fig. 12B).

Furthermore, a comparison of boundary lines shows that when prior growth is slow, hemlock has the greatest release potential followed by chestnut oak and white pine (Fig. 12B). When prior growth is rapid, rankings are reversed with white pine having the greatest release potential followed by chestnut oak and then hemlock (Fig. 12B). Indeed, at prior growth values above 3.0 mm, release potential for white pine is between two and four times as great as hemlock. Thus, the more shade-tolerant species have relatively high levels of slow growth, and are best adapted to respond to disturbance at those growth rates. Species with lower levels of tolerance have relatively high levels of rapid growth and are better adapted to respond to disturbance at these faster growth rates. Thus, there appear to be a trade-offs in release response among species with contrasting levels of understory tolerance.

CONCLUSIONS

This unique methodology represents a new direction in defining dendroecological releases. Past methodologies overly generalize release potential by applying a fixed growth-change threshold to broad categories of diameter, age, or crown class. We propose a more precise method that scales each release by its maximum physiological potential, as defined by prior growth rate. Overall, our procedure can be summarized in a few generalized steps. First, prior growth rate and percent growth change are calculated for each ring in each tree-ring series. Pulses in the percent growth change that exceed 10% are identified, and at the peak year of each pulse, the value of percent growth change and prior growth is retained. The prior-growth boundary line is then used to scale each pulse with respect to its maximum possible value, as predicted by prior growth rates. Those pulses falling within 50–100% and 20–49.9% of the prior-growth boundary line are classified as major and moderate releases, respectively. Use of a universal boundary line for a given species will enable direct comparisons of disturbance histories among multiple stands. However, additional research is still necessary to better calibrate these criteria by determining the specific response levels for a wide spectrum of disturbance types and intensities. Such studies could be conducted in stands with a detailed record of disturbance history, ideally with estimated of crown release for each tree.

Beyond eastern hemlock, this approach is also applicable in white pine and chestnut oak, suggesting that it could be used in a variety of coniferous and deciduous species. Also, calculation of boundary lines for many species would allow for more accurate compilations of disturbance history in mixed-species stands. If prior growth boundary lines are available for all species in a stand, every release can be expressed in terms of species-specific release potentials, as determined by prior growth rate. If, as in the past, a single, flat percent-growth-change threshold is applied to sev-

eral species, shade-tolerant species might be more heavily weighted than the less responsive, intolerant species. This situation could be especially problematic if the shade-tolerant species are longer lived than the intolerants, in which case the magnitude and frequency of disturbances early in the chronology could be over estimated. Our technique would better standardize growth patterns both within and among species, possibly surmounting this problem. Thus, the boundary-line approach offers a high level of flexibility and precision that we believe will yield more accurate estimates of disturbance histories and allow for better comparisons of these disturbance histories among a wide variety of forest stands.

LITERATURE CITED

- Abrams, M. D., C. A. Copenheaver, B. A. Black, and S. van de Gevel. 2001. The dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania, USA. *Canadian Journal of Botany* **79**:58–69.
- Abrams, M. D., C. A. Copenheaver, K. Terazawa, K. Umeki, M. Takiya, and A. Nobuhiro. 1999. A 370-year dendroecological history of and old-growth *Abies-Acer-Quercus* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research* **29**:1891–1899.
- Abrams, M. D., and G. J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bulletin of the Torrey Botanical Club* **119**:19–28.
- Abrams, M. D., and D. A. Orwig. 1995. Structure, radial growth dynamics and recent climate variations for a 320-year-old *Pinus rigida* rock outcrop community. *Oecologia* **101**:353–360.
- Abrams, M. D., S. van de Gevel, R. C. Dobson, and C. A. Copenheaver. 2000. The dendroecology and climatic impacts of old-growth white pine and hemlock on the extreme slopes of the Berkshire Hills, Massachusetts, USA. *Canadian Journal of Botany* **78**:851–861.
- Black, B. A., and M. D. Abrams. 2001. Influences of Native Americans and surveyor biases on metes and bounds witness tree distribution. *Ecology* **82**:2574–2586.
- Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist* **67**:660–669.
- Braker, W. L. 1981. Soil survey of Centre County, Pennsylvania. USDA Soil Conservation Service, Washington, D.C., USA.
- Buell, M. F., H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's Woods. *Bulletin of the Torrey Botanical Club* **81**:253–255.
- Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Volume 1, Conifers, and Volume 2, Hardwoods. USDA Forest Service Agricultural Handbook 654, Washington, D.C., USA.
- Chambers, J. L., T. M. Hinckley, G. S. Cox, C. L. Metcalf, and R. G. Aslin. 1985. Boundary-line analysis and models of leaf conductance for four oak-hickory forest species. *Forest Science* **31**:437–450.
- Clark, J. S., and P. S. Royall. 1995. Transformation of a northern hardwood forest by aboriginal (Iroquois) fire: charcoal evidence from Crawford Lake, Ontario, Canada. *Holocene* **5**:1–9.
- Cook, E. R., R. L. Holmes, O. Bosch, T. Varem-Sanders, H. D. Grissino-Mayer, and P. J. Krusic. 1997. International tree-ring data bank program library, Version 2.1. [Online: (<http://www.ngdc.noaa.gov/paleo/treering.html>)]

- Dahir, S. E., and C. G. Lorimer. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research* **26**: 1875–1892.
- Delcourt, P. A., H. A. Delcourt, C. R. Ison, W. E. Sharp, and K. J. Gremillion. 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak–chestnut forests: paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* **63**(2):263–278.
- Foster, D. R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. *Journal of Ecology* **76**:105–134.
- Foster, D. R., and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal of Ecology* **80**:79–98.
- Frelich, L. E. 2002. *Forest dynamics and disturbance regimes*. Cambridge University Press, Cambridge, UK.
- Grimm, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* **54**:291–311.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* **3**:329–382.
- Hibbs, D. E. 1982. Gap dynamics in a hemlock–hardwood forest. *Canadian Journal of Forest Research* **12**:522–527.
- Lorimer, C. G., S. E. Dahir, and E. V. Nordheim. 2001. Tree mortality in mature and old-growth hemlock–hardwood forests. *Journal of Ecology* **89**:960–971.
- Lorimer, C. G., and L. E. Frelich. 1989. A method for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research* **19**: 651–663.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* **10**:17–25.
- Ludlum, D. M. 1963. *Early American hurricanes: 1492–1870*. American Meteorological Society, Boston, Massachusetts, USA.
- NOAA (National Oceanic and Atmospheric Administration). 2002b. Climate visualization website. [Online: (<http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgrg2.html>).]
- Nowacki, G. J., and M. D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs* **67**:225–249.
- Orwig, D. A., and M. D. Abrams. 1994. Land-use history (1720–1992), composition, and dynamics of oak–pine forests within the Piedmont and Coastal Plain of northern Virginia. *Canadian Journal of Forest Research* **24**:1216–1225.
- Orwig, D. A., and M. D. Abrams. 1999. Impacts of early selective logging on the dendroecology of an old-growth bottomland hemlock–white pine–northern hardwood forest on the Allegheny Plateau. *Journal of the Torrey Botanical Society* **126**:234–244.
- Phipps, R. L. 1985. *Collecting, preparing, cross-dating, and measuring tree increment cores*. U.S. Geological Survey, Water Resource Investigation Report 85–4148, Washington, D.C., USA.
- Ruffner, C. M., and M. D. Abrams. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Canadian Journal of Forest Research* **28**:347–358.
- Russell, E. W. B. 1983. Indian-set fires in the forests of the Northeastern United States. *Ecology* **64**:78–88.
- Schmidt, U., T. Hanspeter, and M. Kaupenjohann. 2000. Using a boundary line approach to analyze N₂O flux data from agricultural soils. *Nutrient Cycling in Agricultural Ecosystems* **57**:119–129.
- Sesischab, F. K., and D. A. Orwig. 1991. Catastrophic disturbance in the presettlement forests of western New York. *Bulletin of the Torrey Botanical Club* **118**:117–122.
- Smith, D. M. 1986. *The practice of silviculture*. John Wiley and Sons, New York, New York, USA.
- Speer, J. H., T. W. Swetnam, B. E. Wickman, and A. Youngblood. 2001. Changes in Pandora moth outbreak dynamics during the past 662 years. *Ecology* **82**:679–697.
- Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* **21**:414–416.

APPENDIX

Tree-ring data sets used in the development of prior-growth boundary lines are available in ESA's Electronic Data Archive: *Ecological Archives* A013-024-A1.