Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, U.S.A.[1]

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Abstract: This study evaluated the use of radial growth averaging as a technique of identifying canopy disturbances in a thinned 55-year-old mixed-oak stand in West Virginia. We used analysis of variance to determine the time interval (averaging period) and lag period (time between thinning and growth increase) that best captured the growth increase associated with different levels of crown release of *Quercus prinus* L. and *Quercus rubra* L. A lag of 3 years and an interval of 7 years yielded the best fit of percent growth change and percent crown release, respectively, for *Q. prinus*; for *Q. rubra*, the radial growth response did not differ significantly when lag and interval were varied from 1 to 3 and 6 to 15 years, respectively. The relationship between percent crown release and percent growth change was linear for both species. This method provides a suitable means of detecting canopy disturbances affecting overstory trees and is potentially applicable to other tree species. When combined with fire histories, these data can provide the basis for reconstructing long-term disturbance regimes. This estimate may also provide a framework for scheduling the rate of stand entry for silvicultural treatments (e.g., thinning) that is consistent with its historic stand development.

Résumé : Cette étude évalue l'utilisation de la croissance radiale moyenne pour identifier les perturbations dans le couvert d'un peuplement mélangé de chênes âgé de 55 ans, situé en Virginie de l'Ouest et qui a été éclairci. Nous avons utilisé l'analyse de variance pour déterminer l'intervalle de temps (période sur laquelle est établie la moyenne) et le temps de réaction (période de temps entre l'éclaircie et l'augmentation de la croissance) qui traduisent le mieux l'augmentation de croissance associée à différents degrés de dégagement des cimes chez *Quercus prinus* L. et *Quercus rubra* L. Un temps de réaction de 3 ans et un intervalle de 7 ans donnent le meilleur ajustement du pourcentage de variation de croissance en fonction du pourcentage de dégagement des cimes chez *Q. prinus*. Chez *Q. rubra*, la réponse en croissance radiale n'est pas significativement différente pour un temps de réaction et un intervalle variant respectivement de 1 à 3 ans et de 6 à 15 ans. La relation entre le pourcentage de dégagement des cimes et le pourcentage de variation de croissance est linéaire chez les deux espèces. Cette méthode constitue une façon adéquate de détecter les perturbations du couvert qui affectent les arbres de l'étage dominant et est potentiellement applicable à d'autres espèces d'arbres. En les combinant à l'historique des feux, ces données peuvent servir de base pour reconstituer les régimes de perturbation à long terme. Cette estimation peut également fournir un cadre de référence pour planifier le rythme d'intervention dans le peuplement pour y effectuer des traitements sylvicoles (p. ex., éclaircie) qui est consistant avec l'historique du développement du peuplement.

[Traduit par la Rédaction]

Introduction

Natural disturbances in forests kill vegetation and release growing space (Oliver and Larson 1996). They are simultaneously a source of mortality for some individuals and a source of establishment and growth for others, and the ongoing process of death and replacement has a profound effect on forest structure and composition. In fact, many features of forests are better understood as responses to different kinds of disturbances rather than the result of a continuous change toward equilibrium (Brubaker 1987). The disturbance regime of a forest represents the sum total of stem- and stand-replacing events, and many studies have characterized individual stands and forest types by disturbance agents, severity, and return time (Barden 1980; Romme and Martin 1982; Runkle 1982, 1985). In mesic, eastern deciduous forests, tree-fall gaps are the dominant disturbance type (Runkle 1982), especially as forests mature. These events create resource heterogeneity along light, temperature, humidity, and soil-resource gradients. In closed canopy, deciduous forests in the east, the amount, timing, and quality of available light may vary as functions of gap size, the depth of shade imposed by the height of the surrounding canopy, solar angle, latitude, and aspect (Canham et al. 1990). Because light levels beneath intact canopies average 1–6% of full sunlight (Canham et al. 1990; Canham and Burbank

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1994), increases in light levels in gaps are perhaps most influential in determining the growth of the survivors. Silvicultural treatments such as crown thinning, crop tree release, and shelterwood system recognize the importance of managing the light environment to favor growth of selected trees and produce changes in light availability comparable with those resulting from natural mortality.

Studies of disturbance regimes of eastern deciduous forests have traditionally taken two approaches. Barden (1980, 1981), Runkle (1981, 1982, 1998), Cho and Boerner (1991), and others have identified gap makers and gap fillers and have measured the frequency of gap formation, gap size, and gap closure rate by sampling along transects. These gap-sampling studies have described the disturbance regimes of relatively large sample areas. However, because it is difficult to interpret gaps older than 15 years (Cho and Boerner 1991), the sampling period of this method is limited to relatively short time intervals. A second approach concentrates on the response of the survivors. It combines analysis of the age structure of forests and their tree-ring record to estimate historic disturbance rates over much longer time periods (Lorimer 1985; Lorimer and Frelich 1989). Dendrochronological studies have been particularly effective in determining long-term forest dynamics (Foster 1988), fire histories (Buell et al. 1954; Sutherland 1997), insect outbreaks (Fajvan and Seymour 1993), and changes in species composition over many decades (Henry and Swan 1974; Abrams et al. 1997).

Radial growth analysis is particularly applicable in closed-canopy, eastern deciduous forests. Except on the most drought-prone sites, these forests are characterized by a relatively high degree of climatic complacency; that is, radial growth patterns show relatively low variability, indicating that tree growth is relatively less affected by variations in climate (Fritts 1976) than by the effects of canopy disturbance and competition for growing space (Phipps 1982; Nowacki and Abrams 1997).

Lorimer and Frelich (1989) proposed a radial-growth averaging technique to identify canopy accession events of shade-tolerant understory trees, such as sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.). They distinguished between the magnitude of growth increases and their duration. Thus, major releases were characterized by mean growth increases ≥100%, while moderate releases involved increases between 50 and 99%. Sustained releases last at least 15 years, while temporary releases last 10–15 years. These criteria were designed to identify canopy accession events of understory saplings and seedlings in canopy gaps and to screen out cases of sidelight responses (Lorimer and Frelich 1989).

Nowacki and Abrams (1997) modified this method for eastern, old-growth, overstory oaks (*Quercus* spp.). They noted that mature overstory oaks responded more conservatively to increased sidelight from canopy gaps than did smaller understory individuals to overhead gaps, and that the release criteria (50–100% growth increase) proposed by Lorimer and Frelich (1989) were not sensitive enough to identify partial crown release events of less shade-tolerant overstory oaks that do not involve an advancement in canopy stratum. They proposed criteria based on a comparison of running 10-year ring-width means to determine canopy disturbance rates, using the formula:

$$[1] \qquad \%GC = \left(\frac{M_2 - M_1}{M_1}\right) \times 100$$

where %GC is percent growth change, M_1 is the preceding 10-year mean radial growth (inclusive of the disturbance year), and M_2 is the subsequent 10-year mean radial growth (exclusive of the disturbance year) (Nowacki and Abrams 1997).

Three parameters are implicit in eq. 1: (*i*) the length of the time period averaged, (*ii*) the lag time between the disturbance and onset of growth increase, and (*iii*) the selection of a minimum %GC level that is both low enough to identify smaller canopy disturbance events (i.e., a single-tree mortality event that releases 25% of a neighboring tree's crown) and high enough to filter out drought-induced growth reduction and subsequent recovery (Nowacki and Abrams 1997). Drought effects in eastern mesic forests have been shown to last for only 2 or 3 years (Cook and Jacoby 1977; Jacobi and Tainter 1988; Orwig and Abrams 1997), and sustained growth declines (approximately 5 years) associated with drought are observed for only the most severe drought events (Rubino and McCarthy 2000). Thus, use of shorter averaging intervals (3–5 years) risks confounding disturbance response with those that occur during drought recovery.

The 1-year lag and 10-year interval were proposed by Nowacki and Abrams (1997), because these time periods are generally consistent with the onset and average duration of growth increases of overstory oaks that are associated with canopy disturbance events (Minckler 1967; Hilt 1979; Cutter et al. 1991). Standard stocking tables for upland oaks are based on a 10-year interval for an understocked (C level) stand to reach the lower level of full stocking (B level), when growing space is fully utilized (Gingrich 1967). However, Gingrich (1967) noted that the time interval between C- and B-level stocking may vary from as long as 12–15 years on poor sites (site index, SI, < 17 m, upland oaks) to 5–8 years on very good sites (SI > 23 m). In addition, Cutter et al. (1991) found a significant differential thinning response of 12 years for scarlet oak (*Quercus coccinea* Muench.) and a lag of 6 or 7 years. White oak (*Quercus alba* L.) released on one or two sides of their crown grew faster than unreleased trees for 20 years after treatment (Schlesinger 1978). In Arkansas, 50-year-old northern red oak (*Quercus rubra* L.) crop trees responded the first year after release; however, the greatest response occurred 5–10 years after release (Graney 1987). In this study, we examine percent growth change over intervals between 6 and 15 years based on this range of values, and a natural gap disturbance regime that most often produces small (<100 m^2; Barden 1981; Runkle 1985) and relatively short-lived canopy gaps (10–15 years; Runkle 1982; Cho and Boerner 1991).

Using data from several eastern oak thinning studies (Hilt 1979; Dale and Sonderman 1984; and Lamson et al. 1990), Nowacki and Abrams (1997) further proposed that a release of 35–40% of an individual crown would yield a 25% GC. When this criteria was tested in three old-growth oak stands in central Pennsylvania, they found that the technique identified 31 of 43 known disturbance events dating as far back as 1684.

In eastern, closed-canopy deciduous forests, many factors act in concert to affect tree growth. Cook (1987) proposed a conceptual model that partitioned tree-ring variance among age- and size-related trends, climatic trends, endogenous disturbances (e.g., small canopy gaps), exogenous disturbances (e.g., larger, stand-wide events), and other random or unexplained variance. This study examines the relative contributions of climate and canopy disturbances to radial growth of canopy oaks, and tests the 10-year radial-growth averaging technique proposed by Nowacki and Abrams (1997) using data from a 1982 thinning study in West Virginia (Lamson et al. 1990). Our objectives were (*i*) to use standard dendroclimatological techniques (Cook and Kairiukstis 1990) to estimate the relative contributions of climatic and nonclimatic variation to radial growth; (*ii*) to examine the relationship between the percentage of tree crown perimeter released and radial growth of overstory, codominant northern red oak and chestnut oak (*Quercus prinus* L.) using the radial-growth averaging technique; (*iii*) in view of the variability of response times for different species, to determine the response lag time and response interval that best captured the radial growth change associated with crown release; and (*iv*) to evaluate the radial growth averaging technique as a method of reconstructing canopy disturbance history.

Materials and methods

Study area and pretreatment stand condition

The study area consists of a 24.3-ha stand located on the 3100-ha West Virginia University Forest, 13 km east of Morgantown, W.V. (39°39′43″N, 79°45′28″W; Lake Lynn 7.5-min quadrangle). Bedrock for the area is part of the Upper Connequenescing sandstones of the Pottsville series, which include conglomeratic sandstones, thin coals, fire clay, and shale. Pottsville sandstones form the protective mantle at the top of Chestnut Ridge and are highly resistant to erosion. Soils are characterized as Dekalb series on well-drained hill slopes and ridgetops and deeper Ernest series on concave slopes bordering streams (USDA 1959). These are loamy-skeletal, moderately deep, and well-drained soils of low natural fertility (USDA 1959). Soil nutrient analysis by Hicks and Frank (1984) in an adjacent watershed found low levels of major plant nutrients in the A and B horizons and substantial iron and manganese. Precipitation is quite acidic; average annual pH was 3.9 for the period 1984–1999, and nitrate deposition for the same period averaged 13.8 $kg \cdot ha^{-1} \cdot year^{-1}$ (Rentch and Hicks 2002).

The stand is located on a northeast-facing upper slope position at an elevation of 640 m; slope inclination ranges from 0 to 15%. Annual precipitation averages 129.4 cm and is fairly evenly distributed throughout the year. The average annual mean temperature is 9.0°C, although temperatures as low as –33.9°C have been recorded in January (Carvell 1983). The frost-free season averages 167 days (April 30 – October 10; USDA 1959).

At the time of treatment (1982) the stand was an overstocked (Gingrich 1967), second-growth forest, approximately 55 years old. Site index is 21.3 m for northern red oak (base age 50). Pretreatment stand conditions averaged 31.7 m^2/ha basal area and 618 trees/ha (diameter at breast height (DBH) ≥ 10 cm) (Graves et al. 2000). Yellow-poplar (*Liriodendron tulipifera* L.) was the dominant species in the stand, followed by the red oak group (including northern red oak; black oak, *Quercus velutina* Lam.; and scarlet oak), the white oak group (including white oak and chestnut oak), and red maple (*Acer rubrum* L.).

Initial study design (1982)

In 1982, a thinning study was conducted using twenty 1.2-ha experiment units, with a 0.2-ha permanent plot located in the center of each experimental unit (all information about the original experimental design is from Lamson et al. (1990)). Three thinning treatments (45, 60, and 75% relative density; Gingrich 1967) and an uncut control were randomly assigned to the experimental units, resulting in five replications of each treatment. After five growing seasons (1986), all trees were remeasured, and all crop trees were assigned a free-to-grow (FTG) rating. Crop trees were defined as vigorous dominant and codominant trees of commercial species with a potential grade 1 butt log, with no more than three epicormic branches, and no significant decay in the main stem. Free-to-grow means that there is enough space (more than 1.5 m) between the crop tree crown and adjacent crowns that the canopy will not close in the subsequent 5 years. FTG ratings were assigned from 0 (no crown release) to 4 (crown fully released) in increments of 0.5. For the current study, FTG ratings were converted to percentages of crown released in 12.5% increments.

Increment core collection and preparation

Because this study is part of a larger study of old-growth oak forests, only dominant and codominant red oak (n = 51) and chestnut oak (n = 52) crop trees were selected for coring. In the 1982 study, all trees ≥2.5 cm DBH were tagged for long-term monitoring. For this study, a random sample of dominant–codominant trees was cored to provide response data by release level. Sample trees were randomly selected from a master list of all crop trees by their level of crown release assigned during the first remeasurement in 1986 and without regard to the three thinning levels. Trees were cored in each of the eight crown release (%CR) levels (12.5, 25, 37.5, 50, 67.5, 75, 87.5, and 100%) and a control. Two cores were extracted at breast height (1.37 m) from each sample tree. The minimum target subsample size for each release level was five, although this could not be attained in some cases because of low numbers of suitable crop trees in the target crown-release group. To increase sample size, trees were pooled into four crown release levels: 25, 50, 75, 100%, and a control. Quadratic mean diameters of the sample trees were 34.5 cm for red oak and 24.6 cm for chestnut oak.

Cores were dried, mounted, and then sanded with progressively finer grit sandpaper to expose the annual rings (Stokes and Smiley 1968). Growth ring widths were measured to the nearest 0.001 mm using a Leica Stereo Zoom-5 binocular microscope, an Acu-rite measuring stage, and a Quik-Chek 1000 digital readout, in conjunction with J2X® software.

Tree-ring series were cross-dated using marker years based on consistently narrow rings (e.g., 1953, 1959, 1988), and dating was validated using the program COFECHA (Grissino-Mayer et al. 1997).

Data analysis

For the climatic portion of the study, age- and diameter-related radial growth trends were removed from each tree-ring series using the program ARSTAN (Cook and Holmes 1997). ARSTAN produces chronologies by detrending each series and then applying a robust estimation of the mean value function to yield a series with a mean of one and equal variance. We used the modified negative exponential model as the detrending method because of its compatibility with the decreasing pattern found in most ring-width series (Cook and Peters 1997). The program first creates a ring-width index (RWI) for each tree, and then an autoregressive model was used to account for autocorrelation in each RWI. In this study, the first-order autoregressive model was sufficient to account for autocorrelation.

We then used a response function analysis to estimate the effect of 32 climatic variables on the radial growth response (RWI) of northern red oak and chestnut oak. Monthly values of total precipitation and mean temperature for June–December of the previous year and January–September of the current year were selected as predictors. Precipitation and temperature data from 1973 to the present were recorded at the Cooper's Rock weather station on site, and data for the years 1932–1973 were interpolated from records from the three closest weather stations. Climatic data were obtained from the U.S. National Climate Data Center, Asheville, N.C.

Response functions were derived using the method of principal components regression (Fritts et al. 1971; Fritts 1976). This method accounts for strong multicollinearity among monthly climatic variables and permits an assessment of the independent effects of each variable. With this method, the original climatic variables are transformed into a new set of uncorrelated variables called principal components of the correlation matrix. This transformation ranks the new uncorrelated variables in order of their importance, and the procedure then involves eliminating some of the principal components to achieve a substantial reduction in variance. We used the eigenvalue product rule (Guiot et al. 1982) to eliminate the last eight principal components, and the remaining 24 components were further screened using stepwise regression with an F value of 0.15 to enter, commonly used in dendroclimatic studies (Fritts 1976; Lindholm et al. 2000). A multiple regression analysis of the response variable against the reduced set of principal components was then performed, using ordinary least squares estimation. Once the regression coefficients for the reduced set of orthogonal variables were calculated, they were mathematically transformed into a new set of coefficients that corresponded to the original correlated set of variables. A 0.05 significance level was used to identify statistically significant climatic predictors.

The correlation matrix of climatic predictors, the eigenvectors of this matrix, and the uncorrelated principal components were computed using the SAS programs (PROC PRINCOMP, PROC STEPWISE; SAS Institute Inc. 1998). Because we were dealing with time series data, we checked normality and independence of the resulting residuals. Normality was tested using the normal probability plot generated in SAS, and independence was tested by plotting the residuals against time and against their lagged values. In both cases the data conformed to the two assumptions.

The proportion of variance (R^2_{climate}) of each species' chronology attributable to the 32 climatic variables used was calculated using the following equations:

$$[2] \qquad \text{SS}_{\text{Regression}} = \text{SS}_{\text{Total}} - \text{SS}_{\text{Residuals}}$$

$$[3] \qquad R^2_{\text{climate}} = \frac{\text{SS}_{\text{Regression}}}{\text{SS}_{\text{Total}}}$$

We calculated response functions separately for each species using their entire data set, and then for each crown-release group (0, 25, 50, 75, and 100%), to see if the R^2_{climate} value changed as a function of crown release.

For the disturbance-history portion of the study we used the technique of Nowacki and Abrams (1997) with several modifications. Although basal area increment provides a better means of comparing the absolute growth among stands, the focus of this study was on detecting relative radial growth changes within individual trees over short time periods to identify canopy disturbances affecting that tree. Thus, the mean of ring widths from two increment cores per tree was the input for the %GC calculation.

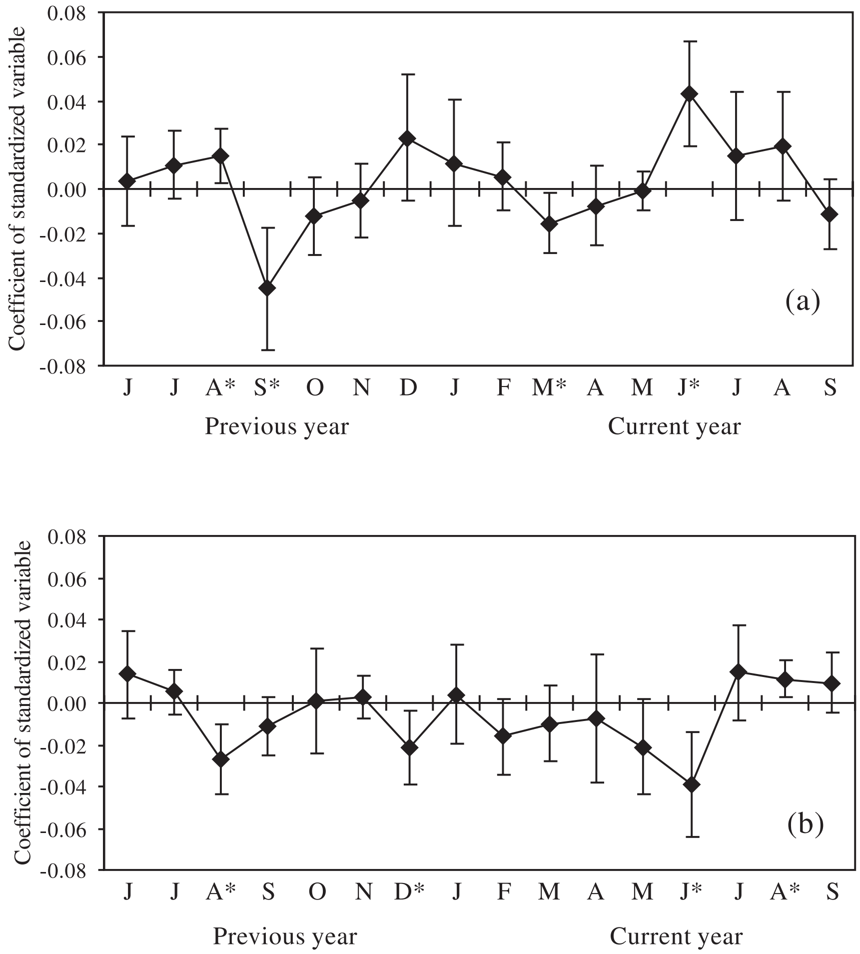
We first calculated %GC values for each tree using eq. 1 for years 1983, 1984, and 1985 (lag of 1–3 years) and for time intervals (M_1 and M_2) ranging from 6 to 15 years. We then analyzed the entire data set, by species, using the general linear models procedure (PROC GLM; SAS Institute Inc. 1998) to test for statistically significant relationships between %GC and %CR. To see if different combinations of lag and time interval better expressed this relationship, we also included lag and interval, as well as their interaction, as independent variables in the analysis. When lag or interval showed a significant effect, we used Fisher's least significant difference (LSD) to identify which level of lag and (or) interval produced statistically different mean %GC values. Finally, for each species, we ran each combination of lag and interval individually using PROC GLM. To see if the trend between release level and %GC was linear, quadratic, or cubic, we used one degree of freedom orthogonal comparisons. Orthogonal comparisons are a priori tests that divide the treatment SS into independent parts (Dowdy and Wearden 1991). The outputs are F statistics and equations of each model. When the appropriate F statistic was significant, the significance of the coefficient (b_n) was tested using a t test.

Results

Climate and radial growth

Response functions for northern red oak and chestnut oak are shown in Figs. 1 and 2. Of the 32 climatic variables considered, a total of eight temperature and six precipitation variables were statistically significant. The overall trends of response functions for the two species were similar. Correlation values for precipitation were generally positive and had greater absolute values than those for temperature. Growing

Fig. 1. Response function of northern red oak. Variables are monthly precipitation (*a*) and mean monthly temperature (*b*) for June–December of the previous year and January–September of the current year. Months marked with an asterisk are significant at $p < 0.05$. Error bars are 95% confidence intervals.



season climatic predictors were also more numerous and greater in absolute value than those of the dormant season. Both species showed significant negative correlations between radial growth and previous-August and previous-December temperature, as well as previous-September precipitation. Correlations with June precipitation and radial growth for both species yielded the highest positive values, results that conform to nearly all dendroclimatic studies of oaks (Estes 1970; Ashby and Fritts 1972; Jacobi and Tainter 1988; Pan et al. 1997; Rubino and McCarthy 2000). Both species also showed a strong negative correlation with June temperature, although the relationship was statistically significant for red oak only.

The small number of significant correlations between these climatic variables and growth, and their low values, illustrate the relative climatic complacency of these species on this site. Mean sensitivity, a statistical measure of the mean change from each measured annual ring width value to the next, and a measure of how much annual variations in precipitation and temperature limit growth on a site (Fritts 1976), was relatively low (0.19 and 0.22 for northern red oak and chestnut oak, respectively). A comparison of the R^2_{climate} values from the principal components regression for the released and unreleased groups suggests the comparative importance of climatic and nonclimatic factors to radial growth in this forest. The values of R^2_{climate} generally declined as the level of crown release increased (Table 1). The proportion of ring width variation attributable to climate for the chestnut oak and red oak control groups (10.6 and 35.9%, respectively) was two to three times greater than the mean of the released groups (4.5 and 8.8%, respectively). Differences were more pronounced for red oak, a species that is generally considered both more climatically sensitive (Parker et al. 1982; Abrams et al. 1998) and more opportunistic in favorable environmental conditions (Dickson 1994; Hicks 1998). For both species, climate, while exerting a significant influence on annual tree-ring variation, was comparatively less influential than nonclimatic events such as crown release and canopy disturbance.

Canopy disturbances and radial growth averaging

The relationship between %CR and %GC was highly significant for both species for all lags and all intervals (Table 2). Lag and interval did not show a significant effect for red oak, suggesting that the strong relationship between %GC and %CR for this species was present regardless of the lag and interval used in the calculation of %GC. For chestnut oak, both lag and interval were statistically significant. The best fit between %GC and %CR occurred when a shorter time interval (7-year) and a longer lag (3-year) were

Fig. 2. Response function of chestnut oak. Variables are monthly precipitation (*a*) and mean monthly temperature (*b*) for June–December of the previous year and January–September of the current year. Months marked with an asterisk are significant at $p < 0.05$. Error bars are 95% confidence intervals.

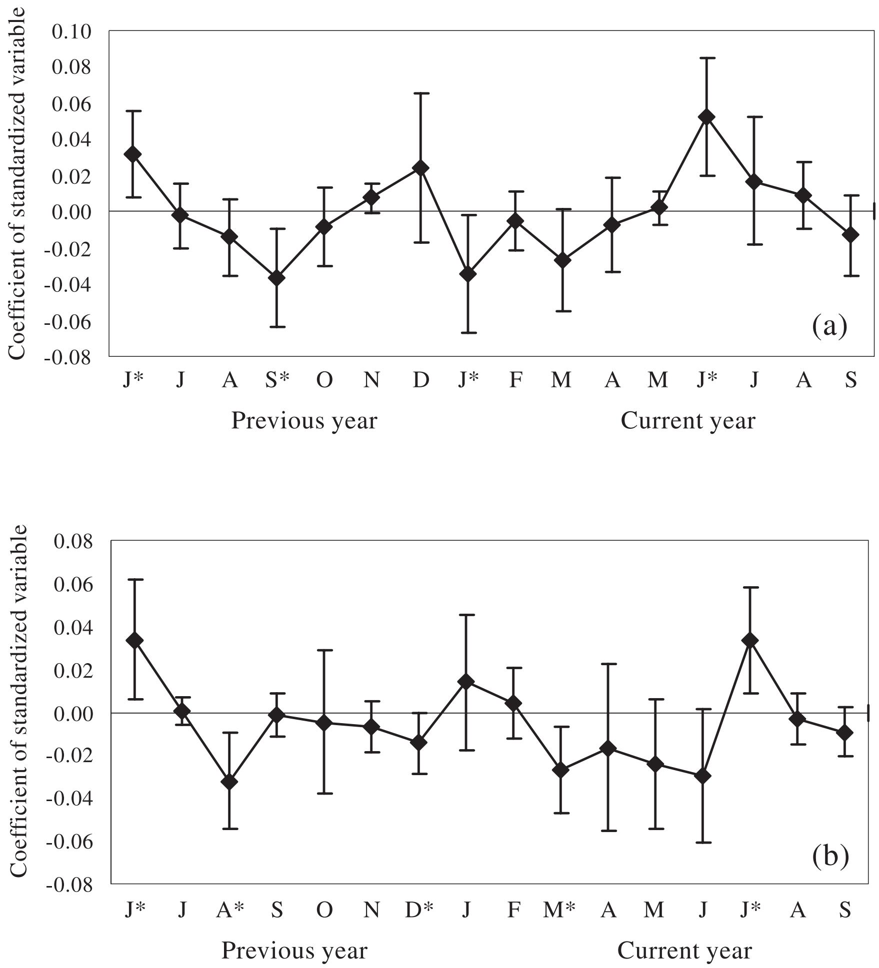


Table 1. Percentage of standardized tree-ring variation (R^2_{climate}) that can be attributed to influence of 32 climatic variables (monthly precipitation and mean monthly temperature for June–December of the previous year and January–September of the current year) by species and crown release level.

Crown release level (%)	Chesnut oak (%)	*n*	Northern red oak (%)	*n*
Control	10.6	10	35.9	10
25	5.7	12	11.2	12
50	6.5	13	4.5	9
75	4.8	11	14.8	14
100	1.2	6	4.9	6
Mean, all released	4.5		8.8	

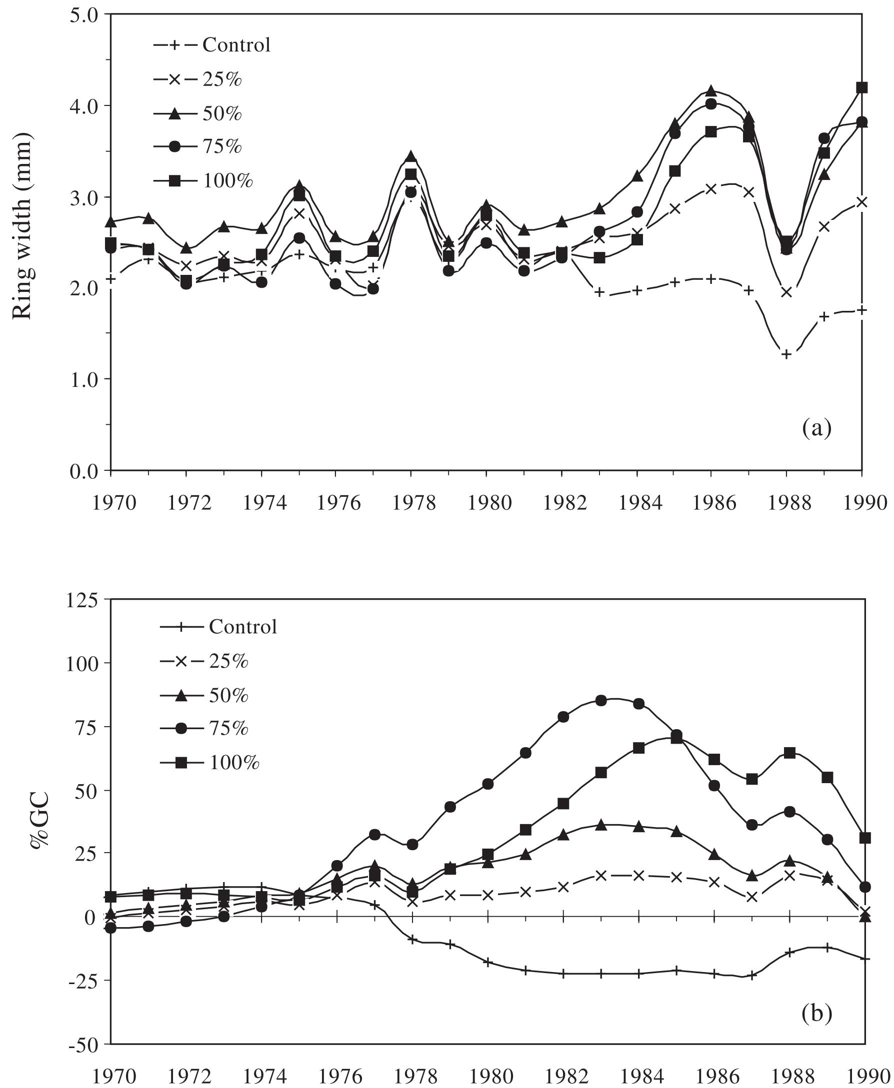
Table 2. Results of analysis of variance of % growth change (%GC, dependent variable) as a function of % crown release (%CR), lag, and time interval (independent variables) using the general linear models procedure (SAS Institute Inc. 1998).

Source	df	MS	*F*	*p*
Northern red oak				
Lag	2	8929	2.27	0.104
Interval	9	3832	0.97	0.461
%CR	4	567 310	145.60	<0.0001
Lag × interval	18	221	0.06	1.000
Chestnut oak				
Lag	2	7179	4.69	0.009
Interval	9	7840	5.12	<0.0001
%CR	4	411 193	270.10	<0.0001
Lag × interval	18	8200	0.30	0.998

used; however, the interaction of lag and interval was not significant ($p = 0.998$). The 3-year lag does not imply that chestnut oak delays its response to canopy release for 3 years. Plots of raw ring widths (Figs. 3*a* and 4*a*) show radial growth increases for both species in 1983, the first year following thinning. However, use of the 3-year lag best captures the maximum mean %GC for chestnut oak.

Plots of %GC for northern red oak (using a 1-year lag and 10-year interval) and chestnut oak (3-year lag and 7-year interval) are shown in Figs. 3*b* and 4*b* for the period 1970–1990. Two features of these plots are important. First, radial

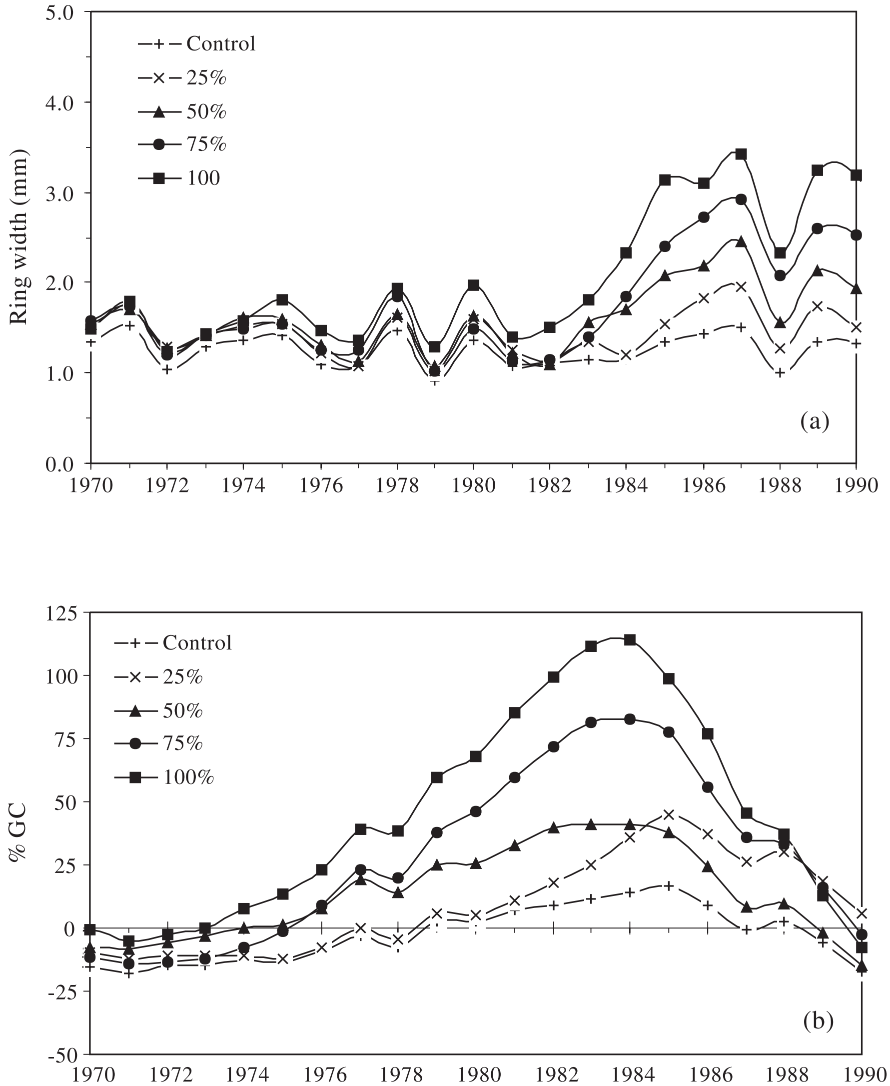
Fig. 3. Mean ring width (*a*) and percent growth change (%GC) (*b*) for five levels of crown release for northern red oak, 1970–1990. Disturbance year is 1982.



growth averaging provides a fairly accurate estimation of the disturbance year. Peak %GC for chestnut oak correctly identified the disturbance year as 1982, while red oak's peak %GC occurred 1 year later for all %CR levels except the 100% level. Second, the trend of increasing %GC associated with increased levels of crown release is also apparent, particularly for chestnut oak. On average, each 25% increment of crown release yielded 26% GC for chestnut oak and 20% GC for red oak. When the response of the two species was analyzed for each individual combination of lag and interval, the relationship between %GC and %CR was best approximated by a straight line ($y = a + bx$, where y is %GC and x is %CR) (Table 3; note that only data for intervals of 7–12 years are shown). The coefficient of the linear model (b) was 0.95 (t = 3.62, p < 0.001) and 1.10 (t = 5.21, p < 0.0001) for red oak and chestnut oak at interval and lag shown in Figs. 3 and 4 and varied between 0.74 and 1.23 over all lag periods and intervals. Using the 1-year lag and 10-year interval as proposed by Nowacki and Abrams (1997), the coefficient for chestnut oak was 0.92, not greatly different from the 3-year lag and 7-year interval. These results provide evidence of an approximate 1:1 relationship between %GC and %CR for these 55-year-old trees and suggest that the magnitude of %GC is highly correlated with disturbance severity.

The increases were synchronous and anamorphous, with several exceptions. Peak %GC in the 25% crown release group for chestnut oak was delayed until 1984. Red oak achieved maximum %GC in the 75% crown release level in 1983, while %GC did not peak in the 100% crown release group until 1985 and at a slightly lower value. The small sample of red oaks in the 100% crown release level (n = 6) may be responsible for this anomaly. The fact that chestnut oak in the control group (i.e., no release) showed a positive %GC (19%) in 1982 is probably due to the fact that 7 of the 10 sample trees in this group occurred in experimental units that were thinned to a relative density of 75%. Although some chestnut oak control trees were not "control" in the strictest sense, their growth change was modeled as a function of changes in each tree's immediate environment (i.e., level of crown release), and all control chestnut oaks met the criterion of zero crown release. In addition, relative density

Fig. 4. Mean ring width (*a*) and percent growth change (%GC) (*b*) for five levels of crown release for chestnut oak, 1970–1990. Disturbance year is 1982.



levels were plot means and do not necessarily indicate density level in the immediate environment of any particular tree. In contrast, all the red oak control trees occurred in unthinned experimental units where only natural mortality unassociated with the treatment occurred.

Discussion

Climatic response

The strongest correlations between radial growth and climate occurred during August and September of the previous year and June of the current year. This trend is consistent with the determinate (Marks 1975) or preformed (Oliver and Larson 1996) growth type (although note that red oak has also been classified as semi-determinate (Tomlinson et al. 1991) or episodic (Dickson 1994)). Previous-year climate is important, because buds that are formed at the end of the growing season contain primordia of all the tissues that will expand during the subsequent growing season, and carbohydrates stored in the previous year fuel next year's initial extension growth (Kozlowski and Keller 1966; Marks 1975; Bormann and Likens 1979). The first significant correlation for current growing season climate occurred for June precipitation and temperature, when "spring" gives way to "summer". Oaks complete their addition of earlywood by the time of leaf-out (Kennedy and Sutherland 1999), mid-May in the central Appalachian region, when stored food reserves from the previous growing season largely determine growth (Hinckley et al. 1979). Beginning in June, growth depends more on currently produced than previously accumulated photosynthates, and competition for photosynthates by more active sinks in other parts of the tree occurs (Hinckley et al. 1976). Consistent with this process are strong negative correlations between radial growth and June temperature for both species (although the relationship was statistically significant only for red oak). High summer temperatures have been linked to reduced radial growth because of high rates of leaf transpiration and soil water evaporation, which together produce premature stomatal closure related to water stress (Fritts 1976; Hinckley et al. 1979), as well as increased respiration and reduced rates of assimilation and hormone synthesis (Kramer and Kozlowski 1960; Fritts

1976). In contrast, cooler June temperatures allow net photosynthesis to continue at a high rate (Jacobi and Tainter 1988).

Radial growth of both species showed negative and significant correlations with previous-September precipitation and previous-August temperature. On well-drained, midslope sites, negative correlations between growth and precipitation during the growing season are difficult to explain. Pan et al. (1997) and Jacobi and Tainter (1988) found a similar response for northern red oak and white oak, respectively, so this correlation is probably not an artifact of the response function analysis. Fritts (1976) reasoned that this may be a case in which growth and precipitation are less directly and causally related to each other, than both related to another physiological factor, for example, cold hardiness. Conditions that initiate cold hardening include low temperatures and short days; however, water stress may also trigger this process (Fritts 1976; Carter and Brenner 1985). While a dry autumn may cause water stress and interrupt current-year growth, early cold hardening reduces the susceptibility of primordial tissue to early fall frost and severe winter cold and results in greater survival of buds. In contrast, cooler than average August temperatures may extend the growing season, reduce respiration, and permit greater accumulation of stored food reserves for the following growing season (Jacobi and Tainter 1988). Thus, while cool August temperatures increase food production, dry Septembers favor bud survival.

Table 3. Coefficients of the linear model: percent growth change (%GC) = $a + b \times$ percent crown release (%CR), for lags of 1–3 years and averaging intervals of 7–12 years for northern red oak and chestnut oak.

		Northern red oak		Chestnut oak	
Lag (years)	Interval (years)	*b*	*t**	*b*	*t**
1	7	0.81	3.39	0.90	5.46
1	8	0.85	3.41	0.90	5.77
1	9	0.90	3.57	0.89	5.95
1	10	0.95	3.62	0.92	6.07
1	11	1.02	3.75	0.98	6.08
1	12	1.03	3.89	0.95	6.25
2	7	0.97	3.46	1.05	5.52
2	8	0.98	3.49	0.99	5.72
2	9	1.04	3.58	1.00	5.84
2	10	1.09	3.70	1.04	5.91
2	11	1.16	3.82	1.07	5.92
2	12	1.16	3.91	1.03	6.13
3	7	1.11	3.53	1.10	5.21
3	8	1.13	3.49	1.07	5.29
3	9	1.18	3.66	1.08	5.46
3	10	1.20	3.78	1.09	5.57
3	11	1.23	3.85	1.10	5.66
3	12	1.21	3.95	1.02	5.84

*A *t* value greater than 2.714 is significant at the 0.05 level.

Radial growth averaging

The dendroclimatic analysis shows that the radial growth of oaks is indeed affected by climate, but the influence of climate assumes relatively less importance as trees undergo canopy disturbance and crown release (Table 1). A critical component of successful radial growth averaging is the selection of a time interval that is long enough to average out high-frequency, short-term climatic responses, while capturing intermediate-length growth increases (i.e., 7–12 years) that are associated with canopy disturbances (Nowacki and Abrams 1997). The efficiency with which the radial growth averaging technique emphasizes intermediate-length growth changes while deemphasizing interannual effects of climatic fluctuations is evident from the species' ring-width and %GC curves (Figs. 3 and 4). In 1988, the study site experienced a severe drought, during which June precipitation was 45% of normal values, and Palmer drought severity indices for the period June–July averaged –3.9 (NCDC 2000). Trees of both species in all crown release levels showed a large growth decline in 1988 (Figs. 3*a* and 4*a*), but predrought growth levels of both species resumed the following year. For chestnut oak, the large fluctuation in radial growth between 1987 and 1989 was not evident in the %GC curve (Fig. 4*a*). For red oak, there was a small spike in 1988, but the increase was not of sufficient magnitude (6–10% increase over the prior year) to be mistaken for a canopy disturbance (Fig. 3*a*).

In view of the different growth characteristics of these two species, some measure of species-specific averaging criteria may appear warranted. For example, a delayed response and a shorter duration of the response are consistent with chestnut oak's overall growth characteristics. Northern red oak outgrows nearly all other oaks in radial growth (Trimble 1969), as well as height extension and lateral expansion (Hicks 1998). When trees of good vigor on better sites are compared, chestnut oak is often overtopped and outcompeted by more rapidly growing species such as northern red oak and yellow-poplar (Trimble 1960; McQuilken 1990). Yetter and Runkle (1986) found red oak height growths of 0.19 m/year in gaps, while the average lateral expansion of red oak crowns in openings was 0.16 m/year in both 16-year-old (Miller 2000) and 50-year-old second growth stands (Trimble and Tryon 1966). In comparison, chestnut oak has a relatively smaller live crown (Hicks 1998), and a lower crown expansion rate (0.12 m/year; Miller 2000). Comparing northern red oak, black oak, and white oak, Graney (1987) found that a more rapid response of intermediate and higher crown class red oak to thinning was probably due to differences in competitive crown size and position in overstocked stands. Red oaks were in better condition to respond and tended to reach dominant crown positions earlier and sustain growth increases longer than other oaks.

Initial tree size and stand characteristics also may influence response time and the magnitude of %GC. More highly stocked stands may show a greater response than lightly stocked ones (Trimble 1968), and the rate of crown closure is faster on better quality sites (Gingrich 1967; Hilt 1979). However, if crown class is controlled, response is independent of initial tree size (Ellis 1979; Trimble 1969; Singer and Lorimer 1997) and basal-area density (Trimble 1969).

An additional issue concerns the degree to which tree age may dampen the response to crown release and increase climatic sensitivity. For this study, the importance of this question may be underestimated by the low mean tree age (55 years at time of treatment) and the fact that a relatively large portion of their age occurred during and after the treatment. As trees age and increase in height, girth, and crown size, the ratio of photosynthetic and nonphotosynthetic tissue usually decreases (Barnes et al. 1998), making them more susceptible to climatic, physical, or other forms of stress (Waring 1987). In taller, older trees, the efficiency of water and nutrient transport may also decrease because of tissue changes associated with age, size, and carbon balance (Ryan and Yoder 1997). As a result, premature stomatal closure and reduced growth may occur not because of climatic drought, but because of the inability to move water rapidly enough from the roots to leaves. Recognizing the reduced growth potential of older trees, common recommendations are to stop thinnings in oak stands on average sites (SI = 17–23 for red oak) at ages 60–70 in the central United States (Roach and Gingrich 1968) and at age 95 in the northeastern United States (Ward 1991). Comparing 5-year growth of FTG versus unreleased 75- to 80-year-old hardwood sawtimber trees, Smith and Miller (1991) found a 44% increase for red oak, and a 56% increase for white oak, but no significant difference was found between diameter increase of released and nonreleased chestnut oak. Recognizing the reduced growth potential of older, overstory oaks, Nowacki and Abrams (1997) suggested that a 35–40% crown release may be required to elicit a 25% GC for presettlement-era oaks.

In this study, the relationship between %CR and %GC for 55-year-old overstory oaks was linear and approximately 1:1, and the 25% GC value was a suitable threshold for detecting minimal (one-side) release events. Perkey and Onken (2000) found a similar relationship between growth and release for 55-year-old red oak crop trees. In Wisconsin, Singer and Lorimer (1997) also found a linear relationship between crown release and growth for 42- to 243-year-old sugar maple but not for white ash (*Fraxinus americana* L.) or black cherry (*Prunus serotina* Ehrh.). However, Ellis (1979) found that fully released 85-year-old sugar maple had a mean diameter growth increase of 94%, comparable with the response in our study. Finally, looking at the 100 largest oak trees per hectare (age 35–100 years), Hilt (1979) found that the heavier the thinning, the greater the response. Younger stands responded somewhat better than older ones, but he attributed that to the interaction between age and stocking. Crown class, rather than age, site (Hilt 1979), vigor, initial DBH, stocking, or site quality (Trimble 1969) was most closely correlated with diameter increase. Further, as stands age, they potentially become more diverse in composition, age distribution, and canopy stratification, and crown class becomes a more reliable predictor of response to thinning and disturbance.

Limitations of radial growth averaging

As a growth model, the percent growth change method evaluated in this study is not intended to account for the wide range of ecological processes associated with either silvicultural thinning or "natural" gap disturbances. Tree mortality initiates a suite of biotic responses and environmental changes that include, in addition to increased crown exposure and lateral extension of gap border trees (Runkle 1985), understory initiation and (or) release (Runkle 1982; Lorimer and Frelich 1989); microsite changes in temperature and humidity (Beatty and Stone 1986); and altered rates of decomposition, nutrient cycling, and energy exchange (Sprugel 1985; Vitousek 1985). In fact, if understory dynamics are the primary focus, the criteria of Lorimer and Frelich (1989) provide the best means of identifying canopy accession events. We were less interested in larger stand-level changes associated with reductions in residual density than the radial growth response of individual codominant trees bordering canopy openings. In this sense, our study more closely resembles crop-tree release studies. Thus, our use of the model is aimed at (*i*) capturing a limited portion of the total change that occurs during crown release, (*ii*) evaluating the model's accuracy in identifying a time period when known canopy disturbances of known magnitude occurred, and (*iii*) establishing its utility as a method of reconstructing canopy disturbance history.

Depending on the lag selected, the radial growth averaging method assumes that the response occurs 1–3 years after the canopy disturbance. However, response time may vary according to the precise timing of the disturbance event. For example, a disturbance in January may precede the growing season enough for a growth increase to occur in the same calendar year, while one in July, after most of the radial growth is complete, would not be apparent until the following year. This factor may be more apparent for northern red oak than chestnut red oak, because of the former's episodic flushing growth habit (Dickson 1994). Differences in individual tree genetics and physiological condition before the disturbance, as well as species-level differences, may also temper the precise timing of the response (Lorimer and Frelich 1989; Schuler and Fajvan 1999).

If the technique is used to construct a site disturbance chronology, some caution should be exercised in attributing %CG evidence of a disturbance in two or more proximate trees to the same disturbance event. This may not always be the case; for example, in this region, high-velocity, localized, and short-duration windstorms associated with thunderstorms are a common form of canopy disturbance (Romme and Martin 1992; NCDC 2001), and more than one disturbance may occur in a sample plot in the same year (Fajvan and Seymour 1993).

Finally, while most evidence supports our assertion that interannual variability in climate is the dominant climatic signal in eastern mesic forests, there is some evidence that longer term climatic trends may be present. Long-term, nonperiodic trends, such as global warming, for example, may increase drought frequency (LeBlanc and Foster 1992) and alter species distributions (Iverson et al. 1999). In addition, current European research suggests that some climatic trends may operate on frequencies comparable with intervals used in radial growth averaging. For example, the North Atlantic Oscillation is an intermittent climate oscillation with temporally active and passive phases. Periods of 5–7, 9–11, 12–14, and 80–90 years have been identified (Appenzeller and Stocker 1998). Although this phenomenon has been linked to winter climate and phenology of herbaceous plants in Europe (Post and Stenseth 1999; Ottersen et al. 2001), its effects in North America have yet to be demonstrated

Applications

The radial growth averaging method is generally applicable in temperate closed canopy forests where competition for sunlight overshadows the effects of climate (Nowacki and Abrams 1997). Theoretically, the technique is applicable to any species that can withstand side shade and that can profit from partial crown release. Thus, for example, the model would probably apply to species such yellow-poplar (Carvell 1964; Beck and Della-Bianca 1975) but not to black cherry (*Prunus serotina* Ehrh.) (Trimble 1968; Miller et al. 1995). In old-growth forests, standwide disturbance years indicated by %GC values for older (>100 years) hickories (*Carya* spp. Nutt.) and white ash closely agreed with those for white oak, northern red oak, and chestnut oak (Rentch 2001). For this study, a 25% growth change threshold appears to identify crown release events for two oak species. For other species with different growth rates and release-response characteristics, further research that quantifies the relationship between crown release and radial growth is needed.

The percent growth change method is particularly applicable in eastern forests where oaks account for a significant portion of the canopy. Here, problems with oak regeneration on better quality sites have stimulated research into conditions that facilitated previous oak establishment. Fire chronologies of older oak forests comprise one approach to estimating ground-level disturbance (Sutherland 1997; Abrams 2000). The percent growth change model can supplement fire history by estimating the historical range of variability of canopy disturbance over a similar time period. When locations of cored trees are mapped, individual tree chronologies from several overstory species and cohorts over a relatively long time period (i.e., several hundred years) can be integrated into a temporal and spatial approximation of the disturbance regime. In fact, for many older forests with only sketchy historical records, this method may be the only way to reconstruct long-term stand dynamics. This estimate may provide a framework for scheduling the rate of stand entry for silvicultural treatments (e.g., thinning) that is consistent with historic stand development.

Conclusion

In oak-dominated forests of eastern North America, where individual and multiple tree-fall gaps comprise the dominant disturbance regime, the influence of climate is primarily expressed as short-term variations in radial growth that rarely last more than 1 year. Competition for growing space dominates growth, and the effect of climate is often overshadowed by canopy disturbances that alter the competitive balance and the distribution of resources. In such a disturbance regime, radial growth averaging is a suitable method for estimating the frequency and intensity of canopy disturbances, and the 25% GC threshold provides a good indication that a small, single-tree event has occurred. The applicability of this method to nonoak species is suggested; however, more research quantifying the relationship between percent growth change and percent crown release is needed. Using this method, individual tree and standwide chronologies may be readily determined, and when combined with spatial analysis, species dynamics and group dynamics can be chronicled. If old-growth trees are available, radial growth averaging makes a comparison of disturbance regimes over a long historical period possible. When combined with fire chronologies, the method provides a useful tool in estimating the historic range of variability of canopy disturbance and may provide the best method of estimating long-term stand dynamics when the historical record (land surveys, human use, etc.) is lacking.

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