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Original article

Dendrochronological analysis of white oak growth patterns across a topographic moisture gradient in southern Ohio

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ABSTRACT

Moisture availability is a key factor that influences white oak (*Quercus alba* L.) growth and wood production. In unglaciated eastern North America, available soil moisture varies greatly along topographic and edaphic gradients. This study was aimed at determining the effects of soil moisture variability and macroclimate on white oak growth in mixed-oak forests of southern Ohio. Using accurately dated and measured tree rings, we analyzed 119 white oaks growing across an integrated moisture index (IMI), a computer-generated GIS model that simultaneously combines topographic and edaphic features into a moisture index scale. Growth trends varied considerably across the IMI, with trees in mesic sites exhibiting patterns much different from those in either xeric or intermediate sites. BAI growth and biomass increments were higher for trees growing in the intermediate and mesic sites than those from the xeric sites. Correlation and response function analyses, and redundancy analysis revealed significant relations between ring-width indices and climate, with current year May–July PDSI, precipitation and temperature as the most important correlates of white oak growth. Additionally, climatic influences on growth rate were variable across the IMI; trees in xeric sites showed much greater coefficients relative to those from the intermediate and mesic sites. Despite these differences, xeric and intermediate trees exhibited similar growth patterns. The present results provide further evidence of the usefulness of the IMI for identifying and comparing white oak growth patterns across the complex, dissected landscape of southern Ohio.

Introduction

Ecologists have long recognized the influence of microsite variability on ecosystem structure and function in topographically dissected landscapes (Boerner, 2006; Ozier et al., 2006; Copenheaver et al., 2007). In unglaciated eastern North America, for example, numerous studies have linked changes in overstory composition with microsite variation related to topographic (slope position, aspect, and steepness) and edaphic gradients (e.g., McCarthy et al., 1984). Microsite gradients, including variations in soil and air temperature, evaporation rate, daily insolation, wind velocity, soil type, and atmospheric moisture often influence soil moisture availability (Dyer, 2009). Furthermore, microsite conditions have been shown to vary greatly from mean regional macroclimatic conditions (Hutchins et al., 1976), thus, permitting a mosaic of communities and habitats across the landscape. However, understanding the influence of macroclimate on growth and productivity is also important for predicting future growth patterns in the face of global climate change (Graumlich, 1993).

The relationship between microsite variability and site quality has also been recognized by many researchers (e.g., Kozlowski et al., 1991; Pinno et al., 2010). In view of this and of the significance of site quality in meeting wood production and conservation needs (Carmean et al., 1989), researchers have developed several metrics to assess how tree growth rates are affected by local environmental conditions. For example, site index curves (i.e., average dominant tree height of a particular species at a given age) have long been used to measure timber production potential in North America. However, application of site index curves can be problematic if certain site and tree conditions are not satisfied – un-injured trees, lack of growth suppression, fully stocked stands, and lack of severe fire and heavy grazing (Carmean et al., 1989; Fralish, 1994).

Having identified the inherent problems associated with the application of site index curves in various forest stands, researchers developed several different techniques to relate growth rate or yield with topographically driven microsite characteristics in Appalachian and Central Hardwood forests. Gaiser (1951), for example, developed a method relating white oak (*Quercus alba*

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L.) site productivity with edaphic (depth of A horizon) and topographic gradients (slope position and slope aspect) in southeastern Ohio. Auchmoody and Smith (1979) analyzed 46 site-derived soil and topographic characteristics to develop an empirical model to predict oak (*Quercus* spp. L.) site quality where application of site index curves is precluded in northwestern West Virginia. A similar investigation linking site productivity with topographic and edaphic gradients was conducted by Fralish (1994) in the Shawnee Hills of Illinois. In these studies, available soil moisture was found to be a key factor influencing site productivity.

In developing productivity indices, researchers have developed methods that attempted to both adequately describe the influence of microsite variability on productivity yet offer users an index that is fairly easy to implement (e.g., Meiners et al., 1984). The integrated moisture index (IMI) is one of such indices developed by Iverson et al. (1997) to help predict forest composition and productivity. The index was created “to provide a relative rating of moisture that can be related to specific processes wherever moisture is seen to be the primary driving factor” (Iverson et al., 1997). The IMI is a simple and general model that can be computed by combining four geographic information system (GIS)-derived topographic and soil features. The input features are hillshade (effect of solar radiation due to slope angle, aspect, and position and shading from adjacent landforms), flow accumulation (accumulated flow of water as it moves downslope due to gravity), curvature (shape of the land) and water holding capacity (depth of A and B soil horizons).

The IMI has been successfully used to reveal patterns in forest composition, soil pH and nitrate levels, and herbaceous layer composition and richness in forests of southern Ohio (Iverson et al., 1997; Hutchinson et al., 1999). Given the well-documented link between available soil moisture and site productivity, and the ability of the IMI to simultaneously account for various complex topographic and edaphic gradients that drive moisture availability, this index is both desirable and suitable for assessing regional microsite productivity in the unglaciated portion of the Allegheny Plateau.

Annual growth of trees is governed by numerous biotic and abiotic factors, with available soil moisture being one of the most important (Fritts, 1976; Oberhuber and Kofler, 2000). Different growth trends in trees growing across sites characterized by contrasting moisture availability (yet experiencing similar macroclimate) have been noted in several dendrochronological studies. For example, Abrams et al. (1998) and Orwig and Abrams (1997) found that drought-induced reductions in growth rate were often more dramatic on xeric sites than in trees growing in mesic sites. Similarly, Tardif and Bergeron (1997) found a “filtering” effect caused by different growing environments; they found droughts to have a greater impact on trees from xeric sites than on trees in sites that were less water-limited. In these respects, successful decomposition of white oak growth patterns across contrasting environments (as represented by the different IMI classes) is of great ecological interest, and should facilitate future assessment of stand dynamics in such heterogeneous landscapes.

Untangling the influence of complex topographic and edaphic gradients and their associated moisture regime on growth rate and productivity can be time and energy intensive. However, through the use of dendrochronological techniques, the influence of site factors on growth rate can be directly estimated (Clark et al., 2001; Rubino and McCarthy, 2002). Dendrochronological analysis offers several benefits. First, productivity analysis can be performed nondestructively so that growth rates among numerous topographic and edaphic conditions can be compared without cutting down trees. Second, by coupling tree-ring widths with stem diameters and bole heights, annual basal area production and annual wood volume increments can be calculated. Third, growth rates over an extended historical context can be examined. Such information may be of great interest given the changes in climate, moisture, atmospheric gas concentrations, and atmospheric deposition currently occurring or predicted for the region.

The objectives of this investigation were several-fold. First, utilizing dendrochronological techniques, we wanted to identify and compare radial-growth rates and biomass of white oak growing across complex topographic and edaphic gradients. Specifically, we wanted to determine how available moisture (as related to microsite variability caused by edaphic and topographic gradients) affects annual wood production. Additionally, we wanted to assess how trees from various microsites respond to similar macroclimatic conditions to determine the influence of climate on white oak growth across the landscape. To achieve these objectives, we used the IMI to model available soil moisture due to its ease of use and previous success in revealing community and ecosystem attributes in relation to available moisture in the region.

Methods

Study sites

This study was conducted in four mixed-oak forests of southern Ohio: Arch Rock (39°12′00″N, 82°23′00″W), Watch Rock (39°11′00″N, 82°22′00″W), Young’s Branch (38°43′00″N, 82°41′00″W) and Blue Grass Ridge (38°36′00″N, 82°31′00″W) (Fig. 1). The first two sites are located close to the Raccoon Ecological Management Area in Vinton County (now known as the Vinton Furnace State Experimental Forest) while the latter two are located in the Wayne National Forest, Lawrence County. The sites are located on the unglaciated Allegheny Plateau and fall within the Low Hills Belt section of the mixed mesophytic forest region of the eastern United States (Braun, 1950). All study areas are dominated by oaks and hickory (*Carya* spp. Nutt.) and were clearcut in the mid-1800s to provide wood for charcoal production (Hutchinson et al., 2008). A complete description of site geology, land use history, and vegetation can be found in Sutherland and Hutchinson (2003). Climate for the region is humid-continental. July is the warmest month (mean = 23.8 °C), and January is the coldest (mean = −0.3 °C). Mean annual precipitation is 105.7 cm; July is the wettest month (mean 11.5 cm of precipitation), and October is the driest (mean = 6.2 cm). Precipitation is fairly evenly distributed throughout the year (National Climatic Data Center and National Oceanic and Atmospheric Administration, 2010).

Field sampling

The IMI was mapped for each of the four study sites, and twenty-seven 25 m × 50 m plots (108 total) were installed at each site. The plots were stratified across the landscape so that approximately one-third of each of the plots was classified into each of the three IMI categories: xeric, intermediate, and mesic (plot characteristics for mesic plots: northeasterly aspect, deep soil, concave slope shape, mid- to low-slope position; for xeric plots: southwesterly aspect, thin soil, steep slope, ridge top). The plots were part of a larger study designed to evaluate the effectiveness of prescribed burning as a restoration tool in mixed-oak forests (see Sutherland and Hutchinson, 2003). All plots were constructed on ridges and slopes with no plots being constructed on valley floors.

Two increment cores (for most trees) were obtained at breast height from two trees just outside of each plot. The trees were located within 10 m of the diagonal plot corners of the plots. To avoid reaction wood, cores were taken parallel to slope contours according to standard dendrochronological procedures (Stokes and

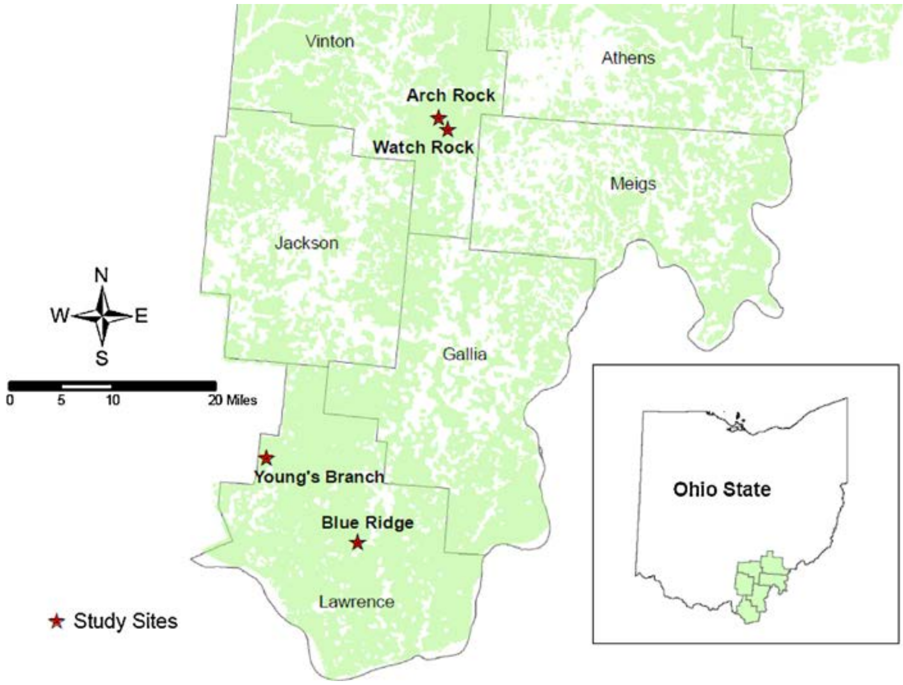

Fig. 1. Map of southeastern Ohio showing the four study areas.

Smiley, 1968). Cores were stored in labeled drinking straws in the field to minimize mechanical damage during transport. Diameter at breast height (DBH) was recorded for each cored stem.

To minimize growth trend variation among species, only cores obtained from white oak were analyzed in this investigation (Fritts, 1976). We chose to analyze only white oak due to its relatively common distribution across various topographic positions and soil types in the region and due to its large regional importance as a lumber species (Griffith et al., 1993; Widmann et al., 2009). White oak is a long-lived tree and is classified as intermediate in shade tolerance (Rogers, 1990). Individuals are able to persist for extended periods of time in the understory as seedlings and as suppressed saplings and pole-sized trees (Rogers, 1990). White oak exhibits annual variation in tree-ring widths, crossdates well, and has proven to be an important tree species for dendrochronological analysis in northeastern North America (Speer et al., 2009). White oak is classified as drought resistant (Rogers, 1990) and is able to persist in drought-affected sites through a suite of morphological and physiological adaptations (Abrams, 2003). Although increment cores for this study were collected in November 1996, we expect the estimates derived from them to be stable over time, given that the same or similar biophysical processes currently influencing white oak growth operated in the past (Guiot, 1991).

Laboratory methods

The increment cores were allowed to air dry and were glued into grooved boards. All samples were prepared for dating and ring-width measurement by sanding with increasingly finer grades of sandpaper (100–400 grit) using belt and random orbit sanders (Stokes and Smiley, 1968). A final hand sanding with 30 and 15 μm particle sanding films was also performed. Tentative dates were assigned to each annual growth ring, and crossdating was performed using both skeleton plots (Stokes and Smiley, 1968) and list method (Yamaguchi, 1991).

Annual increments were measured ($\pm$0.01 mm) with an Olympus SZ40 boom dissecting scope (40$\times$) and a VELMEX unislide measuring table (VELMEX Inc., Bloomfield, NY) connected to a microcomputer. The computer program MEDIR Version 1.13 from the International Tree-Ring Data Bank Program Library, version 2.1 was used during measuring (Krusic et al., 1997). To further ensure that the proper calendar dates were assigned to each tree ring, the program COFECHA was run on the dated and measured samples (Holmes, 1997). COFECHA employs a correlation procedure that enhances time-series characteristics to ensure accurate calendar year assignment to individual tree rings.

Once all dates and measurements were verified, the computer program ARSTAN (Cook and Holmes, 1997) was used to create composite standardized chronologies for trees from xeric, intermediate, and mesic IMI plots. We chose to pool the trees from the various forest sites into IMI composite chronologies so that we could observe the landscape-level response of white oak to available moisture. Standardization produces a dimensionless set of indices and removes undesirable growth trends in the series caused by age and stand dynamics or atypical growth trends particular to individual trees. In the closed-canopy forests of northeastern North America, detection of climatic signals is often difficult due to competition among trees for limiting resources such as light (Cook and Peters, 1981). Furthermore, Phipps (1982) states that growth trends may be more influenced by competition than by climate in northeastern North America. Dendroecological analysis of raw ring-width chronologies reveals episodic releases and suppressions in nearly all chronologies (Hutchinson et al., 2008); such growth trends may greatly hamper detection of a climatic signal (Cook and Peters, 1981). Therefore, detrending was performed via a cubic smoothing spline; we chose a spline with a 50% frequency response of 100 years. Standard dendrochronological statistics (signal:noise ratio, mean sensitivity, standard deviation, first-order autocorrelation, and correlation among trees and all radii) were calculated for the three composite IMI chronologies to compare growth and climatic sensitivity among the IMI classes.

Growth trend analysis

To understand the temporal pattern of growth across the IMI classes, we constructed basal area increment (BAI; the area of wood produced at breast height during 1 year) curves for the period 1966–1996. Radial increments spanning this period were converted to BAIs according to Visser (1995) using DBH for each tree. Further, we computed annual biomass increments (increments in above-ground biomass) by entering reconstructed DBH for successive years into species-specific allometric equation for white oak (Jenkins et al., 2004). The DBH values were reconstructed from radial increments and the DBH measured at the time of coring (Clark et al., 2001; Woolley et al., 2007; Kim et al., 2010). We chose to analyze this time period because we wanted to identify growth patterns in mature, regional mixed-oak forests (all stands were approximately 150 years old) and because this time period was free of silvicultural treatments in all study regions (Hutchinson et al., 2008). Analysis of variance (ANOVA) was performed on the composite BAI and biomass chronologies to determine if they differed significantly among the IMI classes. Post hoc analyses were done using the Bonferroni multiple comparisons test. All analyses were preceded by normality test using the D'Agostino normality test (Hintze, 1997).

Climate–growth analysis

The composite ring-width chronologies for each IMI category were used to determine if trees growing in dissimilar microsites react differently to similar macroclimatic conditions. In other words, will a consistent subset of climatic variables be important correlates to growth rate across the landscape? The indexed ring widths were calibrated against the climate variables, namely, total monthly precipitation, mean monthly temperature, and monthly Palmer drought severity index (PDSI; Palmer, 1965), using bootstrap correlation and response function analyses (Biondi and Waikul, 2004). In each of these procedures, 1000 bootstrapped samples generated from the original ring-width indices were used to more accurately test the significance of the regression coefficients and the stability of the error estimates (Guiot, 1991). These regression models were implemented using the R package *bootRes*. This package computes univariate Pearson correlation coefficients between the ring-width parameters and each of the climatic factors in correlation function analysis, while ordinary least square multivariate estimates are computed for the regression of the ring-width parameters against the principal components of the climatic variables in response function analysis (Zang and Biondi, 2012). The growing season for white oak in southern Ohio covers the period of growth from April through July (Sutherland, 1997). In line with this, climatic variables for January through July of the current year and April through December of the previous year were analyzed (i.e., from the beginning of the previous year growing season to the end of the current year growing season). Previous year climatic variables were analyzed because regional white oak growth rates are often correlated with past climatic events (e.g., droughts; Kozlowski et al., 1991; Rubino and McCarthy, 2000). The climatic data used in the above analyses were obtained for 1895–1996 from the CLIMVIS web page of the National Climatic Data Center and National Oceanic and Atmospheric Administration (2010), and their effects on radial growth were assessed at significance level of 1% ($P \leq 0.01$).

In addition to correlation and response functions, redundancy analysis (RDA) was performed to compare climatic impacts on growth variables across the IMI. RDA is a principal component extension of multiple regression analysis, which is commonly used in dendroecological studies to evaluate the strength and direction of climatic constraints on tree growth (Tardif and Conciatori, 2006). With RDA, the linear correlations among ring-width indices and the climate data were computed. The ordinations were calculated using a correlation matrix and scores were symmetrically scaled to enhance display of results in the ordination space. A Monte Carlo permutation test (999 permutations) was used to determine the most significant climatic factors in relation to white oak growth. RDA, and all other analyses were performed using the R programming language (R Development Core Team, 2012).

Table 1
General chronology statistics for composite white oak chronologies obtained from xeric, intermediate, and mesic microsites (as defined by the integrated moisture index) in southern Ohio.

	Xeric	Intermediate	Mesic
Number of trees	43	39	37
Number or radii	87	77	72
Series length (year)	148	147	145
Time span	1849–1996	1850–1996	1852–1996
Mean sensitivity	0.181	0.192	0.168
Standard deviation	0.165	0.203	0.200
Signal:noise	13.131	12.857	10.718
First-order autocorrelation	0.100	0.149	0.451
Correlation among all radii	0.274	0.264	0.266
Correlation between trees	0.267	0.258	0.257

Results

A total of 119 white oak trees (238 radii) were analyzed across the three IMI categories (Table 1). The three composite IMI chronologies were approximately equal in age and number of samples (Fig. 2, Table 1). Mean sensitivity and standard deviation were highest for the intermediate composite chronology. The signal:noise ratio and correlation among all radii and trees were highest for the xeric composite chronology. First order autocorrelation was highest for the mesic composite chronology (Table 1).

Growth and biomass increment trends

Growth trend analysis using the composite BAI and biomass chronologies revealed several differences among the IMI categories. BAIs were consistently higher in both mesic and intermediate sites than in xeric sites (Fig. 3). Mean BAI values

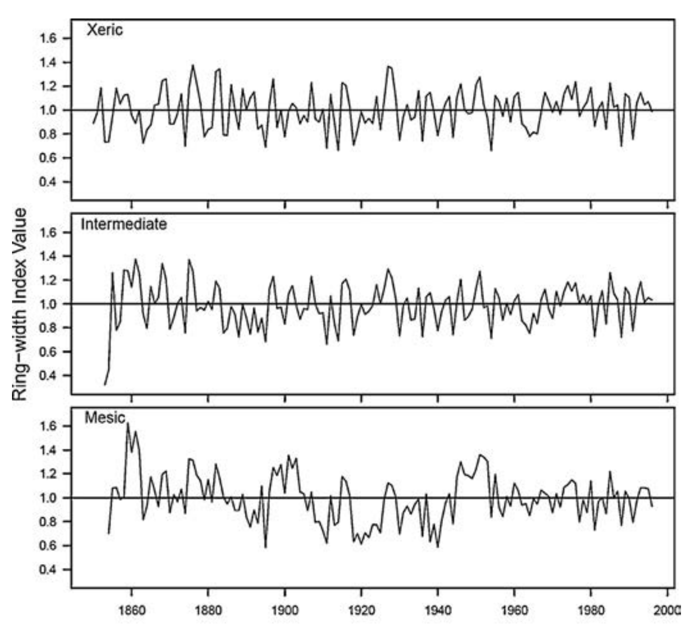

Fig. 2. Composite tree-ring index chronologies for white oaks growing in xeric, intermediate and, mesic microsites (according to the integrated moisture index).

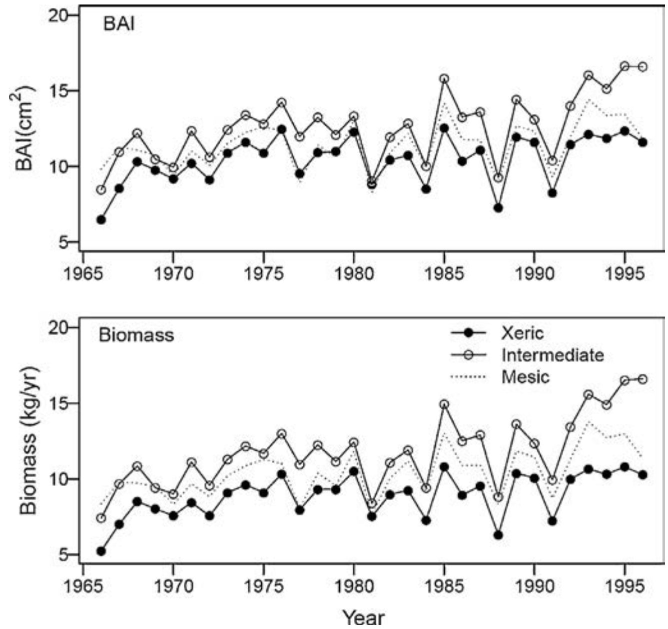

Fig. 3. Mean basal area increment and annual biomass increment chronologies of white oak across the three IMI classes for all sites.

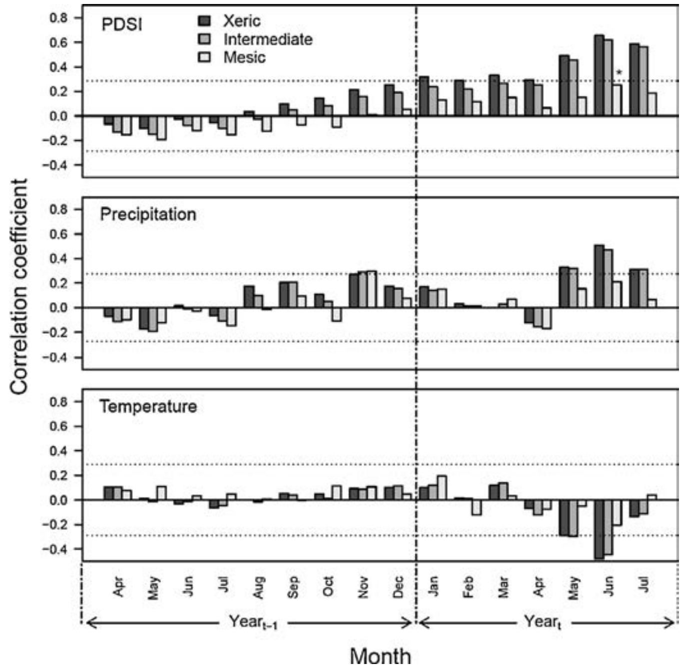

Fig. 4. Correlation function analysis of xeric, intermediate, and mesic tree-ring indices with current year, t, monthly (January–July) and previous year, $t-1$, monthly (April–December) Palmer drought severity index (PDSI), precipitation, and temperature from 1895 to 1996. Horizontal ashed lines or asterisk (*) = significant correlation coefficient (N = 101; α = 0.01).

for xeric, intermediate and mesic sites were 10.47 ± 0.28 (s.e.) $cm^2\ year^{-1}$, $12.6 \pm 0.39\ cm^2\ year^{-1}$ and $11.41 \pm 0.28\ cm^2\ year^{-1}$, respectively. Analysis of variance indicated significant differences among the three chronologies (F = 11.11, P < 0.001). Post hoc multiple comparison of BAI chronologies showed significant difference between intermediate and mesic sites (P < 0.05) and between intermediate and xeric (P < 0.001), but not between xeric and mesic (P > 0.05).

Similarly, biomass increment differed significantly (F = 19.108, P < 0.001) among the IMI classes, with the intermediate IMI category again showing the highest mean biomass production ($6.15 \pm 0.19\ kg\ year^{-1}$; Fig. 3). Mean biomass produced by white oak trees between 1966 and 1996 at the xeric, intermediate and mesic and sites were $8.89 \pm 0.26\ kg\ year^{-1}$, $11.76 \pm 0.42\ kg\ year^{-1}$ and $10.40 \pm 0.29\ kg\ year^{-1}$, respectively. The temporal trends of biomass and BAI were also quite similar across the IMI classes. However, in relation to moisture gradient, both BAI and biomass chronologies did not show as much temporal variability as the ring-width chronologies.

Climatic influence across the IMI classes

Correlation and response function analyses of the three composite IMI tree-ring index chronologies and climatic variables revealed several significant relationships between white oak growth rate and macroclimate. Both current (t) and previous ($t-1$) year climatic variables were significantly correlated with annual growth at α = 0.01 (Fig. 4). With the correlation function analysis, the xeric ring-width chronology was significantly correlated with 13 climatic parameters, while the intermediate and mesic chronologies were significantly correlated with 10 and one (1) climatic parameters, respectively. A total of 12, 8, and 4 significant relationships were observed between PDSI, precipitation, and temperature with yearly growth, respectively.

The xeric chronology was significantly positively correlated with PDSI from January through July of the current year, while the intermediate and mesic chronologies, respectively, were only significantly positively correlated with current year April–July and June PDSI (Fig. 4). None of the chronologies significantly correlated with previous year PDSI values. Radial growth in the xeric and intermediate trees showed significant positive correlation with previous year November and current year May–July precipitation. However, growth of mesic trees was only positively correlated with previous year November precipitation. Growth was negatively correlated with current year May and June temperature, but only in the xeric and intermediate trees. Besides the greater number of significant correlations, PDSI was also more strongly associated with the radial growth than the other climatic factors. Altogether, the correlation coefficients were highest for current year May to July climate variables.

The multivariate response function analysis also showed significant relationships between the ring-width indices and the climatic variables (Fig. 5). However, the number of significant correlates was slightly lower compared to those obtained with the univariate correlation function analysis. Each of the xeric and intermediate chronologies had nine (9) significant response coefficients, whereas the mesic chronology only correlated significantly with three (3) climatic variables. Total significant regression coefficients for PDSI, precipitation and temperature were 9, 10, and 2 respectively. Both xeric and intermediate chronologies were significantly positively correlated with previous year November, and current year May–July PDSI. On the other hand, the mesic chronology was negatively correlated with previous year July and positively correlated with current year March PDSI. All three ring-width chronologies were significantly related to previous year November (positive), current year April (negative) and May (positive) precipitation. However, only the xeric and intermediate chronologies were significantly positively correlated with current year precipitation. Also, only current year June temperature significantly correlated (negative) with tree growth, and this was observed for the xeric and intermediate chronologies.

Redundancy analysis (RDA) highlighted the key monthly climatic factors that influence radial growth of white oak trees in southern Ohio (Fig. 6). Similar to the correlation and response

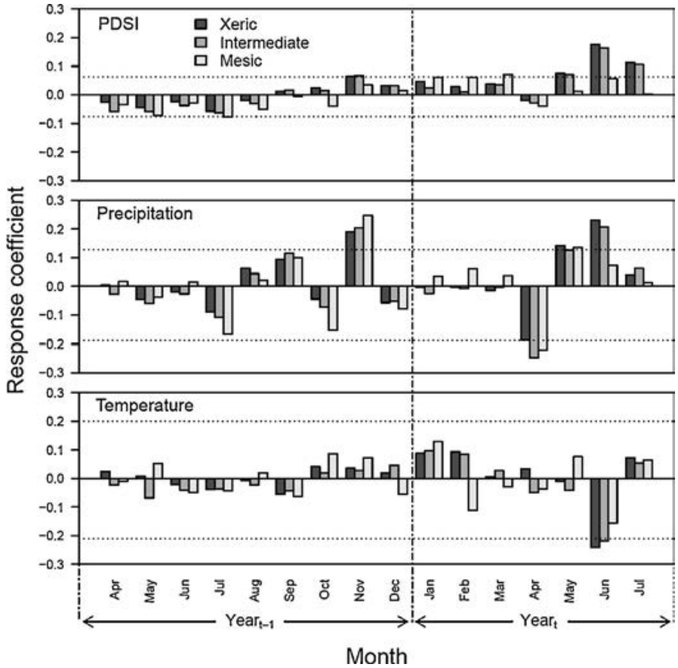

Fig. 5. Response function analysis of white oak ring-width chronologies with current year, *t*, monthly (January–July) and previous year, *t* − 1, monthly (April–December) Palmer drought severity index (PDSI), precipitation, and temperature from 1966 to 1996 compared for xeric, intermediate and mesic sites. Dashed lines = significant correlation coefficient (N = 101; α = 0.01).

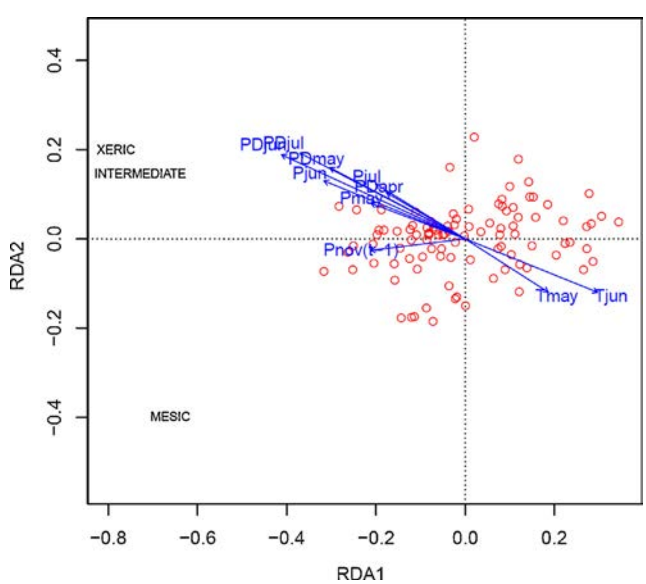

Fig. 6. Redundancy analysis (RDA) of white oak ring-width indices obtained for the period 1895–1996 from three integrated moisture index classes (xeric, intermediate, mesic) in southeastern Ohio. For clarity, only vectors (climatic factors) with highly significant ($P \leq 0.01$) correlations are drawn. PD = Palmer drought severity index, *T* = temperature, *P* = precipitation, (*t* − 1) = previous year. Circles indicate weighted sum of ring-width indices for the period 1895–1996.

function analyses, the RDA technique separated out the xeric and intermediate IMI categories from the mesic site. In RDA plots, arrows point in the direction of the gradients and their lengths indicate the strength of the variable. Thus, the most important positive correlates of white oak growth in the xeric and intermediate sites were current year PDSI for April, May, June and July PDSI. Current year May, June and July total monthly precipitation were also significantly correlated with the xeric and intermediate ring-width chronologies. Current year temperature for May and June also showed strong negative correlations with ring-width indices. In the mesic site, however, previous year November precipitation strongly correlated with radial growth. The RDA ordination axes accounted for 64.13% of the total variance in ring-width indices. Of this, 98.9% were constrained within the first two RDA axes.

Discussion

White oak growth rates and patterns varied substantially among the three IMI categories. These differences were evident in both overall growth trends and in response to macroclimatic conditions and further illustrated by the standard dendrochronological descriptive statistics. The greater signal:noise ratio and the higher correlations among radii for the xeric and intermediate chronologies compared to the mesic chronology were expected because xeric sites are generally thought to be the most moisture-limiting and therefore the most responsive to seasonal and yearly climatic variation (Fritts, 1976; Iverson et al., 1997). Also, the first-order autocorrelation was lowest in the xeric chronology and highest for the mesic chronology. This, too, was expected given that first-order autocorrelation is often higher on less growth-limiting sites (Fritts, 1976).

The higher stand deviation and mean sensitivity for the intermediate chronology (rather than the xeric chronology) may suggest that moisture availability may not have much influence on white oak grow rate. However, as stated by Jacobi and Tainter (1988), deviations from expected chronology statistics may result from different physiological responses to macroclimate across the landscape. For instance, if high water-stress conditions occur during the growing season, cambial activity may stop earlier on xeric sites and thus lead to unexpected growth/climate relationships if conditions improve later in the season. Charton and Harman (1973) also found that chronology statistics do not always provide the best measure of chronology sensitivity for white oak. Finally, the various chronology statistics from this investigation are quite comparable to those obtained from other regional white oak studies (Rubino and McCarthy, 2000).

Growth and biomass trends

Variations in the patterns of white oak growth and biomass increment among the IMI classes reflect the strong mechanistic link between soil moisture availability and oak species growth and agrees well with results obtained by Gaiser (1951) and Auchmoody and Smith (1979). In both of these studies, greater white oak growth potential was observed in sites characterized by increased levels of available soil moisture (e.g., lower slope positions, northeast facing slopes, deeper soil A horizon thickness). It should also be noted that growth curves represent a composite response to several factors affecting regional white oak growth including physiological changes associated with aging and climate (Hornbeck et al., 1988). Thus, the higher BAI and biomass of white oak in the intermediate sites compared to the mesic sites may be due to the effects of other environmental factors when soil moisture is not limiting.

The relatively less temporal variability of BAI and biomass chronologies across the IMI classes compared to the ring-width chronologies appears to reflect control of wood production by factors such as carbon allocation and remobilization besides climate (Mund et al., 2010). Lambers et al. (2008), for instance, argue that biomass production may not coincide with other growth parameters (e.g., stem area or diameter, height, volume, etc.) due to variations in wood density, tree architecture, and differential allocation of carbon. Nonetheless, the high degree of similarity in the pattern of BAI and biomass increment supports the view that BAI approximates wood production of trees well (Visser, 1995).

Climatic response across the IMI classes

The tree-ring chronologies prepared from this investigation exhibited climatic responses quite comparable to growth–climate patterns observed in other regional studies (e.g., Rubino and McCarthy, 2000; Speer et al., 2009). The high number of significant regression coefficients between ring-width indices and climate (particularly PDSI and precipitation) suggest that climate is an important factor when predicting growth rate in the mixed mesophytic forest regions of eastern North America (Braun, 1950). More interesting, however, is the influence of climate among the contrasting microsites encountered throughout the landscape (Tardif and Bergeron, 1997).

Differences in white oak growth across microsites are evident despite similar macroclimatic conditions. Not only were the individual climate correlates of annual growth different across the IMI, but also, the strength of relationships differed considerably. For example, correlation function analysis of the xeric chronology showed that current year monthly PDSI values (January–July) are significantly correlated with growth rate, whereas current year May–July PDSI correlated strongly with the intermediate chronology. However, only current year June PDSI correlated significantly with the mesic chronology. Moreover, the correlation and response coefficients were consistently greater for the correlation between the xeric chronology and PDSI than the intermediate chronology and PDSI.

The above trends indicate that a distinct IMI × climate interaction exists for white oak in southern Ohio. The trees in microsites associated with less available soil moisture appear to track climatic variability closer than trees growing in microsites with more available moisture.

Other dendrochronological analyses of trees growing in microsites with contrasting moisture availability have shown similar results. For example, dendrochronological analysis of northern white-cedar (*Thuja occidentalis* L.) and black ash (*Fraxinus nigra* Marsh.) growing on contrasting sites in Quebec responded differently to similar macroclimate (Tardif and Bergeron, 1997). Additionally, Orwig and Abrams (1997) noted differences in drought response in growth patterns of pignut hickory (*Carya glabra* (Mill.) Sweet), white oak, and Virginia pine (*Pinus virginiana* Mill.) growing across sites varying in soil moisture availability. Similar patterns were observed in Scotch pine (*Pinus sylvestris* L.) by Oberhuber and Kofler (2000) and in several tree species growing on xeric ridge and wet-mesic riparian sites by Abrams et al. (1998).

Further evidence of this climate–growth relation is provided by the RDA plot, which clearly reveals the most important monthly climatic parameters that influence white oak growth in southern Ohio. It is worth noting that RDA results are highly consistent with those from the correlation and response function analyses. These results also conform to those obtained from similar regional studies (LeBlanc and Terrell, 2001; Tardif and Conciatori, 2006; Speer et al., 2009). The above relationships were strongest in the xeric and intermediate IMI sites but almost non-existent in the mesic sites, again reflecting the ability of the IMI to effectively identify sites with distinct moisture status. Based on these correlations, we hypothesize that different resource levels (especially soil moisture) and different physiological stresses are encountered across the IMI classes and that these differences are responsible for the different growth rates in the IMI categories. The RDA was not successful at identifying distinct clusters for xeric and intermediate site trees, suggesting that the variation in growth patterns between these microsites may be minimal.

Using IMI as a predictor of white oak growth

Differences in growth rate, biomass increment, and climatic response were observed among the individual IMI categories. Temporal patterns of growth among IMI categories appeared to be distinct, despite overlaps between xeric and intermediate sites. Numerous factors may be responsible for the lack of strict fidelity between radial-growth patterns and IMI category. For example, competition may be an extremely important factor controlling white oak growth patterns, despite the strong influence of available moisture. Dendroecological analysis of ring widths revealed that large increases in radial-growth rate and productivity were often associated with release from competition (Hutchinson et al., 2008). In closed-canopy forests of this region, competition has been identified as a major determinant of woody biomass production (Phipps, 1982). However, the influence of moisture on response to release will vary based on site conditions. For example, Minckler (1957) found that growth rates of released white oak stems varied with available soil moisture. Secondly, growth trends may not exhibit strict fidelity among IMI classes due to life history characteristics of white oak. For instance, white oak is able to tolerate a wide range of physiological conditions by acclimating to environmental stresses and exhibits great phenotypic plasticity.

Overlap in growth patterns across the IMI may also be due to the assignment of IMI scores to individual plots. Assignment of IMI values may be at a resolution too coarse to accurately model fine-scale interactions between vegetation and microsite variability due to the coarse resolution of certain parameters used to create the IMI (Iverson et al., 1997; Hutchinson et al., 1999; Iverson and Prasad, 2003). Gaiser (1951) found that very slight differences in site quality have a large impact on site productivity. Hence, extremely fine-scale changes in topography or soil that are below the resolution of the input data may lead to inaccurate IMI classification.

The IMI has proven to be an effective tool for modeling numerous ecological patterns and processes at the landscape-level (Iverson et al., 1997; Hutchinson et al., 1999; Iverson and Prasad, 2003). One very important benefit that approaches such as the IMI offer is the ability to stratify the landscape and allow investigators to choose to focus efforts on particular strata according to their study objectives and experimental design. This is an improvement over less objective sampling approaches and consequently aids in the development of management plans and in making management decisions. In this investigation, the IMI was successful in helping to elucidate white oak radial-growth patterns in a topographically complex region. We conclude that variability in growth trends, biomass, and climatic response suggests that only two IMI categories are necessary with regards to white oak productivity: mesic and xeric-intermediate.

Due to the influence of recent and predicted anthropogenic activities (e.g., air pollution) on regional forest growth trends (Jacobi and Tainter, 1988; Hutchinson et al., 2003), understanding how microsite variability affects ecological processes may be exceedingly important. The IMI provides a utilitarian approach for assessing white oak growth patterns and climatic responses across the landscape and may prove to be an effective tool for monitoring and managing white oak productivity where topographic and edaphic gradients cause marked microsite variability.

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