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ORIGINAL ARTICLE

## The influence of winter temperatures on the annual radial growth of six northern range margin tree species

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### Abstract

This study explores the influence of temperature on the growth of six northern range margin (NRM) tree species in the Hudson River Valley (HRV). The HRV has excellent geographic and floristic qualities to study the influence of climate change on forested ecosystems. Indices of radial growth for three populations per species are developed and correlated against average minimum and maximum monthly temperatures from 1897 to 1994. Only positive correlations to temperature are considered for this analysis. Principal component analysis (PCA) is performed on chronologies over the entire HRV and at four subregions. PCA reveals a strong common signal among populations at subregional and regional scales. January temperatures most limit growth at the ecosystem level, supporting the hypothesis that winter temperatures may control vegetational ecotones. Surprisingly, growth of the oak–hickory ecosystem is most limited by January temperatures only in the southern half of the study region. Chestnut and white oak are the primary species driving the geographic pattern. As winter xylem embolism is a constant factor for ring-porous species, snow cover and its interaction on fine root mortality may be the leading factors of the pattern of temperature sensitivity. Species-specific differences in temperature sensitivity are apparent. Atlantic white-cedar (AWC) and pitch pine are more sensitive to the entire winter season (December–March) while oak and hickory are most sensitive to January temperatures. AWC is most sensitive species to temperature. Chestnut and white oak in the HRV are more sensitive to winter temperature than red oak. Pignut hickory has the most unique response with significant relations to late growing season temperatures. Interestingly, AWC and pitch pine are sensitive to winter temperatures at their NRM while oak and hickory are not. Our results suggest that temperature limitations of growth may be species and phylogenetically specific. They also indicate that the influence of temperature on radial growth at species and ecosystem levels may operate differently at varying geographic scales. If these results apply broadly to other temperate regions, winter temperatures may play an important role in the terrestrial carbon cycle.

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**Keywords:** Temperature sensitivity; Temperate forests; Geographic temperature response; White oak subgenus; Eastern North America; Oak–hickory ecosystem

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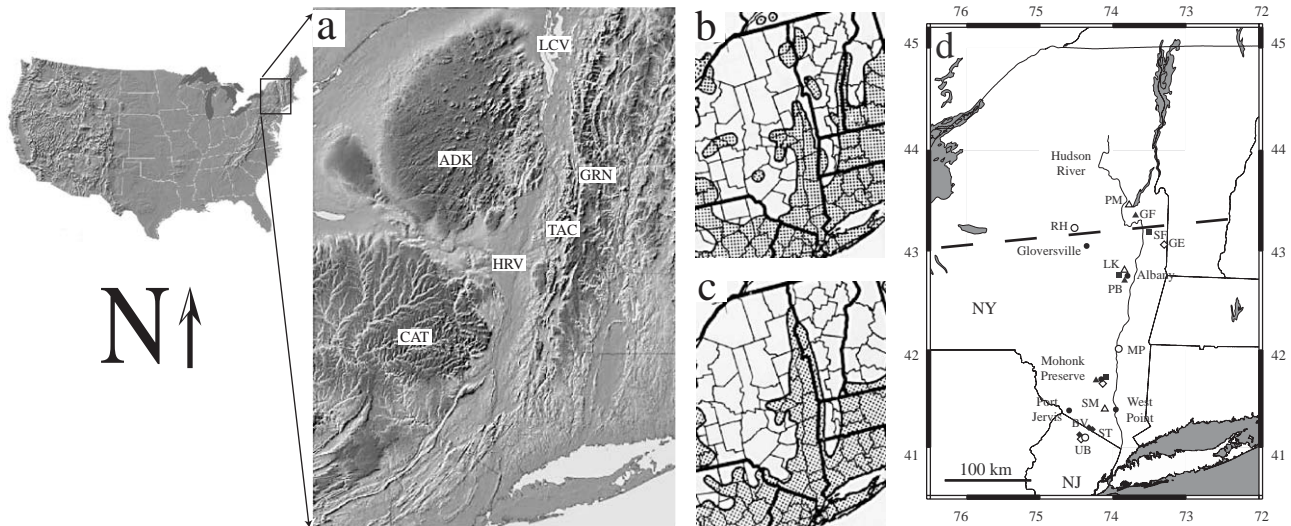
## Introduction

It has been forecast that rapid warming over the next 100 years will substantially alter forested ecosystems (Solomon, 1986; Overpeck et al., 1991; Iverson and Prasad, 1998; Bachelet et al., 2001; IPCC, 2001). However, the impact of such warming on ecosystems is uncertain because existing information describing the influence of temperature on growth for most tree species is lacking (Loehle and LeBlanc, 1996). While temperature has been shown to be an important factor of tree growth and forest ecosystem dynamics at treeline (e.g. Jacoby and D'Arrigo, 1989; Villalba, 1994; Briffa et al., 2001; Buckley et al., 1997; Kullman, 2001), it is not as well understood in temperate forests. Because northern range margins (NRM) represent a “species treeline,” NRM are optimum locations to determine if temperature limits tree growth in temperate regions. Temperate regions possess some of the largest global aboveground terrestrial carbon pools (Myneni et al., 2001) while also directly providing society with goods and services. Therefore, it is critical to understand the influence of climate change on tree growth in temperate regions.

Radial growth studies of NRM populations indicate that temperature may influence individual species differently. For example, in the southeastern US loblolly pine (*Pinus taeda* L.) growth is positively correlated to

winter temperatures only at its NRM locations (Cook et al., 1998). However, eastern hemlock (*Tsuga canadensis* L.) is positively correlated to March temperatures throughout its range in eastern North America (Cook and Cole, 1991). Two mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) populations at high elevation in Alaska are most strongly and positively correlated to March–July temperatures (Wiles et al., 1998). In contrast, a nearby mountain hemlock population at lower elevation has the strongest positive correlation to January–March temperatures (Frank, 1998). An American beech (*Fagus grandifolia* Ehrh.) population near its NRM in eastern Canada is positively correlated to April temperatures (Tardif et al., 2001). These studies show that each species may have a specific temperature response, and therefore, a full understanding of potential changes in forested ecosystems as a result of climatic warming may require the study of many tree species.

We chose six species to investigate the influence of temperature on the radial growth of NRM species in the Hudson River Valley (HRV) (Fig. 1): Atlantic white-cedar (AWC) (*Chamaecyparis thyoides* (L.) B.S.P.), pitch pine (*Pinus rigida* Mill.), chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), and pignut hickory (*Carya glabra* Mill.). In general, these species represent the range of distributions for the 30+ NRM species in the HRV (Little, 1971). For



**Fig. 1.** (a) Topographic map centered on eastern New York State and the Hudson Valley. The darker shades represent mountainous areas and are identified by abbreviations: ADK = Adirondack Mountains; GRN = Green Mountains; TAC = Taconic Mountains; CAT = Catskill Mountains. The two main valleys are designated by: HRV = Hudson River Valley and LCV = Lake Champlain Valley. Distribution maps of (b) pitch pine and (c) chestnut oak. (d) Map of population sites and meteorological stations. Tree species are represented by symbols: (◆) AWC, (▲) pitch pine, (◇) chestnut oak, (△) white oak, (○) red oak, and (■) pignut hickory. Site locations are represented by abbreviations. These populations are (north–south): PM = Prospect Mountain, GF = Glen Lake Fen, RH = Rooster Hill, GE = Goose Egg Ridge, SF = Stott Farm, LK = Lisha Kill, PB = Albany Pine Bush, MP = Montgomery Place, SM = Schunemunk Mountain, BV = Bellvale Mountain, ST = Sterling Forest, and UB = Utertowntown Bog. Meteorological stations are in bold italic and represented by (●). The (---) represents the average position of the convergence of winter Arctic and Pacific Frontal Zones (adapted from Bryson et al., 1970). (a) Adapted from Ray Steiner's Colorlandform Atlas of the United States: <http://fermi.jhuapl.edu/states/states.html>. (b,c) Adapted from Little (1971).

example, AWC distribution is limited to the southern HRV. Distributions of pitch pine, chestnut oak and pignut hickory are primarily confined to the HRV with outlier populations extending into the Lake Champlain Valley (Figs. 1b and c). Northern red and white oak is distributed northward through the Champlain Valley and into the St. Lawrence River valley. However, both species have range margins along the edges of the Adirondack and Green Mountains.

Geographic, climatic and floristic qualities of the HRV and surrounding mountains make it an excellent region to study climate change and forested ecosystems. Despite varying objectives and methods, different geographic studies of vegetation consistently show a distinct boundary at the northern end of the HRV (Bray, 1915; Braun, 1950; Eyre, 1980; Bailey, 1995; Lugo et al., 1999). Two recent reconstructions of northeastern US vegetation patterns using different methods indicate that this ecotone has been present since European settlement (Russell and Davis, 2001; Cogbill et al., 2002). Further, similarity between the spatial distribution of tree species (Little, 1971) and temperature (Fig. 2 in Gajewski, 1988) suggests the regional ecotone may be related to a temperature gradient. Regional ecotones are prime areas of study for understanding the influence of climate change on forested ecosystems (Solomon, 1986; Neilson, 1993; Risser, 1995; Loehle, 2000; Peteet, 2000).

The purpose of this study is to explore the limitation of temperature on radial growth of NRM tree populations in the HRV. We are focusing on temperature because it may be the best-forecast variable of future climate change (IPCC, 2001) and yet may be the least understood factor of tree growth. Water stress is a well-established and well-understood factor in tree growth and forested ecosystems (e.g. Douglass, 1920; Schumacher and Day, 1939; Fritts, 1965; Cook and Jacoby, 1977; Currie and Paquin, 1987; Cook, 1991; Stahle and Cleaveland, 1992; Graumlich, 1993; Orwig and Abrams, 1997; Pedersen, 1998; Stephenson, 1998; Allen and Breshears, 1998; LeBlanc and Terrell, 2001; Cook et al., 1999, 2001). Specifically, we address the following questions: “Does temperature limit the annual radial growth of NRM species?” and “Do winter temperatures limit growth more than growing season temperatures?”

We will focus only on a positive relationship between temperature and growth because a negative correlation to temperature is often related to water stress (Fritts, 1976; Kramer and Kozlowski, 1979). We will compare species to discern if there is a species-specific temperature response. Principal component analysis (PCA) will offer insights into an ecosystem-level temperature response. While the study species do not represent a specific ecosystem, they represent the northern range limit of a southern temperate forest at the regional scale. Previous studies have shown that the temperature

response of different species have distinct geographic patterns (Cook and Cole, 1991; Cook et al., 1998; Hofgaard et al., 1999; Gedalof and Smith, 2001; Peterson and Peterson, 2001). Therefore, we will examine temperature responses at the species and ecosystem levels to determine if a geographic pattern exists in the HRV.

## Methods

### Region of study

The region of study under investigation is centered on the HRV, extending from northern New Jersey to the southern Adirondack Mountains, northwestern Taconic Mountains and southern Champlain Valley. The Catskill Mountains bound the HRV on the west while the Taconic Mountains bound it on the east. The valley is a half-graben formed during the rifting of the North American and African continents prior to formation of the Atlantic Ocean roughly 220 million years ago. The HRV is a classic fjord because its southern end is below sea level. It also represents a northern extension of the Valley and Ridge Provenance (Brouillet and Whetstone, 1993). The valley's structure and connection to the ocean allows northward penetration of warm, maritime air creating a nearly uniform climate. However, a temperature gradient is produced by the juxtaposition of the low lying, broad valley and mountain formations to the north. Also, the average winter convergence of the winter Arctic and Pacific Frontal Zones coincides with the northern end of the HRV (Bryson et al., 1970). Together, geography and circulation patterns help to create the boundary between a permanently humid climate with warm summers to the south and a cool temperate, subcontinental climate to the north (Brouillet and Whetstone, 1993).

HRV flora and fauna distributions may be related to its geographic and climatic patterns. Many southern tree and herpetological species distributions generally conform to the low-lying portion of the HRV (Little, 1971; Stewart and Rossi, 1981; Smith et al., 2001). Convergence of biotic and abiotic factors has likely made it rich in ecosystem and biological diversity (Lynn and Karlin, 1985; Currie and Paquin, 1987; Thorne, 1993; Smith et al., 2001). The HRV was hypothesized to be a corridor for tree migration into the Adirondack Mountains (Whitehead and Jackson, 1990). This can be inferred by the presence of higher percentages of pollen of southern species further north in the HRV region than surrounding regions throughout the Holocene (Gaudreau and Webb, 1985; Gaudreau, 1986). Should significant future warming occur, high HRV diversity may make it a primary source of species migration to the Adirondack, Catskill, Taconic and Green Mountains.

The number of days when the air temperature is above freezing ranges from 120 to 140 days in the north to 160–180 days in the south in our study region (McNab and Avers, 1994). This is reflected in the first-leaf phenology of lilac (*Syringa chinensis* Willd.). First leaf for lilac is nearly 20 days later in the Adirondack Mountains than in northern New Jersey (Eastern North American Phenology Network, 2003). Total annual precipitation ranges from 865 mm in the north to 1350 mm in the south (NOAA, 1994).

### Site selection and descriptions

Three populations per species were sampled throughout the HRV (Fig. 1; Table 1). Sites were selected to at least cover the northern-half of the region, except for AWC. Forests were chosen on the potential for individual trees to be at least 80–120 years old. Secondary considerations of forest selection were trees growing on relatively productive sites with little stand-scale disturbance. No forest met all site preferences. Land-use patterns in the HRV often result in older trees being left on shallower, less productive soils (Glitzenstein et al., 1990). Loss of the American chestnut (*Castanea dentata* L.) in the early 20th century and the current decline of eastern hemlock severely impacted several sites.

The presence of boreal and southern temperate species in a few stands exemplifies the unusual floristics of the region (Table 1). For example, Sterling Forest AWC grows with spruce (*Picea* spp.). Black spruce (*P. mariana* (Mill.) B.S.P.) and eastern larch (*Larix laricina* (Du Roi) K. Koch) grow alongside AWC at Uttertown Bog (Lynn and Karlin, 1985). Northern red oak on Rooster Hill grows with two boreal species, red spruce (*P. rubens* Sarg.) and paper birch (*Betula papyrifera* Marsh.). Nearly one-half of the basal area on the upper, northern slope was red spruce (N. Pederson unpublished data). The canopy of Mohonk Preserve pignut hickory stand is exceptionally diverse considering its northerly latitude. Species composition is evenly distributed among 11 species making it like a mixed-mesophytic forest. However, it is best placed in the Appalachian Oak category since it lacks *Aesculus* spp. (Kuchler, 1964).

### Field methods

Healthy appearing, dominant and co-dominant trees were selected for coring to minimize the influence of competition and disturbance on growth. Cores were extracted using a 5.15-mm diameter increment borer. Data presented here are a part of a larger-scale study in which tradeoffs were made between spatial and sample replication where spatial stand replication was consid-

ered more valuable than sample replication. Target replication was 16–20 trees per species. A second core was taken from at least one-third of cored trees. Sampling additional trees reduces the standard error of the final chronology more efficiently than increasing the number of cores per tree (Fritts, 1976). The first core was removed perpendicular to the lean of each tree. The second core was taken between 90° and 180° from the first. Areas on the stem with defects, burls or potential for rot were avoided. More trees and cores were sampled in old forests to increase chronology length and bolster early chronology replication. Only single cores from 20 AWC trees were collected at Uttertown Bog as this collection was a part of a AWC study ranging from northwestern NJ to southern Maine where sample replication was sacrificed to increase spatial coverage and yet reduce laboratory time (Hopton and Pederson, in press). Despite collecting only a single core from 10 trees per species per site in east Texas, a robust climate response was identified among 12 species (Cook et al., 2001). Though smaller than normal, previous experience suggests that our replication should be adequate.

### Tree-ring analysis

Core samples were prepared and analyzed using standard dendrochronological techniques (Stokes and Smiley, 1968; Fritts, 1976; Cook and Kairiukstis, 1990). Cores were visually crossdated by matching the pattern of narrow and wide rings between all samples in each population (Douglass, 1920; Stokes and Smiley, 1968). Annual rings were measured to at least  $\pm 0.002$  mm. Crossdating was then statistically verified using the program COFECHA (Holmes, 1983). Using these dating methods, annual time series of radial growth were created with dating errors of  $\pm$  zero years. Cores that correlated poorly in COFECHA were removed from the population prior to chronology development. These cores had low year-to-year variability in growth or unusual growth trends compared to the sampled population.

Raw ring-width measurements were processed into tree-ring chronology form using the ARSTAN method (Cook, 1985; Cook and Kairiukstis, 1990). Before standardization could begin, short periods of distorted radial growth in a few cores were modeled and replaced. Distorted radial growth often occurred after a stem injury or as a branch scar heals. It was visually identified as reaction wood. Ring widths for these periods were filled using dummy variables. A new procedure in ARSTAN recognizes the dummy variables and interpolates low-frequency growth using a 20-year spline. Next, a high-pass filter calculates high-frequency information from the mean chronology. Low-frequency data from the 20-year spline is multiplied by the

**Table 1.** Location, elevation, forest type and general disturbance history of populations sampled

Site name	Location	Elevation	Forest type <sup>a</sup>	Forest history
		m MSL		
<i>Atlantic White-Cedar</i>				
Bellvale Mountain	N 41 12.19 W 74 19.72	370	AWC—hardwood <sup>b</sup>	Likely logged—next to an old road
Sterling Forest	N 41 11.16 W 74 16.8	310	AWC—conifer <sup>c</sup>	Logged—corduroy skid roads throughout the swamp
Uttertown Bog	N 41 06.92 W 74 25.20	340	AWC—conifer <sup>c</sup>	No field evidence of logging
<i>Pitch Pine</i>				
Glen Lake Fen	N 43 21.26 W 73 41.41	120	Pitch pine <sup>d</sup>	No field evidence of recent disturbance
Albany Pine Bush	N 42 42.09 W 73 50.34	85	Northeastern pine–oak	Presence of cut stumps and evidence of fire suppression
Mohonk Preserve	N 41 46.72 W 74 08.12	365	Pitch Pine Rock Outcrop <sup>e</sup>	Uncut forest
<i>Chestnut Oak</i>				
Goose Egg Ridge	N 43 03.76 W 73 17.89	500	Appalachian Oak	Primarily uncut forest—one stand selectively cut in the 20th century
Mohonk Preserve	N 41 46.72 W 74 08.12	305	Appalachian Oak and Northern Hardwoods	Likely used as a pasture and wood lot in the 19th century
Uttertown	N 41 06.94 W 74 25.00	340	Appalachian Oak and Northern Hardwoods	Primarily uncut forest—northern portion likely cut in the mid-19th century
<i>White Oak</i>				
Prospect Mountain	N 43 25.30 W 73 34.20	360	Appalachian Oak (northern type)	Tourism (hotel and trolley), burned, cut and likely grazed <sup>f</sup>
Lisha Kill Preserve	N 42 47.49 W 73 51.51	85	Oak—mixed hardwood <sup>f</sup>	Likely grazed and logged—barbed wire and old road present
Schunnnemunk Mountain	N 41.23.69 W 74.6.67	350	Oak—mixed hardwood <sup>f</sup>	Uncut forest
<i>Northern Red Oak</i>				
Rooster Hill	N 43 13.82 W 74 31.55	560	Appalachian Oak and Northern Hardwoods	Base of hill logged; no evidence of logging on northern slope
Montgomery Place	N 42 00.68 W 73 55.24	20	Appalachian Oak (northern type)	Likely an old wood lot—cores show evidence rapid growth in 19th and early 20th centuries
Uttertown	N 41 07.02 W 74 25.02	340	Appalachian Oak and Northern Hardwoods	Sampled north of the chestnut oak—likely cut in the mid-19th century
<i>Pignut Hickory</i>				
Stott Farm	N 43 11.28 W 73 29.93	170	Northern Hardwoods and Appalachian Oak	Family wood lot since the early 20th century—logged at least 3 times
Lisha Kill Preserve	N 42 47.70 W 73 51.60	85	Appalachian Oak (northern type)	Likely grazed and logged—barbed wire and old road present
Mohonk Preserve	N 41 46.72 W 74 08.12	180	Appalachian oak	Cut stumps present in the northern end—no such evidence to the south

<sup>a</sup>Forest types based on Kuchler (1964) except where noted.<sup>b</sup>Common hardwoods were red maple (*Acer rubrum* L.) and black tupelo (*Nyssa sylvatica* Marsh).<sup>c</sup>Common conifers were eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), or spruce (*Picea* spp.).<sup>d</sup>Primarily pitch pine mixed with eastern white pine.<sup>e</sup>Pitch pine with black tupelo and chestnut oak (Abrams and Orwig, 1995).<sup>f</sup>Steve Warne, NYS Forest Manager (personal communication) and (E. Mashig, N. Pederson unpublished data).

high-pass filter data to estimate ring width in place of the distorted growth. This method creates realistic estimates of growth and annual variability for missing or cut data (Fig. 2a). After distorted radial growth was modeled and variance was stabilized using an adaptive power transformation of the raw data (Cook et al., 1992; Cook and Peters, 1997), standardization could proceed.

The goal of standardization was to remove geometric and ecological growth trends while preserving variations that are likely related to climate. Ecological growth trends as defined here result from tree-to-tree competition and stand dynamics that cause short-lived, step-change increases in growth (Lorimer, 1985; Lorimer and Frelich, 1989). Removing ecological growth trends in closed canopied forests is difficult to achieve as disturbance and competition strongly influences growth (Fig. 2b). Our standardization goal was achieved by double detrending each radial growth series. Geometric growth trends were first removed from all series using fitted negative exponential or linear growth curves (Fig. 2c). Second detrending of time series with step-change increases in growth was achieved using flexible cubic smoothing splines (Cook and Peters, 1981) (Figs. 2b) or, occasionally, Hugershoff-form curve (Briffa et al., 2001). The Hugershoff-form curve effectively reduces the influence of short periods of suppressed growth at the beginning of time series while simultaneously preserving long-term trends. Some series had no increase in growth typical of canopy disturbance after the first detrending (Fig. 2d). Growth trends like Fig. 2d are present in several populations region wide. The lack of obvious disturbance in the ring patterns and presence of long-term trends in forests with different histories (Table 1) suggests that these trends may be exogenous and not related to stand dynamics. Therefore, there was no compelling reason to remove these trends. Accordingly, a horizontal line of the arithmetic mean fit was used for the second detrending of these series.

After detrending, individual time series are averaged using a biweight robust mean function to create the mean value function of year-to-year growth for each population (Cook, 1985). Autoregression modeling was used to remove much of the autoregressive properties in the detrended series to create the residual chronology. The residual chronology type contains the least amount of disturbance-related growth, has one of the cleanest expressions of climate, and lacks autocorrelation that can make statistical hypothesis testing difficult (Cook, 1985).

Chronology quality was estimated using  $r_{bar}$  (Briffa, 1995) and expressed population signal statistics (Wigley et al., 1984). EPS and  $r_{bar}$  are the primary tools in evaluating tree-ring chronology quality (Cook and Kairiukstis, 1990).  $R_{bar}$  is the mean correlation of all growth series within a population.  $R_{bar}$  is independent

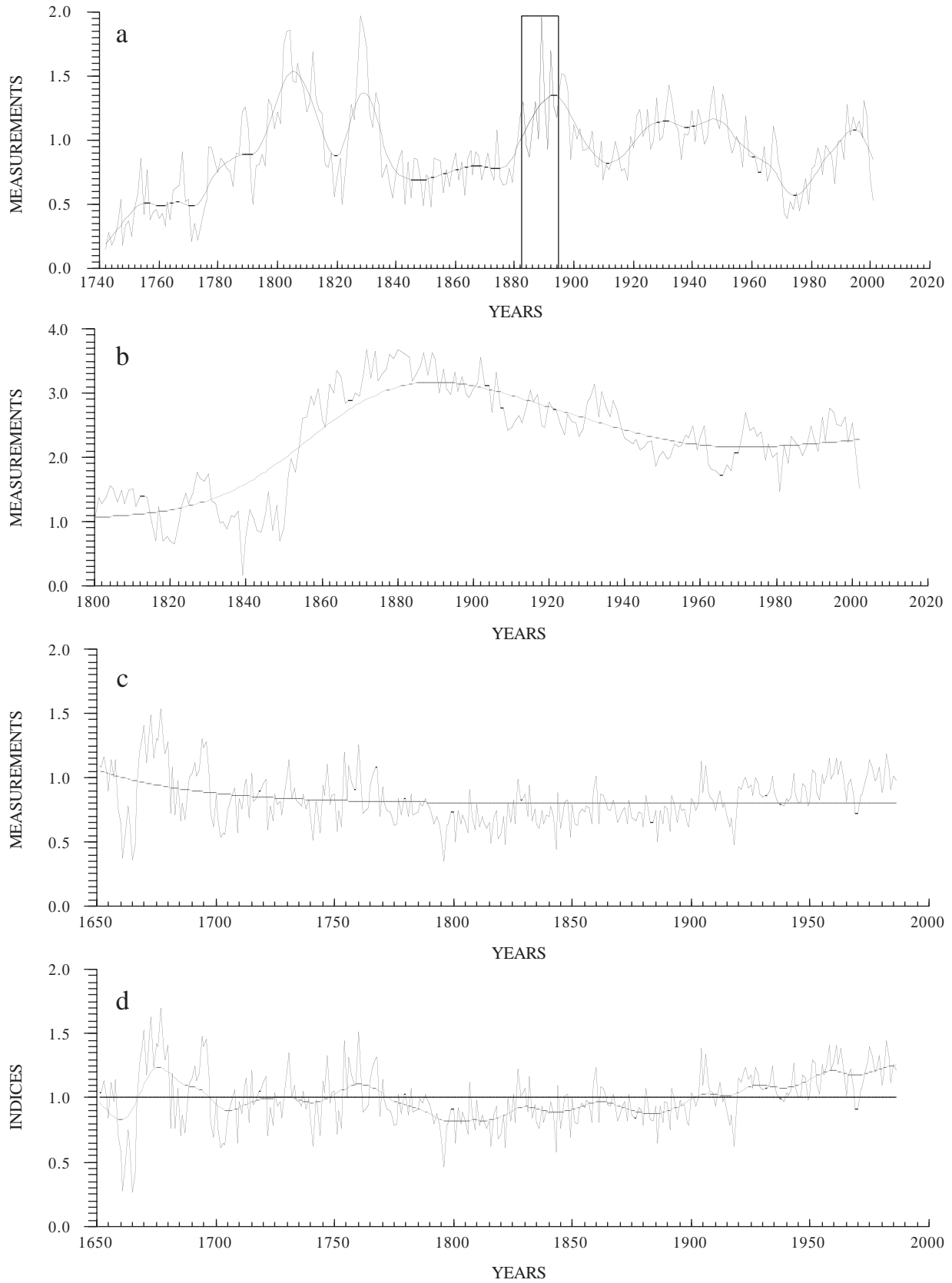
of sample size and unbiased, though caution is needed when interpreting  $r_{bar}$  at very low sample sizes. EPS is a function of  $r_{bar}$  and sample size and describes how well a finite sample size estimates the infinite, hypothetical population.

## Climate data

The US Historical Climatology Network data set (Easterling et al., 1996) was used to study long-term temperature sensitivity. It is one of the longest, high-quality meteorological data available. While growth does not occur at a monthly time step, only monthly climate data offers a dense network of meteorological data before 1930. The following stations in New York State were used: Albany, Gloversville, Mohonk Preserve, Port Jervis and West Point (Fig. 1b). The common period for the meteorological data was from 1896 to 1994. One year of data was lost due to the 20-month climate window. Therefore, temperature analysis was performed over a 98-year period from 1897 to 1994. All meteorological station data were combined using a mean and variance corrected arithmetic average to create a minimum and maximum monthly time series for the entire HRV.

## Temperature response analysis

The temperature response of each population was determined by correlating the residual chronology against a 20-month climate window from prior March to October of the current growth year. Climate during the prior growing season and intervening season can influence a tree's current growth (Fritts, 1976; Kramer and Kozlowski, 1979; Cook and Kairiukstis, 1990). Several physiological factors are responsible for the lag between a prior year's climate and growth. First, pine, oak, and hickory species exhibit determinate growth. Species with determinate growth typically flush once a growing season. Similar to this physiology, some species have preformed shoots in which the number of leaves and amount of growth for the first flush is set during bud formation of the prior year (Kramer and Kozlowski, 1979). For example, shoot elongation in some oaks may occur in less than a month early in the growing season and is a function of the fixed growth in their preformed winter buds (Kozlowski, 1964). Therefore, a good proportion of growth in these species is related to conditions prior to a current year's. Second, non-structural carbon, an important component of bud construction and early leaf development, has a residence time up to 3–5 years in oak (Trumbore et al., 2002). Finally, the season of root growth is longer than shoot growth in some species (Kramer and Kozlowski, 1979). Considering growing season length in the HRV, tree



**Fig. 2.** Examples of: (a) filling of a gap in a series of raw ring width data. The modeled data is the gray line within the boxed area; (b) typical radial growth response to a reduction in competition. The increase in growth following disturbance is detrended using a cubic smoothing spline (Cook and Peters, 1981); (c) detrending of raw ring width data with a fitted negative exponential growth curve; and (d) the resulting indices following detrending of the time series in (c). See text for more details.

phenology, the importance of stored non-structural carbon on growth and its mean residence time, a 20-month climatic window is biologically meaningful. The residual chronology was correlated against prewhitened climate data since time series of temperature data can also have significant autocorrelation.

Each chronology was correlated against the nearest meteorological station. Because there are no long, local meteorological stations in the northern HRV, Gloversville was used in this subregion. Gloversville's relatively high elevation vs. Albany (247 m vs. 84 m MSL, respectively) and location in the Adirondack Mountains foothills better matches the settings of most northern HRV populations. Albany was used for analysis of the north-central HRV populations. The Mohonk Preserve meteorological station was used for analysis of mid-HRV populations. Most sites in the southern end of the transect are on the western side of the Hudson Highlands. Preliminary analysis indicated that Port Jervis station data produced more consistent results vs. most southern populations than the West Point station. The Schunemunk Mountain white oak population, on the eastern side of the Hudson Highlands, was correlated to West Point data.

A one-tailed test was used for correlation analysis since only positive relations between temperature and growth are considered. Temperature was considered a significant factor of growth at the  $p \leq 0.05$  level. During preliminary analysis, it was observed that winter months were an important factor of growth. Correlation analysis was then performed on a common winter season for each species.

### Principal component analysis

A rotated PCA was performed on the residual chronologies to objectively identify common modes of variation through time among species to create a time series of principal component scores. Varimax rotation is the orthogonal rotation of axes of a subset of unrotated principal components. The normalized varimax method of rotating eigenvectors preserves orthogonality of the factor loadings and increases interpretability (Richman, 1986). It eases interpretation because original variables often load onto one or, at most, a few factors and each factor typically is represented by a small number of variables. We use the term "rotated factors" to distinguish the varimax rotation of eigenvectors from the unrotated principal components. The number of eigenvectors retained was determined by the Monte Carlo "Rule- $N$ " method (Preisendorfer et al., 1981). The period of analysis was 1897–1994. PCA enabled us to investigate the temperature sensitivity of the southern temperate ecosystem at regional and subregional scales. Preliminary PCA runs

indicated a specific oak–hickory grouping. Consequently, a separate PCA was performed on the oak and hickory populations at both the geographic scales.

The subregions analyzed were the: (1) northern HRV—composed of Prospect Mountain white oak, Rooster Hill red oak, Glen Lake Fen pitch pine, Goose Egg Ridge chestnut oak and Stott Farm pignut hickory; (2) north-central HRV—composed of Lisha Kill Preserve white oak and pignut hickory and the Albany Pine Bush pitch pine; (3) mid-HRV—composed of Montgomery Place red oak and Mohonk Preserve chestnut oak, pignut hickory and pitch pine; and (4) southern HRV—composed of Schunemunk Mountain white oak, Sterling Forest AWC, and Utertown chestnut and red oak. Only the Sterling Forest AWC population was used for the southern HRV subregion so the southern HRV PCA was not biased towards AWC. Sterling Forest was chosen a priori because of its central location among the AWC populations.

The retained principal component scores for the HRV were correlated against the averaged five station temperature series. Each subregion's scores were correlated against the local meteorological station: Gloversville vs. northern HRV; Albany vs. north-central HRV; Mohonk Preserve vs. mid-HRV; Port Jervis vs. southern HRV. Correlation analysis was performed in the same manner as with the tree-ring records.

## Results

### Tree-ring chronology characteristics

All chronologies met the minimum age requirement of the study and had an average  $EPS > 0.85$  despite frequent forest disturbance and conservative detrending methods (Table 2). Chestnut oak had the highest average EPS across populations while pignut hickory had the lowest. Rbar values indicated a fairly strong overall chronology signal for each population. Pitch pine had the highest average rbar across populations while pignut hickory had the lowest. Chronology statistics indicate a strong common signal in uneven-aged populations.

### Principal component analysis

PCA indicated a significant amount of common growth variation across all populations in the HRV (Table 3). Only two rotated factors were retained. Rotated factor one (RF1) accounted for 27.3% of the common growth variation while rotated factor two (RF2) accounted for 19.9%. Loadings onto RF1 were dominated by oak, primarily by chestnut and white oak, while loadings onto RF2 were dominated by AWC.



**Table 2.** Final chronology sample depth, interval, age structure and signal strength statistics for each population

Site name	No. of trees (# of cores)	Chronology interval	Median minimum age (min./max.) <sup>a</sup>	Average EPS <sup>b</sup>	Average rbar <sup>c</sup>	AR model <sup>d</sup>
<i>Atlantic White-Cedar</i>						
Bellvale Mountain	20 (31)	1843–2001	125 (72/161)	0.926	0.334	3
Sterling Forest	21 (36)	1818–2001	119 (91/184)	0.959	0.433	2
Uttertown Bog	20 (20)	1764–2002	125 (104/238)	0.877	0.319	4
<i>Pitch Pine</i>						
Glen Lake Fen	20 (40)	1881–2001	112 (99/123)	0.963	0.503	1
Albany Pine Bush	16 (34)	1834–2001	132 (103/167)	0.906	0.303	2
Mohonk Preserve	22 (45)	1618–1996	224 (121/379)	0.908	0.456	3
<i>Chestnut Oak</i>						
Goose Egg Ridge	19 (31)	1666–2002	178 (114/338)	0.956	0.430	3
Mohonk Preserve	26 (47)	1655–2002	193 (106/380)	0.945	0.393	2
Uttertown	29 (48)	1577–2002	228 (121/426)	0.920	0.281	3
<i>White Oak</i>						
Prospect Mountain	18 (32)	1659–2001	192 (113/342)	0.966	0.482	2
Lisha Kill Preserve	18 (23)	1816–2002	167 (112/188)	0.911	0.327	3
Schunne-munk Mountain	26 (46)	1648–2000	230 (126/330)	0.895	0.302	2
<i>Northern Red Oak</i>						
Rooster Hill	22 (43)	1778–2002	120 (86/221)	0.920	0.232	3
Montgomery Place	16 (32)	1787–2002	135 (75/220)	0.950	0.413	1
Uttertown	20 (42)	1785–2001	144 (112/218)	0.905	0.396	1
<i>Pignut Hickory</i>						
Stott Farm	18 (27)	1787–2001	106 (83/217)	0.903	0.403	1
Lisha Kill Preserve	14 (27)	1753–2002	170 (153/251)	0.886	0.341	2
Mohonk Preserve	19 (30)	1740–2002	158 (76/265)	0.860	0.186	2

<sup>a</sup>Tree ages are uncorrected number of rings including the first partial ring of the oldest core from each tree used in the final chronology. Minimum age does not include trees with internal rot.

<sup>b</sup>Between tree rbar.

<sup>c</sup>Expressed population signal.

<sup>d</sup>Order of pooled autoregressive model used for standardization.

Varimax rotation delineated between two forest types of the southern species sampled in the HRV, oak–hickory and AWC. However, all populations in the HRV loaded positively onto the first unrotated principal component

(PC1). Because PC1 provides a time series expression of the best-weighted linear combination of variables that collectively explain the most common variance, its temperature response was explored to interpret the

**Table 3.** Principal component analysis loading factors and percent common variance for all residual and only oak and hickory chronologies

Populations	Factor loading			
	All populations			Oak–hickory
	Unrotated eigen. 1	Rotated factor 1	Rotated factor 2	Unrotated eigen. 1
Bellvale Mountain. AWC	0.224	0.064	0.874	—
Sterling Forest AWC	0.230	0.174	0.881	—
Uttertown AWC	0.260	0.075	0.887	—
Glen Lake Fen pitch pine	0.142	0.215	0.319	—
Albany Pine Bush pitch pine	0.111	0.094	0.351	—
Mohonk Preserve pitch pine	0.174	0.312	0.323	—
Goose Egg Ridge chestnut oak	0.282	0.812	0.109	0.335
Mohonk Preserve chestnut oak	0.322	0.747	0.369	0.360
Uttertown chestnut oak	0.274	0.542	0.440	0.301
Prospect Mountain. white oak	0.274	0.703	0.225	0.314
Lisha Kill Preserve white oak	0.262	0.725	0.145	0.307
Schunnemunk Mtn. white oak	0.209	0.568	0.125	0.253
Rooster Hill northern red oak	0.205	0.647	0.002	0.250
Montgomery Place northern red oak	0.234	0.518	0.301	0.260
Uttertown northern red oak	0.272	0.484	0.512	0.292
Stott Farm pignut hickory	0.232	0.588	0.199	0.250
Lisha Kill Preserve pignut hickory	0.203	0.581	0.081	0.260
Mohonk Preserve pignut hickory	0.234	0.513	0.308	0.292
Common variance (%)	36.0	27.3	19.9	44.9

**Table 4.** Principal component analysis loading factors for eigenvector 1 and percent common variance for all residual and only oak–hickory chronologies

Subregion	All populations		Oak–hickory	
	Factor loading	Variance (%)	Factor loading	Variance (%)
<i>Northern Hudson Valley</i>		52.8		62.8
Goose Egg Ridge chestnut oak	0.549		0.565	
Prospect Mountain white oak	0.494		0.516	
Rooster Hill northern red oak	0.442		0.459	
Stott Farm pignut hickory	0.431		0.451	
Glen Lake Fen pitch pine	0.270		—	
<i>North-central Hudson Valley</i>		54.2		75.8
Lisha Kill Preserve pignut hickory	0.656		0.707	
Lisha Kill Preserve white oak	0.647		0.707	
Albany Pine Bush pitch pine	0.387		—	
<i>Mid-Hudson valley</i>		55.9		66.9
Mohonk Preserve pignut hickory	0.552		0.593	
Mohonk Preserve chestnut oak	0.548		0.591	
Montgomery Place northern red oak	0.488		0.547	
Mohonk Preserve pitch pine	0.396		—	
<i>Southern Hudson valley</i>		59.2		70.3
Uttertown northern red oak	0.580		0.617	
Uttertown chestnut oak	0.575		0.622	
Schunnemunk Mountain white oak	0.417		0.482	
Sterling Forest Atlantic white-cedar	0.399		—	
Mean	—	55.5	—	69.0

influence of temperature for the southern temperate ecosystem. PC1 accounted for 36% of the common growth variation among all populations. PCA analysis of oak–hickory populations revealed only one significant principal component, which accounted for 44.9% of the common growth variation. Chestnut and white oak had the highest loadings on this unrotated principal component (PC–OH).

Within each subregion only PC1 was significant. Mean common growth variation among subregional populations was 55.5% (SD = 2.8%) (Table 4). Oak and hickory species loaded nearly equally onto the first principal component in each subregion while conifers consistently loaded the lowest. PCA of oak and hickory populations in each subregion revealed a higher amount of common growth variation (mean = 69.0%, SD = 5.5%). Loading order did not change significantly from the PCA of all species in each subregion. The north-central results must be cautiously interpreted as only two populations were available for analysis.

### Species response to temperature

AWC growth is significantly correlated to winter and growing season temperature (Figs. 3a–c). Winter temperatures (November–March) had the strongest correlation to growth and were significantly correlated at the  $p < 0.001$  level (Table 5). The most consistent correlations during the growing season were minimum temperatures in July and August.

Northern and north-central HRV pitch pine populations were significantly correlated to winter (November–March) temperatures (Figs. 3d and e; Table 5). Prior November and current February temperatures were significant factors of growth in the northern HRV population. North-central HRV growth was significantly correlated to minimum March and April temperatures. The mid-HRV pitch pine population was significantly correlated to prior minimum May and July temperature prior maximum July and August, but not winter (Fig. 3f).

Chestnut oak growth was significantly correlated to winter (December–January) temperatures in the mid- and southern HRV (Table 5). Northern HRV growth was significantly correlated to prior maximum April, May and June and prior minimum October temperatures (Fig. 4a). Mid-HRV growth was significantly correlated to prior July, current January and current minimum September temperatures (Fig. 4b). Southern HRV growth was significantly correlated to prior April temperatures prior maximum December and current January temperatures (Fig. 4c).

White oak growth was significantly correlated to January temperatures in the north-central and southern HRV (Figs. 4d–f; Table 5). The northern HRV population showed very low sensitivity to temperature (Fig. 4d).

The north-central population was only significantly correlated to maximum January temperatures. Southern HRV growth was significantly correlated to current January and October maximum temperatures.

Northern red oak did not have a strong relation to January temperatures (Figs. 5a–c; Table 5). Northern HRV growth was significantly correlated to prior maximum March, minimum October, current maximum January, September and October temperatures.

Pignut hickory was best correlated to winter temperatures only in the mid-HRV (Figs. 5d–f; Table 5). Northern HRV growth was significantly correlated to prior maximum May and June and current minimum July temperatures. North-central HRV growth was significantly correlated to prior and current maximum September and prior November temperatures. Mid-HRV growth was only correlated to current September temperatures.

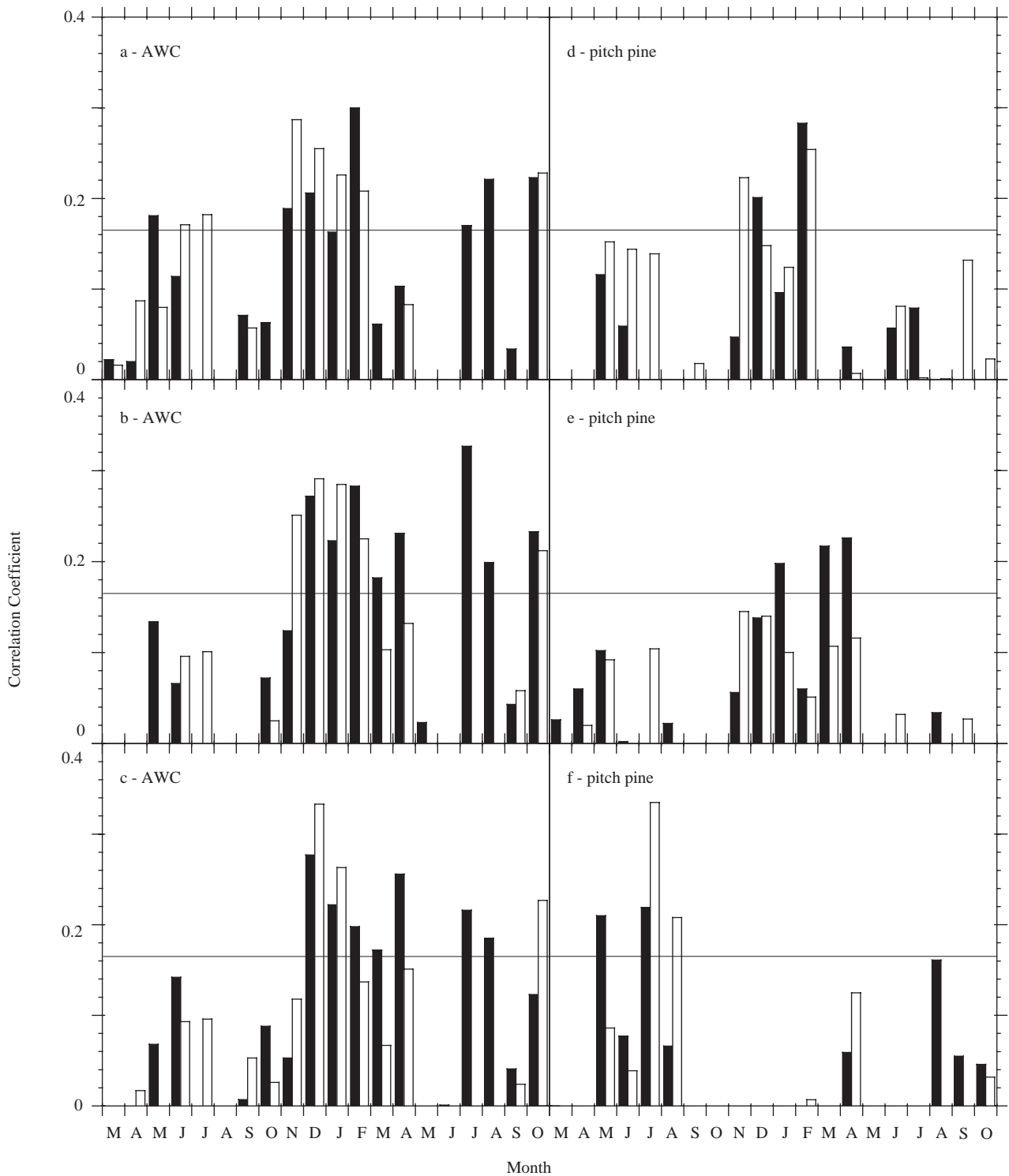
### Ecosystem temperature response

Ecosystem temperature response for the HRV is shown in Fig. 6. RF1 was only significantly correlated to prior minimum October temperatures. RF2 was most strongly correlated to winter (December–February) and April temperatures. RF2 was also significantly correlated to 2 months during the growing season, minimum July and maximum October temperatures. PC1 was significantly correlated to January temperatures. PC–OH was significantly correlated to prior minimum October and current January temperatures.

Subregional ecosystem temperature response revealed a geographic pattern of increasing winter temperature sensitivity moving south (Fig. 7a–d). Northern HRV growth was significantly correlated to prior April and June maximum and current July minimum temperatures. North-central HRV growth was significantly correlated to prior maximum November and current maximum September temperatures. Mid-HRV growth was significantly correlated to prior maximum July and current minimum September temperatures. Southern HRV growth was significantly correlated to prior maximum December, current January and current maximum October temperatures. Temperature response of oak–hickory PCA scores only slightly altered the pattern (Fig. 7e–h). Perhaps the most important change was a significant correlation of growth to January temperatures in the mid-HRV.

### Discussion

Monthly and seasonal winter temperatures are more limiting than growing season temperatures to annual radial growth of NRM species in the HRV (Figs. 3–4 and 6–7; Table 5). At the southern temperate ecosystem level January temperatures had the strongest influence



**Fig. 3.** Correlation between average monthly minimum temperatures (solid bars) and average monthly maximum temperatures (open bars) and residual chronologies of AWC arranged north–south: (a) Bellvale Mountain, NY; (b) Sterling Forest, NY; and (c) Uttertown Bog, NJ and pitch pine arranged north–south; (d) Glen Lake Fen, NY; (e) Albany Pine Bush, NY; and (f) Mohonk Preserve, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

on growth (Fig. 6a). Although an unrotated eigenvector may minimize the complexity of a multivariate system (Dommenget and Latif, 2002), it does isolate the

common variance among all populations. Much of the common variance in PC1 is related to growing season drought (N. Pederson, unpublished data) which helps

**Table 5.** Relations between winter temperatures and radial growth

Site name	Residual chronology correlation ( <i>p</i> value)	
	<i>T</i> <sub>min</sub>	<i>T</i> <sub>max</sub>
<i>Atlantic White-Cedar</i> <sup>a</sup>		
Bellvale Mountain	0.337 <sup>***</sup>	0.317 <sup>***</sup>
Sterling Forest	0.380 <sup>***</sup>	0.409 <sup>***</sup>
Uttertown Bog	0.360 <sup>***</sup>	0.331 <sup>***</sup>
<i>Pitch Pine</i> <sup>a</sup>		
Glen Lake Fen	0.249 <sup>**</sup>	0.213 <sup>*</sup>
Albany Pine Bush	0.252 <sup>**</sup>	0.200 <sup>*</sup>
Mohonk Preserve	−0.076	−0.131
<i>Chestnut Oak</i> <sup>b</sup>		
Goose Egg Ridge	0.072	0.126
Mohonk Preserve	0.187 <sup>*</sup>	0.207 <sup>*</sup>
Uttertown	0.192 <sup>*</sup>	0.198 <sup>*</sup>
<i>White Oak</i> <sup>c</sup>		
Prospect Mountain	0.015	0.070
Lisha Kill Preserve	0.154	0.211 <sup>*</sup>
Schunemunk Mountain	0.168 <sup>**</sup>	0.214 <sup>**</sup>
<i>Northern Red Oak</i> <sup>c</sup>		
Rooster Hill	0.119	0.179 <sup>*</sup>
Montgomery Place	0.105	0.105
Uttertown	0.113	0.140
<i>Pignut Hickory</i> <sup>d</sup>		
Stott Farm	−0.042	−0.091
Lisha Kill Preserve	0.030	0.002
Mohonk Preserve	0.159	0.126

*T*<sub>min</sub> = average minimum monthly temperatures; *T*<sub>max</sub> = average maximum monthly temperatures; \*\*\* represents  $p \leq 0.001$ ; \*\* represents  $p \leq 0.010$ ; \* represents  $p \leq 0.050$ .

<sup>a</sup>Season = November–March.

<sup>b</sup>Season = December–January.

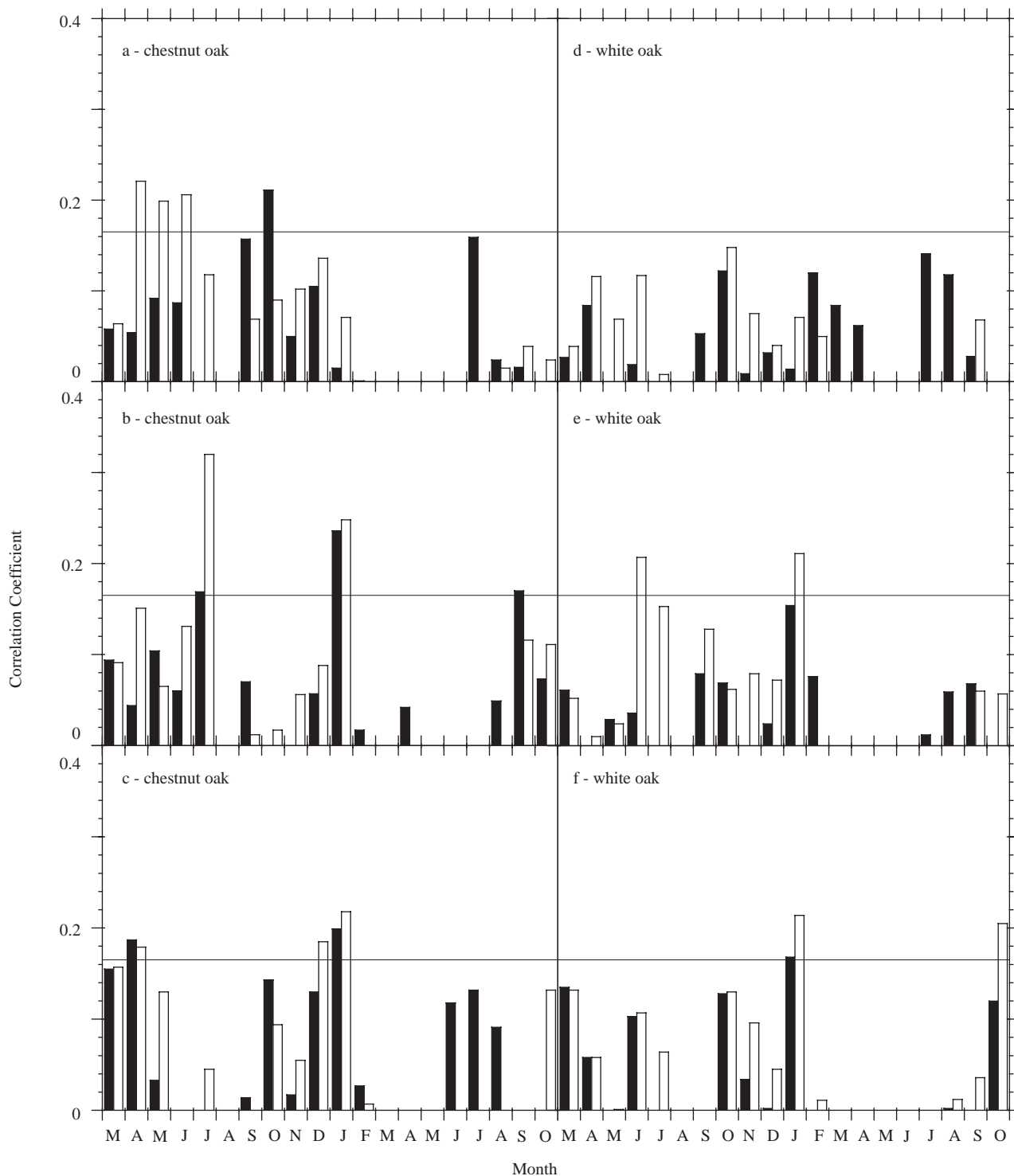
<sup>c</sup>Season = January.

<sup>d</sup>Season = January–February.

explain the rather equitable loadings on PC1 (Table 3). However, growth of populations with the highest loadings on PC1 also tends to be more strongly correlated to winter temperatures or are located in the southern half of the HRV. Therefore, species and geography seem to be most responsible for the large-scale, southern temperate ecosystem response to winter temperatures. The high sensitivity of conifers at the northern and southern end of the HRV (Fig. 3) strengthened southern temperate ecosystem response. The January response of the oak–hickory ecosystem across the HRV (Fig. 6d) is weaker than the southern temperate ecosystem response (Fig. 6a). Winter temperatures have been found to constrain radial growth in different temperate species and ecosystems (Brubaker, 1980; Conkey, 1982; Cook et al., 1987, 2001; D'Arrigo et al., 1997, 2001; Pan et al., 1997; Rubino and McCarthy, 2000; Tardif et al., 2001). Only Brubaker

(1980) demonstrated the importance of winter temperatures for multiple species. Winter temperatures are hypothesized to be one of the dominant controls on ecotone position (Neilson, 1993). The HRV is a northward extension of southern deciduous forest types (Bray, 1915; Braun, 1950; Bailey, 1995) and its position correlates to the average location of the convergence of winter Arctic and Pacific Frontal Zones (Bryson et al., 1970). Our results support the hypothesis that ecotone position may be related to winter temperature sensitivity.

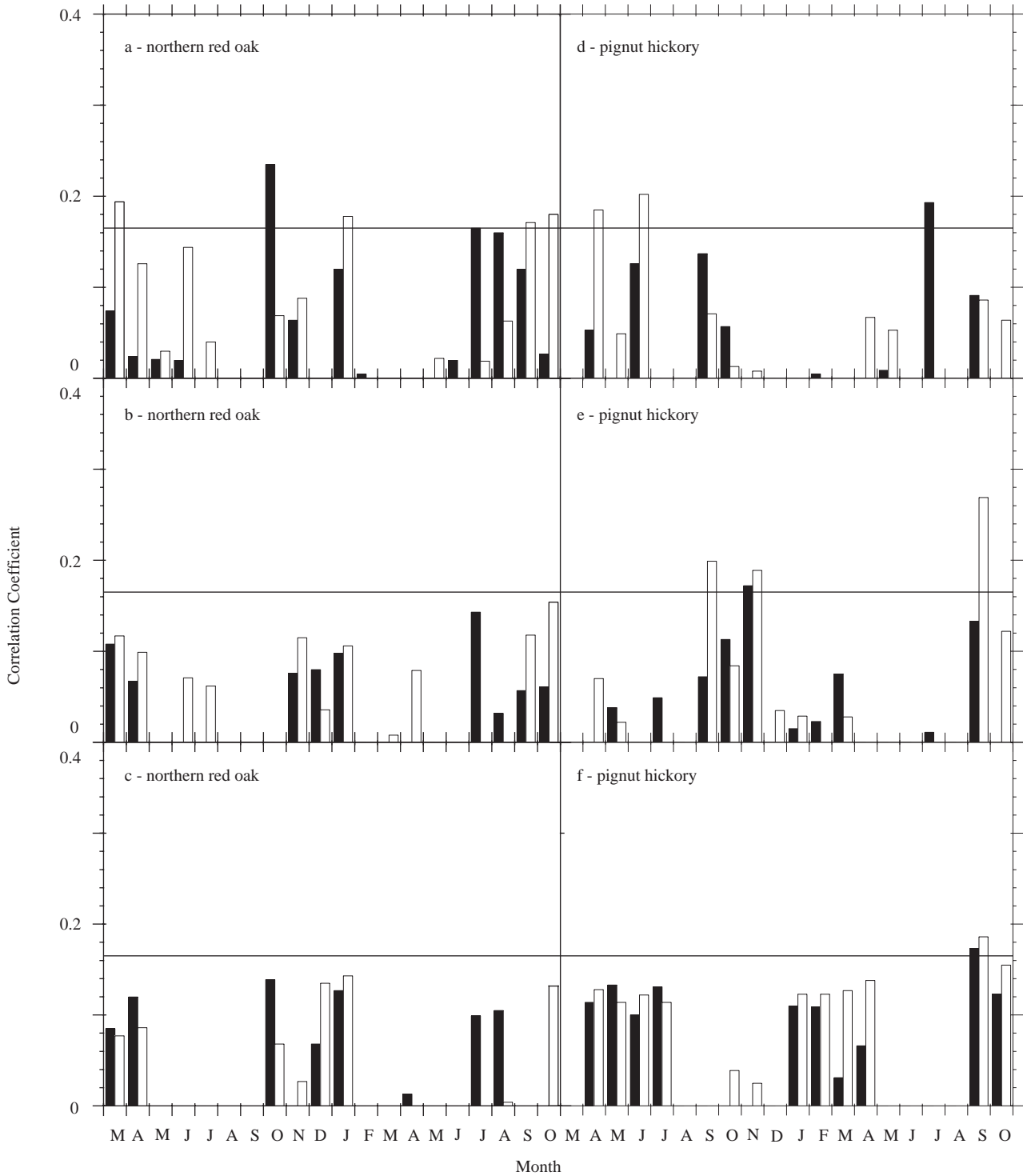
Curiously, there is a geographic pattern of winter temperature response at the subregional scale (Fig. 7). January temperatures most strongly limit radial growth in the lower half of the HRV. Although January temperatures limit oak and hickory growth (PC–OH) across the entire HRV (Fig. 6d), the geographic pattern is driven primarily by the temperature response of chestnut and white oak which often loaded the highest



**Fig. 4.** Same as Fig. 3 except for chestnut oak arranged north–south: (a) Goose Egg State Forest, NY; (b) Mohonk Preserve, NY; and (c) Utertstown, NJ and white oak arranged north–south: (d) Prospect Mountain, NY; (e) Lisha Kill Preserve, NY; and (f) Schunnumunk Mountain, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

first principal component in each subregion. The January response in the southern half of the HRV (Figs. 7(g and h)) strongly resembles the patterns of chestnut and white oak (Fig. 4; Table 5). Northern red

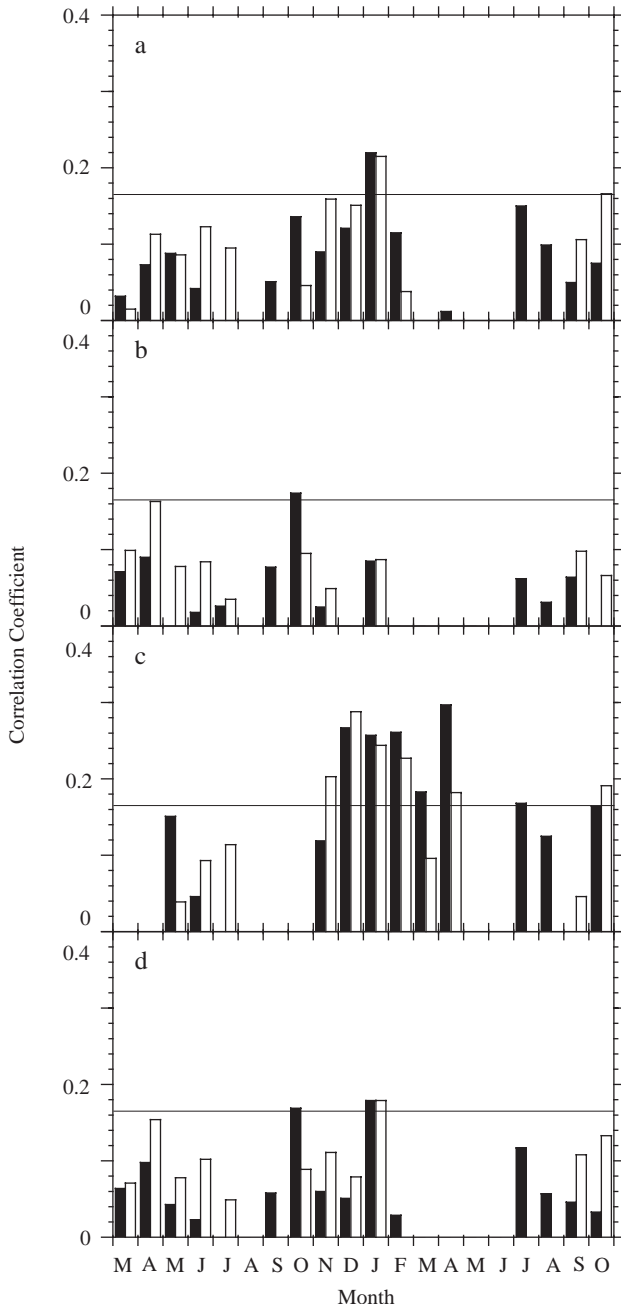
oak and pignut hickory contribute to the geographic pattern, though to a lesser degree (Figs. 5c and f; Tables 3–5). The cause of the geographic pattern is not certain.



**Fig. 5.** Same as Fig. 3 except for northern red oak arranged north–south: (a) Rooster Hill, NY; (b) Montgomery Place, NY; and (c) Uttertown, NJ and pignut hickory arranged north–south: (d) Argyle, NY; (e) Lisha Kill, NY; and (f) Mohonk Preserve, NY. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

Hypothetically, the geographic temperature response could result from the potential negative influence of winter xylem embolisms on growth (Zimmermann, 1983; Cochard and Tyree, 1990; Sperry and Sullivan,

1992; Sperry et al., 1994; Field and Brodrigg, 2001). Winter embolisms disrupt the conductance of water within a tree’s stem. Oaks often have high levels of xylem embolism by winter’s end, even in warm



**Fig. 6.** Correlation between average monthly minimum temperatures (solid bars) and average monthly maximum temperatures (open bars) against HRV PCA scores of (a) unrotated eigenvector 1; (b) rotated eigenvector factor 1; (c) rotated eigenvector factor 2; and (d) eigenvector 1 scores for only oak and hickory species. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

temperate and Mediterranean climates (Cochard and Tyree, 1990; Sperry and Sullivan, 1992; Sperry et al., 1994; Tyree and Cochard, 1996; Tognetti et al., 1998; Cavender-Bares and Holbrook, 2001). Recovery of

water conductance in oaks is made through the production of earlywood (or pore vessels) before leaf-out (Sperry et al., 1994). Energy that could be used for growth would likely be used for winter embolism recovery. Because winter embolism is a physiological limitation of oak and hickory trees, it ought to be a constant factor across the HRV. Consequently, there must be other factors for the observed geographic variation in January temperature sensitivity.

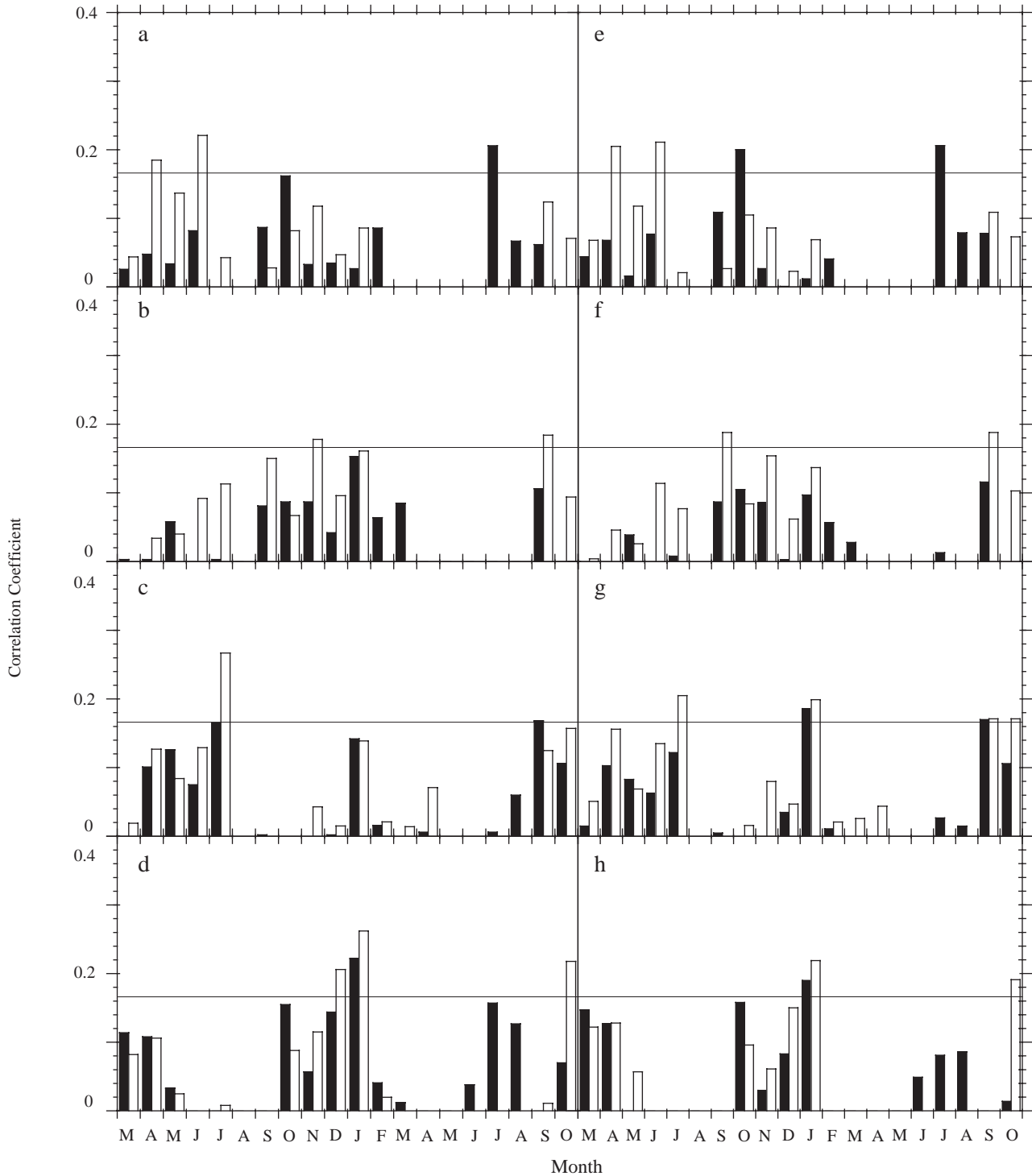
An interaction between snow cover and fine root mortality are additional factors that could account for the stronger winter temperature response in the southern HRV. A deep snow pack in late winter has been shown to effectively reduce radial growth rates by maintaining low soil temperatures and delaying initiation of cambial expansion (Graumlich and Brubaker, 1986; Gedalof and Smith, 2001; Peterson and Peterson, 2001; Peterson et al., 2002). At treeline a lack of snow cover can also have a detrimental effect through increased winter desiccation and erosion of cambium and foliage from wind-blown snow and ice crystals (e.g. Payette et al., 1996; Kajimoto et al., 2002). We hypothesize that reduced snow cover in the southern half of the HRV reduces growth through the increase of fine root mortality.

From December–March average snow cover ranges from 5% to 25% in the southern HRV to >75% in the Adirondack Mountains (Groisman et al., 1994; Groisman and Davies, 2001). Effective freeze-thaw days, which are freeze-thaw days with less than 7.5 cm of snow, occur twice as often in the lower HRV than the Adirondack Mountains (Schmidlin et al., 1987). Snow cover 7.5 cm deep can reduce the daily temperature range by roughly 50% (Geiger, 1957). Differences in snow cover from north to south in the HRV may create a significant gradient in winter soil temperature.

Roots are the least cold hardy part of a plant. When snow cover was removed in a natural forest setting, fine root mortality doubled even though mild winter conditions only occasionally drove upper soil temperatures down to  $-4^{\circ}\text{C}$  (Hardy et al., 2001; Tierney et al., 2001). Root damage combined with stem embolism is more highly correlated to reduced xylem conductance and increased shoot dieback than stem damage alone in yellow (*B. alleghaniensis* Britton) and paper birch (Cox and Malcolm, 1997; Cox and Zhu, 2003). Therefore, the potential impact of annual snow cover on a tree's roots may be the most logical explanation of the geographic relation between winter temperatures and radial growth in the HRV. Further investigation requires comparison of snow depths with temperature data in assessment of radial growth.

Winter temperatures are the strongest temperature factor of NRM growth in the HRV. Increased winter temperatures in areas of inconsistent snow pack may mean less winter damage to roots, which may mean less of a growth limitation. Although future climate





**Fig. 7.** Same as Fig. 6 except for PCA unrotated eigenvector 1 scores at (a) northern Hudson Valley; (b) north-central Hudson Valley; (c) mid-Hudson Valley; and (d) southern Hudson Valley. (e–h) For the same subregions, but do not include conifer populations. Thin, horizontal line indicates a significant correlation at the 95% confidence limit for a one-tailed test.

warming may reduce productivity and carbon uptake in regions that currently have a consistent annual snow pack (Groffman et al., 2001), it could be that warmer winters in regions without a regular snow pack like the

lower HRV may experience increased tree growth and carbon uptake.

The most consistent response of the oak–hickory ecosystem is the significant correlation to prior October

minimum temperatures (Figs. 6b and d). Although rotated and unrotated eigenvector analysis can detect local and global problems differently (Dommenges and Latif, 2002), both RF1 and PC-OH find prior October temperatures to be important for oak–hickory growth. Several physiological processes occur early in the fall season (Kramer and Kozlowski, 1979). For example, between 1883 and 1912 in northern Ohio, at roughly the same latitude as the lower HRV, leaf color change was completed in pignut hickory and white oak around October 6 and October 17, respectively (Fig. 4 in Lechowicz, 1984). Deciduous trees translocate nutrients from leaves into branches and buds before leaf senescence (Chabot and Hicks, 1982). Warmer temperatures may allow an extended period of nutrient recovery or rapid rates of recovery prior to leaf fall. Considering that many oak and hickory have determinate shoot growth, completion of these physiological processes is likely important the following year.

Differences in winter temperature response are apparent between species. AWC and pitch pine are more sensitive to winter temperatures and a longer winter season than oak or hickory (Figs. 3–5; Table 5). Pines are also more sensitive to temperature than hardwoods in the upper Great Lakes (Graumlich, 1993). Differences in winter temperature sensitivity between conifers and broad-leaved trees could result from a couple of mechanisms. Temperate conifers can have a positive carbon gain on warm winter days when their leaves are not frozen (Chabot and Hicks, 1982; Havranek and Tranquillini, 1995). In fact, non-structural carbon in xylem, needles and bark varies in amount and quality due to metabolic activity on warm winter days (Havranek and Tranquillini, 1995). However, maintenance of foliage throughout winter makes conifers more susceptible to damage from freezing, snow and ice accumulation or winter desiccation. Differing winter temperature sensitivities of conifers and broad-leaved species are likely a result of contrasting physiological traits.

Winter sensitivity of AWC and pitch pine in the HRV is similar to loblolly pine at its northern range limit (Cook et al., 2001). Research at southern latitudes is needed to determine if the winter temperature sensitivity exists only at NRM for AWC and pitch pine like loblolly pine.

Oak and hickory are not strongly limited by winter temperatures at NRM locations like AWC and pitch pine (Figs. 4, 5 and 7e). Our results suggest that conifers and oak and hickory may have significantly different temperature sensitivities at NRMs and perhaps, contrasting patterns of winter temperature response across latitudes.

Temperature sensitivity in oaks may be determined at the subgenus level. Chestnut and white oak is more sensitive to January temperatures in the southern half of

the HRV than northern red oak. Our results support physiologically based research that found white oaks to be more susceptible to freezing than red oaks in northern Florida (Cavender-Bares and Holbrook, 2001). White and red oak subgenus groups also have distinct climatic response across a drought gradient in east Texas (Cook et al., 2001). More research is needed to verify whether the differences in temperature response between red and white oaks are consistent for a larger number of species.

AWC growth is most sensitive to temperature followed somewhat closely by pitch pine and distantly by chestnut oak, pignut hickory, white and northern red oak (Figs. 3–5). Only AWC is correlated to summer temperatures. AWC's strong temperature response accounts for the second rotated eigenvector factor of the HRV (Tables 3 and 5). The high sensitivity of AWC agrees with a study of seven separate AWC populations from New Jersey to Maine where temperature was the most important climatic factor of growth along its northern range limit (Hopton, Pederson, *in press*). Of species studied in temperate eastern North America, AWC's sensitivity to temperature is exceptional. Red spruce is as temperature-sensitive as AWC in the northeastern US, especially at high elevations (Conkey, 1986; Cook et al., 1987). However, red spruce's growing season sensitivity was related to wood density, not ring width (Conkey, 1982, 1986). Of the species studied in temperate eastern North America, AWC appears to have the best potential for reconstruction of historical temperature variations.

Chestnut oak is the most sensitive oak (Figs. 4 and 5; Table 5). Its higher sensitivity to spring temperatures may help explain its more southerly distribution and lack of occurrence in the Adirondack Mountains of New York State. A late spring and a shorter growing season may put chestnut oak at a competitive disadvantage in northerly locations.

Pignut hickory's late growing season temperature response is the most different of the species studied (Figs. 5e and f). Its climate response has rarely been studied (Hill, 1982; Liu and Muller, 1993; Orwig and Abrams, 1997; Abrams et al., 1998). Why pignut hickory is most sensitive to late growing season temperatures is not clear. It seems like the late-season temperature response would be related to physiological activities and determinate shoot growth as discussed above.

Most differences in temperature response between species were found at the margins of the growing season and may be related to phenology. Phenology of the temperate forest is thought to be temperature driven (Kramer et al., 2000). It is also thought to be an important contributor to species distribution (Chuine and Beaubien, 2001) and growth response to climate change (Kramer et al., 2000). However, much more

work is needed to determine if differences in radial-growth temperature sensitivity in the HRV contribute to species distribution.

Local site conditions may play an important role in temperature sensitivity. For example, the absence of a winter response in the mid-HRV pitch pine is conspicuous and runs counter to most of our findings (Fig. 3f). This population grows on an outcrop of conglomerate bedrock while the other pitch pine populations grow in deeper soil. Sandy soils, with a higher amount of pore space, are more conducive to cold air seepage (Kramer and Kozlowski, 1979). It is possible that bedrock acts as an insulator of tree roots.

## Conclusion

Winter temperatures are the strongest and most consistent temperature factors of radial growth of NRM species in the HRV. Differences between species suggest that temperature sensitivity may be related to phenology and life history traits. AWC and pitch pine are sensitive to the entire winter season while oak and hickory are primarily sensitive to January temperatures. These differences may have important ecological implications. For example, a shortening of the winter season would favor AWC and pitch pine more than oak and hickory. It is not clear that our results are applicable to the same species in other regions or species from different biomes in our study region. If these results are indicative of the subtle influence of temperature on growth, they suggest that more broad-scale research is needed at the species level.

PCA indicated a strong common signal of radial growth at local and regional scales across multiple species in the HRV. Previous multi-site network studies using multiple species show a strong climate signal across a drought and temperature gradient in eastern North America (Graumlich, 1993; Cook et al., 2001). Our results confirm these prior studies. They also indicate that climate has a strong influence on tree growth in forests with different land-use histories ranging from those in an old-growth condition to those repeatedly cut.

The varying influence of temperature at the species and ecosystem level at different geographic scales has important implications in forecasting the impact of climate change on forested ecosystems. As has been shown for eastern hemlock (e.g. Cook and Cole, 1991), it is unlikely that simulation models capture these differences across the landscape. Incorporation of these results into simulation models may produce important differences from current forecasts of climate change impacts on forests.

Finally, land-use history, elevated nitrogen deposition, elevated carbon dioxide and change in growing

season climate have been implicated as significant factors affecting the terrestrial carbon cycle. Our results suggest that winter temperatures may have a meaningful role in the terrestrial carbon cycle of temperate regions.

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