

Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed

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Abstract

This study used dated and measured tree-ring data to examine relationships between radial growth, topographic aspect, and precipitation for four hardwood species, yellow-poplar (*Liriodendron tulipifera* L.), northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus prinus* L.), and red maple (*Acer rubrum* L.), growing on contrasting aspects in north-central West Virginia (39°39'43"N, 79°45'28"W). The main objectives of the study were to determine variation in growth between northeast and southwest aspects, examine changes in annual growth related to changes in precipitation and Palmer drought severity index (PDSI), and test for the existence of an interaction between species' growth response to drought and topographic aspect.

The study found that all species except northern red oak showed significant differences in growth between the northeast and southwest aspects ($P < 0.05$). Where significant differences were found, all except chestnut oak exhibited higher growth rates at the northeast aspect. The largest and the least difference in growth between the northeast and southwest aspects were found for yellow-poplar and northern red oak, respectively.

Among the four species studied, yellow-poplar showed a sharp decline in growth from the late 1950s to the late 1960s, which was evidently caused by several years of below-average precipitation. The more conservative species, red oak, chestnut oak and red maple, showed a mild response to the drought compared to yellow-poplar which experienced 30–40% less growth relative to its peak growth in the late 1950s. A rapid growth recovery, in the early 1970s, following the decline in the late 1960s was associated with wetter than average conditions of the early 1970s. Analysis of drought effects in 1953, 1966, 1988 and 1991 indicated that most species experienced below-average growth although drought-related growth declines lasted only for a few years and recovery following drought was rapid.

Regarding the interaction of aspect and response to drought, yellow-poplar displayed greater response to periodic droughts at the southwest aspect while the oaks showed little evidence of an aspect-related interaction with drought response. The results of this study are logical in terms of the ecological strategies of the species; yellow-poplar is widely known to be site specific and exploitive, whereas oaks and maples are more conservative.

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1. Introduction

Spatial variability in site quality, species composition, and forest productivity, due to differences in topographic characteristics, has long been recognized by foresters in the eastern United States (Trimble and Weitzman, 1956; Doolittle, 1957, 1958; Olson and Della-Bianca, 1959; Trimble, 1964; Phillips, 1966; Carmean, 1967, 1975; Olson, 1969; Lloyd and Lemmon, 1970; Lee and Sypolt, 1974; Luxmoore et al., 1978; Auchmoody and Smith, 1979; Spurr and Barnes, 1980; Tajchman and Wiant, 1983; Carmean and Kahn, 1983; Frank et al., 1984; Hicks and Frank, 1984; Boyles and Tajchman, 1984; Tajchman and Lacey, 1985; McNab, 1989, 1993). Long recognized as an important topographic variable, aspect affects the amount and daily cycle of solar radiation received at different times of the year and has a strong influence on the microclimate, especially air temperature, humidity, and soil moisture (Rosenberg et al., 1983). For example, a southwestern slope is sunnier and drier than a northeastern slope because the southwest aspect receives more intense solar radiation, which alters the microclimatic conditions of the site. Since aspect, through its control on solar intensity, affects microclimate, a change in aspect across a landscape has been known to result in changes in growth rate, species composition, and site quality. Although it is generally believed that south-facing slopes are drier and soil moisture deficits limit tree growth on these sites, a study by Lee and Sypolt (1974) has shown that, in some years, available soil moisture was not significantly different by aspect in West Virginia. Therefore, an alternative explanation for differential growth rates between forests on north and south-facing slopes relates to differences in energy exchange and thermal regimes rather than differences in soil moisture.

Similarly, variation in annual growth associated with annual changes in climate is likely to vary across a range of aspects or topographic positions. Dendrochronologists, especially in the western states, have known for nearly a century that trees that are located on xeric sites are more sensitive to climatic variation (Fritts, 1976). As a result, dry to xeric sites are most often chosen for dendrochronological studies to facilitate cross-dating among trees, study sites, and also to maximize the variance in radial growth due to varia-

tion in climate (Stokes and Smiley, 1968; Fritts, 1976; Phipps, 1982).

Though much is known about climate-related variation in radial growth of trees in the semi-arid regions of the southwestern United States, not nearly as much is known about climate-related variation in growth of trees in the mixed mesophytic-hardwood forests of the eastern United States. In fact, recent studies (Orwig and Abrams, 1997; Abrams et al., 1998) strongly emphasized that our understanding of the impact of climate and drought on radial growth rates of species across contrasting site conditions is very limited, especially for the eastern United States.

Over the past several decades, numerous dendroclimatological studies in eastern North America (e.g., Bonkougou et al., 1983; McClenahan and Dochinger, 1985; Jacobi and Tainter, 1988; Graumlich, 1992; Luken et al., 1994; Pan et al., 1997; Abrams et al., 1998; Rubino and McCarthy, 2000) have shown the existence of sufficient year-to-year variation to enable cross-dating and permit accurate assignment of calendar years to individual growth rings. However, few studies have focused on the issue of interaction among site condition, species characteristic and radial growth response to drought. For example, Abrams et al. (1998) studied the effects of drought on radial growth of 10 hardwood species across a range of sites in the Ridge and Valley Province of central Pennsylvania. They looked at the effects of drought on trees that were growing in wet-mesic, mesic, dry-mesic, and xeric sites. They found that trees in general suffered the greatest declines in growth on wet-mesic and xeric sites and the trees that suffered the smallest declines were found in the intermediate mesic areas (mesic and dry-mesic sites). The species showing the greatest decline during drought varied among sites and were red maple in the mesic site (valleys), black cherry in the dry-mesic (barrens) and wet-mesic (riparian) sites, and red oak and red maple on the xeric site (ridges).

In a similar study Orwig and Abrams (1997) examined radial growth responses to drought for six species at two contrasting locations (mesic and dry) in northern Virginia. They noted that yellow-poplar growing on mesic sites experienced greater ring-width reductions associated with drought than co-occurring, more drought tolerant white oak and black oak. On the dry sites yellow-poplar also experienced greatly reduced growth as a result of drought, but exhibited significant

growth increases following individual drought events. Although these studies indicate a general trend of higher drought response for trees growing in xeric environments, the results were not entirely conclusive.

In the literature, there are conflicting views, based on two approaches (tree-ring level and leaf physiology level), on species drought tolerance across contrasting sites. At the tree-ring level (Fritts, 1976; Phipps, 1982), complacent trees growing on more favorable sites may exhibit little tree-ring response to climatic variation, whereas sensitive trees growing on severely limiting sites often have significant growth response associated with climate. On the other hand, at the leaf physiology level, studies have reported that tree species on wet-mesic or mesic sites may exhibit greater decreases in gas exchange (or net photosynthesis) during drought than those on xeric sites (Zobel, 1974; Kubiske and Abrams, 1994).

Scarcity of information and lack of agreement concerning drought responses of plants in differing environmental or site conditions justifies the current study. Therefore, the main objective of this study is to determine how annual radial growth as a response to drought varies between a northeast (mesic site) and southwest (xeric site) aspect in four tree species, yellow-poplar (*Liriodendron tulipifera* L.), northern red oak (*Quercus rubra* L.), chestnut oak (*Quercus prinus* L.), and red maple (*Acer rubrum* L.). These species represent a spectrum of adaptation ranging from a species typically associated with mesic sites (yellow-poplar), a species typically associated with xeric sites (chestnut oak) and two species with a wider site amplitude (northern red oak and red maple). In the central Appalachian region, rainfall is plentiful and even the most xeric sites could be characterized as moist by southwestern United States standards. However, it is hypothesized that the species should respond to the fine scale differences in microclimate due to changing topographic aspect. The specific objectives of this study were to (1) compare mean growth rates of the species between mesic and xeric aspects and among species at a site, (2) evaluate variation in drought response between mesic and xeric aspects, and among species at a site, (3) determine if there is an interaction between response to drought and topographic aspect, and (4) identify if there are extended growth declines associated with adverse climate.

2. Description of the study area and methods

2.1. Study area

The study area, Little Laurel Run watershed, is part of Coopers Rock State Forest located approximately 16 km northeast of Morgantown, WV (39°39'43"N, 79°45'28"W). The watershed encompasses approximately 271 ha and is typical of many Appalachian V-shaped valleys with long, steep and rocky slopes. The watershed orientation is from northwest to southeast. The average relief of the watershed is roughly 224 m above sea level (Tajchman and Wiant, 1983). The topography of the area is fairly rugged and the average slope inclination is 14° (25%). The average oak site index is 22.6 m (74 ft). The watershed is covered with an even-aged 60–70-year-old mixed hardwood forest of mostly sprout origin. Roughly 62% of the forest is composed of mixed oak cover types. The predominant species in these stands are white oak, black oak, northern red oak, scarlet oak, and chestnut oak. The remainder, 38% of the forest, is occupied by mesophytic-hardwood stands. These stands occur on the mesic sites and consist primarily of yellow-poplar, red maple, black cherry, and northern red oak (Knight, 1980).

The soils are characterized as Dekalb series on well-drained hill slopes and ridge tops, deeper Ernest series on concave slopes bordering streams. Annual precipitation averages 129.4 cm and is fairly evenly distributed throughout the year. The average annual mean temperature is 9.0 °C, although temperatures as low as –33.9 °C have been recorded in January (Carvell, 1983). The growing season in the study area is approximately May–September and about 47% of the average annual precipitation was received during this critical period of tree growth (Fekedulegn, 2001).

Precipitation data from 1973 to the present were recorded at the Cooper's Rock Weather Station on site, and data for the years 1935–1972 were interpolated using records from the three closest weather stations (Fekedulegn, 2001). Monthly Palmer drought severity index (PDSI) data for the period 1935–1996 were obtained for West Virginia climate district II from CLIMVIS web page of NCDC/NOAA (2001). Using the monthly data, growing season PDSI was computed.

2.2. Vegetation sampling and microclimate data

To document the variation in species composition and dominance between the northeast and southwest aspects, 100 20 m × 20 m, square plots (50 per aspect) were established. At each plot, the diameter at breast height and total height of all trees was measured. Tree species importance values (Phillips, 1959) were then computed for each species by summing the relative density, relative basal area, and relative frequency. For each aspect species importance values were ranked which provides a means for comparing species importance between the two aspects.

To examine differences in microclimate between the two aspects, air temperature readings were taken at 2 h intervals from 6 A.M. to 8 P.M. using a psychrometer at each aspect during two cloudless days: July 14 and 16 of 1997. Temperature readings within the forest were taken at breast height, 1.4 m above ground. The psychrometer consists of two ventilated thermometers, the dry bulb thermometer measured the air temperature directly, while the wet bulb thermometer measured a temperature lowered by an amount determined by the evaporative cooling caused by the ambient air. These data were then used to provide estimates of relative humidity and vapor pressure deficit (Rosenberg et al., 1983; Burman and Pochop, 1994). Vapor pressure deficit (Et) is an approximate measure of potential evapotranspiration in that large values of Et indicate higher rates of evapotranspiration and plant water stress and lower values indicate lower rates.

2.3. Increment core collection and preparation

At each aspect, in October 1996, dominant and codominant trees from four species, yellow-poplar, red oak, chestnut oak, and red maple (Table 1), were identified on plots with average basal area. Following standard procedure, two increment cores were extracted at breast height from each selected tree. Cores were dried, mounted and then sanded with progressively finer grit sandpaper to expose the annual rings (Stokes and Smiley, 1968). Growth ring widths were measured to the nearest 0.001 mm using a Lecia Stereo Zoom-5 binocular microscope, an Acu-rite measuring stage and a Quick-Check 1000 digital readout, in conjunction with J2X[®] software. Tree-ring series were cross-dated using marker years based

Table 1

Summary statistics (mean values) of trees sampled for tree-ring analyses

Species and aspect	<i>n</i> ^a	Diameter (cm) ± S.E. ^b	Age ^c ± S.E.
Yellow-poplar			
Northeast	38	39.5 ± 3.0	62.6 ± 0.6
Southwest	27	30.3 ± 2.8	62.0 ± 0.4
Red oak			
Northeast	36	28.9 ± 2.3	64.6 ± 1.2
Southwest	34	26.7 ± 1.9	60.9 ± 0.9
Chestnut oak			
Northeast	11	17.8 ± 0.9	60.2 ± 0.8
Southwest	39	23.0 ± 1.7	61.8 ± 2.1
Red maple			
Northeast	40	18.8 ± 0.9	58.9 ± 0.6
Southwest	27	15.5 ± 0.4	57.5 ± 1.3

^a Number of trees cored.

^b Standard error.

^c The number of annual rings at breast height.

on consistently narrow rings (e.g., 1953, 1988), and dating was validated using the program COFECHA (Grissino-Mayer et al., 1997). For each tree, ring-width measurements from the two cores were considered as replicates of the same process and hence were averaged. Mean ring-width and basal area increment (BAI) for each species were obtained by calculating mean ring-width and BAI from the two cores for each tree and then averaging these mean values for all trees of the same species.

About 80% of the trees cored (Table 1) at both the mesic and xeric aspects reached their coring height consistently around 1926–1940. According to the site history, the area was logged for timber from 1912 to 1930 (Carvell, 1973). Hence, the period 1935–1996 is considered as the study period and ring-width and climate data during this period constitute the database for this study.

For all species, except chestnut oak, trees sampled at the mesic site had higher mean dbh than those at the xeric site (Table 1). Chestnut oak was extremely infrequent on the northeast aspect and most chestnut oak trees sampled at this site were located near ridge tops. In both stands red maple had the lowest average age and smallest diameter compared to the other three species. Yellow-poplar was the largest in average diameter at coring height.

2.4. Data analyses

ANOVA and *t*-test procedures were used to determine if there were significant differences in mean ring-width and BAI between sites and among species. Due to heterogeneous variance in BAI between the mesic and xeric aspects, and among species, ANOVA was performed on log-transformed values. The method of least significant difference (LSD) was used for mean separation among the four species. Year-to-year variability in growth of each species between the mesic and xeric sites was compared using the coefficient of variation (CV) of BAI. The temporal patterns of mean ring-width and BAI were examined to determine if years with low and high growth are associated with variations in growing season precipitation.

To evaluate the effect of drought on radial growth of the species, three moderate (1953, PDSI = −2.42; 1988, PDSI = −2.65; 1991, PDSI = −2.33) and one extreme (1966, PDSI = −4.00) drought years were selected. Paired *t*-tests were then used to compare growth in drought years with average growth and growth in the prior year. To understand rate of recovery, growth in the year following drought (post-drought growth rate) was compared with the growth in the year prior to drought (pre-drought growth rate). To determine if radial growth rate was suppressed beyond the year of drought, paired *t*-tests were performed comparing the mean growth for the 5 years previous to and the 5 years following each drought (Rubino and McCarthy, 2000; Abrams et al., 1998). Prior to these analyses, the ring-width series of each tree was transformed into ring-width index (RWI) by fitting the modified negative exponential model and calculating RWI as the ratio of actual to expected growth. Model fitting and calculation of RWI was accomplished in SAS (SAS Institute, 1998). In few cases where the modified negative exponential model failed to fit, a smoothing spline of segment length 32 (Cook and Peters, 1981) was used for detrending. Hence, the measure of growth used to evaluate drought effects is the RWI, a standardized measure of growth that is not sensitive to tree size.

Relationships between the species RWI values and growing season precipitation and PDSI were examined using Pearson's product-moment correlation (if the variables are normally distributed) and Spearman rank correlation (if the assumption of normality was not satisfied).

3. Results

3.1. Stand characteristics

The species importance values (Fig. 1) indicates that northern red oak and red maple are important at both aspects while yellow-poplar and chestnut oak are specialists with respect to their aspect preference. Northern red oak and red maple yield above-average species importance values at both aspects, and this reflects the rather broad ecological amplitudes of these species. On the other hand, yellow-poplar and chestnut oak are largely confined to specific aspects suggesting that these two species have defined aspect preference. Yellow-poplar occur primarily on the mesic slopes whereas chestnut oak is a xeric species.

At the time of sampling (1996), stand conditions, basal area and density (>10 cm), averaged 36 m² ha^{−1} and 425 trees/ha at the northeast aspect and 28 m² ha^{−1} and 522 trees/ha at the southwest aspect. Basal area was 30% higher at the mesic site (Table 2). At the northeast aspect, contribution of individual species to the total basal area was yellow-poplar (39%), red oak (19%), chestnut oak (less than 1%), and red maple (12%), while the corresponding estimates at the southwest aspect

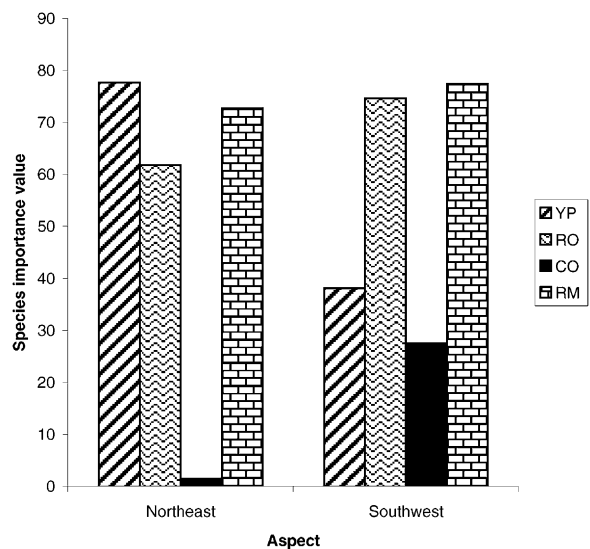


Fig. 1. Species importance values by aspect. At each aspect, species importance values were obtained by summing relative density, relative basal area and relative frequency. Species abbreviations: YP, yellow-poplar; RO, northern red oak; CO, chestnut oak; RM, red maple.

Table 2
Stand characteristics by aspect in the study site at the time of sampling

Species	Basal area (m ² /ha)		Height (m) of dominant and codominant trees	
	Northeast	Southwest	Northeast	Southwest
Yellow-poplar	14.2 ± 1.90	1.5 ± 0.44	30.91 ± 0.29	25.8 ± 1.23
Northern red oak	7.0 ± 1.10	6.3 ± 0.89	27.67 ± 0.39	23.92 ± 0.35
Chestnut oak	0.16 ± 0.20	4.5 ± 0.74	26.5 ± 1.4	20.2 ± 0.95
Red maple	4.3 ± 0.59	3.0 ± 0.30	26.26 ± 0.50	22.33 ± 0.59
Other species	10.4 ± 1.70	12.9 ± 0.56		
Total	36.1 ± 1.83	28.2 ± 2.1		

were yellow-poplar (5%), red oak (23%), chestnut oak (16%) and red maple (11%). These data comply with the result shown in Fig. 1 indicating that yellow-poplar at the xeric site and chestnut oak at the mesic site have the least contribution (importance) confirming their strong aspect preference.

All trees in the dominant and codominant crown classes of the four species on the mesic site were significantly taller ($P < 0.05$, t -test) than their counterparts on the xeric site (Table 2). Most dominant and codominant species on the northeast-facing site had similar mean heights except yellow-poplar which was significantly taller (Table 2, $P < 0.05$, ANOVA). On the southwest aspect, however, mean height of dominant and codominant yellow-poplar trees was not significantly taller than that of the oaks. The stands on both sites had two well-defined (distinct) strata, an overstory stratum (>24 m tall) dominated by less shade-tolerant species and an understory stratum (<14 m tall) dominated by shade-tolerant species. The understory stratum (trees < 12–14 m tall) on the northeast aspect is mostly composed of red maple (63%) and red maple accounts for 46% of the understory vegetation on the southwest aspect as well. Yellow-poplar (40%) and the red oak group (20%) make up 60% of the dominant and codominant trees in the northeast aspect, whereas on the southwest aspect the red oak group (64%) and the white oak group (22%) together account for 86% of the trees in the overstory stratum.

3.2. Microclimate

Fig. 2 shows the diurnal variation of air temperature, relative humidity, and vapor pressure deficit at breast height (1.4 m above ground) during the two

observation periods (July 14 and 16 of 1997). Each plotted point represents an average for 2 days. During early morning, from 7 to 11 A.M., air temperature at the northeast aspect was about 2.74 °C higher while during midday period, from 12 to 4 P.M., the southwest aspect had air temperature about 4.86 °C higher than the northeast aspect. The maximum temperature difference between the dry and mesic site was 5.55 °C and was observed at noon (Fig. 2(a)). A study by Lee and Sypolt (1974) at the WVU Forest demonstrated that the net radiation on south-facing slopes exceeded that on north-facing slope by 24%. Higher midday temperatures at the southwest aspect could be the result of the higher radiant energy received at this aspect. Lower midday breast height temperature at the northeast-facing slope could also be due to higher canopy density (shading) at these aspects.

The amount of water vapor present in the air is one of the most important environmental factors affecting tree growth (Kramer and Kozlowski, 1960) as it directly influences the rate of evapotranspiration. In the present study it was estimated in terms of relative humidity. The relative humidity at the southwest aspects was about 25% lower than that at the northeast aspect during midday periods (Fig. 2(b)). This was due to the higher midday temperatures at the drier aspect. The maximum difference in relative humidity between the two sites was observed between noon and 3 P.M.

The pattern of vapor pressure deficit (Et) follows that of air temperature. The data in Fig. 2(c) shows that evapotranspiration rates on the southwest aspects begin slower in the morning, reaching maximum rates at noon and remain higher throughout the afternoon than that on the northeast aspect. Plant water stress as measured by vapor pressure difference (Et) is about

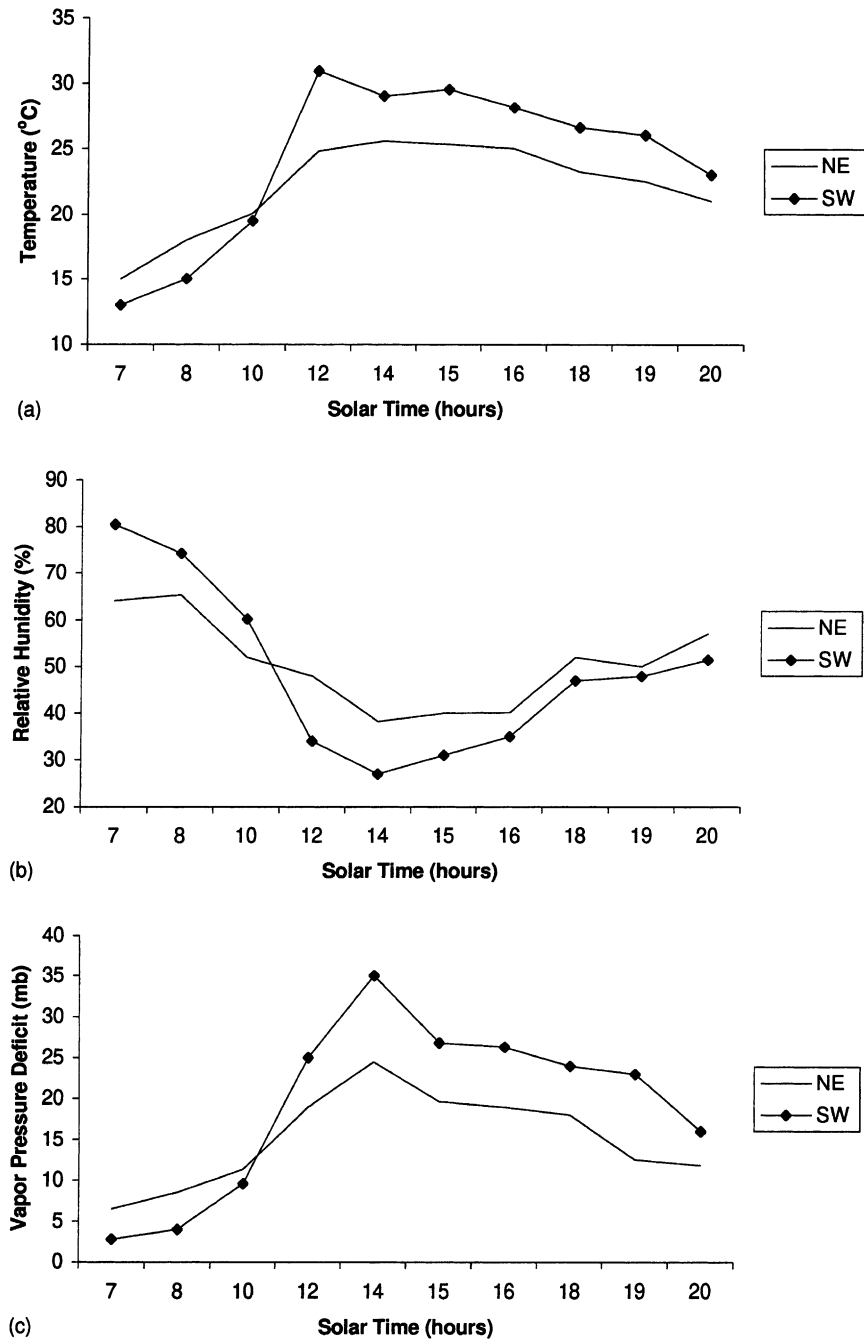


Fig. 2. The diurnal pattern of air temperature (a), relative humidity (b), and vapor pressure deficit (c) at the two aspects during two cloudless days (July 14 and 16 of 1997). Site abbreviations: NE, northeast; SW, southwest.

37% higher on the southwest aspect during midday periods than on northeast aspect.

3.3. Spatial variability in radial and basal area growth

Radial and basal area growth patterns of the species, for the whole study period (1935–1996), are illustrated in Figs. 3 and 4. The radial and basal area growth patterns in Figs. 3 and 4 were derived by averaging data from all trees. The statistics of growth are summarized in Table 3.

All species, except chestnut oak, showed higher mean ring-width and BAI at the mesic site (Table 3). Significant differences ($P < 0.05$, t -test) in growth rates between the mesic and xeric sites were observed for all species except northern red oak (Table 3). At the mesic site, radial growth averaged 3.61, 2.41, 1.44, and 1.52 mm per year for yellow-poplar, red oak, chestnut oak, and red maple respectively. Yellow-poplar was the fastest growing species at this site with mean radial increment significantly higher than the other three species ($P < 0.05$, ANOVA). At the xeric site, however, mean radial growth of yellow-poplar (2.03 mm per year) was not significantly different from that of red oak (2.33 mm per year) and chestnut oak (2.20 mm per year) but was significantly higher than red maple (1.25 mm per year) (Table 3). At both sites red maple grew significantly more slowly than yellow-poplar and red oak.

The largest difference in growth rates between the mesic and xeric sites occurred for yellow-poplar, a species which has a defined aspect preference and the smallest occurred for northern red oak, a species that is a generalist with respect to its aspect preference. Unlike the other three species, chestnut oak showed a significantly larger mean ring-width and BAI at the xeric site. This is possibly due to a competitive advantage of chestnut oak at the xeric site. For example, xeric sites typically carry a lower tree stocking level than mesic sites. Chestnut oak trees, which favor xeric sites, would have more room for crown expansion, permitting greater dbh growth on xeric sites. Therefore, the data indicate that growth rates of yellow-poplar, red maple and chestnut oak showed larger aspect-induced spatial variability compared to northern red oak.

Year-to-year variability in growth as measured by CV of BAI shows that all species exhibited larger

variability at the xeric site (Table 3). Significant and the largest differences in CV of BAI between the mesic and xeric sites were observed only for yellow-poplar.

3.4. Temporal patterns of growth

3.4.1. Radial growth

Fig. 3 shows the similarities and differences in radial growth patterns of the species. Sharp declines in radial growth of all species corresponded to the drought years of 1953, 1988 and 1991, which proved to be good years to cross-date tree-ring series. Increased growth rate (peaks) were observed for most species in 1958, 1980, and 1992. The depressions and peaks in radial growth were present for each species at the mesic and xeric sites indicating that regardless of aspect, the trees were responding similarly to common environmental factors.

The marked declines in growth around years 1953, 1966, 1988, and 1991 are associated with low precipitation. Examination of climatic data from the vicinity of the study site indicates that the annual precipitation for those years were 25–30% below the long-term average. Sharp declines in growth in 1988 and in the mid-1960s were also reported in other dendroclimatic studies (Cook and Jacoby, 1977; Rubino and McCarthy, 2000). Growth spikes in 1958, 1980 and 1992 are associated with increased amount of precipitation that occurred in those years. Growing season precipitation in 1958 and 1980 were 20–30% above the long-term average. In 1992, growing season precipitation was average but the increase in growth from 1991 to 1992 is due to the relative effect of higher precipitation in 1992 compared to the previous year (1991). Growing season precipitation in 1992 (61 cm) was twice larger than that in 1991 (31 cm).

3.4.2. Basal area growth

Basal area growth of all species showed an increasing pattern from 1935 to late 1950s, with a sharp decline in 1953 and a sharp increase in 1958 (Fig. 4). From 1960 to the end of the time series, basal area growth of yellow-poplar showed a more fluctuating pattern while the other three species showed a consistent increasing pattern. The most striking feature is that BAI of yellow-poplar declined for a 10-year period, from 1958 to 1968, with a short period of accelerated growth from 1962 to 1964.

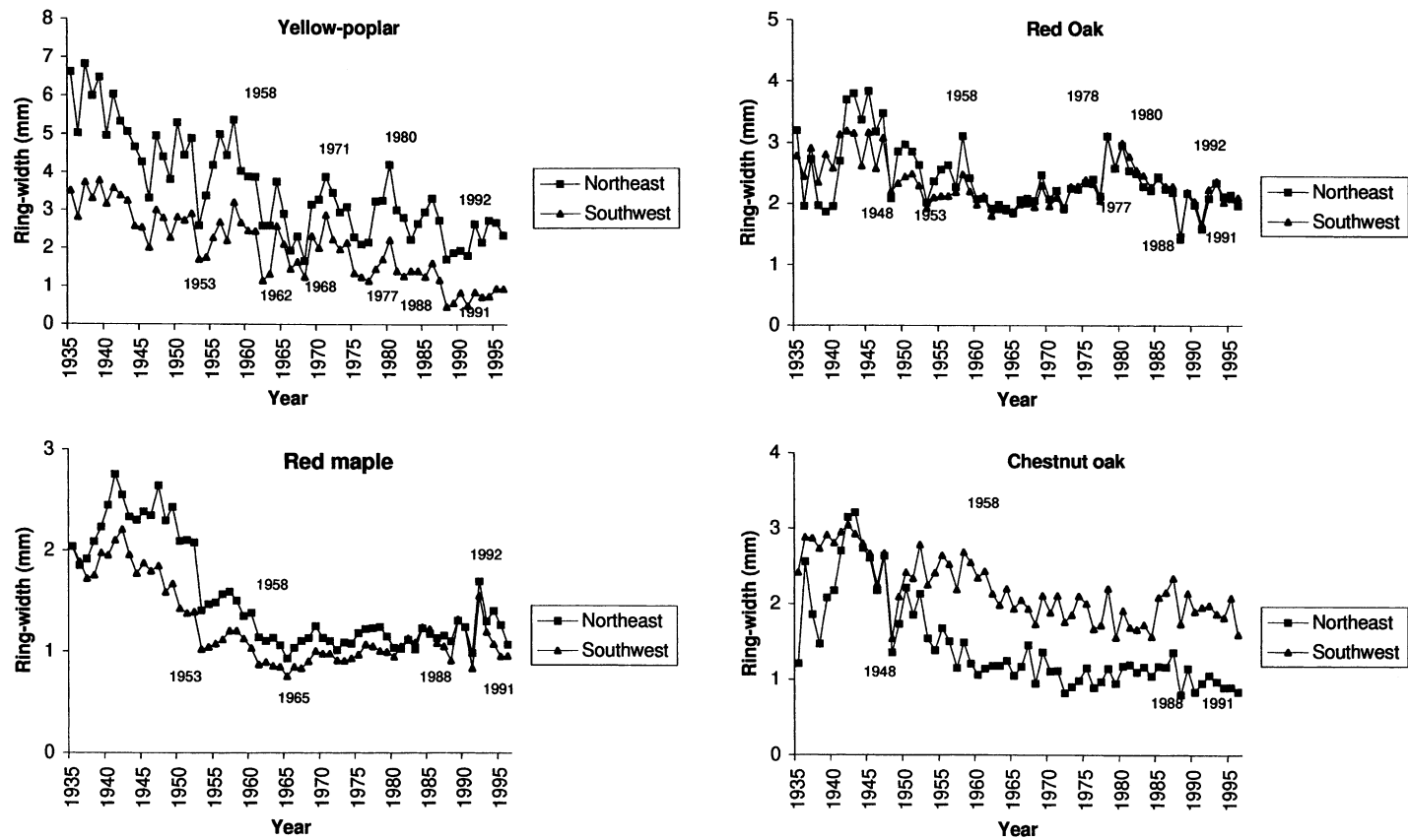


Fig. 3. The pattern of mean radial increment by species and aspect. Ring-width data from all trees of the same species were averaged by aspect. Species abbreviations are as in Fig. 1.

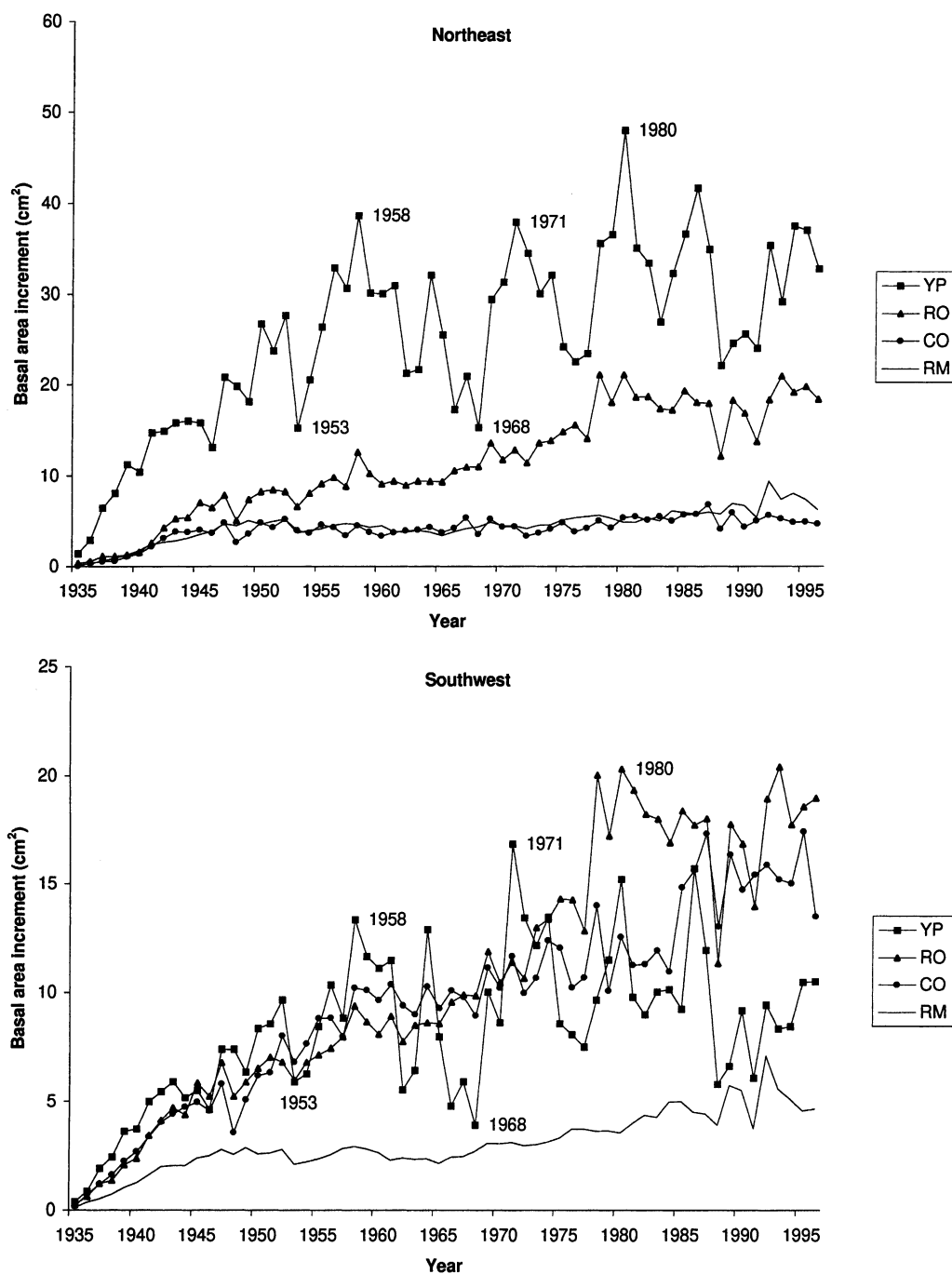


Fig. 4. The pattern of mean BAI by species and aspect. BAI data from all the trees of the same species were averaged by aspect. Species abbreviations are as in Fig. 1.

Table 3
Mean radial and BAI by species and aspect (1935–1996)^a

Species and aspect	dbh (cm)	Radial increment (mm per year)				BAI (cm ² per year)				
		Mean	S.D. ^b	Min ^c	Max ^d	Mean	S.D.	Min	Max	CV ^e
Yellow-poplar										
Northeast	39.5	3.61 a	1.32	1.67	6.82	25.3 a	12.0	1.38	48.0	47.3 a
Southwest	30.3	2.03 b	0.9	0.47	3.78	8.30 b	5.1	0.39	16.8	61.6 b
Red oak										
Northeast	28.9	2.41 c	0.53	1.46	3.84	11.3 c	4.5	0.32	21.1	39.7 a
Southwest	26.7	2.33 cb	0.40	1.42	3.19	10.6 cb	5.3	0.21	20.4	49.8 a
Chestnut oak										
Northeast	17.8	1.44 d	0.61	0.80	3.21	4.0 d	1.4	0.05	6.8	34.5 a
Southwest	23.0	2.20 c	0.42	1.54	3.04	9.4 c	4.3	0.18	17.4	46.5 a
Red maple										
Northeast	18.8	1.52 d	0.51	0.93	2.75	4.5 d	1.3	0.13	9.4	30.6 a
Southwest	15.5	1.25 e	0.39	0.76	2.21	3.1 e	1.4	0.12	7.1	44.3 a

^a Means with the same letter are not significantly different (alpha 0.05).

^b Standard deviation.

^c Minimum.

^d Maximum.

^e CV of BAI (%).

To better understand changes in growth trends, basal area growth of each species was analyzed by 5-year intervals (Fig. 5). The plots in Fig. 5 indicate that yellow-poplar was the only species that showed a pronounced decline in growth from late 1950s to late 1960s.

In the early 1960s, all species showed 10–15% smaller growth relative to late 1950s but the highest decline especially for yellow-poplar was observed in the late 1960s. Compared to mean BAI in late 1950s, BAI of yellow-poplar in the late 1960s was 32 and 38% smaller at the mesic and xeric sites, respectively. Red maple showed, on average, a 5–8% decline in BAI at both the sites. Growth declines in the late 1960s was not observed for the two oak species. The decline in growth from late 1950s to late 1960s is evidently associated with declining precipitation during this period (Fig. 6). Precipitation decreased from late 1950s to late 1960s. The recovery following the decline is associated with the increased precipitation in the early 1970s (Fig. 6).

Three periods characterized with substantial increase in BAI compared to the previous 5 years include the late 1950s, the early 1970s, and early 1980s. These spikes are more noticeable on yellow-poplar than the other three species.

3.5. Drought effects

The majority of the species showed below-average growth at both sites in all the drought years analyzed (Table 4(a)). However, significant below-average growth in all drought years analyzed was observed only for yellow-poplar. Northern red oak exhibited significant declines only in 1988 and 1991 but there were no significant declines for chestnut oak in any of the drought years analyzed. For yellow-poplar, the amount of decline was generally higher at the xeric site except in the extreme drought year (1966) in which case the decline at the mesic site was larger (Table 4(a)).

How did growth rate in drought years compare to pre-drought levels? In all drought years analyzed, yellow-poplar at both the mesic and xeric sites showed significantly smaller growth compared to its pre-drought growth rate (Table 4(b)). The decrease in growth during drought years relative to pre-drought growth rates ranged from 27 to 50% with those at the xeric site experiencing the highest percent reduction (except in 1996). Red oak and chestnut oak showed significant drought-induced reductions in 1988 (both sites) and 1953 (mesic site) compared to pre-drought

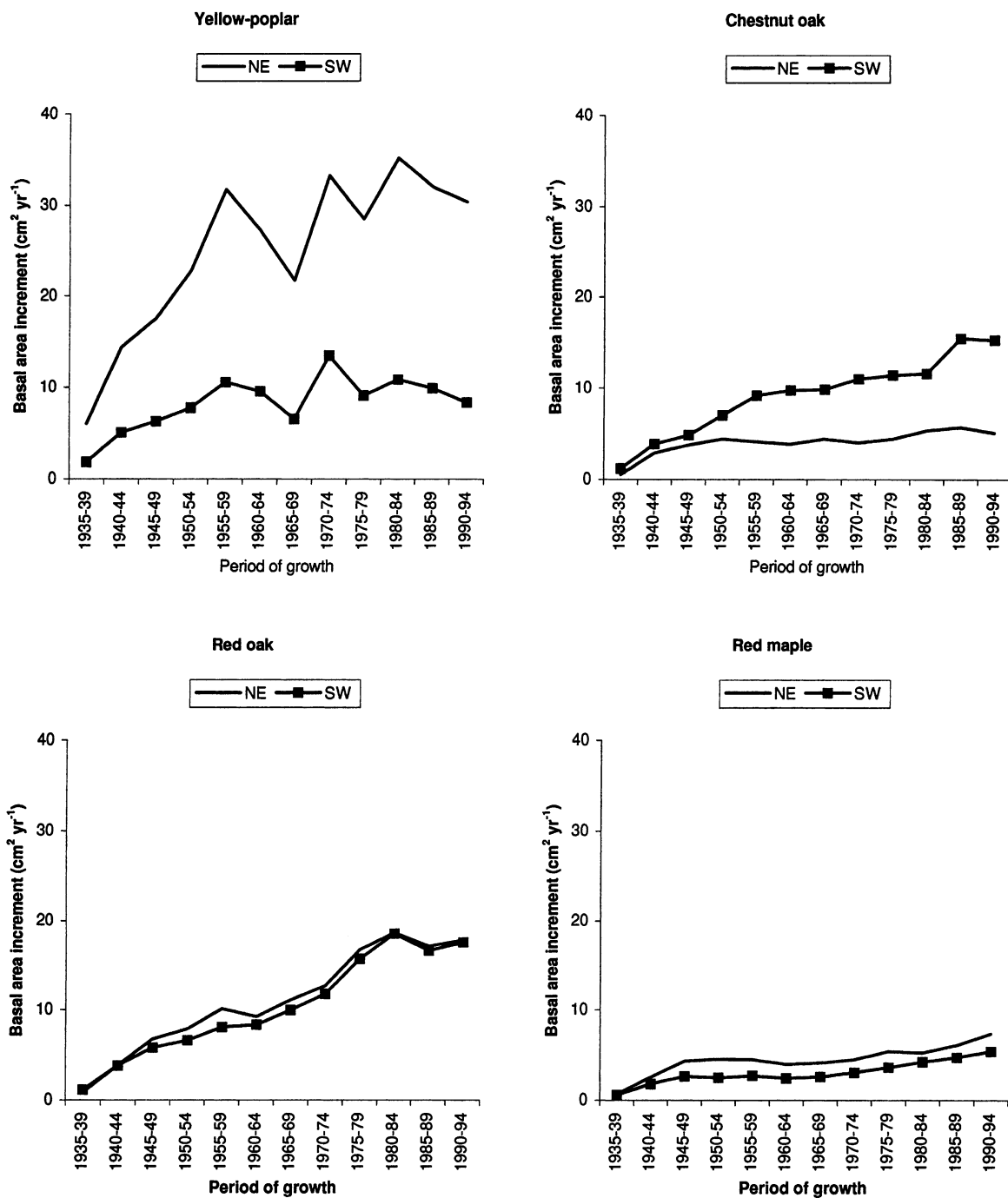


Fig. 5. Mean BAI at intervals of 5 years. Based on all trees of the same species, BAI data were averaged for non-overlapping 5-year intervals. Site abbreviations as in Fig. 2.

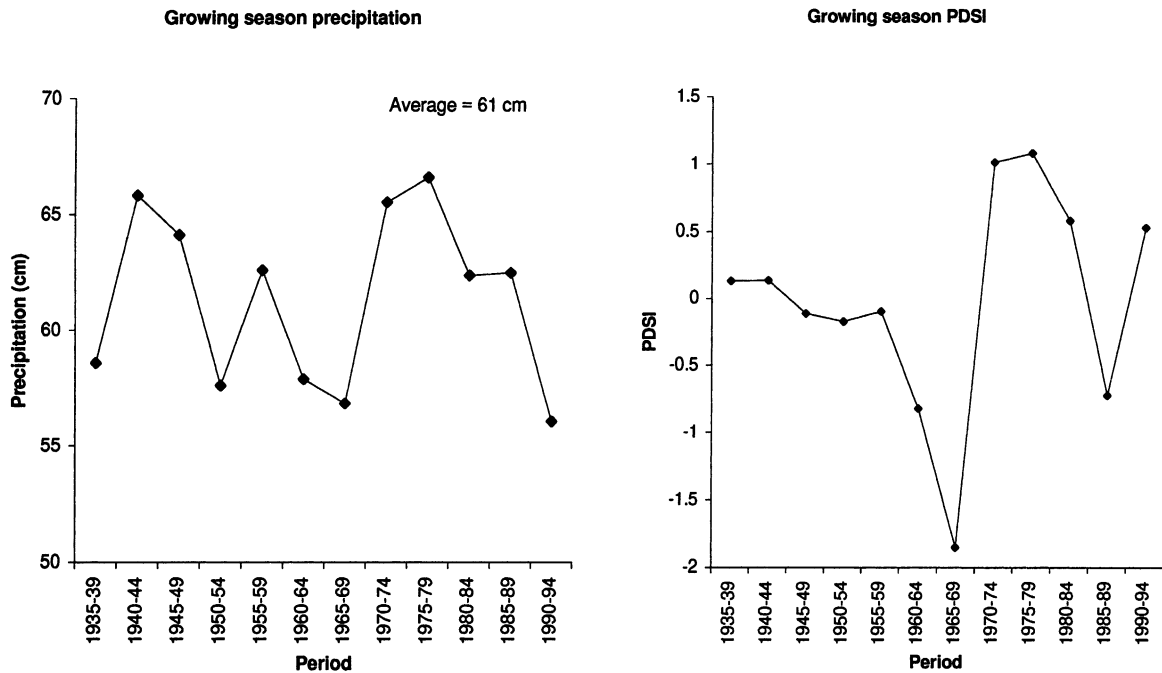


Fig. 6. Growing season precipitation and PDSI by 5-year intervals. Precipitation and PDSI from May to September were averaged for non-overlapping 5-year intervals.

Table 4
Percent growth change^a in RWI

Species	Aspect	(a) Drought year vs. average				(b) Drought year vs. prior year				(c) Pre-drought vs. post-drought				(d) 5-year pre-drought vs. 5-year post-drought			
		1953	1966	1988	1991	1953	1966	1988	1991	1953	1966	1988	1991	1953	1966	1988	1991
Yellow-poplar	Northeast	-36	-40	-32	-26	-46	-33	-38	-6	-28	-18	-30	37	11	0	-21	13
	Southwest	-39	-31	-42	-29	-50	-27	-50	-30	-47	-16	-39	27	-14	21	-22	12
Red oak	Northeast	-21	-14	-33	-26	-24	12	-34	-20	-10	14	1	6	0	15	-8	10
	Southwest	-20	-10	-38	-25	-17	10	-42	-19	-7	10	-5	11	-2	10	-11	6
Chestnut oak	Northeast	-9	-11	-14	6	-27	14	-39	16	-32	44	-13	30	-13	15	-9	-5
	Southwest	-5	-3	-8	8	-21	9	-30	4	-13	2	-10	7	21	-5	3	-8
Red maple	Northeast	-18	-25	1	-8	-32	13	-4	-20	-27	21	14	30	-22	16	19	17
	Southwest	-22	-23	-8	-16	-25	13	-13	-33	-22	12	25	25	-15	17	9	3

^a Percent growth changes in RWI are calculated as follows:

Drought year vs. average (%) = $[(M1 - M2)/M2] \times 100$

Drought year vs. prior year (%) = $[(M1 - M3)/M3] \times 100$

Pre-drought vs. post-drought (%) = $[(M4 - M3)/M3] \times 100$

5-year pre-drought vs. 5-year post-drought (%) = $[(M6 - M5)/M5] \times 100$

where M1: RWI in the drought year; M2: average RWI; M3: RWI 1 year prior to drought; M4: RWI 1 year after drought; M5: average RWI of 5 years prior to drought; M6: average RWI of 5 years after drought. Percent growth changes $< |24|$ were not significant at 5% level.

levels. Red maple growth in 1953 (both sites) and 1991 (xeric site) were significantly smaller compared to pre-drought levels.

Growth comparisons before and after droughts (Table 4(c)) revealed that all species at both aspects grew more slowly following the drought in 1953. Growing season precipitation in 1953 (41 cm) was 32% below average. Yellow-poplar was the only species that experienced statistically significant growth reductions at both sites following the drought in 1953 and 1988. For the recovery period immediately following the extreme drought in 1966, all species, except yellow-poplar, showed higher growth rates compared to pre-drought levels. That is, for red oak, chestnut oak, and red maple, radial growth in 1967 was larger than that in 1965, which was also another moderate drought year with growing season PDSI of -2.1 . All species recovered following the drought in 1991. This was probably because the growing season precipitation in 1992 (61 cm) was twice than that in 1991 (31 cm).

Average growth in the 5-year period following drought events was not significantly smaller for any species or site combination than the corresponding pre-drought growth rates (Table 4(d)). This indicates that drought effects at the study site were short lived. The only exception is a 20% smaller growth in the 5-year period following the 1988 drought for yellow-poplar but it was not significant.

4. Discussion

The ecological growth strategies of the four species is well illustrated in Fig. 4. For example, yellow-poplar, on mesic sites displays a rapid growth rate, indicating that the trees were exploiting the abundant resource to gain an early competitive advantage. On these sites, northern red oak began slower, but sustained its growth. Chestnut oak, although, it displayed a consistent rate of growth, was clearly at a competitive disadvantage on mesic sites while red maple growth was characterized by an early surge, followed by a plateau, then a subsequent increase. This probably relates to overtopping of red maple by faster-growing species followed by a natural thinning process during and after which the shade-tolerant maples were able to respond. On the xeric site, yellow-poplar displayed

the same rapid early growth, as did red maple, but both species slowed dramatically at about age 15–30. The red oak was able to sustain its basal area growth at a more-or-less constant rate, regardless of aspect and the chestnut oak actually grew more on the xeric site, illustrating its competitive advantage on such sites.

Among the four species, yellow-poplar showed declining basal area growth from 1958 to 1968 (Fig. 5) parallel with the pattern of precipitation and PDSI (Fig. 6). This suggests that the decline is most likely linked to below-average precipitation. Consecutive droughts, a moderate drought in 1965 and an extreme drought in 1966, seem to be the causal factor for the reduced growth rate during the late 1960s.

Generally, all species experienced reduced growth rates in the 1960s but the effect on yellow-poplar was the greatest. The apparent one-to-one correspondence between the growth of yellow-poplar and precipitation indicate that yellow-poplar is more sensitive to moisture than the other three species. This can also be seen from the high correlation between radial growth of yellow-poplar and growing season precipitation (Table 5). It was very interesting that in this even-aged mesophytic forest, yellow-poplar was the only species substantially affected by periods of lower than average precipitation.

Table 5
Correlation coefficients between species mean RWI values and growing season precipitation and PDSI

Species and aspect	Growing season precipitation	Growing season PDSI
Yellow-poplar		
Northeast	0.41*	0.25*
Southwest	0.59*	0.27*
Red oak		
Northeast	0.31*	0.22
Southwest	0.35*	0.26*
Chestnut oak		
Northeast	0.28*	0.18
Southwest	0.33*	0.22
Red maple		
Northeast	0.20	0.23
Southwest	0.31*	0.34*

* Coefficients are significant at $\alpha = 0.05$ level.

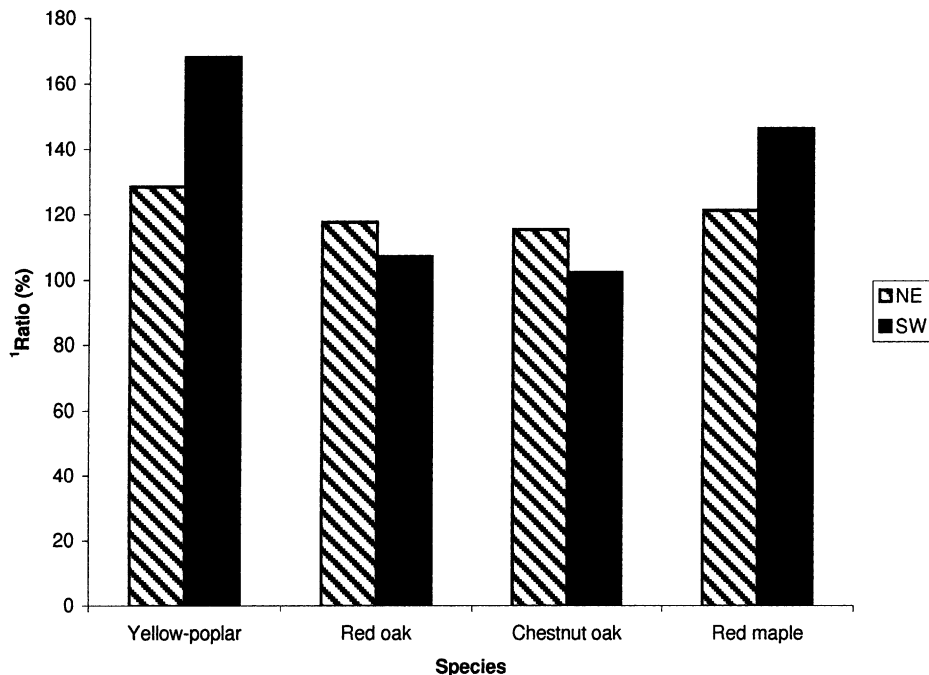
Growth declines in 1960s, especially from 1961 to 1966, have been reported by other researchers in northeastern United States (e.g., Cook and Jacoby, 1977; Lorimer, 1984). The subsequent recovery of growth rates in the 1970s (Fig. 5) suggests that the wetter than average condition of this decade is responsible for this (Fig. 6). The strong recovery in the early 1970s suggests that the decline in the previous years was temporary. In general, in this study, temporary periods of declining growth coincided with periods of documented below-average precipitation and there were no obvious unexplained growth declines.

This study revealed several trends in the ring-width response to droughts. Yellow-poplar showed larger drought induced growth decreases on xeric sites except during the extreme drought year of 1966 where the opposite was true. Due to the development of larger aboveground biomass of trees growing on north east aspects, these trees may become more stressed when subjected to drought than trees on southwest aspects which have a more balanced root:shoot ratio.

This may explain why yellow-poplar trees experienced larger drought-induced growth decrease at the mesic site during the extreme drought year of 1966. For red oak, chestnut oak and red maple, there was no clear trend in drought-induced growth decrease between the mesic and xeric aspects.

The ratio of growth in wet years to dry years (Fig. 7) also suggest a clear drought response–site interaction for yellow-poplar. The data shows that relative to growth during dry years, growth of yellow-poplar in moist years was 30% larger at the mesic site and 68% larger at the xeric site. Red oak and chestnut oak showed negligible difference between the mesic and xeric sites.

Comparison of pre and post-drought growth rates of the species generally indicate that the more conservative species (red oak, chestnut oak and red maple) tend to recover their growth following drought faster than yellow-poplar but when precipitation in the year following the drought is higher (example 1992) the increase in growth rate of yellow-poplar is much larger



$$^1\text{Ratio} = (\text{Average RWI in 8 wet years} / \text{Average RWI in 8 drought years}) * 100$$

Fig. 7. Radial growth in wet years expressed as a percent of drought years.

than the other three species. Generally, the two oak species were less affected by drought compared to yellow-poplar, and red maple was intermediate in response.

Drought and drought-related growth decline in mesic forests of the eastern US have been shown to last for only a few years (Cook and Jacoby, 1977) and growth recovery is relatively rapid (Orwig and Abrams, 1997). For example, reviewing a 374-year chronology of white oak in Ohio, Rubino and McCarthy (2000) found that only one of the 10 severe droughts resulted in an extended (5 years) growth decline. In the current study none of the species showed significant growth declines 5 years following drought events. The longest drought effect observed was for yellow-poplar where mean growth 3 years following the drought in 1988 was 33% smaller than the pre-drought 3-year average.

It is interesting to note that although 1988 is classified as a moderate drought year ($PDSI = -2.65$) compared to 1966 classified as an extreme drought year ($PDSI = -4.00$), the magnitude and frequency of growth declines of the species (especially yellow-poplar) was higher for the drought that occurred in 1988. In addition, growing season precipitation in 1988 (53 cm) was higher than in 1966 (45 cm). Growth declines in 1988 have been reported in other dendroclimatic studies (e.g., Abrams et al., 1998; Rubino and McCarthy, 2000). The two oak species also showed large declines in 1988 compared to 1987 (Table 3) but their growth following the 1988 drought was not reduced as much as that of yellow-poplar compared to pre-drought rates. This supports the conclusion that although drought is a major factor controlling radial growth of trees, it is not the sole factor. Other factors such as temperature, inherent characteristics of species, site interactions and tree age may confound the effects of drought in any given period and may serve to amplify or diminish its impact.

5. Conclusion

Regarding the interaction between drought response and topographic aspect, the study concludes that the difference in drought response between the mesic and xeric site were mild or negligible for the more conservative species and was highly significant for the

exploitive species. The result from such studies can be influenced by severity of drought, site conditions, age, inherent characteristics (e.g., drought tolerance and competitive strategy) of the species and other factors. Although this study evidently indicates the high sensitivity of yellow-poplar to both the changes in climate and topographic aspect, it is a less preferred species, compared to oaks, for dendroclimatic (climate reconstruction) studies. The species has a high potential for such studies and should be considered so.

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