ORIGINAL ARTICLE

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Differential drought responses between saplings and adult trees in four co-occurring species of New England

Abstract Tree-ring characteristics in four species were examined to address whether co-occurring mature trees of different successional status respond differently to drought, and whether saplings of these species have a greater response to drought than mature trees. We examined saplings and mature trees of paper birch, yellow birch, red maple and sugar maple, which varied in successional status (shade-tolerance) and co-occurred at Harvard Forest, Petersham, Mass., USA. Three drought events in 1964–1966, 1981 and 1995 were identified using climate data. For mature trees, there was no significant interspecific difference in relative changes in ring-width index (RWI) during the 1964–1966 and 1995 drought events. However, the interspecific difference was significant in the 1981 drought event. Response function analysis for mature trees showed that the radial growth of sugar maple was mainly controlled by spring and summer precipitation, red maple by spring and summer precipitation and temperature, yellow birch by winter and summer precipitation, and spring and summer temperature, and paper birch by spring and summer precipitation and spring temperature. Saplings of sugar maple and yellow birch, but not red maple and paper birch, showed significant positive correlations between RWI and annual total precipitation. In the 1995 drought event, saplings and mature trees of red maple and paper birch differed significantly in drought responses, but this was not true in sugar maple and yellow birch. Our results do not support a generally greater response in saplings than in mature trees, nor an early- versus late successional difference in drought responses.

Keywords Drought · Dendrochronology · Ontogeny · Temperate forest · Harvard Forest

Introduction

In ecology, experimental results from tree seedlings and saplings are widely used to extrapolate to possible responses of mature individuals (Ehleringer and Field 1993). This approach is particularly common in global change research (Körner 2000; Norby et al. 1999), because experimental manipulations for adult trees in elevated CO_2 and temperature are still subject to major limitations. It is currently unclear how valid this extrapolation is, as many biological processes change in rate as organisms grow and age.

Size-dependence of metabolism has been a central concept in zoology (Krebs 2001). By comparison, size dependence of physiological traits in plants has received much less attention (Thomas and Winner 2002), although evidence from dendrochronology has demonstrated that tree-ring growth responses to climate are age-dependent (Szeicz 1997; Szeicz and MacDonald 1995). As trees develop, they increase both in size and structural complexity. Age-related physiological changes result in part from the volume and depth of soil explored by root systems (Clark 1983), which generally leads to an increase in the magnitude of root systems and overlap of nutrient depletion zones around roots (Berntson 1994). As trees increase in height, distances over which photosynthate and hormone molecules must be transported increase as well. Thus it is possible that the responses to environmental conditions shift with plant life-stages (Bazzaz 1996; Sandquist et al. 1993).

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Recent studies have emphasized the importance of ontogenetic changes in physiological processes between juvenile and mature trees (Bazzaz et al. 1996; Kolb et al. 1998). Frazer and Davis (1988) found differences in seedling and adult water potentials as a function of rooting depth and soil moisture. Donovan and Ehleringer (1991) reported that carbon isotope discrimination values for leaves of two Great Basin species, *Chrysothamnus nauseosus* and *Salix exigua*, were significantly greater for juvenile plants than for adult plants growing in the same habitat, indicating that juvenile plants are less water-use efficient. Studies also showed that leaf characteristics develop in continuous, and potentially nonlinear, patterns during tree ontogeny (Thomas and Ickes 1995). Juvenile and mature plants were also found to differ in ecophysiological characters in several *Quercus* species in the prairies (Bragg et al. 1993; Knapp and Fahnestock 1990), in *Q. laevis* in a sandhill community (Donovan and Pappert 1998), and in *Q. rubra* in New England forests (Cavender-Bares and Bazzaz 2000). For example, photosynthesis of *Q. rubra* was depressed more severely in seedlings than in mature trees in a drought year in comparison with a wet year, and the maximum photosynthetic rate of mature trees of the same species is three- to sixfold greater than that of seedlings in New England (Cavender-Bares and Bazzaz 2000). In a recent review, Thomas and Winner (2002) provided a quantitative summary of studies comparing photosynthetic processes of saplings and mature trees.

For temperate forests, a research framework for scaling seedling responses to mature trees in response to CO_2 elevation has been developed (Bazzaz et al. 1996), which takes into account not only growth environmental differences between seedlings and mature trees, but also ontogenetic differences between seedling and adults. While previous studies have focused mainly on how physiological traits change with life-stage, it is also important to investigate how whole-plant responses change with ontogeny, and how these short-term physiological changes correlate with whole-plant responses.

Theoretical and experimental work suggests that species must differ somehow in resource requirements in order to coexist in a community (Bazzaz 1987; May 1974). Therefore, co-occurring species are assumed to occupy somewhat different niches, with minimal niche overlap (May 1974). Thus, within a tree community, the behavior of species in different successional status and distinct ecological characters might be different (Bazzaz 1987, 1996).

Drought intensity and frequency are considered important influences on plant distribution and productivity around the world (Kramer 1983; Lange et al. 1982; Ogle et al. 2000; Yordanov et al. 2000). Examination of tree-ring patterns in different species and ages may be helpful in elucidating the variation in tree responses to past climate conditions, especially during drought years (Abrams et al. 1998; Cook and Jacoby 1977; Jacobi and Tainter 1998).

This study was designed to assess (1) how co-occurring species in the same soil series differ in radial growth responses to drought, and (2) how juvenile and mature trees differ in responses to drought. Since seedlings and saplings usually have smaller and shallower root systems than mature trees and occur in the soil layers that are most susceptible to soil drying, largely due to transpiration of neighboring trees, we assume that juveniles would be affected by drought stress more severely than mature trees. We further predicted that species with a broader soil moisture tolerance would be less affected by drought stress than those with a narrower soil moisture demand, and these differences might shift with plant life-stages.

Materials and methods

Site characteristics

This study was carried out at the Harvard Forest, Petersham, Mass. (42°30′N, 72°15′W), which has been maintained as an experimental area since 1907. Physically, the Harvard Forest exceeds 1,215 ha in north-central Massachusetts, and includes hardwood and conifer forests, and plantations. The forest is situated in the transition hemlock [*Tsuga canadensis* (L.) Carriere]—white pine (*Pinus strobus* L.)—northern hardwood vegetation zone (Spurr 1956) with altitudes ranging from 220 to 410 m a.s.l. The soils are based on a bedrock dominated by granite, gneiss, and schist, overlain by sandy loam glacial till, producing soils that are moderately to well drained (Stout 1952). The study area comprised principally red oak (*Quercus rubra* L.), hemlock, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), white pine and paper birch (*Betula papyrifera* Marsh.), with scattered individuals of sugar maple (*Acer saccharum* Marsh.) (Foster 1992).

Tree-ring materials

Four species of two dominant genera, red maple, sugar maple, paper birch, and yellow birch, were selected for the study for two reasons. First, these four species differ in successional status, shade tolerance and soil moisture preference (Table 1). Sugar maple is regarded as the most shade-tolerant of the North American broad-leaved species, and appears to have considerable water requirements (Burns and Honkala 1990). In contrast, red maple is widely thought to be less shade-tolerant, and thrives on many landforms under different soil conditions and under widely varying moisture and light regimes (Abrams 1998; Sipe and Bazzaz 1994, 1995). Yellow birch is late successional in New England forests relative to paper birch, but early-successional relative to sugar maple (Wayne and Bazzaz 1993). Paper birch has a broad soil moisture preference, while yellow birch requires moderately high soil moisture levels. Second, two pairs of congeners were selected in order to minimize confounding effects due to phylogenetic constraints. These four species co-occur at Prospect Hill in Harvard Forest due to different land use history and management practice (Spurr 1956).

Table 1 The habitat and life historical traits of four study species (Burns and Honkala 1990; Sipe and Bazzaz 1994, 1995; Spurr 1956; Wayne and Bazzaz 1993)

	Betula papyrifera	*Betula alleghaniensis*	*Acer rubrum*	*Acer saccharum*
Successional status	Pioneer to early	Mid-late	Early-late	Late
Shade tolerance	Intolerant	Moderate tolerant	Tolerant	Very tolerant
Soil moisture preference	Broad-dry	Moderate-high	Broad	High
Longevity (max, mean years)	200+, 75+	300+, 90+	200+, 90+	400+, 150+
Mean mature size				
Height (m)	15+	15–20	18+	20+
Diameter (cm)	25–50	60+	45–75	50–90
Minimum fruiting age (years)	15	60	4	40–60

We collected tree-ring samples from saplings and mature trees at four tracts of Prospect Hill, all on well-drained sandy loam soils to minimize differences between site features. At each tract, two cores per tree were collected from five mature canopy trees of each species (located at the center, east, west, north and south of each tract) following Fritts (1976). In total, 160 cores were collected (2 cores × 5 individuals × 4 species × 4 tracts). Stem discs of 2–3 cm in thickness were collected from five saplings of each species at a height of 0.1 m. Saplings were selected in open sites so that the light conditions were similar to the mature individuals. A total of 80 discs were obtained for saplings (1 disc × 5 individuals × 4 species × 4 tracts). It should be noted that, in the present study, saplings were defined as having a basal stem diameter of 2.8–8.5 cm, not yet reproductive, and ranging in age from 7 to 15 years old. Mature trees were defined as those whose crowns fully extended into the canopy, and were reproductive, with stems between 20 and 58 cm in diameter at breast height (DBH), and ages between 30 and 115 years old (Table 2). Compared to the average longevity of 75–150 years for the four species, our sample trees are relatively mature.

The core and disk samples were prepared and sanded to enhance ring boundaries before measurement. Ring-width measurement was conducted using a uni-slide tree ring measuring system (Velmex, New York, N.Y., Measure J2+ measuring software), with a measurement precision of 0.01 mm. All cores were cross-dated using a method as described by Yamaguchi (1991), and the quality of cross-dating was examined by COFFECHA program (Holmes 1983).

Data analysis

Three severe drought events in 1964–1966, 1981 and 1995 were identified in Harvard Forest since 1960 using annual and summer (April–September) precipitation data (Harvard Forest Archives) and the Palmer Drought Severity Index (PDSI) of central Massachusetts (NOAA Online Climate Data, http://www.ncdc.noaa.gov/oa/climate/climatedata. html) (Fig. 1). PDSI incorporates the current conditions (i.e., for the current month) and the past conditions (the preceding several months), based on a water budget model that incorporates the balance between water supply, soil moisture, runoff, and water demand. PDSI values normally range from −4 (extremely dry) to +4 (extremely wet), and values near 0 are considered to reflect normal conditions (Palmer 1965). The three drought periods were selected because they contained the lowest growing season PDSI (April–September) during the past 40 years in central Massachusetts. The 1964–1966 drought event contained the second lowest growing season PDSI, and was the longest drought event in the twentieth century. The 1995 drought event was the severest drought in the past 30 years, but the following year, 1996, had the fourth highest growing season PDSI in the century with a PDSI value of 2.66 during the growing season. Therefore, the severity and length of these four drought events were different.

The cross-dated ring-width series were standardized to remove the age-related growth trend using the program ARSTAN (Grissini-Mayer et al. 1993), in which the detrending curve selected was a negative exponential curve, a horizontal line, or a straight line with negative slope. Ring-width index (RWI) chronologies for each species were

Table 2 Diameter at breast height (DBH) and age of the samples collected at four sites in Harvard Forest, Petersham, Mass., USA

| Species	Sample number	DBH (cm)				Age (years)			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Mature									
Betula papyrifera	20	25.9	4.47	20.0	34.7	43.0	6.71	30	60
Betula alleghaniensis	20	27.4	5.36	20.1	38.1	49.6	11.18	39	94
Acer rubrum	20	29.3	6.71	20.5	43.0	62.4	13.41	28	93
Acer saccharum	18	39.0	9.83	21.9	58.0	77.4	12.96	34	115
Saplings									
Betula papyrifera	20	6.4	1.16	3.8	8.5	10.0	3.58	7	15
Betula alleghaniensis	19	5.3	1.25	3.0	7.1	14.8	4.92	8	17
Acer rubrum	20	3.8	0.76	2.8	6.0	9.8	0.89	9	12
Acer saccharum	20	5.3	0.80	3.6	6.6	10.2	1.34	8	14
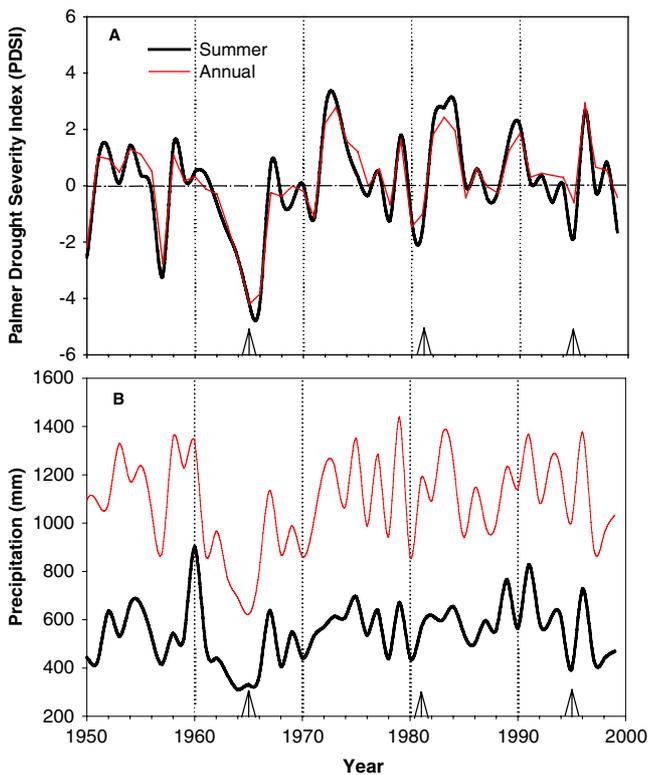
Fig. 1 Annual and summer (April–September) values of the Palmer Drought Severity Index (PDSI) in central Massachusetts (**a**) and annual and summer values of precipitation at Harvard Forest (**b**) for the time period 1950–1999. *Arrows* indicate the three severe drought periods examined in this study. The drought in the mid-1960s continued from 1964 to 1966

derived by averaging the standardized tree-ring series among the mature or juvenile individuals (Fritts 1976).

For mature trees, relationships between RWI and climatic variables are identified using the techniques of response function and correlation analysis. The response function, obtained by computer program PRECON (Fritts 1996), is a linear multiple regression technique that uses the principal components of monthly climatic variables to estimate tree-ring growth. This method overcomes the inter-correlation problems among climatic variables (Fritts et al. 1971). The response functions were calculated for the period of 1948–1999, which included at least ten sample replications for all species. During this period, there were no large-scale insect outbreaks nor pathogen attacks reported at Harvard Forest (Harvard Forest Archive). Correlation analysis helps to understand the climate-growth relationships by calculating Pearson's correlation coefficients between climate variables and tree growth. For mature trees, we calculated correlation coefficients between annual total precipitation and RWI. In case of saplings, it was only possible to carry out correlation analyses due to the brevity of the interval examined (<15 years).

The relative changes were calculated for each core as the change in RWI during drought years normalized to the 5 years prior and following the drought. For the 1995 drought event, however, the relative changes in RWI after the drought were normalized to 4 years (1996–1999).

During the 1964–1966 drought event, average RWI from 1964 to 1966 was calculated as the RWI of the drought year. For the 1995 drought event, the relative changes (%) in RWI were calculated for both mature trees and saplings. A three-way analysis of variance (ANOVA) was performed on species' relative growth values using the general linear model (GLM) procedure in SAS to determine the effect of species, sites, life-stage, and their interactions. Scheffé post hoc tests were used for subsequent multiple comparisons (SAS 1999).

Results

Ring-width chronology and drought responses

Generally, RWI of mature trees declined to various extents during the 1964–1966, 1981, and 1995 drought periods (Fig. 2, Table 3). The decreases in ring-width chronologies were greatest in the 1981 drought event, with all species experiencing dramatic decreases in RWI (Table 3). Except for red maple, all species experienced significantly below-average growth during the severe drought in 1965. During
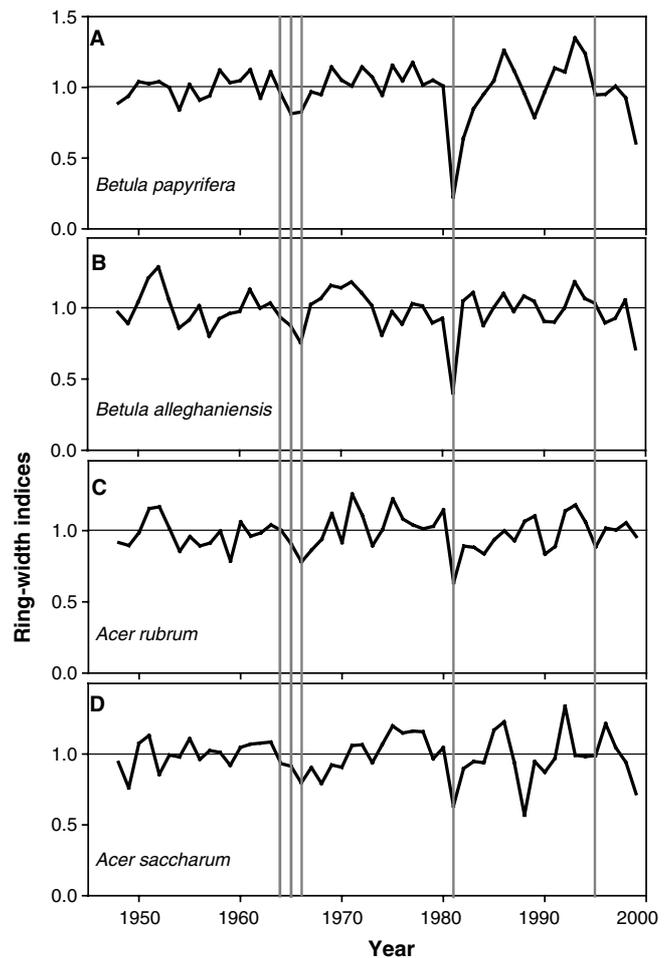

Fig. 2 Standardized ring-width indices for mature trees across four research sites at Harvard Forest. Sample size of each species was shown in Table 2. *Vertical bars* indicate the three severe drought periods examined in this study

Table 3 Relative changes (%, +1 SE) in ring-width index of mature trees for four species during three drought events. The relative changes were calculated for each core as the change in RWI during drought years normalized to the 5 years prior and following the drought. For the 1995 drought event, the relative change in RWI af-ter the drought was normalized to 4 years (1996–1999). During the 1964–1966 drought event, average RWI from 1964 to 1966 was calculated as the RWI of the drought year. Means in a column followed by the same letter are not significantly different at $P < 0.05$ by Scheffé post hoc tests for multiple comparisons

Species	1995 drought		1981 drought		1964–1966 drought	
	Mean	SE	Mean	SE	Mean	SE
From pre- to drought						
Betula papyrifera	−12.23 a	6.65	−77.69 c	1.97	−17.88 a	3.27
Betula alleghaniensis	−0.78 a	4.67	−53.42 b	4.88	−11.24 a	5.37
Acer rubrum	−9.37 a	6.22	−38.46 a	2.96	−4.98 a	4.95
Acer saccharum	−2.72 a	4.05	−40.60 a	2.71	−13.78 a	3.58
From drought to post						
Betula papyrifera	−4.75 a	5.32	494.90 b	74.50	20.94 a,b	3.91
Betula alleghaniensis	1.17 a,b	8.46	346.72 b	91.45	34.71 b	5.60
Acer rubrum	22.59 b	7.79	47.66 a	5.85	23.05 a,b	7.29
Acer saccharum	7.10 a,b	5.02	68.58 a	6.06	7.80 a	4.75

the 1995 drought there were large variations in the relative RWI changes as shown by standard error, although on average all species exhibited reductions in RWI (Table 3). There was no significant interspecific difference in relative changes in RWI in the 1964–1966 and 1995 drought events. However, the difference was significant in the 1981 drought event. Drought responses did not correspond perceptibly with successional status (Table 3).

The ring-width chronologies of saplings (Fig. 3) showed that sugar maple and yellow birch RWI decreased during the 1995 drought event, whereas paper birch RWI remained normal, and red maple RWI increased. The interspecific difference is significant at the 95% confidence level (statistical results are 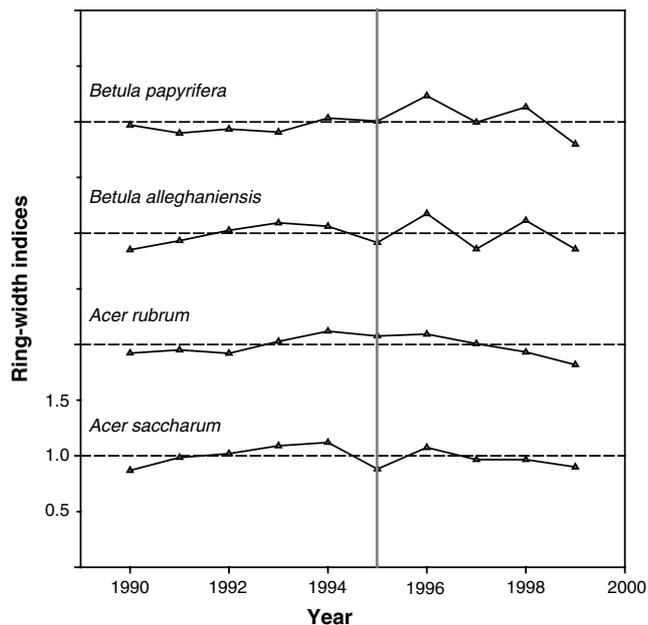not shown). Except red maple, the other three species experienced above-average growth immediately following the 1995 drought event.

Climate-growth relationships

The response functions of mature trees' ring-width chronologies with monthly mean temperature and monthly total precipitation are presented in Fig. 4. The RWI of
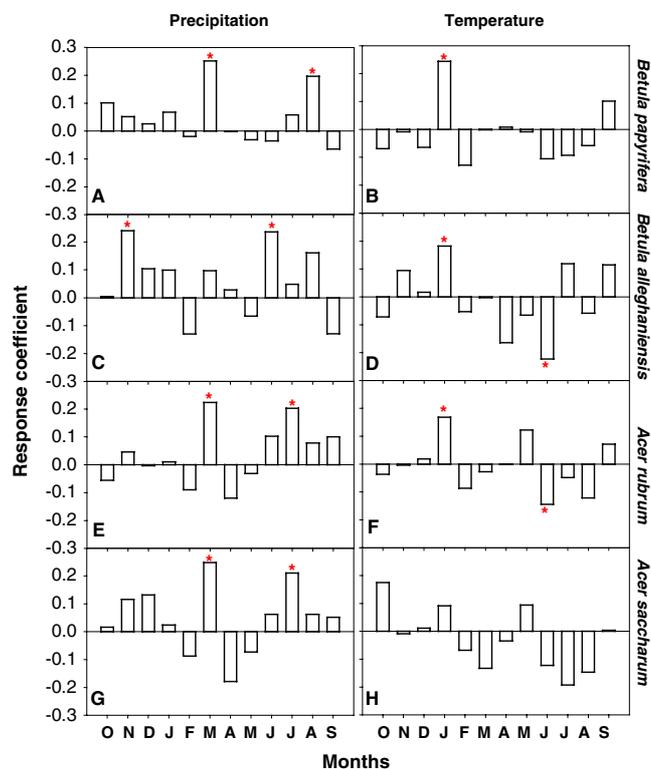
Fig. 3 Standardized ring-width indices for saplings across four research sites for the time period of 1990–1999 at Harvard Forest. Sample size of each species was shown in Table 2. *Vertical bar* indicates the severe drought in 1995

Fig. 4 Response functions of tree-ring chronologies. Monthly precipitation and temperature for the interval 1948–1999 are used to explain the variance in RWI. The *asterisks* above columns represent a significant ($P < 0.05$) effect of precipitation or temperature on RWI
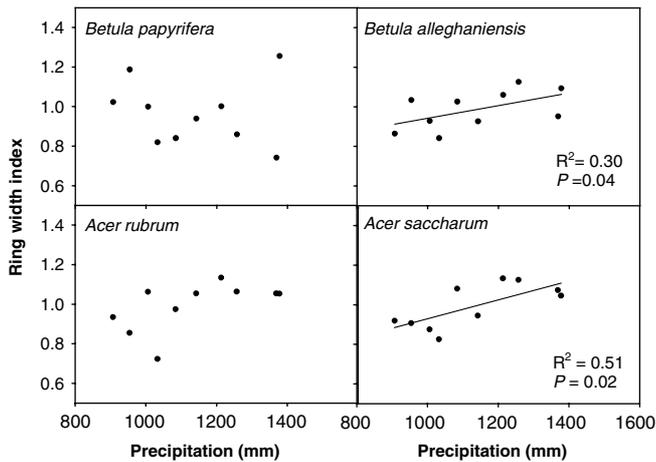
Fig. 5 The correlations between RWI and annual precipitation for saplings. Annual precipitation for the interval 1988–1999 was used

Fig. 6 Relative changes (%) in radial growth of saplings and mature trees for the 1995 drought. Sample size was shown in Table 2. *Error bars* represent 1 SE of the mean. The significance between saplings and mature trees (Scheffé post hoc comparisons, *$P<0.05$, ***$P<0.001$) are shown above each column pair. *B. allegha = B. alleghaniensis*

sugar maple and red maple are positively correlated with the March and July precipitation of the growth year. The RWI of yellow birch is positively correlated with the June precipitation of the growth year, and that of November of the previous year (Fig. 4). The RWI of paper birch is positively correlated with the precipitation in March and August of the growth year.

The response functions also demonstrate that the RWI of red maple and yellow birch are correlated positively with January temperature, but negatively with July temperature of the growth year. The RWI of paper birch is positively correlated with January temperature. However, the RWI of sugar maple does not significantly correlate with the temperatures of any month.

Thus, among mature trees, the relationships between RWI and climate differ between species. The RWI is positively correlated with precipitation in March (paper birch, red maple, and sugar maple), June (yellow birch), July (sugar maple and red maple), or November of the previous year (yellow birch). Additionally, the RWI is positively correlated with January temperature (paper birch, yellow birch, and red maple), and negatively correlated with July temperature.

The ring-width chronologies of saplings only cover a period of 10 years, which precludes the use of response function analysis. Pearson's product-moment correlation
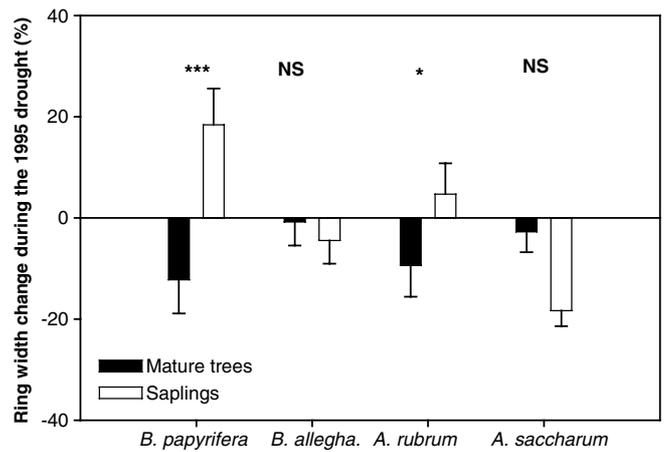
showed that annual RWI is positively correlated with annual total precipitation in late-successional sugar maple and yellow birch, but not in early- to mid-successional red maple and paper birch (Fig. 5). We also found that annual total precipitation is not significantly correlated with RWI for any of the mature species (figures not shown).

Differences in growth response between saplings and mature trees during the 1995 drought

Among the three drought events studied, only the 1995 drought can be used to compare the difference between mature trees and saplings, because the saplings only cover a period of about 12 years. In the 1995 drought event, the RWI of mature trees decreased on average from 0.78 to 12.23 %, with no significant interspecific differences (Table 3). Among saplings, sugar maple and yellow birch RWI decreased by 18.3 and 4.45%, respectively (Fig. 6). In contrast, both red maple and paper birch sapling RWI increased by 4.71 and 18.4% on average, respectively, exhibiting significant interspecific differences between sapling responses (statistical results not shown). Moreover,

Table 4 Analysis of variance on the effects of species, sites (tract), life-stage, and their interactions for relative changes (%) in ring-width index (RWI) of saplings and mature trees for the 1995 drought. The relative changes in RWI of both mature trees and saplings were cal-

culated for each core or disc as the difference between RWI in 1995 and the average RWI from 1990 to 1994 divided by the average RWI from 1990 to 1994

Sources of variation	Sum of squares	df	Mean squares	F value	P
Species	5,452	3	1,817	1.57	0.198
Site	1,863	3	6,21	0.54	0.658
Life-stage	3,547	1	3,647	3.15	0.077
Species × site	9,438	9	1,049	0.90	0.522
Species × life-stage	20,878	3	6,959	6.00	0.001
Site × life-stage	3,236	3	1,079	0.93	0.427
Species × site × life-stage	9,009	9	1,001	0.86	0.559

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the differences in relative changes in RWI between mature trees and saplings are significant in both red maple and paper birch, demonstrating an interaction between species and life-stage (Table 4, Fig. 6). From Table 3, large variations (standard error) in the relative changes for all species are obvious, indicating that, although RWI of saplings of red maple and paper birch increased on average, the RWI of a fraction of the population of both species decreased during the 1995 drought event.

Discussion

Interspecific differences in drought responses

In general, late successional plants are more sensitive to declining moisture levels than early successional plants (Bazzaz 1979). Leaf-level physiological studies had reported an inverse relationship between species successional status and drought tolerance (Abrams and Mostoller 1995; Bazzaz 1979). For example, photosynthesis of early-successional plants declines at lower negative water potentials (Bazzaz et al. 1996). Abrams and Mostoller (1995) also showed that both sunfleck and sun leaves of early successional species exhibited smaller decreases in area-based net photosynthesis than leaves of other species in response to drought. The results of a field study were consistent with the idea that seedlings of late successional sugar maple exhibit "conservative" water use patterns and have low drought tolerance (Ellsworth and Reich 1992). Similarly, we found that in this study that saplings of mid-successional yellow birch and late successional sugar maple exhibited reduced growth during the 1995 drought event. In contrast, mid-successional red maple and early successional paper birch both increased growth on average during the same event.

Several studies of seedling physiology have produced results diverging from those of the present study. For example photosynthesis of paper birch seedlings was more sensitive to decreasing soil moisture levels than that of yellow birch seedlings in a controlled experiment (Catovsky and Bazzaz 1999). Another study found that gas exchange reduction in response to drought stress was minimal in sugar maple compared to sweetgum (*Liquidambar styraciflua*) and American sycamore (*Platanus occidentalis*) (Tschaplinski et al. 1995). These short-term physiological changes, however, seem decoupled from whole-plant responses to drought. Processes that involve the transport and partitioning of carbon, nutrients and water between different parts of the plant may help explain this discrepancy between leaf- and plant-level activities (Wolfe et al. 1998).

Saplings and mature trees differ in drought response: life-stage shift

We found significant differences in relative changes in red maple and paper birch between saplings and mature trees. This is consistent with previous studies which found physiological parameters related to carbon and water relations may change with plant size and developmental stage (Cavender-Bares and Bazzaz 2000; Donovan and Ehleringer 1991; Donovan and Pappert 1998; Parrish and Bazzaz 1985). However, we observed different trends in response to drought with development among co-occurring species, i.e., saplings of red maple had no growth reduction and saplings of paper birch increased in radial growth, whereas mature individuals of both species experienced growth reductions during the 1995 drought event.

Generally, the difference between saplings and mature individuals has been considered to be due, in part, to the fact that saplings and mature trees may occupy different microhabitats (Donovan and Pappert 1998). As their shoot and root systems develop, seedlings and saplings begin to integrate into the environment, becoming less sensitive to small-scale fluctuations. Thus, mature plants may be buffered against changes in soil moisture because of their rooting patterns, and against changes in temperature and nutrient availability by their large above- and below-ground mass, enabling them to better access resources (Bazzaz et al. 1996). A recent study found that photosynthetic rates of seedlings and saplings of red oak were affected by drought more severely than mature trees, due both to their shallower rooting as well as to their inability to fix carbon at low water potentials (Cavender-Bares and Bazzaz 2000). In the current study, RWI of mature yellow birch trees correlated positively with November precipitation in the previous year, suggesting that mature trees with deep root systems may use deeper water reserves.

Previous studies have shown that plants have the ability to adjust water use efficiency during development. For example, mature trees appear to be able to increase their water use efficiency to a much greater extent during drought than seedlings (Cavender-Bares and Bazzaz 2000; Donovan and Ehleringer 1992). In contrast to our primary assumption, we found that red maple and paper birch saplings did not show growth reductions during the 1995 drought. Why are saplings with a shallow root system more resistant to drought than mature trees of deeper-root system? Ontogenetic effects may account for this puzzling result, as these differences may have a genetic and/or environmental origin (Donovan and Ehleringer 1991). In addition, the juvenile phase of plants lasts from germination to the onset of reproduction, and for woody plants the transition to reproduction is often a function of plant size (Harper 1977). Because of potential size differences among plants (both above and belowground), characteristics of juvenile and reproductive plants may vary in response to microenvironmental differences. The ecophysiological characteristics favored in each life-history phase may be distinct since juveniles are potentially under different selective pressures than reproductive plants.

Implication for scaling: evidence from this study

The objective of studies on seedlings and saplings is to extrapolate seedling establishment and sapling growth

to predict ultimate regeneration success and mature tree response to environment (Carlton and Bazzaz 1998; Ehleringer and Field 1993). From this study, it is apparent that the life-stage scaling factors between seedling and sapling differ across species. The feasibility of scaling depends on a thorough evaluation of these effects and how they vary under different environmental conditions. We found that growth responses of early successional tree species, like paper birch and red maple, were influenced to a greater extent by life-stage than later successional species.

Our results also suggest that scaling factors between seedlings and mature trees may vary with community types as well, or a scaling factor from individual to community should be considered. As co-occurring species differ in tolerance to drought, when water is limited in the soil, the more sensitive species may first respond by decreasing stomatal conductance. Thus, the community can maintain relatively higher water potential in the soil, and the less sensitive species will be minimally affected. As shown in Fig. 6, when saplings of sugar maple and yellow birch experienced growth reductions in the 1995 drought, co-occurring red maple and paper birch showed an average or above-average growth. The situation will be different when the plants are growing with different neighbors, i.e., different communities. The fact that the life-stage differences may depend on community types presents a challenge when scaling between seedlings and mature trees, potentially adding greater complexity to models of community response to climate change.

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