

# Population-level variation of *Fraxinus americana* (white ash) is influenced by precipitation differences across the native range

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**Summary** We investigated the potential of *Fraxinus americana* L. to adapt to climate change by comparing diameter growth, survival and physiological status of 44 populations of 30-year-old trees originating from throughout the species range and grown in a common garden. Populations originating closest to the latitude of the common garden had the most rapid diameter growth and the highest survival. Among populations originating within a narrow latitudinal band along an east–west gradient of decreasing precipitation, those from the drier western end were best adapted to the dry climate of the common garden site, as judged by survival, stem circumference, leaf and wood carbon isotope ratios, leaf mass per area and leaf nitrogen concentration. These findings suggest that eastern populations may not perform well under the hotter and drier conditions predicted by climate change scenarios. Moreover, in the event of significant climate change, the short-term acclimation responses (within a generation) of *F. americana* may be insufficient to ensure the continued vigor or survival of this species throughout much of its present range.

**Keywords:** carbon isotope ratios, climate change, common garden, fitness, global change, intraspecific variation, photosynthesis, physiological adaptation, stem circumference, stomatal conductance, temperate trees, tree rings, water stress.

## Introduction

If, as anticipated, there is rapid climate change during the 21st century, temperate tree species may be vulnerable to decline or extinction unless they are able to either migrate as rapidly as forest climate zone boundaries or adapt to the ongoing climate change within their current geographic range (Condit 1998, Gunter et al. 2000, Thuiller et al. 2006). It has been predicted that the survival of tree species will increasingly depend on evolutionary change, rather than migration (Davis and Shaw 2001, Etterson and Shaw 2001), because, according to even conservative climate change scenarios, forest climate zone boundaries will move more rapidly than tree species can migrate (Davis 1984, Davis and Zabinski 1992, Higgins and Harte 2006). Furthermore, tree migration will be impeded by fragmentation of forests as a result of agricultural and urban development, and species establishment may be unsuccessful

at new sites currently occupied by other species (Solomon and Kirilenko 1997).

In the short-term, the potential of tree species to respond to climate change will depend in part on phenotypic plasticity and in part on intraspecific genetic variation in adaptive traits (Ward and Strain 1997, Ward et al. 2000, Ward and Kelly 2004). Species with large ranges covering more than one climate zone usually exhibit large intraspecific variation in physiology, morphology and growth rate (Donselman and Flint 1982, Geber and Dawson 1993, Abrams 1994, Aspelmeier and Leuschner 2004). Several studies have documented that differences in physiological traits among tree populations reflect differences in climate at the place of origin (Schuler 1994, Palmroth et al. 1999, Aspelmeier and Leuschner 2004). Unfortunately, models that predict species redistribution with climate change often largely ignore population-level genetic variation (Hampe and Petit 2005, but see Zhang and Marshall 1995, Persson and Beuker 1997, Rehfeldt et al. 1999, Marshall et al. 2001, Rehfeldt et al. 2002), which may extend the predicted range of a species over a broader climate zone than previously assumed (Higgins and Harte 2006).

Of the few studies that have assessed the relationship between physiological traits and species fitness (Dawson and Ehleringer 1993, Farnsworth et al. 1996, He et al. 2005), most have focused on short-lived herbaceous species (Potvin and Toussignant 1996, Ward et al. 2000, Etterson and Shaw 2001). In this study, we examined intraspecific variation in physiology and growth among 44 populations of the temperate deciduous tree *Fraxinus americana* L. (white ash) grown in a common garden.

The natural range of *F. americana* includes the eastern half of the United States and extends into parts of southern Canada (see Figure 1; Schlesinger 1990). Within this range, the risk of severe drought is expected to increase in the central regions of the United States (McCarthy et al. 2001), and a reduction in summer precipitation is expected in the southeastern United States due to climate change (National Assessment Synthesis Team 2000, Mearns et al. 2003). Models predicting suitable habitat for tree species under future climate change scenarios indicate that the range of *F. americana* will decrease as the zone providing optimum growth conditions shifts northward (Iverson and Prasad 1999).



Figure 1. Sources (● and ○) of the 44 *F. americana* populations grown in the common garden, located at Nelson Environmental Study Area in northeastern Kansas, USA (Ú). Ten populations originating from along an east–west precipitation gradient are identified by open circles. The shading shows the natural range of *F. americana* in North America (USDA Forest Service, [www.na.fs.fed.us](http://www.na.fs.fed.us)).

Common garden studies with *F. americana* provide a means of investigating intraspecific variation in physiology and growth. The common garden in which this study was conducted is located in northeastern Kansas, at the western edge of *F. americana*'s current range (Figure 1). In this marginal habitat, where the required degree of adaptation may exceed the limits of phenotypic plasticity in some genotypes, one might expect the fullest expression of range-wide genetic variation in response to the particular stresses of the test site (Stanton et al. 2000, Paschke et al. 2003).

Our overall goal was to determine the capacity of *F. americana* to adapt to climate change by comparing population-level differences in physiological traits, survival and growth in a common garden. Our specific objectives were to: (1) quantify population-level variation in physiological traits; (2) examine if populations originating along an east–west precipitation gradient vary in adaptation to drought; and (3) determine if variation in physiological traits is correlated with variation in survival and overall growth.

## Materials and methods

### Common garden location and climate

*Fraxinus americana* trees selected for study were grown in a common garden planted in 1976 at the western edge of the species' current range (University of Kansas, Lawrence, Nelson Environmental Study Area (39.0° N, 95.1° W, 299 m a.s.l.; Figure 1). At the common garden site, mean annual precipitation is 879 mm, with large interannual variation ( $\pm 200$  mm SD); mean annual temperature is 11.9 °C, and mean temperature during the growing season (April–September) is 20.4 °C (Table 1, see Jefferson county, Kansas). Trees in the common

garden were 30 years old at the time of the study and were derived from open-pollinated seeds collected from native parent trees of each provenance (Table 1, Figure 1). There were 25 trees from each of 44 provenances. Climate data for the place of origin of each provenance were obtained from the meteorological station nearest to each site (National Oceanic and Atmospheric Administration National Climatic Data Center 2002, 2004; Table 1).

### Growth and survival

Growth of all populations in the common garden was assessed by measurement of stem circumference of surviving individuals at a height of 0.6 m above the ground (to avoid trunk bifurcation). Percent survival was recorded in spring 2004, 28 years after planting.

### Physiological variation along an east–west precipitation gradient

A subset of 10 populations originating within a narrow latitudinal range along an east–west precipitation gradient at the latitude of the common garden were selected for separate study (Table 1 and Figure 1). Mean annual precipitation at the source of these populations ranges from 765 mm year<sup>-1</sup> in the west (Otoe, NE) to 1261 mm year<sup>-1</sup> in the east (Tucker, WV). Populations in the common garden were compared for leaf morphology, gas exchange and stable carbon isotope ratios (leaves and wood).

### Leaf morphology

Leaf mass per area (LMA) was measured in the common garden for nine populations ( $n = 5$  trees) originating from within the east–west precipitation gradient, with sampling occurring during July 8–11, 2005. We also measured the LMA of five trees that were growing in close proximity to the common garden, which were similar to the common garden trees in stem circumference (Jefferson County, KS population). Only sun leaflets from the south side of each tree were collected for analysis. Leaflet tissue was dried at 70 °C for at least 48 hours.

### Gas exchange

Light-saturated photosynthesis ( $A_{\text{sat}}$ ) and stomatal conductance ( $g_s$ ) were measured in the common garden for nine populations ( $n = 5$  trees) from along the east–west precipitation gradient during July 8–11, 2005. Spring precipitation (April–June 2005) in the measurement year was similar to the 29-year mean for the common garden site. The month of June 2005 was wetter than the 29-year mean (207.2 mm versus 143 mm). There was only one substantial rain event in the period immediately preceding the measurements (22.9 mm on July 3). Mean predawn water potential of the trees was  $-0.769 \pm 0.048$  MPa on July 10. Measurements were made on leaflets from the south side of each tree with an open-flow infrared gas analyzer equipped with a red-blue light source (LI-6400, Li-Cor, Lincoln, NE) between 1000 and 1400 h. Inside the leaf cuvette, the CO<sub>2</sub> concentration was 380 ppm, irradiance was 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and the leaf block temperature was 30 °C.

Table 1. Climate at the common garden site (Jefferson, KS) and at the sources of 44 *Fraxinus americana* provenances (listed by county) grown in the common garden. Numbers in parenthesis indicate the number of populations from a single county, if more than one. The subset of populations representing the east–west precipitation gradient are shown in bold. Annual precipitation (mm) and temperature (°C) means are for the period 1931–2000 (National Oceanic and Atmospheric Administration 2002). Abbreviation: VPD = vapor pressure deficit.

Location	Latitude (° N)	Longitude (° W)	Elevation (m)	Annual precipitation (mm)	Annual temperature (°C)	Growing season VPD (kPa)
Jefferson, KS (Common garden site)	39.0	95.1	299	879	11.9	0.633
Ontonagon, MI	46.6	89.5	408	820	4.3	0.400
Forest, WI (2)	45.7	89.0	511	777	5.6	0.428
Presque Isle, MI	45.3	83.6	198	749	6.1	0.509
Penobscot, ME (2)	44.8	69.0	85	1083	6.2	0.519
Benzie, MI	44.7	86.0	236	793	6.4	0.530
Onondaga, NY	42.7	76.1	381	940	8.3	0.579
Washtenaw, MI (2)	42.2	83.7	259	799	9.0	0.637
<b>Wayne, OH</b>	<b>40.7</b>	<b>82.0</b>	<b>265</b>	<b>969</b>	<b>9.7</b>	<b>0.592</b>
<b>Otoe, NE</b>	<b>40.6</b>	<b>95.7</b>	<b>259</b>	<b>765</b>	<b>10.8</b>	<b>0.639</b>
<b>Adams, IL</b>	<b>39.8</b>	<b>90.7</b>	<b>213</b>	<b>943</b>	<b>10.9</b>	<b>0.633</b>
<b>Preble, OH</b>	<b>39.6</b>	<b>84.7</b>	<b>305</b>	<b>1035</b>	<b>11.7</b>	<b>0.699</b>
<b>Tucker, WV</b>	<b>39.1</b>	<b>79.5</b>	<b>762</b>	<b>1261</b>	<b>9.3</b>	<b>0.463</b>
<b>Effingham, IL</b>	<b>39.1</b>	<b>88.4</b>	<b>183</b>	<b>1025</b>	<b>11.9</b>	<b>0.631</b>
<b>Effingham, IL</b>	<b>39.0</b>	<b>88.4</b>	<b>177</b>	<b>1025</b>	<b>11.9</b>	<b>0.631</b>
<b>Randolph, WV</b>	<b>38.9</b>	<b>79.7</b>	<b>975</b>	<b>1261</b>	<b>9.3</b>	<b>0.463</b>
<b>Jackson, IN</b>	<b>38.9</b>	<b>86.0</b>	<b>191</b>	<b>1142</b>	<b>12.3</b>	<b>0.670</b>
<b>Jackson, IL (2)</b>	<b>37.7</b>	<b>89.4</b>	<b>158</b>	<b>1097</b>	<b>13.3</b>	<b>0.760</b>
Gallatin, IL	37.6	88.3	152	1125	13.3	0.680
Muhlenberg, KY	37.3	87.2	128	1220	13.9	0.547
Hopkins, KY (2)	37.3	87.6	139	1220	13.9	0.547
Overton, TN (3)	36.5	85.4	357	1408	13.6	0.627
Marion, AR (2)	36.4	92.8	274	1155	14.5	0.672
Boone, AR	36.4	93.0	274	1164	14.2	0.652
Bledsoe, TN (2)	35.5	85.2	396	1408	13.6	0.680
McMinn, TN	35.3	84.5	251	1263	13.9	0.690
Franklin, TN (2)	35.2	85.9	357	1408	13.6	0.680
Pickens, SC	35.0	83.0	229	1295	15.6	0.779
Union, GA	34.8	83.9	914	1378	15.3	0.738
Oktibbeha, MS (3)	33.4	88.8	116	1383	17.2	0.639
East Baton Rouge, LA (2)	31.5	91.0	9	1559	19.3	0.686
George, MS	30.8	88.8	76	1602	19.4	0.732

After stabilization of instrument and leaf responses (particularly  $c_i$ ), four measurements were recorded over a period of two minutes and averaged to determine  $A_{\text{sat}}$  and  $g_s$  of individual leaflets.

After the gas exchange measurements, the measured leaflets were harvested and assayed for total N on an area basis ( $N_a$ ). Leaf tissue for N analysis was dried at 70 °C and ground to a powder in liquid nitrogen. The N concentration of 4–5 mg of ground leaf tissue was measured with a C/N autoanalyzer (CE Instruments, Milan, Italy).

#### Carbon isotope ratios of leaves and tree rings

The mean carbon isotope ratio ( $\delta^{13}\text{C}$ ) of leaf tissues was determined for the 10 *F. americana* populations ( $n = 3–6$  trees) originating from sources located on the east–west precipitation gradient and grown in the common garden. In addition, six *F. americana* trees of similar stem circumference to the common garden trees and growing in close proximity to the com-

mon garden (Jefferson County, KS provenance) were also measured. Sun leaflets from each sampled tree were collected on August 27, 2004 from the south side of the canopy at a height of about 7.6 m and transported to the laboratory and oven-dried (70 °C, for at least 48 hours). Three leaflets from each tree were combined and ground to a fine powder in liquid nitrogen for  $\delta^{13}\text{C}$  analysis.

The  $\delta^{13}\text{C}$  of  $\alpha$ -cellulose from tree rings formed over a decade (1996–2005) was analyzed for five of the 10 populations ( $n = 3$  trees, with the exception of the Tucker, WV population where  $n = 1$ ), representing the ends and the mid-point of the precipitation gradient (Otoe, NE; Adams, IL; Preble, OH; Tucker, WV; Jackson, IN).  $\alpha$ -Cellulose was extracted as described by Ward et al. (2002).

We measured  $\delta^{13}\text{C}$  of both foliar tissue and wood  $\alpha$ -cellulose (1.8–2.2 mg per tin capsule) with an elemental analyzer (Carla Erba, Model 1110, Milano, Italy) coupled to a ThermoFinnigan Delta Plus gas isotope mass spectrometer (Bremen, Germany) at the Stable Isotope Mass Spectrometry Labora-

tory (Kansas State University, Manhattan, KS). Values of  $\delta^{13}\text{C}$  were calculated according to standard delta notation:

$$\delta = (R_{\text{sample}}/R_{\text{standard}} - 1)1000 \quad (1)$$

where  $R$  is the ratio of the heavy isotope ( $^{13}\text{C}$ ) to the lighter isotope ( $^{12}\text{C}$ ). The standard was belemnite carbonate from the PeeDee Formation, SC, and the precision of  $\delta^{13}\text{C}$  measurements was  $\pm 0.15\text{‰}$ .

#### Data analysis

The effects of the discrete variable, population, on stem circumference and tree survival was evaluated by a one-way analysis of variance (ANOVA). Within the subgroup of populations from along the east–west precipitation gradient, population effects on LMA, gas exchange measurements, leaf N and foliar  $\delta^{13}\text{C}$  were evaluated by ANOVA. The  $\delta^{13}\text{C}$  of  $\alpha$ -cellulose results for tree rings for five provenances from sources on the east–west precipitation gradient, selected a priori to represent the ends and mid-point of the precipitation gradient, were analyzed. The 10-year tree-ring  $\alpha$ -cellulose  $\delta^{13}\text{C}$  values were subjected to a two-way ANOVA, with population and date (or year) as the main effects and population  $\times$  date as the interaction term. All data were tested for normality with the Shapiro and Wilk's test ( $P \leq 0.05$ ). Logarithmic and power transformations were used to fit responses to a normal distribution when necessary. Relationships among measured variables and precipitation at the provenance site of origin of each provenance were evaluated by linear regression.

## Results

### Population-level responses from the species range

**Growth and survival** After 30 years of growth in the common garden, there were significant differences among the 44 *Fraxinus americana* provenances in stem circumference ( $P < 0.0001$ ) and survival ( $P < 0.0001$ ) (Figures 2a and 2b). Populations originating closest to the latitude of the common garden ( $39.0^\circ\text{N}$ ,  $95.1^\circ\text{W}$ ) tended to have the greatest stem diameters (Figure 2a) and the highest survival rates (Figure 2b). Growth and survival were highly correlated ( $P < 0.0001$ ; Figure 2c). The populations (Jackson, IL and Overton, TN) with the highest mean stem circumference (70 and 72 cm, respectively) and survival (100% and 88%, respectively) originated from latitudes close to that of the common garden ( $37.7^\circ\text{N}$  and  $36.5^\circ\text{N}$ , respectively). There was 100% mortality in the common garden in the population originating from the southern-most edge of the species' range (East Baton Rouge, LA), whereas the northern-most population (Ontonagon, MI) had a mean stem circumference of only 17 cm and a mean survival of 44%.

### Responses of populations from an east–west precipitation gradient

**Growth and survival** Mean stem circumference of the 10 populations originating from locations across the east–west

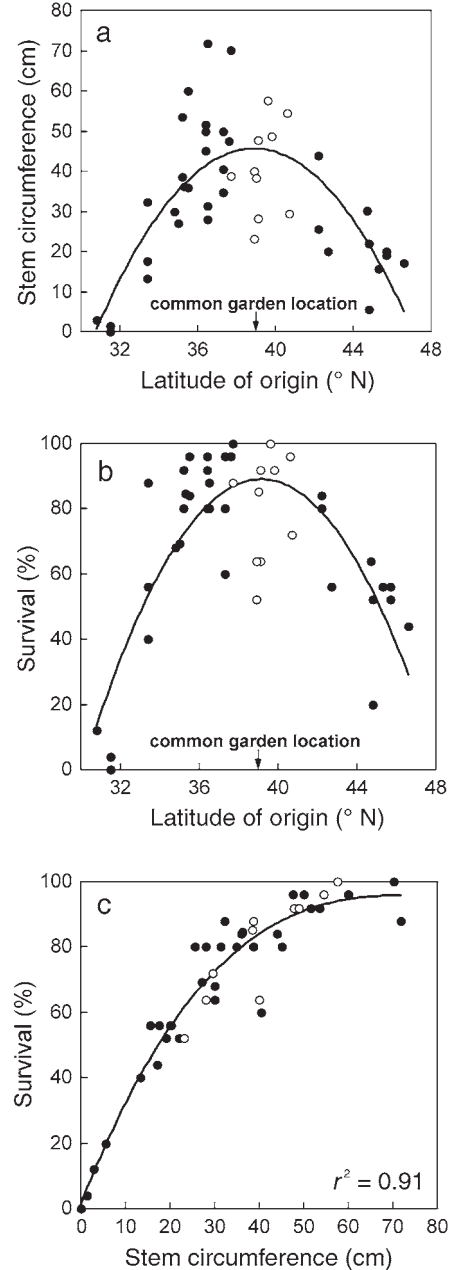


Figure 2. (a) Stem circumference ( $n = 1-25$ ) and (b) survival ( $n = 25$ ) regressed against latitude of origin for the 44 *Fraxinus americana* populations grown in the common garden located in Jefferson County, KS. (c) The regression of survival against stem circumference for the same *F. americana* populations. In all panels, populations representing an east–west precipitation gradient along latitude  $39^\circ\text{N}$  are identified by the open symbols.

precipitation gradient ranged from  $23.17 \pm 5.89$  cm (Randolph, West VA) to  $57.60 \pm 4.02$  cm (Preble, OH), and survival in these populations ranged between 52 and 100% (Figures 2a and 2b (open symbols) and Figures 3a and 3b). Populations from the eastern end of the precipitation gradient, where mean annual precipitation is highest, had lower growth and survival than populations from the drier, western end of the precipita-

tion gradient, which is closer to the common garden (Figures 3a and 3b). Among populations from locations along the precipitation gradient, there were significant positive correlations between both growth and survival and mean annual precipitation at the population source ( $r^2 = 0.48$ ,  $P = 0.0254$  for growth;  $r^2 = 0.65$ ,  $P = 0.0243$  for survival; Figures 3a and 3b).

**Leaf morphology and leaf nitrogen** The LMA of trees grown in the common garden varied significantly ( $P = 0.0041$ ) among the 10 populations (including the local population) originating from the east–west precipitation gradient, with populations from drier, more western regions having thicker leaves than populations from wetter, more eastern regions (Figure 4a). Values of LMA correlated with longitude of provenance origin ( $r^2 = 0.45$ ,  $P = 0.0350$ , data not shown) and mean annual precipitation at the provenance origin ( $r^2 = 0.58$ ,  $P = 0.0103$ ; Figure 4a) of the provenances. In conjunction with this finding,  $N_a$  was significantly correlated with mean annual precipitation at the provenance origin ( $r^2 = 0.44$ ,  $P = 0.0373$ ; Figure 4b), with populations from wetter locations (which had thinner leaves) exhibiting a lower  $N_a$  than populations from drier locations (which had thicker leaves). Foliar nitrogen concentration on a leaf mass basis varied significantly ( $P = 0.0379$ ) among populations, although among populations originating from the east–west precipitation gradient, the variation did not show a specific relationship with longitude (data not shown).

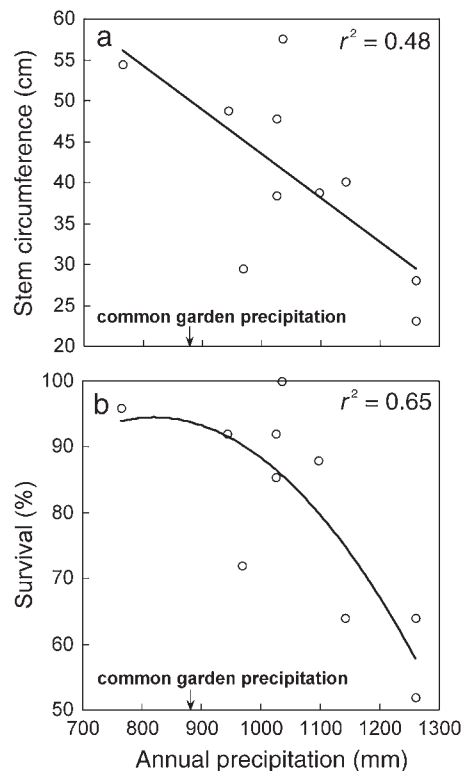


Figure 3. (a) Mean stem circumference ( $n = 16–25$ ) and (b) survival ( $n = 25$ ) of ten *Fraxinus americana* provenances from an east–west precipitation gradient grown in a common garden and regressed against mean annual precipitation at the population source.

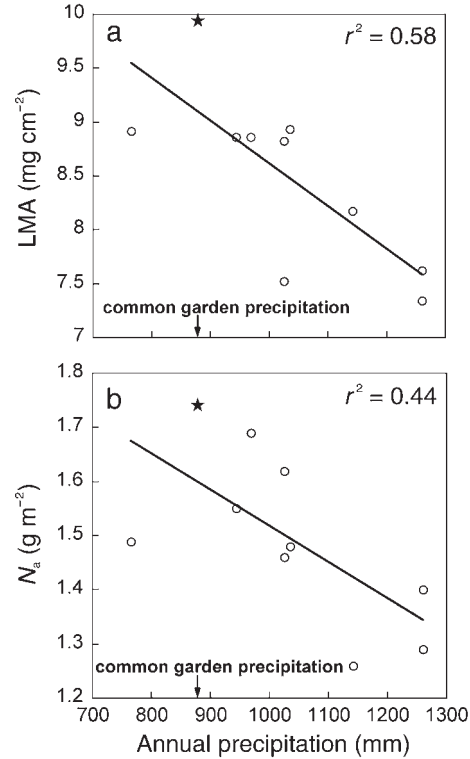


Figure 4. (a) Mean leaf mass per area (LMA;  $n = 5$ ) and (b) foliar nitrogen concentration on a area basis ( $N_a$ ;  $n = 5$  trees) of 10 *Fraxinus americana* provenances from an east–west precipitation gradient grown in a common garden regressed against mean annual precipitation at the population source. The Jefferson county, KS provenance, growing in close proximity to the common garden is identified by the filled star.

**Gas exchange and water relations** Leaf gas exchange parameters of  $A_{sat}$  and  $g_s$  did not vary significantly ( $P = 0.2377$  and  $P = 0.9123$ , respectively) among nine populations originating from the east–west precipitation gradient and grown in the common garden (Table 2). Mean  $A_{sat}$  was  $16.74 \pm 0.47 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  among the nine populations, and mean  $g_s$  was  $0.347 \pm 0.010 \text{ mmol m}^{-2} \text{ s}^{-1}$ . Similar results were reported by Bassow and Bazzaz (1997) for *F. americana*.

We found significant variation in 10-year foliar  $\delta^{13}\text{C}$  values ( $P = 0.0001$ ; Figure 5), which were highly correlated ( $r^2 = 0.75$ ,  $P = 0.0012$ ) with mean annual precipitation at the sources (Figure 5). Although the overall range was narrow (from  $-29.25\text{‰}$  to  $-27.62\text{‰}$ ), provenances from wetter sites had significantly lower foliar  $\delta^{13}\text{C}$  than populations originating from drier sites (Figure 5), and populations from wetter sites had lower survival at the drier common garden site (Figure 3b;  $r^2 = 0.55$ ,  $P = 0.0134$ ). Furthermore, foliar  $\delta^{13}\text{C}$  values were correlated with survival ( $r^2 = 0.55$ ,  $P = 0.0628$ , marginal significance; Figure 6a) and overall growth (stem circumference;  $r^2 = 0.54$ ,  $P = 0.0151$ ; Figure 6b) for the 10 populations grown in the common garden. Populations with the highest growth and survival in the common garden exhibited the highest foliar  $\delta^{13}\text{C}$  and, hence, the most conservative water use.

Table 2. Light-saturated photosynthesis ( $A_{\text{sat}}$ ) and stomatal conductance ( $g_s$ ) in *Fraxinus americana* populations ( $n = 5$  trees per population) from across an east–west precipitation gradient when grown in a common garden. There were no significant differences in  $A_{\text{sat}}$  ( $P = 0.24$ ) or  $g_s$  ( $P = 0.91$ ) among populations.

Population	Longitude (°W)	$A_{\text{sat}} \pm \text{SE}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$g_s \pm \text{SE}$ ( $\text{mmol m}^{-2} \text{s}^{-1}$ )
Otoe, NE	95.7	$17.50 \pm 1.26$	$0.36 \pm 0.02$
Adams, IL	90.7	$17.75 \pm 0.53$	$0.33 \pm 0.03$
Effingham, IL	88.4	$17.41 \pm 0.46$	$0.34 \pm 0.02$
Effingham, IL	88.4	$16.91 \pm 0.15$	$0.36 \pm 0.03$
Jackson, IN	86.0	$15.34 \pm 0.31$	$0.38 \pm 0.01$
Preble, OH	84.7	$16.58 \pm 0.62$	$0.35 \pm 0.04$
Wayne, OH	82.0	$17.41 \pm 1.07$	$0.34 \pm 0.04$
Randolph, WV	79.7	$17.06 \pm 0.92$	$0.37 \pm 0.05$
Tucker, WV	79.5	$14.73 \pm 1.58$	$0.30 \pm 0.05$

When all years were combined, the  $\delta^{13}\text{C}$  of  $\alpha$ -cellulose from tree rings formed between 1996 and 2005 in the common garden differed significantly ( $P = 0.0224$ ) among the five analyzed populations from the precipitation gradient (Figure 7). In addition, there was a significant effect ( $P = 0.0018$ ) of year on  $\alpha$ -cellulose  $\delta^{13}\text{C}$  measurements. In some years, such as 1997 and 1999, there were large differences in the mean  $\alpha$ -cellulose  $\delta^{13}\text{C}$  among these five populations. In other years (e.g., 2003), all five populations had similar  $\alpha$ -cellulose  $\delta^{13}\text{C}$ . Despite some interannual variation within populations during the 10-years when the sampled wood was formed, the overall rank order of  $\alpha$ -cellulose  $\delta^{13}\text{C}$  in these populations was consistent from one year to the next (no significant population  $\times$  year interaction,  $P = 0.99$ ). The population originating from the eastern portion of the species range (Tucker, WV) had the lowest carbon isotope ratios from 1996 through 2005, whereas populations originating from drier, more western regions (Otoe, NE and Adams, IL), exhibited higher carbon isotope ratios, particularly before 2002.

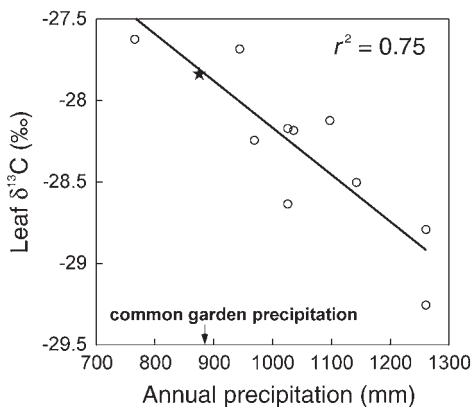


Figure 5. Foliar carbon isotope ratios of *Fraxinus americana* populations ( $n = 3$ –6) from an east–west precipitation gradient when grown in a common garden. The population originating from Jefferson county, KS, near the common garden is indicated by the filled star.

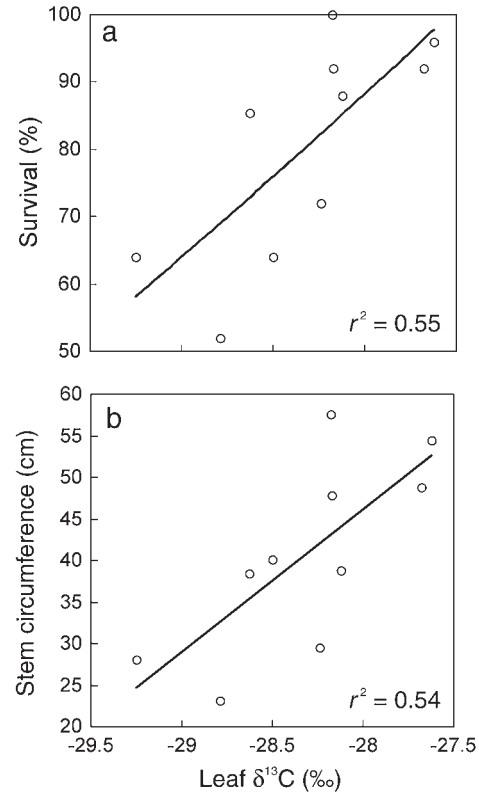


Figure 6. (a) Survival and (b) stem circumference regressed against foliar carbon isotope ratios for 10 populations from an east–west precipitation gradient that were grown in a common garden.

## Discussion

In this study, we quantified population-level variation among 44 provenances of 30-year-old *Fraxinus americana* trees grown in a common garden located at the western edge of the species' native range (northeastern Kansas, USA). Conditions at the common garden site are drier than over much of the spe-

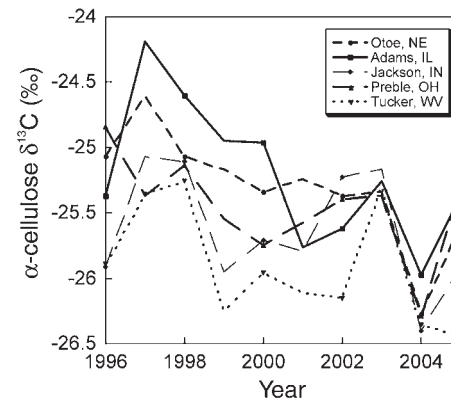


Figure 7. Carbon isotope ratios of  $\alpha$ -cellulose from whole-tree rings formed between 1996 and 2005 in five *Fraxinus americana* populations ( $n = 1$ –3) that originated from an east–west precipitation gradient and were grown in a common garden.

cies' current range and resemble conditions anticipated in more easterly regions of the species' range in the near future.

Among the 44 *F. americana* provenances in the common garden, stem circumference and survival varied significantly among the populations and were highest among populations that originated from locations closest to the common garden (Figure 2). Schuler (1994) obtained similar results in a comparison of *F. americana* provenances grown for 15 years in a common garden located at the opposite end of the species' east–west range, in north central West Virginia: populations originating from the immediate vicinity of that common garden having the highest growth and survival. Both studies thus indicate that adaptive differentiation has occurred within *F. americana* in response to range-wide climatic variation.

In our study and Schuler's (1994), survival and growth in the common garden were lower in provenances originating either to the north or south of the common garden (Figures 2a and 2b). There is a close inverse relationship ( $r^2 = 0.80$ ,  $n = 31$ ) between source latitude and precipitation, which might explain the decline in survival and growth with increasing southward distance from the common garden to the provenance source. However, the decline in performance with increasing northward distance from the common garden to the provenance source cannot be explained by the trend in precipitation, and thus indicates that there must be range-wide adaptation of *F. americana* to factors other than precipitation, e.g., temperature (Alexander et al. 1984) or growing season duration.

The responses of provenances from across a narrow latitudinal band, encompassing that of the common garden, suggest wide-range adaption of *F. americana* to local moisture regime, as precipitation at the source of these provenances was closely correlated with longitude ( $r^2 = 0.66$ ,  $n = 10$ ). For example, in the common garden survival was only about 50% for the eastern-most population (Randolph, West Virginia), but rose to 96% for the western-most population originating closest to the common garden (Otoe, Nebraska). Stem circumference in the eastern-most populations (Tucker, West Virginia; Randolph, West Virginia; Wayne, Ohio) was only about half that in the western-most populations (Otoe, Nebraska; Adams Illinois). Similar range-wide adaption of populations to local climate, in particular precipitation, has been observed in *Picea abies* (Oleksyn et al. 1998) and *Juglans nigra* (Bresnan et al. 1994).

In the common garden, differentiation in LMA and  $N_a$  was evident among *F. americana* populations from across the east–west precipitation gradient. Increases in LMA and  $N_a$  indicate increases in the quantity of photosynthetic apparatus per unit leaf area (Fitter and Hay 2002) and, thus, increases in water-use efficiency (Li et al. 2000, 2004). The superior growth and survival of provenances originating from the western edge of the species' range where the climate is driest when transplanted to the dry climate of the Kansas common garden (Figures 4a and 4b) is thus likely attributable, at least in part, to their high LMA and  $N_a$ .

The stable carbon isotope ratio of leaves (foliar  $\delta^{13}\text{C}$ ) provides a time-integrated measure of the ratio of leaf inter-cellular  $\text{CO}_2$  concentration to atmospheric  $\text{CO}_2$  concentration

( $c_i/c_a$ ). The  $c_i/c_a$  ratio depends on stomatal conductance and photosynthetic demand for  $\text{CO}_2$ , and thus indicates water-use efficiency (Farquhar et al. 1989, Ehleringer 1991). In this common garden study, foliar  $\delta^{13}\text{C}$  results provide evidence of a strong correlation between the physiological responses of an *F. americana* population grown in the common garden and the amount of annual precipitation at the population source (Figure 5). Specifically, eastern populations from wetter regions exhibited lower  $\delta^{13}\text{C}$  values, and were therefore less conservative in their water use compared with western populations that originated from drier climates. A more conservative strategy for water use may have contributed to higher survival (Figure 6a), particularly when considering that the common garden experienced periods of extreme drought during the 30-year study.

In the five *F. americana* populations from the precipitation gradient that were analyzed, the  $\alpha$ -cellulose  $\delta^{13}\text{C}$  of tree rings indicated that population differences in water use occurred not only in 2004, but extended over much of the decade during which the sampled wood was formed (Figure 7). From 1996 to 2005, the eastern-most population (Tucker, WV) consistently had the lowest  $\alpha$ -cellulose  $\delta^{13}\text{C}$  when grown in the common garden, indicating a less conservative water use strategy over an extended time period. The two populations that consistently had the highest  $\alpha$ -cellulose  $\delta^{13}\text{C}$  in tree rings (i.e., the most conservative water use) were from Otoe, NE and Adams, IL, at the western-most end of the east–west precipitation gradient. In 2003, however, the mean  $\alpha$ -cellulose  $\delta^{13}\text{C}$  values among all five populations were similar, perhaps reflecting a response to the severe drought that occurred during the previous year (2002).

The physiological differences among the provenances investigated as reflected in differences in tree-ring  $\delta^{13}\text{C}$  values can evidently persist for up to 30 years during which all provenances experienced the same climate. This finding indicates that the genetic diversity of *F. americana* populations will play a greater role than phenotypic plasticity in determining growth and survival in a changing climate.

Although evidence for adaptation to changes in water availability was found in many of the examined parameters (and most strongly in those that integrated long time scales), no variation in  $A_{\text{sat}}$  was detected among the *F. americana* populations from across the precipitation gradient (Table 2), although  $A_{\text{sat}}$  has been shown to vary among population in other tree species, such as *Betula pendula* Roth. and *Fraxinus pennsylvanica* Marsh. (Abrams 1994, Aspelmeier and Leuschner 2004). Stomatal conductance did not vary significantly among populations of *F. americana* (Table 2). The absence of differences in  $g_s$  may have been a result of the wetter than average conditions during the month preceding our measurements (June), which may have masked long-term population-level differences.

Our findings indicate that models assuming that all *F. americana* trees will respond similarly to climate change are incorrect. Western populations of *F. americana* are better adapted to drier conditions than eastern populations, indicating that east-

ern populations may not perform well under future climate change scenarios predicted for that region. Furthermore, this work suggests that the continued persistence of tree species within their current range will depend largely on pre-existent adaptive mechanisms (i.e., adaptations to past climatic changes).

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