Stability of Provenance Differences during Development of Hard Maple Seedlings Irrigated at Two Frequencies

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Abstract. Traits associated with drought resistance vary with provenance of hard maples (*Acer* sp.), but the stability of differences *ex situ* and over time is unknown. We compared growth, dry-matter partitioning, leaf anatomy, and water relations of seedlings from central Iowa, eastern Iowa, and the northeastern United States over 2 years. Some seedlings from each of the three provenances were used as well-irrigated controls. The remaining seedlings were drought-stressed and irrigated based on evapotranspiration. Across irrigation treatments, plants from Iowa had shorter stems and higher specific weight of lamina, root : shoot dry-weight ratios, and root : lamina dry-weight ratios than did plants from the northeastern United States when treatments began. Biomass partitioning did not differ based on provenance after irrigation treatment for 2 years, but leaves from central Iowa had a higher specific weight, and their abaxial surfaces had more stomates and trichomes, than did leaves from the Northeast. Drought stress reduced conductance only in plants from central Iowa. Across provenances, drought stress reduced stomatal frequency, surface area of laminae, and dry weights of laminae and roots, and increased root : shoot dry-weight ratio. Leaf water potential of plants subjected to drought was lower at predawn and higher at midday than that of control plants. Drought did not cause osmotic adjustment in leaves. We conclude that the stability of foliar differences among provenances of hard maples validates using these traits as criteria for selecting ecotypes for use in managed landscapes prone to drought.

Members of the Saccharina Pax. section of the Aceraceae, known collectively as hard maples, include many taxa of economic and aesthetic significance. Although cultivars of sugar maple (*Acer saccharum* Marsh.) often are specified by landscape personnel, the impact of these taxa often is reduced by symptoms of stress on trees installed at disturbed sites, particularly in urban areas (Close et al., 1996). Episodes of drought may be exacerbated in managed landscapes by the limited soil volume available for root expansion and the runoff of precipitation on impermeable

surfaces. Limited water availability can reduce shoot growth and cause sugar maples to develop scorch and marginal necrosis of leaf blades (Pair, 1991). Strategies to select ornamental hard maples with superior resistance to drought stress are needed.

One strategy for selection might be to focus on individuals native to relatively xeric habitats. Many popular sugar maple cultivars originated in the northeastern United States, a region more mesic than areas farther west where hard maples also are native. Bark and foliar traits of certain hard maples in the Midwestern United States are unique. Taxonomists commonly place individuals with dark bark and three-lobed leaves with pilose abaxial surfaces in a subspecies of sugar maple, *Acer saccharum* Marsh. ssp. *nigrum* (Michx. f.) Desmarais (Griffiths, 1994). These trees also have been considered to be a different species, *Acer nigrum* Michx. f. (Griffiths, 1994; Rehder, 1940), and are known commonly as black maples. Selecting genotypes for landscapes prone to drought could be facilitated by establishing a relationship between geographic origin and traits of drought resistance among sugar maples and black maples.

Some evidence exists to support the hypothesis that western forms of hard maples may be more drought-resistant than their eastern counterparts. During the first year of development of seedlings from various Midwestern locations, both root weight per unit shoot weight and specific leaf weight were greater in black than in sugar maples (Graves,

1994). Trichome frequency on leaf blades of indigenous, mature hard maples increased from ≈ 0 to 1200-cm^{-2} near 43°N latitude along a continuum from 70°W longitude in the north-eastern United States to 94°W in the Midwest (St. Hilaire and Graves, 1999). Trees with high root : shoot ratios, high specific leaf weights, and densely arranged foliar trichomes may be desirable because these traits can confer drought resistance (Abrams et al., 1990; Schuepp, 1993). Selecting hard maples with these traits for use in managed landscapes has been proposed (St. Hilaire and Graves, 1999), but would be tenable only if the traits are stable *ex situ* and over time.

We have gathered new information on how hard maples with different geographic origins compare with regard to traits associated with drought resistance. Specifically, our objective was to resolve two unsettled issues in the literature: 1) how seedlings from the Midwest and the northeastern United States compare in growth and dry-matter partitioning; and 2) whether foliar traits associated with drought resistance previously observed on trees *in situ* across the eastern half of the country are expressed in plants grown *ex situ* in a common environment.

Materials and Methods

Plant material. In Sept. 1995, samaras were obtained from five trees of hard maple in each of three provenances. We collected fruits in two provenances, eastern and central Iowa. Samaras from eastern Iowa were from two trees in Yellow River State Forest (lat. $43^\circ 17' \text{N}$, long. $91^\circ 25' \text{W}$), one tree in Palisades State Park (lat. $41^\circ 91' \text{N}$, long. $91^\circ 51' \text{W}$), and two trees in Backbone State Park (lat. $42^\circ 62' \text{N}$, long. $91^\circ 56' \text{W}$). In central Iowa, samaras were from two trees at Iowa State Univ. (lat. $42^\circ 15' \text{N}$, long. $93^\circ 35' \text{W}$), one tree at the YMCA woodland (lat. $42^\circ 14' \text{N}$, long. $93^\circ 94' \text{W}$), and two trees in Dolliver Memorial State Park (lat. $42^\circ 39' \text{N}$, long. $94^\circ 08' \text{W}$). Samaras from Iowa were stratified at 4°C in damp sphagnum moss. On 11 Jan. 1996 we received cold-stratified samaras from one tree each in Strafford, N.H. (lat. $43^\circ 17' \text{N}$, long. $71^\circ 04' \text{W}$), Underhill, Vt. (lat. $44^\circ 31' \text{N}$, long. $72^\circ 56' \text{W}$), and Starksboro, Vt. (lat. $43^\circ 13' \text{N}$, long. $73^\circ 03' \text{W}$), and from two trees in Lake Placid, N.Y. (lat. $44^\circ 16' \text{N}$, long. $73^\circ 58' \text{W}$). All 15 trees from which fruits were obtained were native at their respective sites. We judged all trees from which seeds were collected in central Iowa and the northeastern United States to be black maple and sugar maple, respectively. All trees sampled in eastern Iowa were phenotypically intermediate between the two taxa but were more similar to sugar maple than to black maple.

Experimental units. On 19 and 20 Mar. 1996, samaras from the 15 maternal parent trees (15 half-sibling groups) were sown in plastic pots (top diameter = 11.4 cm ; Belden Plastics, St. Paul, Minn.) filled with 700 cm^3 of 3 coarse perlite : 1 medium-grade vermiculite (by volume; Strong-Lite, Seneca, Ill.). Plastic screens were placed over drainage holes to

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prevent loss of the growth medium. Seedlings were held on a glasshouse bench where incandescent lamps maintained the photoperiod at 16 h. Mean midday temperature and photosynthetically active radiation were monitored at canopy level every day throughout the experiment with a model 1600 steady-state porometer (LI-COR, Lincoln, Nebr.) and averaged 28 °C and 380 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The surface of the medium was misted daily with tap water until 27 Mar. Thereafter, pots were drenched from the top until solution drained from the medium once daily through 20 May with 3 Peters® Excel All Purpose 21N–2.2P–16.6K : 1 Peters® Excel Calcium-Magnesium Special 15N–2.2P–12.5K (by weight; Grace Sierra, Milpitas, Calif.) that provided nitrogen at 175 $\text{mg}\cdot\text{L}^{-1}$. Each single seedling in a pot was an experimental unit.

Initial harvest. On 21 May 1996, 20 visually uniform seedlings from each of the 15 half-sibling groups, along with additional seedlings for border rows, were arranged in a completely randomized design in the glasshouse. Ten plants from each source were assigned randomly to a drought treatment. The other 10 plants from each source were assigned to a control treatment in which plants were irrigated every 2 d. Also on 21 May, one plant from each of the 30 factorial combinations of irrigation treatment and half-sibling group was randomly selected for harvest. Stem length of these plants was measured. Area of lamina ≥ 2.5 cm long was determined with a LI-3100 area meter (LI-COR). Dry weight of the shoots, including 3 cm of the hypocotyl, was determined. The remainder of the hypocotyl was included with root dry weight. A disc (0.79 cm^2) of laminar tissue was taken between the midvein and the first-order vein from a leaf of the third oldest pair of fully expanded leaves. Specific weight was determined by dividing the disc dry weight by disc area.

Treatment in 1996. Every 2 d from 21 May until 8 Sept., all plants in the control treatment were drenched from the top until solution drained from the medium. Drought cycles were monitored and ended consistently across half-sibling groups by measuring evapotranspiration as described by Graves (1994). Six plants assigned to drought within each half-sibling group were the indicator pots, and, within half-sibling groups, cycles ended with irrigation when 40% weight loss had occurred (Graves, 1994). This degree of evapotranspiration was chosen because it evoked leaf wilting during a preliminary experiment. Measures with a model HH1 Theta Probe and a model ML1 sensor (Delta-T Services, Cambridge, England) showed that mean volumetric water content of the upper 6 cm of the medium was 3.7% when combined weight of indicator pots had decreased 40%. Irrigated pots drained 2 h before a new weight of indicator pots was taken for determining subsequent decreases in pot weight. Treatments were applied until 8 Sept., when all half-sibling groups had completed four consecutive cycles of drought. Eleven of the 270 plants

were dead when irrigation treatments ended. Each of these plants was in the drought treatment; one was from central Iowa, while four and six plants were from the northeastern United States and eastern Iowa, respectively. On 9 Sept., all living plants were prepared for vernalization by moving them to a glasshouse at 13 °C, where plants were irrigated with tap water as needed to keep the surface of the medium moist. On 1 Nov., the plants were moved to a dark cooler at 5 °C. Plants were irrigated every 10 d with tap water during a 16-week vernalization.

Treatment in 1997. Plants were moved from the cooler to the glasshouse on 27 Feb 1997. Seven plants from the northeastern United States, eight from eastern Iowa, and 11 from central Iowa did not break bud. Twenty-five of these 26 plants were in the drought treatment. Of the 233 plants that broke bud, 82 (44 controls and 38 in the drought treatment) had died by 26 Mar. and were diagnosed with *Fusarium* wilt. The number of plants with *Fusarium* by provenance ranged from 23 (eastern Iowa) to 31 (central Iowa). The 151 plants that had broken bud and appeared healthy on 26 Mar. were retained in the irrigation treatment they received during 1996 and arranged in a completely randomized design. There were 51, 53, and 47 plants retained from the northeastern United States, eastern Iowa, and central Iowa, respectively; the number of these in the drought treatment was 17, 23, and 21, respectively. Within irrigation treatments, two to nine seedlings from each of the 15 half-sibling groups were retained. Irrigation was as in 1996 until all half-sibling groups completed at least five more drought cycles. The 14 groups of half-siblings that completed a fifth drought cycle before the last group did were subjected to additional cycles so that all plants were the same age when treatments ended and final data on growth were collected.

Leaf water relations. The date when the fifth drought cycle ended varied with half-sibling groups because of differences in evapotranspiration. As groups reached this stage, half-siblings subjected to drought were not irrigated as was done to end previous cycles. Instead, predawn leaf water potential (ψ_{pd}) of one leaf of the youngest fully expanded pair on all plants in that group was estimated the next morning by using a pressure chamber (PMS Instruments, Corvallis, Ore.). Between 1030 and 1430 hr, stomatal conductance of the opposite leaf was measured with a model 1600 steady state porometer (LI-COR), and midday water potential and (ψ_{md}) of that leaf was determined. The pair of leaves immediately basipetal to leaves removed for ψ_{pd} and ψ_{md} then was removed from two plants selected randomly from both irrigation treatments. Petioles were cut under and held in tap water, and leaf blades were enclosed in plastic and kept in the dark at 4 °C to promote rehydration. A pressure-volume curve (Tyree and Hammel, 1972) was developed for one leaf from each plant to estimate osmotic potential at full turgor ($\psi_{\text{r}}^{\text{FT}}$). Two discs were removed from the opposing laminae, one from each side of the midvein 2 to 3 cm distal from the petiole. One

disc was dried at 67 °C for 3 d. Its dry weight was divided by 0.79 cm^2 to determine specific leaf weight. The other disc from each plant was used for microscopy.

Microscopy. Laminar discs were divided into three sections of similar area by making two parallel, transverse cuts. Sections were preserved in formalin-acetic acid-alcohol (Berlyn and Miksche, 1976). One of the two outer sections of each disk was chosen randomly and rehydrated into water through 50%, 30%, and 10% ethanol. That section was used to determine stomatal frequency within a 0.05- mm^2 grid, average length and width of a guard cell within each of three pairs, and the length of the aperture between each pair (St. Hilaire and Graves, 1999). The middle section of each disc was dehydrated in a graded series of ethanol-tertiary butanol and embedded in paraplast-xtra (Oxford Labware, St. Louis, Mo.). Serial 8- μm sections were stained with safranin-fast green. Thickness of the entire laminae, abaxial and adaxial epidermal surfaces, and palisade and spongy parenchyma were measured. Surface areas of the laminae from which discs were removed were determined with an area meter after filling the cut area with opaque adhesive tape, and dry weight of discs was estimated from leaf specific weight. After lamina area was measured, trichomes were counted on the abaxial surface within the field of view (0.237 cm^2) of an Olympus SZ60 (Olympus Optical, Tokyo) stereomicroscope fitted with fiber optic lighting. A mean count was determined from counts of three areas, one along the midvein 3 cm from the apex of the central lobe and two areas immediately distal to where the discs had been removed.

Final harvest. Drought treatments were sustained until 27 July 1997, when all groups of half-siblings had completed at least five cycles. All plants were harvested on 31 July. Epicotyl length, lamina area, and shoot and root dry weight were determined as was done during the initial harvest. Leaves used for pressure-volume curves and microscopy were included in the total lamina area and dry weight.

Data analysis. Data from the 10 experimental units per provenance from the initial harvest were subjected to an analysis of variance [ANOVA; Statistical Analysis System (SAS), Cary, N.C.] appropriate for the completely randomized design. Measures of $\psi_{\text{r}}^{\text{FT}}$, which were determined from the linear portion of pressure-volume curves with the Reg procedure of SAS, and developmental traits measured during 1997 were analyzed in accordance with the completely randomized experimental design by using the GLM procedure of SAS. Variation due to the two irrigation treatments, three provenances, and 15 half-sibling seed sources was examined. Half-sibling groups were nested within provenances and used as error for the provenance main effect. The interaction of irrigation treatment and half-sibling group within provenance was used as error to test the irrigation treatment main effect and the interaction of irrigation treatment and half-sibling group across provenances.

Table 1. Growth, biomass partitioning, and specific leaf weight of seedlings of hard maples from three provenances. Data were collected 21 May 1996, immediately before irrigation treatments began, when the seedlings were ≈ 2 months old. The plants were grown in individual pots in a glasshouse from stratified seeds collected in late 1995. Values are means of 10 replicates, two seedlings from each of five half-sibling groups from each provenance.

Dependent variable	Provenance of origin			LSD ^z
	Northeastern United States	Eastern Iowa	Central Iowa	
Stem length (mm)	68	53	43	13
Specific leaf wt (mg·cm ⁻²)	3.8	4.4	4.8	0.5
Shoot dry wt (mg)	640	590	630	NS
Surface area of laminae (cm ²)	167	119	114	NS
Root : shoot dry-wt ratio	0.21	0.28	0.30	0.05
Root : lamina dry-wt ratio	0.27	0.38	0.43	0.10

^zFisher's least significant difference ($P = 0.05$) values are shown for dependent variables that differed significantly based on provenance.

^{ns}Nonsignificant.

Results

Seedling size and the partitioning of dry matter between roots and shoots differed among provenances before irrigation treatments. Seedlings from the Northeast had the longest stems ($P = 0.0407$) and the lowest specific leaf weight ($P = 0.0057$) (Table 1). Shoot dry weights and surface areas of laminae did not differ significantly among provenances ($P = 0.8936$ and 0.0907 , respectively). Seedlings from Iowa had highest mean root : shoot dry weight ($P = 0.0210$) and root : lamina dry weight ($P = 0.0137$) ratios (Table 1).

All drought-stressed half-sibling groups completed four drought cycles in 1996, and the mean time required to complete a cycle was 27, 25, and 27 d for groups from the northeastern United States, eastern Iowa, and central Iowa, respectively. Differences in evapotranspiration caused the number of drought cycles among half-sibling groups to range from five to eight during 1997. Averaged over the five half-sibling groups from each provenance, the mean number of drought cycles for seedlings from the northeastern United States was 5.6, and the average time to

complete a drought cycle was 15 d. The corresponding values for seedlings from eastern Iowa were 6.8 and 13 d; values for central Iowa were 5.8 and 15 d.

When treatments ended in 1997, weight and dry-matter partitioning varied with irrigation treatment but not provenance. Controls had higher lamina surface area ($P = 0.0001$), higher lamina ($P = 0.0001$) and root ($P = 0.0001$) dry weight, and lower root : shoot dry weight ratio ($P = 0.0074$) than did drought-stressed plants (Table 2). Drought led to reduced ψ_{pd} ($P = 0.0301$) and to increased ψ_{md} ($P = 0.0002$) (Table 2). Pressure-volume analysis showed that ψ_{π}^{FT} averaged -1.51 MPa and did not vary with provenance or irrigation treatment.

Trichome frequency ($P = 0.0095$) and specific leaf weight ($P = 0.0002$) varied with provenance. While leaves from Iowa had several hundred trichomes per square centimeter, leaves from the northeastern United States were glabrous (Table 3). The mean specific weight of leaves from central Iowa was 13% and 20% higher than the mean for plants from the northeastern United States and eastern

Iowa, respectively (Table 3). Stomate frequency varied with provenance ($P = 0.0309$) and irrigation ($P = 0.0072$). Leaves from central Iowa had 22% and 32% more stomates per unit surface area, respectively, than did leaves of plants from eastern Iowa and the northeastern United States (Table 3), and drought stress reduced stomate frequency by 19% overall (Table 3). Width (mean = $16 \mu\text{m}$) and length (mean = $15 \mu\text{m}$) of guard cells, length of the stomatal aperture (mean = $5 \mu\text{m}$), thickness of laminae (mean = $91 \mu\text{m}$), and thickness of epidermal and parenchymal layers did not vary with provenance or irrigation treatment.

Data on stem length, shoot dry weight, total dry weight, and stomatal conductance in 1997 showed interactions of provenance and irrigation treatment. For stem length and seedling weight, differences between the control plants from the three provenances were responsible for the interactions. We judged such interactions to be of low significance for characterizing provenance differences in responses to water supply because the influence of drought was similar regardless of plant origin. In contrast, the interaction ($P = 0.0296$) of provenance and treatment for stomatal conductance was caused by an irrigation effect that existed only among plants from central Iowa (Table 3).

Discussion

Previous research to compare development of sugar and black maples focused only on seedlings native to the Midwest (Graves, 1994), and foliar variation has been studied only among trees in native stands (Dansereau and Desmarais, 1947; Desmarais, 1952; Kriebel, 1957; St. Hilaire and Graves, 1999). We analyzed plants from both the Midwest and the northeastern United States grown in a common setting to test whether provenance differences were caused by environmental or ge-

Table 2. Dependent variables affected by irrigation treatment but not by provenance of origin of hard maple seedlings from the northeastern United States, eastern Iowa, and central Iowa. Irrigation $\times$ provenance interactions were non-significant for these variables. Values are means of 90 (control) or 61 (drought) replicates treated in 1996 and 1997. The plants were grown in individual pots in a glasshouse from stratified seeds collected in late 1995. Control seedlings were irrigated every 2 d, while drought-stressed seedlings were subjected to repeated cycles during which soil moisture content was reduced to $\approx 3.7\%$.

Dependent variable	Irrigation treatment		LSD ^z
	Control	Drought	
Surface area of laminae (cm ²)	1675	397	260
Lamina dry wt (g)	10.4	2.3	1.6
Root dry wt (g)	7.1	3.8	2.2
Root : shoot dry-wt ratio	0.24	0.66	0.17
ψ_{pd} (MPa)	-0.77	-0.85	0.08
ψ_{md} (MPa)	-1.92	-1.44	0.19

^zFisher's least significant difference, $P = 0.05$.

Table 3. Dependent variables affected only by provenance of origin of hard maples (trichome frequency and specific leaf weight) or by both provenance of origin and irrigation treatment (stomate frequency and stomatal conductance). The interaction of provenance and irrigation treatment was significant for stomatal conductance but not for stomate frequency. Therefore, means for stomatal conductance for all treatment combinations are shown. Seedlings were grown in individual pots in a glasshouse from stratified seeds collected in late 1995. All measurements were made in 1997 after 2 years of growth. Controls were irrigated every 2 d, while drought-stressed seedlings were subjected to repeated cycles during which soil moisture content was reduced to $\approx 3.7\%$. Provenance values for the first three dependent variables are means for 20 replicates. Irrigation values for stomate frequency are means for 30 replicates. Values for stomatal conductance are means for 17 to 34 replicates, depending on treatment combination.

Dependent variable	Provenance of origin			LSD ^z	Irrigation treatment		LSD ^z
	Northeastern United States	Eastern Iowa	Central Iowa		Control	Drought	
Trichome frequency (no./cm ²)	0	360	531	314			
Specific leaf weight (mg·cm ⁻²)	5.3	5.0	6.0	0.3			
Stomate frequency (no./cm ²)	475	516	628	112	596	483	92
Stomatal conductance (mmol·m ⁻² ·s ⁻²)							
Control	38	28	46	3			
Drought	38	25	25				

^zFisher's least significant difference for each dependent variable is shown ($P = 0.05$).

netic variance. Some differences previously reported in situ clearly are not dependent on the environment. For example, the high stomate and foliar trichome frequencies of plants native to Iowa (Table 3) are consistent with observations of trees in nature (Dansereau and Desmarais, 1947; Desmarais, 1952; Ware, 1983) and with data taken on detached leaves from trees indigenous to these areas (St. Hilaire and Graves, 1999). Pronounced trichome development is a trait of black maple (Rehder, 1940), a western variant of sugar maple. We considered all our germplasm from central Iowa to be black maple, the only form of hard maple native there (St. Hilaire and Graves, 1999). The taxonomy of trees from the other two provenances is less clear. Black maples occur among the sugar maples of New England and New York (Rehder, 1940), and the two taxa are sympatric in eastern Iowa (St. Hilaire and Graves, 1999). Assuming foliar pubescence is an accurate marker for taxonomic distinction, data on trichomes (Table 3) suggest that the plants we studied included densely pubescent black maples (central Iowa), glabrous sugar maples (eastern United States), and intermediate forms with moderate pubescence (eastern Iowa). The lack of irrigation effect on trichome frequency (Table 3), and the similarity in our data for seedlings vs. that for trees in nature (St. Hilaire and Graves, 1999), indicate foliar trichome frequency is a stable trait across environments and stages of tree ontogeny.

As was found for trichomes, the frequency of stomates varied with provenance, but stomate frequency also was reduced by drought (Table 3). Provenance differences we found are similar to those reported previously for leaves of trees in nature (St. Hilaire and Graves, 1999), confirming that high stomatal frequency of hard maples in western portions of the Midwest is a stable trait in different environments. This is consistent with previous reports that show populations of other woody species native to relatively xeric areas have higher stomatal frequencies than populations in mesic areas (Donselman and Flint, 1982; Ehleringer, 1980). Having numerous stomates that are sensitive to drought may permit a plant both to optimize carbon fixation when the environment is favorable and to limit water loss when adverse conditions prevail. This may explain the relatively high stomatal conductance of well-irrigated control plants from central Iowa and the proportionally large decrease in stomatal conductance when plants of that provenance were subjected to drought (Table 3). Field research is needed to test whether stomatal regulation of water loss varies among hard maples from different provenances. The lack of an interaction between provenance and irrigation treatment for ψ_{pd} and ψ_{md} suggests that any difference that may exist between provenances in stomatal regulation of water

loss during drought was not sufficient to confer different states of leaf water status in the glasshouse used for this study.

Both genetic variation and environment appear to influence another foliar trait, specific weight. Data in Tables 1 and 3 demonstrate provenance differences independent of environment that are consistent with data on specific leaf weight of seedlings from only the Midwest (Graves, 1994). In contrast, St. Hilaire and Graves (1999) found that specific leaf weight did not differ among indigenous trees in the provenances where seeds for this study were collected. Moreover, there are conflicting reports regarding how leaf thickness, which can account for differences in specific weight but was consistent among provenances in our study, varies among hard maples (Powers, 1967; Preston, 1989). The fact that we found differences in specific weight among provenances but not in total leaf thickness nor its components indicates that specific weight varied because of differences in cell density or some other factor, such as frequency of chloroplasts (Kloppel and Adams, 1995). An increase in specific leaf weight follows drought as an adjustment mechanism in some plants, including Freeman maple (*Acer xfreemanii* E. Murray) (Zwack et al., 1998), but we have no evidence for this among seedlings of hard maple (Table 3).

Biomass partitioning differed among provenances very early in seedling growth, but differences were not sustained over 2 years. Very young plants from central Iowa had less laminar area and relatively large root systems per unit weight of shoot or lamina (Table 1). This is consistent with the data of Graves (1994), who reported that seedlings of black maple from central Iowa had a lower mean shoot dry weight and shoot : root weight ratio during their first season of growth than did sugar maples from the Midwest. Development of a large root system per unit shoot may favor establishment of seedlings in western provenances, where drought is relatively common. The fact that only one of the 11 plants that succumbed to the first year of drought was from central Iowa is consistent with this idea. Although there are no data to support the observation that western forms of black maple sustain particularly large root systems as they age (Ware, 1983), hard maples as a group developed relatively small shoot systems per unit root during drought (Table 2). This adjustment to low water supply may be especially important for these taxa, which data from this study and others (Ellsworth and Reich, 1992; Kolb et al., 1991) suggest do not show osmotic adjustment consistently in response to water deficits.

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