Variation among Red and Freeman Maples in Response to Drought and Flooding

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Abstract. Freeman maples (*Acer ×freemanii* E. Murray) are marketed as stress-resistant alternatives to red maples (*Acer rubrum* L.). Our objective was to compare two cultivars of Freeman maple ['Jeffersred' (Autumn Blaze®) and 'Indian Summer'] and five red maples ['Franksred' (Red Sunset®), 'Autumn Flame', 'PNI 0268' (October Glory®), 'Fairview Flame', and unnamed selection 59904] for effects of flooding and water deficit on plant growth, biomass partitioning, stomatal conductance, and leaf osmotic potential. Plants grown from rooted cuttings in containers were subjected to three consecutive cycles during which root-zone water content decreased to 0.12, 0.08, and 0.02 m³·m⁻³, respectively. Additional plants were flooded for 75 days, while plants in a control treatment were irrigated frequently. Stomatal conductance immediately before imposing drought and after three drought cycles did not differ among genotypes and averaged 220 and 26 mmol·s⁻¹·m⁻², respectively. Differences in stomatal conductance after recovery from the first drought cycle and at the end of the second drought cycle did not vary with species. Drought reduced estimated leaf osmotic potential similarly for all genotypes; means for drought-stressed and control plants were -1.92 and -1.16 MPa, respectively. Freeman maples had a higher mean root : shoot weight ratio and a lower leaf surface area : root dry-weight ratio than did red maples. Across genotypes, stomatal conductance of flooded plants initially increased by ≈20% and then fell to and remained below 50 mmol·s⁻¹·m⁻². Stomatal conductance of 'Indian Summer' decreased to ≈20 mmol·s⁻¹·m⁻² after 8 days of flooding, indicating that this cultivar may be particularly sensitive to root-zone saturation.

The physical environment of urban landscapes is very heterogeneous. Both excessive and deficient soil moisture are common and may impact trees within the same landscape simultaneously, even at adjacent sites (Berrang et al., 1985). Water deficiencies can be attributed to compaction and restricted volumes of soil and to competition among plants (Kozlowski, 1985). Heat loads of some urban soils (Graves and Dana, 1987) also may hasten evaporation or increase water use by plants. Excess soil moisture can arise from textural problems and poor drainage after soils become compacted (Kawase, 1981). Inundation of urban soils also results from overflowing rivers and streams, storms, the construction of dams, and excessive irrigation (Kozlowski, 1985).

Tree taxa that maintain landscape function during episodes of variable and adverse soil moisture are needed. Red maple and silver

maple (*Acer saccharinum* L.) are commonly found in urban areas. Red maples are valued for their ornamental features, while silver maples are considered to be adapted to soil conditions that limit use of other, more desirable species (Dirr, 1998). Putative hybrids of these species, known as Freeman maples, include numerous cultivars marketed for use in urban areas. Bachtell (1989) speculated that Freeman maples could be both more resistant to stress than red maples and more ornamental than silver maples. Data are needed to support or refute suspected differences in responses to water availability between red maples and Freeman maples, and among genotypes within the species (Santamour, 1993).

Previously, Townsend and Roberts (1973) found that water stress resistance varied among red maple seedlings originating from different seed sources. Abrams and Kubiske (1990) observed variation in responses to drought between red maples from bog vs. upland sources, and Zwack et al. (1998) described responses to drought among three cultivars of Freeman maple. None of these studies, however, directly compared the impact of drought on red maples and Freeman maples. Responses of red maple to flooding have been considered. Will et al. (1995) found no interactions between flooding and the hydrologic conditions

where red maples were obtained. 'Franksred' (Red Sunset®) showed a 22% mortality rate after 118 d of continuous flooding (Nash and Graves, 1993), while red maples studied by McDermott (1954) recovered rapidly from as much as 32 d of continuous flooding. Peterson and Bazzaz (1984), Hosner (1960), and Hosner and Boyce (1962) studied the effects of flooding on silver maple, but little is known about responses of Freeman maple to flooding. Our objective was to compare leaf water relations, and biomass accumulation and partitioning of red maples and Freeman maples grown in containers with excessive, moderate, and deficient root-zone moisture.

Materials and Methods

Production and maintenance of propagules. Stock plants of 'Jeffersred' (Autumn Blaze®) and 'Indian Summer' Freeman maples, and the red maples 'Franksred' (Red Sunset®), 'Autumn Flame', 'PNI0268' (October Glory®), 'Fairview Flame', and one unnamed selection (59904, a cross of 'Autumn Flame' and October Glory®) were grown in a greenhouse with natural photoperiod at lat. 42°N in Ames, Iowa. Plants were fertilized as described by Zwack et al. (1998). We took 5-cm-long, single-node stem cuttings from actively growing stock plants on 17 May 1997, and rooted them by using a subirrigation method (Zwack et al., 1998). Environmental conditions were monitored at several locations in the greenhouse 3 d per week during plant development. Average daily midday air temperature, relative humidity (RH), and photosynthetic photon flux (PPF) during rooting, measured with a model 1600 steady-state porometer (LI-COR, Lincoln, Nebr.), ranged from 20.8 to 23.3 °C, 25% to 54.6%, and 77 to 705 μmol·s⁻¹·m⁻², respectively. Rooted cuttings were potted 12 June 1997 in containers (bottom diameter = 152 mm, top diameter = 200 mm, height = 157 mm) in perlite and vermiculite (volume 2250 cm³) as described by Zwack et al. (1998), held under natural photoperiod, and fertilized every other day to container capacity with tap water containing N at 10.8 mol·m⁻³ from Peters Excel All-purpose 21N-2.2P-16.6K fertilizer (Scotts, Marietta, Ga.). The pH of the fertilizer solution was 6.0 to 6.6. Treatments began 17 July 1997, the day the last regular irrigation was provided. Mean length from the apex to the shoot origin of the one stem allowed to develop on each plant ranged from 20 ('Indian Summer') to 51 (Red Sunset®) cm 1 d before treatments began. Average daily air temperature, RH, and PPF from the time cuttings were potted to when treatments began were measured with the porometer and ranged from 22.1 to 25.5 °C, 44% to 68.7%, and 104 to 753 μmol·s⁻¹·m⁻², respectively.

Treatments. Plants were subjected to three consecutive cycles of drought separated by irrigation to container capacity with a fertilizer solution. The moisture content by volume of the upper 6 cm of the medium in each container was measured at 0800 hr every day with a model HH1 Theta Probe equipped with a model ML1 sensor (Delta-T Services, Cam-

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bridge, England). Moisture content of the rooting medium was allowed to decrease from $\geq 0.35 \text{ m}^3\cdot\text{m}^{-3}$ at container capacity to 0.120, 0.080, and $0.020 \text{ m}^3\cdot\text{m}^{-3}$ during three consecutive drought cycles, respectively. These values were chosen because they were associated with a similar degree of wilting assessed visually during the three cycles. Each cycle was ended by rehydration of the medium to container capacity with fertilizer solution. Immediately before treatments began, we tagged one of the leaves of the youngest fully expanded pair. Stomatal conductance of these leaves was measured from 0900 to 1130 hr the day when a plant completed a drought cycle and again 2 d later to assess recovery after irrigation. When all plants of a cultivar finished a cycle, new leaves were tagged for measurements so that one of the two leaves in the youngest fully expanded pair was used consistently. Different rates of evapotranspiration resulted in differences among plants in the time required to finish drought cycles, so the drought status of each plant was assessed individually. When a plant completed a drought cycle, it was irrigated to container capacity and a new drought cycle was initiated that same day. As plants that progressed through drought cycles relatively rapidly completed their third cycle, new cycles were initiated that terminated at a moisture content of $0.020 \text{ m}^3\cdot\text{m}^{-3}$ until the plant that progressed most slowly through the treatments had completed three cycles.

Containers of plants in the flooding treatment were placed singly in larger containers without drainage holes. Tap water (pH 9.1, electrical conductivity $0.43 \text{ mS}\cdot\text{cm}^{-1}$, alkalinity $1.00 \text{ meq}\cdot\text{L}^{-1}$) added between the two containers entered the drainage holes of the smaller containers and rose through and saturated the entire rooting volume of each plant. Water was added as needed to maintain it at the upper surface of the root medium. Flood water was replaced for all plants of a genotype on days that those plants completed the first, second,

and third drought cycles. To replace the water, we removed the plants from the large pots, flushed the root zone with the fertilizer solution (pH 6.0 to 6.6), and replaced the tap water in the outer container. Stomatal conductance of the youngest fully expanded leaf of three randomly selected, flooded plants of each genotype was measured with the porometer during the first 30 d of treatment and then at 3- and 5-d intervals.

After 75 d of inundation, which was the day the drought treatments ended, we removed the youngest fully expanded leaf on each of three randomly selected plants in the control and flood treatments for color analysis. Leaves were scanned into Adobe Photoshop 4.0, and an area of 76×76 pixels was cut from a standard, interveinal position near the midrib of each leaf. For each pixel in this area, the intensity of red, green, and blue was determined by using Visilog software (Noesis, St-Laurent, Que.). Increasing color intensities were represented by increasing values on a scale of 0 to 255. We summed the products of each scaled value and the number of corresponding pixels. This sum was divided by the total number of pixels, 5776, to find the mean intensity per pixel. We analyzed the ratio of intensity of green to red to test for effects of genotype and irrigation treatment. We also drained the flood water on day 75 and irrigated plants in the flood treatment daily thereafter with tap water to maintain the medium near container capacity. Stomatal conductance of the youngest fully expanded leaf was measured after 3 weeks.

Root-zone water content of plants in the control treatment was maintained near container capacity as described by Zwack et al. (1998). All plants of a cultivar were fertilized when that cultivar completed a drought cycle (Zwack et al., 1998). The porometer was used to measure stomatal conductance of three randomly selected control plants on days when measurements were taken on flooded plants. Measures of the environment around the plants

also were taken with the porometer at these times. Daily air temperature, RH, and *PPF* ranged from 19.0 to 24.8°C , 34.6% to 83%, and 57 to $1130 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$, respectively, during the treatment period.

Destructive harvest. We harvested the drought and control plants 1 d after completion of the third cycle. About four fully expanded lamina were removed from each plant in drought and control treatments, sealed in separate plastic bags, and kept frozen for 10 d. Samples were thawed at room temperature for 20 min and centrifuged at $3824 g_n$ for 20 min to express leaf sap. We estimated leaf osmotic potential by measuring osmolality of this foliar water with a Wescor 5500 vapor pressure osmometer (Logan, Utah). We reduced all measured osmotic potential values by 15% to account for the inclusion of apoplastic water in the leaf sap. This value has been applied to osmotic potential data obtained by using similar methods with red maple (Graves et al., 1989), is within the range of apoplastic water percentage typically observed among other taxa (Boyer and Potter, 1973; Tyree et al., 1978), and was applied with the assumption that our treatments did not alter partitioning of water between the apoplast and symplast.

Stem length was measured from the apex to the shoot origin on the cutting, and xylem diameter was measured 1.5 cm above the origin. We cut a 1.54-cm^2 disc from the youngest fully expanded leaf remaining on each plant for determination of specific weight. Discs were taken from the same interveinal position for each lamina, near the midrib about equidistant from the leaf base and tip, and were dried at 67°C for at least 7 d before being weighed. We also determined the relationship of lamina area and weight within genotype and irrigation treatment combination by using fully expanded leaves of each plant. Areas of these lamina were measured with an area meter (LI-3100; LI-COR), and dry weights were measured after tissues were held at 67°C for 3 to 7 d. Remaining shoot parts were dried at 67°C

Table 1. Variables measured after five genotypes of red maple and two genotypes of Freeman maple were subjected to three consecutive cycles of drought separated by fertilization to container capacity or to 75 d of continuous flooding. Means were separated by using Fisher's LSD ($P = 0.05$).

Treatment	Stem elongation (cm) ^y	Root DW ² (g)	Leaf DW (g) ^y	Leaf surface area : root DW (cm ² ·g ⁻¹) ^y	Leaf surface area : xylem diam (cm ² ·mm ⁻¹) ^y	Estimated leaf osmotic potential (-MPa)	Specific leaf weight (mg·cm ⁻²)	Root : shoot DW ratio ^y
<i>Genotype</i>								
Red maples								
Red 59904	45.9	10.0	11.7	201	252	1.37	5.5	0.44
'Autumn Flame'	62.7	11.9	13.8	245	311	1.50	4.9	0.33
'Fairview Flame'	45.0	11.2	10.0	193	229	1.58	4.8	0.47
October Glory®	48.5	16.0	15.8	199	320	1.54	4.9	0.43
Red Sunset®	69.9	17.2	23.9	261	449	1.72	5.5	0.35
Freeman maples								
Autumn Blaze®	44.7	18.8	16.6	174	377	1.55	5.2	0.57
'Indian Summer'	42.1	12.2	13.1	208	330	1.60	5.0	0.53
Genotype LSD _{0.05}	6.2	3.6	3.4	28	32	0.09	0.4	0.05
Red vs. Freeman maple contrast (<i>P</i>)								
	0.0001	0.05	0.76	0.002	0.0002	0.22	0.33	0.0001
<i>Irrigation</i>								
Control	106.7	19.5	21.4	212	384	1.16	5.2	0.38
Drought	35.1	8.9	9.9	221	280	1.92	5.3	0.48
Flood	18.6	---	---	---	---	---	4.9	---
Irrigation LSD _{0.05}	3.8	1.8	1.3	14	16	0.05	0.2	0.02

²DW = dry weight.

^yVariable for which interaction of genotype and irrigation treatments was significant at $P \leq 0.05$.

for at least 7 d before being weighed. Total lamina area per plant was estimated by applying the relationship of lamina area to weight that we determined for each treatment combination to total lamina weight data and adding the lamina areas of the leaves removed for determination of osmotic potential. Root systems were separated from the growth medium, placed in bags, and dried at 67 °C for at least 7 d before weighing.

Experimental design and data analysis. We used a factorial treatment design of three irrigation treatments and seven genotypes. Rooted cuttings were assigned randomly to treatments and placed on a greenhouse bench in a completely randomized design. There were eight replicates (plants) per treatment combination for 'Autumn Flame' and October Glory®, seven for Red Sunset®, six for 59904, five for Autumn Blaze®, and three for both 'Fairview Flame' and 'Indian Summer'. Data were analyzed by using the Statistical Analysis System (SAS Institute, Cary, N.C.). Analyses of variance (ANOVA) were performed by using the General Linear Model procedure. Treatment means were separated by using Fisher's least significant difference (LSD) ($P = 0.05$). Means for all combinations of irrigation treatments and genotypes were plotted vs. the mean over irrigation treatments by genotype to examine the source of interactions revealed by ANOVA.

Results

Effects of drought. Genotype $\times$ irrigation interactions existed for stem elongation, leaf dry weight, leaf surface area : root dry weight, leaf surface area : xylem diameter, and root : shoot ratio. For these variables, plots of the data illustrated that differences between genotypes in the control treatment were the main sources of the interactions. We judged such interactions to be of low significance for characterizing genotypic differences in resistance to water stress. Therefore, only main effect means for such variables are presented (Table 1). Drought reduced root dry weight and estimated leaf osmotic potential, and no interaction of genotype and irrigation treatment existed (Table 1). There also was no genotype $\times$ irrigation interaction for specific leaf weight, which was not altered by drought (Table 1). The mean number of days to reach the end of the third drought cycle differed among genotypes. Red Sunset®, Autumn Blaze®, October Glory®, 'Autumn Flame', 'Indian Summer', 59904, and 'Fairview Flame' required 27, 35, 39, 44, 50, 57, and 65 d, respectively, to complete the third drought cycle ($LSD = 9$). Plants survived three cycles of increasingly severe drought without visible leaf damage or abscission.

Stomatal conductance of plants subjected to drought differed among genotypes and drought cycles, and there was no interaction between these main effects. Averaged across all sampling dates, droughted plants of Red Sunset® had higher stomatal conductance than did all other genotypes except 'Indian Summer' (Table 2). Stomatal conductance was

Table 2. Mean stomatal conductance of five genotypes of red maple and two genotypes of Freeman maple subjected to three cycles of drought or to 75 d of continuous flooding. Values representing all dates are means of 18 to 43 measurements taken when volumetric water content of the root zone ranged from 0.010 to 0.400 $m^3 \cdot m^{-3}$. Other values for plants subjected to drought are means of three to eight replicates. For flooded plants, stomatal conductance was measured on 18 of the final 54 d of treatment on three replicates of each genotype, so each value in the column that represents the last 54 d is a mean of 54 measures. Values for stomatal conductance after 21 d of relief from flooding are means of three replicates of each genotype. Means within columns were separated by using Fisher's LSD ($P = 0.05$).

Genotype	Stomatal conductance ($mmol \cdot s^{-1} \cdot m^{-2}$)				
	All dates	2 d after first drought cycle	At end of second drought cycle	Over last 54 d of flooding	21 d after relief from flooding
Red maples					
Red 59904	89	146	42	24	44
'Autumn Flame'	93	182	26	57	154
'Fairview Flame'	97	119	16	27	42
October Glory®	98	219	23	24	41
Red Sunset®	120	224	19	56	101
Freeman maples					
Autumn Blaze®	73	123	28	33	78
'Indian Summer'	119	180	38	10	6
LSD _{0.05}	22	80	14	32	79

Fig. 1. Stomatal conductance over time for five red maple genotypes and two Freeman maple genotypes during 75 d of continuous flooding followed by a 21-d recovery period. Each point is a mean of 21 measurements averaged across genotypes. Data on control plants after recovery were not collected because they were harvested with plants in the drought treatment after 75 d.

similar across genotypes on the first day of treatment ($220 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$) and at the end of the first, second, and third drought cycles ($26 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$). The averages for droughted plants 2 d after completion of the first and second drought cycles were 179 and $158 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$, respectively. These data also were analyzed by drought cycle to determine during which stages of the drought treatment the genotypes differed. Genotypes differed 2 d after the completion of the first drought cycle ($P = 0.035$) and at the end of the second drought cycle ($P = 0.005$) (Table 2). Estimated leaf osmotic potential of genotypes differed across irrigation treatments. Red Sunset® had the lowest osmotic potential (-1.72 MPa) and 59904 had the highest (-1.37 MPa) (Table 1).

Effects of flooding. Flooding reduced stem elongation and specific leaf weight (Table 1). Mean stomatal conductance across genotypes increased to $>250 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ during the first days of flooding, then decreased until

about day 30 (Fig. 1). It remained near or below $50 \text{ mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ until treatments ended on day 75 (Fig. 1). After 8 d of inundation, 'Indian Summer' had lower stomatal conductance than the other genotypes, which caused an irrigation $\times$ genotype interaction (Fig. 2). Genotypes differed in their mean stomatal conductance over the last 54 d of flooding, and in their capacity to increase stomatal conductance after termination of flooding (Table 2). During the 75 d of treatments and 3 weeks after flooding, one out of eight replicates of 'Autumn Flame' and October Glory®, two out of six replicates of red maple 59904, and two out of three replicates of 'Indian Summer' died. Genotypes varied in the extent to which flooding reduced the ratio of green : red leaf color intensity; only in 'Autumn Flame' was this ratio not reduced (Fig. 3). Autumn Blaze® leaves turned a deeper red during flooding than did leaves of any other genotype. Our method of quantifying color provided data

Fig. 2. Stomatal conductance of plants in the control and flood treatments for each genotype vs. mean stomatal conductance for all plants within the genotype after 8 d of continuous flooding. Genotypes are arranged from left to right in order of increasing mean conductance after combining data from plants in the control and flood treatments. The nonparallel nature of the lines illustrates interaction between main effects. The genotype $\times$ irrigation interaction on day 8 can be attributed to the low conductance of 'Indian Summer' in the flood treatment. Each point is a mean of three single-plant replicates.

Fig. 3. Mean green : red leaf color intensity of plants of each genotype in the control and flood treatments vs. mean green : red leaf color intensity for all plants of each genotype after 75 d of continuous flooding. Genotypes are arranged from left to right in order of increasing mean ratio of green to red after combining data from plants in the control and flood treatments. The nonparallel nature of the lines indicates interaction between main effects. Each point is a mean of three single-plant replicates, except for flooded 'Indian Summer', which is represented by a single value.

consistent with this observation (Fig. 3). We observed but did not quantify leaf wilting, leaf epinasty, and hypertrophied lenticels on the submerged portion of the stem for all genotypes.

Discussion

Red maples and Freeman maples tolerated drought and flood stress by adjusting water use and growth. Although differences in growth and water relations among genotypes under favorable conditions were observed, we found

limited evidence for variation among individual genotypes in mechanisms of drought tolerance or the magnitude of expression of drought responses. For example, decreases in stomatal conductance and leaf osmotic potential in response to drought were similar for all genotypes. Yet when genotypes of the two species were contrasted statistically to obtain broad comparisons, differences between red maples and Freeman maples in magnitude of response for variables related to biomass partitioning suggested that the potential of Free-

man maples to avoid stress may be greater than that of red maples. Variation among individual genotypes in responses to flooding were evident. 'Indian Summer' responded more rapidly than did other genotypes; stomatal conductance was reduced after 8 d of inundation (Fig. 2). This suggests that 'Indian Summer' is a particularly flood-sensitive cultivar.

Near the end of the first drought cycle, severe foliar wilting was observed for all genotypes. Despite increasingly severe drought during the second and third cycles, foliar wilting became less severe, which suggests that plants adjusted to the stress. As foliar wilting decreased, so did stomatal conductance. Mean conductance across genotypes 2 d after the end of the second drought cycle was 21 and 62 $\text{mmol} \cdot \text{s}^{-1} \cdot \text{m}^{-2}$ lower than that 2 d after the end of the first drought cycle and at the beginning of treatments, respectively. Such conservative stomatal response in plants that have been exposed to stress has been observed in *Acer saccharum* Marsh. (sugar maple) (Close et al., 1996; Pereira and Kozlowski, 1978), *Betula papyrifera* Marsh. (Pereira and Kozlowski, 1978), and 'Marmo', 'D.T.R. 102', and 'Celzam' Freeman maple (Zwack et al., 1998). Davies and Kozlowski (1977), however, reported that red maple and sugar maple reopened their stomata within 1 d after an irrigation that ended a single drought episode. These authors suggested that the maples might not compete successfully with other species on dry sites, and noted that neither maple species regained full stomatal conductance after drought, which is consistent with our results after the first drought cycle.

Stomatal activity alone probably does not account for turgor maintenance at low moisture levels in the root zone. Osmotic adjustment requires active solute accumulation in leaf cells that allows for turgor maintenance despite low plant water potential. Osmotic adjustment in red maple seedlings from different ecotypes was reported by Abrams and Kubiske (1990), while Nash and Graves (1993) reported no differences in osmotic potential at full turgor between drought-stressed and well-hydrated plants of 'Franksred' red maple. Zwack et al. (1998) found an osmotic adjustment of 0.24 MPa for droughted plants of 'Celzam', 'D.T.R. 102', and 'Marmo' Freeman maples. We estimated leaf osmotic potential of drought-stressed plants to be 0.76 MPa more negative than that of controls maintained at a root-zone moisture content near container capacity. Genotypes also differed, but there was no interaction of genotype and irrigation effects. Red Sunset[®] had the lowest osmotic potential across both irrigation treatments and 59904 had the highest (Table 1). Control plants of Red Sunset[®], however, were very vigorous and tended to extract more water from the root zone between daily irrigations than did controls of the other genotypes. Consequently, mild stress near the end of treatments among control plants of Red Sunset[®] could have contributed to the overall lower osmotic potential of this genotype.

Continuous flooding reduced stomatal conductance of all seven genotypes in our experi-

ment. Stomatal closure has been reported as one of the first responses to flooding in green ash (*Fraxinus pennsylvanica* Marsh.), with closure beginning 1 or 2 d after inundation (Sena Gomes and Kozlowski, 1980). Will et al. (1995) reported that stomatal conductance of red maple seedlings was reduced to 70% of the conductance of controls after 1 d and to 49% of the conductance of controls after 3 d of continuous flooding, with a recovery to 70% of the conductance of controls after 9 d. During our study, stomatal conductance across genotypes increased among flooded plants during the first few days of inundation, and a reduction to 70% of the initial conductance required ≈ 9 d of flooding (Fig. 1). At no time during the 75 d of inundation did the average conductance recover to 70% of that of controls. The slower response of stomatal conductance in our experiment could be attributed to a less severe flooding treatment than others have used. Most reports of experiments with flooding involve several centimeters of standing water above the matrix of the root zone (Day, 1987; Peterson and Bazzaz, 1984; Will et al., 1995). Because we did not inundate plants above the surface of the rooting medium, oxygen diffusion near the roots may have lessened the severity of the stress.

'Indian Summer' responded to flooding more rapidly than did the other six genotypes, as evidenced by the interaction of genotype and irrigation treatments for stomatal conductance after 8 d of flooding (Fig. 2). Two of the three flooded plants of 'Indian Summer' died during treatment, which also suggests this Freeman maple is particularly prone to flooding stresses; the next highest mortality rate among flooded plants was 33% for 59904. The variation among genotypes in response to flooding is also illustrated by the degree to which stomatal conductance increased after termination of flooding. After 3 weeks near container capacity, conductance ranged from $154 \text{ mmol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ for 'Autumn Flame' to $6 \text{ mmol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ for 'Indian Summer' (Table 2). If such differing capacities for recovery are consistent regardless of plant age and time of year, the potential to select genotypes with superior flood resistance would be feasible. Although the reason genotypes differed in green : red leaf color intensity in response to flooding is not known, the only genotype that did not respond, 'Autumn Flame', also had relatively high stomatal conductance during flooding

and after recovery (Table 2). Day (1987) reported that flooding appeared to increase red pigmentation of red maple but did not quantify this. Future studies could address flooding effects on foliar anthocyanins and chlorophylls, as well as factors underlying differences among cultivars in the effects of stress on these pigments.

Whether Freeman maples are consistently more resistant to water stress than red maples under landscape conditions remains unknown, but our results provide relevant information. Some red maples showed as much drought and flooding tolerance as some Freeman maples. However, single-degree-of-freedom contrasts of the five red maples and two Freeman maples revealed species differences for five variables. Freeman maples as a group had less stem elongation, greater root dry weight, lower leaf surface area : root dry weight, higher root : shoot ratios, and a higher ratio of leaf surface area to xylem diameter (Table 1). All of these except leaf surface area : xylem diameter might be considered advantageous during drought because they represent a potentially more favorable balance between tissues that obtain water and tissues that lose water.

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