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Genotypic Variability in Photosynthesis, Water Use, and Light Absorption among Red and Freeman Maple Cultivars in Response to Drought Stress

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Abstract. **Cultivars of red (*Acer rubrum* L.) and Freeman maple (*Acer ×freemanii* E. Murray) are popular ornamental plants which are commonly placed in a variety of landscapes. To date, little information quantifies the capacity to tolerate and recover from drought among cultivars of red and Freeman maple. The objective of this study was to compare the effects of water stress on the physiology of five different maple cultivars of marketable size including four red maple genotypes, 'Summer Red', 'October Glory' (October Glory), 'Autumn Flame', and 'Franksred' (Red Sunset), as well as one hybridized Freeman maple genotype, 'Jeffersred' (Autumn Blaze). Two-year-old cloned genotypes of red and Freeman maple were subjected to two treatments: irrigated daily to container capacity or irrigation withheld for one drought and recovery cycle. Light absorption, gas exchange, and chlorophyll fluorescence measurements were conducted under well-watered and drought stress conditions that approached 0.070 $m^3 \cdot m^{-3}$. Compared to well-watered conditions, drought stress conditions of 0.090 $m^3 \cdot m^{-3}$ had a significant main effect that reduced the amount of light absorption in four of the five genotypes. Additionally, absorption among genotypes was different under both well-watered and water stress conditions. Over the course of drought stress and a recovery phase, net photosynthesis and stomatal conductance were different among genotypes. Maximum photosystem II (PSII) efficiency of dark-adapted leaves (F_v/F_m) was lowered by the water stress condition. The efficiency of excitation capture by open PSII reaction centers (F_v'/F_m') was variable among genotypes. Photochemical quenching was higher in Autumn Blaze, October Glory, and 'Summer Red' under drought conditions, which corresponded with a low degree of closure of PSII centers. Additionally, the fraction of excess excitation energy was also lower. Lastly, water deficit caused an increase in PSII efficiency in all genotypes except Autumn Blaze. This research demonstrated physiological variation among commercially available red and Freeman maple genotypes that may be selected for drought tolerance based on site moisture characteristics.**

Container-grown plants are often subjected to periods of severe drought. Drought-induced depression of photosynthesis can be the consequence of patchy stomatal closure and/or collapse of the mesophyll due to loss of turgor as a result of low lateral CO_2 diffusion capacity (Cornic and Massacci, 1996). As a result, leaf photosynthetic efficiency and capacity can be compromised. During periods of drought when stomata close and CO_2 assimilation is reduced, the photosynthetic reduction of O_2 via photorespiration increases and serves as a sink for excess excitation energy in the photosynthetic apparatus (Cornic and Briantais, 1991). The photorespiratory increase in O_2 reduction may not be sufficient to dissipate excess excitation energy in PSII antennae and as a consequence, energy dissipation occurs as heat in order to minimize damage to PSII reaction centers (Baker, 1993). Such effects can have significant consequences on the photosynthetic productivity of plants (Long et al., 1994). Analyzing changes in chlorophyll fluorescence emission via a pulse modulated fluorescence system (Schreiber et al., 1994) has been used to study both photosynthetic electron transport and thermal dissipation in leaves (Demmig-Adams and Adams, 1992; Genty et al., 1989) and can elucidate photo-damage to PSII reaction centers in response to stress.

Variation in water stress tolerance of photosynthetic and respiratory systems can be a principal factor in differential growth under drought stress. Considerable differences in response to drought are known to exist among genotypes of red maple (Abrams and Kubiske, 1990), and it may be possible to select for this variability to manage cultivars in nursery and landscape conditions. The intent to tailor other tree species to soil conditions (e.g., *Populus*) through selective breeding, interspecific hybridization, and cloning has been based on genetic diversity within species (Stettler et al., 1988). Red maple (*Acer rubrum* L.) occurs naturally along a hydrologic continuum from wet to dry (Golet et al., 1993; Walters and Yawney, 1990) and has shown genotypic variability among sites of different soil moisture availability (Abrams and Kubiske, 1990; Anella and Whitlow, 1998, 2000; Townsend and Roberts, 1973). In addition to the potential genetic diversity within the species, red maple can cross-pollinate with silver maple (*Acer saccharinum* L.), the hybrid of which is known as Freeman maple (*Acer ×freemanii* E. Murray). The high adaptability of red maple to different soils and climates together with its wide distribution across the eastern United States, and its ability to cross-pollinate with silver maple, could favor differentiation, providing a basis for cultivar development.

Variations in photosynthesis and transpiration rates coupled with chlorophyll fluorescence and light absorption parameters provide a quick and noninvasive way to characterize plant responses to water stress. Photoprotective processes are thought to occur in light-harvesting antenna of PS II (Horton et al., 1996). Fluorescence can decipher the amount of quenching within the PS II reaction center and, therefore, quantify damage to the PS II antenna. The technique quantifies the response of the photosynthetic apparatus to stress and variability within the measured

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parameters, and could indicate genotypic tolerance and adaptation to water deficits.

In this study, genotypic variation in the response of commercially available red and Freeman maple genotypes to drought and drought recovery was quantified to address the following questions: 1) To what extent is the capacity for tolerance to drought and recovery of photosynthesis a variable among red and Freeman maple genotypes? 2) To what extent do changes in water status and stomatal conductance explain differences in genotypic response to carbon assimilation, photosystem II function, and light absorption?

Genotypes of red maple and a hybrid Freeman maple were chosen for this study because they are popular ornamental trees grown commercially in nurseries. There is already considerable basic information on their photosynthetic responses to drought stress (Abrams, 1988; Abrams and Kubiske, 1990; Briggs et al., 1986; Nash and Graves, 1993; Townsend and Roberts, 1973; Zwack et al., 1998, 1999). Preliminary studies using a modulated fluorescence system and an integrating sphere have indicated a robust photosynthetic apparatus tolerant of extended water deficits (unpublished preliminary study). Two-year-old cloned cultivars were chosen, rather than cuttings, to provide data on the drought response of plant material commonly available to a consumer and subject to drought in the nursery during shipping, and/or in the hands of the consumer.

Materials and Methods

Plant material. Four South Carolina grown (Parsons Nursery, Georgetown, S.C.) red maple cultivars ['Summer Red', 'October Glory' (October Glory), 'Autumn Flame', and 'Franksred' (Red Sunset] and one Freeman maple cultivar 'Jeffersred' (Autumn Blaze) were transplanted into 56.7-L Spin Out (Nursery Supplies Inc., United States) treated plastic pots containing a mixture of 20 pine bark: 1 sand (v:v), fertilized with 8.3 kg·m^{-3} of Nutricote 20N–3.0P–8.3K type 360 (Chiso-Asahi Inc., Japan), and placed on an outdoor gravel pad. After the 1.5 m tall trees were transplanted on 7 to 14 Apr. 2001, they were grown under natural photoperiod and irradiance at the local outdoor nursery (Parson's Nursery). Plants were irrigated four times daily to container capacity with pressure compensating drip emitters (ML Irrigation Inc., Laurens, S.C.), determined by the visual sign of container flow through. Plants were shipped to Clemson University on 7 Aug. 2001, transferred to an outdoor gravel pad, and fitted with identical pressure-compensating drip emitters. Pots were spaced 1.5 m center-to-center. Initially, all pots were watered to saturation and permitted to drain for 18 h. Plants were irrigated four times daily to container capacity before imposing drought. To eliminate evaporation from the substrate surface and/or water penetration in case of rain, white plastic bags were cut and sealed to the stem with Parafilm (American National Can, Greenwich, Conn.). The bottom ends of the bags were left open and secured to the lip of the pots with an elastic plastic ring. Wrapping the exterior of each container with aluminum foil reduced the radiation load on containers. For each genotype, treatments consisted of a well-watered control (n = 6) watered four times daily as before and a drought treatment where water was withheld (n = 6) until reaching a volumetric water content of 0.090 m^3·m^{-3}. At the initiation of the study, plant size was of wholesale marketable quality for either 56.7-L and/or 1.27-cm-diameter landscape material.

Water measurements. After drainage and thereafter every other day, bulk volumetric water content of each container was measured in four locations with a Theta Probe type ML2 (Delta-T Devices, Cambridge, England) at 10 and 20 cm below the substrate surface and measurements were pooled. Readings were taken in four predrilled locations (two each on opposite sides of the pot). Drilled holes were large enough to allow the probe adequate movement and contact with the substrate surface within the container. The readings were then averaged to estimate bulk volumetric water content for each container.

To minimize variation within the drought stress episode, the volumetric water content of each plant was assessed individually. When the substrate of an individual replicate of a given genotype reached a bulk volumetric water content of 0.090 m^3·m^{-3}, a timed drought and recovery cycle was initiated. During this cycle, leaves were sampled on days 1, 3, 5, 6, 7, and 9. Plants were rewatered to container capacity the evening of the fifth day and tracked for recovery responses for 4 d of poststress observations. When a plant completed its cycle, it was terminated from the study.

To minimize the chances of leaf abscission and variation in bulk volumetric water content, a preliminary experiment (n = 6) was conducted to derive nonlethal bulk volumetric water content over time (data not shown). We undertook an additional preliminary experiment to construct substrate moisture release curves on representative substrate samples (n = 6). Our pressure plate apparatus was capable of –1.5 MPa. For our substrate, the data indicate that a substrate moisture status of –1.5 MPa equates to a 22% volumetric water content (unpublished data). The data were used purely as an indication of the level of water status of the substrate.

Measurements of leaf gas exchange and chlorophyll fluorescence. Randomly selected plants from each source and treatment combination were chosen for repeated sampling of gas exchange, chlorophyll fluorescence, and light absorption measurements (n = 6). Before arrival at a moisture status of 0.090 m^3·m^{-3}, plants were measured every 2 d, and during the drought and recovery cycle, plants were measured at the same times as soil moisture status as described above. Net photosynthesis (A_{net}) and leaf conductance (g_s) were measured on the first fully expanded leaf in full sun using a portable steady state gas-exchange system (CIRAS-I, PP Systems, Haverhill, Mass.) equipped with a light- and temperature-controlled cuvette (model PLC5 (B); PP Systems). On the terminal tip, measurements were taken on the youngest fully expanded non-damaged leaf from 0900 to 1230 HR. The leaves were tagged and on any given day, measurements were taken in random order to compensate for any effects caused by time of sampling. All leaves were south oriented and fully exposed to reduce environmental interactions. Leaf temperature within the cuvette was controlled at 25 °C, photosynthetic photon flux (*PPF*) was maintained at 1000 μmol·m^{-2}·s^{-1} with the cuvette light source, and vapor pressure deficit in the cuvette kept at 1.3 ± 0.4 kPa. Temperature set points were taken as those optimum for temperate-zone C_3 species (Kozlowski and Pallardy, 1997). Saturating *PPF* set points were derived from Bauerle (2001) and vapor pressure deficit set points were determined in a preliminary study (unpublished data). Measurements were recorded after reaching steady state.

Chlorophyll fluorescence was measured on individual leaves using a portable modulated fluorometer (OS5-FL; Opti-Sciences, Tyngsboro, Mass.). Maximum fluorescence (F_m) and minimum fluorescence (F_o) of dark-adapted leaves were equilibrated for a minimum of 30 min using a dark-adapting leaf clip and measured at twilight. Measurements were taken on the same leaves and relatively the same leaf area used for gas exchange. For leaves exposed

to natural sunlight, fluorescence values F'_m, F'_o, and F'_v were obtained by imposing a 0.8-s saturating flash of ≈ 20,000 μmol·m^{-2}·s^{-1} *PPF* at the end of the fiber optic to the leaf. At twilight, the efficiency of excitation capture of open PSII centers was measured and at solar noon the PSII photochemical efficiency was calculated by dividing the maximum light adapted fluorescence (F'_m) by the change in minimal and maximal light adapted fluorescence (F'_v) (Genty et al., 1989) at ambient light (usually above 1500 μmol·m^{-2}·s^{-1}). The same leaves and leaf area surface on a leaf were used for dark-adapted and solar noon measurements.

Chlorophyll fluorescence nomenclature followed that of van Kooten and Snel (1990). The quantum efficiency of PSII (F_v/F_m) for dark-adapted leaves was calculated where F_v is the difference between minimal and maximal fluorescence. For leaves exposed to natural sunlight, the coefficient for non-photochemical quenching (q_N) was calculated as $q_N = 1 - (F'_v)/F_m - F_o$, whereas the photochemical quenching coefficient (q_P) was calculated as $q_P = (F'_m - F_s)/(F'_m - F'_o)$ where F_s is steady state fluorescence (Demmig-Adams and Adams, 1996; Schindler and Lichtenthaler, 1996; Schreiber et al., 1994). An estimate of the PSII reduction state (PSII closure) is derived as $1 - q_P$. Nonphotochemical quenching (NPQ) was calculated as $(F_m - F'_m - 1)$ (Bilger and Björkman, 1990; Demmig-Adams and Adams, 1996; and Demmig-Adams et al., 1997). Quantum efficiency of PSII (open centers) under natural light was calculated as $(F'_v)/F'_m$. Actual PSII efficiency (PSII) was calculated using steady state fluorescence (F_s) as $(F'_m - F_s)/F'_m$ (Genty et al., 1989). The fraction of absorbed *PPF* potentially going into singlet oxygen formation ($^1O_2$) was estimated as $(F'_v/F'_m) \times (1-q_P)$ (Demmig-Adams and Adams, 1996).

Measurements of light absorption. At the peak of drought stress (≈0.090–0.070 m^3·m^{-3}), a spectroradiometer with the 1800-12S integrating sphere attachment (LI-1800; LI-COR Inc., Lincoln, Nebr.) was used to measure leaf reflectance and transmittance on the youngest fully expanded, nondamaged leaf on the first lateral from the terminal tip. Each leaf remained attached to the stem until immediately before absorption determinations. To investigate potential absorption changes in the photosynthetic absorption range, a reference scan and a sample scan were made from 400–700 nm immediately upon excision at 2-nm intervals for both reflectance and transmittance. The sample scan was divided by the individual reference scan for each leaf at each particular measurement and integrated over the wavelength range to obtain an average. Sample absorption was calculated as absorption = (1 – reflectance – transmittance).

Experimental design and data analysis. Treatments were applied in a completely random repeated measures design with a factorial arrangement between the two irrigation treatments (control and drought) and five genotypes. Red and Freeman maple cloned genotypes were assigned randomly to treatments and placed on a gravel pad in a completely randomized design. There were six replications per treatment genotype combination. Data were analyzed using analysis of variance (SAS Institute Inc., 1989). A Fisher's protected least significance difference test ($P \leq 0.05$) was used to characterize the relationship among genotypes.

Results

Substrate water potential. Substrate moisture release curves indicated –1.5 MPa occurred at 22% water by volume in the pine bark, sand substrate used in the study. The threshold substrate volumetric water content of 0.090 m^3·m^{-3} (a predetermined value that caused wilting across genotypes in a preliminary study) was equal to 9% water by volume in our substrate.

Chlorophyll fluorescence. In spite of the level of drought stress imposed, fluorescence values presented an overall nonsignificant treatment effect for all but the fraction of PSII centers that reached closure ($1–q_P$). With respect to F_v/F_m, q_N, q_P, $1 - q_P$, NPQ, F'_v/F'_m, PS II, and $^1O_2$, only $1–q_P$ indicated a difference in the relative variation of genotype means at $P \leq 0.05$. To compare possible genotypic variability, fluorescence values under irrigated conditions are reported since the drought treatment did not result in significant changes in all but one fluorescence parameter. The F_v/F_m values were slightly lower than 0.83 (Table 1), a reference value reported as optimal for an unstressed higher plant (Björkman and Demmig, 1987; Johnson et al., 1993). Although ANOVA showed a statistical difference among genotypes for this parameter, the relative variation of genotype means was only 1.46%; thus this is an unlikely source of significant genotype variation under irrigated conditions. In addition, F_v/F_m values remained relatively unchanged in response to drought. Table 1 also shows values of thermal dissipation of excitation energy, indicated by both NPQ and q_N. Although the relative variation in NPQ and q_N was high, the standard errors in NPQ explain the lack of statistical significance, whereas q_N values were different among genotypes. The efficiency of excitation capture by open PSII centers (F'_v/F_m') was different among genotypes at $P \leq 0.01$. Photochemical quenching (q_P) did not indicate a high degree of variation among genotypes, whereas the fraction of PSII closure

Table 1. Chlorophyll fluorescence parameters of irrigated plants of five genotypes of maple. Results are given as mean ± SE of six replications. Volumetric water contents (V) (m^3·m^{-3}) are given for well watered irrigated conditions. Dark adapted photochemical efficiency (F_v/F_m) was measured using a dark adapted leaf at twilight. Nonphotochemical quenching coefficient (q_N), photochemical quenching coefficient (q_P), estimate of the PSII reduction state ($1 - q_P$), nonphotochemical quenching (NPQ), efficiency of excitation capture by open PSII centers (F'_v/F'_m), actual PSII efficiency (PSII), and the fraction of absorbed PPF potentially going into singlet oxygen formation ($^1O_2$) were measured at solar noon.

Cultivar	V	F_v/F_m	q_N	q_P	$1-q_P$	NPQ	F'_v/F'_m	PSII	$^1O_2$
Autumn Blaze	> 0.5	0.792 ± 0.006 a	0.273 ± 0.025 b	0.873 ± 0.015	0.126 ± 0.014	0.146 ± 0.015	0.500 ± 0.016 a	0.486 ± 0.011 a	0.066 ± 0.010 b
Autumn Flame	> 0.5	0.803 ± 0.005 ac	0.167 ± 0.024 a	0.871 ± 0.013	0.129 ± 0.013	0.126 ± 0.015	0.514 ± 0.016 a	0.471 ± 0.010 ac	0.075 ± 0.009
October Glory	> 0.5	0.817 ± 0.006 b	0.187 ± 0.026 a	0.844 ± 0.013	0.156 ± 0.013	0.144 ± 0.016	0.567 ± 0.017 b	0.501 ± 0.010 ad	0.097 ± 0.009 c
Red Sunset	> 0.5	0.805 ± 0.005 a	0.173 ± 0.024 a	0.851 ± 0.012	0.149 ± 0.012	0.120 ± 0.014	0.553 ± 0.015 b	0.493 ± 0.010 a	0.091 ± 0.009
Summer Red	> 0.5	0.787 ± 0.005 ad	0.190 ± 0.023 a	0.846 ± 0.013	0.154 ± 0.013	0.113 ± 0.014	0.502 ± 0.015 a	0.454 ± 0.010 b	0.090 ± 0.009
Relative variation of cultivar means		1.46	21.71	1.65	9.94	11.23	5.82	3.88	15.22
P		**	*	NS	NS	NS	**	**	NS
Drought		NS	NS	NS	NS	NS	NS	NS	NS

[z]Mean separation by Fischer's LSD at $P \leq 0.05$. The relative variation of cultivar means is shown as a percentage. Significant differences between cultivars at $P \leq 0.05$ are designated by letters.

NS,*,**Nonsignifican or significant at $P \leq 0.05$ or 0.01, respectively.

$(1 - q_P)$ was relatively high in variation between genotypes as was the fraction of absorbed PPF potentially going into $^1O_2$ formation though none significantly varied. Nonphotochemical quenching showed 21.71% variation among genotypes, with Autumn Blaze presenting the highest q_N coefficient. The efficiency of excitation capture by open PSII centers (F'_v/F'_m) and the actual PSII efficiency exhibited significant cultivar variation (Table 1).

Gas exchange. Drought (connected symbols) values for A_{net} and g_s are presented as percent of control (Fig. 1). Before subjecting the cultivars to drought, baseline A_{net} and g_s values were similar among the five cultivars under study (data not shown). For purposes of clarity, gas exchange significant differences greater than $P \leq 0.05$ are stated as significantly different in the text. Effects of drought were more pronounced on A_{net} and g_s for 'Autumn Flame' during the drought period than the other cultivars under study. Photosynthesis was reduced ≈90% and g_s was reduced 55% five days after arriving at a threshold 0.090 $m^3 \cdot m^{-3}$ moisture status (Fig. 1). The decline, particularly in A_{net}, from initial irrigated levels to threshold substrate moisture was more pronounced in the remaining four genotypes, whereas 'Autumn Flame' retained A_{net} and g_s levels closer to control values. The A_{net} for 'Autumn Flame' was higher than that for Autumn Blaze, Red Sunset, and 'Summer Red' on day 1 of the drought cycle and 'Summer Red' on day 3 of the drought cycle. A_{net} for Red Sunset was significantly higher than 'Autumn Blaze', 'Autumn Flame,' October Glory, and 'Summer Red' at the end of the study. The g_s for 'Autumn Flame' was significantly higher than that for all other genotypes on day 1 of the drought cycle; there were no differences on day 3; and on day 5, only Red Sunset and 'Summer Red', were different. On the first and second day into recovery, day 6 and 7, there were no genotypic differences in either A_{net} or g_s. Four days after rewatering (day 9 of the cycle), 'Summer Red' rebounded to its original A_{net} level and within 20% of initial g_s. At the same time, mean separation indicated 'Summer Red' was different from October Glory for A_{net} and different from Autumn Blaze and October Glory for g_s.

Light absorption. Genotypes presented differences with respect to the amount of absorbed light both under control and drought stress conditions (Fig. 2). In response to drought stress (the main treatment effect), percent absorbed light decreased slightly in all genotypes except for Autumn Blaze ($P \leq 0.05$). The relative reduction of absorption was similar among the four, excluding Autumn Blaze, in both transmitted and/or reflected light in response to drought stress. Under well-watered conditions, Autumn Blaze was different from all other genotypes, whereas 'Autumn Flame', Red Sunset, October Glory and 'Summer Red' were the same. Drought stress resulted in the same pattern among genotypes with the only discrepancy being a nonstatistical difference between Autumn Blaze and October Glory.

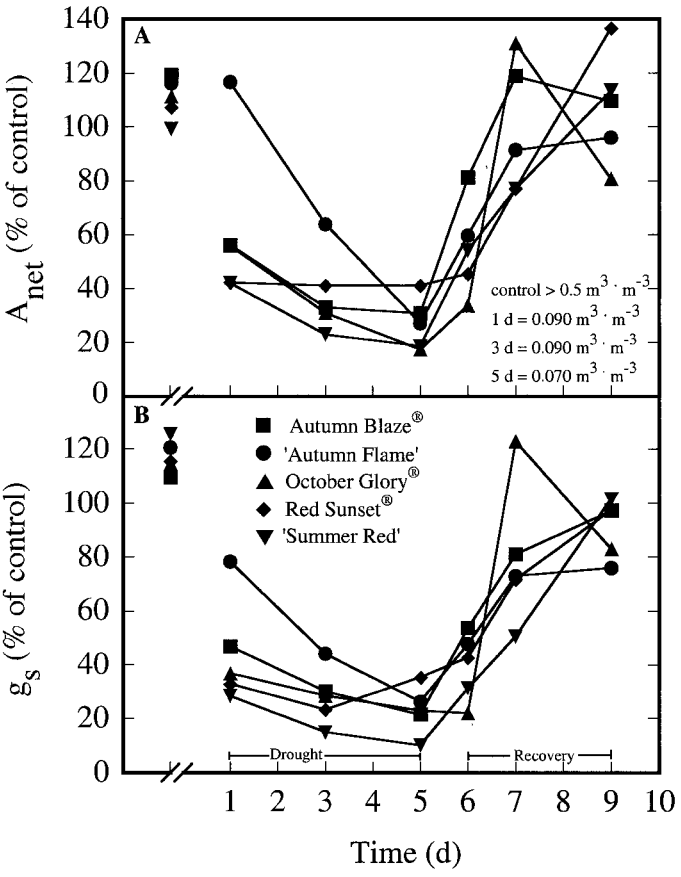

Fig. 1 (**A**) CO_2 assimilation rate (A_{net}) and (**B**) stomatal conductance (g_s) during a timed drought and recovery cycle for 'Autumn Blaze' (■), 'Autumn Flame' (●), October Glory (▲), 'Red Sunset' (◆), and 'Summer Red' (▼) genotypes of maple. Legends apply to all figures. Means (n = 6) are for individual genotypes for the drought treatment expressed as a percentage of that genotype's control. The volumetric substrate water content at days 1, 3, and 5 is denoted in the figure legend.

Discussion

These results indicate that a relatively short duration drought stress, which could occur under nursery and or landscape conditions, causes significant changes in foliar gas exchange and light absorption but not in most chlorophyll fluorescence parameters in maple genotypes. The primary changes included a decrease in A_{net}, g_s, and absorbed light, and an increase in the fraction of PSII center closure. A major effect of drought treatment was a reduction in g_s, which simultaneously reduced both water loss and carbon assimilation. Chlorophyll fluorescence data depicted a functioning PSII, even under stress conditions. This likely indicates CO_2 depletion as the primary factor limiting photosynthesis under

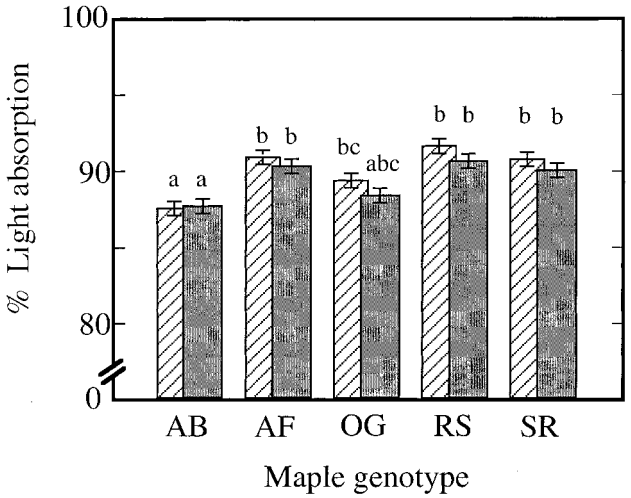

Fig. 2. Percentage of leaf light absorption within the photosynthetic 400 to 700 nm wavelength range for 'Autumn Blaze' (AB), 'Autumn Flame' (AF), 'October Glory' (OG), 'Red Sunset' (RS), and 'Summer Red' (SR) genotypes of red and freeman maple. Means (n = 6) for individual genotypes are hatched for irrigated and solid for the drought treatment. The means followed by the same letter are not significantly different at $P < 0.05$. Bars represent SE.

drought (Whitehead, 1998). It may be that the photosynthetic reduction of O_2 via photorespiration increased, which then provided a sink for excess excitation energy (Cornic and Briantais, 1991). The O_2 reduction alone would not be adequate to dissipate all of the excess excitation energy; other possibilities would be loss of energy as heat and an overall increase in reflected and or transmitted radiation (Baker, 1993; Cornic, 1994). In addition, abscisic acid (ABA) accumulation in the guard cells may be responsible for stomatal closure preventing both water loss and photosystem degradation (Whitehead, 1998). The role of ABA in the regulation of stomatal aperture in drought stressed plants has been documented (Borel et al., 1997; Trejo et al., 1995). In regards to genotypic variation, however, response to water deficit may be mediated by variable responsiveness to ABA (Bauerle, unpublished data). The end product of variable ABA responsiveness is responsible for variation in regulating stomatal control (Cellier et al., 1998). Our results were different from research on cuttings, where Raschke and Hedrich (1985) found that high ABA levels under water-stress could affect photosynthetic rates by prompting stomatal closure and/or mesophyll degradation that affects the photosynthetic apparatus.

In contrast to CO_2 gas exchange measurements where various drought-induced effects have been reported for red maple (Zwack et al., 1998, 1999), little data on chlorophyll fluorescence and light absorption under water stress are available. By dark adapting the leaf, photoinhibition can easily be determined by measuring potential quantum yield (Genty et al., 1989). Values for F_v/F_m were not different among genotypes. Moreover, F_v/F_m was insensitive to stress under short periodic drought and only $1–q_P$ showed effects of stress when measured after illumination. It is unlikely that increased internal recycling of photorespired CO_2 could have resulted in the continuation of uninterrupted CO_2 fixation in stressed leaves. In addition, the rate of photosynthesis could vary greatly with only small effects on fluorescence parameters (Massacci and Jones, 1990). Although chlorophyll fluorescence may not be the best tool for investigation of the response to drought stress, it has been demonstrated that genotypic differences can be deciphered with respect to the composition of NPQ (Johnson et al., 1993). Moreover, the most powerful and elegant application of fluorescence is to use it in conjunction with other techniques such as gas exchange measurements to obtain a full picture of the plant response to environmental stress (Maxwell and Johnson, 2000). Within this study, the chlorophyll fluorescence and light absorption parameters alone are unlikely to indicate the net photosynthesis response to stress, making gas exchange a necessary measurement for an interpretation of the plant response to stress.

Considerable genetic variability exists within red maple populations for traits including drought tolerance (Abrams and Kubiske, 1990; Reaves et al., 2002; Townsend and Roberts, 1973), ozone tolerance (Townsend and Dochinger, 1974), growth and phenology (Townsend, 1977), response to light (Sibley et al., 1997), seed germination syndrome where different amounts of vernalization are required (Anella and Whitlow, 1998) and response to flooding (Anella and Whitlow, 1999, 2000). The variation may open up the possibility of quantifying the capacity both to tolerate drought stress and recover from drought. We found variation among individual genotypes in response to drought. This was most evident at the beginning and end of the drought cycle. Contrary to other reports on red maple by Davies and Kozlowski (1977) and Zwack et al. (1999), one genotype, October Glory, did regain full g_s two days after drought relief. Similar to those reports, the overall trend was to lower g_s and conserve water use up to four days after drought relief, even though photosynthesis was at or near predrought levels in most genotypes.

Variation in gas exchange traits among individual genotypes in response to drought was evident. During the first three days of the drought cycle, 'Autumn Flame' maintained a higher level of both A_{net} and g_s than did other genotypes, but after 5 d of a 0.090 $m^3 \cdot m^{-3}$ or less volumetric water content, Red Sunset maintained a higher level of A_{net} and g_s. The one Freeman maple of the group (Autumn Blaze) gave no indication that its tolerance of drought stress may be greater than that of the red maple genotypes. The outcome contradicted observations with rooted cuttings by Zwack et al. (1999) in relation to biomass partitioning. The more important observation herein was to quantify the effects of drought on the photosynthetic apparatus in relation to gas exchange and light absorption.

In conclusion, our results showed that under realistic nursery potential water stress levels, variation in cultivar physiological response occurred. We found marketable quality 56.7-L/1.27-cm diameter maple genotypes to have a photosynthetic apparatus that appears to be maintained under periods of brief water stress, the mechanism of which may involve heat dissipation and increases in reflected and transmitted radiation. Alternatively, genotype chlorophyll content could be affected by drought and chlorophyll degradation could therefore reduce leaf light absorption (Bauerle, unpublished data). Results were dependent on the duration of drought. Genotypes of red maple already on the market can be selected for drought tolerance based on physiological response to water deficit. Genotypes, which rebound to original or near original physiological levels, are more likely to survive and tolerate drought episodes compared to those that do not recover. Such information can benefit both growers and the landscape community as to the level and consequence of drought stress on maple selections.

Literature Cited

Abrams, M.D. 1988. Comparative water relations of three successional hardwood species in central Wisconsin. Tree Physiol. 4:263–273.

Abrams, M.D. and M.E. Kubiske. 1990. Photosynthesis and water relations during drought in *Acer rubrum* L. genotypes from contrasting sites in central Pennsylvania. Funct. Ecol. 4:727–733.

Anella, L.B. and T.H. Whitlow. 1998. Germination of *Acer rubrum* seeds collected from wet and dry habitats. Seed Sci. Technol. 26:755–762.

Anella, L.B. and T.H. Whitlow. 1999. Flood tolerance ranking of red and Freeman maple cultivars. J. Arboricult. 25:31–37.

Anella, L.B. and T.H. Whitlow 2000. Photosynthetic response to flooding of *Acer rubrum* seedlings from wet and dry sites. Amer. Mid. Nat. 143:330–341.

Baker, N.R. 1993. Light-use efficiency and photoinhibition of photosynthesis in plants under environmental stress, p. 221–235. In: J.A.C. Smith and H. Griffiths (eds.). Water deficits: plant responses from cell to community. Bios Scientific Publ., Oxford.

Bauerle, W.L. 2001. The water relations of *Acer rubrum* L. ecotypes from contrasting hydrologic habitats. PhD diss. Cornell Univ, Ithaca, N.Y.

Bilger, W. and O. Björkman. 1990. Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in *Hedera canariensis*. Photosyn. Res. 25:173–185.

Björkman, O. and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence at 77K among vascular plants of diverse origins. Planta 170:489–504.

Borel, C., T. Simonneau, D. This, and F. Tardieu. 1997. Stomatal conductance and ABA concentration in the xylem sap of barley lines of contrasting genetic origins. Austral. J. Plant Physiol. 24:607–615.

Briggs, G.M., T.W. Jurik, and D.M. Gates. 1986. Non-stomatal limitation of CO_2 assimilation in three species during natural drought conditions. Physiol. Plant. 66:521–526.
Cellier, F.G., G. Conéjéro, J.C. Breitler, and F. Casse. 1998. Molecular and physiological responses to water deficit in drought-tolerant and drought-sensitive lines of sunflower. Plant Physiol. 116:319–328.
Cornic, G. 1994. Drought stress and high light effects on leaf photosynthesis, p. 297–313. In: N.R. Baker and J.R. Boyer (eds.). Photoinhibition of photosynthesis from molecular mechanisms to the field. Bios Scientific Publ., Oxford.
Cornic, G. and J.M. Briantais. 1991. Partitioning of photosynthetic electron flow between CO_2 and O_2 reduction in a C_3 leaf (*Phaseolus vulgaris* L.) at different CO_2 concentrations and during drought stress. Planta 183:178–184.
Cornic, G. and A. Massacci. 1996. Leaf photosynthesis under drought stress, p. 347–366. In: N.R. Baker (ed.). Photosynthesis and the environment. Kluwer Academic Publ., The Netherlands.
Davies, W.J. and T.T. Kozlowski. 1977. Variations among woody plants in stomatal conductance and photosynthesis during and after drought. Plant Soil 46:435–444.
Demmig-Adams, B. and W.W. Adams, III. 1992. Photoprotection and other responses of plants to high light stress. Annu. Rev. Plant Physiol. Plant Mol. Biol. 43:599–626.
Demmig-Adams, B. and W.W. Adams. 1996. Xanthophyll cycle and light stress in nature: Uniform response to excess direct sunlight among higher plant species. Planta 198:460–470.
Demmig-Adams, B., W.W. Adams, III, and S.C. Grace. 1997. Physiology of light tolerance in plants. Hort. Rev. 18:215–246.
Genty, B., J.M. Briantais, and N.R. Baker. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta 990:87–92.
Golet, F.C., A.J.K. Calhoun, W.R. DeRagon, D.J. Lowry, and A.J. Gold. 1993. Ecology of red maple swamps in the glaciated northeast: A community profile. 12. U.S. Dept. of the Interior, Lafayette, Ind.
Horton, P., A.V. Ruban, and R.G. Walters. 1996. Regulation of light harvesting in green plants. Annu. Rev. Plant. Physiol. Plant Mol. Biol. 47:655–684.
Johnson, G.N., A.J. Young, J.D. Scholes, and P. Horton. 1993. The dissipation of excess excitation energy in British plant species. Plant Cell Environ. 16:673–679.
Kozlowski, T.T. and S.G. Pallardy. 1997. Physiology of woody plants. 2nd ed. Academic Press, San Diego.
Long, S.P., S. Humphries, and P.G. Falkowski. 1994. Photoinhibition of photosynthesis in nature. Annu. Rev. Plant Physiol. Plant Mol. Biol. 45:633–662.
Massacci, A. and H.G. Jones. 1990. Use of simultaneous analysis of gas-exchange and chlorophyll fluorescence quenching for analyzing the effects of water stress on photosynthesis in apple leaves. Trees Structure and Function 4:1–8.
Maxwell, K. and G.N. Johnson. 2000. Chlorophyll fluorescence—A practical guide. J. Expt. Bot. 51:659–668.
Nash, L.J. and W.R. Graves. 1993. Drought and flood stress effects on plant development and leaf water relations of five taxa of trees native to bottomland habitats. J. Amer. Soc. Hort. Sci. 118:845–850.
Raschke, K. and R. Hedrich. 1985. Simultaneous and independent effects of abscisic acid on stomata and photosynthetic apparatus in whole leaves. Planta 163:105–118.
Reaves, M., T. Whitlow, and J. Comstock. 2002. Physiological response of red maple under drought conditions. HortScience 37:438.
SAS Institute, Inc. 1989. SAS user's guide. Statistics. 6th ed. SAS Institute, Inc. Cary, N.C.
Schindler, C. and H.K. Lichtenthaler. 1996. Photosynthetic CO_2-assimilation, chlorophyll fluorescence and zeaxanthin accumulation in field grown maple trees in the course of a sunny and a cloudy day. J. Plant Physiol. 148:399–412.
Schreiber, U., W. Bilger, and C. Neubauer. 1994. Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of in vivo photosynthesis, p. 49–70. In: E.D. Schulze and M.M. Caldwell (eds.). Ecophysiology of photosynthesis. Springer-Verlag, Berlin.
Sibley, J. L., D.J. Eakes, C.H. Gilliam, G.J. Keever, and W.A. Dozier Jr. 1997. Photosynthetic response of selected red maple cultivars to light. J. Arboricult. 23:100–105.
Stettler, R.F., R.C. Fenn, P.E. Heilman, and B.J. Stanton. 1988. *Populus trichocarpa* x *Populus deltoides* hybrids for short-rotation culture: Variation patterns and 4-year field performance. Can. J. For. Res. 18: 745–753.
Townsend, A.M. 1977. Characteristics of red maple progenies from different geographic areas. J. Amer. Soc. Hort. Sci. 102:461–466.
Townsend, A.M. and L.S. Dochinger. 1974. Relationship of seed source and development stage to the ozone tolerance of *Acer rubrum* seedlings. Atmos. Environ. 8:957–964.
Townsend, A.M. and B.R. Roberts. 1973. Effect of moisture stress on red maple seedlings from different seed sources. Can. J. Bot. 51:1989–1995.
Trejo, C.L., A.L. Clephan, and W.J. Davies. 1995. How do stomata read abscisic acid signals? Plant Physiol. 109:803–811.
van Kooten, O. and J.F.H. Snel. 1990. The use of fluorescence nomenclature in plant stress physiology. Photosyn. Res. 25:147–150.
Walters, R.S. and H.W. Yawney. 1990. *Acer rubrum* L., red maple, p. 654. In: Silvics of North America. Agr. Hndbk. II. Hardwoods. U.S. Dept. Agr., Wash., D.C.
Whitehead, D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiol. 18:633–644.
Zwack, J.A., W.R. Graves, and A.M. Townsend. 1998. Leaf water relations and plant development of three Freeman maple cultivars subjected to drought. J. Amer. Soc. Hort. Sci. 123:371–375.
Zwack, J.A., W.R. Graves, and A.M. Townsend. 1999. Variation among red and freeman maples in response to drought and flooding. HortScience 34:664–668.