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Response of five temperate deciduous tree species to water stress

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Summary

Gas exchange, tissue water relations, and leaf/root dry weight ratios were compared among young, container-grown plants of five temperate-zone, deciduous tree species (*Acer negundo* L., *Betula papyrifera* Marsh, *Malus baccata* Borkh, *Robinia pseudoacacia* L., and *Ulmus parvifolia* Jacq.) under well-watered and water-stressed conditions. There was a small decrease (mean reduction of 0.22 MPa across species) in the water potential at which turgor was lost (Ψ_{tlp}) in response to water stress. The Ψ_{tlp} for water-stressed plants was −1.18, −1.34, −1.61, −1.70, and −2.12 MPa for *B. papyrifera, A. negundo, U. parvifolia, R. pseudoacacia*, and *M. baccata*, respectively. Variation in Ψ_{tlp} resulted primarily from differences in tissue osmotic potential and not tissue elasticity. Rates of net photosynthesis declined in response to water stress. However, despite differences in Ψ_{tlp}, there were no differences in net photosynthesis among water-stressed plants under the conditions of water stress imposed. In *A. negundo* and *M. baccata*, water use efficiency (net photosynthesis/transpiration) increased significantly in response to water stress. Comparisons among water-stressed plants showed that water use efficiency for *M. baccata* was greater than for *B. papyrifera* or *U. parvifolia*. There were no significant differences in water use efficiency among *B. papyrifera, U. parvifolia, A. negundo*, and *R. pseudoacacia*. Under water-stressed conditions, leaf /root dry weight ratios (an index of transpiration to absorptive capacity) ranged from 0.77 in *R. pseudoacacia* to 1.05 in *B. papyrifera.*

Introduction

The ability of plants to survive and grow on dry sites varies among species. For example, *Robinia pseudoacacia* L. (Bunger and Thomson 1938), *Ulmus parvifolia* Jacq. (Dirr and Richards 1989), *Malus* spp. (Lakso 1983, Flint 1985), and *Acer negundo* L. (Hatton 1935, Dewers 1981) are reported to be relatively tolerant of dry sites compared to other temperate, deciduous tree species. In contrast, *Betula papyrifera* Marsh appears to be intolerant of dry sites (Pomerleau and Lortie 1962).

A plant's capacity to resist drought depends on a variety of adaptive characteristics and mechanisms (Turner 1979, Jones 1980). Based on the classification system presented by Turner (1979), these adaptations may enable plants either to maintain high tissue water potentials (Ψ_w) during drought or to increase their tolerance of low plant water potentials.

The purpose of this study was to compare leaf gas exchange, leaf/root dry weight ratios, and the capacity to maintain turgor at low tissue water potentials in five deciduous tree species under both well-watered and water-stressed conditions.

Materials and methods

Plant material

Bare-root seedlings of *Acer negundo* (box elder), *Malus baccata* Borkh (Siberian crabapple), (*Robinia pseudoacacia* (black locust), *Ulmus parvifolia* (Chinese elm), and *Betula papyrifera* (paper birch), ranging in height from 45 to 60 cm, were pruned to a single stem 25 cm above the root crown. Root systems were pruned to a maximum length of 20 cm below the crown.

On May 3, 1988, plants were potted in 19-liter white plastic containers filled with a pasteurized mixture of vermiculite/sphagnum peat moss/soil (1/1/1/ v/v). Before the irrigation treatments were begun, plants were grown outside in Ithaca, NY under natural conditions for 16 weeks. They were kept well-watered and fertilized weekly with a 10/10/10, $N/P_2O_5/K_2O$ solution containing N at a concentration of 200 mg l^{-1}. For the experiment, the plants were moved to a glass greenhouse and the irrigation treatments begun on August 22, 1988, at which time plants were similar in size, with a mean total shoot length of 307 cm.

Irrigation treatments

The experiment was a two-way factorial (five species × two irrigation treatments) randomized complete block design with eight replications per treatment. The control (well-watered) plants of each species were irrigated every evening to container through-flow, whereas the plants subjected to water stress were irrigated with only sufficient water to restore a container weight corresponding to a bulk soil water potential of −1.1 MPa, based on a soil water release curve. This irrigation regime can result in some variation in soil water content within a container at certain times, but it makes it possible to subject a number of plants to similar amounts of water stress for extended periods of time. The degree of water stress imposed was chosen to provide a bulk soil water potential above the turgor loss point reported for most temperate-zone deciduous tree species. Treatments were imposed for 30 days.

Plant water relations

Tissue water potential was determined with a pressure chamber (Plant Moisture Status Console, Soilmoisture Equipment Corp., Santa Barbara, CA). Tissue water relations were determined during the last 10 days of the 30-day experiment using pressure-volume methodology (Tyree and Hammel 1972). Samples were collected and measurements taken on a block by block basis. Because of the small leaf size of *U. parvifolia*, terminal shoots (12 cm long) with 8 to 10 leaves were used for pressure-volume measurements. Fully exposed sun-leaves (5th most recently fully expanded leaf) were used for all other species. Samples were collected before dawn, re-cut under water, enclosed in a polyethylene bag, placed in the dark, and allowed to rehydrate for 2 h. Tissue water potentials and corresponding leaf weights were then measured periodically on each sample over a range of tissue water potentials from 0 to −4.0 MPa. Between measurements, samples were allowed to transpire freely outside the pressure chamber (Hinckley et al. 1980, Ritchie and Roden 1985). A gas mixture of 98% N_2 and 2% O_2 was used to pressurize the chamber. The chamber pressure was changed at a rate not exceeding 0.02 MPa s^{-1} to avoid tissue injury.

Pressure-volume data were analyzed by means of a segmented, non-linear regression model (model "PVD," Schulte and Hinckley 1985).

Bulk tissue osmotic potential, Ψ_π, was described by the function:

$$\Psi_\pi = \frac{\Psi_{\pi,\mathrm{sat}}}{1 - \dfrac{1 - \mathrm{RWC}}{\mathrm{SWF}}}, \tag{1}$$

where $\Psi_{\pi,\mathrm{sat}}$ is the osmotic potential at full tissue saturation, RWC is the relative water content and SWF is the symplastic fraction of the total water content. Bulk turgor potential, Ψ_p, was described by the function:

$$\Psi_p = -\Psi_{\pi,\mathrm{sat}} \left(\frac{\mathrm{RWC} - \mathrm{RWC_{tlp}}}{1 - \mathrm{RWC_{tlp}}} \right)^b, \tag{2}$$

where $\mathrm{RWC_{tlp}}$ is the relative water content at the turgor loss point and b is a constant, both of which were estimated in the regression. Bulk modulus of elasticity, ε, was then calculated as described by Jones and Turner (1980):

$$\varepsilon = \frac{d\Psi_p}{d\mathrm{RSWC}}, \tag{3}$$

where RSWC is the relative symplastic water content and is calculated as:

$$\mathrm{RSWC} = 1 - \frac{1 - \mathrm{RWC}}{\mathrm{SWF}}. \tag{4}$$

Differentiation of Equation 3 gives:

$$\varepsilon = \frac{-\Psi_p\, b}{\mathrm{RSWC_{tlp}} - \mathrm{RSWC}}, \tag{5}$$

where $\mathrm{RSWC_{tlp}}$ is the RSWC at the turgor loss point.

Gas exchange measurements

Net photosynthesis (P_N), stomatal conductance to water vapor (g_s), water use efficiency (WUE) and photosynthetically active radiation were determined with a portable gas exchange system (Li-Cor model LI-6200, Lincoln, NE). Measurements were taken between 1000 and 1500 h EDT on September 15, 1988. Cuvette air temperature ranged from 26 to 32 °C. Leaf to air vapor pressure difference ranged cuvette where the air is well stirred will tend to minimize boundary-layer resistance. Thus, variation in WUE among treatments, measured within a cuvette, will typically represent differences in leaf anatomy and physiology more than leaf morphology.

Plant dry weights

Plants were harvested 30 days after the irrigation treatments commenced. Dry weights of harvested plants and abscised leaves (which were collected throughout the experiment) were determined after drying at 70 °C for 96 h.

Results

Plant water relations

Leaves of water-stressed plants showed a small decrease in Ψ_{tlp} compared to well-watered plants (Table 1). The main-effect mean for Ψ_{tlp} for well-watered plants

Table 1. Osmotic potential at full hydration ($\Psi_{\pi,sat}$), total water potential at the turgor loss point (Ψ_{tlp}), relative symplastic water content at the turgor loss point ($RSWC_{tlp}$), power exponent (*b*), and the bulk modulus of elasticity at a turgor of 1.0 MPA ($\varepsilon_{1.0}$) derived from pressure-volume measurements taken over the period of 20–30 days after irrigation treatments began.

Treatments	$\Psi_{\pi,sat}$ (−MPa)	Ψ_{tlp} (−MPa)	$RSWC_{tlp}$	*b*	$\varepsilon_{1.0}$ (MPa)
Well-watered					
Betula papyrifera	1.08	1.33	0.82	1.38	8.32
Acer negundo	1.34	1.54	0.87	1.35	13.34
Ulmus parvifolia	1.30	1.61	0.81	1.38	9.15
Robinia pseudoacacia	1.41	1.60	0.88	1.24	14.55
Malus baccata	1.95	2.55	0.76	1.45	9.76
Water-stressed					
Betula papyrifera	1.18	1.45	0.81	1.39	8.48
Acer negundo	1.34	1.62	0.84	1.66	12.97
Ulmus parvifolia	1.61	2.02	0.80	1.38	9.88
Robinia pseudoacacia	1.70	1.91	0.89	1.48	20.51
Malus baccata	2.12	2.76	0.77	1.42	10.43
Factorial analysis[1]					
Irrigation treatment	**	**	NS	*	NS
Species	**	**	**	NS	**
Irrigation x species	*	NS	NS	*	NS
$LSD_{0.05}$	0.16	0.20	0.04	0.18	3.84

[1] NS, *, ** nonsignificant or significant at the 5% or 1% level, respectively, $n = 7$.