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Comparative drought resistance among six species of birch (*Betula*): influence of mild water stress on water relations and leaf gas exchange

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Summary

Responses of plant water relations and leaf gas exchange to mild water stress were monitored and compared among six species of birch; monarch birch (*Betula maximowicziana* Reg.), river birch (*B. nigra* L.), paper birch (*B. papyrifera* Marsh.), European white birch (*B. pendula* Roth.), 'Whitespire' Japanese birch (*B. platyphylla* var. *japonica* Hara. 'Whitespire'), and gray birch (*B. populifolia* Marsh.). Before imposition of water stress, 'Whitespire' Japanese birch and river birch maintained the highest stomatal conductances and net rates of photosynthesis of the species examined. After irrigation was withheld, stomatal conductance and rate of net photosynthesis gradually declined for most species. After 28 days without irrigation, 'Whitespire' Japanese birch maintained significantly higher stomatal conductance and rate of net photosynthesis than did the other species despite having one of the lowest midday water potentials. There was no evidence of osmotic adjustment by any of the species in response to the imposed drought. However, there was substantial variation in the water potential at the turgor loss point among the species, from a high of −1.34 MPa for river birch to a low of −1.78 MPa for 'Whitespire' Japanese birch. Stomatal conductance and net photosynthesis under mild water stress (average predawn leaf water potential of −0.61 MPa) were negatively correlated with leaf osmotic potential at full turgor and leaf water potential at the turgor loss point. Thus, the greater net photosynthesis of 'Whitespire' Japanese birch under water stress compared with the other species appears to have resulted from a superior capacity to maintain turgor at low leaf water potentials, which in turn provided for greater stomatal conductance and CO_2 uptake. These results indicate that 'Whitespire' Japanese birch is better adapted to dry sites than the other species.

Introduction

The genus *Betula* has many species with traits of ornamental value. Some of the ornamental species are native to cool, moist climates and perform poorly on dry sites, e.g., European white birch (*B. pendula* Roth.), paper birch (*B. papyrifera* Marsh.), and river birch (*B. nigra* L.) (Weaver 1978, Dirr 1983). Among the approximately 40 species of birch, however, there may be some that are well adapted to drier environments.

The capacity to maintain turgor pressure as plant water potential decreases can contribute to drought resistance. Turgor is a prerequisite for cell expansion (Lockhart 1965) and stomatal opening (Ehret and Boyer 1979, Richter et al. 1981) and is often positively correlated with photosynthesis and plant growth under water stress (Johnson 1978, Ludlow 1987, Osonubi and Davies 1978). The capacity to maintain turgor pressure at decreasing plant water potentials is primarily a function of bulk tissue osmotic potential and tissue elasticity (Tyree and Jarvis 1982). Tissues with lower osmotic potentials and greater elasticity (lower bulk modulus of elasticity) will maintain positive turgor to lower tissue water potentials.

The objective of this experiment was to evaluate and compare water relations and leaf gas exchange of six species of birch subjected to mild water stress.

Materials and methods

Plant material

Between March 20 and April 4, 1989, bare-root seedlings of monarch birch (*Betula maximowicziana* Reg.), (see Santamour and Meyer 1977, for species description), river birch (*B. nigra* L.), paper birch (*B. papyrifera* Marsh.), European white birch (*B. pendula* Roth.), 'Whitespire' Japanese birch (*B. platyphylla* var. *japonica* Hara. 'Whitespire'), and gray birch (*B. populifolia* Marsh.), ranging in height from 0.6 to 1.0 m, were planted in 11.4-liter, black, plastic containers filled with a mixture of milled pine bark (< 13 mm)/sand/sphagnum peat moss (14/5/5 v/v) amended with 4.2 kg m^{-3} dolomitic limestone, 1.2 kg m^{-3} superphosphate, 0.9 kg m^{-3} KNO_3, 3.6 kg m^{-3} Esmigran (Sierra Chemical Co., Milpitas, CA), 59 ml m^{-3} Sequestrene Fe 330 (Ciba-Geigy Co., Greensboro, NC), and 40 ml m^{-3} Solubor (sodium borate, U.S. Borax and Chemical Co., Los Angeles, CA). Plants were initially grown outdoors at the Mountain Horticultural Crops Research Station, Fletcher, NC and received daily irrigation. On June 6, 1989, all plants were pruned to a height of 0.6 m above the stem–root junction. On July 20, 1989, one tree of each species was transplanted to each of six plywood boxes (1.0 m × 2.2 m × 0.4 m) filled to a depth of 0.3 m with 0.66 m^3 of the same growing medium. The boxes were placed in a polyethylene-covered house. Plants were grown in natural lighting and were well irrigated for 57 days (until September 15, 1989) when they were similar in size and approximately 1.2 m in height. Thereafter, irrigation was withheld. The experimental design was a randomized complete block with six replications. Data were assessed statistically by the analysis of variance using the SAS software package (SAS Institute, Cary, NC).

Plant water relations

Leaf water potential (Ψ) was determined with a pressure chamber (Plant Moisture Status Console, Soil Moisture Equipment Corp., Santa Barbara, CA). Components of Ψ were estimated by pressure-volume methodology (Tyree and Hammel 1972). Leaf samples were collected for pressure-volume measurement during four separate 3-day periods: (1) before withholding irrigation (September 12–14, 1989), (2) between 5–7 days without irrigation (September 19–21, 1989), (3) between 12–14 days without irrigation (September 26–28, 1989), and (4) between 25–27 days without irrigation (October 10–12, 1989). Samples were collected and measured on a block by block basis whereby all experimental units in a given block were sampled on a given day providing for three replicates for each time period. Fully exposed sun-leaves (fifth most recently fully expanded leaf) were collected before dawn. With the petioles submerged in distilled water, they were enclosed in a polyethylene bag and allowed to rehydrate for 2 hours before measurement. Leaf water potential and corresponding leaf weights were then measured periodically on each sample over a range of Ψ from 0 to −4.0 MPa (typically at intervals from 0.3 to 0.4 MPa). Between measurements, samples were allowed to transpire freely outside the pressure chamber (Hinckley et al. 1980, Ritchie and Roden 1985). A mixture of 98% N_2 and 2% O_2 was used to pressurize the chamber. Chamber pressure was changed at a rate not exceeding 0.02 MPa s^{-1} to avoid tissue injury. Pressure-volume data were analyzed using a segmented, non-linear regression model (model "PVD," Schulte and Hinckley 1985; SAS, NLIN procedure, SAS Institute, Cary, NC). Curves typically consisted of eight data points with four in the region below the point of turgor loss. The R^2 values for individual regression analyses were greater than 0.98 in all cases.

The Ψ at the turgor loss point (Ψ_{tlp}) was calculated as:

$$\Psi_{tlp} = \frac{\Psi_{\pi,sat}}{1 - \frac{1 - RWC_{tlp}}{SWF}},$$

where $\Psi_{\pi,sat}$ is the bulk tissue osmotic potential at full saturation, RWC_{tlp} is the relative water content at the turgor loss point, and SWF is the symplastic water fraction at full saturation. Bulk modulus of elasticity was defined as the change in turgor pressure per change in the relative symplastic water content (Jones and Turner 1980). Differentiation and calculation at full turgor, i.e., where the relative water content = 1 and turgor pressure = $-\Psi_{\pi,sat}$, gives the maximum bulk modulus of elasticity (ε_{max}):

$$\varepsilon_{max} = \frac{\Psi_{\pi,sat} \times b}{RSWC_{tlp} - 1},$$

where b is a constant estimated by the regression analysis (model "PVD") and $RSWC_{tlp}$ is the relative symplastic water content at the turgor loss point.

Gas exchange measurements

Net photosynthesis (P_n), stomatal conductance to water vapor (g_s), and photosynthetically active radiation (PAR, 400–700 nm) were measured between 1030 and 1400 h EDT with a portable gas exchange system (Li-Cor model LI-6200, Lincoln, NE). Supplemental light was provided with a halogen lamp to ensure a minimum irradiance of 1200 μmol m^{-2} s^{-1} of photosynthetically active radiation. Gas exchange readings were recorded as CO_2 was depleted from 330 to 318 ppm for each leaf. Following measurement of gas exchange rates, leaves were immediately excised and Ψ was measured. Samples were measured and collected on a block by block basis.