

Response of five temperate deciduous tree species to water stress

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Received October 23, 1989

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_{tip}) in response to water stress. The Ψ_{tip} 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_{tip} 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_{tip} , 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/P₂O₅/K₂O 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% N₂ and 2% O₂ 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:

$$\Psi_{\pi} = \frac{\Psi_{\pi, \text{sat}}}{1 - \frac{1 - \text{RWC}}{\text{SWF}}}, \quad (1)$$

where $\Psi_{\pi, \text{sat}}$ 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:

$$\Psi_p = -\Psi_{\pi, \text{sat}} \left(\frac{\text{RWC} - \text{RWC}_{\text{tlp}}}{1 - \text{RWC}_{\text{tlp}}} \right)^b, \quad (2)$$

where 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):

$$\epsilon = \frac{d\Psi_p}{d\text{RSWC}}, \quad (3)$$

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

$$\text{RSWC} = 1 - \frac{1 - \text{RWC}}{\text{SWF}}. \quad (4)$$

Differentiation of Equation 3 gives:

$$\epsilon = \frac{-\Psi_p b}{\text{RSWC}_{\text{tlp}} - \text{RSWC}}, \quad (5)$$

where 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

from 2.1 to 5.7 kPa. Supplemental light from high intensity discharge lights was provided to ensure a minimum photosynthetically active photon flux of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were taken on a block by block basis. Because WUE is highly sensitive to the leaf to air vapor pressure difference (Flore et al. 1985), an analysis of covariance was performed to evaluate differences in WUE at a common leaf to air vapor pressure difference. Measurements of transpiration rates inside a 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 ($\Psi_{\pi,\text{sat}}$), 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 ($\epsilon_{1.0}$) derived from pressure-volume measurements taken over the period of 20–30 days after irrigation treatments began.

Treatments	$\Psi_{\pi,\text{sat}}$ (-MPa)	Ψ_{tlp} (-MPa)	RSWC_{tlp}	b	$\epsilon_{1.0}$ (MPa)
Well-watered					
<i>Betula papyrifera</i>	1.08	1.33	0.82	1.38	8.32
<i>Acer negundo</i>	1.34	1.54	0.87	1.35	13.34
<i>Ulmus parvifolia</i>	1.30	1.61	0.81	1.38	9.15
<i>Robinia pseudoacacia</i>	1.41	1.60	0.88	1.24	14.55
<i>Malus baccata</i>	1.95	2.55	0.76	1.45	9.76
Water-stressed					
<i>Betula papyrifera</i>	1.18	1.45	0.81	1.39	8.48
<i>Acer negundo</i>	1.34	1.62	0.84	1.66	12.97
<i>Ulmus parvifolia</i>	1.61	2.02	0.80	1.38	9.88
<i>Robinia pseudoacacia</i>	1.70	1.91	0.89	1.48	20.51
<i>Malus baccata</i>	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
$\text{LSD}_{0.05}$	0.16	0.20	0.04	0.18	3.84

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

was -1.73 MPa compared with -1.95 MPa for water-stressed plants, demonstrating a small but significant (main-effect contrast, $P < 0.01$) increase in the capacity for water-stressed plants to maintain turgidity at more negative Ψ_w . Differences among species were much greater, however, than differences between irrigation treatments. Under water-stressed conditions, leaves of *M. baccata* maintained Ψ_p to a Ψ_w of -2.76 MPa (Table 1). *Robinia pseudoacacia* and *U. parvifolia* had intermediate Ψ_{tip} values and *A. negundo* and *B. papyrifera* had the highest Ψ_{tip} values.

Differences in Ψ_{tip} can result from variation in both $\Psi_{\pi,sat}$ and tissue elasticity (Tyree and Jarvis 1982). *Acer negundo* and *B. papyrifera* showed no significant decrease in $\Psi_{\pi,sat}$ (i.e., osmotic adjustment) in response to water stress, whereas *M. baccata*, *R. pseudoacacia*, and *U. parvifolia* showed significant decreases in $\Psi_{\pi,sat}$ of 0.17, 0.29, and 0.31 MPa, respectively (Table 1). Comparisons of $\Psi_{\pi,sat}$ among water-stressed plants showed that *M. baccata* had the most negative $\Psi_{\pi,sat}$ (Table 1). *Robinia pseudoacacia* and *U. parvifolia* had similar $\Psi_{\pi,sat}$ followed by *A. negundo* and *B. papyrifera* with the least negative $\Psi_{\pi,sat}$ values.

Variations in ϵ as influenced by Ψ_p are shown in Figure 1. Because ϵ is often a function of Ψ_p (Cheung et al. 1976, Roberts et al. 1981), ϵ was calculated at a Ψ_p of 1.0 MPa ($\epsilon_{1.0}$). There was little effect of water stress on tissue elasticity of the species studied except in *R. pseudoacacia* (Table 1). Under conditions of water-stress, $\epsilon_{1.0}$ varied from 8.48 MPa for *B. papyrifera* (most elastic) to 20.51 MPa for *R. pseudoacacia* (least elastic).

Gas exchange

Under well-watered conditions, the rate of light-saturated P_N ranged from 10.3 to 4.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *M. baccata* and *B. papyrifera*, respectively (Table 2). Rates of P_N and g_s were much lower in all water-stressed plants and there were no significant differences among species under the water stress imposed (Table 2). Water use efficiency (adjusted for differences in vapor pressure difference) increased significantly in *A. negundo* and *M. baccata* in response to water stress (t -test, $P < 0.05$) (Figure 2). Comparisons among water-stressed plants showed that WUE of *M. baccata* was significantly higher than that of *B. papyrifera* or *U. parvifolia*. *Acer negundo* and *R. pseudoacacia* had intermediate WUE values that were not significantly different from those of the other species.

Leaf and root weights

Leaf/root dry weight ratios (LRR) are presented as an index of the balance between the capacities for transpiration and absorption (Table 3). *Betula papyrifera* and *R. pseudoacacia* had lower LRR under water-stressed conditions than under well-watered conditions. This difference may reflect an effect of water stress on dry matter partitioning, as well as on leaf abscission. In water stressed plants, LRR ranged from a low of 0.77 for *R. pseudoacacia* to 1.05 for *B. papyrifera*.

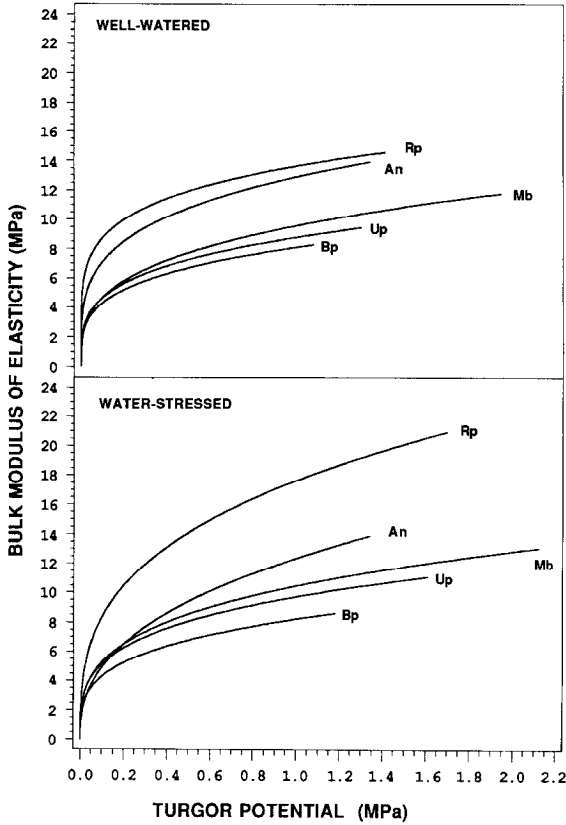


Figure 1. Bulk modulus of elasticity (ϵ) of well-watered and water-stressed *Acer negundo* (An), *Betula papyrifera* (Bp), *Malus baccata* (Mb), *Robinia pseudoacacia* (Rp), and *Ulmus parvifolia* (Up). ϵ was calculated as: $(b - \Psi_p)/(RSWC_{tp} - RSWC)$. See Table 1 for parameter estimates and statistical comparison of ϵ at a turgor of 1.0 MPa.

Discussion

The tissue water potential at which turgor was lost (Ψ_{tlp}) in water-stressed plants varied from 1.45 MPa for *B. papyrifera* to 2.76 for *M. baccata*. Although a more elastic tissue (lower ϵ) will contribute to maintenance of turgor at low Ψ_w (Tyree and Jarvis 1982), *B. papyrifera* (with the most elastic tissue, lowest $\epsilon_{1.0}$) lost turgor at the least negative Ψ_w . Because Ψ_{tlp} is influenced by both ϵ and $\Psi_{\pi, sat}$ this result shows that in *B. papyrifera* the effect of low ϵ on Ψ_{tlp} was more than offset by the influence of high $\Psi_{\pi, sat}$. Furthermore, these results suggest that, for these species, Ψ_{tlp} is influenced to a much greater degree by variation in $\Psi_{\pi, sat}$ than ϵ . This finding supports the supposition of Jones et al. (1985) that variation in ϵ must be large before substantial changes in Ψ_{tlp} result.

Malus baccata demonstrated the greatest turgor maintenance capacity, maintaining a positive Ψ_p to -2.76 MPa Ψ_w . This capacity resulted primarily from low $\Psi_{\pi, sat}$ (-2.12 MPa). Field studies of *Malus domestica* "MacIntosh" have shown $\Psi_{\pi, sat}$

Table 2. Net photosynthetic rate (P_N), stomatal conductance to H_2O (g_s), and tissue water potential (Ψ_w) measured 24 days after initiation of treatments.

Treatments	P_N ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	Ψ_w (-MPa)
Well-watered			
<i>Betula papyrifera</i>	4.7	0.10	0.81
<i>Acer negundo</i>	6.3	0.10	1.00
<i>Ulmus parvifolia</i>	8.1	0.14	0.89
<i>Robinia pseudoacacia</i>	5.4	0.06	0.95
<i>Malus baccata</i>	10.7	0.20	1.40
Water-stressed			
<i>Betula papyrifera</i>	0.9	0.01	1.18
<i>Acer negundo</i>	1.6	0.02	1.33
<i>Ulmus parvifolia</i>	2.0	0.02	1.72
<i>Robinia pseudoacacia</i>	2.0	0.02	2.33
<i>Malus baccata</i>	1.5	0.01	1.69
Factorial analysis ¹			
Irrigation treatment	**	**	**
Species	**	**	**
Irrigation \times species	**	**	**
LSD _{0.05}	1.6	0.04	0.33

¹ NS, *, ** nonsignificant or significant at the 5% or 1% level, respectively, $n = 8$. Cuvette air temperature ranged from 26–32 °C, and leaf to air vapor pressure difference ranged from 2.1 to 5.7 kPa over the measurement period. Light levels exceeded 1000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ for all measurements.

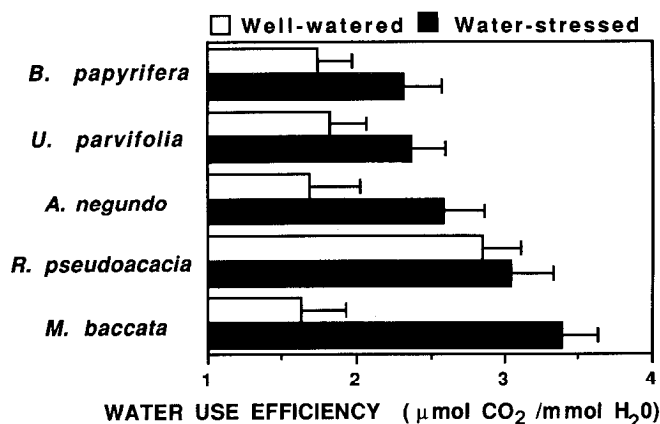


Figure 2. Instantaneous water use efficiency (net photosynthesis/transpiration) of well-watered and water-stressed *Betula papyrifera*, *Ulmus parvifolia*, *Acer negundo*, *Robinia pseudoacacia*, and *Malus baccata*. Values are least-square means ($n = 8$) \pm SEM. Mean leaf to air vapor pressure gradient was 3.8 kPa.

values ranging from -2.00 MPa (Davies and Lakso 1979) to -4.0 MPa (Lakso et al. 1984). The ability of *M. baccata* to maintain positive turgor under water stress did not result in greater P_N under the imposed water stress. Even though the Ψ_{tip} for *M.*

Table 3. Leaf/root dry weight ratios measured after 30 days of irrigation treatments and total weight of abscised leaves collected throughout the experiment.

Treatments	Leaf/root dry weight ratio	Abscised leaf weight (g)
Well-watered		
<i>B. papyrifera</i>	1.40	3.00
<i>A. negundo</i>	1.20	8.39
<i>U. parvifolia</i>	0.75	3.04
<i>R. pseudoacacia</i>	1.31	6.52
<i>M. baccata</i>	0.64	5.18
Water-stressed		
<i>B. papyrifera</i>	1.05	15.67
<i>A. negundo</i>	0.98	7.09
<i>U. parvifolia</i>	0.77	4.49
<i>R. pseudoacacia</i>	0.60	38.73
<i>M. baccata</i>	0.86	4.74
Factorial analysis ¹		
Irrigation treatment	**	**
Species	**	**
Irrigation × species	**	**
LSD _{0.05}	0.27	7.90

¹ NS, *, ** nonsignificant or significant at the 5% or 1% level, respectively, $n = 8$.

baccata was -2.8 MPa (Table 1), which is considerably lower than the measured midday Ψ_w of -1.7 MPa (Table 2), P_N was reduced as a result of water stress, indicating that stress-induced reductions in g_s and P_N were due to factors other than loss of turgor. However, *M. baccata* has the potential to maintain P_N to a more negative Ψ_w than the other species. Lakso (1979) found that excised leaves of *Malus domestica* "McIntosh" maintained P_N to Ψ_w as low as -5.0 MPa. The maintenance of Ψ_p and P_N at low Ψ_w coupled with a high WUE (cf. Flore et al. 1985) can be effective mechanisms for resisting water stress (Lakso 1983).

These adaptations may be particularly important for *Malus* spp. which are characterized by a low root density (Atkinson and Thomas 1985), a high resistance to water flow (Davies and Lakso 1978), and a low midday Ψ_w (Davies and Lakso 1978, 1979). Although depth of rooting in *Malus* spp. may exceed 2 m, most of the root system is typically within the surface 0.5 m of soil (Atkinson and Thomas 1985), further limiting water availability during periods of drought.

Of the species examined, *U. parvifolia* and *R. pseudoacacia* were intermediate in their ability to maintain Ψ_p at low Ψ_w . Furthermore, both of these species exhibited low leaf/root dry weight ratios (LRR) under water stress compared with the other species. The low LRR of *U. parvifolia* occurred under both well-watered and water-stressed conditions, suggesting that LRR is inherently low in this species. The low LRR of water-stressed plants of *R. pseudoacacia* resulted primarily from leaf abscission in response to the water stress. Leaf abscission greatly reduces transpiration and can be an important mechanism in avoiding the development of extreme

water stress (Kozlowski 1976). In addition to low LRRs, *Ulmus* and *Robinia* can develop unusually deep roots. Bunger and Thomson (1938) found that *R. pseudoacacia* and *Ulmus pumila* (a close relative to *U. parvifolia*) have a maximum rooting depth exceeding 8 m. These observations indicate that deep rooting and low LRR are both important mechanisms of drought resistance in *U. parvifolia* and *R. pseudoacacia*.

Acer negundo was intermediate in its capacity to maintain Ψ_p at low Ψ_w and in its LRR. Field studies have shown that the root system of *A. negundo* is very adaptable, being shallow and wide-spreading in alluvial soils, but very deep (> 4 m), with a dominant taproot, on upland soils (Biswell 1935). Such morphological adaptability may account for the success of the species on dry sites.

Betula papyrifera had the lowest turgor maintenance capacity, the highest LRR under water stress and one of the lowest WUEs under water stress. The combination of these factors most likely contributes to the poor success of *B. papyrifera* on dry sites. Field studies have shown that *B. papyrifera* is shallow rooted (Pomerleau and Lortie 1962) with a mean rooting depth of only 0.5 m in mature trees.

Success of plants growing on dry sites results from the integration of characteristics that contribute to stress tolerance at both high and low tissue Ψ_w . However, the effectiveness of any combination of traits in conferring drought resistance is dependent on environmental conditions. Potential for deep rooting, as with *R. pseudoacacia* and *U. parvifolia*, would contribute little to drought resistance where soils are shallow or root systems are confined. In such cases, turgor maintenance at low Ψ_w and high WUE, as with *M. baccata*, may be of particular importance in conferring resistance to drought. Alternatively, where soils are deep and well-drained, plants with lower LRR and deep rooting habits may be better adapted to drought.

The variety of plant characteristics that contribute to drought resistance and the variation in site characteristics makes plant selection for dry sites difficult. A greater understanding of the physiology, adaptive characteristics, and response to water stress of different species will enhance our ability to select more appropriate species and genotypes for specific sites.

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