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Foliar dehydration tolerance of twelve deciduous tree species

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Abstract

The potential for foliar dehydration tolerance and maximum capacity for osmotic adjustment were compared among 12 temperate, deciduous tree species, under standardized soil and atmospheric conditions. Dehydration tolerance was operationally defined as lethal leaf water potential (ψ): the ψ of the last remaining leaves surviving a continuous, lethal soil drying episode. *Nyssa sylvatica* Marsh., and *Liriodendron tulipifera* L. were most sensitive to dehydration, having lethal leaf ψ of -2.04 and -2.38 MPa, respectively. *Chionanthus virginicus* L., *Quercus prinus* L., *Acer saccharum* Marsh., and *Quercus acutissima* Carruthers withstood the most dehydration, with leaves not dying until leaf ψ dropped to -5.63 MPa or below. Lethal leaf ψ (in MPa) of other, intermediate species were: *Quercus rubra* L. (-3.34), *Oxydendrum arboreum* (L.) D.C. (-3.98), *Halesia carolina* L. (-4.11), *Acer rubrum* L. (-4.43), *Quercus alba* L. (-4.60), and *Cornus florida* L. (-4.88). Decreasing lethal leaf ψ was significantly correlated with increasing capacity for osmotic adjustment. *C. virginicus* and *Q. acutissima* showed the most osmotic adjustment during the lethal soil drying episode, with osmotic potential at full turgor declining by 1.73 and 1.44 MPa, respectively. Other species having reductions in osmotic potential at full turgor exceeding 0.50 MPa were (in MPa) *Q. prinus* (0.89), *A. saccharum* (0.71), *Q. alba* (0.68), *H. carolina* (0.67), *Q. rubra* (0.60), and *C. florida* (0.52).

Key words: Dehydration tolerance, lethal leaf water potential, maples, oaks, temperate trees.

Introduction

Plants have evolved many physiological, morphological, anatomical, and phenological characteristics for responding to and resisting drought stress. Certain characteristics and responses to drought do not occur at random but appear to coincide, leading to the sometimes loose but useful categories of perennial plants as drought avoiders or drought tolerators (Ludlow *et al.*, 1983). Drought avoiders have tissues that are very sensitive to dehydration. They tend to have characteristics that allow them to avoid tissue water deficits when soil moisture limitation occurs: e.g. deep roots to maximize water uptake and sensitive stomates to minimize leaf water loss. Drought tolerators have leaves that can tolerate dehydration, and they tend to have poorly developed responses for avoiding dehydration. Tolerators rely on osmotic adjustment to survive drought (Ludlow *et al.*, 1985). Ludlow (1989) has profiled the mechanistically linked characteristics that classify these two drought resistance strategies.

In the spectrum of responses ranging from extreme drought avoidance to extreme tolerance, perhaps the single most important determinant of drought resistance strategy is the dehydration tolerance of the species, which is a measure of tissue capacity for withstanding desiccation (Ludlow, 1989). Dehydration tolerance has been operationally defined as the water potential (ψ) or relative water content (RWC) of the last surviving leaves (called the lethal value) on a plant subjected to a slow, continuous soil drying episode (Ludlow, 1989). Drought avoidance, a strategy possessed by both annuals and perennials, is characterized by relatively high lethal leaf ψ and RWC and relatively little osmotic adjustment during drought. In contrast, drought tolerators, mostly perennials, have

lower lethal leaf water status values and typically display much more active accumulation of solutes when subjected to drought.

Although there is a continuous range of responses to water stress and not all plants fit closely into one or the other category, the division of plant responses into categories or strategies can be a valuable aid to understanding the ecological consequences for a species: e.g. potential for carbon acquisition and growth during drought, metabolic costs of resistance mechanisms, long-term plant survival. Although lethal leaf ψ have been measured in several herbaceous species (citations above), such characterizations have not been made of tree species. The objective here was to characterize and compare the potential for foliar dehydration tolerance and maximum capacity for osmotic adjustment in several temperate, deciduous tree species, under standardized soil and atmospheric conditions, and under light levels commonly found in deciduous forests. Knowing the dehydration tolerance of foliage can assist in the interpretation of tree behaviour in the forest. Eleven tree species native to the southeastern United States were selected for study, representing a range of natural habitat and hence probable leaf dehydration tolerance, and an additional oak, for comparative purposes.

Materials and methods

Plant culture

Two- to three-year-old saplings of the following tree species, ranging in height from about 0.5–1.5 m, were transplanted singly into 16 or 28 l plastic pots (ten trees per species per pot size, 240 pots total) in the spring of 1995: red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), fringe tree (*Chionanthus virginicus* L.), flowering dogwood (*Cornus florida* L.), carolina silverbell (*Halesia carolina* L.), tulip poplar (*Liriodendron tulipifera* L.), black gum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboreum* [L.] DC.), sawtooth oak (*Quercus acutissima* Carruthers), white oak (*Quercus alba* L.), chestnut oak (*Quercus prinus* L.), and red oak (*Quercus rubra* L.). All saplings were container-grown from seed obtained from local provenances, except for *Q. prinus*, *Q. alba* and *A. saccharum*, which were obtained bare-root from a nursery. Pots of different size were used to vary the time required for plants to reach the lethal point. Trees were grown in a standard nursery mix: 4 pine bark/1 sand (v/v), to each m^3 of which was added 4 l of dolomitic lime, 4 l 17–6–10 osmocote plus minor elements and 2 l Epsom salt (MgSO$_4$). To approximate forest lighting and temperature conditions, the experiment was conducted in a rain shelter (20 m × 7.7 m × 5 m), covered with shade cloth which allowed exposure of foliage to about 3–4% of ambient light. This enabled characterization of drought response under light levels that these species commonly encounter as saplings in their native habitats. Maximum and minimum air temperatures, average daily relative humidity and maximum daily *PPFD* (as hourly means) are given in Fig. 1. Following the final transplanting, trees were adequately watered and allowed to grow for 2 months, until the drought treatment began.
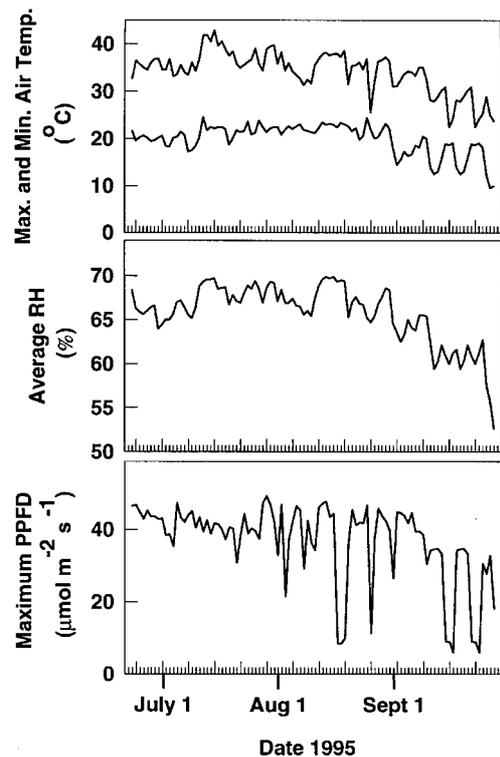

Fig. 1. Maximum and minimum daily temperatures, average daily relative humidity and maximum daily *PPFD* (hourly mean) during the lethal drying episode.

Drought treatment and water relations measurements

On 15 June 1995, all plants were watered to the drip point and subsequently subjected to a continuous soil drying episode by withholding water from pots. One leaf from each plant was collected on the previous day between 08:30 h and 10:30 h EST for measurement of initial (pre-drought) osmotic potential at full turgor (ψ_π^{100}). Leaves were rehydrated overnight by placing petioles in a beaker of distilled water in an enclosed chamber in the dark, then placed in a syringe, frozen in liquid N$_2$ and kept at $-80\,°C$ pending further analysis. Syringes were thawed until samples reached room temperature, and the ψ_π of expressed sap was measured with a vapour pressure osmometer (model 5500XR, Wescor, Inc. Logan, UT). Other trials with these 12 species indicated that carefully washing and drying leaves prior to excising them had no effect on ψ_π values (i.e. leaf surface solutes were negligible under these cultural conditions), so leaves were not washed before sampling for either pre- or post-drought ψ_π (described below).

Foliar dehydration tolerance was characterized by measuring lethal leaf ψ and lethal leaf *RWC*. Dehydration tolerance has been operationally defined as the ψ (called the lethal ψ) of the last surviving leaves on a plant subjected to a slow, continuous soil drying episode (Ludlow, 1989). The extent of soil drying required to kill foliage was characterized as the lethal soil *RWC*. Each tree was checked daily after beginning the drying episode and lethal measurements begun when fewer than eight live leaves with minimal necrotic areas (less than 25% of total leaf area) remained. Preliminary trials were conducted on extra trees to determine the visible signs of the lethal drought point for each species, by excising leaves at various levels of dehydration to ascertain which would rehydrate and which had died. For most species, determining when to sample leaves was

fairly clear, as leaves developed extensive necrotic areas as they died. Sampling of lethal values was performed between 08 : 30 h and 10 : 30 h EST beginning on 5 July 1995 and continuing until 3 October 1995, when foliage of some species had begun to develop autumn colour.

Lethal leaf ψ determinations were performed on two leaves per tree with two SC-10 thermocouple psychrometers (Decagon Devices, Inc., Pullman, WA) calibrated daily with a graded series of NaCl solutions. Psychrometer sample changers were connected to NT-3 nanovoltmeter thermometers (Decagon Devices), used to derive temperature and μV readings for conversion into ψ values. Lethal ψ determinations were performed on strips cut from leaf laminae adjacent and parallel to mid-veins and placed inside the psychrometer chamber with abaxial sides exposed to the centre of sample cups. Preliminary tests indicated that leaf samples of each species generally reached thermal and water vapour equilibrium in the psychrometer chamber within 6 h; all samples were allowed to equilibrate, then, for about 6 h. Leaf RWC was determined on two whole leaves per tree using fresh weight (FW) at excision, saturated weight (SW) after 24 h rehydration on distilled water (petioles submerged) at $4 \,°C$ in the dark, and dry weight (DW) after oven drying 48 h at $80 \,°C$: leaf $RWC \, (\%) = (FW - DW)/(SW - DW) \times 100$. Lethal, post-drought ψ_π^{100} was measured as for pre-drought samples on two leaves per tree. Leaf osmotic adjustment (ψ_π^{100}) during the drying episode was assessed as $\psi_\pi^{100} = $ pre-drought $\psi_\pi^{100} - $ post-drought ψ_π^{100} (this procedure for estimating maximum osmotic adjustment integrates both phenologically-induced and drought-induced solute changes). Lethal soil RWC was measured on soil samples extracted from the root zone, 18-25 cm below the soil surface near the centre of the pot. Soil RWC was defined similarly to leaf RWC (above): soil $RWC \, (\%) = (FW - DW)/(SW - DW) \times 100$, where FW, SW and DW refer to soil fresh weight, weight at field capacity and oven-dry weight, respectively.

Experimental design and statistical analysis

The experiment used a completely randomized design with 20 plants of each species (with the exception of *A. saccharum*, for which $n = 10$, in 28 l pots). Data were evaluated with General Linear Models Procedure (SAS, Cary, NC) and means separated by Duncan's Multiple Range Test ($P = 0.05$). The size of each leaf used in lethal ψ determinations and the number of days trees dried were included in the statistical model as covariates.

Results

Pot size did not affect most measured parameters of most species, so data for trees in 16 and 28 l pots were grouped for analysis.

Figure 2 ranks the 12 tree species in terms of foliar dehydration tolerance, operationally defined by lethal leaf ψ. Lethal leaf RWC (Fig. 3) has also been used to define dehydration tolerance and is probably a useful measure of dehydration tolerance within a species. Throughout the remainder of this paper, lethal leaf ψ is used to classify the relative foliar dehydration tolerance among species, as ψ has traditionally been used as the best comparative (thermodynamically sound) measure among species (Kramer and Boyer, 1995).

N. sylvatica and *L. tulipifera* were most sensitive to foliar dehydration, reflecting the low drought tolerance
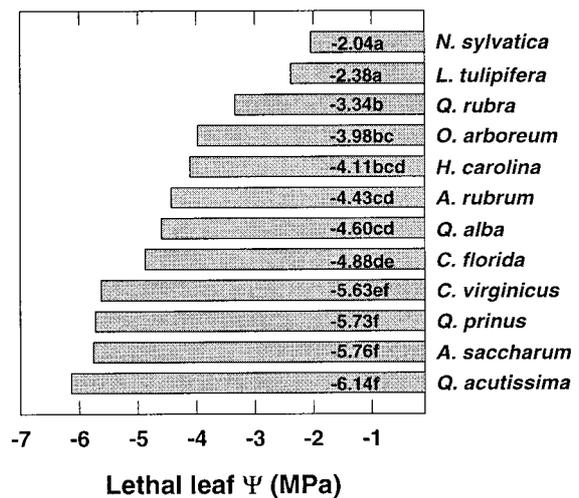

Fig. 2. Lethal leaf water potential (ψ) of 12 deciduous tree species. Measurements were made on the last surviving leaves of plants subjected to a continuous drying episode. Numbers within bars give the exact length of the bar and indicate averages of 8–20 plants. Each plant was subsampled twice. Numbers followed by the same letter are statistically similar (Duncan's Multiple Range Test, $P > 0.05$).
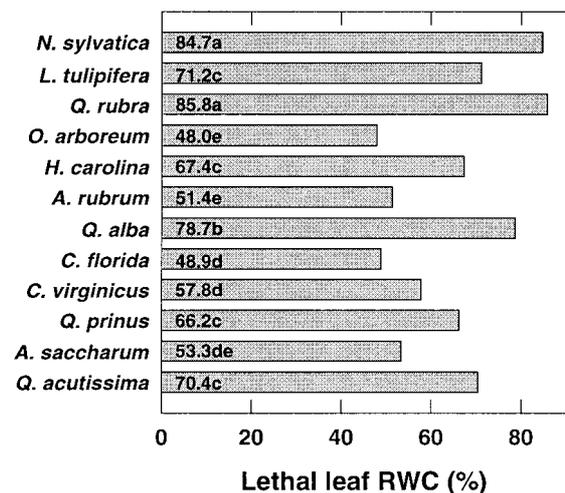

Fig. 3. Lethal leaf relative water content (RWC) of 12 deciduous tree species. Measurements were made on the last surviving leaves of plants subjected to a continuous drying episode. Numbers within bars give the exact length of the bar and indicate averages of 8–20 plants. Each plant was subsampled twice. Numbers followed by the same letter are statistically similar (Duncan's Multiple Range Test, $P > 0.05$).

usually attributed to these two species. Other mesic hardwoods, *O. arboreum*, *H. carolina* and *A. rubrum*, also had relatively high lethal leaf ψ. *C. virginicus*, *Q. prinus*, *A. saccharum*, and *Q. acutissima* withstood the most dehydration, with leaves not dying until leaf ψ dropped to an average of -5.63 MPa or below. Although lethal leaf ψ and lethal leaf RWC were not correlated across species ($r = 0.48^{NS}$), the three species having the highest lethal leaf ψ also had relatively high lethal leaf RWC. *O. arboreum* and *A. rubrum*, intermediate in lethal leaf ψ, had the lowest lethal leaf RWC.

The two species having the highest lethal leaf ψ, *N. sylvatica* and *L. tulipifera*, also had high lethal soil *RWC* (Fig. 4). One of the most dehydration-tolerant species, *Q. acutissima*, also had very low lethal soil *RWC*.

Pre-drought ψ_π^{100} varied among species, with *C. virginicus* having the lowest values and *N. sylvatica* and *H. carolina* having the highest values (Fig. 5). Among the oaks, *Q. acutissima* and *Q. rubra* had relatively high pre-drought ψ_π, and *Q. prinus* and *Q. alba* and relatively low pre-drought ψ_π. *C. virginicus* had much lower post-drought ψ_π^{100} than other species (Fig. 5). Three of the oaks (*Q. acutissima*, *Q. prinus* and *Q. alba*) also had low post-drought ψ_π^{100} (below -2 MPa). Among the maples,

A. saccharum had both lower pre- and post-drought ψ_π^{100} than *A. rubrum*.

Osmotic adjustment ($\Delta\psi_\pi^{100}$) was computed as the difference between pre-drought and post-drought ψ_π^{100}. This measure of active accumulation of solutes during the drying episode includes seasonal or developmental changes as well as drought-induced changes in ψ_π^{100}. It was not feasible to try to sample several undroughted controls for each species each time one droughted tree reached the lethal point, as lethal points were reached and post-stress ψ_π^{100} required measurement on 44 different days during the drying episode. Most of the solute changes responsible for $\Delta\psi_\pi^{100}$ were probably drought-induced, given the extreme (leaf-killing) severity of the drought.

C. virginicus and *Q. acutissima* showed the most osmotic adjustment during the lethal soil drying episode, with $\Delta\psi_\pi^{100}$ of 1.73 and 1.44 MPa, respectively (Fig. 5). Other species having declines in ψ_π^{100} exceeding 0.50 MPa were (in declining order of adjustment) *Q. prinus*, *A. saccharum*, *Q. alba*, *H. carolina*, *Q. rubra*, and *C. florida*. Decreasing lethal leaf ψ of species was significantly and negatively correlated with increasing capacity for osmotic adjustment (Fig. 6). The two species having the highest lethal leaf ψ also showed little (*L. tulipifera*) or no (*N. sylvatica*) osmotic adjustment. *A. rubrum* and *O. arboreum* showed no osmotic adjustment.

Mean drying time across species, from initially withholding water to the lethal point, was 44 d (drying times for individual species are listed in Fig. 7). The ability of plants to acclimate to drought is often a function of rate of soil drying (e.g. extent of osmotic adjustment, Turner and Jones, 1980), and average time of drying of trees to their lethal points varied among species. Among species,
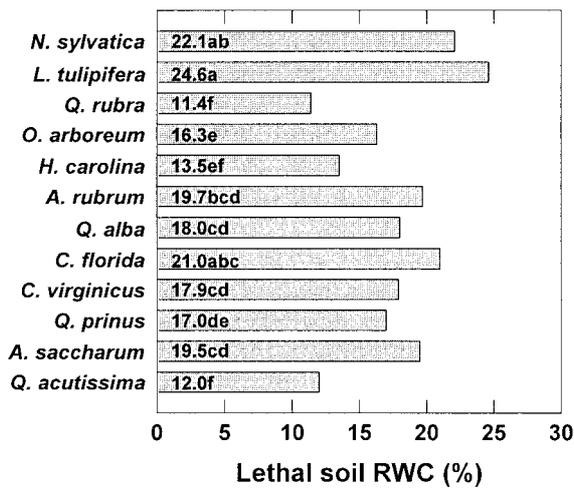

Fig. 4. Lethal soil relative water content (*RWC*) of 12 deciduous tree species. Numbers within bars give the exact length of the bar and indicate averages of 8–20 plants. Numbers followed by the same letter are statistically similar (Duncan's Multiple Range Test, $P > 0.05$).
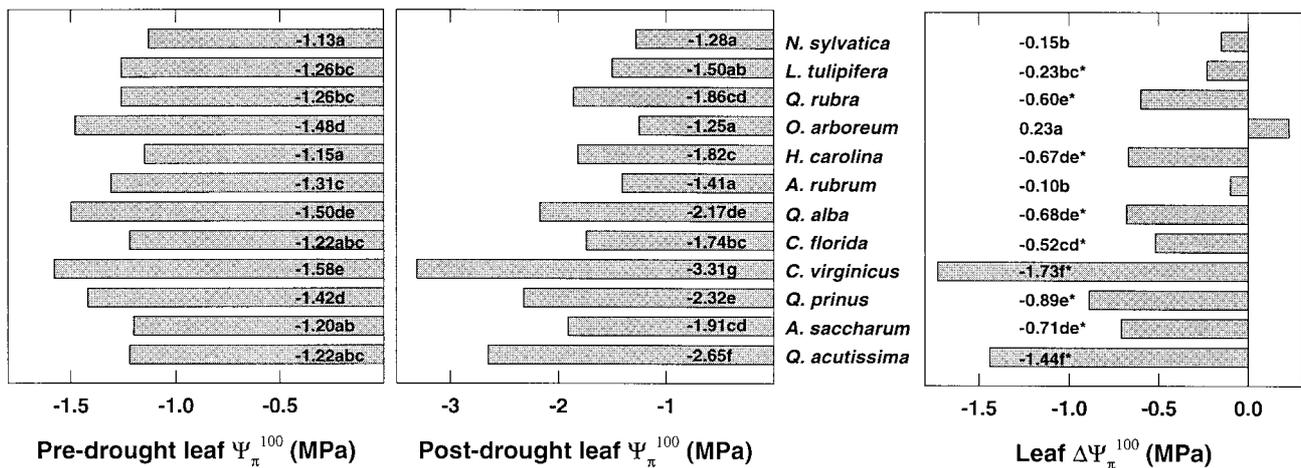

Fig. 5. Pre-stress and post-stress leaf osmotic potential at full turgor (ψ_π^{100}), and pre-stress–post-stress leaf ψ_π^{100} ($\Delta\psi_\pi^{100}$, osmotic adjustment) of 12 deciduous tree species. Pre-stress ψ_π^{100} were measured the day before the drying cycle began. Post-stress (lethal) ψ_π^{100} were measured at the same time as lethal leaf ψ and *RWC*. Numbers within bars give the exact length of the bar and indicate averages of 8–20 plants. Numbers followed by the same letter are statistically similar (Duncan's Multiple Range Test, $P > 0.05$). For $\Delta\psi_\pi^{100}$, numbers highlighted by an asterisk signify that post-stress ψ_π^{100} were significantly different ($P \leq 0.05$) than pre-stress ψ_π^{100} for that species (i.e. osmotic adjustment occurred). Each plant was subsampled twice for post-stress ψ_π^{100} and once for pre-stress ψ_π^{100}.
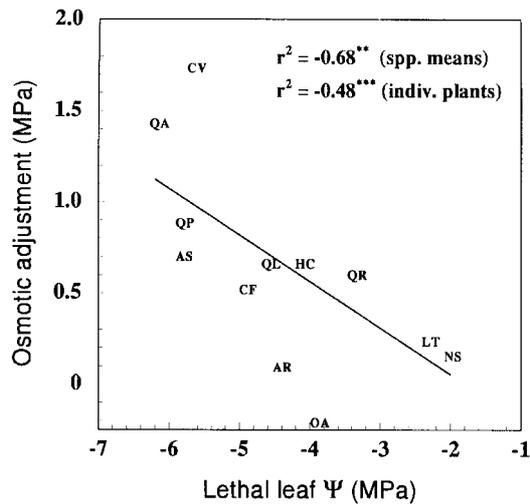
Fig. 6. The relationship between maximum osmotic adjustment (adjustment occurring during a lethal drying episode) and lethal leaf ψ. Data point abbreviations show values for each of the 12 species. ** and *** indicate significance of the correlation at $P \leq 0.01$ and 0.001, respectively.
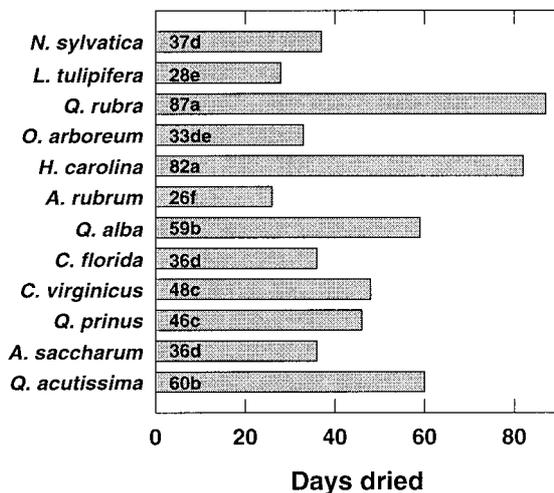

Fig. 7. Length of the continuous, lethal soil drying episodes for the 12 tree species. Numbers within bars give the exact length of the bar and indicate averages of 8–20 plants. Numbers followed by the same letter are statistically similar (Duncan's Multiple Range Test, $P > 0.05$).

however, drying time was not correlated with lethal leaf ψ ($r = -0.06^{NS}$), lethal leaf RWC ($r = 0.55^{NS}$) or osmotic adjustment ($r = -0.39^{NS}$). Hence, estimates of relative species foliar dehydration tolerance did not appear to be confounded by differences in rates of soil drying, which were in some instances probably related to differences in plant size. Not surprisingly, lethal soil RWC was correlated with drying time ($r = -0.81^{P \leq 0.001}$); those plants whose foliage died at lower soil RWC took longer to dry down to those soil RWC.

For lethal leaf ψ, length and width of each leaf were measured, as a gauge of relative leaf age within species,

and these data were incorporated into the statistical model. Leaf size (age) did not affect lethal leaf ψ.

Discussion

Many experimental factors can influence foliar responses to severe drought stress: plant status (nutrition, age, overall vigour), edaphic conditions (aeration, ion content, microbial activity, soil drying rates), and atmospheric factors (irradiance, air temperature, *VPD*). The approach was to standardize these conditions as much as possible, growing trees of similar age in soils that would maximize vigour and promote adequate nutrition, then conducting the experiment in a rain shelter constructed to simulate the ambient light and atmospheric conditions common to the understorey of deciduous forests of the southeastern United States. Soil drying rate was not controlled, either among or within species, but it did not materially affect lethal leaf ψ, RWC or changes in ψ_π.

Ranking of species according to foliar dehydration tolerance under these standardized conditions reveals some interesting relationships among species. For instance, previous works have ranked the drought resistance of *Q. alba*, *Q. rubra*, *A. saccharum*, and *C. florida* in that order as sites moved from xeric to mesic (Bahari *et al.*, 1985). Yet leaves of *A. saccharum* were able to withstand more desiccation (lower lethal leaf ψ and RWC) than either of the two oaks, despite the fact that soil ultimately became as dry (*Q. alba*) or much drier (*Q. rubra*) in the oaks than in *A. saccharum*. The similar foliar dehydration tolerance and osmotic adjustment of *A. saccharum*, considered a drought-sensitive species in nature (Graves, 1994; Berkowitz *et al.*, 1995), and *Q. alba*, a drought-tolerant species, underscores the value of determining lethal leaf ψ. The implication is that, in nature, *Q. alba* must have some other means of more successfully avoiding leaf dehydration than *A. saccharum*, such as a deeper root system, and this has been indicated by root experiments comparing the two species (Pallardy and Rhoads, 1993). In nature, flowering dogwood usually exhibits relatively little drought tolerance, perhaps because of its inability to avoid low ψ (Bahari *et al.*, 1985), but its leaves withstood as much or more dehydration than any of the native oaks or maples studied. This suggests that *C. florida* probably has poorly developed drought avoidance mechanisms such as deep rooting, and in fact it is considered to have shallow root systems. *Q. rubra* had perhaps surprisingly high lethal leaf ψ, but others have observed mortality in this species when predawn leaf ψ fell to -3.6 MPa or below (Viven *et al.*, 1993). Obviously, red and white oak possess other mechanisms than leaf dehydration tolerance that allow them to grow on drier sites than sugar maple and flowering dogwood.

Not surprisingly, the mesic hardwoods *N. sylvatica*, *L.*

tulipifera, *O. arboreum*, *H. carolina*, and *A. rubrum*, species tending to inhabit moist or bottomland sites, had the most dehydration-sensitive foliage in this study. Red maple is usually considered to be less drought resistant than sugar maple, and this is reflected by the leaf dehydration tolerances of the two species observed here. Among the oaks, *Q. rubra*'s relatively high lethal leaf ψ is consistent with its usual ranking as a mesic *Quercus* species (Timbal and Lefebvre, 1995). Others have concluded that differences in drought mortality among oak species were due to differences in ability to tolerate dehydration and not to drought avoidance (Viven *et al.* 1993). *L. tulipifera* and *Q. rubra* had relatively similar lethal leaf ψ and *RWC*; these two species previously showed similar leaf hydraulic properties in a study comparing drought response of diffuse and ring porous tree species (Shumway *et al.*, 1993).

With lethal leaf ψ near -2 MPa, foliage of *N. sylvatica* and *L. tulipifera* were as sensitive to dehydration as the most sensitive herbaceous crop species, cowpea (*Vigna unguiculata*) and *V. mungo* (Sinclair and Ludlow, 1986). The four most dehydration-tolerant deciduous tree species studied here were about mid-range in terms of the range of foliar dehydration tolerance reported to date (Ludlow, 1989); the lowest published lethal leaf ψ are near -12 MPa (for several C_4 grasses; Ludlow, 1989).

Quercus alba and *Q. rubra* have previously shown lower leaf ψ_π^{100} under drought than *A. saccharum* and *C. florida* (Bahari *et al.*, 1985), but post-drought leaf ψ_π^{100} or osmotic adjustment induced by lethal drought did not differ much among these species in the current study. Others have observed no osmotic adjustment in *Q. rubra* relative to the considerable adjustment in the more xeric *Q. prinus* (Kleiner *et al.*, 1992). Although osmotic adjustment of 0.60 MPa was observed in *Q. rubra*, perhaps not surprising given the extreme drought to which trees were exposed, *Q. prinus* also showed more osmotic adjustment than *Q. rubra* in the current study. *A. rubrum* has previously shown no osmotic adjustment with drought (Nash and Graves, 1993), and even lethal drought failed to induce active osmotic adjustment in this species in the current study. The limited osmotic adjustment of *L. tulipifera* here is in accord with another study in which this tree showed no osmotic adjustment during two drought cycles (Abrams and Kubiske, 1994).

A linear relationship frequently exists between dehydration tolerance (lethal leaf ψ) and osmotic adjustment when comparing these parameters among a range of species varying widely in tolerance (Ludlow, 1989; Sinclair and Ludlow, 1986), but this is not always the case when considering just a few species (O'Neill, 1983; Chapman and Augé, 1994). Generally, a positive relationship would be expected between leaf dehydration tolerance and osmotic adjustment, because plants with low dehydration tolerance and high osmotic adjustment would die from

dehydration, unless the plant had exceptionally deep roots as in phreatophytes (Ludlow, 1989). For these 12 tree species, lethal leaf ψ was correlated with leaf $\Delta\psi_\pi^{100}$ (Fig. 6); generally, the higher the dehydration tolerance, the greater the capacity for osmotic adjustment. This relationship was as strong or stronger for these deciduous trees as has been observed before for other kinds of plants (e.g. 22 forage legumes; Ludlow, 1989).

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