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Physiological Mechanisms of Drought Resistance in Four Native Ornamental Perennials

Douglas S. Chapman and Robert M. Augé
Department of Ornamental Horticulture and Landscape Design, University of Tennessee, Knoxville, TN 37901-1071

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Abstract. **Understanding physiological drought resistance mechanisms in ornamentals may help growers and landscapers minimize plant water stress after wholesale production. We characterized the drought resistance of four potted, native, ornamental perennials: purple coneflower [*Echinacea purpurea* (L.) Moench], orange coneflower [*Rudbeckia fulgida* var. *Sullivantii* (Beadle & Boynt.) Cronq.], beebalm (*Monarda didyma* L.), and swamp sunflower (*Helianthus angustifolius* L.). We measured a) stomatal conductance of leaves of drying plants, b) lethal water potential and relative water content, and c) leaf osmotic adjustment during the lethal drying period. Maintenance of stomatal opening as leaves dry, low lethal water status values, and ability to osmotically adjust indicate relative drought tolerance, with the reverse indicating drought avoidance. *Echinacea purpurea* had low leaf water potential (ψ_L) and relative water content (RWC) at stomatal closure and low lethal ψ_L and RWC, results indicating high dehydration tolerance, relative to the other three species. *Rudbeckia fulgida* var. *Sullivantii* had a similar low ψ_L at stomatal closure and low lethal ψ_L and displayed relatively large osmotic adjustment. *Monarda didyma* had the highest ψ_L and RWC at stomatal closure and an intermediate lethal ψ_L, yet displayed a relatively large osmotic adjustment. *Helianthus angustifolius* became desiccated more rapidly than the other species, despite having a high ψ_L at stomatal closure; it had a high lethal ψ_L and displayed very little osmotic adjustment, results indicating relatively low dehydration tolerance. Despite differences in stomatal sensitivity, dehydration tolerance, and osmotic adjustment, all four perennials fall predominantly in the drought-avoidance category, relative to the dehydration tolerance previously reported for a wide range of plant species.**

Water is the earth's most abundant compound, yet lack of water is the single most important resource limiting plant distribution and productivity throughout the world (McWilliam, 1986; Turner and Kramer, 1980). Plants have evolved various physiological and morphological responses (or mechanisms) to endure periods of water stress (Begg, 1980; Levitt, 1980; Morgan, 1980). Identifying drought-resistance responses and their influences on productivity and yield is essential to drought-resistance selection and breeding programs and for developing water-conserving agricultural practices.

Plants that have tissues with low dehydration tolerance and that depend on avoiding water deficits for survival are known as drought avoiders (Ludlow et al., 1983; Turk et al., 1980). Drought avoiders have mechanisms that maximize water uptake, minimize water loss, or combine the two. Drought avoiders typically minimize water loss with stomata that close rapidly with decreases in atmospheric humidity (Nagarajah and Shulze, 1983) or leaf water status (Ludlow and Ibaraki, 1979; Nobel, 1977), or with morphological characteristics such as leaf shedding, reduced leaf size, or deep, extensive root systems (Begg, 1980; Kummerow, 1980). In contrast, plants with tissues that are dehydration tolerant and that have only moderate avoidance mechanisms are known as drought tolerators. These plants rely on osmotic adjustment to survive drought (Ludlow et al., 1985). Osmotic adjustment helps maintain turgor and hence sustains metabolic activity during drought; stomata remain partially open (Flower and Ludlow, 1986; Ludlow, 1980a), and net photosynthesis continues, although at a reduced rate (Ackerson and Hebert, 1980). There is a spectrum in response ranging from extreme drought avoidance to extreme drought tolerance, and, although the terms avoidance and tolerance are useful in categorizing drought resistance, not all plants fit closely into one or the other category.

The purpose of this research was to characterize and compare physiological drought-resistance responses of four native, ornamental perennials that are indigenous to contrasting natural habitats. *Echinacea purpurea* and *Rudbeckia fulgida* var. *Sullivantii* grow on open, sunny sites such as meadows and prairies, where dry conditions frequently prevail, whereas *Monarda didyma* and *Helianthus angustifolius* usually occur on wetter sites adjacent to streams or bogs (Radford, 1968). The four species are widely cultivated and commercially grown for ornamental use in gardens and landscapes. In this experiment, stomatal behavior, dehydration tolerance, and osmotic adjustment during prolonged soil-drying cycles were investigated.

Materials and Methods

Stomatal behavior experiments

Plant material and culture. Twenty 4- to 6-week-old seedlings of *E. purpurea*, *R. fulgida* var. *Sullivantii*, *M. didyma*, and *H. angustifolius* were planted on 5 May 1991 in 8-liter plastic pots (top width 21 cm, bottom width 17 cm, height 25 cm) containing a 4 bark : 1 sand medium (v/v) amended with dolomitic lime at 2.0 $kg\cdot m^{-3}$, slow-release fertilizer (20N–1.7P–8.3K; O.M. Scotts and Sons, Marysville, Ohio) at 1.78 $kg\cdot m^{-3}$ and soluble trace elements (Peters Fertilizer Products, W.R. Grace, Fogelsville, Pa.) at 0.48 $g\cdot m^{-3}$. Medium pH was 4.7 to 5.0 at transplanting. A water-soluble fertilizer (20N–8.8K–16.6P; Peters) was applied at a rate of 237 mM N every 7 to 10 days at watering. All plants were grown under natural daylight in a greenhouse in Knoxville, Tenn., and they remained well watered until the drought treatment began.

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Drought treatment and water relations measurements. On 10 July 1991, four plants of each species were arranged randomly on a greenhouse bench, watered, and subsequently subjected to a continuous soil-drying cycle by withholding water from pots. Leaf diffusive conductance (Cs), leaf temperature, photosynthetic photon flux (PPF), leaf water potential (ψ_L), leaf osmotic potential (ψ_π), and leaf relative water content (RWC) were measured on each leaf beginning on day 1 of the soil-drying cycle and continuing until Cs declined to $<0.5\ \text{mm}\cdot\text{s}^{-1}$ ($\approx$7 to 21 days, depending on species). All measurements were performed daily between 0900 and 1330 HR on healthy, unshaded, recently fully expanded leaves. PPF was measured with each Cs measurement and ranged from 150 to 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on sunny days with no supplemental light and from 300 to 750 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on cloudy days under supplemental 400-W high-pressure sodium lights (Voigt Lighting Industries, Leonia, N.J.). Preliminary tests indicated that Cs did not change predictably within these diurnal or irradiance ranges. Sodium-vapor lights were used on all cloudy days and were turned on at least 1 h before measurements began. Leaf temperature ranged from 22 to 34C and greenhouse relative humidity ranged from 40% to 75% during the experiment at the time of porometry measurements. Numbers of leaves sampled per species on each day varied according to daily declines in Cs and ψ_L, such that a wide spectrum of values for Cs, ψ_L, ψ_π, and RWC could be collected for each species during the drying cycle.

Cs and leaf temperature were measured adjacent to the mid-vein on abaxial leaf surfaces with an automatic-cycling porometer (model AP-4; Delta T Devices, Cambridge, England). PPF was measured for each leaf sample with a quantum sensor (LI-COR, Lincoln, Neb.) attached to a datalogger (model 21X; Campbell Scientific, Logan, Utah). Immediately after determining Cs and leaf temperature, leaf samples were wrapped in plastic cling-film to minimize moisture loss and excised, and ψ_L was determined with a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara. Calif.). Balance points were observed on cut petioles with a microscope. Leaf RWC was determined on leaf tips (2 to 5 cm^2) excised from the same leaf sample used to determine ψ_L and ψ_π, rehydrated for 4 h at 4C, and calculated as RWC = (FW – DW)/(SW – DW), where FW, DW, and SW were the fresh weight at excision, dry weight after oven-drying for at least 48 h at 80C, and saturated weight of leaf tip, respectively. The remainder of the leaf was used to determine ψ_π immediately after measuring ψ_L. The leaf was inserted into a 1- or 3-ml plastic syringe, frozen in liquid N, and thawed at room temperature for 20 to 60 min. Leaf osmotic potential was determined with a vapor-pressure osmometer (model 5500; Wescor, Logan, Utah), calibrated with a graded series of NaCl solutions, on sap expressed onto 6-mm filter paper disks. Leaf turgor potential (ψ_p) was calculated as $\psi_p = \psi_L - \psi_\pi$. The experiment was repeated 7 to 24 Aug. 1991 with a new set of plants. The above measurements were made quickly by three investigators working together to minimize water loss from samples. Preliminary tests showed that quickly pressurizing wrapped leaves did not usually depress values of subsequent RWC and ψ_π measurements more than $\approx$1%.

Experimental design. The experimental design was a 4 × 2 (species × drying cycle) factorial with four replicates for each treatment combination. Since in the analysis of variance (ANOVA) [General Linear Models (GLM) Procedure, SAS, Cary, N.C.] there were no significant species × drying cycle interactions, results from the two drying cycles were pooled for regression analysis. Pooled standard errors of the means were calculated by taking square roots of the error mean squares and dividing them by the square root of the number of observations in a mean.

Dehydration tolerance and osmotic adjustment experiment

Plant material and culture. Twelve 4- to 6-week-old seedlings of *E. purpurea*, *R. fulgida* var. *Sullivantii*, *M. didyma*, and *H. angustifolius* were planted in 20-liter plastic pots (top width 29 cm, bottom width 25 cm, height 29 cm) containing a 4 bark : 1 sand medium (v/v) on 7 and 8 June 1991. Medium pH and amendment rates of lime, slow-release fertilizer, and micronutrients were identical to those used for the stomatal behavior experiments. A water-soluble fertilizer (20N–8.8K–16.6P; Peters) was applied at a rate of 237 mM N every 7 to 10 days at time of watering. Plants remained growing in a greenhouse in Knoxville until December 1991, when it was necessary to impose a cold treatment for plants to break dormancy induced by short fall days. After foliage was cut back to 5 to 10 cm above soil level, plants were placed into refrigeration (12C) on 3 Dec. 1991. On 6 Jan. 1992, plants were moved back into a greenhouse, and irrigation and fertilization were immediately resumed using the same type and rate of water-soluble fertilizer applied previously.

Drought treatment and water relations measurements. On 21 Apr. 1992, plants were randomly arranged on a growing bench, well watered, and subsequently subjected to a slow, continuous soil-drying cycle by withholding water. At the start of soil drying, *E. purpurea*, *R. fulgida* var. *Sullivantii*, and *H. angustifolius* plants were about the same height (40 to 60 cm) and width (25 to 40 cm) and had 25 to 50 leaves. *Monarda didyma* was more compact ($\approx$20 cm high and $\approx$40 cm wide) but had more leaves per plant (40 to 100).

Leaf osmotic potential at full turgor (ψ_π^{100}) was determined between 1200 and 1300 HR on the first day (day 0) of the soil-drying cycle on one leaf from each plant. Procedures for determining ψ_π^{100} were the same as those used for measuring ψ_π in the stomatal behavior experiment. To assess ψ_π^{100} after drought, one leaf per plant was excised at time of sampling for dehydration tolerance (see procedures for lethal measurements below), rehydrated by floating (petiole submerged) on distilled water for 4 h at 3C, and blotted dry, and ψ_π^{100} was determined as above. Leaf osmotic adjustment ($\Delta\psi_\pi^{100}$) was assessed as $\Delta\psi_\pi^{100} = \psi_\pi^{100(b)} - \psi_\pi^{100(a)}$, where $\psi_\pi^{100(b)}$ and $\psi_\pi^{100(a)} = \psi_\pi^{100}$ before and after drought, respectively.

Dehydration tolerance of the four species was characterized by measuring lethal leaf ψ_L, lethal RWC, and lethal soil water potential (ψ_s). Dehydration tolerance has been operationally defined as the ψ_L or RWC of the last surviving leaf (called the lethal value) on a plant subjected to a slow, continuous soil-drying cycle (Ludlow, 1989). Plants were checked daily after beginning the drying cycle and lethal measurements begun when only five to six live leaves with minimal necrotic areas (<25% of total leaf area) remained. Sampling was performed between 0800 and 1000 HR beginning on 5 May 1992 and continued until 12 June 1992.

Lethal ψ_L determinations were performed with two thermocouple psychrometers (model SC-10; Decagon Devices, Pullman, Wash.) calibrated daily with a graded series of NaCl solutions, following standard psychrometer precautions (Oosterhuis and Wullschleger, 1987). Psychrometer sample changers were connected to nanovoltmeter thermometers (model NT-3; Decagon Devices) used to derive temperature and μV readings for conversion into ψ values. Lethal ψ_L was determined on strips cut from leaf laminae adjacent and parallel to mid-veins and placed inside the psychrometer chamber with abaxial sides exposed to the center of sample cups.

Lethal ψ_s values were determined on the same plants from which other lethal values were measured with the thermocouple psychrometers described above on soil samples extracted from the root zone, 18 to 25 cm below the soil surface near the center of the pot. Preliminary tests indicated that leaf and soil samples generally reached thermal and water-vapor equilibrium in the psychrometer chamber in 2 h; all samples were allowed to equilibrate for a minimum of 2 h. Thermocouple psychrometers were used to determine ψ_L in this experiment because the pressure chamber gave inconsistent values at very low ψ_L and because psychrometers are not subject to these pressurization errors. Leaf RWC was determined as before on another leaf sample excised from each plant.

Experimental design and statistical analysis. The experiment used a completely randomized design with 10 plants of each species (40 plants total) subjected to one prolonged lethal soil-drying cycle. Mean separation of lethal ψ_L, lethal ψ_s, lethal RWC, $\psi_\pi^{100(b)}$, $\psi_\pi^{100(a)}$, and $\varnothing\psi_\pi^{100}$ was performed using ANOVA (GLM, SAS) and Duncan's multiple range test ($P \leq 0.05$).

Results

Stomatal behavior. Stomatal conductance decreased in a similar curvilinear manner during the drying cycle in *E. purpurea* and *R. fulgida* var. *Sullivantii*, with rapid initial declines slowing below about –1.50 MPa ψ_L and 3 mm·s^{-1} Cs (Fig. 1a). At high ψ_L, Cs of *M. didyma* was about one-fourth that of *H. angustifolius* and *R. fulgida* var. *Sullivantii* and one-third that of *E. purpurea* (Fig. 1b). Stomatal conductance of *M. didyma* fell most rapidly at high ψ_L, slowing at about –0.75 MPa ψ_L and 2 mm·s^{-1} Cs. Conductance fell more rapidly with declining ψ_L in *H. angustifolius* than in the other three species (Fig. 1b). At about –1.0 MPa ψ_L and 4 mm·s^{-1} Cs, the decline in Cs began to slow. Conductance measurements in all species stopped when leaves began dying (i.e., when samples were incapable of rehydration for RWC measurements). To get an indication of ψ_L and RWC at or near stomatal closure, we computed mean ψ_L and RWC between 0.5 and 1.5 mm·s^{-1} Cs (Fig. 2), as leaf conductance never became zero. Mean ψ_L near stomatal closure ($\psi_L^{\rightarrow 0}$) was lower in *E. purpurea* (–2.79 MPa) and *R. fulgida* var. *Sullivantii* (–2.46 MPa) than in *M. didyma* (–1.21 MPa) and *H. angustifolius* (–1.47 MPa) (Fig. 2a). The lowest ψ_L reached in *H. angustifolius* and *M. didyma* was 1.0 to 1.5 MPa higher than low values in *E. purpurea* and *R. fulgida* var. *Sullivantii*.

In *E. purpurea* and *R. fulgida* var. *Sullivantii*, Cs fell with decreasing leaf RWC in a similar curvilinear fashion during the soil-drying cycle, with rapid initial declines slowing at ≈0.70 g·g^{-1} RWC and 3 mm·s^{-1} Cs (Fig. 3a). At high leaf RWC, Cs for *M. didyma* was about one-third as high as Cs for *E. purpurea* and *R. fulgida* var. *Sullivantii* and one-fourth as high as for *H. angustifolius* (Fig. 3b). As leaf RWC declined, Cs fell very little in *M. didyma*. Conductance in *H. angustifolius* fell rapidly at high leaf RWC, with initial declines slowing at ≈0.70 g·g^{-1} RWC and 3 mm·s^{-1} Cs. Mean leaf RWC near stomatal closure (RWC$^{\rightarrow 0}$) was lower in *E. purpurea* (0.56 g·g^{-1}) and *H. angustifolius* (0.47 g·g^{-1}) than in *R. fulgida* var. *Sullivantii* (0.62 g·g^{-1}) and *M. didyma* (0.78 g·g^{-1}) (Fig. 2b).

In *E. purpurea* and *R. fulgida* var. *Sullivantii*, the relationship of ψ_L to RWC was very similar, as reflected by the slopes of the linear regressions (Fig. 4a). *Monarda didyma* and *H. angustifolius* each displayed smaller decreases than *E. purpurea* or *R. fulgida* var. *Sullivantii* in ψ_L as leaf RWC declined (Fig. 4b). At lower leaf RWC, ψ_L in *H. angustifolius* was higher than in the other three species.

The relationship of leaf ψ_p to ψ_L was plotted using data representing ψ_L higher than –2.10 MPa in *E. purpurea* and *R. fulgida* var. *Sullivantii*, –1.60 MPa in *M. didyma*, and –1.40 MPa in *H. angustifolius*. At ψ_L below the values above, the pressure chamber began to return unrealistically high ψ_L estimates, likely indicative of damage to droughted tissues at high pressurization. Leaf ψ_p declined with decreasing ψ_L in a similar manner in *E. purpurea* and *R. fulgida* var. *Sullivantii* (similar slopes, Fig. 5a), with ψ_p remain-

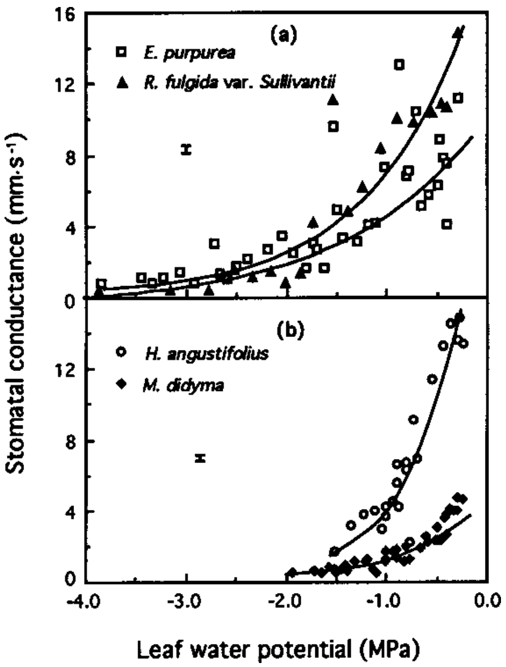


Fig. 1. Stomatal conductance as a function of leaf water potential for (**a**) *Echinacea purpurea* [$y = 9.64 \times 10^{(0.32x)}$ (R^2=0.59)] and *Rudbeckia fulgida* var. *Sullivantii* [$y = 22.65 \times 10^{(0.44x)}$ (R^2 = 0.56)] and (**b**) *Helianthus angustifolius* [$y = 20.56 \times 10^{(0.74x)}$ (R^2 = 0.48)] and *Monarda didyma* [$y = 5.11 \times 10^{(0.61x)}$ (R^2 = 0.66)]. Each symbol represents the mean of four observations. Plots were constructed from individual observations from both drying cycles. Vertical bars = SEs of the means.

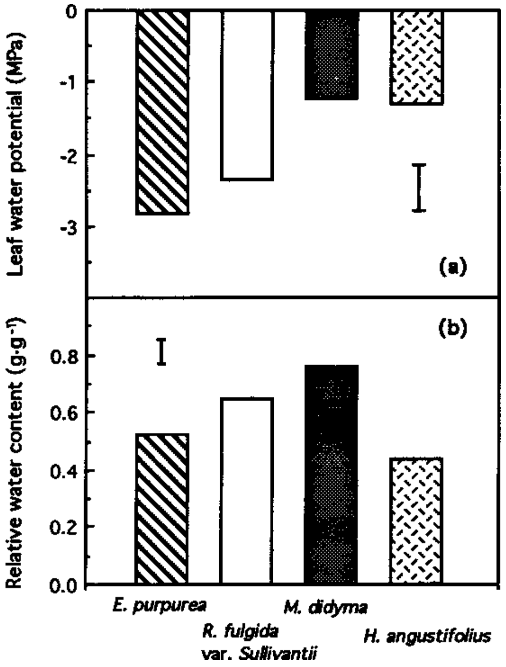


Fig. 2. Mean leaf water potential (**a**) and leaf relative water content (**b**) near stomatal closure (0.5 to 1.5 mm·s^{-1} leaf diffusive conductance) of *Echinacea purpurea*, *Rudbeckia fulgida* var. *Sullivantii*, *Monarda didyma*, and *Helianthus angustifolius*.

ing slightly higher in *R. fulgida* var. *Sullivantii* than in *E. purpurea* at any given ψ_L. Leaf water potential at turgor loss ($\psi_p{}^0$) values were computed from regressions illustrated in Fig. 5 and represent treatment composites (sample size = 1, hence no statistics were computed). The estimated ψ_L at $\psi_p{}^0$ was slightly lower in *R. fulgida* var. *Sullivantii* (-2.02 MPa) than in *E. purpurea* (–1.86 MPa). In *M. didyma*, ψ_p at high ψ_L was similar to that of *E. purpurea* (Fig. 5b), and ψ_L at $\psi_p{}^0$ in *M. didyma* (–2.05 MPa) was similar to that of *R. fulgida* var. *Sullivantii*. Leaf ψ_p for *H. angustifolius* was lower than for the other three species at high ψ_L, and this trend continued during the drying cycles (Fig. 5b). The estimated ψ_L at $\psi_p{}^0$ in *H. angustifolius* (–1.71 MPa) was highest among the four species.

Leaves of all four species wilted during the drying cycle. Leaves of *H. angustifolius* dried more rapidly (abruptly, after 2 to 3 days) and more severely than those of the other three species. Most leaves of *H. angustifolius*, in contrast to those of the other species, did not recover after rewatering. Leaves of *E. purpurea* and *R. fulgida* wilted gradually during the drying cycle (after ≥10 days of soil drying). Upon rewatering, both species recovered within a few days to one week, and their appearance was respectable; these two species are very rugged, drought-resilient perennials in the landscape (D.S. Chapman, personal observations). Leaves of *M. didyma* did not wilt until the end of the soil-drying cycles (in both stomatal and lethal experiments). Its physical appearance was least affected by drought compared to the other three species. Like *E. purpurea* and *R. fulgida*, it recovered within a few days of rewatering.

Dehydration tolerance and osmotic adjustment. Echinacea purpurea had relatively low lethal ψ_L (Fig. 6a) and lethal leaf RWC (Fig. 6c), yet had a high lethal ψ_s (Fig. 6b) and displayed little $\Delta\psi_\pi{}^{100}$ (Fig. 7b). *Rudbeckia fulgida* var. *Sullivantii* had low lethal ψ_L (Fig. 6a) and lethal ψ_s (Fig. 6b), displayed a large $\Delta\psi_\pi{}^{100}$ (Fig. 7b), but had a relatively high lethal leaf RWC (Fig. 6c). *Monarda didyma* had a relatively high lethal ψ_L (Fig. 6a) and high lethal leaf RWC (Fig. 6c), yet showed a relatively large $\Delta\psi_\pi{}^{100}$ (Fig. 7b). *Helianthus angustifolius* had one of the highest lethal ψ_L and little $\Delta\psi_\pi{}^{100}$, yet had a low lethal leaf RWC.

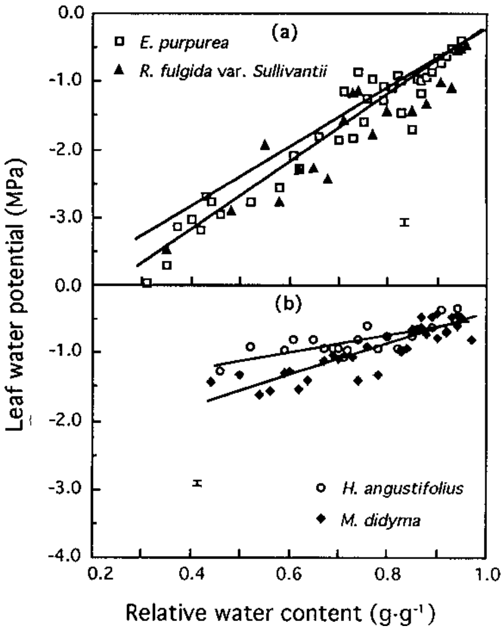


Fig. 4. Leaf water potential as a function of leaf relative water content for (**a**) *Echinacea purpurea* [y = (–5.19) + 4.96x (R^2 = 0.75)] and *Rudbeckia fulgida* var. *Sullivantii* [y = (–4.54) + 4.37x (R^2 = 0.51)] and (**b**) *Helianthus angustifolius* [y = (–1.77) + 1.28x (R^2 = 0.23)] and *Monarda didyma* [y = (–2.56) + 2.05x (R^2= 0.38)]. Plots were constructed and regression coefficients computed from individual observations from both drying cycles. Each data symbol represents the mean of four observations. Vertical bars = SES of the means.

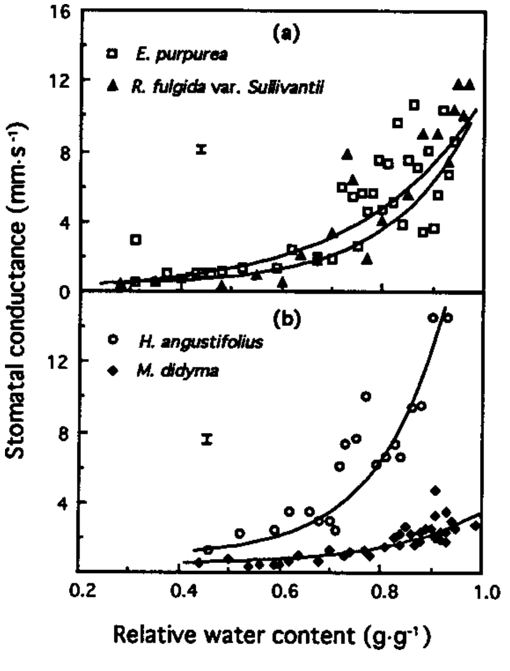


Fig. 3. Stomatal conductance as a function of leaf relative water content for (**a**) *Echinacea purpurea*[$y = 0.14 \times 10^{(1.83)}$ (R^2 = 0.63)] and *Rudbeckia fulgida* var. *Sullivantii* [$y = 4.27\,e - 2 \times 10^{(2.36x)}$ (R^2 = 0.57)] and (**b**) *Helianthus angustifolius* [$y = 0.11 \times 10^{(2.21x)}$ (R^2 = 0.61)] and *Monarda didyma* [$y = 4.54\,e - 2 \times 10^{(1.84x)}$ (R^2 = 0.60)]. Plots were constructed and regression coefficients computed from individual observations from both drying cycles. Each symbol represents the mean of four observations. Vertical bars = SES of the means.

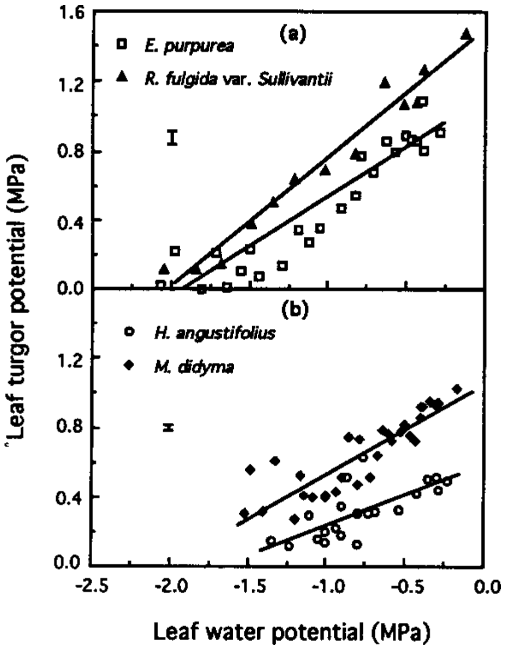


Fig. 5. Leaf turgor potential as a function of leaf water potential for (**a**) *Echinacea purpurea* [y = 1.07 + 0.55x (R^2= 0.56)] and *Rudbeckia fulgida* var. *Sullivantii* [y = 1.50 + 0.74x (R^2= 0.83)] and (**b**) *Helianthus angustifolius* [y = 0.58 + 0.34x (R^2 = 0.19)] and *Monarda didyma* [y = 1.01 + 0.44x (R^2 = 0.25)]. Plots were constructed and regression coefficients computed from individual observations from both drying cycles. Each data symbol represents the mean of four observations. Vertical bars = SES of the means.

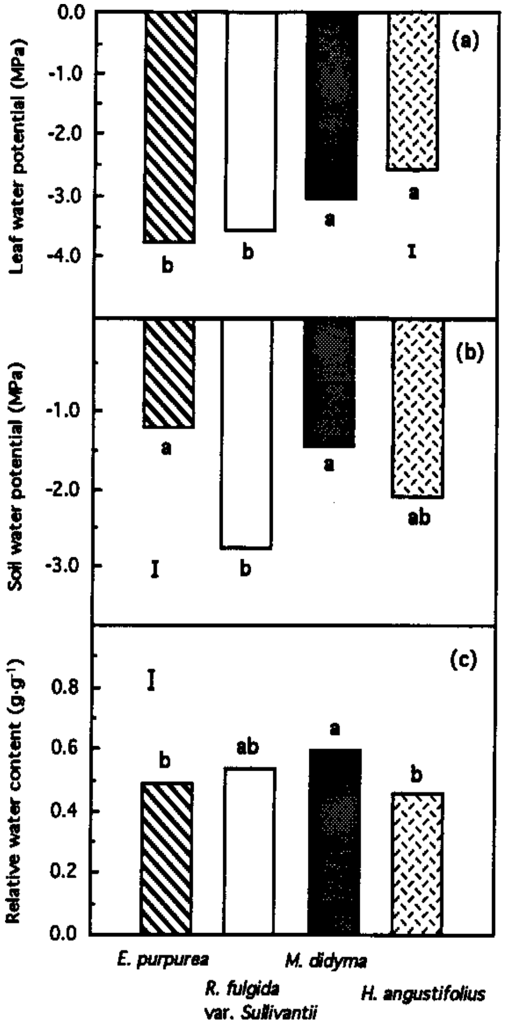


Fig. 6. Lethal leaf water potential (**a**), lethal soil water potential (**b**), and lethal leaf relative water content (**c**) of each species after a prolonged continuous soil drying cycle. Vertical bars = SES of the means; n = 10. Mean separation by Duncan's multiple range test, $P \leq 0.05$.

Discussion

As dehydration tolerance increases (as lethal ψ_L and RWC decline), there is generally a linear decrease in $\psi_L^{\to 0}$ (Ludlow, 1989; Ludlow et al., 1983; Sinclair and Ludlow, 1986) and a corresponding increase in the capacity for $\varnothing\psi_\pi^{100}$ (Ludlow, 1989; Sheriff et al., 1986; Sinclair and Ludlow, 1985; Wilson et al., 1980). For example, $\psi_L^{\to 0}$ in five accessions of a drought-tolerant tropical legume, *Centrosema*, ranged from –5.9 to –8.0 MPa and had a corresponding lethal ψ_L of –8.0 to –12.1 MPa, whereas $\psi_L^{\to 0}$ and lethal ψ_L in a drought-avoiding pasture legume, siratro [*Macroptilium atropurpureum* (DC) Urb.], were –1.9 MPa and –2.4 MPa, respectively (Ludlow et al., 1983). The extremely drought-tolerant tropical pasture legume, *Galactia striata* Urb., exhibited $\Delta\psi_\pi^{100}$ up to 2.3 MPa, whereas $\Delta\psi_\pi^{100}$ in *M. atropurpureum*, was <0.26 MPa (Sheriff et al., 1986).

Comparisons of the dehydration tolerance (expressed as lethal ψ_L) of *H. angustifolius*, *M. didyma*, *R. fulgida* var. *Sullivantii*, and *E. purpurea* to those of some tropical crops and pasture species ranging from extreme drought avoidance to extreme drought tolerance are shown in Table 1. Relative to the tropical crops and pasture species, the four ornamental perennial species that we investigated are predominantly drought avoiders. Drought-avoidance mechanisms (minimizing water loss and maximizing water uptake) are essential for survival during moderate to severe water deficits because drought avoiders have low dehydration tolerance (high lethal ψ_L and RWC) (Ludlow, 1989; Ludlow et al., 1983; Sinclair and Ludlow, 1986) and display little $\Delta\psi_\pi^{100}$ (Ludlow et al., 1985). Most mesophytic species fall into the avoidance category because they close stomata at high ψ_L and RWC to postpone tissue desiccation, having generally evolved in climates where rainless periods are brief (Fitter and Hay, 1987; Levitt, 1980). Stomatal closure is one of the primary defense mechanisms protecting plants from desiccation (Chaves, 1991; Mansfield and Davies, 1981).

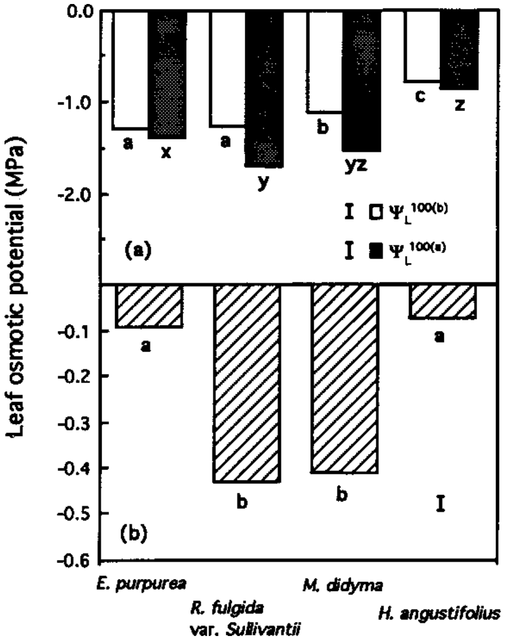
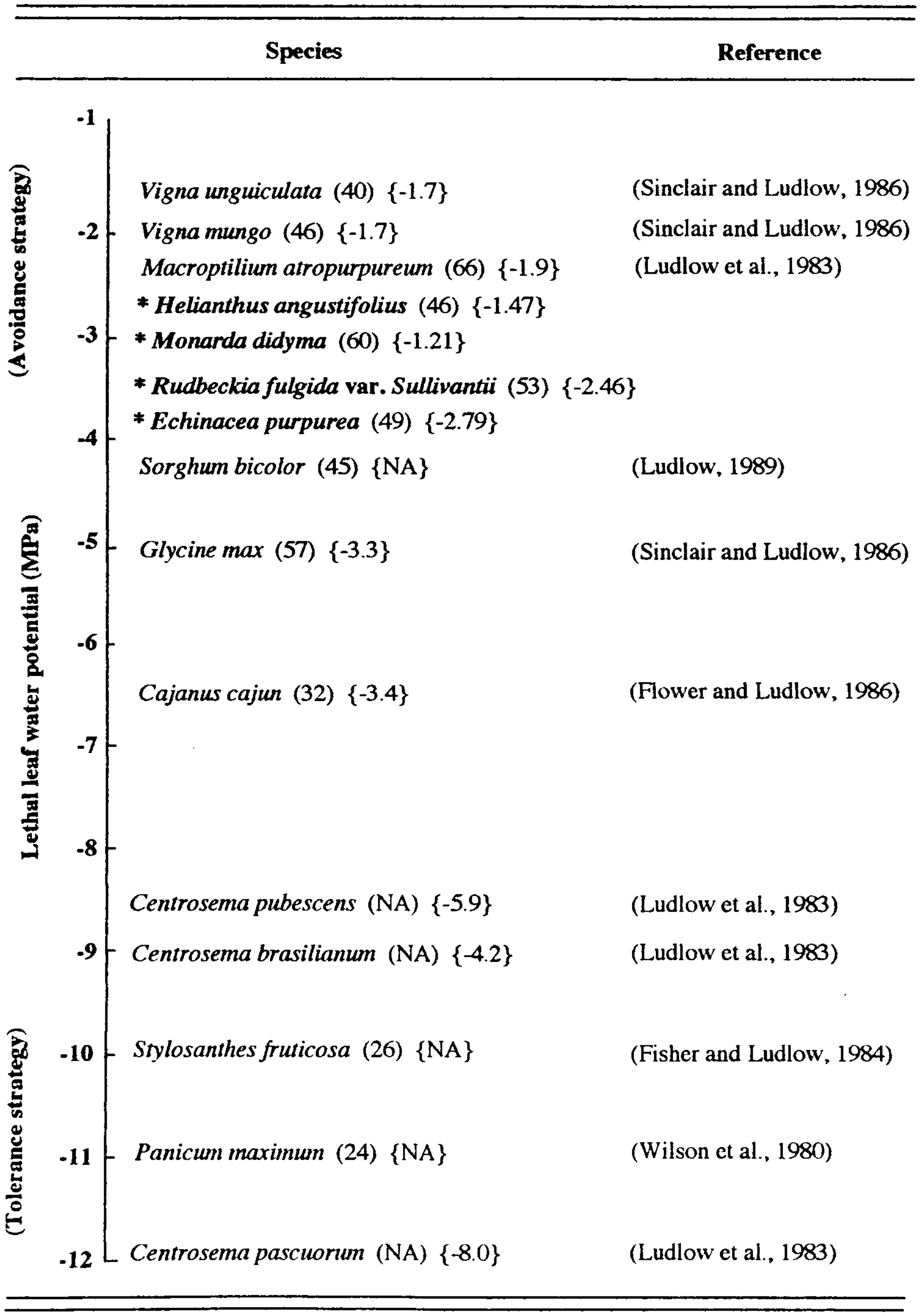


Fig. 7. Leaf osmotic potential at full turgor before ($\psi_\pi^{100(b)}$) and after ($\psi_\pi^{100(a)}$) the drying cycle (**a**) and leaf osmotic adjustment for each species (**b**). Vertical bars = SES of the means; n = 10. Mean separation by Duncan's multiple range test, $P \leq 0.05$.

In some species, Cs remains relatively constant until a threshold or critical ψ_L or RWC is reached, below which Cs begins to decline (Hsiao, 1973; Ludlow, 1980a, 1980b). In other species, as in the four perennials we investigated, Cs falls in a linear or curvilinear fashion from high ψ_L and RWC (Begg and Turner, 1976). Traditionally, ψ_L has been considered to be the primary parameter controlling stomatal behavior during drought (Beardsell and Cohen, 1975; Ludlow, 1980a), but others (Hsiao, 1973; Turner, 1974) have indicated that stomatal closure was better correlated with leaf ψ_p^0; recent investigations suggest that stomatal closure is directly linked to soil drying (decreasing ψ_s) (Bates and Hall, 1981; Gollan et al., 1986). When water stress is moderate to severe, a close correlation between $\psi_L^{\to 0}$ and ψ_L at ψ_p^0 frequently exists (Turner et al., 1985; Wilson et al., 1980), but this was not observed in our investigation. In *E. purpurea* and *R. fulgida* var. *Sullivantii*, the estimated ψ_L at ψ_p^0 was 0.44 to 0.93 MPa higher than $\psi_L^{\to 0}$ and corresponded more closely to the ψ_L at which Cs leveled off, i.e., stomata remained open for quite awhile after bulk leaf ψ_p reached zero. In *H. angustifolius* and *M. didyma*, the estimated ψ_L at ψ_p^0 was 0.24 to 0.84 MPa lower than $\psi_L^{\to 0}$, i.e., stomates closed before bulk leaf ψ_p was lost. These differences may reflect contemporary views of stomatal behavior—that stomata are likely affected by a combination of factors that vary in concert with ψ_L (Chaves, 1991), including leaf ψ_p (Bradford and Hsiao, 1982), $\varnothing\psi_\pi^{100}$ (Kaiser,

Table 1. Dehydration tolerance, expressed as lethal leaf water potential (MPa), of *Echinacea purpurea, Rudbeckia fulgida* var. *Sullivantii, Monarda didyma,* and *Helianthus angustifolius* compared to some tropical crops and pasture species ranging from plants that use the avoidance strategy to those that use the tolerance strategy. Data were obtained from different studies under widely varying conditions. Lethal leaf relative water content (%) is shown in parentheses and leaf water potential at stomatal closure is shown in brackets. Table adapted from Ludlow (1989).



Species	Reference
Vigna unguiculata (40) {-1.7}	(Sinclair and Ludlow, 1986)
Vigna mungo (46) {-1.7}	(Sinclair and Ludlow, 1986)
Macroptilium atropurpureum (66) {-1.9}	(Ludlow et al., 1983)
*** *Helianthus angustifolius*** (46) {-1.47}	
*** *Monarda didyma*** (60) {-1.21}	
*** *Rudbeckia fulgida* var. *Sullivantii*** (53) {-2.46}	
*** *Echinacea purpurea*** (49) {-2.79}	
Sorghum bicolor (45) {NA}	(Ludlow, 1989)
Glycine max (57) {-3.3}	(Sinclair and Ludlow, 1986)
Cajanus cajun (32) {-3.4}	(Flower and Ludlow, 1986)
Centrosema pubescens (NA) {-5.9}	(Ludlow et al., 1983)
Centrosema brasilianum (NA) {-4.2}	(Ludlow et al., 1983)
Stylosanthes fruticosa (26) {NA}	(Fisher and Ludlow, 1984)
Panicum maximum (24) {NA}	(Wilson et al., 1980)
Centrosema pascuorum (NA) {-8.0}	(Ludlow et al., 1983)

1987), leaf RWC (Boyer, 1989; Sinclair and Ludlow, 1985), leaf epidermal water relations (Tardieu and Davies, 1992), and chemical components coming from the roots (Zhang and Davies, 1989).

Helianthus angustifolius had the most robust drought-avoidance features of the four species we investigated, as demonstrated by its high $\psi_L^{\rightarrow 0}$, high lethal ψ_L, and lack of $\Delta\psi_\pi^{100}$. Surprisingly, its RWC$^{\rightarrow 0}$ and lethal RWC were relatively low, features generally found in drought tolerators (Ludlow, 1989). In *H. angustifolius*, $\psi_L^{\rightarrow 0}$ and lethal ψ_L were similar to those of three drought avoiding legumes—cowpea [*Vigna unguiculata* (L.) Walp.] (Hall and Schulze, 1980; Sinclair and Ludlow, 1986), mung bean [*Vigna mungo* (L.) Hepper] (Ludlow et al., 1985), and *M. atropurpureum*, (Sheriff et al., 1986), which also demonstrate high $\psi_L^{\rightarrow 0}$ and high lethal ψ_L. Deep, extensive root systems (maximizing water uptake) coincide with rapid stomatal closure in some drought avoiders (Markhart, 1985; Sheriff and Ludlow, 1984; Sheriff et al., 1985), providing the plant with a two-fold survival mechanism. The advantage of having these combined avoidance characteristics has been demonstrated by *M. atropurpureum*, which survived longer during drought than the drought-tolerant *Centrosema* species when both plants were grown under the same environmental conditions (Ludlow et al., 1985; Sinclair and Ludlow, 1986). In *H. angustifolius*, the restriction of water loss (i.e., stomatal closure) may not be the primary mechanism of drought avoidance because stomatal closure failed to prevent rapid water loss. We observed severe leaf desiccation in *H. angustifolius* 4 to 7 days after water withholding in the stomatal behavior experiment, whereas leaves of the other three species were not severely wilted until after day 13. We did not investigate root development in our experiment, but it is possible that *H. angustifolius* relies primarily on a deep, extensive root system to maximize water uptake, rather than rapid stomatal closure, to minimize water loss. If this is the case, growing *H. angustifolius* in containers probably increased the rate of tissue desiccation by limiting root development.

The high $\psi_L^{\to 0}$ and $\mathrm{RWC}^{\to 0}$, and high lethal ψ_L and RWC displayed by *M. didyma* were also similar to those found in drought-avoiding legumes (Ludlow et al., 1983; Sinclair and Ludlow, 1986). The extremely low Cs at high ψ_L and the small decreases in Cs with declining ψ_L in *M. didyma* are indicative of the conservative role its stomata have in regulating water loss. This feature might indicate that *M. didyma* is exclusively a drought avoider, but its relatively large $\Delta\psi_\pi^{100}$ is a feature usually found in drought-tolerant species (Flower and Ludlow, 1986; Hsiao et al., 1984). Among the four species in our investigation, *E. purpurea* had the greatest dehydration tolerance in terms of $\psi_L^{\to 0}$, $\mathrm{RWC}^{\to 0}$, lethal ψ_L, and lethal RWC, but displayed little $\Delta\psi_\pi^{100}$. The relatively low $\psi_L^{\to 0}$, low lethal ψ_L, and large $\Delta\psi_\pi^{100}$ found in *R. fulgida* var. *Sullivantii* reflect some degree of drought tolerance, but its lethal RWC was higher than those of a few extreme drought avoiders (Sinclair and Ludlow, 1986). Lethal ψ_L in *E. purpurea* and *R. fulgida* var. *Sullivantii* was similar to that of *Sorghum bicolor* (L.) Moench, which has a slightly lower ψ_L, yet is considered to be a drought avoider because it displays little $\Delta\psi_\pi^{100}$ (Ludlow, 1989).

Leaf $\Delta\psi_\pi^{100}$ is defined as the lowering of the tissue osmotic potential arising from the net active accumulation of solutes in cells (vs. passive accumulation from decreases in cell volume) in response to water deficits and salinity (Turner and Jones, 1980). Leaf $\Delta\psi_\pi^{100}$ assists in turgor maintenance, which sustains stomatal opening (stomatal adjustment) and hence allows photosynthesis and leaf expansion to continue during periods of water stress (Hsiao, 1973; Ludlow et al., 1985). However, $\Delta\psi_\pi^{100}$ seems to be as important to plant survival as it is to maintaining ψ_p (Flower and Ludlow, 1986; Hsiao et al., 1984). A linear relationship between dehydration tolerance (lethal ψ_L) and $\Delta\psi_\pi^{100}$ frequently exists when comparing these parameters among a wide range of species (drought avoiders to drought tolerators) (Ludlow, 1989; Sinclair and Ludlow, 1986), but this is not always the case when considering only a few species (Bjorkman et al., 1980; O'Neill, 1983), as demonstrated by *M. didyma* and *E. purpurea* in our experiment. Generally, a linear relationship would be expected, since a drought avoider (low dehydration tolerance) with high $\Delta\psi_\pi^{100}$ would die from dehydration unless the plant had exceptionally deep roots, as in phreatophytes (Ludlow, 1989). There was a consistent linear relationship between $\psi_L^{\to 0}$ and lethal ψ_L among the four species we investigated, a result that complies with that found among a wide range of species (Ludlow, 1989; Sinclair and Ludlow, 1986). A linear relationship between lethal ψ_L and lethal RWC can also be found (Ludlow, 1989), but, among the species we investigated, this was not the case. Lethal leaf RWC in *H. angustifolius* was lower than those of the more drought-tolerant species, *R. fulgida* var. *Sullivantii* and *M. didyma*. A similar situation was observed in *V. unguiculata* and *V. mungo*, which died at a high ψ_L but at lower lethal RWC than the more drought-tolerant soybean [*Glycine max* (L.) Merr.] (Sinclair and Ludlow, 1986). Therefore, as in $\Delta\psi_\pi^{100}$/lethal ψ_L, the linear relationship in lethal ψ_L/lethal RWC becomes more evident when comparing values among a wide range of species. Recently, it was suggested that lethal RWC is a more precise measure of dehydration tolerance than lethal ψ_L because a particular species dies within a smaller range of lethal RWC (Flower and Ludlow, 1986).

Our results were from plants growing in containers in a controlled environment, but dehydration tolerance, $\psi_L^{\to 0}$, and $\mathrm{RWC}^{\to 0}$ can vary with growing conditions. Generally, stomata in field-grown plants are not as sensitive to decreases in ψ_L. Stomata in creosote bush (*Larrea divaricata* Cav.), a drought-tolerant desert shrub, closed at –4.0 MPa when grown in a controlled environment in containers and at –5.8 MPa when grown in the field. In the drought-avoiding faba bean (*Vicia faba* L.), the same values were –0.6 and –1.0 MPa, respectively (Fitter and Hay, 1987). Therefore, it is likely that we would find a different set of values for the parameters we measured under field conditions.

Variations in drought resistance (dehydration tolerance and the mechanisms involved) generally correspond to the natural range of the species (Ludlow et al., 1983). We might expect to find a stronger expression of drought avoidance in species like *H. angustifolius* and *M. didyma* because they have evolved in microclimates close to water and in temperate climates with frequent rainfall. In contrast, *E. purpurea* and *R. fulgida* var. *Sullivantii* have evolved in dry, open microclimates, and, in the case of *E. purpurea*, a prairie species, in a climate with significant fluctuations in rainfall. As a result, *E. purpurea* and *R. fulgida* var. *Sullivantii* have combined some degree of dehydration tolerance with moderate avoidance responses. This combination may provide plants with a capacity to survive a wide range of environments (Ludlow, 1989).

Moisture stress is one of the major causes of losses in plant quality after wholesale production (Nelson and Carlson, 1987). Understanding a plant's drought resistance may help growers and landscapers to select and develop cultural methods that correspond to the specific mechanisms of the plant. These cultural methods could effectively minimize water stress after wholesale production.

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