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Scientia Horticulturae 98 (2003) 511–516

SCIENTIA HORTICULTURAE

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Short communication

Comparative dehydration tolerance of foliage of several ornamental crops

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Accepted 14 January 2003

Abstract

Cultivars of *Dahlia*, *Pentas*, *Salvia* and two *Impatiens* were subjected to severe soil drying, and their foliar water relations were measured when fewer than eight live leaves remained (defined as the lethal point). *Salvia* was the most dehydration tolerant of the four genera, as characterized by lethal leaf water potential, and showed the highest osmotic adjustment. *Dahlia* and the two *Impatiens* cultivars had similar water relations at the lethal point. Length of the drying period, which was varied by growing plants in three pot sizes, did not affect any leaf water relations parameter. The paper also provides a ranking of the foliar dehydration tolerance of 25 other ornamental plants, measured in additional experiments. Foliage of woody species tended to be more tolerant of dehydration than foliage of herbaceous species.

Keywords: *Dahlia*; Drought stress tolerance; Floriculture crops; *Impatiens*; Lethal water potential; Osmotic adjustment; *Pentas*; *Salvia*

1. Introduction

Potted horticultural crops are frequently exposed to severe water deficits at point of sale. As growers and scientists, we develop opinions about the relative ability of various crops to withstand drought, but little has been published regarding the actual dehydration tolerance of ornamental plants.

Abbreviations: RWC, relative water content; Ψ, water potential; Ψ_{π}^{100}, osmotic potential at full turgor

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0304-4238/$ – see front matter
doi:10.1016/S0304-4238(03)00037-2

Plants have evolved many physiological and morphological strategies which allow them to cope with drought stress. In the spectrum of plant responses ranging from extreme drought avoidance to extreme tolerance, one of the most important determinants of drought resistance strategy is the dehydration tolerance of the species. Dehydration tolerance is a measure of tissue capacity for withstanding desiccation and has been defined for several agronomic species as the water potential (Ψ) of the last surviving leaves (called the lethal value) on a plant subjected to a slow, continuous soil drying episode (Ludlow, 1989).

Here we describe an experiment comparing lethal leaf Ψ and other lethal water relations parameters of five potted floricultural crops. The experiment was designed to test whether length of the drought period affected the lethal values and evaluate drought tolerance among the studied species. The paper also summarizes results of additional experiments, providing a comparative ranking of the dehydration tolerance of 30 ornamental species.

2. Materials and methods

2.1. Plant culture

Dahlia × *hybrida* (Willd.) Desf. 'Figaro', *Salvia splendens* Sellow ex Roem. and Schult. 'Sizzler White', *Impatiens wallerana* Hook 'Rosebud Pink', *Impatiens* sp. New Guinea hybrid 'Kientzler Aurore' and *Pentas lanceolata* (Forssk.) Defl. 'Ruby Glow' were grown in a commercial potting mix consisting of 55% Canadian sphagnum peat moss, 25% vermiculite and 20% perlite (v/v/v), with a starter nutrient charge and wetting agent (Fafard Mix no. 2, Fafard, Agawam, MA, USA). To vary the time required for plants to reach the lethal point, each species was grown in three soil volumes, with pot size adjusted for species according to growth rate and habit. *Dahlia*, *I. wallerana* and *Salvia* were grown in 10.9, 7.1 and 3.9 l plastic pots, and *Impatiens* sp. New Guinea hybrid and *Pentas* were grown in 5.5, 3.1 and 1.8 l plastic pots.

Plants were grown in a greenhouse in Knoxville, TN, USA, under 50% shade (~1000 $\mu mol\ m^{-2}\ s^{-1}$ on a clear day) with heating/cooling set for 21/18 °C day/night. Plants were kept adequately watered until drought was imposed. With each irrigation plants were given Peters Excel 15N–5P–15K (CalMag, Grace-Sierra, Milpitas, CA, USA) at 14.3 mM N. Plant height, width (at the widest point) and leaf number were measured just prior to the drying period.

2.2. Drought treatment and water relations measurements

Seven weeks after potting, all plants were subjected to a continuous soil drying episode by withholding water from pots. One leaf from each plant was collected on day 0 (last day plants were watered) for measurement of initial (pre-drought) osmotic potential at full turgor (Ψ_{π}^{100}) using a vapor pressure osmometer (5500XR, Wescor, Logan, UT, USA) on expressed sap as described before (Chapman and Augé, 1994). Each plant was visibly checked daily after beginning the drying period and lethal measurements begun when fewer than eight live leaves with minimal necrotic areas (less than 25% of total leaf area) remained. Extra plants were sacrificed in preliminary trials 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.

At the lethal point for each plant, three leaves were excised for measurement of total Ψ, relative water content (RWC) and Ψ_π^{100}. For the two *Impatiens* cultivars, two to three leaves were used for Ψ_π^{100} because one leaf did not yield sufficient sap. Leaf Ψ was determined with thermocouple psychrometers (Decagon Devices, Pullman, WA, USA) as described before (Augé et al., 1998). RWC was calculated as described before (Chapman and Augé, 1994) using fresh weight of whole leaves at excision, turgid weight after 24 h rehydration with petioles submerged in distilled water in a covered container at 4 °C, and dry weight after oven drying 48 h at 80 °C. Leaf osmotic adjustment during the drying period was assessed as pre-drought Ψ_π^{100}–post-drought Ψ_π^{100}; this procedure for estimating osmotic adjustment integrates both phenologically induced and drought-induced solute changes. Sampling for water relations measurements was performed between 08:30 and 10:30 h EST.

Lethal leaf Ψ of the following ornamental plants were measured in three additional experiments, performed as described above except that plants were grown in one pot size: *Acer ginnala* Maxim., *Cornus kousa* Hans., *Heuchera villosa* Michx. 'Palace Purple', *Hypericum patulum* Thunb. 'Sungold', *Nepeta cataria* L., *Malus* 'Hopa', *Pelargonium* × *hortorum* L.H. Bail. 'Designer Scarlet' and *Rosa hybrida* L. 'Double Delight'.

2.3. Experimental design and statistical analysis

Plants were arranged in a randomized complete block design, blocked by growing bench, with eight replicates of each species in each pot size (120 plants total). Data were analyzed by ANOVA using the general linear models procedure (PROC GLM) with mean separations (Fisher's protected LSD), and by correlation analyses (Pearson correlation coefficients) (SAS, Cary, NC, USA).

3. Results and discussion

3.1. Rate of soil drying

One objective was to determine how rate of soil drying affected the ultimate degree of dehydration at which leaves died. The ability of plants to acclimate to drought can depend on the rate of soil drying (Turner and Jones, 1980) and we speculated that lethal values of leaf Ψ, Ψ_π^{100} or RWC might vary with drying time. To test this, we varied length of the lethal drying period by growing plants with similar-sized shoots in different soil volumes. Pot size did not affect plant height, width or leaf number at the onset of the drying period (data not shown). Pot size did affect drying times; averaged across species, drying times were 24.1 ± 1.7 days for the smallest pots, 34.6 ± 2.5 days for intermediate-sized pots and 41.2 ± 2.7 days for the largest pots. Rate of soil drying did not affect foliar dehydration tolerance of these five taxa; none of the lethal leaf water relations parameters were affected by pot size (P values for ANOVA main effect of the pot size exceeded 0.05 for all Ψ, Ψ_π and RWC variables). This is consistent with a previous study, in which rate of soil drying did not affect foliar dehydration tolerance of ornamental trees (Augé et al., 1998).

Table 1
Lethal leaf water relations of *Impatiens*, *Dahlia*, *Salvia* and *Pentas*

Species	Lethal Ψ (MPa)	Initial Ψ_{π}^{100} (MPa)	Lethal Ψ_{π}^{100} (MPa)	Osmotic adjustment (MPa)	Lethal RWC (%)	Days to lethal point
I. wallerana	−2.06a[a]	−0.52a	−0.86a	−0.34b	0.73a	55.2a
Dahlia × *hybrida*	−2.29a	−0.66b	−1.08b	−0.41b	0.64b	25.9c
Impatiens sp. New Guinea hybrid	−2.37a	−0.66b	−1.14bc	−0.47b	0.77a	32.6b
P. lanceolata	−4.27b	−1.16d	−1.25c	−0.09a	0.41d	17.3d
S. splendens	−5.16c	−0.81c	−1.48d	−0.64c	0.48c	35.4b

[a] Values represent means for each water relations variable across three pot sizes, $n = 24$. Within columns, means followed by different letters are significantly different at $P \leq 0.05$ (Fisher's LSD).

3.2. Lethal water relations of flowering annuals

Because pot size did not affect lethal water relations parameters, species comparisons are shown with values averaged across pot size for each species (Table 1, species ordered by lethal leaf Ψ). On average, *Dahlia* and the two *Impatiens* had similar and high lethal leaf Ψ, close to the highest previously reported lethal values for any plant species (*Vigna unguiculata* and *Phaseolus* sp., Augé et al., 2001; Ludlow, 1989). These three ornamentals also had the lowest full turgor solute concentrations (the highest Ψ_{π}^{100}) before exposure to drying, and they showed mostly similar osmotic adjustment during the lethal drought period (0.34–0.47 MPa). The two *Impatiens* had the highest lethal RWC. Foliage of *Salvia* was most tolerant of dehydration among the five taxa, having the lowest Ψ, the lowest Ψ_{π}^{100} and the second lowest RWC at the lethal point. Salvia also showed the highest osmotic adjustment. Lethal Ψ of *Salvia* was similar to that previously reported for *Glycine max* (−4.9 MPa, Ludlow, 1989), and the lethal Ψ for *Pentas* was 0.5 MPa lower than that reported before for *Sorghum bicolor* (−3.8, Ludlow, 1989).

Others have observed a loose correlation between lethal leaf Ψ and capacity for osmotic adjustment (Ludlow, 1989; Augé et al., 1998), and this was also observed in the current experiment. Lethal Ψ and osmotic adjustment were not significantly correlated within species but were correlated across species ($P = 0.04, r = 0.65$). Species having similar lethal Ψ also had similar osmotic adjustment (*Dahlia* and the two *Impatiens*), and the species with the lowest lethal Ψ also had the largest osmotic adjustment (*Salvia*). *Pentas* was the exception; it showed the least osmotic adjustment but had relatively high dehydration tolerance (low lethal leaf Ψ and the lowest lethal leaf RWC).

3.3. Comparative foliar dehydration tolerance of several ornamental species

Table 2 shows lethal leaf Ψ measured in several experiments, providing a ranking of the foliar dehydration of 30 ornamental tree, shrub, and herbaceous annual and perennial species. Foliage of woody plants is typically considered to be more tolerant of dessication than foliage of herbaceous plants, and that is loosely borne out by Table 2. Ten of the 15 most dehydration tolerant plants were trees or woody shrubs, and four of the five most tolerant were trees. *Quercus* sp. tended to be the most dehydration tolerant trees, consistent

Table 2
Foliar dehydration tolerance of several woody and herbaceous ornamental species, ranked by lethal leaf Ψ[a]

Species	Common name	Lethal leaf Ψ (MPa)
Pelargonium × hortorum 'Designer Scarlet'	Geranium	−2.01a[b]
Nyssa sylvatica[c]	Black gum	−2.04a
Impatiens wallerana 'Rosebud Pink'	Double impatiens	−2.06a
Heuchera villosa 'Palace Purple'	Coral bells; alum root	−2.15ab
Ocimum basilicum 'Italian Large Leaf Cal Select'[d]	Basil	−2.16ab
Dahlia × hybrida 'Figaro'	Dahlia	−2.29ab
Impatiens sp. New Guineas hybrid 'Kientzler Aurore'	New Guinea impatiens	−2.37ab
Liriodendron tulipifera[c]	Tulip poplar	−2.38ab
Malus 'Hopa'	Flowering crabapple	−2.49abc
Helianthus angustifolia[e]	Swamp sunflower	−2.58abc
Monarda didyma[e]	Beebalm	−3.02bcd
Quercus rubra[c]	Red oak	−3.34cde
Rudbeckia fulgida var. Sullivanii[e]	Orange coneflower	−3.56def
Halesia carolina[c]	Carolina silverbell	−3.58def
Echinacea purpurea[e]	Purple coneflower	−3.77defg
Oxydendrum arboreum[c]	Sourwood	−3.98efg
Cornus kousa	Kousa dogwood	−4.01efg
Rosa hybrida 'Double Delight'	Rose	−4.16efg
Acer ginnala	Amur maple	−4.19efg
Pentas lanceolata 'Ruby Glow'	Star-cluster	−4.27fgh
Acer rubrum[c]	Red maple	−4.43fghi
Cornus florida[c]	Flowering dogwood	−4.46fghi
Quercus alba[c]	White oak	−4.60ghi
Salvia splendens 'Sizzler White'	Scarlet sage	−5.16hij
Nepeta cataria	Catnip	−5.17ij
Chionanthus virginicus[c]	Fringe tree	−5.63jk
Quercus prinus[c]	Chestnut oak	−5.73jk
Acer saccharum[c]	Sugar maple	−5.76jk
Quercus acutissima[c]	Sawtooth oak	−6.14kl
Hypericum patulum 'Sungold'	Goldencup St. John's wort	−6.67l

[a] Data were obtained from four previously unpublished and three previously published experiments in our lab.
[b] Means followed by different letters are significantly different at $P \leq 0.05$ (Fisher's LSD; data blocked by experiment). Sample size ranged from 8 to 24, with most samples representing the average of two subsamples.
[c] Data previously published in Augé et al. (1998).
[d] Data previously published in Kubikova et al. (2001).
[e] Data previously published in Chapman and Augé (1994).

with their typically relatively high drought resistance in the field. *Nyssa* and *Liriodendron* had the most dehydration intolerant foliage of the woody species tested. *Pelargonium* and *I. wallerana* were the most dehydration intolerant herbaceous plants. *Nepeta* and *Hypericum* were the most dehydration tolerant herbs, with the semi-evergreen *Hypericum* having the lowest lethal leaf Ψ of all 30 species measured.

We recognize the limitations inherent in experiments attempting to compare species and ascertain absolute values that are independent of experimental conditions. Our approach was to grow plants under standard greenhouse and nursery conditions, with culture (fertilization, pre-stress irrigation, environmental conditions) designed to optimize plant health. Measurements were made on plants of a size typical for marketing conditions. The values listed in Table 2 would likely vary somewhat if the experiments were repeated under different conditions. For example, values for lethal leaf Ψ of different cultivars of *V. unguiculata* (cowpea) varied by about 0.25 MPa between two reports (Augé et al., 2001; Ludlow, 1989). Yet Table 2 gives us a fairly robust look at the comparative foliar dehydration of a variety of ornamental species representing a wide variety of taxa and habit.

When soil dries, plants in the ground can favor root growth, sending roots further and deeper into the soil profile to scavenge water. When constrained to limited soil volumes in pots, plant shoots have essentially two means of withstanding drought stress: retaining their water (dehydration avoidance), or enduring dehydration (dehydration tolerance). Our main objective was to begin to develop a quantitative gauge of the foliar dehydration tolerance of ornamental species. The ranking in Table 2 is not a ranking of drought resistance; plants with very sensitive stomata, for instance, may retain leaf water and survive for a very long time even if their symplasm is not tolerant of dessication (e.g. *Pelargonium*, Table 2; *V. unguiculata*, Ludlow, 1989). But, in concert with morphological and stomatal avoidance mechanisms, knowing the dehydration tolerance of ornamental species helps us understand the physiology underlying their relative drought resistance.

Acknowledgements

This research was supported by the Tennessee Agricultural Experiment Station, by the US Department of Agriculture under award no. 00-35100-9238, and by the Biological and Environmental Research Program (BER), US Department of Energy, through the Southeast Regional Center of the National Institute for Global Environmental Change (NIGEC) under cooperative agreement no. DE-FC03-90ER61010. We are grateful to Dr. Arnold Saxton for statistical advice.

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