Transpiration and Drought Stress Recovery of Three Zinnia Cultivars[1]

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Abstract

Transpiration and drought stress recovery were investigated in three container-grown zinnia cultivars [*Zinnia elegans* Jacq. ('Lilliput' and 'Thumbelina') and *Z. haageana* Reger ('Persian Carpet')] by measuring daily changes in the normalized transpiration ratio (NTR) of well-watered (control), water-stressed, and water-stressed/re-watered plants. Transpiration of plants grown in gradually drying substrate did not decline until the fraction of transpirable substrate water (FTSW) reached 0.16 to 0.12. Symptoms of plant-water stress (i.e. foliar wilt) were first observed on the leaves of 'Persian Carpet', which was also the cultivar with the highest average daily transpiration rate. By comparison, the remaining two cultivars ('Lilliput' and 'Thumbelina') exhibited lower average daily transpiration rates and took significantly longer to reach the same dry-down endpoint (NTR $\leq$0.15). Drought stress recovery was assessed by comparing xylem water potential and root and shoot dry weight in well-watered and in drought-stressed plants following a 7-day stress amelioration period. Xylem water potential of all three drought-stressed cultivars increased (i.e. became less negative) one week after re-watering. Root biomass and root:shoot ratio were both significantly greater in water-stressed plants than in well-watered plants of the same cultivar, a finding that suggests the likelihood of osmotic adjustment in response to drought.

Index words: normalized transpiration ratio, fraction of transpirable substrate water, foliar wilt, containerized horticultural crops.

Species used in this study: 'Lilliput' and 'Thumbelina' zinnia (*Zinnia elegans* Jacq.), 'Persian Carpet' zinnia (*Zinnia haageana* Reger).

Significance to the Horticulture Industry

Data from the current study illustrate differences in drought tolerance and drought stress recovery between container-grown zinnia species and between cultivars of the same species. Seedlings of *Zinnia haageana* 'Persian Carpet', seeded in plug trays and transplanted into marketable pots after 4 weeks, transpired at a faster rate and took significantly less time to reach a prescribed substrate dry-down endpoint than did similar seedlings of *Zinnia elegans* ('Lilliput' and 'Thumbelina'). Within the same species, the normalized transpiration ratio of both 'Lilliput' and 'Thumbelina', when plotted as a function of the fraction of transpirable substrate water (FTSW), showed that the decline in transpiration for 'Lilliput' occurred at a higher FTSW than for 'Thumbelina', indicating that the former cultivar is more water-conserving and better able to withstand drier substrate conditions. All three drought-stressed cultivars recovered well during the stress amelioration period, especially *Z. haageana* 'Persian Carpet', where xylem water potential decreased from -2.47 MPa to -0.54 MPa one week after re-watering. The data from this study suggest that plant-water efficiency in zinnia production can be improved by testing changes in the transpiration rate of different genotypes in response to substrate drying.

Introduction

Effective water management decisions are critical in the environmental and economic sustainability of nursery and greenhouse-grown crops (Southern Nursery Assn. 2013). With the advent of increasingly strict water-use regulations, higher water procurement costs, and limited groundwater resources, it is important for growers to minimize water use during the production cycle while, at the same time, maximizing plant water-use efficiency. Nowhere is this need more evident than in the production of high-value, container-grown horticultural crops, where a variety of species are grown and numerous production methods are employed, some of which require different irrigation regimes (Lea-Cox et al. 2013).

Most plants follow a predictable pattern in their response to progressively drying soil. Initially, the supply of moisture is sufficient to support plant growth and development, but gradually soil water becomes limited, resulting in stomatal closure, a rapid decline in transpiration, and a concomitant reduction in CO_2 assimilation. Studies with agronomic crops (Zaman-Allah et al. 2011, Belko et al. 2012, Gholipoor et al. 2010) have shown that the transpiration ratio of drying to well-watered plants, referred to as the normalized transpiration ratio (NTR), decreases in a two-phase response to substrate drying when expressed as a fraction of plant available water. In the first phase, drying plants transpire at the same rate as well-watered plants (NTR = 1.0), while in the second phase, NTR declines rapidly as the stomates close (Miller, 2000; Cathey et al. 2011). Previous studies have shown genetic variability among cereals and legumes in the fraction of transpirable substrate water (FTSW) at which soil moisture stress begins to influence transpiration (Vadez et al. 2014). While FTSW data can be found for many field-grown crops, similar information is limited for container-grown crops, yet could prove useful in developing plants with greater drought tolerance. Whereas previous studies have focused on the plant response to changes in preset irrigation schedules (i.e. changing the interval between

[1]Received for publication May 17, 2018; in revised form July 31, 2018. We thank Dr. William Cannon and Nathan Madonich for helpful reviews of this paper, and Gerald Nimis for advice on the experimental design and statistical analyses used in this investigation.

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irrigation events) (Roberts et al. 2017), in the present investigation we monitored the response of zinnia cultivars to progressively drying substrate, and irrigation was based on the transpiration status of each plant. The objectives of this study were: (1) to compare the time required for each cultivar to reach a prescribed substrate dry-down endpoint; (2) to determine the breakpoint at which the transpiration rate declined for drought-stressed versus well-watered plants of the same cultivar; and (3) to evaluate the recovery of drought-stressed cultivars following a 7-day stress-amelioration period.

Materials and Methods

Single seeds of *Zinnia elegans* Jacq., 'Lilliput' and 'Thumbelina', and *Zinnia haageana* Regel, 'Persian Carpet' (Livingston Seed Co., Columbus, OH) were sown into separate 50-cell plug trays filled with soilless substrate (Sunshine Mix #5) consisting of 80% peat and 20% fine perlite (Sun Gro Horticulture, Agawan, MA). After seeding, each tray was covered with plastic wrap and sub-irrigated with tap water to keep the substrate moist. The seeded trays were placed in a laboratory environment [20-22C (68-72F); 45-70% RH] beneath LED lights (160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation; 12 h photoperiod) and, after radicle emergence (one week), the plastic wrap was removed and the germinated seedlings allowed to grow for an additional three weeks under the same light source. During this time the seedlings were sub-irrigated weekly with a water-soluble fertilizer [20N-2.6P-18.3K (JR Peters, Inc., Allentown, PA)] at a N rate of 200 $mg \cdot L^{-1}$ (0.01 $oz \cdot 1.10\ qt^{-1}$). By the end of week 4 the seedlings had developed three pairs of true leaves and were ready for transplanting into marketable containers.

At the time of transplanting, 18 uniformly-sized seedlings of each cultivar were removed from the plug trays and replanted into square plastic pots [volume = 450 cm^3 (27.5 in^3). The base of each pot was fitted with nylon screen above which a 1.5 cm (0.6 in) layer of pea gravel was added to facilitate drainage. Each seedling was planted in soilless substrate (Sunshine Mix #5), and the substrate surface covered with a 0.5 cm (0.2 in) layer of white aquarium gravel, allowing substrate irrigation while curtailing surface evaporation. The transplants were placed back beneath the LED lights and allowed to become established over a 10-day period during which they were hand-watered daily and sub-irrigated once with the same water-soluble fertilizer used previously. The day prior to the start of the study, all 54 seedlings were thoroughly watered to the point at which water drained freely from the bottom of each pot. The following day, after drainage had ceased, each pot was weighed to obtain the drained substrate water capacity. At this time, a 9 cm^2 (3.5 in^2) plastic petri dish was placed beneath each pot as a precautionary measure to collect any excess substrate drainage; however no drainage was observed during the course of the experiment.

The study consisted of three randomly-assigned treatments [a well-watered (control) treatment, and two drought stress treatments], replicated six times for each of the three zinnia cultivars, for a total of 54 plants. Each of the 54 pots was weighed every day at 1500 h to determine transpiration (Ts) over the previous 24 h period. The control plants were kept well-watered by returning the daily pot weight to a value no less than 85% of each pot's original drained pot capacity, thereby preventing the substrate from becoming over-saturated while still providing adequate substrate moisture. Re-watering was accomplished by adding water back to each pot using a plastic squeeze bottle, applying the water directly to the gravel surface while the pot was still on the balance. For drought stress-treated plants, the substrate was allowed to dry-down gradually by adding back only enough water, if necessary, to return the daily pot weight to a maximum of 17 g (0.60 oz) below the net pot weight of the previous day. The 17 g represents the average daily Ts rate for all 54 seedlings prior to the start of the dry-down period. Again, re-watering, when required, was accomplished as previously described. Moisture status of the drought stress treatments was monitored daily by dividing the Ts loss of each dry-down plant by the mean Ts loss of all six well-watered (control) plants from the same cultivar (i.e. Ts ratio). To account for differences in plant size, the Ts ratio was further divided by the average Ts rate of the same plants under well-watered conditions (i.e. Ts during the first 2-4 days of the study when all plants had adequate substrate moisture). This final calculation, referred to as the normalized transpiration ratio (NTR), resulted in a value centered on 1.0 for drought stress-designated plants during the initial stages of the dry-down cycle (Cathey et al. 2011).

In the present study, the substrate in drought-stressed pots was allowed to dry-down until the plants showed signs of severe foliar wilt. This occurred at an NTR of ≤ 0.15, which was then defined as the dry-down endpoint for this experiment. Upon reaching the endpoint, each pot was re-weighed to obtain the final pot weight, and this value used to calculate the daily fraction of transpirable substrate water (FTSW) (Miller 2000). At the dry-down endpoint, half of the drought-stressed plants from each cultivar were immediately harvested, while the remaining half were re-watered back to their original starting weight (85% of drained pot capacity) and maintained at this moisture threshold for seven days before harvesting. Well-watered (control) plants were harvested at the end of the study period. At harvest, the following measurements were recorded for each plant: height, two-dimensional crown width, xylem water potential (Ψ_x) measured using the pressure chamber technique (Scholander et al. 1965), leaf area, shoot and root dry weight. From these measurements, growth index [GI; height + two-dimensional crown width / 3; (Monterusso et al. 2005)], transpiration efficiency (TE; total biomass per liter of water transpired), and root:shoot ratio were calculated. The experiment was designed as a 3 by 3 factorial with three stress treatments and three cultivars, each with six replications. A model for the experimental design was fit and analyzed using statistical software [*Statistix 10* (Analytical Software, Tallahassee, FL)], and differences between treatment means were compared using Tukey's pairwise comparison test, $P \leq 0.05$. A plot of NTR as a function of FTSW for each cultivar was made using segmented linear regression

Table 1. **Transpiration (Ts), Ts efficiency and number of days to reach the dry-down endpoint for three zinnia cultivars subjected to drought stress based on the normalized transpiration ratio of drying to well-watered substrate[z].**

Cultivar	Treatment[y]	Total Ts (g)	Ts rate ($g \cdot cm^2 \cdot d^{-1}$)	Ts efficiency ($g \cdot L^{-1}$)	Days to dry-down endpoint
Lilliput	WW	551.0	0.071	3.26	—
	DS	215.3	0.122	6.35	12.5
	DS+RW	303.3	0.060	3.43	13.8
Persian Carpet	WW	632.8	0.101	2.95	—
	DS	238.5	0.183	5.60	11.2
	DS+RW	305.8	0.086	3.11	13.0
Thumbelina	WW	490.7	0.053	3.84	—
	DS	235.7	0.112	5.75	12.8
	DS+RW	292.7	0.068	2.55	14.2
F-test probabilities:					
	Cultivar (CV)	***	***	***	NS
	Treatment (T)	***	***	***	***
	CV x T	***	*	NS	NS

[z]Each value represents the mean of six replications. NS, nonsignificant; *, ***, significant at $P \leq 0.05$ and $P \leq 0.001$, respectively (Tukey).

[y]WW (well-watered; control) - substrate maintained at 85% of drained pot capacity (DPC), plants harvested at end of study; DS (drought-stressed) - substrate dried to ≤0.15 endpoint, plants harvested immediately; DS+RW (drought-stressed/re-watered) - substrate dried to ≤0.15 endpoint, substrate re-watered and maintained at 85% DPC for 7 days prior to plant harvest.

analysis [R statistical program (version 3.4.0) with the 'segmented' package (R Core Team 2017, Muggeo 2003, Muggeo 2008)]. For simplicity and ease of discussion, the treatments used in this investigation will henceforth be designated as follows: well-watered (WW) plants; drought-stressed (DS) plants; drought-stressed/re-watered (DS+RW) plants.

Results and Discussion

Transpiration. Data collected on the quantity of water extracted from the substrate by the three zinnia cultivars used in this study (total Ts) show the presence of a significant cultivar by treatment interaction (Table 1). Here, the total Ts of WW 'Persian Carpet' seedlings (632.8 g) was significantly greater than it was for any of the other cultivar by treatment combinations. As expected, total Ts was always significantly greater for WW plants than for water-stressed plants (either DS or DS+RW treatments) of the same cultivar. For DS+RW seedlings, total Ts showed a consistent trend that was generally higher for seedlings of the same cultivar that were not re-watered (DS treatment). Looking at the rate of water loss expressed as the quantity of water transpired per unit leaf area per day, the data again reveal a significant cultivar by treatment interaction (Table 1). In this instance, the Ts rate of DS-treated 'Persian Carpet' was significantly greater than the Ts rate for any of the other cultivar by treatment combinations. Averaged across all treatments, the Ts rate of 'Persian Carpet' was 46% greater than 'Lilliput' and 58% greater than 'Thumbelina'. Among all three cultivars, Ts rate was significantly higher for DS-treated plants than for either DS+RW-treated or WW plants.

Transpiration data from the present study indicate that, of the three zinnia cultivars investigated, 'Persian Carpet' should be the most drought susceptible based on greater total Ts and a higher daily Ts rate under drought stress conditions. The remaining cultivars ('Lilliput' and 'Thumbelina') both exhibited lower total Ts values and lower Ts rates, making it likely that either of these cultivars would better tolerate drought stress conditions. The cultivar differences in Ts noted here are reflected in the average length of time it took for DS-treated seedlings to reach the NTR dry-down endpoint (≤0.15). For 'Persian Carpet' the endpoint was reached after 11.2 days, while for 'Lilliput' and 'Thumbelina' the endpoint was attained after 12.5 and 12.8 days, respectively (Table 1). A longer time to reach the endpoint suggests a lower rate of water use. The length of the dry-down periods recorded for zinnia in the present study are in general agreement with those reported for other plant species (Cathey et al. 2011, Miller 2000).

Transpiration efficiency (TE), the ratio of biomass produced per liter of water transpired, is considered an important trait for determining drought tolerance (Stokes et al. 2016, Vadez and Ratnakumar 2016). In the current study, no significant TE differences were found between zinnia cultivars, but there was a significant treatment effect (Table 1). In this case, cultivars grown in substrate gradually dried-down to the ≤0.15 endpoint (DS treatment) exhibited TE values significantly higher than those for WW plants of the same cultivar or for those that were re-watered after exposure to drought and allowed to recover (DS+RW treatment). These results are similar to those reported by Changhai et al. (2010), who found that drought-stressed wheat plants exhibited a higher TE than non-stressed plants, a finding attributed to differential changes in stomatal conductance under drought-stressed and well-watered conditions.

A plot of NTR as a function of FTSW during a typical dry-down cycle is shown for each of the three zinnia cultivars used in this investigation (Fig. 1). The two-segmented response curves seen here appear to accurately describe the FTSW relationship for each cultivar as indicated by the r^2 values, which ranged from 0.849 for 'Thumbelina' to 0.984 for 'Lilliput'. The FTSW at which NTR begins to decline indicates the breakpoint for stomatal closure, and plants that close their stomates at higher FTSW values normally take longer to reach the dry-down endpoint (Miller 2000). In the current study, NTR break-points were calculated at FTSW values ranging from 0.12

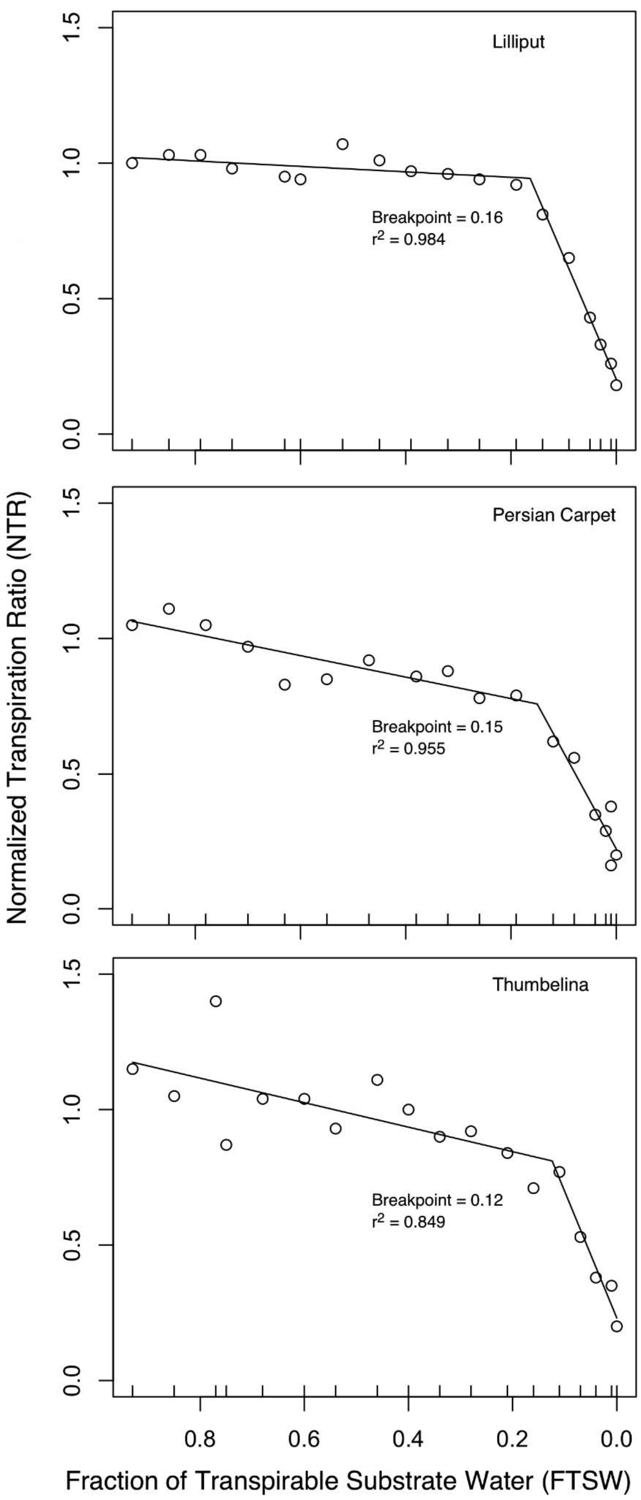

Fig. 1. The normalized transpiration ratio (NTR) of three zinnia cultivars plotted as a function of the fraction of transpirable substrate water (FTSW) during a typical dry-down cycle with an NTR endpoint of 0.15. Breakpoint is defined here as the FTSW at which NTR begins to decline as a result of substrate dry-down.

('Thumbelina') to 0.16 ('Lilliput') (Fig.1). These values are somewhat lower than those reported for other plant species (Johnson et al. 2009), and could be the result of a higher water retention rate for the soilless substrate used in this study. Since a lower breakpoint indicates the potential for extracting more substrate water prior to stomatal closure, a lower threshold could be beneficial under moderate drought conditions. However, under severe stress, a higher breakpoint would result in stomatal closure early in the dry-down cycle, thereby ensuring water conservation and enhancing the chances for survival (Ray and Sinclair 1997, Miller 2000). Thus, in the present investigation, 'Thumbelina' should best survive moderate water stress conditions, while 'Lilliput' should have a better chance of tolerating prolonged periods of drought.

Table 2. Growth and xylem water potential of three zinnia cultivars subjected to drought stress based on the normalized transpiration ratio of drying to well-watered substrate[z].

Cultivar	Treatment[y]	Leaf area (cm^2)	Shoot dry wt. (g)	Root dry wt. (g)	Water potential (MPa)
Lilliput	WW	289.3	1.43	0.38	−0.42
	DS	146.8	0.91	0.66	−1.57
	DS+RW	253.6	1.01	0.33	−0.53
Persian Carpet	WW	225.8	1.52	0.34	−0.52
	DS	118.5	1.00	0.48	−2.47
	S+RW	179.7	0.99	0.29	−0.54
Thumbelina	WW	335.7	1.57	0.31	−0.43
	DS	168.9	0.90	0.53	−2.03
	DS+RW	216.4	0.75	0.08	−0.61
F-test probabilities:					
	Cultivar (CV)	***	NS	**	*
	Treatment (T)	***	***	***	***
	CV x T	*	NS	NS	NS

[z]Each value represents the mean of six replications. NS, nonsignificant; *, **, ***, significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively (Tukey).

[y]WW (well-watered; control) - substrate maintained at 85% drained pot capacity (DPC), plants harvested at end of study; DS (drought-stressed) - substrate dried to ≤0.15 endpoint, plants harvested immediately; DS+RW (drought-stressed/re-watered) - substrate dried to ≤0.15 endpoint, substrate re-watered and maintained at 85% DPC for 7 days prior to plant harvest.

Drought recovery. The degree to which the zinnia cultivars were able to recover from drought stress was determined by a series of growth measurements taken at harvest (Table 2). These data show that leaf area was greater in WW plants than in DS plants of the same cultivar. Leaf area of DS+RW plants was significantly greater than for similar plants of the same cultivar that were not re-watered (DS treatment). Leaf growth recovery was particularly prominent in seedlings of 'Lilliput', where leaf area for DS+RW plants (253.6 cm^2) was only 14% lower than the leaf area of WW controls (Table 2). The impact of drought stress on leaf area is well documented (Jones 1992), and FTSW readings of <0.40 have been shown to reduce both leaf area and stem elongation in turfgrass (Masinde et al. 2005). Research by Salih et al. (1999) has shown that, under conditions of limited soil moisture, water absorption is largely dependent on leaf area. Ts data from the present investigation indicate that 'Lilliput', with more total leaf area and an ability to recover quickly after re-watering, should better tolerate lower soil moisture conditions than 'Persian Carpet'. This supposition is borne out by the number of days required for each of these drought-stressed cultivars to reach the dry-down endpoint which, as indicated earlier (Table 1), was 11.2 days for 'Persian Carpet' and 12.5 days for 'Lilliput'.

While no significant differences in shoot dry weight were observed between the three zinnia cultivars included in this study, shoot biomass was always greater in WW plants than in drought-stressed plants of the same cultivar (Table 2). For roots, dry weight was greater in 'Lilliput' than in 'Thumbelina', and consistently greater in DS-treated seedlings than in either WW seedlings or in seedlings of the same cultivar that were re-watered following drought (DS+RW treatment) (Table 2). These results can be explained based on the differential response of roots and shoots to drought stress (Franco et al. 2008). In root tissue, when plant-water potential becomes more negative because of drought, osmotic adjustment occurs quite rapidly, thereby allowing the roots to regain at least partial turgor and resume growth. In shoot tissue, on the other hand, osmotic adjustment under drought conditions occurs much slower, and the wall "loosening" ability of plant cells may actually decrease, causing shoot growth inhibition (Hsiao and Xu 2000). Since root growth is normally less affected by drought than shoot growth, an increase in the root:shoot ratio of drought-stressed plants is frequently observed. This was the case in the present study where, for each cultivar tested, root:shoot ratio was consistently higher in drought-stressed plants (DS and DS+RW treatments) than in WW plants.

Xylem water potential, Ψ_x, a measure of the magnitude of plant-water stress, was determined for each plant at the time of harvest (Table 2). The data show that the average Ψ_x for drought-stressed zinnia cultivars grown in drying substrate ranged from -1.57 MPa for 'Lilliput' to -2.47 MPa for 'Persian Carpet'. Signs of foliar wilt began to appear first on the foliage of drought-stressed 'Persian Carpet' followed later by similar symptoms on the leaves of drought-stressed 'Lilliput' and 'Thumbelina'. Within two weeks after beginning the dry-down cycle, depending on cultivar, the leaves on all plants had lost turgor and were severely wilted, some even showing marginal necrosis. Of the three zinnia cultivars investigated, 'Persian Carpet' was the most sensitive to drought based on the first appearance of foliar wilt symptoms, the number of days to reach the dry-down endpoint, and the degree of plant-water stress (Ψ_x) at harvest. However, the recovery exhibited by DS+RW plants of all three cultivars during the stress amelioration period suggests a certain robustness amongst the cultivars investigated in this study. Despite being subjected to severe drought-stress conditions, Ψ_x improved 66% for 'Lilliput', 70% for 'Thumbelina', and 78% for 'Persian Carpet' after the 7-day stress recovery period, and the final Ψ_x readings for DS+RW-treated plants were not significantly different than those for well-watered plants of the same cultivar (Table 2).

In summary, data from these experiments indicate important differences between certain cultivars of *Z. haageana* and *Z. elegans* in their response to gradual substrate dry-down. Drought stressed seedlings of *Z. haageana* 'Persian Carpet' exhibited a faster rate of water loss and took less time to reach the substrate dry-down endpoint than did *Z. elegans* ('Lilliput' or 'Thumbelina'). Even within the same species, differences in the Ts breakpoint were observed between 'Lilliput' (breakpoint = 0.16) and 'Thumbelina' (breakpoint = 0.12). In terms of drought recovery, all three cultivars recovered well, with no measureable differences between species or between cultivars of the same species. And, despite the presence of some residual leaf damage, the water potential of all three drought-stressed cultivars improved substantially by the end of the 7-day stress amelioration period. The findings of this investigation suggest possible options for improving plant-water efficiency in zinnia production by testing and selecting cultivars with lower rates of water use and/or cultivars with faster recovery rates during stress amelioration.

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