

Influence of Spring and Fall Drought Stresses on Growth and Gas Exchange during Stress and Posttransplant of Container-grown *Magnolia ×soulangiana* ‘Jane’

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ABSTRACT. Responses of *Magnolia ×soulangiana* (Soul.-Bod.) ‘Jane’ (‘Jane’ saucer magnolia) to consecutive short term pretransplant drought stresses and recovery after transplanting were evaluated beginning October 1997 and June 1998. Plants were subjected to one (mild) or two (moderate) 3-day drought stress periods or a two 3-day and one 4-day (severe) drought stress period, each separated by two rewatering periods over 24 hours. One day after each stress period, plants were transplanted into the field and well watered to monitor recovery from stress. Plant response was determined by measuring whole-plant CO₂ assimilation, leaf gas exchange (CO₂ assimilation, transpiration, stomatal conductance) and canopy growth throughout stress and recovery periods. Whole-plant and leaf CO₂ assimilation were lower for the stressed treatments for most of the measurements taken during stress in the fall and spring. After release from stress and transplanting, leaf CO₂ assimilation returned to control levels for mild and moderate fall stresses within 2 to 3 d by the next measurement, while it was over 3 weeks until recovery from the severe stress. There was no difference in leaf gas exchange following release from stress and transplanting during the spring stress. More rapid defoliation occurred for the severe fall-stressed plants compared to the controls after release from stress in the fall. Flower number was reduced in spring for the fall-stressed plants. At termination of the experiment, the growth index was lower for severe fall-stressed plants but there were no differences for other fall stress treatments. There was no increase in growth for control or stressed plants for the spring experiment.

There are many circumstances where container plants can be subjected to water stress between production and establishment in the landscape. Container substrates are designed to be well drained and container nurseries frequently irrigate daily to runoff resulting in plants acclimated to well watered conditions. The time involved in shipping as well as delays, and inadequate watering by retailers, landscapers, and homeowners while holding plants before planting can result in drought stress. Frequently in these situations, plants are not watered unless they manifest symptoms of water stress even though plants may be under physiological stress prior to visible symptoms.

Several studies have shown that reducing water stress in the interim between nursery production and planting improves performance and survival of bare-root nursery trees (Englert et al., 1993; Gebre and Kuhns, 1993; Insley and Buckley, 1985; Kozlowski and Davies, 1975; Lefevre et al., 1991). However, there is little information regarding the impact of water stress during the postproduction pretransplant interim on transplant performance of container nursery plants. Harris and Bassuk (1995) found a single drought episode prior to transplanting reduced posttransplant trunk growth but had no effect on plant height, dry weight, or photosynthesis of container plants.

Drought stress has been shown to reduce leaf CO₂ assimilation for many woody species (Abrams et al., 1990; Fernandez et al., 1997; Harris and Gilman, 1993; Ni and Pallardy, 1991; Quick et al., 1992). Photosynthesis is essential for plant growth as the primary source of carbohydrate production and carbon for organic molecules. Leaf growth and canopy development result in production of photosynthesizing tissue and affect interception of light which in turn affects growth; thus, there is an interrelationship between growth and whole plant photosynthesis. Reductions in photosynthesis can have a lasting impact on plant performance.

Trees are transplanted at two major times of year, fall and spring. ‘Jane’ saucer magnolia (*Magnolia ×soulangiana*) is a popular spring flowering, small deciduous tree. Purchasing and planting of spring flowering trees and shrubs is driven by the presence of flowers even though it may not be the best time of year for planting of a particular species (Harris and Bassuk, 1994). The objectives of this study were to determine the effects of increasing degrees of postproduction, pretransplant drought stress on plant growth and photosynthetic response during these periods, and to determine effects on growth, photosynthetic response and flowering of ‘Jane’ saucer magnolia after subsequent field planting.

Materials and Methods

Sixty ‘Jane’ saucer magnolias in 19-L containers were received from a wholesale nursery in Aug. 1997 and Mar. 1998. Container substrate was a 4 pine bark fines : 1 river sand (by volume) amended with pelletized dolomitic limestone at a rate of 6 kg·m⁻³. The 48 most uniform plants received in August and March were selected for use in an Oct. 1997 (fall) study and a repeat of the study in June 1998 (spring), respectively. The experiments were conducted at the South Carolina Botanical Garden, Clemson Univ., Clemson, S.C., in an outdoor container nursery area. Two weeks before imposition of

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treatments, plants were fertilized to runoff with a 20N–8.6P–16.6K water-soluble fertilizer (Scotts-Sierra, Marysville, Ohio) at an N rate of 250 mg·L⁻¹.

Beginning on 4 Oct. 1997 and 1 June 1998 (day 1), the magnolias were subjected to a one (mild) or two (moderate) 3-d drought stress period or a two 3-d and one 4-d (severe) drought stress period. Each stress period was separated by two irrigation periods over 24 h, when drought stressed plants were watered to runoff. Control plants were watered to runoff daily. Plants were watered at 1500 HR and all measurements were taken prior to irrigating each day. Rain water was excluded from all plants by covering individual containers with R3 residential sheathing insulation (extruded polystyrene, Dow Chem. Co., Midland, Mich.) sealed with duct tape. Since the magnolias were multitrunk, a collar was made of 10 cm diameter polyvinyl chloride pipe (PVC) cut ≈10 cm in length, split in half, secured around the base of the trunks and filled with polyurethane foam (polymeric diisocyanate and polyols mixture, Great Stuff, Flexible Products Co., Joliet, Ill.) to form a seal for the sheathing. Eight replicates of control and stress treatments were used for each drought stress interval to provide comparisons after transplanting at different dates. Following release from each stress interval, eight control and eight drought stressed plants were field planted, watered at 2.5 cm·d⁻¹ and monitored for recovery. Soil type was a Cecil sandy loam (clayey, kaolinitic, thermic Typic Kanhapludults). A completely randomized design with a 1 × 1-m spacing was used for both the container and field plots.

Volumetric substrate moisture content (SMC) was measured at least every second day during stress using a θ -probe type ML1 (Delta-T Devices, Cambridge, United Kingdom) set on the organic soil moisture setting. The θ -probe gives an integrated measure of SMC over a volume with a 6 cm length and 2 cm diameter (19 cm³). Measurements were taken at the substrate surface vertically downward and horizontally at access holes cut in the middle of the containers (10 cm below container rim) and the bottom (20 cm below container rim). Access holes were sealed between measurements by taping the excised portion of the containers back in place.

Whole-plant CO₂ assimilation (WPA) was measured with an infrared gas analyzer (IRGA) (CIRAS-1; PP Systems, Haverhill, Mass.) during stress using a system modified from Corelli-Grappadelli and Magnanini (1993) and Miller et al. (1996). Sheets of Mylar M-30 film (polyethylene terephthalate, polyvinylidene chloride coated, DuPont, Wilmington, Del.) were used to form chambers to fit over the plants leaving minimum excess room along the sides to increase turbulent air mixing. Mylar was chosen due to its high light transmission and low permeability to CO₂, H₂O, and O₂ (Miller et al., 1996; Pauly, 1989). The mylar chambers were secured with tent zippers (Outdoor Wilderness Fabrics, Inc., Nampa, Ind.) to R3 residential sheathing insulation cut to fit over the top of the container and around the PVC collar. Air flow was provided to eight chambers at once by a squirrel-cage blower (model 4C592; Dayton Electric Manufacturing Co., Chicago, Ill.) connected to 10 cm diameter PVC schedule 40 pipe with 45° angle “Y” branches and 90° elbows to each chamber. The air outlet was provided where the mylar sheets were joined together around a 7 cm diameter plastic ring taped to form an opening at the top of the chambers. The IRGA was used to measure the CO₂ differential (Δ CO₂ in mL·L⁻¹) between ambient air and air inside the mylar chambers near the air outlet. Measurements were taken on days with irradiance >1000 mmol·m⁻²·s⁻¹ from 1000 to 1230 HR as often as possible during stress. Measurements were taken only on control and severe stressed plants since there were no differences in treatment for severe, mild, and moderate stressed plants during stress. The 16 plants were measured

eight at a time in random order. Air flow through the chambers was determined by averaging the air flow from three locations across the diameter of the outlet using a thermal anemometer (model 37000-00; Cole-Parmer, Chicago, Ill.). Air flow was converted to air volume and whole-plant CO₂ assimilation was calculated as described by Miller et al. (1996). The thermal anemometer also was equipped with a thermocouple. Changes in air temperature can affect WPA, so air temperature inside versus outside the mylar chambers was monitored with the thermal anemometer.

Leaf gas exchange [CO₂ assimilation (A), transpiration (E), and stomatal conductance (g_s)] was measured on the same days as WPA during stress periods and for 33 d after transplanting in both fall and spring. Measurements of leaf gas exchange were taken using the same IRGA connected to a Parkinson broad-leaf chamber (CIRAS-1 Parkinson leaf cuvette, PP Systems, Haverhill, Mass.) on one recently mature, fully expanded leaf per plant. Leaf gas exchange measurements took ≈20 min per group of 16 plants and were begun following WPA measurements during stress, at ≈1300 HR, or beginning at 1100 HR after the end of all stress treatments. Leaf gas exchange was measured during stress only of the control and severe stressed plants since there were no differences in treatment for severe, mild and moderate stressed plants during stress. All plants were measured during recovery after transplanting.

For the fall stress, three growing shoots per plant were marked ≈5 cm below the apex at the beginning of stress and shoot growth was measured from this mark to the apex on 1, 2, 6, 10, and 16 d after imposition of the fall stress (DAFS). Plant height and width were measured for the spring stress on 0, 2, 6, 14, 21, 28, 36, 88, and 160 d (4 Feb. 1999, plants dormant) after the first spring stress (DASS) to monitor recovery. Plant height and width were measured 226 (prior to spring growth), 261, 285, 328, and 488 (4 Feb. 1999, plants dormant) DAFS to determine effects of stress from the previous season on transplant growth. Growth index was calculated from height and width measurements as (height + width)/2. Leaf number was monitored from the end of stress treatment until total defoliation for the fall stress. Flower number was determined for fall-stressed plants in Spring 1998.

Data were subjected to analysis of variance using the PROC ANOVA procedure of SAS (SAS Inst., Inc., Cary, N.C.). Mean separation was by t test and Tukey's studentized range test (HSD). Regression analysis was conducted using the PROC GLM procedure of SAS.

Results and Discussion

Substrate moisture content was lower for the stress treatments than controls by 3 DAFS for all container locations measured (Fig. 1). Substrate moisture content remained lower throughout the remainder of the stress even after rewatering between stress periods. Substrate moisture content within a treatment was lower in the top of containers (Fig. 1A) than in the middle for the first two measurements (Fig. 1B) and the bottom for most sampling times (Fig. 1C). There was a linear decrease in SMC over days during drought treatments in the fall (Fig. 1) but not spring (Fig. 2). Substrate moisture content decreased most rapidly for fall-stressed plants in the bottom of containers followed by the middle and then the top. All portions of the containers were at a similar level by the end of the severe stress. Lower SMC was found in spring-stressed plants at the bottom of the container starting 1 DASS (Fig. 2C). Substrate moisture content remained lower for stress treatments from 3 DASS throughout the stress periods for all measurement locations (Fig. 2) except 5 DASS for the bottom of the container. Irrigation between

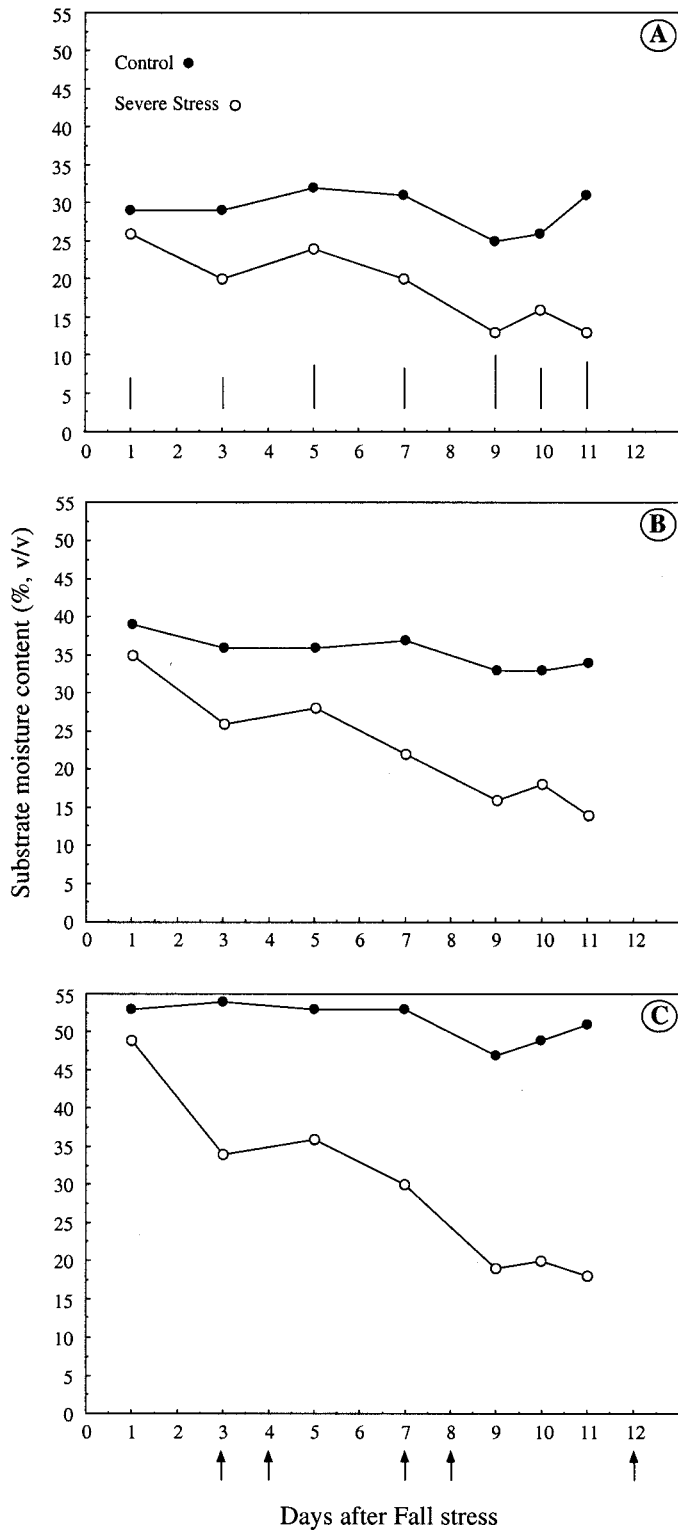


Fig. 1. Substrate moisture content during the fall stress (day 1, 4 Oct 1997) for control and severe stress. Measurements were taken at (A) the container surface, and at access holes (B) 10 cm and (C) 20 cm below the container rim. Arrows indicate days irrigation was applied to stressed plants between drought periods. Controls were watered daily. Vertical bars in A represent Tukey's HSD at $P \leq 0.05$ for comparisons of all means for each date. Regression analysis was conducted on all data for each treatment ($n = 56$). Regression was significant only for drought treatments, equations: $y = -1.37x + 31.20, R^2 = 0.57$; $y = -2.28x + 42.72, R^2 = 0.67$; $y = -3.22x + 58.27, R^2 = 0.64$, for A, B, and C, respectively. All R^2 were significant at $P \leq 0.001$.

stress periods seemed only to slow drying of the substrate during fall stress rather than replenishing water back to control levels. During spring, irrigation of drought treatments between stresses was more effective in replenishing SMC but still not sufficient to return to

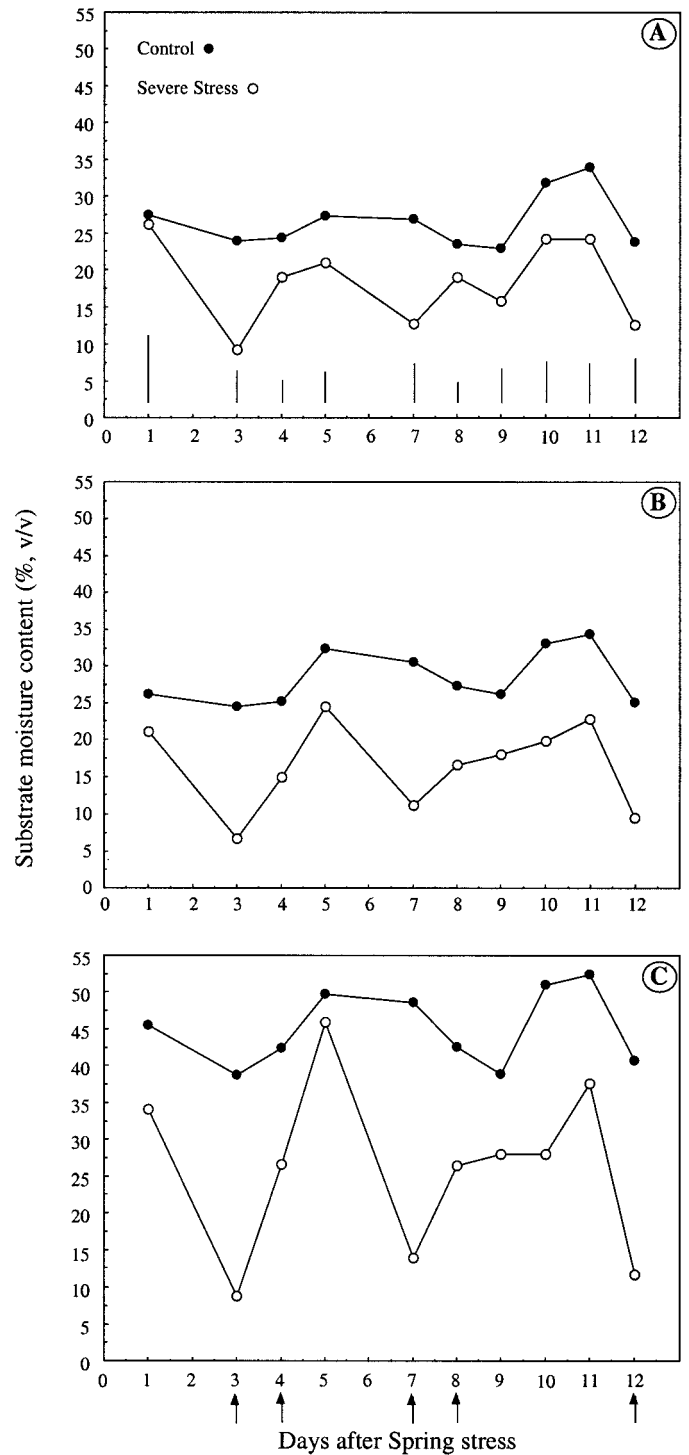


Fig. 2. Substrate moisture content during the spring stress (day 1, 1 June 1998) for control and severe stress. Measurements were taken at (A) the container surface, and at access holes (B) 10 cm and (C) 20 cm below the container rim. Arrows indicate days irrigation was applied to stressed plants between drought periods. Controls were watered daily. Vertical bars in (A) represent Tukey's HSD at $P \leq 0.05$ for comparisons of all means for each date. Regression analysis was conducted on all data for each treatment ($n = 56$) but was not significant for any treatment.

control levels. The response of SMC to drought treatments is reflective of the difficulty of rewetting substrates based on pine bark (Airhart et al., 1978; Regulski, 1984), which becomes more difficult after each additional drought period. The apparent lag in SMC response of drought treatments to watering is because SMC was measured in the morning prior to irrigation, therefore, the response to irrigation does not appear until the following day. There was a rise in SMC during the third stress period in the spring on 10 and 11 DASS likely due to rain leaking in on those dates. However, the SMC of drought treatments was still much lower than controls.

Substantial reductions in WPA were found in water-stressed plants for most sampling dates over the 12 d of the stress treatments (Fig. 3). Whole-plant CO₂ assimilation was lower for drought stressed versus control plants for all sampling dates during fall except 6 DAFS (Fig. 3A), and spring except 11 DASS (Fig. 3B). The exception on 6 DAFS may have been due to the lag in response to watering and on 11 DASS to the rainfall that leaked in. There was no difference in air temperature during WPA measurements between the inside and outside of the mylar chambers for fall or spring except on 7 DASS (Fig. 4), with no difference due to treatment (data not presented). Whole-plant CO₂ assimilation was found to be affected quickly by drought stress in this study as well as a previous study by Percival et al. (1998). This may be because WPA integrates

several factors such as differences in shoot extension, leaf area, chlorophyll fluorescence, and stomatal conductance which may not show responses to drought individually (Fernandez et al., 1997).

In fall-stressed plants, leaf gas exchange and stomatal conductance were lower than controls by 3 DAFS and remained lower except on 5 DAFS for E and g_s (Fig. 5). There were no differences in leaf gas exchange between control and mild or moderate fall-stressed plants after transplanting (data not presented). However, leaf gas exchange of severe fall-stressed plants remained lower than controls after transplanting until 31 DAFS, reflecting 19 d of adequate moisture (Fig. 5). The large decrease in A (Fig. 5A) for both treatments on day 45 (Nov. 14) was most likely due to fall dormancy.

Leaf gas exchange was lower on only 3 DASS during the spring for stressed versus control plants (Fig. 6). Response of mild and moderate stress was similar to severe stress, therefore, only the severe stress is shown. The low rates of A following transplanting regardless of treatment, including 2 d with negative A (respiratory loss of carbon), indicate plants were suffering from transplant shock.

In addition to lower A, there were substantially fewer leaves on severe stressed plants from 16 DAFS onwards (Table 1). There were also fewer leaves 31 DAFS for mild stressed plants but no differ-

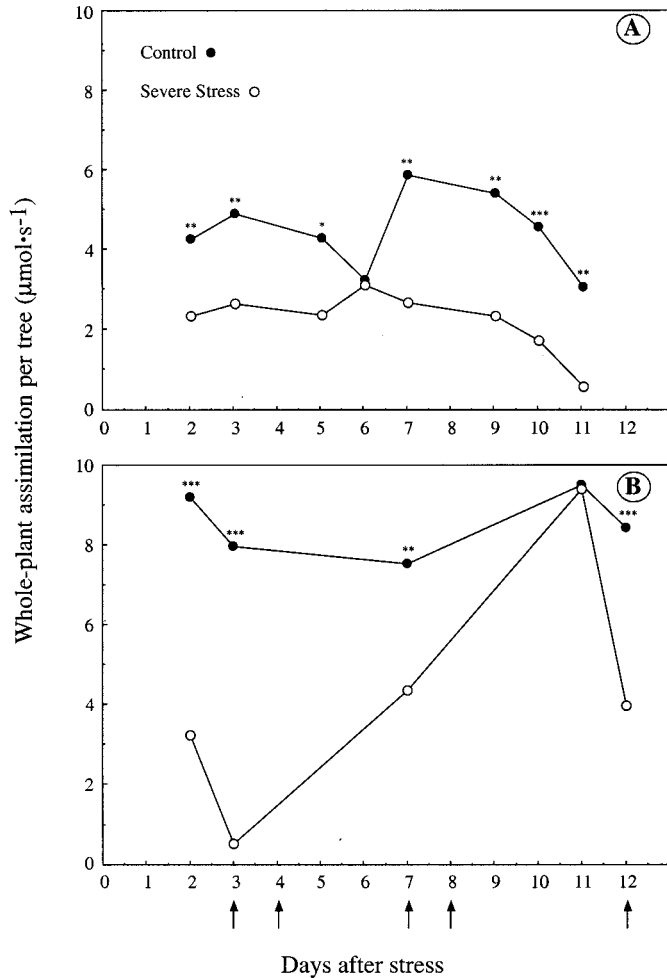


Fig. 3. Whole-plant CO₂ assimilation during stress periods for (A) the fall stress (day 1, 4 Oct. 1997) and (B) the spring stress (day 1, 1 June 1998) for control and severe stress (n = 8). Arrows indicate days irrigation was applied to stressed plants between drought periods. Controls were watered daily. ***, **, *Significantly different at *P* = 0.05, 0.01, or 0.001, respectively, by *t* test (unpaired).

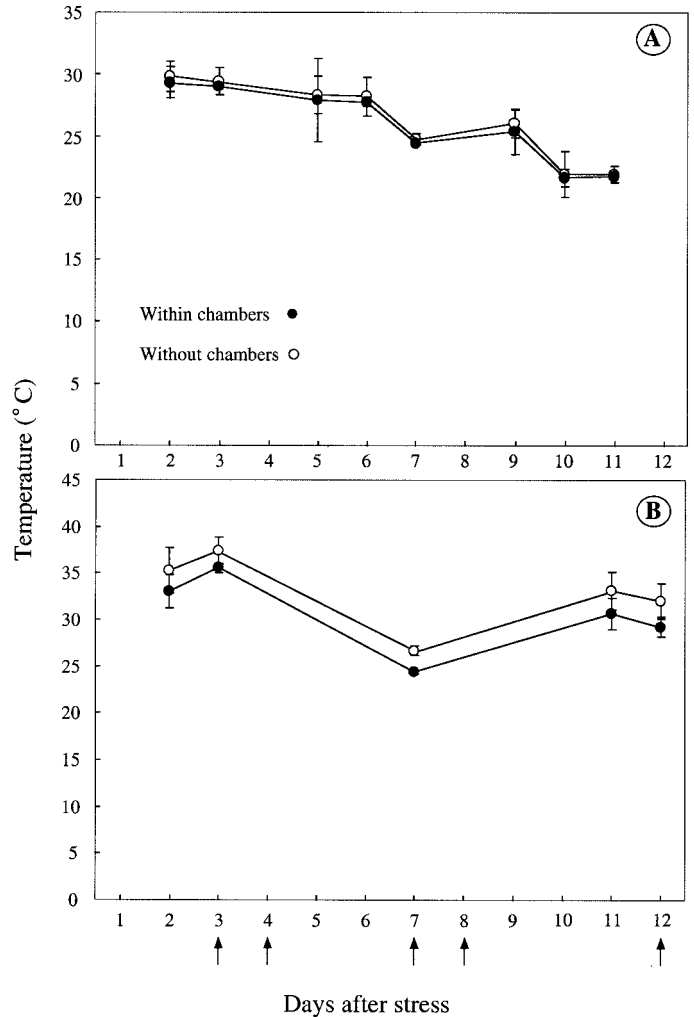


Fig. 4. Air temperature (\pm SD) (n = 8) during whole-plant CO₂ assimilation measurements within and without whole-plant chambers for (A) the fall stress (day 1, 4 Oct. 1997) and (B) the spring stress (day 1, 1 June 1998).

ences on other days. There was no loss of leaves observed during the spring stress (data not presented). Reduction in leaf number has been proposed as a mechanism of stress avoidance by Struve and Joly (1992), who found a reduction in leaf number of red oak (*Quercus rubra* L.) but no change in A. However, in this study the large reduction in the number of leaves for the severe stressed plants

occurred simultaneously with lower A. Fewer leaves result in less photosynthetic area, which, in turn, would result in substantial reductions in WPA. Whole-plant CO₂ assimilation would be lower for severe stressed plants versus controls through 29 DAFS based on the recorded reductions in leaf number and A.

Transpiration decreased throughout the remainder of the fall sampling period after release from stress for both control and severe stressed plants while g_s and A exhibited a pattern similar to prestress measurements (Fig. 5). However, differences in E between control

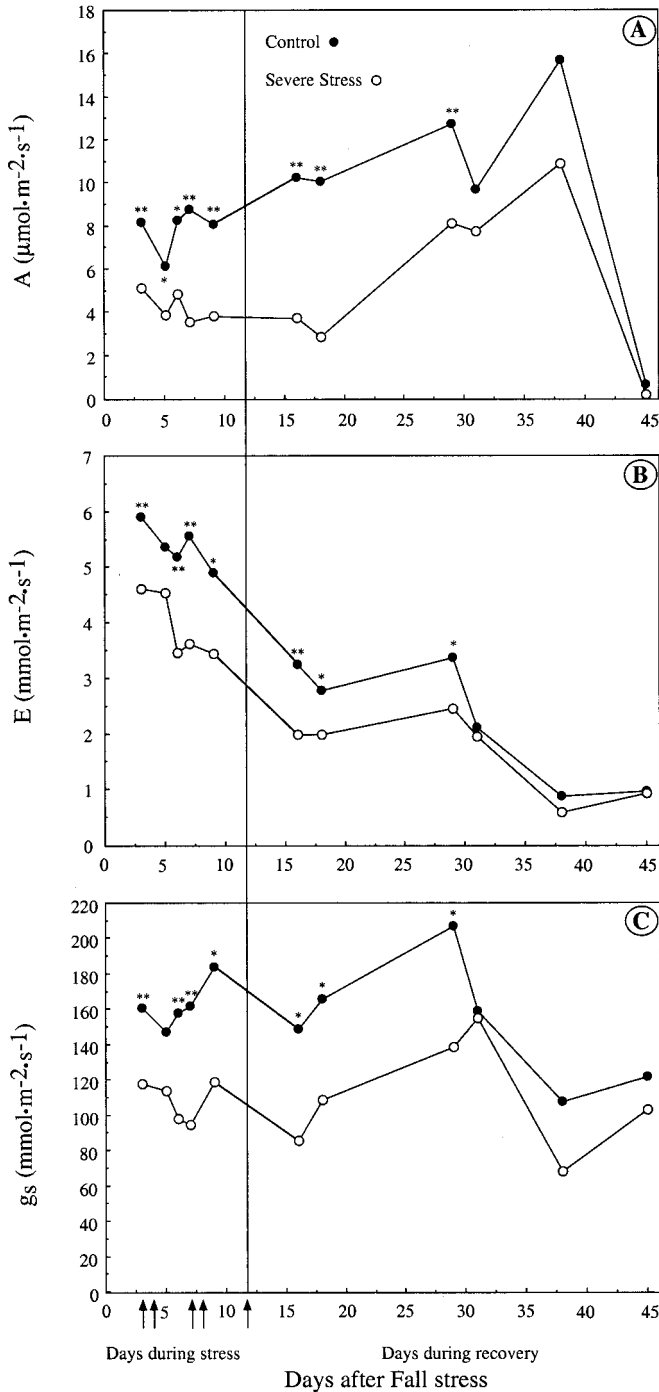


Fig. 5. Leaf gas exchange (n = 8) during stress and recovery for the fall stress (day 1, 4 Oct 1997). (A) CO₂ assimilation (A), (B) transpiration (E), and (C) stomatal conductance (g_s) for control and severe stress. Arrows indicate days irrigation was applied to stressed plants between drought periods, controls were watered daily. *,**Significantly different at P = 0.05 or 0.01, respectively, by t test (unpaired).

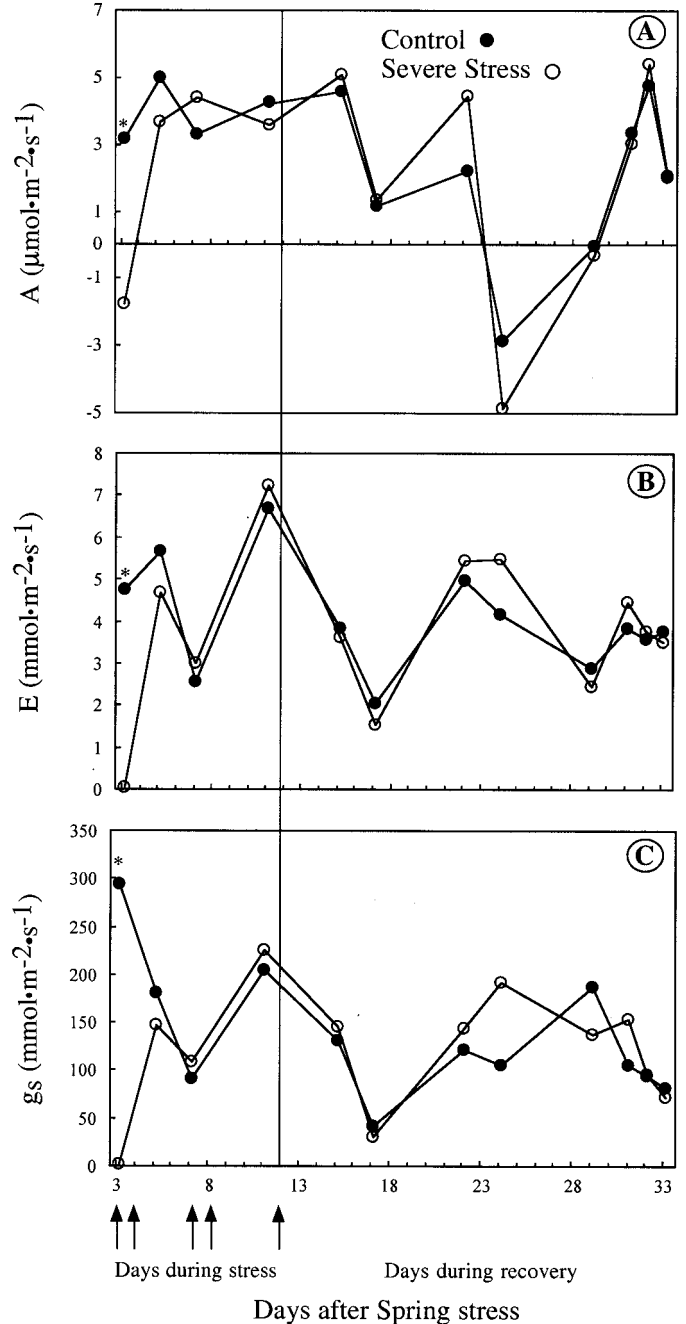


Fig. 6. Leaf gas exchange during stress and recovery for the spring stress (day 1, 1 June 1998). (A) CO₂ assimilation (A), (B) transpiration (E) and (C) stomatal conductance (g_s) for control and severe stress. Arrows indicate days irrigation was applied to stressed plants between drought periods, controls were watered daily. *,**Significantly different at P = 0.05 by t test (unpaired).

Table 1. Average leaf number per plant (n=8) for *Magnolia* × *soulangiana* 'Jane' during the fall stress treatments. Day 1 of the fall stress was 4 Oct. 1997. The last day of the severe stress was 16 Oct.

Treatment	Days after fall stress			
	3	16	31	45
Mild stress control	---	212	155	52
Mild stress drought	---	194	132	36
	---	NS	NS	NS
Moderate stress control	---	208	153	40
Moderate stress drought	---	201	123	33
	---	NS	*	NS
Severe stress control	260 ^z	226	158	46
Severe stress drought	257 ^y	175	80	22
	NS	*	**	*

^zLeaf number for all control treatments (mild, moderate, and severe control plants).

^yLeaf number for all stress treatments (mild, moderate, and severe stressed plants).

NS,*,** Nonsignificant or significant at $P = 0.05$ or 0.01 , respectively, by t test (unpaired).

and severe stressed plants were similar to those for A and g_s. The decrease in E was most likely due to the decrease in evaporative demand with the onset of cooler temperatures.

There was a slight increase in shoot growth during the fall stress, however, there were no differences in shoot growth between fall-stressed and control plants in 1997 (data not presented). Growth index for severe fall-stressed plants was lower than control plants from 226 through 488 DAFS (Table 2). Growth index also was lower for mild fall-stressed plants compared to controls twice during 1998 but no differences were found by the final measurement on 488 DAFS. The three consecutive short-term stresses in fall had a negative effect on performance in the succeeding year. There was no increase in growth index from planting through 160 DASS for control or stressed plants from the spring stresses. This indicates that the fall-stressed plants were able to recover overwinter from transplanting, except from the severe stress, and increase growth in the following year while the spring-stressed plants, including controls, were still suffering from transplant shock. This also indicates that transplant shock was more stressful than the spring stresses by affecting growth of nonstressed trees to the same extent as stressed trees.

There was a difference in flower number for the fall-stressed plants only due to the main effect of stress. There were eight flowers per plant for the stressed treatments versus 12 per plant for controls (n = 24, $P = 0.03$). Due to the large flower size of 'Jane' saucer magnolia, even a small reduction in flower number on young plants can be noticed aesthetically. Aborted flower buds were found on seven of the stressed plants with an average of 2 ± 0.3 flower buds aborted per plant. Only two control plants had aborted flower buds with 3 ± 2 buds aborted. Flower bud initiation and development of saucer magnolia occurs during the summer through fall of the year preceding bloom. Reductions in WPA during stress, lower A, and fewer leaves during recovery indicate substantial reductions in carbohydrate production, especially for the severe stress. Reductions in carbohydrate content (Goldschmidt and Golomb, 1982) and carbon assimilation (Crane and Davies, 1988) have been linked to reduced flowering. The reduction in carbon assimilation during the fall stress most likely affected flower formation.

Time of year has been shown to affect transplant performance and survival of several species (Harris and Bassuk, 1994; Harris et al., 1996). In a study comparing seasonal transplanting effects on

Table 2. Growth index (n = 8) [(height (cm) + width (cm))/2] during recovery of *Magnolia* × *soulangiana* 'Jane' exposed to consecutive short term drought stress in fall. Day 1 of the fall stress was 4 Oct. 1997. The last day of the severe stress was 16 Oct.

Treatment	Days after fall stress				
	226	261	285	328	488
Mild stress control	91	93	93	93	113
Mild stress drought	87	87	87	89	107
	NS	*	*	NS	NS
Moderate stress control	87	92	91	90	107
Moderate stress drought	88	88	88	87	105
	NS	NS	NS	NS	NS
Severe stress control	89	92	93	92	109
Severe stress drought	83	86	85	85	99
	*	*	*	*	*

NS,* Nonsignificant or significant at $P = 0.05$, by t test (unpaired).

four taxa, Harris and Bassuk (1994) found coarse rooted plants to have a lower survival rate than finer rooted plants during late spring transplanting, possibly due to poor root to soil contact resulting in inability to supply adequate water. Saucer magnolia is a coarse rooted plant and the poor performance following spring transplanting of drought and control treatments may be due to poor root to soil contact. Saucer magnolia flowers in early spring and is at peak demand during this period. These results indicate that spring may not be the best time of year for transplanting container-grown saucer magnolia.

Future performance of plants exposed to extended periods of drought between harvest at the nursery and installation in the landscape can be adversely affected and it is critical to maintain adequate water relations during this period. Visible symptoms of drought stress, such as leaf wilting, discoloration and defoliation, were not noticed until the last 2 d of the severe fall and spring stresses. However, reductions in whole-plant photosynthesis and leaf gas exchange had occurred by day 2 or 3 and SMC was lower by day 3 for drought stressed plants of the fall and spring stresses and usually remained lower than controls throughout the remainder of the stress periods. Plants were able to recover with few adverse effects from mild and moderate stresses and transplanting in the fall. However, the reductions in WPA, A and leaf number of severe fall-stressed plants resulted in less growth by termination of the experiment. Additionally, flower number was reduced by drought for fall-stressed plants. The effects of spring stress on response following transplanting were possibly masked by transplant shock, since neither control nor stressed treatments of the spring stress grew after transplanting.

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