ARTICLE

Maintenance of water uptake and reduced water loss contribute to water stress tolerance of *Spiraea alba* Du Roi and *Spiraea tomentosa* L.

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Two primarily eastern US native shrubs, *Spiraea alba* Du Roi and *Spiraea tomentosa* L., are typically found growing in wet areas, often with standing water. Both species have potential for use in the landscape, but little is known of their environmental requirements, including their adaptation to water stress. Two geographic accessions of each species were evaluated for their response to water stress under greenhouse conditions. Above-ground biomass, water relations and gas exchange were measured in well-watered and water stress treatments. In both species, water stress resulted in reduced growth, transpiration and pre-dawn water potential. However, both species also exhibited the ability to osmotically adjust to lower soil water content, resulting in maintained midday leaf turgor potential in all accessions. Net CO_2 assimilation was reduced only in one accession of *S. alba*, primarily due to large reductions in stomatal conductance. *S. tomentosa* lost a larger proportion of leaves than *S. alba* in response to water stress. The primary water stress tolerance strategies of *S. alba* and *S. tomentosa* appear to be the maintenance of water uptake and reduced water loss.

INTRODUCTION

The managed landscape presents a number of biotic and abiotic stresses for plants. These include high and/or low light, nutrient deficiency and/or excess, and water deficit due to inadequate rainfall and/or irrigation, soil compaction and impermeable surfaces above the root zone.[1,2] Transplanted seedlings and plants are often exposed to water stress immediately after planting and this stress can result in poor establishment and sometimes mortality.[3]

Plant response to water deficit is dependent on the level of the deficit, but growth and survival can be achieved through desiccation avoidance or tolerance.[4] Desiccation tolerance, or tolerance of low water potential, often results in plant responses such as wilting that are not desired in plants used in gardens and landscapes.[5] Desiccation avoidance strategies allow for avoidance of low plant water potentials by reducing water loss or increasing water uptake, accomplished via reduced stomatal aperture, reduced leaf area and/or osmotic adjustment.[6] These responses are more likely to be tolerated in landscape plantings, but the degree to which reduced leaf area is achieved through leaf abscission and/or senescence is also an important factor.

There is growing interest in gardening with native plants not only for their novelty, but also to take advantage of their adaptation to local climates.[7–9] Drought events are increasing in frequency in the United States[10] and the identification of native species capable of maintaining their appearance in a formal landscape under water stress conditions is important to both the landscape production and maintenance industry and consumers.[11–13] This has led to renewed interest in documenting water use of both native and exotic landscape plants.[14–16] However, most species recommendations are made based on anecdotal evidence and not systematic and/or comparative studies of water stress tolerance.

The native shrubs *Spiraea alba* Du Roi and *Spiraea tomentosa* L. have potential as landscape plants due to their relatively small size (1–1.5 m tall) and their long and showy flowering period.[17] *S. tomentosa* was used in the landscape as early as 1736.[18] Both species are now mainly used in habitat restoration, although there is revived interest in their use as landscape plants.[19,20] Both *S. alba* and *S. tomentosa* are often found thriving in sites with saturated soils[21–24] or periodic flooding[25–28] and therefore, they are recommended for wet landscape sites.[29] They are adapted to a wide range of soils, including serpentine soils,[30] but their salt tolerance is unclear.[31,32] There is some indication that both species can be grown in dry soils;[33–36] however, water stress tolerance has not been evaluated in these species.

Water stress responses were determined in *S. alba* and *S. tomentosa* following a dry-down period under controlled conditions. Growth, water relations and gas exchange were used to determine the relative water stress tolerance of these two species and of two Midwest accessions within each species.

MATERIALS AND METHODS

Design and analysis

The goal of this experiment was to test differences in growth and physiology of two seed source accessions (Illinois=IL and Michigan=MI) of each of *S. alba* and *S. tomentosa* grown under well-watered (WW) or water stress (WS) treatments. The experiment was arranged as a split-plot on a randomized complete block design. Each of six blocks consisted of two treatments (subplots): one WW and one WS container in which one replicate of each of the species and accessions within species (four plants total: one plant×treatment replicate each) was randomized within each subplot (Supplementary Figure S1). Two-way analysis of variance was conducted to determine significant differences between treatments and among accessions with treatment (water) and accession as fixed effects and block as a random effect using PROC GLIMMIX of the statistical software SAS 9.2 (SAS Inc., Cary, NC, USA).

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Plant materials and growth conditions

All plants were grown from seed germinated in the spring of 2008 by collaborating commercial nurseries and provided as plugs or grown from seed planted in spring of 2008 in the Purdue Horticulture greenhouses. S. alba and S. tomentosa were grown from seed collected in Will County, Illinois and Jackson County, Michigan. Each accession was given a unique abbreviation: the first letter indicates species (A=S. alba and T=S. tomentosa) and the next two letters are the postal code of the state in which the seed for that accession was collected (IL=Illinois and MI=Michigan).

Uniform plugs of all plants were planted on 13 February 2009. One plant of each accession was planted in Fafard® Growing Mix 2 soilless media (Conrad Fafard, Inc., Agawam, MA, USA) in a 0.6 m×0.9 m×0.2 m (ca 0.108 m^3 media) black plastic container (Shape Products, LLC, Menomonie, WI, USA) with holes drilled to allow drainage of the media, allowing for direct comparison of genotypes under similar media water content (Supplementary Figure S1). After planting, plants were pruned to 10 cm from media level and containers were irrigated to field capacity with a significant leaching fraction. On 14 July, all containers were irrigated (the last irrigation for WS treatments) and all plants were pruned to 17 cm from media level. The WW containers were irrigated three more times (sufficient to maintain growth given the large volume of the containers used) and the last irrigation was on 27 August, the day before final measurements were made.

Plants were fertilized with acidified water supplemented with 15N–2.2P–12.5K water-soluble fertilizer (Excel Cal-Mag; Scotts, Marysville, OH, USA) to provide the following (in mg L^{-1}): 200 N, 29 P, 167 K, 67 Ca, 27 Mg, 1.0 Fe, 0.5 Mn and Zn, 0.24 Cu and B, and 0.1 Mo. Irrigation water was supplemented with 93% sulfuric acid (Ulrich Chemical, Indianapolis, IN, USA) at 0.08 mL L^{-1} to reduce alkalinity to 100 mg L^{-1} and pH to a range of 5.7–6.3.

The greenhouse day and night mean temperatures were 22 and 18 ℃, respectively, and maximum day and night RH was ca 60% and 50%, respectively. To provide a 16-h photoperiod throughout the experiment, supplemental lighting from metal halide and high pressure sodium lamps contributed 100 μmol m^{-2} s^{-1} at plant height from 0600 HR to 2200 HR.

Measurements

Gas exchange was measured on all plants 16 days before and 45 days after cessation of irrigation in the WS treatment on a recently developed, fully expanded leaf using a Li-Cor 6400XT (Li-Cor, Inc., Lincoln, NE, USA). Measurements were made between 1000 HR and 1400 HR, using an external light source set at 1500 μmol m^{-2} s^{-1} and a flow rate of 400 μmol s^{-1}. The vapor pressure deficit during measurements was between 0.7 and 1.5 kPa. Because the leaves were too small to fill the chamber opening, leaves were photographed in the chamber prior to measurements, leaf area was calculated using Image J ×1.38 (National Institutes of Health, Bethesda, MD, USA), and gas exchange values were adjusted accordingly. For each measurement, the leaf was positioned on the thermocouple in the chamber to ensure accurate measurement of leaf temperature for calculation of stomatal conductance. In addition to plants grown for the water stress treatment, an additional set of plants grown from seed collected in northern Indiana were used to measure photosynthetic light curves.

Chlorophyll fluorescence was measured on recently matured, fully expanded, dark-adapted leaves 1 day prior to gas exchange measurements using a Hansatech Handy PEA chlorophyll fluorometer (Hansatech Instruments Ltd, Norfolk, UK). Leaves were dark adapted for 15 min prior to measurements, based on preliminary tests of dark adaptation time. The ratio of variable to maximum fluorescence (F_v/F_m) was used as an indicator of the maximum quantum efficiency of photosystem II.

All water relations measurements were made pre-dawn (ca 0200–0600 HR) and midday (ca 1100–1400 HR). Plant water potential (pre-dawn Ψ_w and midday Ψ_w) was measured on stems (ca 10 cm) that included ca 13 leaves, three of which were fully expanded. Each stem was cut from the plant with a sharp razor blade and inserted into a rubber stopper, which was then placed in a pressure chamber (PMS Instrument Company, Corvallis, OR, USA) for determination of total water potential.

Leaf osmotic potential was determined on leaves from the same stem used for the total water potential measurements. One to two fully expanded leaves were removed from each shoot and placed in a mesh insert (Life Science Products, Inc., Frederick, CO, USA) inserted in a microcentrifuge tube and immersed in liquid nitrogen until completely frozen. They were then kept on ice until they could be stored at −20 ℃ until processing. To extract cell sap, leaves were thawed in sealed tubes for 20 min and centrifuged at 13 000 r.p.m. for 10 min. Ten microliters of the extracted liquid was placed in a vapor pressure osmometer (Wescor 5500; Wescor Inc., Logan, UT, USA).

The osmolality was converted to osmotic potential by the equation $\Psi_\pi=-C_sRT$, where Ψ_π is osmotic potential, C_s is the osmolality, R is the gas constant and T is temperature. The osmotic potential at full turgor ($\Psi_{\pi100}$) was calculated as $\Psi_\pi \times RWC$ (defined below).

Relative water content (RWC) was determined on a fully expanded leaf from the stem that was used for the total water potential measurements. A scintillation vial was filled with 5 mL of de-ionized water and weighed. As each leaf was cut from the plant, it was immediately placed in a vial with the petiole down and the difference in weight provided the leaf fresh weight (LFW). The leaves were left to imbibe water for 5 h before they were removed, quickly blotted dry to remove surface water and weighed to obtain the leaf turgid weight (LTW). The leaves were then dried to a constant weight at 70 ℃ (LDW). Relative water content was calculated as RWC=(LFW–LDW)/(LTW–LDW). Leaf succulence was calculated as LFW/LDW.

After determination of LTW, the leaf used for determining RWC was photographed next to a ruler with a digital camera prior to drying. Leaf area (LA) was determined using ImageJ ×1.38 software (National Institutes of Health, Bethesda, MD, USA). Specific leaf area (SLA) was calculated as SLA=LA/LDW. Media water content was determined immediately after completion of gas exchange and water relations measurements from a media core 4 cm in diameter extending from the surface of the media to the bottom of each container. The media samples were placed into sealed containers of known weight and weighed (MFW). The media was then dried to a constant weight at 70 ℃ (MDW). Percent media water content was calculated as MWC=((MFW–MDW)/MFW)×100.

After all physiological measurements were completed, the plants were cut at media level and above-ground biomass was dried to a constant weight at 70 ℃ for determination of total above-ground dry weight. Most of the leaves that died during the experiment remained attached to the plants and were thus included in dry weight values.

RESULTS

Media water content

Media water content among the six control (WW) containers was very consistent at 77.7%±0.1% (mean±s.e.). The MWC of the WS containers was significantly different from the WW containers ($p<0.0001$), but the variability among WS containers was high (38.8%±4.6%) after 45 days of water stress (Supplementary Figure S1). Among WS containers, MWC of blocks 1–3 averaged 29.2%±2.1%, whereas the MWC of blocks 4–6 averaged 48.5%±2.9%. This difference in MWC within the WS treatment was not due to larger plants in blocks 1–3, potentially leading to greater transpirational water loss (no significant differences in above-ground dry weight among blocks), but is likely due to differences in light across the experiment. However, the split plot design allowed for direct comparison of accessions within a single subplot, so that all plants in that subplot would be subjected to approximately the same MWC. It should be noted that MWC was only collected at the end of the experiment, so while it does confirm differences between treatments and indicate differences among plots, the amount of time the plants were growing under these different MWC conditions is not known.

Growth

After 45 days without irrigation, a greater proportion of older leaves had senesced on S. tomentosa plants than S. alba plants, based on visual observations (Figure 1). Within S. alba, the Michigan accession appeared to have greater senescence and more leaf loss than A-IL, whereas differences between the S. tomentosa accessions were less obvious (Figure 1). Individual leaf area was not affected by WS, except in A-IL, in which leaves that developed during the WS were ca 60% the size of WW leaves (Supplementary Figure S2), and the average SLA was 283 cm^2 g^{-1}, with no differences between accessions and/or treatments. Although individual leaf area was reduced by water stress only in A-IL plants, total above-ground biomass was lower in WS plants in all accessions except T-MI (Figure 2), suggesting that leaf initiation was suppressed in plants exposed to WS. It is important to note that plant biomass included senesced leaves that remained on the plants at the time of harvest (Figure 1).
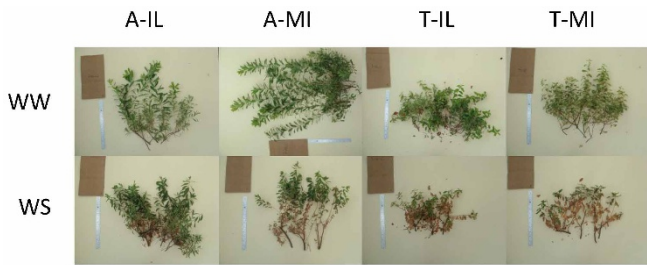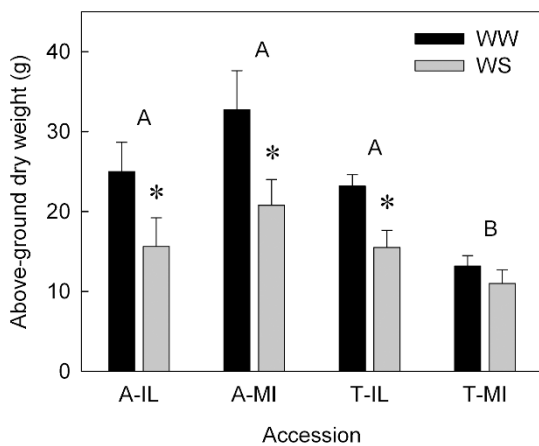
Figure 1. Representative photographs of *S. alba* and *S. tomentosa* accessions from Illinois (A-IL and T-IL) and Michigan (A-MI and T-MI) exposed to well-watered (WW) or 45 days of water-stress (WS) treatments.
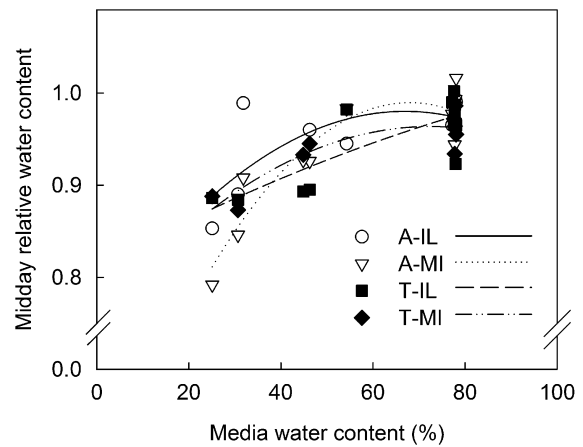
Water relations

All water relations measurements were collected at predawn (*ca* 0200–0600 HR) to assess the water status of plants at equilibrium when transpirational demand should be minimal and at midday (*ca* 1000–1400 HR) to assess the relative effects of WS on the accessions of the two species. Midday RWC decreased in response to WS in leaves of all accessions (Figure 3). Leaf RWC recovered overnight in WS plants of all accessions so there was no difference between WW and WS plants at predawn (data not shown). Leaf succulence did not change significantly between predawn and midday periods and was 3.01 ± 0.34 overall. Although WS resulted in lower RWC, midday succulence was different between WW (3.27 ± 0.17) and WS (2.74 ± 0.05) plants only in A-MI, presumably because RWC was still relatively high in WS plants.

Water stress resulted in reduced predawn Ψ_w in all accessions (Figure 4a), whereas midday Ψ_w was lower in response to WS only in *S. alba* accessions (Figure 4b). Differences in Ψ_w between WW and WS plants in blocks 4–6 were much less than in blocks 1–3, likely due to differences in MWC described above.

The patterns of leaf Ψ_π and $\Psi_{\pi100}$ were similar among accessions and treatments, so only $\Psi_{\pi100}$ is presented to demonstrate osmotic adjustment (i.e., corrected for leaf water content). Leaf Ψ_π did not differ between predawn and midday periods in any accessions, and WS plants had lower Ψ_π in all cases (data not shown). When Ψ_π was

Figure 2. Above-ground dry weight of *S. alba* and *S. tomentosa* accessions from Illinois (A-IL and T-IL) and Michigan (A-MI and T-MI) exposed to well-watered (WW, black columns) or 45 days of water-stress (WS, gray columns) treatments. Columns are means ($n=6$) and bars are $\pm$s.e. Asterisks above pairs of columns indicate significant differences between treatments within an accession at *$p<0.05$. Accessions (pairs of columns) with the same letter are not significantly different based on Tukey's Honestly Significant Different Test.

Figure 3. Relationship between media water content and midday RWC. The relationship was quadratic for Illinois ($y=-0.519x^2+0.6969x+0.746$; $R^2=0.5441$) and Michigan ($y=-0.97x^2+1.319x+0.5413$; $R^2=0.8707$) accessions of *S. alba* (A-IL and A-MI) and the Michigan ($y=-0.4031x^2+0.5817x+0.7536$; $R^2=0.8012$) accession of *S. tomentosa* (T-MI) and linear for the Illinois ($y=0.1853x+0.8314$; $R^2=0.6679$) accession of *S. tomentosa* (T-IL).

adjusted for RWC to calculate $\Psi_{\pi100}$, the same pattern was evident: all accessions responded to WS with a lower $\Psi_{\pi100}$ (Figure 4c and 4d).

In all plants and at both predawn and midday, $\Psi_{\pi100}$ (and Ψ_π) was lower than Ψ_w, which resulted in maintained leaf turgidity (Ψ_p) in all accessions (Figure 4e and 4f). The fact that RWC was lower in WS plants and that the osmotic potential corrected for RWC ($\Psi_{\pi100}$) was lower in all cases suggests that osmotic adjustment occurs in both species. The predawn osmotic adjustment (difference in $\Psi_{\pi100}$ between WS and WW plants) in A-IL, A-MI, T-IL and T-MI was 0.70, 0.50, 0.72 and 0.63 MPa, respectively. Calculated midday values were similar among accessions, but lower due to the reduction in midday RWC.

Gas exchange and chlorophyll fluorescence

In response to WS, net CO_2 assimilation was reduced by 60% of WW plants in A-MI, but was not reduced in any other accessions (Figure 5a). Transpiration and stomatal conductance were both lower in WS plants with no differences among accessions (Figure 5b and 5c). In the WW treatment, F_v/F_m was higher in *S. alba* (0.800 ± 0.004) than *S. tomentosa* (0.737 ± 0.015); however, F_v/F_m was not reduced by WS in any of the accessions (0.776 ± 0.010).

DISCUSSION

Two accessions each of *S. alba* and *S. tomentosa* were grown under greenhouse conditions to assess their response to and mechanisms of water stress tolerance. These species are typically found in wet areas,[1,24–28,37] so we sought to test the hypothesis that they are able to withstand short periods of water deficit, as anecdotally proposed by others.[33–35] In previous studies, both species have demonstrated adaptation to light levels[38] and root zone pH[39] that differ from their typical native habitats, and there are examples of other plants native to wet soils that perform suitably under managed landscape systems.[16]

When either of these species is exposed to rapid dry-down, as is typical in small production containers, both *S. alba* and *S. tomentosa* exhibit wilting and eventually shoot tip necrosis (personal observations). However, when grown in large containers in this study, the water stress occurred more slowly (over approximately 2 weeks), more resembling natural or landscape conditions and allowing time
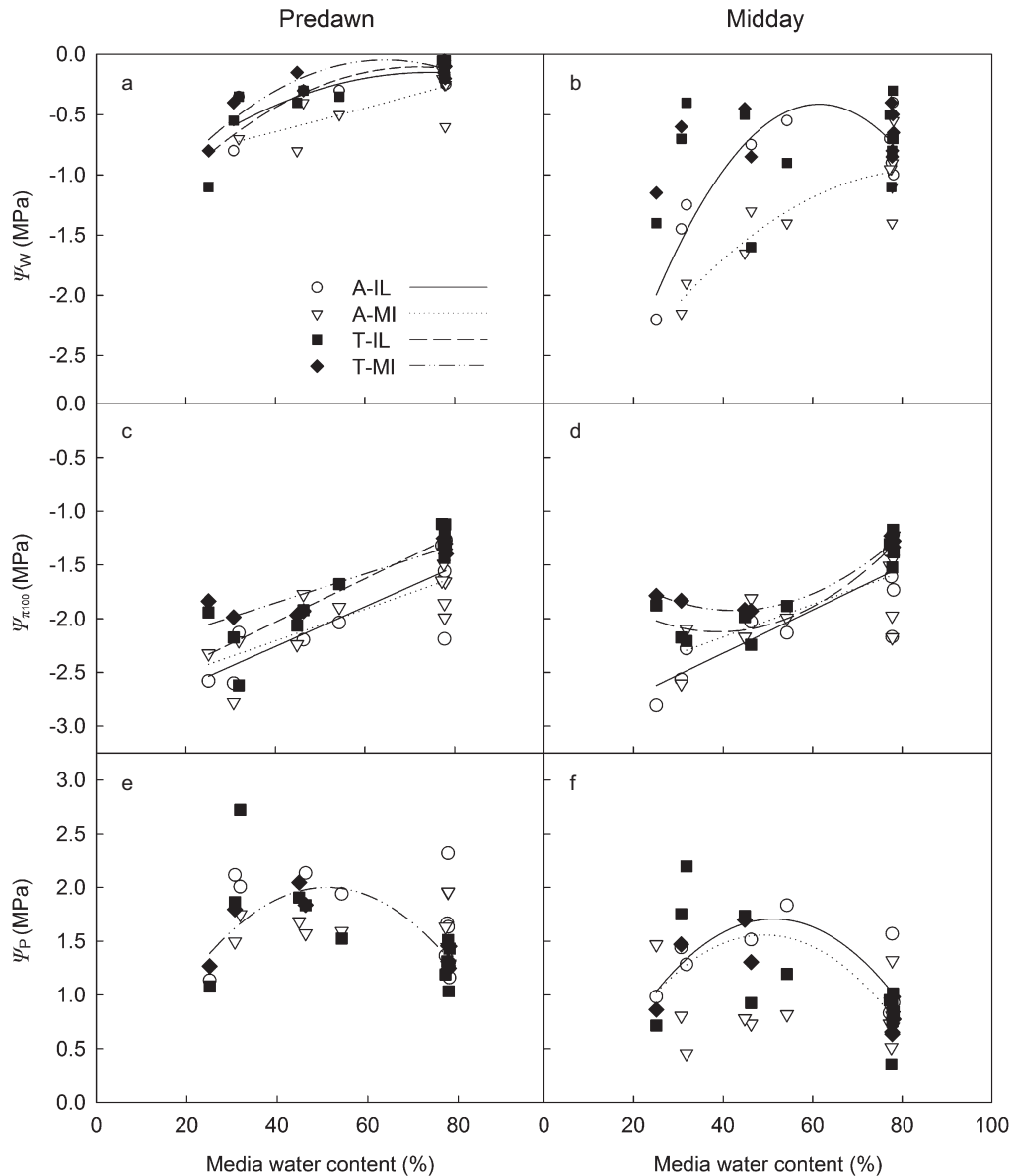
Figure 4. Predawn (**a**, **c** and **e**) and midday (**b**, **d** and **f**) water potential (Ψ_w, **a** and **b**), osmotic potential at full turgor ($\Psi_{\pi 100}$, **c** and **d**) and turgor potential (Ψ_p, **e** and **f**) of *S. alba* and *S. tomentosa* accessions from Illinois (A-IL and T-IL) and Michigan (A-MI and T-MI) as a function of media water content after 45 days of water stress. Significant relationships are indicated by a fitted line.

for adaptation to the water stress. Wilting was not observed under these conditions, and older leaves appeared to be more affected than developing leaves. Both accessions of both species were grown in a fixed media volume, so differences in root characteristics (e.g., rooting depth) could not be expressed.

The general growth response to water stress in these species is a reduction in shoot growth, as opposed to changes at the leaf level: there were no differences between WW and WS plants in individual leaf area (except A-IL), SLA, or succulence. Some species have reduced SLA under water stress,[40] presumably due to reduced net carbon assimilation. This was not observed in this experiment (data not shown). Total leaf area was reduced in most accessions in response to water stress through reduced growth as indicated by biomass measurements (Figure 2) and leaf senescence (Figure 1). These strategies are typical in water-stressed woody shrubs[4,14,41] and are often due to an altered allocation of resources from shoots

to roots.[42] The relative reduction in biomass in response to WS was similar in all accessions except T-MI, which had no reduction in growth in response to WS, but was also the smallest accession in the WW treatment (Figure 2). Fast apical growth rates were correlated with water use efficiency and drought tolerance in *Prunus* rootstocks,[43] as in this study except for T-MI. Overall, this accession exhibited more leaf senescence (Figure 1), suggesting that this species may be less suited to dry landscape situations.

Reduction in individual leaf area is often a consequence of water deficit, but may also provide an adaptive advantage, due to a smaller boundary layer, allowing for more efficient dissipation of heat through convection and conduction when water stress leads to stomatal closure and a subsequent reduction of evaporative cooling.[44] Leaves of A-IL were smaller as a consequence of water stress (data not shown), but all accessions were able to maintain relatively high RWC under water stress (Figure 3).
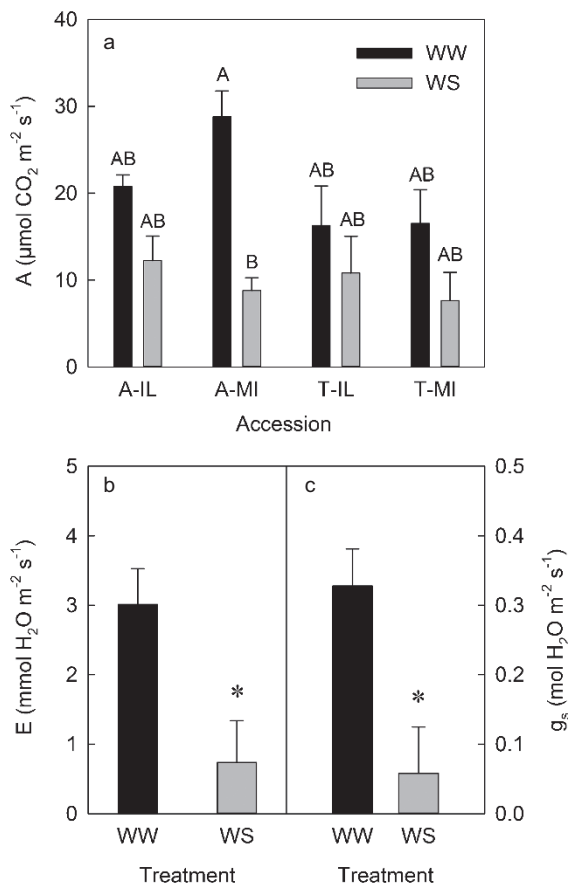
Figure 5. Net CO_2 assimilation rate (A, **a**) of *S. alba* and *S. tomentosa* accessions from Illinois (A-IL and T-IL) and Michigan (A-MI and T-MI) exposed to well-watered (WW, black columns) or 45 days of water-stress (WS, gray columns) treatments. Columns are means ($n=4$–5) and bars are $\pm$s.e. Transpiration rate (E, **b**), and stomatal conductance (g_s, **c**) of well-watered (WW, black columns) or 45 days of water-stress (WS, gray columns) treatments. Asterisks indicate significant differences between treatments at *$p<0.05$.

In the WW treatment, *S. alba* and *S. tomentosa* maintain similar leaf water potentials and stomatal conductance[45] (Figures 4b and 5c). Predawn Ψ_w recovered in both accessions of both species, but in all cases, WS plants were not able to fully recover to control plant values (Figure 4a), suggesting that, regardless of differences in adaptation, all plants were under water deficit stress. The midday Ψ_w of the WS plants in this study were well above levels typically resulting in mortality in woody plant species, but low enough in *S. alba* plants to result in reduced shoot extension as others have also demonstrated.[3]

Young leaves typically maintain lower water potential than older leaves,[46] so it is important to note that shoot segments were used for the determination of water potential, rather than individual leaves (see the section on 'Materials and methods'). It is therefore possible that the Ψ_w values obtained are actually lower than that of mature leaves in these species. Furthermore, if measurements were made on shoots in which growth had ceased due to WS, the Ψ_w of these plants would be higher than WW plants, simply due to leaf composition. Because differences in Ψ_w between older and younger leaves is often small,[47] shoot segments were used because it was extremely difficult to obtain Ψ_w values using a pressure chamber on individual leaves in these species.

Changes in pre-dawn water relations were similar among all accessions (Figure 4). Whereas *S. tomentosa* plants maintained a similar Ψ_w between WW and WS plants, *S. alba* plants exhibited reduced Ψ_w during the day (Figure 4b), presumably because the extent of osmotic adjustment in response to the WS was greater in *S. alba* (Figure 4d). In the WW treatment, the MI *S. tomentosa* accession was the smallest of the accessions in the experiment (Figures 1 and 2), which likely resulted in a low transpirational demand per plant, allowing this accession to maintain midday Ψ_w (Figure 4b) with a relatively (compared to other accessions) small osmotic adjustment (Figure 4d).

Osmotic adjustment can maintain a high RWC even at low leaf water potential, resulting in maintenance of turgor and prevention of tissue desiccation.[48] Typically, osmotic adjustment can occur when plants have adequate time for the adaptation.[49] Osmotic adjustment under WS in all accessions resulted in maintenance (*S. tomentosa*) or a lowering (*S. alba*) of total water potential and an increased ability to extract water from the media. At both predawn and midday measurements, and in both WW and WS plants, $\Psi_{\pi100}$ was lower in *S. alba* than *S. tomentosa* (Figure 4c and 4d), which may allow *S. alba* plants to extract more soil water and to maintain more green leaf area (Figure 1). However, this did not result in maintained growth (Figure 2) or net CO_2 assimilation (Figure 5a) under WS in this species.

All accessions were able to maintain Ψ_p under WS (Figure 4e and 4f). In three cases, Ψ_p values are higher in WS plants. This may be due to the method used to obtain Ψ_w. As discussed previously, if WW plants had actively growing leaves when Ψ_w was measured, the value obtained may be lower than the equivalent shoots of WS plants that may not have actively expanding leaves with lower Ψ_w than fully expanded leaves. This could result in an artificially high Ψ_p in WS plants. However, the differences in Ψ_w between fully expanded and expanding leaves are likely to be small,[47] so the data imply a maintenance of turgor in all accessions under WS, rather than an increase in turgor.

Both species had high net CO_2 assimilation rates (Figure 5), which is consistent with the observation that they both have high net CO_2 assimilation relative to other coexisting deciduous species.[50] Net CO_2 assimilation in these species in the WW treatment (Figure 5a) is correlated with their biomass accumulation in this (Figure 2) and past studies.[38] Net CO_2 assimilation in *S. tomentosa* is lower than in *S. alba* (Figure 5a and Supplementary Figure S3) in the accessions used in this study and in another set of plants grown from seed collected in northern Indiana (Supplementary Figure S4). Under WS, net CO_2 assimilation was not reduced in *S. tomentosa*, despite a similar reduction in transpiration to *S. alba* in T-MI (Figure 5). Water use efficiency (net CO_2 assimilation/transpiration) was higher in WS plants, but did not differ among accessions in either treatment.

Both species maintained turgor during water stress by osmotic adjustment and reducing water loss through reduced stomatal conductance, which decreased by *ca* 80% (Figure 5c). Stomatal closure led to reduced transpiration (Figure 5b), but also likely led to the observed reduction in net CO_2 assimilation (Figure 5a) and growth (Figure 2). The reduction of stomatal conductance under WS likely allowed both species to maintain high Ψ_w (Figure 4b), even when root zone water content is very low (Figure 3b). Because these species are able to maintain Ψ_w via stomatal closure, it is likely that they would be able to tolerate long-term water deficit in a landscape situation, perhaps longer than other species that continue to lose water and dehydrate. The rapid wilting of these plants exposed to water stress in small containers suggests that the response to water stress observed in this experiment is possible only when plants have sufficient acclimation time. Despite the reduction in net CO_2 assimilation, it appears that there was no damage to the photosynthetic apparatus of WS plants, since chlorophyll fluorescence did not change in response to WS, providing further evidence that both species are able to tolerate water stress.

CONCLUSIONS

Both *S. alba* and *S. tomentosa* survived water deficits down to 20% media water content. Although we did not examine recovery in these plants, the RWC (Figure 3) and Ψ_w of the plants at this low root zone water content suggests that they would have survived upon re-watering because cavitation of xylem vessels at these high Ψ_w are unlikely.[51] Overall, both species exhibited an isohydric model of drought tolerance by a reduction in stomatal conductance that resulted in maintained leaf water potential and the ability to osmotically adjust to maintain leaf turgor in the WS treatment. This apparent adaptive ability is despite the fact that both species typically grow in wet to flooded soils.

Plants that are able to tolerate drought conditions without wilting are more desirable as landscape plants,[5] and neither species exhibited wilting during the gradual water stress event in this experiment. Growth was inhibited by water stress, but this would not detract from their landscape potential. However, significant leaf necrosis did occur and to a larger extent on *S. tomentosa* plants, suggesting that *S. alba* may be better suited for the driest areas of a landscape. While the experimental design employed allowed for a slow dry-down, in a typical landscape loam soil, the decrease in water availability would likely be even slower, perhaps allowing for greater potential to adapt to the reduced water availability. Indeed, field observations of multiple accessions of these species growing under minimal irrigation support the fact that they are capable of growing in soils drier than those of their native habitats.[17]

CONFLICT OF INTERESTS

The authors have no conflict of interest to report.

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