Apparent Tolerance of Low Water Availability in Temperate Asian Bamboos[1]

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Abstract

Suitable plant water dynamics and the ability to withstand periods of low moisture input facilitate plant establishment in seasonally arid regions. Temperate bamboos are a major constituent of mixed evergreen and deciduous forests throughout temperate East Asia but play only an incidental role in North American forests and are altogether absent in the Pacific Northwest forest. Many bamboo species are classified as mesic or riparian, but none are considered drought tolerant. To assess their ability to withstand low water, we subjected five Asian temperate and one North American temperate bamboo species to three irrigation treatments: 100%, 50%, and 10% replacement of water lost through evapotranspiration. Plants were irrigated every four days over a 31-day period. Plant response to treatments was measured with stomatal conductance, leaf xylem water potentials, and intrinsic water use efficiency (*iWUE). Pleioblastus distichus* and *Pseudosasa japonica* showed significant reductions in conductance between high and low irrigation treatments. *Sasa palmata* had significantly lower stomatal conductance in all treatments. *Pleioblastus chino* displayed significantly higher *iWUE* in the mid irrigation treatment and *Arunindaria gigantea* displayed significantly lower *iWUE* than *P. chino* and *S. palmata* in the low irrigation treatment. The Asian bamboo species examined here tolerate low water availability and readily acclimate to different soil moisture conditions.

Index words: Temperate bamboos, irrigation response, stomatal conductance, intrinsic water use efficiency.

Species used in this study: Giant Cane [*Arundinaria gigantea* (Walt.) Muhl.]; *Pleioblastus chino* (Franchet & Savatier) Makino; *Pleioblastus distichus* (Mitford) Nakai; *Pseudosasa japonica* (Makino); *Sasa palmata* (Bean) Nakai.

Significance to the Horticulture Industry

Temperate bamboos are a booming market in the specialty nursery field. Much marketing emphasis has been placed on their frost tolerance and shade tolerance for low-maintenance plantings, but their watering and irrigation requirements and responses to low soil water conditions are poorly documented (Mulkey 1986, Cochard et al. 1994, Dierick et al. 2010). Our results indicate that several species of temperate Asian bamboos are well adapted to withstand long periods of low moisture input.

Introduction

Plant water dynamics including their response to precipitation and water availability are collectively causal factors in plant distributions. In addition to greatly influencing the composition of plant communities, precipitation often influences the establishment of introduced species (Davis et al. 2000, Mote 2003, Callaway 2007). Species that display highly plastic responses to water availability (e.g. changes in stomatal response and internal water potential) are more likely to establish and reside in areas of high variability in seasonal precipitation because of their greater control over transpiration and water uptake (Alpert et al. 2000).

We examined the water relations of a collection of Asian temperate bamboos because of their increasing popularity as introductions in horticulture throughout North America. For example, more than 100 retail suppliers in the Pacific Northwest, USA (Bambooweb 2017) currently specialize in frost-tolerant bamboos, most of which display leptomorphic or "running" rhizome morphology (McClure 1993). This morphology allows bamboos to capture resources within resource-limited environments and reflects their evolutionary history within forests (Soderstrom and Calderon 1979). In their native habitats, Asian coniferous and mixed broadleaf temperate forests, temperate Asian bamboos experience monsoonal precipitation patterns in late summer (August and September) as well as persistent snowfall in winter (Box and Choi 2003) producing evenly distributed annual precipitation (Kemp et al. 2012). Cochard et al. (1994) found that the Panamanian tropical vining bamboo *Rhipidocladum racemiflorum* (Steud.) McClure was highly resistant to xylem cavitation and could rapidly respond to changes in soil moisture. Additionally, Mulkey (1986) discovered that some herbaceous bamboos in tropical forest understories developed increased water use efficiency when exposed to light gaps with high irradiance. The Pacific Northwest climate differs markedly from cool temperate forests in east Asia, with a pronounced dry period during summer and precipitation in early fall through late spring (Waring and Franklin 1979, Waring and Running 2007) (Fig. 1). For bamboos to survive in this climate, unaided by irrigation,

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[1] Received for publication September 29, 2017; in revised form February 20, 2018. We would like to thank Charles Cody, greenhouse manager at WSU School of Biological Sciences, and his staff for their immense help in preparing and caring for experimental plants. Jennifer Ringwood-Connolly helped with plant care and obtaining data. Much of this work was supported by a cooperative agreement with USDA Animal Plant Health Inspection Service, under the supervision of Al Tasker. Trade names or commercial products in this publication have been mentioned solely for the purpose of providing specific information and it does not imply recommendation or endorsement by the USDA. The USDA is an equal-opportunity employer and provider.

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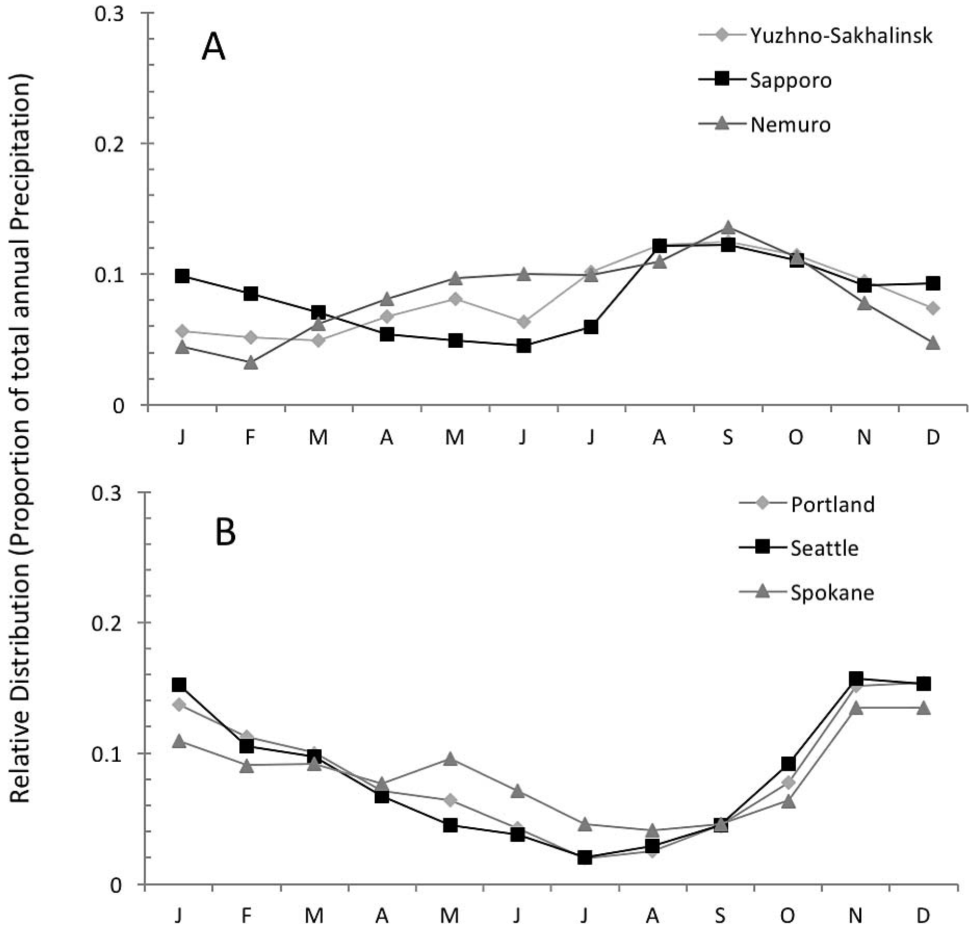

Fig. 1. Monthly distribution of precipitation for selected stations in: A) Temperate East Asia: Yuzhno-Sakhalinsk, Russia, 46°N, 142°E, 87 cm (55 in) annual precipitation, Sapporo, Japan, 43°N, 141°E, 113 cm (45 in) annual precipitation, and Nemuro, Japan, 43°N, 145°E, 104 cm (41 in) annual precipitation (Kemp et al., 2012). B) Selected stations in Pacific Northwest cities: Portland, OR, 45°N, 122°W, 98 cm (39 in) annual precipitation, Seattle, WA 47°N, 122°W, 99 cm (39 in) annual precipitation, and Spokane, WA 47°N, 117°W, 42 cm (17 in) annual precipitation.

they must acclimate rapidly to the changing water availability.

One of the primary modes plants regulate water consumption is by limiting water vapor lost through the stomata during photosynthesis (Kramer 1983, Buckley and Mott 2002). Stomata rapidly contract in response to temperature and moisture dynamics, allowing plants to avoid lethally negative internal xylem pressure potentials (Saliendra et al. 1995). Water loss is mitigated when stomata are closed, but at the sacrifice of photosynthetic production. Plants with optimal water efficiency are those that assimilate the most CO_2 while minimizing water loss (Lambers et al. 2008). With unlimited water resources, C3 photosynthetic plants (including all bamboos) rarely constrict stomata during daylight hours in order to maximize photosynthetic production (Tambussi et al. 2007). In water-limited environments, C3 plants often close their stomata when diurnal temperatures are highest, reducing productivity but also decreasing water loss through transpiration (Berryman 1992, Flexas and Medrano 2002, Saliendra et al. 1995). Stomatal conductance responses are often adaptations to long-term climate patterns or the result of highly plastic stomatal hydraulics (Roy and Mooney 1982). The stomatal response of introduced plants when water is limiting could be an indicator of the potential performance associated with a new habitat (Funk and Vitousek 2007, Levine et al. 2003).

Two interacting forces influence xylem water potentials within plants: soil moisture, which governs water supply, and transpiration, which governs water loss (Lambers et al. 2008). If a plant receives a continuous supply of water, leaf water potentials will remain at a relative constant. When roots uptake soil water while stomata are still transpiring, water potentials may become increasingly negative unless transpiration decreases through stomatal closure (Jarvis 1976, McDowell et al. 2008). Plants typically withstand negative pressure potentials to approximately -1.3MPa in water-limited conditions without suffering embolism and tissue death (Flexas and Medrano 2002, Jones and Sutherland 1991).

We investigated the physiological response to water availability of a group of commercially available temperate Asian bamboos and the most common native North American bamboo. All of these species are native to regions that receive precipitation during summer; therefore we hypothesized these species will not readily acclimate to reduced water availability. We also hypothesized that the native North American bamboo, *Arundinaria gigantea*

(Walt.) Muhl., which is common from the mid-Atlantic United States through Georgia and Alabama, is maladapted to low soil moisture due to its native habitat in riparian and mesic communities. Without mechanisms to control water loss, temperate Asian bamboos would need significant irrigation during summer in areas without summer precipitation.

Materials and Methods

Plants. We purchased all six species in equal numbers from three retailers in Oregon and Washington (Tradewinds Bamboo, Gold Beach, OR, Bamboo Gardens, North Plains, OR and Bamboo Gardens of Washington, Redmond, WA) to increase the potential genetic variability. Within-species genetic variation is low in temperate running bamboos owing to their low recombination rate and the use of extensive vegetative propagation within the nursery industry (Triplett and Clark 2010). We chose one species of native North American bamboo and five species of temperate Asian bamboos for this study: *Arundinaria gigantea* (USA), *Bashania fargesii* (E.G. Camus) Keng & Yi (China), *Pleioblastus chino* (Franchet & Savatier) Makino (China and Japan), *Pleioblastus distichus* (Mitford) Nakai (China and Japan), *Pseudosasa japonica* (Makino) (Japan), and *Sasa palmata* (Bean) Nakai (Japan and Korea). All the bamboo species examined here are characterized as shade tolerant, frost tolerant [will survive temperatures in excess of -10 C (14 F)] and have a leptomorphic (running) rather than pachymorphic (clumping) rhizome morphology (Ohrnberger 1999, Soderstrom and Calderon 1979).

Rhizomes from purchased plants were split into thirty segments with at least two internodes and within 10% fresh weight of each other and planted in 11-liter (3-gal) PVC pots without drainage holes with a 50-50 mixture of coarse sand and LC-1 potting mix (sphagnum peat moss, coarse grade perlite, gypsum, Dolomitic lime, Sungro Horticulture, 770 Silver Street, Agawam, MA, USA 01001) in February 2009. Pots were housed in a greenhouse at Washington State University (Pullman, WA) in June 2009 and June 2010 with ambient light and cooled temperatures [cooling provided by convective water cooling, 18 C to 2 C (64 F to 68 F)]. Thirty replicates of each species/treatment combination were organized into blocks with the greenhouse bench as the blocking factor. Plants were randomly distributed within the bench and redistributed every four days. Pots were stored in a shaded outdoor lath house from July 1 to September 15, and then moved into a greenhouse from September to October with no additional warming [average daily temperature 12 C (54 F)]. From October to February, the greenhouse was heated to -2 C to 8 C (2 F to 46 F), and from February to May, the greenhouse was further heated to 10 C to 25 C (50 F to 77 F). All pots were watered as needed with a 5% nutrient solution of 20-20-20 NPK (Pete's Fertilizer (now sold as Jack's Classic), J.R. Peters, INC 6656 Grant Way, Allentown, PA, 18106) in the greenhouse and lath house.

Irrigation treatments. Irrigation treatments were applied to the pots as a function of the volume of water lost through evapotranspiration. Potted plants were initially watered to near field capacity (-0.5 MPa ± 0.1 MPa) as measured by a T8 soil moisture tensiometer [Decagon Devices (now Meter Group), 2365 NE Hopkins Ct, Pullman, WA 99163] and weighed. Plants were then divided at random into three irrigation treatments: the lowest irrigation treatment was replaced with 10% of the water weight lost, the middle treatment received 50% of the weight lost, and for the highest water treatment, 100% of the water lost through evapotranspiration was replaced. We irrigated plants every four days and water was applied through 3-liter per minute (0.8 gal min^{-1}) drip applicators to the pots to minimize water loss through the bottom of the pots. No fertilizer was applied during the irrigation treatments.

Response parameters were measured 24-h after water application. Stomatal conductance readings were taken with a SC-1 leaf porometer [Decagon Devices (now Meter Group)]. Stomatal conductance is calculated as a function of the difference in the porometer's humidity readings, the distance between the sensors and ambient temperature (SC-1 Leaf Porometer Operator's Manual, 2016). All measurements were made between 900 hr and 1200 hr to detect highest stomatal conductance (Farquhar and Sharkey 1982, Jones and Sutherland 1991, Saliendra et al. 1995). Immediately following leaf stomatal conductance readings, we measured gas exchange rates on the same leaf with a LI-6400 Portable Gas Exchange System equipped with a 2 by 3 cm chamber with Red/Blue LED Light source (Licor, INC, Lincoln, NE, USA). Leaves were then excised and placed into a 100% humidity chamber until leaf xylem water potentials could be measured.

Leaf water potentials were measured with a Scholander-Type Pressure Chamber (Model 1000, PMS Instruments, Albany, Oregon). The pressure chamber was fitted with a grass compression gland that forms a better seal around the pseudopetiole, which is placed into the gland with the tip exposed. Nitrogen was then slowly injected into the chamber to increase the pressure. A 10× hand lens was used to detect cavitation, i.e., when the water column broke and water flowed from the end of the pseudopetiole.

Leaf stomatal conductance (g_s) and leaf water potential (Ψ) were measured directly from the LI-6400. Intrinsic water use efficiency (*iWUE*) was calculated by dividing the rate of CO_2 assimilation (A) by the rate stomatal conductance (A/g_s). In this case g_s was the measurement stored simultaneously with A in the LI-6400.

This experiment was conducted within seven 4-day periods in June 2009 and 2010. Year had no significant interaction (ANOVA, $P > 0.05$) and consequently data from two sample years were pooled. For all normally distributed data, we performed a repeated measures two-way ANOVA with the bench as a blocking factor. For all significant treatment and species effects, we performed a post-hoc Tukey's Honestly Significant Differences pairwise comparison. When normality assumptions were not met, a Kruskal-Wallis rank sum test was applied with post-hoc pairwise comparisons using the Mann-Whitney U-test. All analyses were performed with R statistical software version 2.11.1 (R Development Core Team 2014).

Table 1. **Stomatal conductance, leaf water potentials, and *iWUE* responses among irrigation treatments ± 1 SE. All values represent pooled results from three 30-day test periods. Water was replaced at 100%, 50% or 10% of water lost (by weight) through evapotranspiration. Values (g_s, *Ψ*, *iWUE*) in bold are different treatment effects within species (N= 12, $P < 0.05$, Mann-Whitney U-test for g_s, and Tukey's HSD for *iWUE*) with lower case letters to indicate significant differences.**

Species	Water Replaced	Stomatal Conductance (μmol $m^{-2}s^{-1}$)	Ψ (MPa)	iWUE (μmol CO^2 mol^{-1} H_20)
Arundinaria gigantea	100%	129.9 ± 34.8	-0.74 ± 0.21	50.5 ± 12.2
	50%	154.5 ± 26.8	-0.84 ± 0.19	56.1 ± 27.3
	10%	130.6 ± 26.4	-0.83 ± 0.24	38.5 ± 25.4
Bashania fargesii	100%	140.6 ± 10.9	-0.93 ± 0.27	57.8 ± 29.7
	50%	117.6 ± 13.4	-0.91 ± 0.32	56.8 ± 20.3
	10%	101.9 ± 21.3	-1.03 ± 0.38	67.0 ± 25.4
Pleioblatus chini	100%	170.1 ± 18.2	-0.81 ± 0.13	65.7 ± 25.7
	50%	156.3 ± 22.8	-0.78 ± 0.15	95.6 ± 17.2
	10%	129.1 ± 20.3	-0.92 ± 0.28	83.7 ± 30.9
Pleioblatus distichus	100%	**274.8 ± 33.8^a**	-0.9 ± 0.17	67.5 ± 29.6
	50%	275.2 ± 30.3	-1.01 ± 0.21	70.2 ± 21.8
	10%	**179.4 ± 29.1^b**	-1.01 ± 0.20	71.7 ± 25.3
Pseudosasa japonica	100%	**311.6 ± 26.5^a**	-0.91 ± 0.24	64.7 ± 15.1
	50%	335.1 ± 46.8	-0.95 ± 0.21	65.6 ± 17.7
	10%	**235.7 ± 48.7^b**	-0.91 ±0.16	67.2 ± 32.9
Sasa palmata	100%	96.8 ± 24.4	-0.83 ± 0.25	**54.8 ± 17.1^a**
	50%	92.4 ± 17.5	-0.92 ± 0.30	81.3 ± 27.6
	10%	116.1 ± 19.9	-1.02 ± 0.16	**83.9 ± 18.1^b**

Results and Discussion

Stomatal conductance. Within species, a significantly lower stomatal conductance was observed over the 30-day measurement periods within *P. distichus* (ANOVA, $F_{2,24} = 4.34$, $P < 0.05$) and *P. japonica* (ANOVA, $F_{2,18} = 3.56$, $P = 0.05$) between the 100% replacement treatment and 10% replacement treatment (Tukey HSD, $P < 0.04$, $P < 0.05$ respectively, Table 1, Fig. 2). No other species displayed a significant within species difference between irrigation treatments. Greater overall stomatal conductance was also measured in *B. fargesii* than *S. palmata* (Mann-Whitney U-test, $P = 0.0014$) (Fig. 2). *Pleioblastus distichus* and *P. japonica* exhibited similarly high stomatal conductance under mid and high irrigation treatments and their stomatal conductances were significantly greater than those for other species (Mann-Whitney U-test, $P < 0.05$) (Fig. 2). *Sasa palmata* also displayed significantly lower stomatal conductance than *P. chino* in the mid-level irrigation (Mann-Whitney U-test, $P = 0.01$) and the lowest stomatal conductance among the species (Fig. 2). Within the low-irrigation treatment, *P. japonica* had significantly higher stomatal conductance than *P. chino* (Mann-Whitney U-test, $P = 0.04$). All treatments of *Arundinaria gigantea* had significantly lower stomatal conductance than *P. japonica* and *P. distichus* (Tukey HSD, $P < 0.05$ for all pairwise comparisons) (Fig. 2).

Leaf water potentials. Leaf water potential was not significantly different over the course of each 30-day study period within species for any treatment (ANOVA, $P = 0.38$). Nor were there any significant differences between species for any treatment (ANOVA, $P = 0.24$, Table 1).

Intrinsic water use efficiency. Pleioblastus chino and *Sasa palmata* showed a significant treatment effect for water use efficiency. For *P. chino,* plants in the mid-irrigation treatment displayed significantly higher *iWUE* than plants in the high irrigation treatment (ANOVA, $F_{5,5.55} = 31.03$, $P < 0.001$, Tukey HSD, $P < 0.01$) (Fig. 3). *Sasa palmata* in the mid and low irrigation treatments displayed significantly higher *iWUE* than plants in the high irrigation treatment (ANOVA, $F_{5,5.55} = 33.04$, $P < 0.001$, Tukey HSD, $P < 0.01$) (Fig. 3). No significant differences between species were observed within the high watering treatment (ANOVA, $P = 0.26$). Species did however respond with significant differences to the mid and low irrigation treatments (ANOVA, $F_{5,58} = 3.36$, $P < 0.01$, $F_{5,58} = 4.01$, $P < 0.005$ respectively). For the mid-level irrigation treatment, *P. chino* displayed higher *iWUE* than *A. gigantea* (Tukey HSD, $P < 0.001$)*, B. fargesii* (Tukey HSD, $P < 0.001$) and *S. palmata* (Tukey HSD, $P < 0.05$). The North American native species, *A. gigantea,* had a lower *iWUE* in the low-irrigation treatment than *P. chino* and *S. palmata* (Tukey HSD, $P < 0.05$).

Species response. Species' responses to these watering treatments usually were minimal: only two Asian species, *P. distichus* and *P. japonica,* and *Arundinaria gigantea* displayed differences in stomatal conductance between treatments. Most of the species showed no changes in stomatal response: *iWUE,* stomatal conductance and leaf water potentials were not significantly altered for over a month even when only 10% of the water lost was replaced. Bamboos, which are all C3 grasses, rely on stomatal control and hydraulic conductance to minimize water loss (Farquhar and Sharkey 1982, Flexas and Medrano 2002). In their native range *P. distichus* and *P. japonica* inhabit the drier, more wind-shorn Pacific side of Honshu and Hokkaido islands (Numata 1979), suggesting that the observed stomatal plasticity may be an adaptation to unpredictable water availability. The other temperate Asian species examined inhabit forests on the leeward side of the Japanese archipelago and continental Asia, and receive more predictable precipitation, particularly during summer monsoons (Numata 1979, Box and Choi 2003). Many

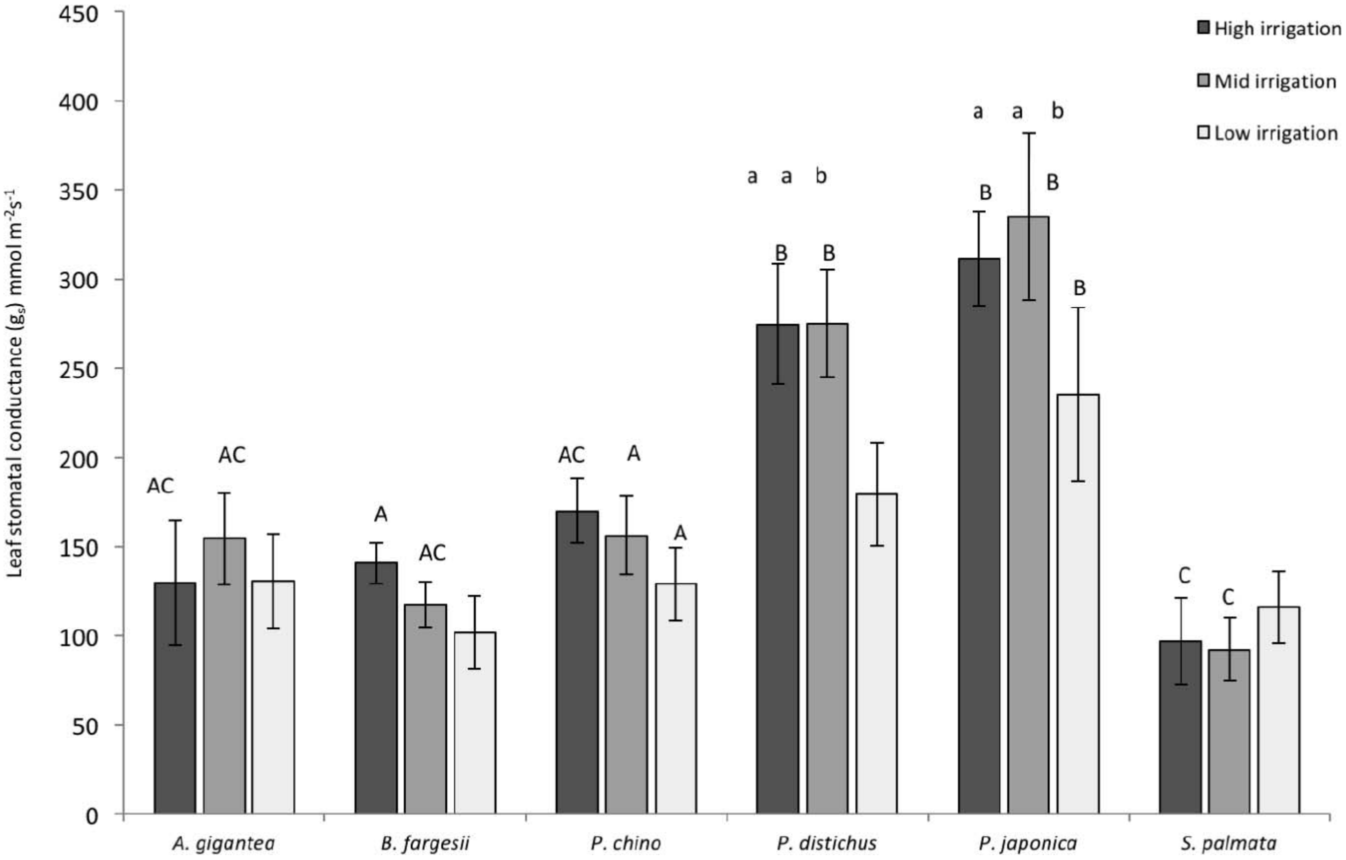

Fig. 2. **Stomatal conductance for five Asian bamboo species and one native North American bamboo (*A. gigantea*). Significance within-species differences are signified by lower case letters ($P < 0.05$, Mann-Whitney U-test). Significant within treatment differences are delineated with upper case letters ($P < 0.05$, Mann-Whitney U-test). *Pleioblastus distichus* and *Pseudosasa japonica* show significant (ANOVA, $P < 0.05$) treatment differences between the high and low irrigation treatments. Significant results for species effects are indicated by lower case letters and significant differences between species are indicated by upper case letters.**

species (*A. gigantea, B. fargesii, P. japonica, S. palmata*) displayed leaf rolling, a response that may reduce the amount of radiation absorbed by the leaf surface as well as reduce the boundary layer conductance (Lambers et al. 2008). No plants died during the course of the study, but the North American native riparian species, *Arundinaria gigantea,* showed visible signs of wilting. None of the Asian species displayed signs of wilting or cavitation.

Leaf water potentials suggest that most of these species can withstand periods of low water availability with the exception of *A. gigantea*. Leaf water potentials were conserved within and between species, suggesting that although only 10% and 50% of the water lost was replaced in the low and mid irrigation treatments, these treatments did not induce responses indicating water stress responses (e.g., stomatal closure and embolism). These results correspond with *iWUE* responses, which showed few differences between species or between treatments within species. *Pleioblastus chino* was the only species that exhibited a treatment effect and increased its *iWUE* in the mid-irrigation treatment.

Many of the temperate Asian bamboos currently being sold in the Pacific Northwest have native ranges that receive higher precipitation during July and August compared to the precipitation in summer in the Pacific Northwest. But total precipitation is similar between temperate East Asia and the Pacific Northwest, with amounts ranging between 800 mm to 1200 mm (32 into–47 in) (Kemp et al. 2012) (Fig. 1). In the driest months in Asia (May and June), sites receive on average over 50 cm (20 inches) of precipitation, whereas in the driest months in the Pacific Northwest (July and August), sites receive less than 8 in. In both regions, July and August are the hottest months with temperatures often above > 25 C (77 F). The disparity in precipitation could be a barrier to species with low tolerance to drought, but we have shown that several of the temperate bamboo species we tested tolerate water draw down without consequences. Higher elevations in the Pacific Northwest regularly receive high amounts of snowfall that persists through much of summer, supplementing the precipitation falling as rain. Snowmelt maintains high soil moisture indices in many areas and contributes to the high primary productivity in Pacific Northwest coniferous forests (Daubenmire and Daubenmire 1968, Gholz 1982, Coops et al. 2011).

Drought tolerant grasses frequently display multiple adaptations to summer drought including reduced growth and leaf senescence (Volaire and Norton 2006). Many grasses from summer drought-dominated regions, such as the Mediterranean Basin, enter summer dormancy after flowering when resources are shunted to storage organs that can withstand significant drying while still maintaining the

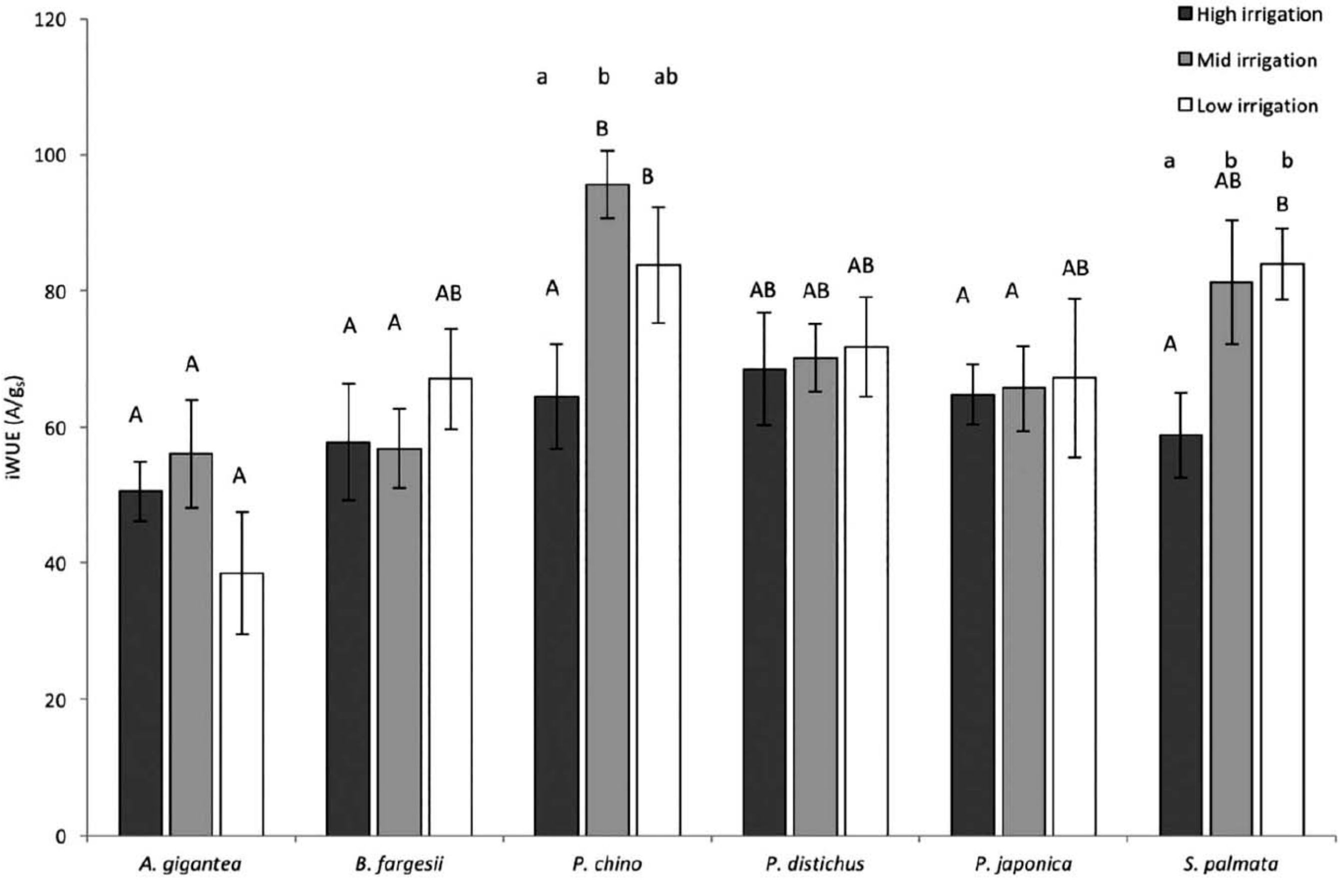

Fig. 3. Intrinsic water use efficiency (*iWUE*) for five Asian bamboo species and one native North American bamboo (*A. gigantea*) averaged over three 30-day trail periods. Significant differences within-species is marked by lower case letters (Tukey's HSD, $P < 0.05$). Significant within-treatment differences are demarcated with upper case letters (Tukey's HSD, $P < 0.05$). With the exception of *P. chino,* no within species differences were detected. Within the middle irrigation treatment, results for *P. chino* are significantly different than results for *A. gigantea, B. fargesii,* and *P. japonica*. In the low irrigation treatment, results for *S. palmata* were significantly different from results for *A. gigantea,* and results for *A. gigantea* were significantly lower than results for *P. chino*. Significant results for species effects are indicated by lower case letters and significant differences between species are indicated by upper case letters.

ability to opportunistically grow when water reappears (Crabbé 1994, Volaire and Norton 2006). Bamboos may also lose leaves but do not have additional storage organs other than the rhizome, which differs in morphology between the two large bamboo types (running vs. clumping). In a recent study of the effects of drought on the temperate dwarf clumping bamboo, *Fargesia rufa* (Yi), (Liu et al. 2015) found reduced light response parameters (e.g. max photosynthetic output, light compensation point, quantum yield), increased amylase activity and starch degradation and increased ammonium concentration in response to drought. However, *F. rufa* was able to regulate its C and N metabolism to produce metabolites that protected against cell damage and accelerated recovery after watering (Liu et al. 2015). Although this study did not focus on plants' response to light, the results confirm that running bamboos' resistance to drought is similar to that displayed by *F. rufa,* a clumping bamboo.

One of two scenarios describe the observed responses in most of the temperate Asian bamboo species: 1) these species withstand periods (at least one month) of reduced water availability without consequences (e.g., leaf death from cavitation) or 2) we did not sufficiently withhold water long enough for these species to elicit a measurably different response between treatments. Because summer conditions persist for nearly three months, future tests should measure responses for the entire season. Our findings, however further the support for limited and highly controlled plantings of running bamboos. Running bamboos have strong propensities for outgrowing barriers and becoming locally invasive (EDDMapS.org). The outcome of our examinations show that these running bamboos acclimate sufficiently to shifting water availability and would likely grow without irrigation intervention even in areas with pronounced summer dry periods.

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