

Gas exchange in *Paulownia* species growing under different soil moisture conditions in the field

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Abstract: In order to evaluate their responses to drought, we determined the photosynthetic activity, water potential, stomatal conductance, transpiration, water use efficiency, photosynthetic photon flux density and leaf temperature of *Paulownia imperialis*, *P. fortunei* and *P. elongata* in three different soil moisture conditions in the field. Our results showed that *P. imperialis* had greater photosynthesis ($8.86 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and instantaneous water use efficiency ($0.79 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) than either *P. elongata* ($8.20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.71 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) or *P. fortunei* ($3.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.07 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$). The rapid growth of *Paulownia* did not appear to be correlated with photosynthetic rates. *Paulownia fortunei* showed more transpiration ($48.78 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and stomatal conductance ($840 \text{ mmol m}^{-2} \text{ s}^{-1}$) than *P. imperialis* ($20 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and $540 \text{ mmol m}^{-2} \text{ s}^{-1}$) and *P. elongata* ($20 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and $410 \text{ mmol m}^{-2} \text{ s}^{-1}$), which allowed these two *Paulownia* species to increase their tolerance to low soil moisture, and maintain higher water use efficiency under these conditions. According to our physiological gas exchange field tests, *Paulownia imperialis* does appear to be capable of successful growth in semiarid zones.

Key words: *Paulownia*, Drought, Photosynthesis, Gas exchange, Stomatal conductance
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Introduction

Native to China, *Paulownia* exhibits rapid growth and high wood quality. This species is commonly used in manufacturing furniture, musical instruments, and fencing (Yao, 1990). *Paulownia* has been introduced as a crop into semi-arid and arid regions of Spain and Australia. More recently, there has been some consideration for introducing *Paulownia* to an arid northwest region in Baja California Sur, Mexico. However, its physiology and drought-adaptive characteristics must be carefully studied to ensure a successful introduction.

The rapid growth of *Paulownia* may be the result of either high photosynthetic rates, large allocation to photosynthetic tissues, or low energy construction costs for stem and leaves (Baruch and Goldstein, 1999). *Paulownia* apparently grows faster by producing low-density wood (Yao, 1990), which decreases the energetic cost of tissue growth (Villar and Merino, 2001). Some studies have shown that certain species are able to survive drought conditions, and that *Paulownia imperialis* is a more resistant species than *P. elongata* or *P. fortunei* (Yao, 1990).

Water stress in plants induces cellular, physiological, and developmental changes. Plants adapt to water stress by inducing rapid physiological responses, such as opening and closing stomata and changing the angles of leaves (Parsons, 1987), and inducing longer developmental responses such as increasing the production

of new, smaller leaves and deeper roots (Parsons, 1987). Biochemical responses may be rapid or slow, such as the production of osmotically active compounds like proline, malate, citrate, betaine, sucrose, pinitol, and aldose (Bray, 1993; Handa et al., 1983).

In this study, we evaluated physiological aspects of drought resistance by measuring gas exchange in three *Paulownia* species. In order to evaluate their response to drought conditions, we studied their physiological activities under field conditions with three different soil moisture levels.

Materials and Methods

Plant husbandry and tissue collection: Seeds of *Paulownia imperialis*, *Paulownia fortunei* and *Paulownia elongata* were germinated under tissue culture conditions. Seeds were sanitized with 95% ethyl alcohol (v/v) for 5 seconds and in 20% commercial NaClO for 5 minutes, and then rinsed thoroughly four times with sterilized deionized water. WPM culture media (Woody Plant Medium; Trigiano and Gray, 2000) was prepared for sowing seeds. The pH of the media was adjusted to 5.8 before the addition of agar, and the media was autoclaved at 121°C and 15 lb for 15 minutes. Sanitized seeds were sown in tissue culture vessels containing 20 ml of solidified WPM supplemented with 3% sucrose and 0.8% agar (Sigma). Plants were maintained in a growth chamber at $25 \pm 2^\circ\text{C}$ under continuous fluorescent light. After one month of germination, we transplanted one plant into each vessel with 20 ml WPM medium. After one month, they were transplanted to 5 l black polyethylene

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bags filled with two parts peat moss (Pro-Mix™, Premier Tech, Dorval, Quebec, Canada) to one part sand. They were maintained in a greenhouse at 23°C and 72% relative humidity. After three months, the trees were transplanted to the sandy soil of an experimental field at the Centro de Investigaciones Biológicas del Noroeste (CIBNOR) 17 km west of La Paz, Baja California Sur, Mexico (23°29' N, 109°43' W). Average annual temperature at this site was 24.8°C, with an annual average maximum of 31.5°C and an annual average minimum of 17.3°C. Annual precipitation was 170 mm. The plants were 17 months old at the time of sampling. The sample size was 12 for each species.

Permanent wilting: We determined the turgor loss point of five *Paulownia imperialis* leaves with a pressure chamber (PMS Instrument Company, Model 1000, Corvallis, Oregon) following the procedure of Schulte and Henry, (1992). Leaves were placed overnight upright in flasks of water covered with plastic. The next morning, leaves were taken out from the flask, and excess water was eliminated by blotting. The leaves were weighed and immediately placed in the pressure chamber. Pressure was gradually increased until liquid was observed at the xylem surface. The leaf was weighted and left to dry under room conditions. We calculated pressure volume curves, and these were used to determine the permanent wilting point (pwp). Pressure volume curves were also used to determine the turgor loss point. Relationship between water potential and soil moisture

We collected 3 kg of soil from the field, which was then moisturized until it reached field capacity. The soil was dried in a gravity convection oven (DX 600 Yamato, Santa Clara, California), while soil moisture (HH2 moisture meter from AT Delta Devices, Cambridge) and water potential (Dewpoint Potentiometer WP4-T of Decagon Devices, Pullman WA) were measured.

Physiological analyses: Plant physiological analyses were performed under three soil moisture conditions (ranging from 7 to 26%). The measurements were taken in July 2006, at which time growing conditions for *Paulownia* species were considered to be at maximum temperature and minimum moisture. Photosynthesis, stomatal conductance, transpiration, leaf temperature and photosynthetic flux density were measured four times daily (7-9AM, 10-12AM, 15-17PM, 18-20PM) with the portable photosynthesis measuring system LI-6200 (LICOR, Lincoln, Nebraska). Water use efficiency was obtained from the instantaneous rates of photosynthesis and transpiration under three different treatments.

Statistical analysis: One-way ANOVA was performed using the NCSS statistical package (NCSS, 2000, Kaysville, Utah). Mean comparisons were tested at 5% probability using a Tukey multiple comparison test.

Results and Discussion

Permanent wilting: Analyzing the pressure volume curves of *P. imperialis*, we found that permanent wilting occurred at -1 MPa. In general, plants exhibit permanent wilting at -1.5 MPa (Larcher, 1995). Williams et al., (1997) found fall of leaves when leaf water potential was -0.5 to -1 MPa in fully deciduous species and soil moisture in

the dry months of 5% at 50 cm and 10% at 100 cm. Zhao et al. (1986) reported in *Paulownia* roots at depths higher than 100 cm.

Relationship between water potential and soil moisture: The soil moisture between 11.6 at 4% supported a water potential of 0 MPa. This value was obtained by measuring water potential at different soil moisture levels from soil samples obtained in the field. At 11% moisture, soil showed a water potential of -0.07 MPa. The water potential was -0.34 MPa at 9.3% soil moisture, and was even lower (-83.2 MPa) at 3.8% moisture. This relationship between water potential and soil moisture is likely due to the high sand content of the soil (Larcher, 1995). The results were similar to those found by Young and Nobel (1986) in the North-Western Sonoran Desert.

Physiological analysis: Little is known about the physiology of *Paulownia* species. Our study is one of the few to characterize *Paulownia* photosynthetic and gas exchange parameters as they relate to soil moisture field conditions. The goal of our work was to understand the performance of *Paulownia* species under semiarid and arid growth conditions.

Fig. 1-3 and Table 1 show the results of the gas interchange parameters as measured in the three species of *Paulownia* grown in the field under different soil moisture conditions. In low soil moisture, plants of all three species were near the point of permanent wilting according to our pressure chamber data.

Photosynthetic Photon Flux Density: Photosynthetic Photon Flux Density (PPFD) increased in the morning and was highest at 10-12 AM (Fig. 1), subsequently decreasing in the afternoon. We observed a decrease in photosynthesis correlated with high afternoon PPFD levels. PPFD was similar to the change of the soil moisture in the soil. Bassow and Bazzaz (1998) measured PPFD from 8 AM to 6 PM in *Quercus rubra*, *Acer rubrum*, *Betula papyrifera* and *Betula alleghaniensis* and found that PPFD was highest between 10 AM and 4 PM. Photosynthesis was highest from 8-10 AM. Fanjul and Barradas (1987) measured (PPFD) from 8 AM to 8 PM in trees of deciduous dry forest *Trichilia trifolia* L. and *Thouinia paocidentata* Poit and found that PPFD was highest between 12 and 2 PM.

Leaf temperature: We observed a decrease in photosynthesis correlated with increasing leaf temperature (Table 1), although we did not observe an increase in photosynthesis with increasing radiation. The level of photosynthesis was correlated with the temperature of the leaves, and the measurements were taken when the leaf temperatures were between 27.7 and 50°C. Leaf temperature fluctuated in a manner similar to the changes in soil. Leaf temperature was lowest in the morning and increased at 10-12 hr and 15-17 hr, decreasing at 18-20 hr. Zhao et al. (1986) reported that the optimal temperature for *Paulownia* growth is 24 to 29°C. Larcher (1995) observed that the primary processes of photosynthesis are among the first processes inhibited at high temperatures.

Photosynthesis: Photosynthetic rates were significantly lower in *P. fortunei* than in *P. elongata* or *P. imperialis* under conditions of

Table 1: Soil moisture, hour, leaf temperature, photosynthesis and transpiration of *P. elongata*, *P. fortunei* and *P. imperialis* under different soil moisture conditions in the field. Values are the mean \pm SD

Species	Soil moisture (%)	Hour (hr)	Leaf temperature (°C)	Photosynthesis ($\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$)	Transpiration ($\text{mmol m}^{-2}\text{s}^{-1}$)
<i>Paulownia elongata</i>	25.6 \pm 1.6	7-9	34.8 \pm 1.4 ^a	5.54 \pm 2.87 ^{a*}	12 \pm 2.08 ^a
		10-12	48.37 \pm 0.66 ^b	4.31 \pm 1.04 ^a	17.85 \pm 4.95 ^a
		15-17	49.32 \pm 1.37 ^b	2.54 \pm 1.22 ^a	18.40 \pm 4.14 ^a
		18-20	41.06 \pm 2.53 ^c	2.18 \pm 2.04 ^a	13.20 \pm 1.80 ^a
<i>Paulownia elongata</i>	13.6 \pm 0.7	7-9	34.38 \pm 1.6 ^a	8.20 \pm 3.25 ^{b*}	11.57 \pm 1.12 ^a
		10-12	48.61 \pm 0.56 ^b	2.49 \pm 1.88 ^b	13.50 \pm 1.62 ^a
		15-17	47.02 \pm 0.97 ^b	0.66 \pm 0.54 ^a	12.93 \pm 0.74 ^a
		18-20	42.67 \pm 1.55 ^c	0.51 \pm 0.11 ^a	12.23 \pm 1.28 ^a
<i>Paulownia elongata</i>	10.3 \pm 1.3	7-9	34.45 \pm 2.03 ^a	2.20 \pm 1.71 ^{a*}	10.95 \pm 4.22 ^a
		10-12	48.76 \pm 2.74 ^b	-0.14 \pm 0.65 ^a	19.18 \pm 2.28 ^b
		15-17	48.05 \pm 0.78 ^b	-0.20 \pm 0.07 ^a	19.23 \pm 4.99 ^b
		18-20	42.12 \pm 3.35 ^c	0.17 \pm 0.25 ^a	11.20 \pm 1.71 ^a
<i>Paulownia fortunei</i>	25.2 \pm 0.8	7-9	41.7 \pm 1.6 ^c	0.25 \pm 0.14 ^{a*}	23.95 \pm 5.59 ^a
		10-12	49.46 \pm 3.25 ^b	-0.51 \pm 0.47 ^a	37.13 \pm 5.31 ^a
		15-17	49.60 \pm 2.51 ^b	-0.23 \pm 0.23 ^a	37.00 \pm 8.84 ^a
		18-20	36.13 \pm 1.63 ^a	-0.59 \pm 0.13 ^a	26.25 \pm 14.87 ^a
<i>Paulownia fortunei</i>	12.1 \pm 1.2	7-9	40.75 \pm 1.32 ^c	0.60 \pm 1.75 ^{a*}	30.7 \pm 2.65 ^a
		10-12	48.89 \pm 0.49 ^b	1.62 \pm 0.73 ^a	31.90 \pm 11.68 ^a
		15-17	47.15 \pm 0.51 ^b	1.83 \pm 2.68 ^a	40.40 \pm 10.40 ^a
		18-20	38.19 \pm 1.34 ^a	-0.26 \pm 0.54 ^a	27.05 \pm 9.17 ^a
<i>Paulownia fortunei</i>	7.4 \pm 0.8	7-9	38.44 \pm 1.54 ^a	3.26 \pm 1.50 ^{b*}	48.78 \pm 33.15 ^a
		10-12	47.98 \pm 1.23 ^b	0.07 \pm 0.05 ^a	47.03 \pm 16.96 ^a
		15-17	45.51 \pm 1.61 ^b	0.42 \pm 0.08 ^a	47.95 \pm 21.77 ^a
		18-20	36.15 \pm 1.52 ^a	-0.31 \pm 0.30 ^a	27.98 \pm 12.80 ^a
<i>Paulownia imperialis</i>	26.8 \pm 1.5	7-9	30 \pm 1.3 ^a	7.02 \pm 0.84 ^b	11.82 \pm 3.11 ^a
		10-12	47.08 \pm 0.6 ^b	3.60 \pm 0.58 ^a	22.30 \pm 5.08 ^b
		15-17	46.42 \pm 0.74 ^{bc}	3.28 \pm 0.44 ^a	21.65 \pm 1.35 ^b
		18-20	44.62 \pm 1.2 ^c	2.23 \pm 0.15 ^a	16.00 \pm 3.51 ^{ab}
<i>Paulownia imperialis</i>	12.5 \pm 0.6	7-9	29.46 \pm 2.38 ^a	8.86 \pm 3.28 ^b	11.2 \pm 2.75 ^a
		10-12	46.44 \pm 0.82 ^{bc}	1.61 \pm 0.08 ^a	17.30 \pm 7.28 ^a
		15-17	47.97 \pm 0.82 ^b	1.71 \pm 1.13 ^a	16.85 \pm 3.04 ^a
		18-20	44.4 \pm 1.02 ^c	0.44 \pm 0.04 ^a	13.15 \pm 1.63 ^a
<i>Paulownia imperialis</i>	10.2 \pm 1.5	7-9	27.66 \pm 1.46 ^a	3.34 \pm 1.23 ^a	10.93 \pm 3.37 ^a
		10-12	50.21 \pm 2.78 ^b	2.22 \pm 1.61 ^a	20.25 \pm 4.95 ^b
		15-17	48.20 \pm 2.51 ^b	1.23 \pm 1.04 ^a	20.28 \pm 2.12 ^b
		18-20	3.68 \pm 0.53 ^c	1.03 \pm 0.75 ^a	15.15 \pm 2.20 ^{ab}

Letters means differences between time of measure of each species, * = Significant differences between soil moisture of each species

medium and high moisture, although *P. fortunei* photosynthesis was higher than either of the other species under low soil moisture conditions (Table 1). *P. elongata* and *P. imperialis* showed higher rates of photosynthesis in high and medium soil moisture (Table 1). In *P. elongata* and *P. fortunei*, significant differences were found in photosynthesis at high versus low moisture conditions. Under conditions of medium soil moisture, *P. elongata* and *P. imperialis* had higher rates of photosynthesis (8.20 \pm 3.25 and 8.86 \pm 3.28 $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ respectively, Table 1), compared to *P. fortunei*. Our results appear to contradict the previous results of Yao (1990), although this previous work does not report units of photosynthetic rates.

Photosynthesis was highest in the morning, and decreased over the course of the day ($p \leq 0.05$ with a Tukey Test). In *P. fortunei*, low moisture correlated with significant differences between the values in the morning (3.26 \pm 1.5 $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$) and the values during different parts of the day (0.07 to -0.31 $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$). In *P. elongata* and *P. fortunei*, significant differences were detected between the different levels of soil moisture, although *P. imperialis* did not show significant differences in photosynthesis between different moisture levels (%). Consistent with our results, previous data from *Prosopis juliflora* showed that a maximum photosynthetic rates of 17.6 $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ occurred at 8 AM, while negative values

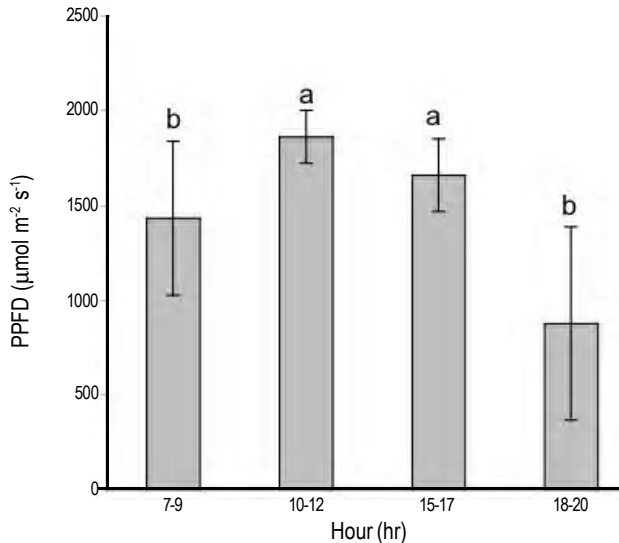


Fig. 1: Photosynthetic photon flux density (PPFD) in three *Paulownia* species at different hours during the day (7-9, 10-12, 15-17 and 18-20)

occurred from 11 AM to 4 PM when the radiation was 600 to 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and the air temperature was 39 to 46°C (Elfadl and Luukkanen, 2006).

Rapid growth of the species of *Paulownia* may be related to high rates of photosynthesis. However, the photosynthetic capacity of the species *Paulownia* is lower than photosynthesis of other similar deciduous trees and bushes (Larcher, 1995). Field experiments of Yao (1990) showed higher photosynthesis of *P. elongata* than *P. imperialis* (7.65 and 6.23, unknown units in the original paper).

We did not, however, find significant differences between the two species (8.2 and $8.86 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$). Ni and Pallardy (1992) report that *Juglans nigra*, photosynthesis decreased with decreases in soil moisture from 4.73 to $0.52 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$.

Stomatal conductance: Stomatal conductance for these species peaked in the morning and decreased during the hours of highest irradiation, with the greatest photosynthetic differences measured in the afternoon (Fig. 2). Stomatal conductance in *P. fortunei* and *P. imperialis* increased as soil moisture decreased, a pattern similar to that of photosynthesis in *P. fortunei*, and inverse of that seen in *P. imperialis*. In *P. fortunei*, stomatal conductance was significantly different and two times higher under conditions of low moisture, but only 25% higher in *P. imperialis* (Fig. 2). *P. elongata* exhibited the lowest stomatal conductance ($150 \pm 10 \text{ mmol m}^{-2} \text{s}^{-1}$), at all soil moisture levels. Stomatal conductance in *P. fortunei* showed significant differences between the high and low soil moisture conditions. Stomatal conductance in *P. elongata* and *P. imperialis* was consistent between different levels of soil moisture. In high moisture conditions, stomatal conductance in *P. elongata*, *P. fortunei* and *P. imperialis* was lower than in *Schinus terebinthifolius*, a rapidly growing tree native to arid environments (Stratton and Goldstein, 2001). At low soil moisture, stomatal conductance in *P. elongata* was two to three times higher, *P. imperialis* was two to five times higher, and *P.*

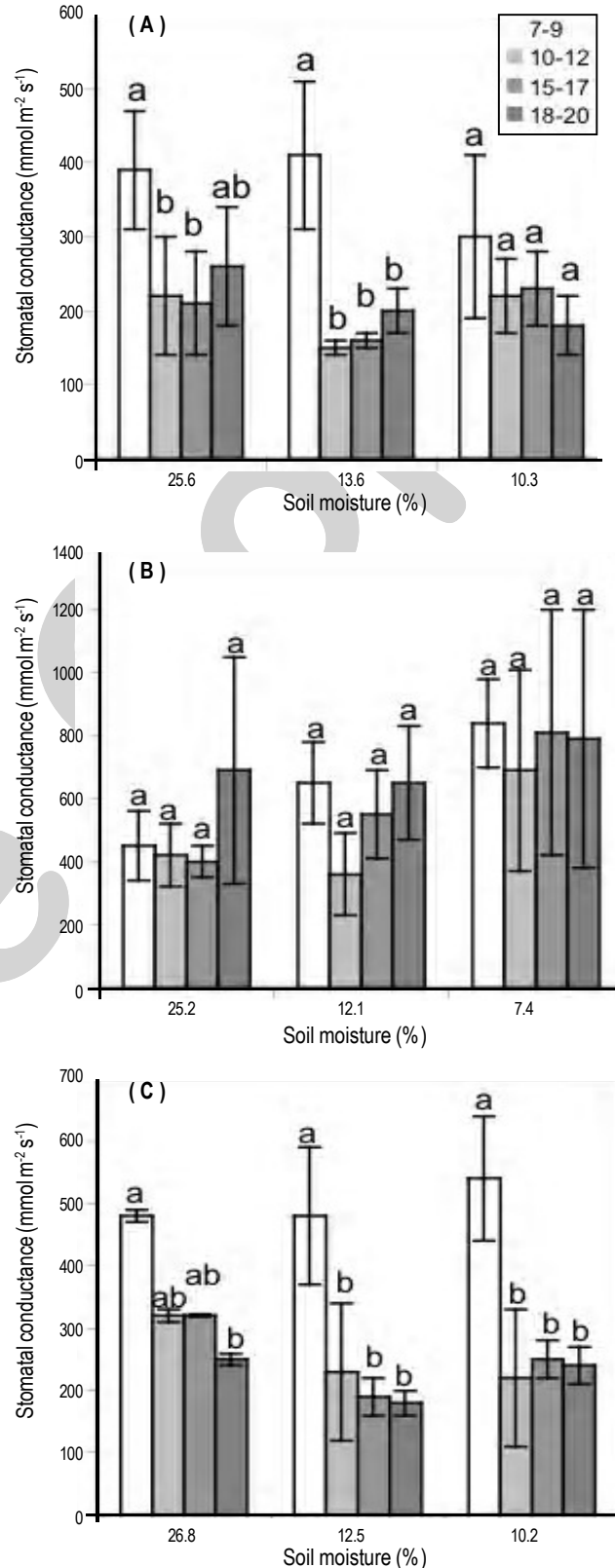


Fig. 2: Stomatal conductance in A) *Paulownia elongata*, B) *Paulownia fortunei* and C) *Paulownia imperialis* under different soil moisture conditions in the field (% humidity in soil), at different times (7-9, 10-12, 15-17, 18-20 hr)

fortunei was eight times higher than stomatal conductance in *S. terebinthifolius* (Stratton and Goldstein, 2001). The fine control of stomatal conductance in *P. elongata* and *P. imperialis* than in *P. fortunei* demonstrates a greater amount of plasticity. There is more plasticity in plants that grow well under low-moisture conditions (Williams *et al.*, 1995). Differences in photosynthesis were related to stomatal conductance. When stomatal conductance was low and the drought stress was elevated, both photosynthesis and transpiration decreased (Fig. 2). Yao (1990) presents similar transpiration values for *P. imperialis* and *P. fortunei*, and nearly 50% higher in *P. elongata*. Stomatal conductance depends on stomatal density and the size of the stomatal pores (Opik and Rolfe, 2005). Stomatal conductance in the *Paulownia* species was higher than stomatal conductance seen in other similar deciduous trees and bushes (Larcher, 1995).

Transpiration: In general, transpiration followed a pattern inverse to stomatal conductance during the day. Maximal rates of transpiration were measured in *P. fortunei* ($48.78 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), with *P. imperialis* and *P. elongata* showing less transpiration ($20 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$; Table 1). Stomatal conductance and transpiration in *P. fortunei* increased when soil moisture was lower. In *P. imperialis* and *P. elongata*, rates of transpiration did not reflect differences in stomatal conductance or soil moisture. This indicates that ranges did not change, even under decreased moisture conditions (Table 1). Similarly, decreases in transpiration and stomatal conductance with drought stress have been reported in deciduous species such as *Juglans regia* x *nigra*, which shows transpiration decreases from 1 to less 0.1 relative transpiration and decreases in stomatal conductance from 300 to $30 \text{ mmol m}^{-2} \text{ s}^{-1}$ under drought conditions (Cochard *et al.*, 2002). The increases in transpiration with higher radiation may be due to the associated increased leaf temperatures. Kaipainen and Pelkonen (2007) measured transpiration in *Salix* sp. and found transpiration to increase with temperature. *P. imperialis* and *P. elongata* survived after the duration of the experiments, but *P. fortunei* died six months after the tests were performed. This is likely due to the fact that *P. imperialis* and *P. elongata* have lower rates of transpiration (22.30 and $19.23 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ respectively) than *P. fortunei*, which has a transpiration rate of $48.78 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. Similar to the study by Tyree *et al.* (1991) of the rapidly growing tree *Schefflera morototoni*, we observed an elevated transpiration rate, which may prevent the formation of embolisms caused by high stomatal conductance and transpiration. This increased rate of transpiration allows survival in periods of severe water stress and high stomatal conductance, and prevents drought stress in the stems and the embolism. A similar situation may occur in *P. fortunei*, since this species has higher stomatal conductance and transpiration than *P. imperialis* or *P. elongata*.

Instantaneous water use efficiency: *P. imperialis* and *P. elongata* showed similar instantaneous water use efficiencies (WUE) at all moisture conditions tested (WUE of 0.79 and $0.71 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$ respectively) and *P. fortunei* showed a lower WUE ($0.07 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$; Fig. 3). These results differ from those of Yao (1990), where *P. fortunei* exhibited higher water use efficiency than *P. elongata* and *P. imperialis*. Water use efficiency was higher in *P.*

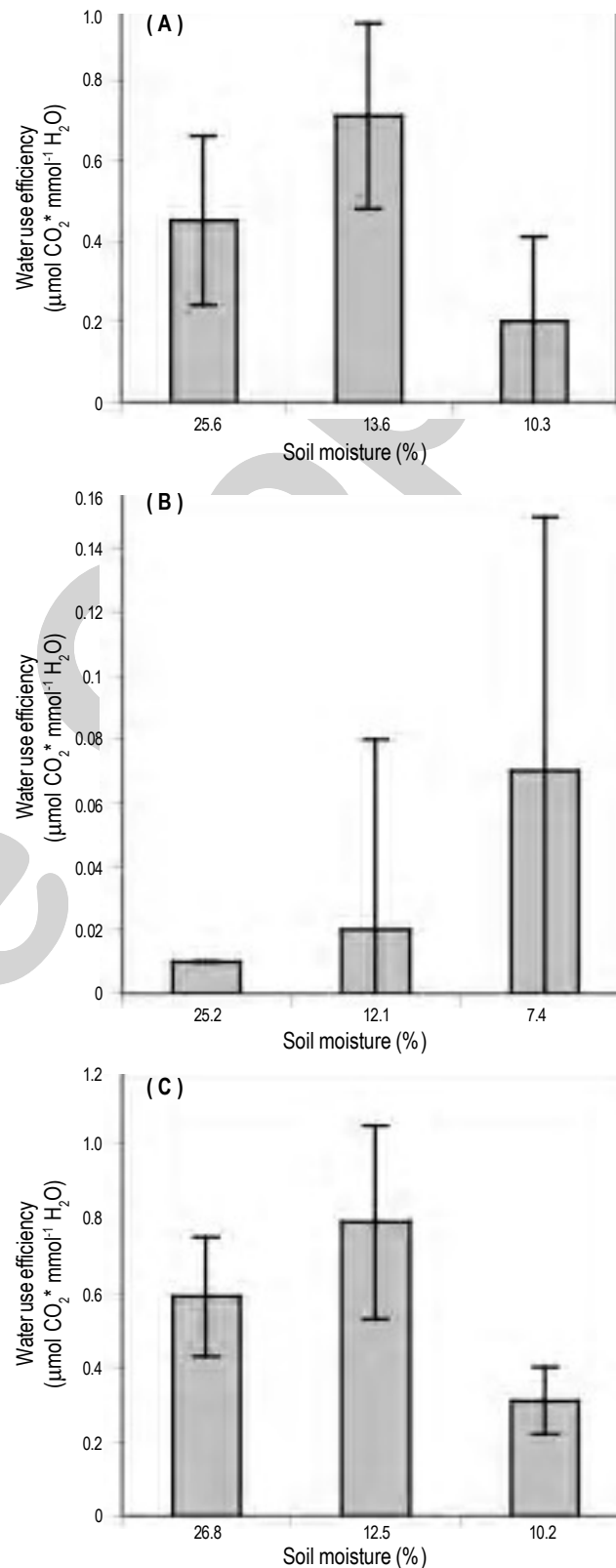


Fig. 3: Water use efficiency in (A) *Paulownia elongata*, (B) *Paulownia fortunei* and (C) *Paulownia imperialis*, under different soil moisture conditions in the field (% humidity in soil), at 7-9 hr

elongata and *P. imperialis* when environmental conditions were most favorable (7 to 9 am), and we obtained a value of 0.79 at 0.01 $\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$.

Similar to the study by Fatih *et al.* (2008) found water use efficiency higher in the morning. Instantaneous WUE was higher for *P. imperialis* and *P. elongata* than for *P. fortunei* because they experience elevated rates of photosynthesis and transpiration. Fig. 3 shows the extreme variation in instantaneous WUE between 7 and 9 am.

In general, plants increase water use efficiency under drought conditions by producing photosynthetic enzymes to increase the drawdown of internal CO_2 and by increasing the rate of photosynthesis, even during decreased stomatal conductance (Wright *et al.*, 2001). Increases in WUE with increased drought stress have been described in *Acer saccharum*, *Juglans nigra* and *Ulmus americana*, and the efficiency generally decreases once drought conditions are alleviated (Ni and Pallardy, 1991; Reich *et al.*, 1989). Instantaneous WUE in *P. elongata*, *P. fortunei* and *P. imperialis* were similar to the instantaneous WUE measured in other trees from northern China, which ranges from 0 to 2.5 $\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$ (Jiang *et al.*, 1999). However, the instantaneous WUE of all three species of *Paulownia* was lower than instantaneous WUE of *P. euphratica*, a tree that grows in more arid regions of Asia (0 to 5000 $\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$) (Chen *et al.*, 2006).

Studying physiological variables, we found that the species *P. imperialis* and *P. elongata* are somewhat tolerant to drought, and both are more drought resistant than the species *P. fortunei*. We conclude that the first two species are more suitable for growth under the semiarid conditions of Baja California Sur. Studies like ours employing physiological tests for drought-adapted growth and survivorship can be implemented for new or exotic species being introduced for the first time into new areas.

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