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Gas exchange, photochemical efficiency, and leaf water potential in three *Salix* species

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Abstract

Gas exchange, photochemical efficiency, and leaf water potential (Ψ_l) of *Salix matsudana* (non-indigenous species), *S. microstachya* and *S. gordejevii* (indigenous species) were studied in Hunshandak Sandland, China. Ψ_l of all the three species decreased from 06:00 to 12:00, and increased afterwards. *S. matsudana* showed higher values of Ψ_l than others. Net photosynthetic rate (P_N) and stomatal conductance (g_s) of *S. matsudana* were the lowest among all, with the maximum P_N at 10:00 being 75 % of that of *S. gordejevii*. Compared with the indigenous species, the non-indigenous *S. matsudana* had also lower transpiration rate (*E*) and water use efficiency (WUE). The values of F_v/F_m in all the species were lower from 06:00 to 14:00 than those after 14:00, indicating an obvious depression in photochemical efficiency of photosystem 2 in both non-indigenous and native species. However, it was much more depressed in *S. matsudana*, the non-indigenous tree. P_N was positively correlated to g_s and negatively related to Ψ_l. The relationship between g_s and vapour pressure difference (VPD) was exponential, while negative linear correlation was found between g_s and Ψ_l.

Additional key words: chlorophyll fluorescence; diurnal courses; leaf water potential; net photosynthetic rate; non-indigenous species; *Salix* species; stomatal conductance; transpiration rate; water use efficiency.

Introduction

In arid and semi-arid areas, precipitation, irradiance, and temperature fluctuate more than in moisture areas (Polis 1995). A majority of the indigenous plants developed in the arid regions possess the best adaptation strategies through a long-term evolution. For example, some plants modulate growth activity response to the environmental conditions (De Lillis and Fontanella 1992), some show very sensitive stomatal control of water loss (Tenhunen *et al*. 1990, Long *et al*. 1994, Sala and Tenhunen 1994), and others adjust the activity of photosystem 2 (PS2) to environment perturbations (Baker 1991). Therefore, a large number of indigenous species usually have fast and active adaptation in response to the instant changes of environmental conditions (Deans *et al*. 2003). However, the response pattern to environmental habitats from non-indigenous species is still poor understood in an arid area where exotic species are artificially planted.

Hunshandak Sandland is one of the four largest sandlands in China. Some 50 years ago, it was vigorous grassland. However, it has been so seriously degraded that most of the sandlands have become shifted. For the sake of stabilising the shifting sands, some non-indigenous trees, such as *Populus* spp. and *Salix matsudana* have been introduced to this region since ten years ago (Han *et al.* 2002). But their eco-physiological responses to the new habitats have not been clear to both ecologists and decision-makers for a long time. Therefore, a careful and comparative investigation on the eco-physiological adaptations of both indigenous and non-indigenous species, especially trees introduced from other places, is urgently needed. Our hypothesis of this study is that *S. microstachya* and *S. gordejevii* might be more tolerant to environmental press than *S. matsudana* in both gas exchange and water use capacity. The aims of this study are: (*1*) To compare the responses to environmental stresses of both photosynthesis and leaf water potential in two indigenous species and one non-indigenous species, all belonging to the same genus, *Salix.* (*2*) To analyse the

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Abbreviations: *E* – transpiration rate; g_s – stomatal conductance; LAR – leaf area ratio; LWC – leaf water content; P_N – net photosynthetic rate; PPDF – photosynthetic photon flux density; PS2 – photosystem 2; T_l – leaf temperature; VPD – vapour pressure difference between air and leaf; Ψ_l – leaf water potential.

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mechanism of eco-physiological adjustment to high irradiance in order to understand how those physiological processes are differently regulated in these species.

Materials and methods

Site description: The experiment was conducted at Hunshandak Sandland Ecosystem Research Station (43º56´47"N, 116º08´15"E) of the Chinese Academy of Sciences, based in Xilingel League of Inner Mongolia Autonomous Region of China. The prevailing climate is of the temperate arid and semi-arid type. The average annual temperature is about 1.7 °C. It receives annual precipitation of about 350 mm, with uneven distribution throughout the years, while evaporation is 2 000~2 700 mm annually. The annual total radiation time is 3 000~3 200 h.

Plants: *S. matsudana*, a mesophyte tree, was artificially introduced to Hunshandak Sandland approximately 10 years ago. *S. microstachya* and *S. gordejevii*, however, are indigenous shrubs widely spread in this area. Both tolerate high irradiance, severe drought, and serious windy sandstorms.

Physiological measurements: The experiments were conducted on clear days from 4 to 6 July 2002. For the photosynthetic photon flux density (PPFD) of experiment days and leaf temperature (T_l) see Fig. 1*AB*. Net photosynthetic rate (P_N), stomatal conductance (g_s), and vapour pressure difference (VPD) between air and leaf were determined with a portable gas exchange system (*LCA-4*, *ADC*, Hoddesdon, UK) in current foliage from each species. Chlorophyll fluorescence was measured using a portable plant efficiency analyser (*PEA*, *Hansatech*, King's Lynn, UK). F_0 (minimal fluorescence), F_m (maximal fluorescence), and F_v (variable fluorescence) were measured by keeping the leaf 30 min in dark before measurement. Leaf water potentials (Ψ_l) were determined with a Dewpoint Potential Meter (*WP4*, *Decagon Devices*, Pullman, USA). Three replicates of current foliage from each individual were measured after gas exchange measurements. Leaf water content (LWC) and leaf area ratio (LAR) were measured as described in Beadle (1993), on 5 June, 8 July, and 10 August 2002. Each measurement was determined by three replicates.

Data analysis: The large data set was entered into an *EXCEL* spreadsheet. Analysis of variance of leaf traits was carried out on each measurement and the significance of species determined by testing against the error mean square. The least significant differences between the means were estimated at 95 % confidence level. Calculations and linear regressions were performed in *SPSS*. Significant differences among different plants are reported at $p<0.05$, if not otherwise indicated.

Results

Changes in leaf water status: Ψ_l of both indigenous and non-indigenous species decreased from 06:00 to 12:00, and then increased. All three species reached their lowest values between 10:00 and 12:00, then the values increased and the steady status was maintained till 18:00 (Fig. 1*G*). Ψ_l of *S. matsudana* was higher than that of other indigenous species, while *S. microstachya* had the lowest values of Ψ_l during the daily course. In addition, *S. matsudana* had significantly higher LWC than *S. gordejevii* (Fig. 2*A*) and lower LAR than *S. microstachya* (Fig. 2*B*). But the variation in both LAR and LWC along with different development stage was not statistically significant in all the three species.

Diurnal courses in gas exchange: P_N of *S. matsudana* was lower than that of other species during the days, the maximal value at 10:00 being 75 % of that of *S. gordejevii* (Fig. 1*C*). The diurnal trends of P_N in *S. matsudana* and *S. gordejevii* showed typical two peaks, one around 10:00 and the other around 14:00. However, only one peak (at 10:00) was found in *S. microstachya*. Accordingly, the two indigenous species had higher g_s (Fig. 1*D*), *E* (Fig. 1*E*), and WUE (Fig. 1*F*) than the non-indigenous species. The trends of these parameters were similar to that of P_N.

Diurnal changes in chlorophyll fluorescence: The values of maximal photochemical efficiency of PS2 (F_v/F_m) were lowest in *S. matsudana* during the daily course, while *S. gordejevii* and *S. microstachya* showed similar values of F_v/F_m (Fig. 1*H*). An obvious depression in photochemical efficiency of PS2 was found in all the species from 06:00 to 14:00, the most serious depression being in *S. matsudana*. Only after 14:00 did they recover to normal levels in all three species.

Relationship between gas exchange and water status: P_N was linearly positively correlated to g_s (Fig. 3*A*), while a negative correlation was observed between P_N and Ψ_l (Fig. 3*C*). The relationship between g_s and vapour pressure difference (VPD) was exponential (Fig. 3*B*), while negative linear correlation was found between g_s and Ψ_l (Fig. 3*D*).

Discussion

The variation in the timing of rainfall in arid areas was regarded as the major stochastic factor influencing primary productivity (Noy-Meir 1973, Ludwig 1987). In the present study site, Hunshandak Sandland, the precipitation is highly unpredictable, especially in July. However, indigenous plants have special photosynthetic mechanism to adapt to such fluctuating environmental conditions through the long-term adaptation. For instance, the depression of g_s or PS2 photochemical efficiency, by which plants could reduce water transpiration or protect the photosynthetic apparatus from destroying, can result in decrease of net P_N (Knapp and Smith 1999, Jiang and Zhu 2001). In addition, reduced leaf water status also contributed to the P_N decrease (Brodribb and Field 2000). The reduced Ψ_l values play a key role in maintaining the plant water status within a security range in order to avoid xylem cavitation (Cochard *et al.* 1996). Nevertheless, in the tested three plant species the closing of stomata, coping with depression of PS2 photochemical efficiency, led to decreases in P_N at midday (Fig. 1*C,D,H*). Nevertheless, we found greater depression of these physiological traits for non-indigenous species than for the indigenous ones under the comparable conditions. This suggested that the non-indigenous species, *S. matsudana*,

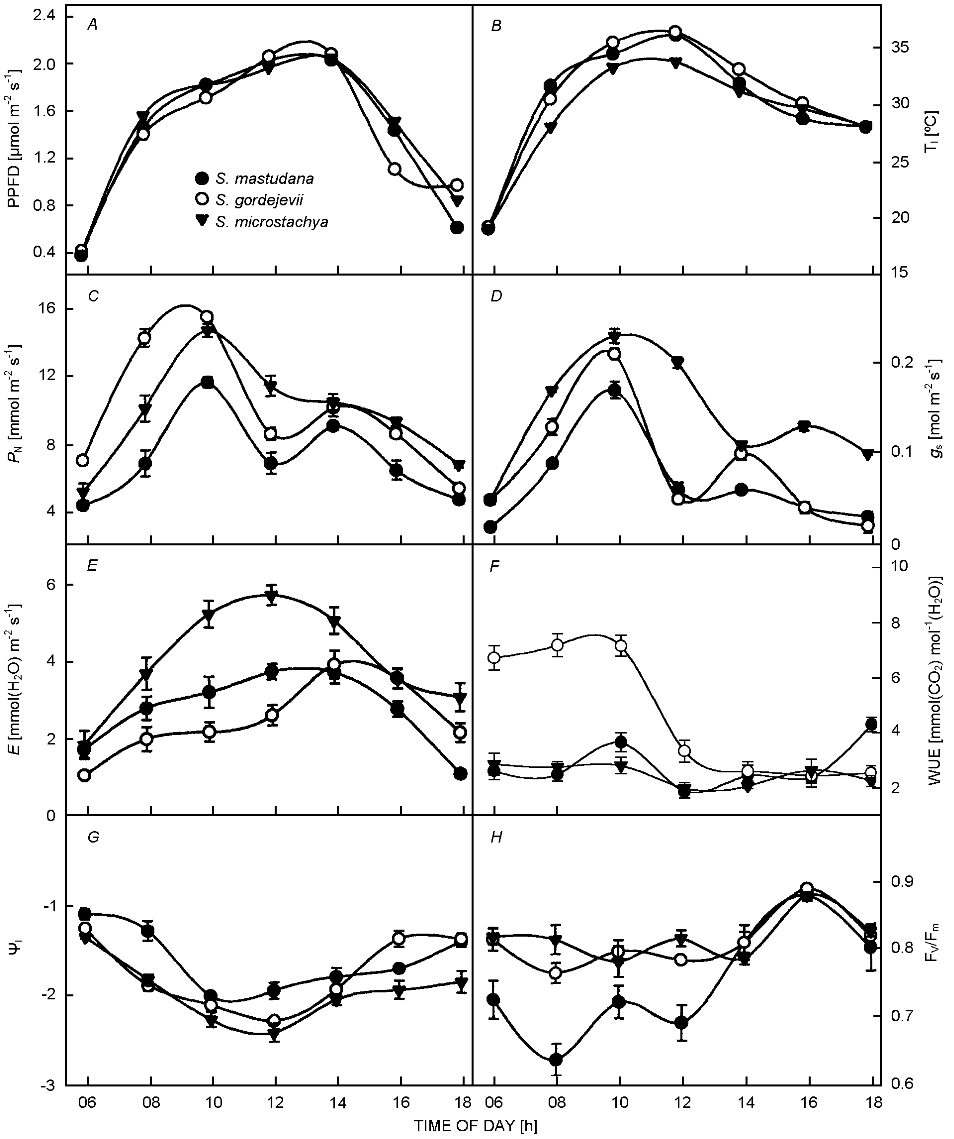

Fig. 1. Diurnal changes of photosynthetic photon flux density (PPFD), average leaf temperature (T_l), net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), water use efficiency (WUE), leaf water potential (Ψ_l), and photochemical efficiency of photosystem 2 (F_v/F_m) of three *Salix* species during the experiment days in Hunshandak Sandland. Means±SE.

may be less tolerant to high irradiance and temperature, and scarce soil water than other two indigenous species, *S. gordejevii* and *S. microstachya*, although they belong to the same genus.

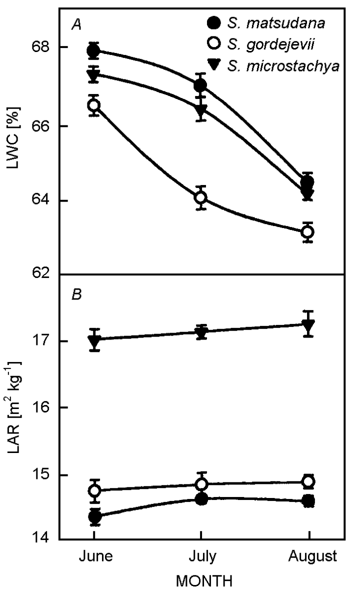

Fig. 2. Leaf area ratio (LAR) (*A*) and leaf water content (LWC) (*B*) of three *Salix* species from June to August in Hunshandak Sandland. Error bars are ±SE.

Generally, *S. matsudana* showed much lower P_N and WUE than others during the whole day, while high Ψ_l was noted. This trend consisted with the previous reports that species responding to their habitats present different eco-physiological characteristics although they can grow in similar habitats (Landnauser *et al.* 1997, Valladares *et al.* 1997). These trends could be explained as follows:

Firstly, leaf water potential (Ψ_l) was physically associated with the stomatal activity, especially for those settled in arid areas (Kozlowski *et al.* 1991, Comstock and Mencuccini 1998, Marcelo *et al.* 2000). Therefore, the low g_s of *S. matsudana* could be mainly derived from a higher Ψ_l (Figs. 1*G* and 3*D*), which results in a loss of hydraulic conductance in the soil-plant-atmosphere continuum (Küppers 1984, Reich and Hinckley 1989, Meinzer *et al.* 1995, Tyree *et al.* 1995). A small change of VPD between air and leaf led to a great change in g_s, as revealed by the exponential relationship between VPD and g_s (Fig. 3*B*). As a result, lowering g_s led to a great decrease in P_N for *S. matsudana*, as reflected by the linear negative relationship between P_N and g_s (Fig. 3*A*). The other two indigenous species showed a high resistance to cavitation in contrast to *S. matsudana*, which showed lower Ψ_l (Fig. 1*G*) and high g_s (Fig. 1*D*). Similar results have been documented in some woody species in analogous environments (Christiane and Ludger 1999, Brodribb and Field 2000). In addition, photosynthesis is partly limited by reduced intercellular CO_2 concentration due to stomata closure (Cornic and Briantais 1991, Quick et al. 1992). Our investigation suggested that the indigenous species would have higher endurance to both air and soil drought than the non-indigenous ones when drought accidents occur.

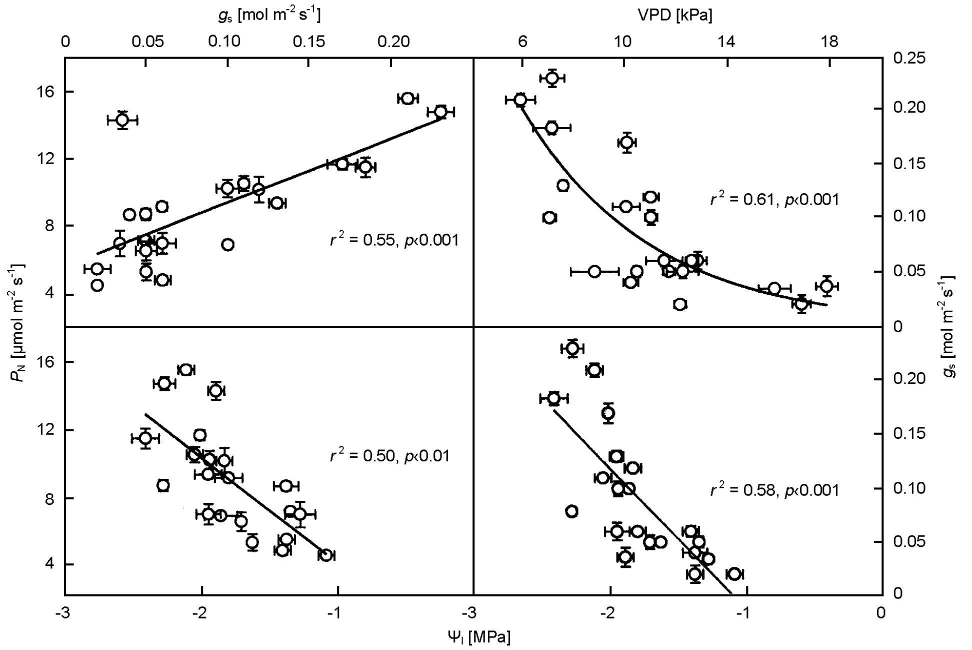

Fig. 3. Relationship between net photosynthetic rate (P_N) and stomatal conductance (g_s) (*A*) or leaf water potential (Ψ_l) (*C*), between g_s and vapour pressure difference (VPD) (*B*) or Ψ_l (*D*). Error bars are ±S.E.

Secondly, the decreased P_N could also be interpreted by the competition capacity for resource. Ψ_l also reflects the capability of plants to resist unfavourable environmental conditions, and is generally considered as a good index of water extraction capacity by the root system of plants (Aranda *et al.* 2000). Compared with the indigenous species, *S. matsudana* showed much higher Ψ_l under the analogous irradiance and leaf temperature. So it probably had a more inferior ability to tract enough water for synthesis and carbon skeleton than the indigenous species under a water stress, which could result in the lower carbon accumulation when it coexists with other indigenous species.

Thirdly, the lower P_N in carbon fixing of non-indigenous species might account for the living habitats. Ni and Pallardy (1991) reported that the hardwood species more tolerant to drought had larger gas exchange rates than the less tolerant ones. In this study, *S. matsudana* behaves like a mesophyte, which is indicated by high LWC and low LAR (Fig. 2*AB*). Hence it might have a lower photosynthetic capacity compared with the xerophyte species. Because the climate in Hunshandak Sandland is of arid and semi-arid type, precipitation greatly fluctuates among years. Therefore, *S. matsudana* should not be suggested, both practically and scientifically, as a good sandstorm defending species for Hunshandak Sandland.

In conclusion, under similar irradiance and leaf temperature the non-indigenous species *S. matsudana* showed lower P_N and g_s due to the higher Ψ_l than both indigenous species, *S. gordejevii* and *S. microstachya*. Correspondingly, lower WUE was found in the non-indigenous species. Additionally, higher maximal photochemical efficiency might reveal less tolerance of drought and high temperature in *S. matsudana*. Our results suggest that it would be difficult for *S. matsudana* to extract enough water from soil layers when water competition occurs owing to decreasing soil water availability in this area in future. *S. matsudana* should not be chosen for restoring degraded sand dunes in Hunshandak Sandland, but indigenous species should be taken into account firstly.

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