PHOTOSYNTHETICA 45 (1): 133-138, 2007

Photosynthetic response to precipitation/rainfall in predominant tree (*Ulmus pumila*) seedlings in Hunshandak Sandland, China

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Abstract

The responses of gas exchange and chlorophyll fluorescence of field-growing *Ulmus pumila* seedlings to changes in simulated precipitation were studied in Hunshandak Sandland, China. Leaf water potential (Ψ_{wp}), net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) were significantly increased with enhancement of precipitation from 0 to 20 mm ($p<0.01$), indicating stomatal limitation of *U. pumila* seedlings that could be avoided when soil water was abundant. However, P_N changed slightly when precipitation exceeded 20 mm ($p>0.05$), indicating more precipitation than 20 mm had no significant effects on photosynthesis. Maximum photochemical efficiency of photosystem 2, PS 2 (F_v/F_m) increased from 0.53 to 0.78 when rainfall increased from 0 to 10 mm, and F_v/F_m maintained a steady state level when rainfall was more than 10 mm. Water use efficiency (WUE) decreased significantly (from 78–95 to 23–27 μmol mol^{-1}) with enhancement of rainfalls. P_N showed significant linear correlations with both g_s and Ψ_{wp} ($p<0.0001$), which implied that leaf water status influenced gas exchange of *U. pumila* seedlings. The 20-mm precipitation (soil water content at about 15 %, v/v) might be enough for the growth of elm seedlings. When soil water content (SWC) reached 10 %, down regulation of PS2 photochemical efficiency could be avoided, but stomatal limitation to photosynthesis remained. When SWC exceeded 15 %, stomatal limitation to photosynthesis could be avoided, indicating elm seedlings might tolerate moderate drought.

Additional key words: drought stress; leaf water potential; maximum photochemical efficiency; water use efficiency.

Introduction

Rainfall is a main driving force in shaping different functional composition of vegetation and distribution of arid ecosystems (Smit and Rethman 2000). Plants adapt to their habitats with different ecological strategies in water utilization, as reflected by their diverse eco-physiological patterns (Prado and De Moreas 1997).

Plants in arid environments tend to adapt to drought by various physiological adjustments, such as leaf water status (Arndt *et al.* 2000, Marron *et al.* 2002, Franks 2004) and stomatal and non-stomatal limitations of photosynthesis (Cornic 2000, Flexas *et al.* 2004, Maroco *et al.* 2004). As a good example, plants can minimize vapour pressure deficit (VPD) between leaf and environments to cope with the drought disturbance in most arid areas (Gebre *et al.* 1998). Therefore, leaf water potential can be used as a suitable indicator of plant water status studies. Moreover, maximum photochemical efficiency of photosystem 2, PS2 (F_v/F_m) is widely recognized as a most sensitive parameter for detecting environmental stress (Govindjee 1995, Briantais *et al.* 1996). For tree species such as *Ulmus pumila* L. which grow in the semi-arid region, it is crucial to develop drought tolerance traits that enable them to survive under soil water deficits in long or short time scales (Tschaplinski *et al.* 1998).

Highlighting semi-arid areas, down regulation of gas exchange (Long *et al.* 1994, Ladjal *et al.* 2000, Jiang and Zhu 2001) and growth rate (Atkinson *et al.* 2000) have been extensively reported in different plant species. Effects of sand burial on survival, growth, gas exchange, and biomass allocation of *U. pumila* seedlings have also been evaluated (Shi *et al.* 2004). However, uncertainness still remains as concerns responses of natural trees to soil moisture in arid areas. Especially physiological traits affected by superabundant soil water or severe drought

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Received 7 July 2005, *accepted* 14 November 2005.

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Acknowledgements: This study was finically supported by the “973“ Project of the China (No. 2007CB106800), the Key Innovative Project of the Chinese Academy of Sciences (No. KZCX2-XB2-01), and Beijing Natural Science Foundation (No. 07D0143 and No. 8062017).

for short or long-term periods are seldom reported. The understanding of the traits such as photosynthesis, transpiration, water potential, and maximum photochemical efficiency of PS2 under different soil water condition will provide insights on the distribution patterns of trees in microhabitats. Unfortunately, such integrative study in semiarid regions is missing.

Hunshandak Sandland is blamed as the source of sand dust storms occurring in North China (State Environmental Protection Administration of China 2001). In order to solve such problems, the Chinese government has invested a great deal of funds for planting trees including *U. pumila*. Moreover, it seems that those *U. pumila* trees have acclimated to moderate drought on the sand dunes.

In Hunshandak Sandland, depression in plant net photosynthetic rate (P_N) can occur because of stomatal limitation under drought condition, but P_N again increases with higher soil water content as reported in *Agriophyllum squarrosum* (Liu *et al.* 2003) and *Hedysarum fruticosum* (Niu *et al.* 2004). Therefore, we chose natural elm seedlings distributed on the dunes in the same region to carry out this study. The aims of this research were: (*1*) to compare the leaf water potential, gas exchange, and maximum photochemical efficiency of PS2 under various rainfalls, and (*2*) to evaluate the drought tolerance of elm seedlings. Such an investigation will be helpful in protecting the natural elm seedlings in Hunshandak Sandland.

Materials and methods

Study area: The investigation was conducted at Hunshandak Sandy Ecosystem Research Station of the Chinese Academy of Sciences (42º13′N, 116º33′E). The prevailing climate is of temperate semi-arid type. Annual mean temperature is 1.7 °C with minimum in January (average –11.1 °C) and maximum in July (average 25.1 °C). The average annual rainfall is 365 mm, 80 % of which occurs in the growth season from June to August. The maximum midday irradiance is often >2 000 μmol m^{-2} s^{-1} and leaf surface temperature is >35 °C. The region is covered with shifting dunes, fixed dunes, lowland, and wetland. Soil water content of arid and humid seasons is listed in Fig. 1. There were no significant differences in soil moisture of soil layers deeper than 55 cm.

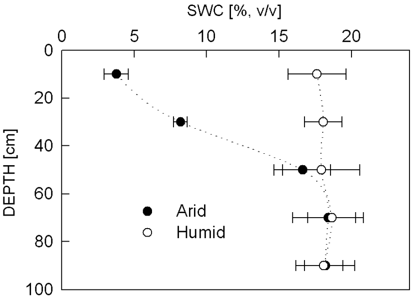

Fig. 1. Soil water content, SWC [% v/v] at different depths under different rainfall observed in 2002. “Arid” means no rainfall for at least 15 d and “humid” means 24 h after a rainfall of 30 mm.

Plants: Huanshandak Sandland is a typical sparse-elm grassland ecosystem. Vegetation is dominated by sandy grasses, with scattered elms (*U. pumila*) randomly distributed on the dunes. Elm is the predominant tree species accounting for 95 % of tree individuals (Li *et al.* 2003b). Four-years-old natural elm seedlings distributed on a protected fixed dune were sampled in a plot of 100×100 m. These seedlings had a height of 31.6±10.8 cm, root depth of 91.2±8.6 cm, and root horizontal length of 53.6±4.9 cm.

Experimental design: Plate plastics frames (600×600×600 mm, L×W×H) were vertically wedged into soil with 5 cm above ground to prevent horizontal soil water exchange. Each frame was a plot enclosing one sample seedling. To prevent rainwater, the target seedlings were sheltered for 15 d before simulated rainfall was applied. The water treatments were done twice at 18:00 on July 10 and August 8, each with seven “rainfall” levels, *i.e.* 0, 5, 10, 15, 20, 25, and 30 mm. Three seedlings for each “rainfall’ level were treated as three replications.

Soil water content (SWC): Prior to each measurement of leaf traits, SWC was monitored with a Soil Moisture Meter (*Delta-T*, Cambridge, England). Five records were taken at 20 cm depth intervals in a 0–100 cm soil layer.

Gas exchange was measured 1 d after watering. P_N, stomatal conductance (g_s), and transpiration rate (E) were determined with a portable Gas Exchange System (*LCA-4*, *ADC*, Hoddesdon, England) and water use efficiency (WUE) was calculated as the ratio of P_N to g_s. To avoid high temperature and irradiation stresses, the measurements were conducted from 10:00 to 12:00 when the photosynthetic photon flux density (PPFD) was 1 800±100 μmol m^{-2} s^{-1}, vapour pressure deficit (VPD) was 2.2±0.2 kPa, and leaf surface temperature was 35±0.5 °C. During operation, the natural orientation of the leaves was maintained as far as possible. Three youngest fully expanded functional leaves of each treated plant were used.

Chlorophyll (Chl) fluorescence: After gas exchange measurement, the same leaves which were used for gas exchange measurement were selected for fluorescence measurement using a portable Plant Efficiency Analyzer (*FMS-2*, *Hansatech*, King’s Lynn, UK). Maximum photochemical efficiency of PS2 (F_v/F_m) was recorded immediately after 30-min dark adaptation. A single saturation pulse of 3 000 μmol m^{-2} s^{-1} was utilized for measurements.

Leaf water potential (Ψ_{wp}) was measured with a Dewpoint Potential Meter (*WP4*, *Decagon Devices*, Pullman, WA, USA). Five youngest fully expanded elm leaves with their petiole similar to those used for gas exchange were sampled for measurement of Ψ_{wp}. he leaves were kept in a sealed plastic bag immediately after sampling and stored in an ice-box until transportation to the laboratory, about 1 500 m away from the experimental site.

Data analysis: Analysis of variance (ANOVA) of leaf traits was carried out on each measurement and the significance of plant mean square was determined by test against the error mean square. Least significant differences (LSD) were calculated for the determination of significant differences between individual treatments when the *F*-test of the ANOVA was significant at p=0.05. Each variable represented the mean of three replications. Statistical analyses were performed using the *SPSS* package (version *10*, *SPSS*, Chicago, IL, USA).

Results

SWC: Simulated rainfall increased SWC with enhancement of rainfall treatment from 0 to 30 mm. However, there was no significant difference between the 25 and 30 mm "rainfall" treatments (Fig. 2*B*).

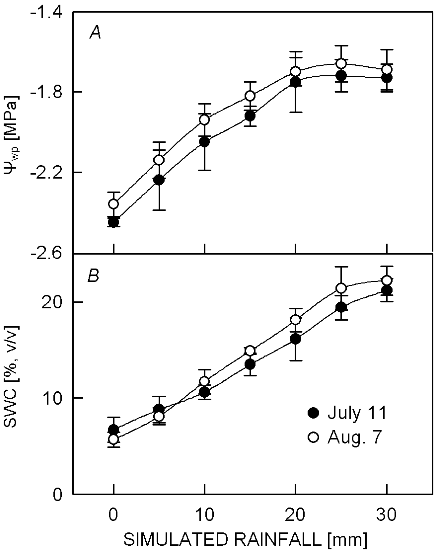

Fig. 2. Midday leaf water potential (Ψ_{wp}, *A*) of elm seedlings and 20–40 cm soil water content (SWC, *B*) on fixed dunes of Hunshandak Sandland under different simulated rainfalls. *Error bars* are ±S.E.

Ψ_{wp} of elm seedlings increased sharply with enhancement of rainfall treatment up to 20 mm; thereafter it increased slowly, and peaked at 25 mm. Ψ_{wp} was in steady state at 25–30 mm rainfalls (Fig. 2*A*).

Chl fluorescence: F_v/F_m of elm seedlings increased sharply from 0 to 10 mm rainfall, afterwards a non-significant increase was observed with further enhancement of rainfall treatment. The lowest values of F_v/F_m (0.51, July 11; 0.55, August 8) were observed at 0 mm while the highest F_v/F_m values (0.78–0.82) were observed at 10–30 mm rainfalls (Fig. 3).

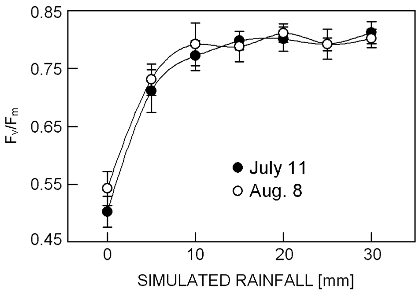

Fig. 3. Midday photochemical efficiency of elm seedlings on fixed dunes of Hunshandak Sandland under different simulated rainfall. *Error bars* are ±S.E.

Gas exchange and WUE: P_N increased with enhancement of simulated rainfalls from 0 to 20 mm, then it declined with further enhancement of rainfall. The lowest P_N was observed at 0 mm, while the highest (15 μmol m^{-2} s^{-1}, August 8) was found at 20-mm rainfall (Fig. 4*A*). g_s and *E* of the seedlings followed a similar trend over the rainfall treatments showing a gradual enhancement from 0 to 20 mm; thereafter it remained almost static with further increase in rainfall (Fig. 4*B*,*C*). WUE gradually decreased with enhancement of rainfall treatments; the highest WUE was observed at 0 mm, while the lowest was found at 30-mm rainfall (Fig. 4*D*).

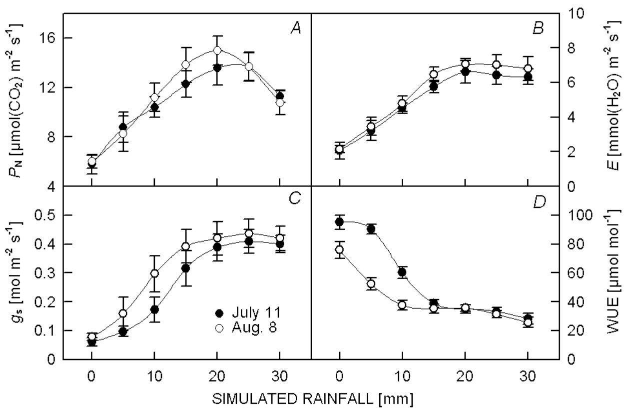

Fig. 4. Net photosynthetic rate, P_N, (*A*), transpiration rate, *E* (*B*), stomatal conductance, g_s (*C*), and water use efficiency, WUE (*D*) of elm seedlings in Hunshandak Sandland under different simulated rainfalls. *Error bars* are ±S.E.

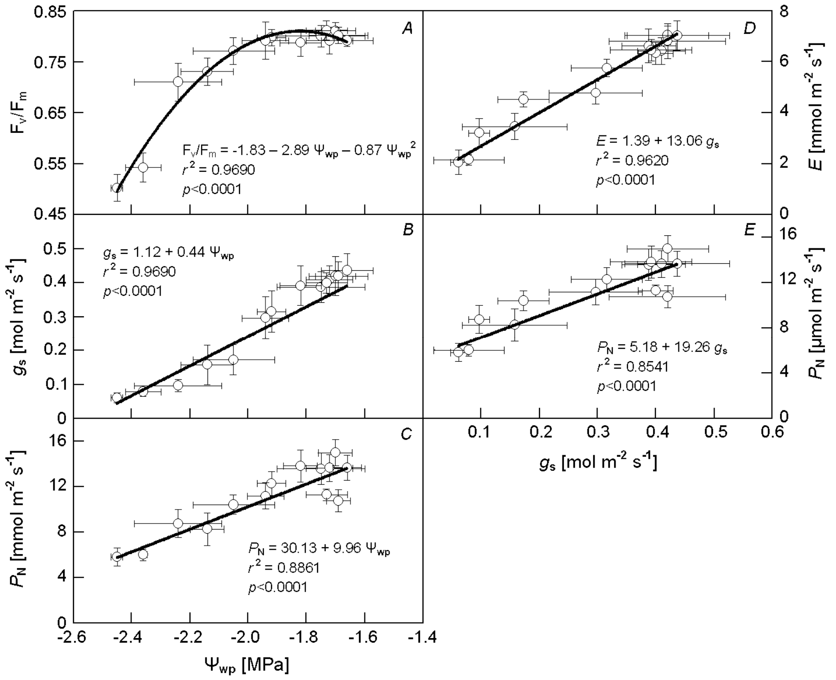

Fig. 5. Relationships between leaf water potential and photochemical efficiency of photosystem 2, F_v/F_m *vs.* Ψ_{wp} (*A*), stomatal conductance, g_s *vs.* Ψ_{wp}, (*B*), net photosynthetic rate, P_N *vs.* Ψ_{wp} (*C*), g_s *vs.* transpiration rate, *E* (*D*), and P_N *vs.* g_s (*E*) through the entire dataset of July 11 and August 8. *Error bars* are ±S.E.

Relationships between P_N, F_v/F_m, *E*, WUE, Ψ_{wp}, and g_s: The regression between Ψ_{wp} and F_v/F_m showed that maximum photochemistry efficiency of PS2 had significant quadratic relationship with Ψ_{wp} (Fig. 5*A*). Significant linear correlations were found between Ψ_{wp} and g_s (Fig. 5*B*), Ψ_{wp} and P_N (Fig. 5*C*), g_s and *E* (Fig. 5*D*), and g_s and P_N (Fig. 5*E*).

Discussion

Under drought stress, plants can decline the conductivity of water flow among the soil-plant-atmosphere water pathway (Lovisolo and Schubert 1998), which can reduce water loss and improve WUE. Specific hydraulic conductance is not only in the regulation of water losses by transpiration but also in carbon uptake (Aranda *et al.* 2005). Plants suffering drought can maintain leaf water balance by osmotic adjustment (Patakas and Noitsakis 1999, Shangguan *et al.* 1999), which is often reflected in decreases of Ψ_{wp} (Jongdee *et al.* 2002, Bucci *et al.* 2004). Down regulation of g_s is also considered as the drought tolerance indicator (Flexas and Medrano 2002, Silva *et al.* 2004). The drought response dominated by stomatal limitations accounts for about 75 % of the total limitation (Wilson *et al.* 2000). Our results showed that gradual reductions in Ψ_{wp}, P_N, and g_s of the elm seedlings were observed with both a decrease in SWC and rainfall (Figs. 2*A* and 4*A,C*). This indicates that stomatal limitation of *U. pumila* can be avoided when water supply is abundant.

Investigators have often observed the down regulations in F_v/F_m along a precipitation gradient (Karavatas and Manetas 1999, Miszalski *et al.* 2001). Drought-tolerant species display declines in midday g_s, and higher resistance to CO_2 influx, protecting through either proportional increase in non-irradiative dissipation of excess energy or photo-inactivation of PS2 (Martīnez-Ferri *et al.* 2000). The resistance of a particular plant parameter (*e.g.* F_v/F_m) to water deficit can be defined as the slope of the relationship between that parameter and a measurement of water deficit such as leaf water content. It is therefore likely that lower leaf water content of some plant species (Hsieh *et al.* 2002) correlates with lower soil water content. In this case, for a given change in soil water content, again the F_v/F_m of WT plants is more resistant to water stress. We found that F_v/F_m decreased significantly when soil water deficit occurred or Ψ_{wp} was lower than –2.0 MPa (Fig. 5*A*), and higher F_v/F_m values were observed when the "rainfall" was above 10 mm (Fig. 3), suggesting the damage of PS2 might occur only in severe drought season, *i.e.* elm seedlings tolerate moderate drought.

Water is one of the limiting environmental factors not only for the growth of plants (Souch *et al.* 1998, Yordanof *et al.* 2000), but also for the distribution of plants (Porporato *et al.* 2001). The fixation of shifting dune is vital for survival of elm seedlings; lowland and wetland are not suitable for the germination and growth of elms (Li *et al.* 2003a). All evidences of our investigation indicated that more "rainfall" than 20 mm was most appropriate for elm; however, higher soil water content could not improve the gas exchange features. This might be an important reason why elms are widely distributed in the semiarid regions.

Alternative approaches of plant drought stress responses such as the promotion of root elongation in response to soil drying (Sharp and Davies 1985), or altering stomatal sensitivity to changes in soil water content are the most documented ways of avoiding water deficit. In this context, the decline of g_s (Fig. 4*C*) and deeper root system (91.6 cm in vertical direction *vs.* 53.6 cm in horizontal direction) of elm seedlings may be an important survival opportunity.

The environmental cost of water use by plantations must be weighed against their economic and environmental values in regions where water resources are limited (Morris *et al.* 2004). The annual rainfall of less than 350 mm is inadequate for forest distribution. Here, sparse-elm (*U. pumila*) grassland is the characteristic landscape and elms are more ecological and economic tree species to prevent removal of dunes. *U. pumila* can maintain higher water use efficacy in arid season (Fig. 4*D*) and should be first considered for the revegetation in Hunshandak Sandland.

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