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Gas exchange and water use efficiency of three native tree species in Hunshandak Sandland of China

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Abstract

Only three tree species, *i.e. Ulmus pumila*, *Malus baccata,* and *Prunus padus*, are distributed in Hunshandak Sandland (HS) in Inner Mongolia, China. Field studies of gas exchange and chlorophyll (Chl) fluorescence of these three tree species were conducted in three arid periods of growth season 2002. Net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and F_v/F_m of *U. pumila* were higher than in *M. baccata* and *P. padus*, especially in the midday. Hence *M. baccata* and *P. padus* were more sensitive to high temperature and irradiance than *U. pumila* in HS. This may be a reason for wide distribution of *U. pumila* in HS. *M. baccata* and *P. padus* are adapted to the back slope of fixed dune, because the micro-habitat is relatively cool and less irradiated than the slope facing sun. Water use efficiency (WUE) of *U. pumila* was lower than that of *M. baccata* and *P. padus*, and thus *U. pumila* does not form forests in this region, because the soil is dry.

Additional key words: drought; ecological restoration; high irradiance; high temperature; *Malus baccata*; photochemistry efficiency; photosynthesis; plant tolerance; *Prunus padus*; *Ulmus pumila*; water use efficiency.

Introduction

Typical two-peak curves are often found in diurnal photosynthetic dynamics of temperate, broad-leaved trees. The down regulation of photosynthesis was explained as the suppression by high irradiance (HI) or high temperature (HT) (Matos *et al.* 1998). However, the patterns of change in photosynthesis induced by HI vary in different species.

Different species in arid areas adapt to the environment by different eco-physiological or structural adjustments at different time scales, *e.g.* by modulation of growth activity (De Lillis and Fontanella 1992, Chimenti *et al.* 2002), maximal carbon fixation early and later in the day (Jiang and Zhu 2001), sensitive stomatal control of water loss (Gabriel 2000, Flexas and Medrano 2002), or by adjustment of activity of photosystem 2 (PS2) to environmental stress (Baker 1991, Medrano *et al.* 2002). In some desert ecosystems, drought, HI (photosynthetic photon flux density, PPFD > 2 000 μmol m^{-2} s^{-1}), and HT (T_{leaf} > 45 °C) for long periods may dramatically influence the gas exchange patterns of plant and limit their production (Jiang and Zhu 2001). Such environmental conditions seldom occur in subtropical areas but can frequently occur in arid or semi-arid areas, especially in deserts. However, the studies on the relation of drought, HT, and HI on characteristics of gas exchange and photochemical efficiency are rare.

HS area is one of the five major sand areas with desert characteristics of China that face serious desertification problems. This area is covered mostly with shifting sand dune, fixed sand dune, and lowland. The sand of this area is the major source of sandstorm to Beijing (State Environmental Protection Administration of China 2001). Most plant species in HS are native. There are more than 400 plant species in this region, among them *Ulmus pumila*, *Malus baccata*, and *Prunus padus* are widely distributed trees and *U. pumila* is the major species with > 95 % proportion.

Physiological characteristics of these sand tree species had not been studied previously. In the present study, we compared the responses of photosynthesis of these three tree species to drought, HT, and HI during growth season at their natural habitat.

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Materials and methods

Site: The study was conducted in HS in Inner Mongolia Autonomous Region, North China (42º23′N, 116º23′E). The prevailing climate is of temperate semi-arid type, with an annual mean temperature of 1.7 °C and average temperatures of –11.1 °C (January) to 25.1 °C (July), annual precipitation of 250-350 mm, and evaporation of >1 950 mm. Soil moisture of 40-100 cm in the fixed dune ranged from 10 (arid season) to 18 (humid season) % (v/v). It was always lower than 15 % during the plant growth season. However, the arid sandy habitats in HS are suitable for the survival of different plant species and formed characteristic landscapes of *U. pumila* grassland. Native tree species, such as *U. pumila*, *M. baccata*, and *P. padus,* are of great ecological and economic importance, not only because they can survive in this region but also they can stop the disposal of sands by wind. In the centre of HS we selected three fixed dunes with typical distribution of the three plant species, and investigated five-year-old seedlings.

Photosynthesis: The experiments were done in three vegetation periods, *e.g.* early summer (17 June), mid summer (7 July), and late summer (11 August) of 2002. Incident photosynthetic photon flux density (PPFD), air temperature (T_a), net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were determined with a portable gas exchange system (*LCA-4, Analytical Development Company*, Hoddesdon, England). Water use efficiency (WUE) was calculated as P_N/E. Natural orientation of the typical functional leaves was maintained during measurements. The experiments were done on clear days. Both the temperature and irradiance were higher on 7 July than on 17 June and 11 August (Fig. 1). Diurnal course of gas exchange of the three species was monitored at 2-h intervals. Five replications were made.

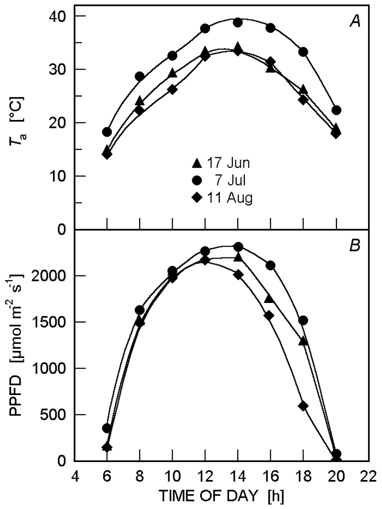

Fig. 1. Diurnal course of average incident photosynthetic photon flux density, PPFD (*A*) and air temperature, T_a (*B*) of early summer (17 June),mid summer (7 July), and late summer (11 August) in Hunshandak Sandland.

Chl fluorescence: F_0, F_m, F_v, and F_v/F_m were measured or calculated with a portable *FMS-2* Plant Efficiency Analyser (*PEA*, *Hansatech*, King's Lynn, UK). Prior to measurements, the samples were dark-adapted for 30 min using clips. To make a record, the *PEA* sensor unit is held over the clip and the shutter opened. The single push button activates the HI LED array within the sensor head providing a maximum irradiance of 3 000 μmol m^{-2} s^{-1}, sufficient for F_m to be reached in all species investigated. Data acquisition is triggered at a rate of 100 kHz (10 μs intervals) with 12-bits resolution. As the fluorescence induction slows down, lower acquisition rates are applied for the remaining recording season. All data were put into a portable computer where customary 32-bit *Windows*® software permitted re-scaling.

Soil moisture in 0-100 cm layer was measured with a soil moisture meter (*HH*$_2$, *ΔT*-device, Cambridge, England), and the records were taken for every 10 cm interval (Fig. 2). Soil moisture in early summer was lower than that in middle and late summer.

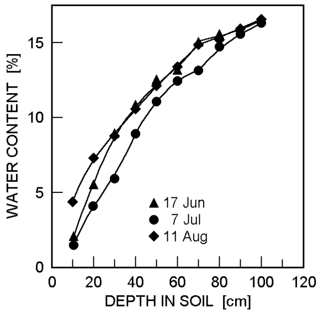

Fig. 2. Average soil moisture in different depths in early summer (17 June), mid summer (7 July), and late summer (11 August).

Data analysis: The large data set of F_v/F_m, P_N, g_s, E, and WUE was entered into an *EXCEL* spread sheet in *Office XP*. Analysis of variance of leaf traits was carried out on each measurement. The least significant differences (LSD) between the means were estimated at 95 % confidence level. Calculation and linear regression were performed in a *Sigma-plot 8.0* program. Significant differences among different plant species were reported at $p < 0.05$ if not otherwise indicated.

Results

Daily courses of gas exchange under HT and HI: In the midday, PPFD was 2 100-2 300 μmol m^{-2} s^{-1}. PPFD values were in the order of mid summer > late summer > early summer (Fig. 1*B*). The maximum T_a in the midday was 32-38 °C, and it was higher in mid summer (38 °C); however, there was no significant difference between early and late summer for maximum T_a of 32 °C (Fig. 1*A*).

Diurnal courses of P_N of the three tree species showed typical two peaks, one at 08:00–10:00 and the other at 16:00–18:00. P_N of *U. pumila* was significantly higher than those of *M. baccata* and *P. padus*. For the time after 10:00, a serious decline in P_N was found in each species, and valleys appeared at 14:00 (Fig. 3*D,H,L*).

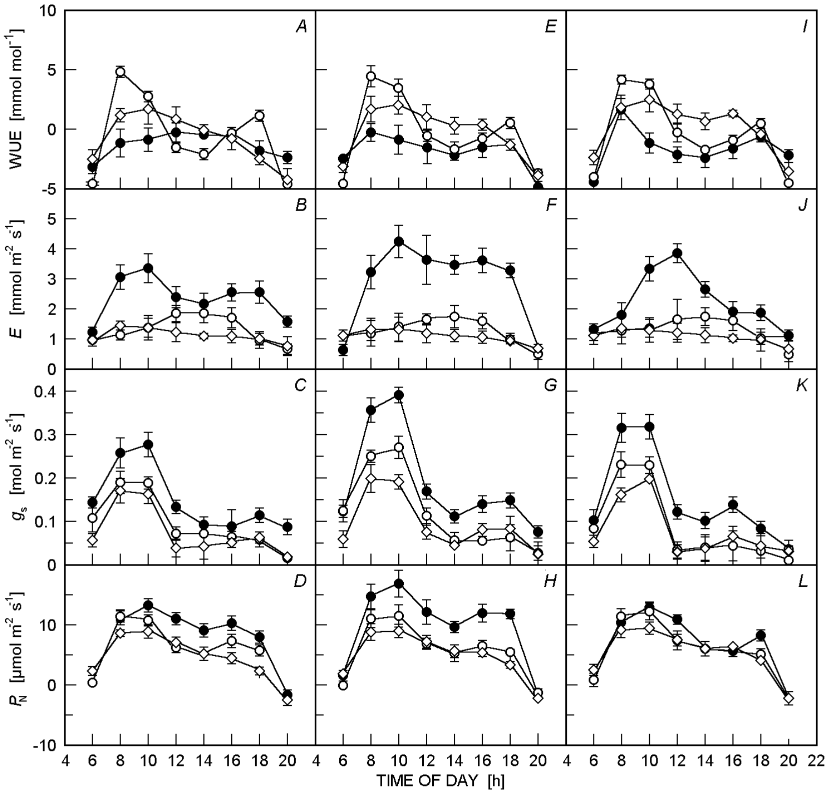

Fig. 3. Diurnal courses of net photosynthetic rate, P_N (*D, H, L*), transpiration rate, *E* (*B, F, J*), water use efficiency, WUE (*A, E, I*), and stomatal conductance, g_s (*C, G, K*) of *U. pumila* (●), *M. baccata* (○), and *P. padus* (◊) measured on 17 June (*A, B, C, D*), 7 July (*E, F, G, H*), and 11 August (*I, J, K, L*) in Hunshandak Sandland.

The values of g_s were parallel to those of P_N (Fig. 3*C,G,K*). Again, the g_s values of *U. pumila* were significantly higher ($p < 0.05$) than those of *M. baccata* and *P. padus*. The same tendency was found in the diurnal courses of *E* (Fig. 3*B,F,J*). However, the diurnal courses of WUE were different: in early summer (June 17), a single peak was observed in *U. pumila* and *P. padus* and a double peak in *M. baccata.* In the morning, WUE of

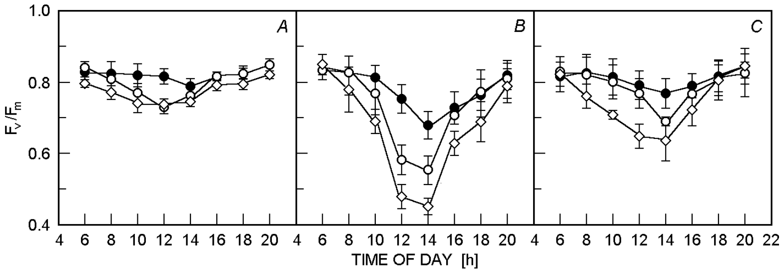

Fig. 4. Diurnal courses of photochemical efficiency (F_v/F_m) of *U. pumila* (●), *M. baccata* (○), and *P. padus* (◊) measured on 17 June (*A*), 7 July (*B*), and 11 August (*C*) in Huanshandak Sandland.

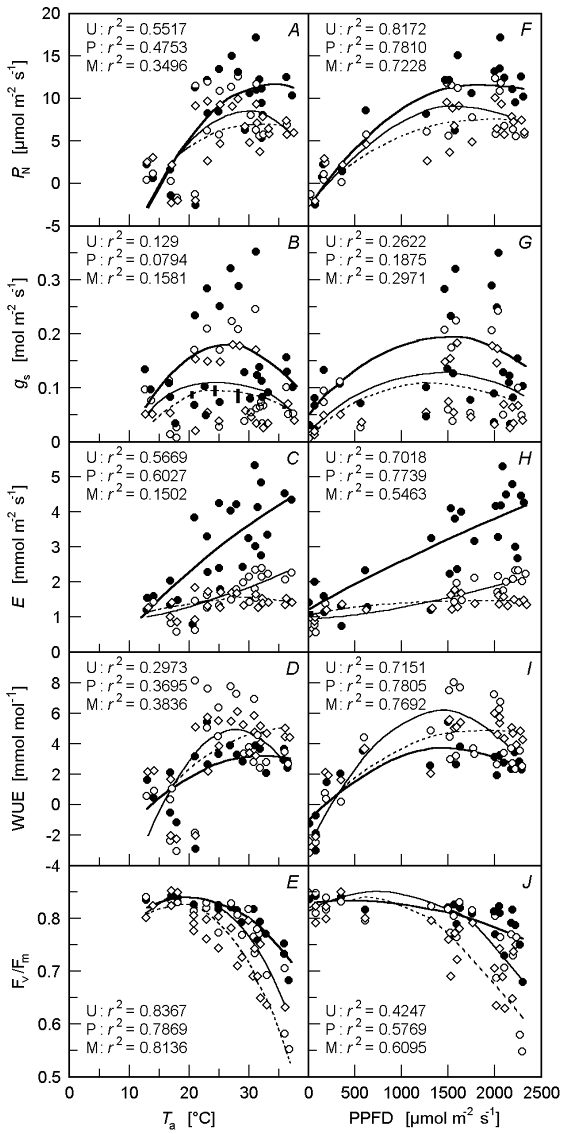

Fig. 5. Relationship between T_a and F_v/F_m, WUE, E, g_s, and P_N, and relationship between T_a and F_v/F_m, WUE, E, g_s, and P_N using values measured in early, mid, and late summer of *U. pumila* (● and —), *M. baccata* (○ and —), and *P. padus* (◊ and - - -) with the expressions of y = ax^2 + bx + c and r^2 ("U" for *U. pumila*; "M" for *M. baccata*; and "P" for *P. padus*) were listed (n = 24).

U. pumila was lower than that of the other species. In midday, the difference with *P. padus* or *M. baccata* was not significant (Fig. 3*A*). In the mid and late summer (July 7 and August 11), double peaks appeared for each species. WUE of *U. pumila* was lower ($p < 0.05$) than those of *P. padus* and *M. baccata* in the morning or midday (Fig. 3*E,I*).

Chl fluorescence: Photochemical efficiencies of PS2 (F_v/F_m) of the three species were similar in the morning or evening, and their values were close to 0.80; moreover, the lowest F_v/F_m was found at 14:00 under both HI and HT (Fig. 4*A,B,C*). Diurnal courses of F_v/F_m values of those three tree species in early summer did not decrease as sharply as in mid and late summer. From 08:00 to 14:00, F_v/F_m values of *U. pumila* were higher than those of *M. baccata* and *P. padus* ($p < 0.05$).

Response of gas exchange and photochemical efficiency to T_a and PPFD: Changes of F_v/F_m, WUE, E, g_s, and P_N under different air temperature or irradiance showed curvilinear regression with expressions of y = ax^2 + bx + c (Fig. 5). P_N values of *U. pumila* were higher and did not decrease when T_a exceeded 30 °C, however, those of *M. baccata* and *P. padus* were relatively low and declined under HT (Fig. 5*A*). P_N values under HI (above 1 500 μmol m^{-2} s^{-1}) had the same tendency as under HT (Fig. 5*F*).

When T_a exceeded 25 °C or PPFD exceeded 1 500 μmol m^{-2} s^{-1}, g_s of the three tree species decreased, values of *U. pumila* being higher than those of *M. baccata* and *P. padus* (Fig. 5*B,G*). E values increased with the increase of T_a and PPFD, especially for *U. pumila*, and values of *U. pumila* were higher than those of *M. baccata* and *P. padus* (Fig. 5*C,H*). WUE of *U. pumila* was lower than that of *M. baccata* and *P. padus* when T_a exceeded 20 °C and PPFD exceeded 500 μmol m^{-2} s^{-1} (Fig. 5*D,I*).

With the increase of T_a and PPFD, F_v/F_m values decreased; this decrease was sharper when T_a exceeded 25 °C or PPFD exceeded 1 500 μmol m^{-2} s^{-1}. Among the three tree species, WUE of *U. pumila* decreased more slowly than that of *M. baccata* and *P. padus* (Fig. 5*E,I*).

Discussion

Gas exchange of desert species responds to environment (Oechel *et al.* 1981, Filella *et al.* 1998, Zunzunegui *et al.* 1999, Jiang and Zhu 2001). Down regulation of g_s has been considered as the drought tolerance indicator (Sparks and Black 1999, Atkinson *et al.* 2000). However, when considered independently from deciduous tree leaf age, the drought response was dominated by stomatal limitations, accounting for about 75 % of the total limitation (Wilson *et al.* 2000). The general response patterns we report here were similar to those found in former studies. The serious depression in P_N (Fig. 3*D,H,L*) in the midday was due to the closure of stomata as shown by the decrease of g_s (Fig. 3*C,G,K*).

Values of F_v/F_m of different plant species differ greatly under environmental stress (Nieva *et al.* 1999). Chl fluorescence parameters are down regulated along the environmental gradient (Karavatas and Manetas 1999). In response to midday heat and irradiance stress, the drought-tolerant species show a decline in midday g_s, and the higher resistance to CO_2 influx in needles does not result in either a proportional increase in non-radiative dissipation of excess energy or photo-inactivation of PS2 (Martínez-Ferri *et al.* 2000). However, steady-state Chl fluorescence also shows a high dependence on g_s (Medrano *et al.* 2002). We found that F_v/F_m of the three species decreased significantly at HT or HI, especially in *M. baccata* and *P. padus* (Fig. 4), which implied the damage of PS2 in these species. Nevertheless, the relatively high values of F_v/F_m in *U. pumila* in hot summer (Fig. 4*B*) suggested another mechanism of depression of photosynthesis, *i.e.* the down regulation of PS2. This destruction was recoverable, since the values could reach their normal values in the evening. On the other hand, PS2 of *M. baccata* and *P. padus* might be damaged under HT and HI, although F_v/F_m values could reach their normal values in the evening. Those two species showed different patterns in gas exchange and fluorescence values, because their values decreased more sharply than that of *U. pumila*. Moreover, *U. pumila* could keep higher P_N than *M. baccata* and *P. padus* in the midday (Fig. 3*D,H,L*, Fig. 5*A,F*), which implies that *U. pumila* can be widely distributed in HS; on the other hand, *M. baccata* and *P. padus* are adapted to the back slope of fixed dune, because the micro-habitat is relatively cooler and less irradiated than the slope facing sun.

The deficit of water is a restrictive factor for plants in any arid region. Therefore, the study of stomatal biology and WUE is central for understanding the physiology of plants (Davies *et al.* 2002, Webb and Baker 2002), such as maize (Kang *et al.* 2002, Liu *et al.* 2002) and oak (Ponton *et al.* 2002). Values of g_s (Fig. 3*C,G,K*) and *E*, (Fig. 3*B,F,J*) of *U. pumila* were higher than those of *M. baccata* and *P. padus*, however, WUE of *U. pumila* was significantly lower than in the other two species, which implies that *U. pumila* can not form forest in this region, because the soil is dry.

Because the severe sand dust storms threaten the ecological safety of North China, some trees should be planted in HS as an ecological barrier to stop these storms. Therefore, sparse elms (*U. pumila*) grassland is the characteristic landscape in HS, and *U. pumila* is a most ecological and economic tree species in this region. It can keep relatively high P_N and photochemical efficiency under drought, HT, and HI (Fig. 5*A,F,E,I*). In the practices of vegetation restoration of HS, the native *U. pumila* should be preferentially chosen, because it will suffer the stress existing here.

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