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Different patterns of gas exchange and photochemical efficiency in three desert shrub species under two natural temperatures and irradiances in Mu Us Sandy Area of China

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Abstract

Field studies of gas exchange and chlorophyll fluorescence of three desert shrub species, *Hedysarum fruticosum* var. *mongolicum*, *Artemisia ordosia,* and *Salix pasmmophylla*, showed different patterns under different leaf temperature (T_l) and incident photosynthetic photon flux density (PPFD). *H. fruticosum* var. *mongolicum* and *A. ordosia* exhibited higher P_N and g_s than *S. pasmmophylla*, especially under very high T_l (>46 °C) and high PPFD (>2 100 μmol m^{-2} s^{-1}) in hot summer. The decreases of P_N with the diurnal course were due mainly to stomata closure. However, P_N of *S. pasmmophylla* was seriously depressed by very high temperature from midday to evening as shown by the negative P_N in hot summer, whereas none of such depression was found in spring. Maximal spring photochemical efficiency of photosystem 2 (PS2), *i.e.*, F_v/F_m, was the lowest at 16:00, indicating the injury of PS2 by heat at this stage. In hot summer again, all the three shrubs underwent pronounced midday depression of P_N and g_s, while in spring they showed a one-peak response. And the first peak appeared 2 h earlier in hot summer than in spring for all the three shrubs. It was the high temperature that led to the different patterns of gas exchange and the serious depression of P_N in *S. pasmmophylla. H. fruticosum* var. *mongolicum* and *A. ordosia* were much more tolerant to heat and high irradiance than *S. pasmmophylla*, which fixed most of CO_2 at the fast growing stage in spring. Nevertheless, in hot summer it had to survive the severe hot environment through strong respiration and storage of CO_2 only in the early morning.

Additional key words: *Artemisia ordosia*; chlorophyll fluorescence; diurnal courses; *Hedysarum fruticosum* var. *mongolicum*; high irradiance; high temperature; photosynthetic rate; photosystem 2; stomatal conductance; *Salix pasmmophylla*.

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 or temperature (*e.g.*, Matos *et al.* 1998, Zhang and Gao 1999). However, the patterns of changes in photosynthesis induced by high irradiance vary in different species, especially in different ecotypes. Under similar temperature, the irradiances inducing depression of photosynthesis in mesophyte species may not affect xerophyllous species. Meanwhile, under similar irradiances, different temperatures may have different effects on the functioning of photosynthesis (Pastenes and Horton 1996).

Different species in the 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), maximal carbon fixation early and late in the day, sensitive stomatal control of water loss (Tenhunen *et al.* 1990, Long *et al.* 1994, Sala and Tenhunen 1994), or by adjustment of activity of photosystem 2 (PS2) to environmental perturbations (Baker 1991). In some desert ecosystems, drought, high irradiance (PPFD >2 000 μmol m^{-2} s^{-1}), and high temperature (T_l >45 °C) for short or long periods may dramatically influence the gas exchange patterns of plants and limit their production. Such environmental conditions seldom occur in subtropical areas but can frequently occur in arid or sub-arid areas. However, the study on the relation of both very high temperature and PPFD on the pattern of gas exchange of different sub-arid species received less attention in the past years.

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Abbreviations: Chl – chlorophyll; F_v/F_m – maximal photochemical efficiency of photosystem 2; g_s – stomatal conductance; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS – photosystem; T_l – leaf temperature.

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In the present study, therefore, we analysed the responses of photosynthesis of some desert shrubs to both the high irradiance and high temperature in a natural site. Our hypothesis was that *A. ordosica* and *H. fruticosum* var. *mongolicum* would present a more heat-tolerant gas exchange pattern than *S. pasmmophylla*, since the latter species is an exotic one. And, that this difference might be even bigger under severe stress (*e.g.*, very high temperature). We studied their leaf gas exchange and chlorophyll (Chl) fluorescence under normal (spring) and hot (summer) conditions in their natural habitats, in order to understand whether these eco-physiological processes were differently regulated in the species studied.

Materials and methods

Study area: The experiment was conducted in Mu Us Sandy Area (37°20'~39°50'N; 107°10'~111°45'E), Inner Mongolia Autonomous Region of China, which is in a warm desert area of China. The main features of environment and climates are available in Jiang and He (1999). Because of the extensive coverage of sand and remarkable landscape heterogeneity, the substrates here are greatly diversified, creating the highly varied microhabitats (Chen and Xie 1994), with shifting and fixed sand dunes, lowland and wetland being the main habitats. Shrub species such as *H. fruticosum* var. *mongolicum*, *S. pasmmophylla*, *A. ordosia*, *Sibina vulgaris*, *Caragana intermedia*, and *Gynanchum komarovii* are common in shifting sandy dunes. Such environments are characterised with better water availability beneath the sand layer. However, environmental variables here change greatly during the season, severe temperature stress being common in mid-summer (Guo *et al.* 2000). Table 1 compares some environmental variables of two seasons (spring and summer) in a shifting sandy dune where the experiment was conducted.

Plants: Some 20 years ago, *S. pasmmophylla* (*Salicaceae*), shallow-rooted exotic shrub, was artificially planted from cuttings to stop windy sands in the shifting sand dunes. For the western parts of Mu Us Sandy Area with precipitation of <250 mm, no individuals of this species could be found. *H. fruticosum* var. *mongolicum* (*Leguminosae*) and *A. ordosica* (*Compositae*), however, are deep-rooted native shrubs which can tolerate severe drought, and are wide spread in the whole sandy areas.

Photosynthesis measurement: The experiments were done during 29 and 30 May 1998 (late spring, the normal season for sandy plants), and 24 and 25 July (middle summer, with the hottest days of the year) of 1999. Incident PPFD, leaf temperature (T_l), net photosynthetic rate (P_N), and stomatal conductance (g_s) were determined with a portable gas exchange system (*LCA*-4, *ADC*, Hoddesdon, England). As far as possible, the natural orientation of the leaves was maintained during measurements. The experiments were done on clear days, but the species in the midsummer experienced very high temperature and strong irradiance. Daytime course of gas exchange of the three species was monitored at 2-h intervals.

Chl fluorescence was measured using a portable plant efficiency analyser (*PEA, Hansatech*, King's Lynn, UK). F_0 (minimal fluorescence), F_m (maximal fluorescence), F_v (variable fluorescence), and F_v/F_m (maximal photochemical efficiency of PS2) were measured by keeping the leaf 30 min in dark before measurement. A red irradiance of 2 000 µmol m^{-2} s^{-1} was used for measurements. Three replications were made.

Data analysis: The large data set was entered into an *EXCELL* spread sheet which included physiological measurements, leaf areas, times, and cultivars. Analysis of variance of leaf traits was carried out on each measurement and the significance of plant mean square determined by testing against the error (species × replicate) mean square. The least significant differences (LSD) between the means were estimated at 95 % confidence level. Calculations and linear regressions were performed in a *Sigma-Plot 4.0* program. Significant differences among different plant functional types in different habitats are reported at $p < 0.05$ if not otherwise indicated.

Results

Daily courses of gas exchange under high temperature and PPFD: On 24 and 25 July 1999, PPFD was 77-100 µmol m^{-2} s^{-1} in the morning, 1 900-2 100 µmol m^{-2} s^{-1} in the midday, and 0-240 µmol m^{-2} s^{-1} in the evening, the maximum PPFD being 2 107 µmol m^{-2} s^{-1} (Fig. 1*AB*). T_l started with 18-21 °C in the morning, reaching maximum of 46.9 °C (25 July) in the midday, then fell down to 27-29 °C in the evening (Fig. 1*F*). The relatively higher T_l of *S. pasmmophylla* was noted at each stage of both days, maximum difference of 15.6 °C with *H. fruticosum* var. *mongolicum* being recorded (Fig. 1*DF*).

Diurnal courses of P_N of the two native shrubs, *H. fruticosum* var. *mongolicum* and *A. ordosica*, showed typical two peaks, one around 08:00 and the other around 16:00 (Fig. 2*EG*). However, under high temperature and high PPFD, only one peak (at 08:00) was found in the exotic shrub, *S. pasmmophylla* (Fig. 2*G*). For times after 10:00, serious depression in P_N was found in this species, with negative P_N. Among the three shrubs, *H. fruticosum* var. *mongolicum* had the highest P_N (24.02 µmol m^{-2} s^{-1}), followed by *A. ordosica* (18.41 µmol m^{-2} s^{-1}), *S. pasmmophylla* being the last (about 5 µmol m^{-2} s^{-1}). The two days' results showed almost the same patterns and values.

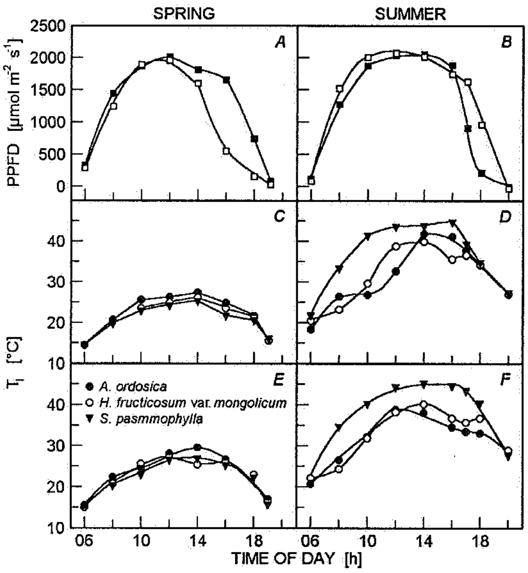

Fig. 1. Diurnal course of average incident photosynthetic flux density (PPFD) of spring (*A*: □, 29 May; ■, 30 May 1998) and summer (*B*: □, 24 July; ■, 25 July, 1999), and leaf temperature, T$_l$ on 29 May (*C*) and 30 May (*E*) 1998, and 24 July (*D*) and 25 July (*F*) 1999 of three shrubs measured at Mu Us Sandy Area, China.

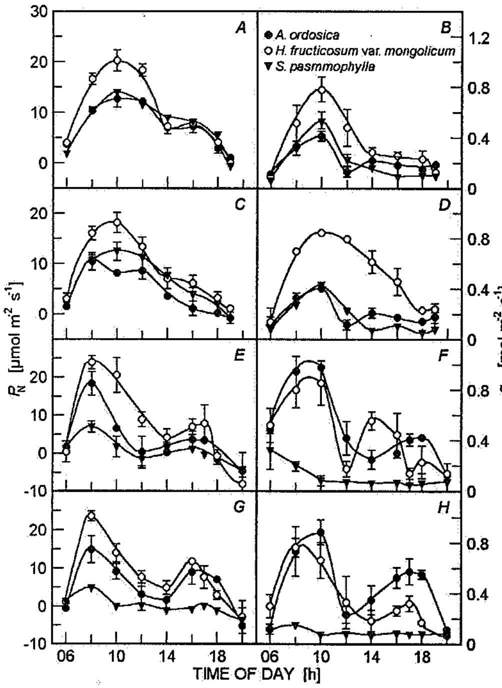

Fig. 2. Diurnal course of net photosynthetic rate, P_N (*left*) and stomatal conductance, g_s (*right*) in leaves of *S. pasmmophylla*, *A. ordosica*, and *H. fruticosum* var. *mongolicum*. *A-B*, *C-D*, *E-F*, and *G-H* correspond to 29 and 30 May 1998, and 24 and 25 July 1999, respectively. Error bars are ±S.E.

The values of g_s were parallel to those of P_N (Fig. 2*FH*), with exception of the second peak being around 14:00 rather than 16:00 for *H. fruticosum* var. *mongolicum* on 24 July (Fig. 2*F*). Again, the two native species had higher g_s than the exotic shrub. For example, g_s of *H. fruticosum* var. *mongolicum* and *A. ordosica* reached 0.8-0.9 mol m^{-2} s^{-1} in the morning, while *S. pasmmophylla* had its maximum g_s of only 0.18 mol m^{-2} s^{-1} at 06:00. Sensitivity of g_s to high temperature and high PPFD was found in *S. pasmmophylla* after 10:00.

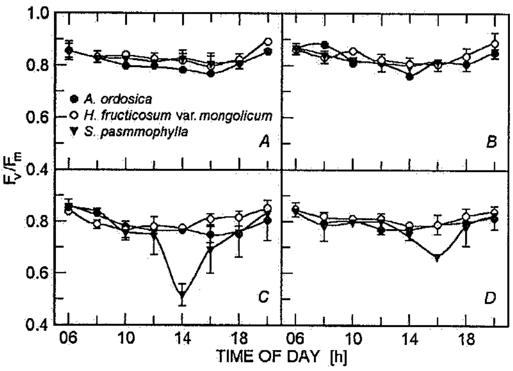

Fig. 3. Diurnal course of photochemical efficiency of photosystem 2 (F_v/F_m) of *S. pasmmophylla*, *A. ordosica*, and *H. fruticosum* var. *mongolicum*. *A* and *B* correspond to 29 and 30 May 1998, and *C* and *D* to 24 and 25 July 1999, respectively. Error bars are ±S.E.

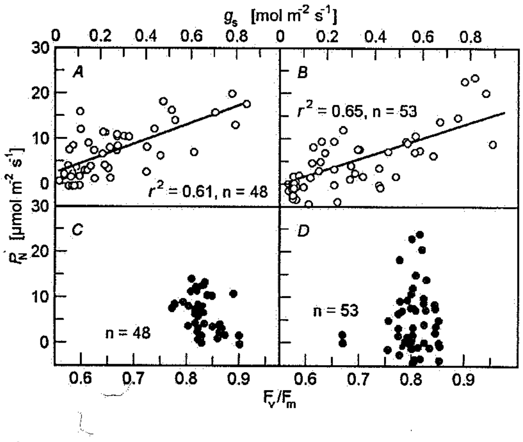

Fig.4. Relationship between net photosynthetic rates (P_N) and stomatal conductance, g_s (*A*, *B*) or F_v/F_m (*C*, *D*) using values measured in spring of 1998 (*A*, *C*) and summer of 1999 (*B*, *D*).

Daytime courses of gas exchange under normal temperature and PPFD: Under normal temperature and irradiance, midday PPFD was 1 600-2 030 µmol m^{-2} s^{-1}, with the maximum value of 2 029 µmol m^{-2} s^{-1}, similar to that for hot summer (Fig. 1*AB*). However, there were great differences in leaf temperature. Under habitats of normal temperature and irradiance, all three shrubs did not show great differences in T_l (Fig. 1*CE*). The maximum T_l was 30 °C around 14:00 in spring (30 May 1998). Under such conditions, all the shrubs showed the typical one peak in both P_N (Fig. 2*AC*) and g_s (Fig. 2*BD*). Their peaks appeared at 10:00, 2 h later than in hot summer. Again, *H. fruticosum* var. *mongolicum* had the highest P_N and g_s, but *S. pasmmophylla* had similar values as *A. ordosica*. And no serious depression in P_N was found in *S. pasmmophylla* except the normal decrease in P_N after 10:00. The plant stores net carbon during the whole daytime (from 06:00 to 17:00) under normal growth conditions.

Changes in Chl fluorescence: Under both high temperature and high PPFD environments, the values of maximal photochemical efficiency of PS2 (F_v/F_m) of the three species were similar during the whole day course, except at 14:00 (on 25 July 1999 it was at 17:00) when an apparent decrease of F_v/F_m in *S. pasmmophylla* occurred. This indicated a serious depression in photochemical efficiency of PS2 (Fig. 3*CD*). The values of F_v/F_m for most measurements were around 0.750-0.850, however, low values of 0.517 (24 July 1999) and 0.670 (25 July 1999) were found under heat stress. Such low F_v/F_m could recover to its normal level in the evening, which began to increase after 16:00.

However, under normal temperature and irradiance, all the three species showed a similar pattern in F_v/F_m (Fig. 3*AB*) ranging between 0.800-0.850. There was no depression in photochemical efficiency of PS2 in all three shrubs.

Relationships between gas exchange variables and Chl fluorescence in different seasons (Fig. 4): P_N was significantly correlated with g_s for the three shrubs in both seasons ($p<0.001$). However, no linear correlation was found between P_N and F_v/F_m.

Discussion

Photosynthesis is affected by environmental factors such as irradiance, temperature, air humidity, and wind speed. However, photosynthesis is mainly limited by reduced intercellular CO_2 concentration due to stomata closure (Kaiser 1987, Cornic and Briantais 1991, Quick *et al.* 1992) affected by those external environmental factors. Other mechanisms were also suggested, such as the activation of ribulose-1,5-bisphosphate carboxylase/oxygenase or of stromal fructose-1,6-bisphosphatase (Lal *et al.* 1996), of the photosynthetic electron flow and PS2 reaction centre (Krause and Weis 1991, Mohammed *et al.* 1995, Sánchez-Rodríguez *et al.* 1999). The response of gas exchange of desert species to environment has been documented, *e.g.*, by Oechel *et al.* (1981), Tenhunen *et al.* (1990), Filella *et al.* (1998), and Zunzunegui *et al.* (1999). Though the general response patterns we report here were similar to those found in former studies, the serious depression in photosynthesis was the first of its type. The closure of stomata was the main factor of P_N decrease for most situations (Fig. 4). Another reason may be the depression of photochemical efficiency of PS2, as shown by the non-linear relationships between P_N and F_v/F_m. Nevertheless, the very low values of F_v/F_m in *S. pasmmophylla* in hot summer (Fig. 3*CD*) suggested another mechanism of depression of photosynthesis, *i.e.*, the damage of PS2. However, this kind of destruction was recoverable, since the values could reach their normal values in the evening. The extremely high PPFD (>2 100 μmol m^{-2} s^{-1}) and the high T_l (up to 47 °C) in hot summer contributed mainly to the low P_N, especially for *S. pasmmophylla*. Because of normal T_l in spring, the leaf could store CO_2 during the whole daytime (Fig. 2*AC*). The maximum T_l in spring was 29.7 °C, while in hot summer it was 46.9 °C, but maximum leaf irradiances were close (Table 1).

The three species showed different patterns in gas exchange and fluorescence values. *H. fruticosum* var. *mongolicum*, the leguminous native species, had always the highest P_N and g_s. In another study comparing P_N of different species, most leguminous species had values of P_N and g_s as large as the C_4 species (Jiang and He 1999).

Table 1. Comparison of variables of seasonal environment in a shifting sandy dune. Averages of midday time (10:00-14:00) of 29 and 30 May 1998 (spring), and 24 and 25 July 1999 (summer). Precipitation and soil water contents (0-80 cm) for May and July, respectively. Except soil water content and precipitation, all the microclimate values were gained by a *LCA*-4 Photosynthesis System. *From Guo *et al.* (2000).

Variable	Spring	Summer
PPFD [μmol m^{-2} s^{-1}]	1 772±190	1 850±210
Maximum PPFD [μmol m^{-2} s^{-1}]	2 029	2 107
Air temperature [°C]	23±1.2	34.4±4.5
Maximum air temperature[°C]	30.8	42.5
Air water content [kPa]	0.78±0.24	2.09±0.27
Leaf temperature [°C]	25.1±2.3	39.9±4.7
Maximum leaf temperature [°C]	29.7	46.9
Soil water content [%]*	2.5	4.4
Precipitation [mm]*	26.7	100.8

A. ordosica is also a native species widely distributed in Mu Us Sandy Area. It can assimilate CO_2 under very high temperature and irradiance. But for *S. pasmmophylla*, when T_l was larger than 40 °C, no P_N was detected. Even though, *S. pasmmophylla* must have a special mechanism to protect its photosynthesis systems from heat destruction. Such mechanism could be strong photorespiration because only negative values of P_N were measured between 12:00 and 18:00. Rossa and Willert (1999) found a substantial increase of photorespiration with the increase of temperature of some geophytes in semi-arid areas. Role of photorespiration during drought stress was also stressed by Wingler *et al.* (1999). The photochemical efficiency of PS2 of *S. pasmmophylla* was depressed under very high temperature, but not damaged since the normal values of F_v/F_m were regained in the evening. And in the second morning, when temperature was low, the plant began to store carbon again. Our results show that the two native species tolerate heat and high irradiance much better than the exotic one. To cope with the serious windy sand problems in that area, use of more native species should be taken into account.

Different temperatures might have the profound effects on the shapes of gas exchange during the daytime. For the two native shrubs, the shapes of gas exchange in hot summer were typical two peaks, but in spring, only one peak was noted. *S. pasmmophylla* could reach its second peak in the afternoon in hot summer, but because of the extremely high T_l, normal performance of photosynthesis was not possible. For the most mesophyte species, the first peak is normally around 10:00 in the morning (*e.g.*, Zhang and Gao 1999), but here all the species reached the first peak at 08:00 in hot summer, 2 h earlier. This indicated that the desert shrubs must quickly utilise radiant energy and water resources before the serious environmental hazard happens.

Drought diminishes photosynthetic CO_2 uptake by increasing stomatal limitation (Teskey *et al.* 1986, Stewart *et al.* 1995). But this study did not measure the water potentials of the studied species as affected by high leaf temperatures or drought in the hot summer. Details of mechanism of changes in gas exchange induced by other environmental variables such as water potential need further investigation.

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