Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tplb20

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Accepted author version posted online: 24 Oct 2014.Published online: 28 Nov 2014.

To cite this article: L. Zhang, K. Yan & H. Shao (2014) Photosynthetic characterization of three dominant plant species in the saline-alkaline soil of the Yellow River Delta, China, Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana, 148:6, 1247-1254, DOI: 10.1080/11263504.2014.980354

To link to this article: http://dx.doi.org/10.1080/11263504.2014.980354

Plant Biosystems, 2014
Vol. 148, No. 6, 1247–1254, http://dx.doi.org/10.1080/11263504.2014.980354

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ORIGINAL ARTICLE

Photosynthetic characterization of three dominant plant species in the saline–alkaline soil of the Yellow River Delta, China

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Abstract
The diurnal variations of photosynthesis of three dominant species, including *Glycine soja*, *Phragmites australis*, and *Cynanchum chinensis*, in the Yellow River Delta in China have been studied under the same natural conditions using a Li-6400 portable photosynthesis system. The results showed that the curves of diurnal variations of net photosynthetic rate (P_N) of the three plants were different. The diurnal variation of P_N on *C. chinensis* was a midday depression pattern and had two peaks. However, P_N of *G. soja* and *P. australis* showed single-peak curves. The transpiration rate (E) of *G. soja* was significantly higher than that of *P. australis* and *C. chinensis*, both showed single-peak curves. In general, the diurnal course of stomatal conductance (g_s) followed the same pattern of P_N. A similar diurnal pattern of intercellular CO_2 concentration (C_i), vapor pressure deficit (VPD), and water use efficiency (WUE) was observed among different species. VPD showed single-peak curves, while WUE was characterized by double-peak curves, which was contrary to C_i. Linear correlations among photosynthetic variables and key environmental factors indicate high positive correlations between P_N and E, P_N and photosynthetic active radiation, P_N and leaf temperature (T_{leaf}), P_N and VPD, and between P_N and g_s except *C. chinensis*. Negative correlations among P_N and relative humidity, P_N and C_i were found. The irradiance response curves derived from the leaves were substantially affected by different species. *C. chinensis* showed highest apparent quantum efficiency, followed by *P. australis* and *G. soja*, while apparent dark respiration (R_d), convexity (k), light saturation point, and maximum gross CO_2 assimilation rate (P_{max}) of *G. soja* were higher than those of *P. australis* and *C. chinensis*. The irradiance response curve of P_N and WUE of different plant species followed the same order: *G. soja* > *C. chinensis* > *P. australis*. They were both higher than most of other species. It was concluded that plant species adapting to the saline–alkaline habitat showed higher photosynthesis. In addition, *G. soja* is also effective to improve saline–alkaline soil quality.

Keywords: *Photosynthesis, diurnal variation,* Glycine soja, Phragmites australis, Cynanchum chinensis

Introduction

Photosynthesis is the only natural conversion mechanism of photon energy into chemical energy and it is responsible for 90–95% of the plant biomass accumulation (Gomez et al. 2005). Approximately 40% of a plant's dry mass consists of carbon, fixed in photosynthesis. Net photosynthetic rate (P_N) in plant leaves is often influenced by environment factors such as irradiance, temperature, and water supply, and also by leaf age, leaf position, and developmental stage (Zhang et al. 2005; Ephrath et al. 2012; Lideman et al. 2013). Plant photosynthetic rate can be calculated using single leaf net photosynthetic rate (P_N), responses to photosynthetic active radiation (PAR) and air temperature (T_a), leaf area index, radiation interception, and transmission and distribution through the canopy depending on crop architecture (Liu et al. 2012; Yan et al. 2013). Photosynthesis is an essential process for developing the simulation models that enable estimating plant growth and productivity. Higher photosynthetic rates reflect the potential of a species to accumulate more biomass (Naumann et al. 2010).

The Yellow River Delta (YRD) is the fastest growing delta and the most active land–ocean interacting region among the large river deltas in the world (Wang et al. 2012a), because the Yellow River brings great quantities of muddy sand into the Bohai Sea. YRD located at Bohai sea gulf is one of

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the three biggest deltas in China. It has a total land area cover of 12,000 km^2, with average of 0.5 hm^2 per capita, and arable land of 0.19 hm^2 per capita in the region. The YRD regarded as the "Golden Triangle" due to its great exploitation potential and development gets more and more attention. It receives less rainfall and so the mineral content in underground water becomes high. These conditions cause soil salinization and alkalization. Therefore, land degradation is a typical problem in the field. It receives less rainfall and so the mineral content in underground water becomes high. These conditions cause soil salinization and alkalization. Therefore, land degradation is a typical problem in the field. Through analysis of land use-cover change and driving force in YRD, it could be concluded that these natural factors such as more evaporation, less rainfall, poorer fresh water limited land use. Soil salinization easily occurs. Meanwhile, a variety of Yellow River hydrology and human disturbances of land environment are also important driving factors (Xing & Zhang 2006).

In this zone, vegetation destruction, caused by adverse environmental and extreme climate conditions together with inappropriate human activities, has led to serious soil erosion, a reduction in soil fertility, and general environmental deterioration. A key factor in the degradation of the soil is the loss of plant cover, allowing increased erosion and salinization processes to occur (Albaladejo et al. 1994). The presence of vegetation in this area is important since it provides physical protection and contributes to organic matter that enhances soil water holding capacity and soil fertility characteristics (Wang et al. 2012a, 2012b; Zhang et al. 2013a, 2013b).

Glycine soja, or wild soybean (previously *G. ussuriensis*), is an annual plant of the legume family. It is the wild ancestor of soybean, an important crop. *Phragmites australis* is one of the most important, widespread, and constructive wetland plant species over the YRD. There was about 2600 ha of *P. australis* wetland in the YRD. It provides staging, wintering, and breeding sites for birds which may directly benefit from ecological restoration engineering for wetlands (Wu et al. 2009). *P. australis* adapts to this area very well and is a dominant species. The reed shows considerable morphological variations among populations of different salinity.

Glycine soja, *Phragmites australis*, and *Cynanchum chinensis* are three dominant plant species adapted to the saline–alkaline habitat in the YRD region; however, less information is known about their photosynthetic characteristics. This work was carried out to investigate the diurnal variation in photosynthesis of *G. soja*, *P. australis*, and *C. chinensis* grown under identical saline soil conditions, considering their relationship with the variation of key environmental factors.

Materials and methods

Site description

This study was conducted in the Yellow River estuary, located in the Nature Reserve of the YRD (37°35′–38°12′N, 118°33′–119°20′E) in Dongying City, Shandong Province, China. The nature reserve has a typical continental monsoon climate with distinctive seasons; summer is warm and rainy while winter is cold. The annual average temperature is 12.1°C, the frost-free period is 196 days, and the effective accumulative temperature is about 4300°C. Annual evaporation is 1962 mm and annual precipitation is 551.6 mm, with about 70% of precipitation occurring between June and August. The soils in the study area are dominated by intrazonal tidal soil and salt soil.

Gas-exchange and environmental measurements

Gas-exchange measurements were conducted in August 2010, aiming to evaluate such physiological traits in a range of environmental conditions. Net photosynthesis rate (P_N), transpiration rate (E), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were determined simultaneously on fully expanded leaves of each species using a portable open-flow gas exchange system Li-6400 (LI-COR Biosciences, Lincoln, NE, USA). The respective results were expressed as μmol (CO_2) $m^{-2} s^{-1}$, mol (H_2O) $m^{-2} s^{-1}$, and μmol (CO_2) mol^{-1}. Measurements were taken at 7:00, 9:00, 11:00, 13:00, 15:00 and 17:00 h on sunny days in August 2010. Measurements were repeated three times for each leaf, for three leaves per plant, and the averages were recorded. PAR, air temperature (T_a), relative humidity (RH), air CO_2 concentration (C_a), and vapor pressure deficit (VPD) were determined concurrently. The water use efficiency (WUE) was calculated as the ratio of P_N/E.

The irradiance response curve

The irradiance response curve was recorded automatically in the same leaf inserted into the leaf chamber by means of operation program. Light response curves were obtained on six randomly selected, fully expanded, healthy leaves of each species using the same portable photosynthesis system, equipped with an artificial light. Measurements were made between 9:00 and 11:00 in August 2010. CO_2 assimilation in response to PAR of 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, and 0 μmol $m^{-2} s^{-1}$ at the leaf surface was measured. Each PAR step lasted 3 min and data were recorded three times. An atmospheric CO_2 concentration of 365 ± 5 μmol mol^{-1}, a temperature of 28°C, and RH of 60% were maintained in the chamber. The data obtained for each leaf were

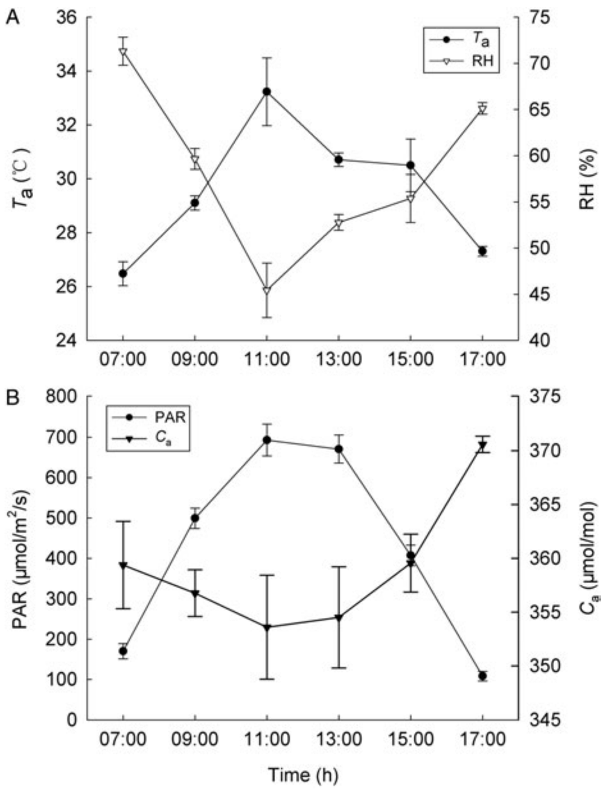

Figure 1. Diurnal courses of average air temperature (T_a), RH, PAR and air CO_2 concentration (C_a).

analyzed with the program photosynthetic assistant (Version 1.1, Dundee Scientific, Dundee, UK) to obtain saturation irradiance of three species. This software utilizes a function described by Prioul and Chartier (1977) to model photosynthetic A–Q. Based on A–Q curves, the maximum rate of photosynthesis (P_{max}), apparent dark respiration (R_d), and convexity (k) were modeled.

Statistical analysis

All experiments were based on three replicated measurements. Data were analyzed by one-way analysis of variance (ANOVA) using the statistical software SPSS 18.0 (SPSS, Chicago, IL, USA). The treatment mean values were compared by post hoc least significant difference (LSD) test. Statistical LSD tests were performed among 07:00, 09:00, 11:00, 13:00, 15:00, and 17:00. The term significant indicates differences for which $P \leq 0.05$. The relationship between photosynthetic variables of different species and environmental factors was analyzed using linear correlation analysis.

Results

Environmental conditions

T_a was lowest (26.48 ± 0.44°C) at 7:00 and increased to maximum (33.23 ± 1.26°C) at 11:00, then it decreased to 27.31 ± 0.18°C at 17:00. On the contrary, RH was highest at 7:00 and decreased to 45.43 ± 2.95% at 11:00, then increased (Figure 1 (A)). Daily PAR and atmospheric CO_2 concentration, which showed a contrary tendency, ranged from 108.27 ± 11.97 to 692.93 ± 39.47 $\mu mol\,m^{-2}\,s^{-1}$ and from 353.60 ± 4.83 to 370.59 ± 0.76 $\mu mol\,mol^{-1}$, respectively (Figure 1(B)).

Diurnal course of leaf gas exchange

Comparative study of the rate of photosynthesis (P_n) during the day showed that diurnal variations in P_N of *C. chinensis* (1.39 ± 0.33–7.32 ± 0.35 $\mu mol\,m^{-2}\,s^{-1}$) were characterized by double-peak curves with higher values at 9:00 and 13:00. While P_N of *G. soja* and *P. australis* (varied from 2.49 ± 0.28 to 12.62 ± 0.44 $\mu mol\,m^{-2}\,s^{-1}$ and from 1.87 ± 0.30 $\mu mol\,m^{-2}\,s^{-1}$ to 8.05 ± 0.78 $\mu mol\,m^{-2}\,s^{-1}$, respectively) showed single-peak curves. Their maximum values were at 13:00 and 9:00, respectively (Figure 2(A)).

The E of *G. soja* (varied from 0.99 ± 0.20 to 4.64 ± 0.40 $mmol\,m^{-2}\,s^{-1}$) was significantly higher than *P. australis* and *C. chinensis* (varied from 0.40 ± 0.07 to 1.45 ± 0.16 $mmol\,m^{-2}\,s^{-1}$ and from 0.62 ± 0.13 to 2.00 ± 0.26 $mmol\,m^{-2}\,s^{-1}$, respectively) (Figure 2(B)). The maximum values of E were at 11:00 for *G. soja* and *C. chinensis*, but at 9:00 for *P. australis*.

The gas exchange of the plant was characterized by measuring the leaf stomatal conductance (g_s) throughout the day on the same dates (Figure 2(C)). The g_s of *G. soja* increased until 13:00, reaching maximum values at that time, and then decreased. The g_s of *P. australis* was significantly lower than *G. soja* and *C. chinensis*, except at 9:00. In general, the diurnal course of g_s followed the same pattern of P_N. The maximum of g_s values occurred in the early morning except *G. soja*. The highest g_s of *G. soja* reached 0.25 $mol\,m^{-2}\,s^{-1}$ at 13:00, followed by 0.23 $mol\,m^{-2}\,s^{-1}$ of *C. chinensis* at 7:00 and 0.11 $mol\,m^{-2}\,s^{-1}$ of *P. australis* at 9:00.

A similar diurnal pattern of C_i was observed among different species (Figure 2(D)). The diurnal patterns of VPD and WUE were also similar among three species. VPD showed single-peak curves, with the maximum values at 11:00 (Figure 2(E)), while WUE was characterized by double-peak curves with higher values at 9:00 and 13:00 or 15:00 (Figure 2 (F)), which was contrary to C_i.

Linear correlations among photosynthetic variables and key environmental factors indicate high positive correlations between P_N and E, P_N and PAR, P_N and T_{leaf}, P_N and VPD, and P_N and g_s except *C. chinensis* ($r = 0.35$, $P > 0.05$) (Tables I–III).

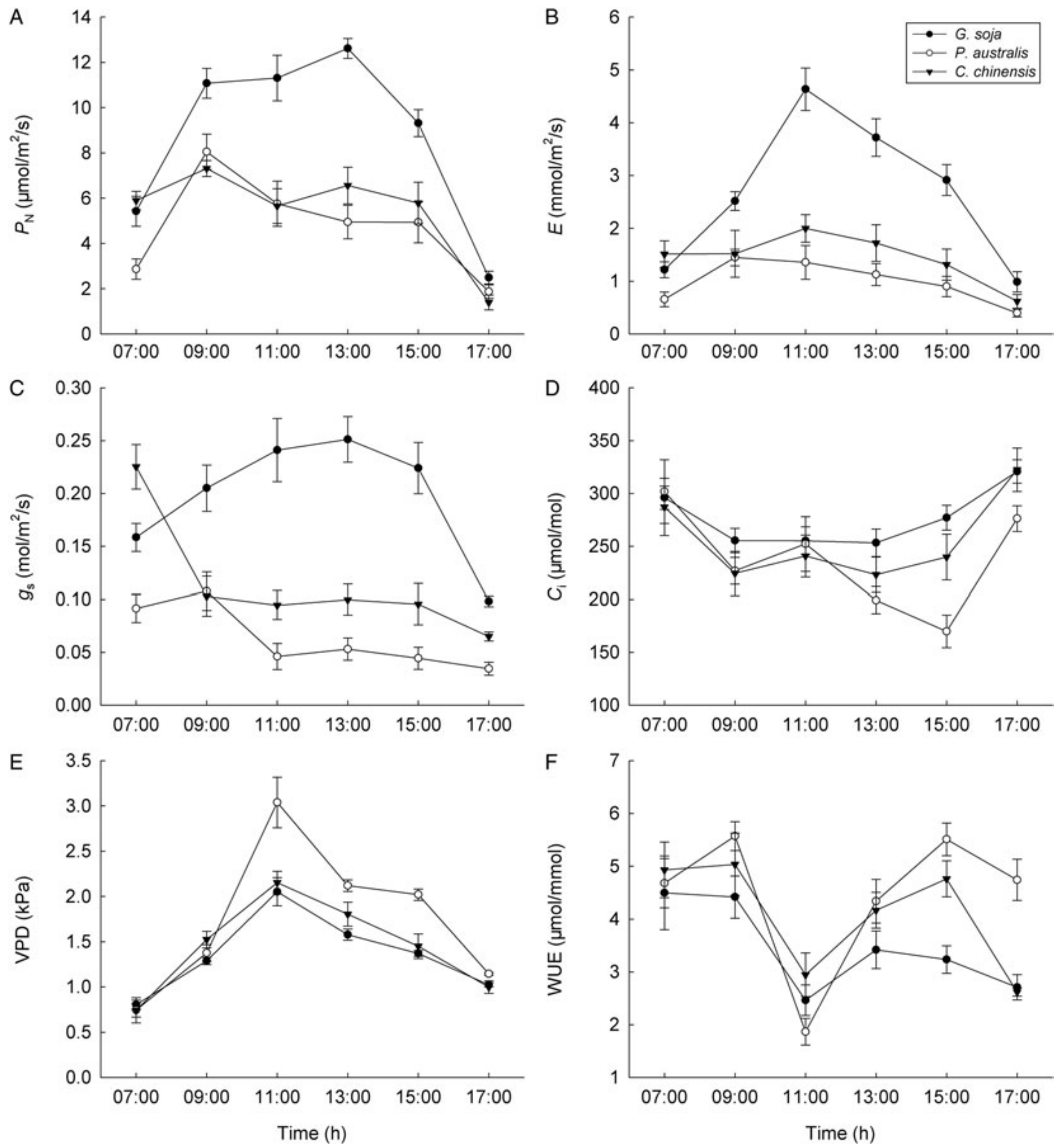

Figure 2. Diurnal courses of net photosynthesis rate (P_N, A), transpiration rate (E, B), stomatal conductance (g_s, C) and intercellular CO_2 concentration (C_i, D), VPD (E) and WUE (F) for three dominant species.

Whereas negative correlations between P_N and RH, and P_N and C_i were found.

The irradiance response curve

The irradiance response curves derived from the leaves were substantially affected by different species (Figure 3). *G. soja* maintained significantly higher P_{net} rate on an area basis than *P. australis* and *C. chinensis*, but there was no significant difference between *P. australis* and *C. chinensis* (Figure 3(A)). The same patterns of diurnal course of E and g_s were observed in all species, with their values increasing with PAR (Figure 3(B),(C)). The irradiance response curve of WUE of different plant species followed the following order: *G. soja* > *C. chinensis* > *P. australis* (Figure 3(D)). They both increased to the maximum when PAR ranged from 400 to 600 μmol mmol^{-1}, then decreased gradually. WUE of *P. australis* and *C. chinensis* was both below zero at dark conditions except *G. soja*.

C. chinensis showed highest apparent quantum efficiency, followed by *P. australis* and *G. soja*, while R_d, k, light saturation point (LSP) and P_{max} of *G. soja* were higher than those for *P. australis* and *C. chinensis* (Table IV).

Discussion

In situ patterns of leaf-level photosynthesis are created by interactions between a suite of ambient environmental conditions and the species-specific sensitivity to these combined factors (Tel-Or & Forni 2011; Zuccarini & Kampus 2011; Giorio & Nuzzo

Table I. Linear correlations among photosynthetic variables of *G. soja* and environmental factors.

	E	PAR	T_{leaf}	RH	C_i	VPD	g_s	WUE
P_N	0.849**	0.944**	0.806**	−0.643**	−0.920**	0.718**	0.895**	0.060
E		0.919**	0.963**	−0.875**	−0.727**	0.917**	0.873**	−0.396*
PAR			0.899**	−0.786**	−0.895**	0.856**	0.829**	−0.141
T_{leaf}				−0.956**	−0.746**	0.983**	0.791**	−0.443*
RH					0.617**	−0.979**	−0.613**	0.595**
C_i						−0.703**	−0.706**	−0.217
VPD							0.675**	−0.505**
g_s								−0.119

Note: *$P < 0.05$, **$P < 0.01$, $n = 30$.

2012). In other words, environmental conditions may be similar surrounding the study species, but the photosynthetic responses of the species were different (Wu et al. 2011).

Irradiation appears to be one of the most important environmental factors governing plant development and survival, and has been suggested to be one of the main factors influencing plant growth (Noda et al. 2004). We observed that the photosynthetic dynamics of three species were mainly influenced by PAR. *G. soja* and *C. chinensis* owe their greater adaptability to higher PAR, and prevent light destroying their tissues through utilizing a greater ratio of PAR (e.g. higher photosynthetic rate). They dissipate unwanted light energy by adjusting their photoreactions via a proportionally higher ratio of carotenoids to zeaxanthins (Ribeiro et al. 2005; Desotgiu et al. 2012; Promis et al. 2012).

A higher conductance would only marginally increase CO_2 assimilation, but would significantly increase transpiration, since transpiration increases linearly with g_s, as a result of the constant difference in water vapor concentration between the leaf and the air. Thus variations in E were closely associated with variations in g_s. During the day, g_s and E had a similar behavior. Nevertheless, increments in E cannot be explained only by increments in g_s, but also by increases in VPD. In the morning, the decrease in g_s of *P. australis* and *C. chinensis* from 9:00 to 11:00 was related to the increase in VPD, a response also observed in citrus (Machado et al. 2002; Vitale et al. 2012) to prevent excessive shoot dehydration. Even under low g_s at 11:00, the higher VPD caused increased E. High values of VPD (1.5 kPa) affect the leaf gas exchange. Higher air temperature and VPD negatively affect CO_2 assimilation due to stomatal closure (Han et al. 2012; Niu et al. 2012; Tretiach et al. 2012). *G. soja* has lower resistance and higher transpiration; thus having the ability to cope with high temperatures. C_i of *G. soja* decreased from 7:00 to 13:00 due to increases in P_N. C_i tended to increase after 13:00 as P_N decreased, also indicating the coupling between P_N and C_i. This result may be used to estimate the leaf capacity to incorporate atmospheric CO_2.

The diurnal course of gas exchange followed the pattern mentioned by Kozlowski and Pallardy (1997) for tropical trees, that is, P_N was low in the early morning and coupled with low PAR, increased sharply and reached a maximum around midday. Afterwards, the decrease in P_N until late afternoon may be related to the higher afternoon T_a and VPD. Similar pattern was shown by palms such as coconut (Passos et al. 2009), as well as by other tree species such as citrus (Machado et al. 2002). Temperature can influence enzymatic reactions, and the physiological and biochemical responses of cell membranes, and thus became the main factor to impact photosynthetic dynamics of the plant (Li et al. 2011; Chen et al. 2012; Oukarroum et al. 2012; Suleman et al. 2013).

The results of correlation analysis of the above data showed that P_N was positively correlated with g_s,

Table II. Linear correlations among photosynthetic variables of *P. australis* and environmental factors.

	E	PAR	T_{leaf}	RH	C_i	VPD	g_s	WUE
P_N	0.853**	0.564**	0.480**	−0.368*	−0.472*	0.403*	0.458*	0.016
E		0.675**	0.580**	−0.465**	−0.354	0.521**	0.441*	−0.247
PAR			0.865**	−0.816**	−0.613**	0.837**	−0.201	−0.409*
T_{leaf}				−0.980**	−0.532**	0.993**	−0.412*	−0.595**
RH					0.541**	−0.980**	0.552**	0.579**
C_i						−0.455*	0.232	−0.320
VPD							−0.466**	−0.662**
g_s								0.306

Note: *$P < 0.05$, **$P < 0.01$, $n = 30$.

Table III. Linear correlations among photosynthetic variables of *C. chinensis* and environmental factors.

	E	PAR	T_{leaf}	RH	C_i	VPD	g_s	WUE
P_N	0.656**	0.689**	0.503**	−0.216	−0.740**	0.350	0.308	0.639**
E		0.734**	0.626**	−0.385*	−0.493**	0.520**	0.313	0.173
PAR			0.951**	−0.794**	−0.784**	0.888**	−0.206	0.081
T_{leaf}				−0.936**	−0.734**	0.982**	−0.410	−0.081
RH					0.607**	−0.978**	0.651**	0.268
C_i						−0.671**	0.175	−0.378*
VPD							−0.517**	−0.189
g_s								0.498**

Note: $^*P < 0.05$, $^{**}P < 0.01$, $n = 30$.

but negatively correlated with C_i, implying that g_s is one of the determinants of P_N difference (Zhang et al. 2005). Our results indicated that the determinant of leaf photosynthetic capacity is g_s, because high P_N is always accompanied by high g_s and they are always positively correlated with each other, as noted in earlier reports (Sonobe et al. 2009).

A pronounced sensitivity of photosynthesis to VPD has been observed, and a significant negative correlation was found between stomatal conductivity and VPD (Bunce 1997). All plant species showed a positive correlation between VPD and P_N, which was different from Tucci et al. (2010). Their results indicated that peach palms showed a negative correlation between VPD and P_N, but a correlation of higher magnitude was observed between P_N and VPD, indicating a stomatal regulation in order to cope with high atmospheric demand. While Lamade and Setiyo (1996) related significant differences among clones in the relationship between P_N and VPD. In general, stomatal closure in many species has been considered as a response due exclusively to soil water deficit (Tsonev et al. 2011; Quentin et al. 2012; Brandao et al. 2013).

In general, the irradiance response curve of P_N and WUE of different plant species followed the same order: *G. soja* > *C. chinensis* > *P. australis*. They were both higher than most of the other plant species. It was concluded that plant species adapted to the saline–alkaline habitat showed higher photosynthesis (Rewald et al. 2011; Akhani et al. 2012; Li et al. 2012; Sandoval-Gil et al. 2012; Wang et al.

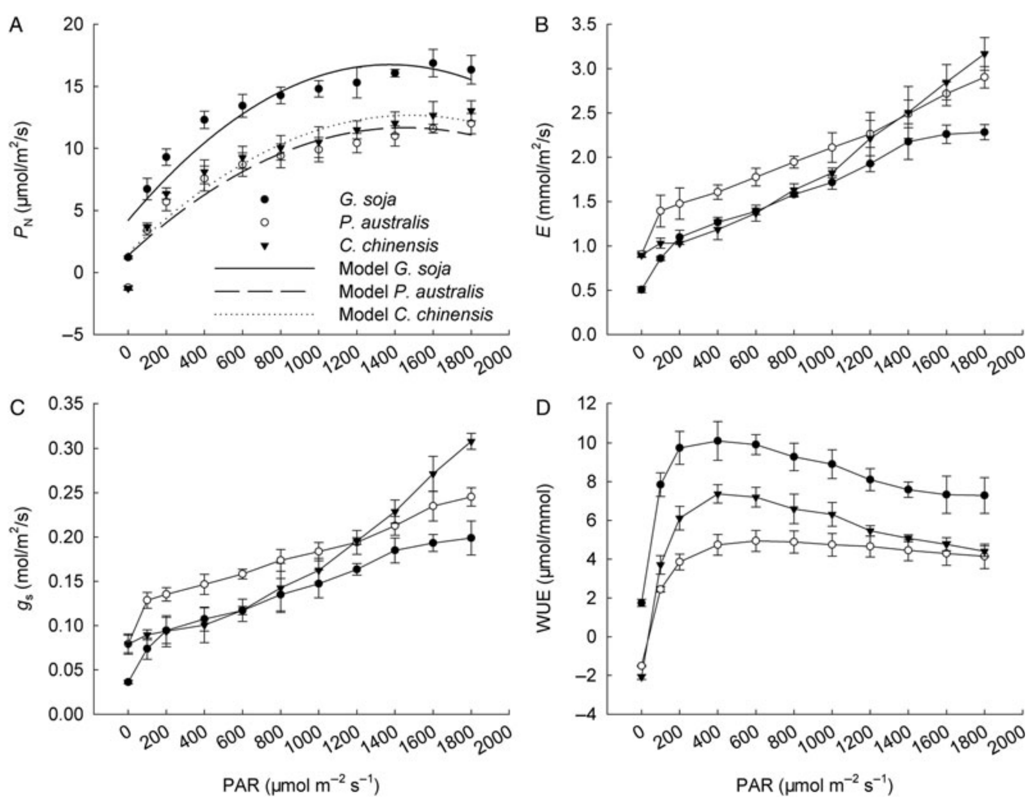

Figure 3. The response of net photosynthesis rate (P_N, A), transpiration rate (E, B), stomatal conductance (g_s, C), and WUE (D) to PAR for three dominant species.

Table IV. Modeled photosynthetic light response curve parameters of different species on a leaf area basis.

	P_{max}	R_d	k	LSP	LCP	AQE
G. soja	17.323	1.213	1.023	1695.6	0	0.079
P. australis	14.576	−1.216	0.912	1551.6	18	0.081
C. chinensis	15.832	−1.269	0.912	1652.4	18	0.085

Note: P_{max}, maximum gross CO_2 assimilation rate; R_d, apparent dark respiration; k, convexity; LSP, light saturation point; LCP, light compensation point; AQE, apparent quantum efficiency.

2013). In addition, *G. soja* exhibits higher LSP, can prevent destruction of photosynthetic tissues from high irradiance and high temperature. So *G. soja* is most effective to revegetate in saline–alkaline soils for its higher photosynthesis to accumulate more biomass.

Funding

This work was jointly supported by Important National Basic Research Program of China [grant number 2013CB430403]; the Important Direction Project of CAS [grant number KZCX2-YW-JC203]; One Hundred-Talent Plan of the Chinese Academy of Sciences (CAS); National Natural Science Foundation of China [grant number 41171216], [grant number 41001137]; the CAS/SAFEA International Partnership Program for Creative Research Teams; the Science & Technology Development Plan of Shandong Province [grant number 2010GSF10208]; Yantai Science & Technology Development Project [grant number 2011016]; the Strategic Priority Research Program of the Chinese Academy of Sciences (CAS) [grant number XDA05030404]; Yantai Double-hundred High-end Talent Plan [grant number XY-003-02]; CAS Visiting Professorship [grant number 2012T1Z0010] and 135 Development Plan of YIC-CAS.

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