

Photosynthetic activity and efficiency of *Bothriochloa ischaemum* and *Lespedeza davurica* in mixtures across growth periods under water stress

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Abstract Photosystem II (PSII) plays an especially important role in the photosynthetic response of higher plants to environmental perturbations and stresses. In this study, a pot experiment was conducted to investigate the differences in the photochemical efficiency and activity of PSII between *Bothriochloa ischaemum* and *Lespedeza davurica* in mixtures under three soil water regimes [80 ± 5 % FC (field capacity) (HW), 60 ± 5 % FC (MW) and 40 ± 5 % FC (LW)]. The maximum PSII quantum yield (F_v/F_m), non-photochemical quenching (NPQ), photochemical quenching (qP) and rapid light curve-derived parameters (rETR_{max}, maximum relative electron transport rate; I_k , minimum saturating irradiance; α , initial slope of the curve) of each species were investigated during the heading period (HP), flowering period (FP) and mature period (MP). The results showed that under HW and MW regimes, the averaged F_v/F_m values of *B. ischaemum* in mixtures at the HP were significantly higher than in monoculture, and the mean rETR_{max} values of *B. ischaemum* during the HP and FP in mixtures were significantly higher than in monoculture. F_v/F_m

values of *B. ischaemum* in the HP were significantly lower than in the other two growth periods under LW regime. During the MP, the averaged F_v/F_m values of *L. davurica* in mixtures were significantly higher than in monoculture under the HW regime, and the mean rETR_{max} values of *L. davurica* in mixtures were significantly higher than in monoculture under each water regime. In the same mixture ratio, NPQ values of *B. ischaemum* were significantly higher than those of *L. davurica*, but the rETR_{max} and I_k values of *B. ischaemum* were significantly lower than those of *L. davurica* under each water regime. The results indicated that application of mixture planting enhanced the photosynthetic performance of both species depending on the developmental stage of the individual plant. *B. ischaemum* showed the maximal photosynthetic performance in the HP and FP while *L. davurica* in the MP under both sufficient water supply and water stress conditions.

Keywords Chlorophyll fluorescence · Native species · Photosynthetic performance · Rapid light curve · Water stress

Abbreviations

α	Initial slope of the curve
I_k	Minimum saturating irradiance
FC	Field capacity
F_m	Maximal fluorescence yield
F_o	Minimal fluorescence yield
F_v/F_m	Maximum PSII quantum yield
NPQ	Non-photochemical quenching
PSII	Photosystem II
qP	Photochemical quenching
rETR _{max}	Maximum relative electron transport rate
Φ_{PSII}	Effective quantum yield of PSII

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Introduction

Photosynthesis is the physico-chemical process by which plants use light energy to drive the synthesis of organic compounds, and it is the basis of plant production (Whitmarsh 1999). Within photosynthetic organisms, photosystem II (PSII) plays a very important role in the photosynthetic response of plants to environmental stress (Baker 1991; Krall and Edwards 1992). The operating quantum efficiency of electron transport through PSII in leaves is related to CO₂ assimilation (Genty et al. 1989), which is most likely to be affected by water shortage. However, the photosynthetic apparatus appears to be very resistant to drought stress, and a mild or moderate water deficit does not induce a significant decrease in the quantum yield of the primary photochemistry of PSII (Cornic and Fresneau 2002; Cornic and Massacci 2004), whereas the structures and functions of PSII would be strongly limited under more severe drought stress (Liu et al. 2006; Oukarroum et al. 2009). Generally, decreases in PSII quantum yield can result from the photo-protective increase in thermal energy dissipation induced by an excess of adsorbed light energy (Colom and Vazzana 2003). The most important photo-protective mechanism of plants is the ability to dissipate excess light energy in PSII through non-photochemical quenching (NPQ) under environmental stress, which was assumed to be the actual physiological photo-protection capacity of the photosynthetic organism (Lambrev et al. 2012; Ruban and Murchie 2012). In contrast, photochemical quenching (qP) reflects the share of light energy absorbed by PSII antenna pigments, which are used for photochemical electron transfer (Schreiber et al. 1986). NPQ and qP values vary with the growth period or with changing environmental factors; one desert perennial species was found to have higher NPQ during the summer months, allowing more excess light energy to be dissipated for its growth, but with higher qP in the spring months, allowing more light energy to be used in photochemical processes (Barker et al. 2002). Therefore, the measurement and analysis of chlorophyll fluorescence have become one of the most powerful and widely used methods of assessing photosynthetic efficiency under stressful environment (Ralph et al. 2002; Schreiber 2004). The fluorescence rapid light curves can provide detailed information on the saturation characteristics of electron transport, and on photosynthetic activity (Ralph and Gademann 2005).

Many studies have been conducted to assess the photosynthetic efficiency and activity of species in isolation as single plant or in monoculture under natural or artificial water stress conditions (Balaguer et al. 2002; Christen et al. 2007; Duan et al. 2012), while less attention has been paid to species in competitive environments or in more complex mixtures. Within multi-species systems, individuals may affect each other indirectly through intermediaries, such as shared

resources or common enemies, which will compete for multiple potentially limiting environmental resources (i.e., light, water and nutrients) or benefit from their symbiotic relationship (Chesson et al. 2004; Silvertown 2004). Mixing species with differences in life-form traits (i.e., photosynthetic pathway, symbiotic nitrogen fixation, root architecture) could affect their physiological response to water availability, and the plant species in mixtures responses to environmental drought may be very different from those grown in isolation as single plants or as monocultures (Dijkstra et al. 2010). Accordingly, the competitive environment and water stress could eventually result in the alteration of the photosynthetic performance of each species. Therefore, it is necessary to understand their photosynthetic response to interspecific competition under different water regimes.

Water shortage is the major limiting factor that affects plant photosynthesis, growth, production and distribution in the semiarid region on the Loess Plateau of China (Shan et al. 2000; Xu et al. 2007). *Bothriochloa ischaemum* L. Keng (a C₄ herbaceous grass) and *Lespedeza davurica* (Laxm.) Schindl. (a C₃ leguminous subshrub) are two native, co-occurring dominant species in natural grassland communities in the area. In addition, they are excellent natural pasture species, and have many agronomic attributes that make the two wild species ideal forage species due to their high adaptability and quality (Xu et al. 2011a, b). These two species have strikingly different life forms and eco-physiologies, and there have been no direct comparisons of the leaf photosynthetic physiology in the context of variation in soil water availability under competitive environment, which would improve our knowledge of their co-existence mechanisms and eventually be useful for taking appropriate measures for using them in practice (Xu et al. 2011b). Thus, we investigated the interactive effects of water stress and interspecific competition on the photosynthetic activity and efficiency of the two species across three growth periods. The aims were: (1) to compare the F_v/F_m , NPQ, qP, and the rapid light curve-derived parameters (rETR_{max}, I_k and α) of both *B. ischaemum* and *L. davurica* under water stress; (2) to determine the photosynthetic activity and efficiency of each species in monocultures or mixtures; and (3) to identify the differences between the two species across the growth periods.

Materials and methods

Plant materials and growth conditions

Seeds of *B. ischaemum* and *L. davurica* were collected in the autumn of 2011 from the experimental fields at Ansai

Research Station (ARS) of the Chinese Academy of Sciences (CAS) (altitude of 1,068–1,309 m, 36°51'N, 109°19'E) located at the centre of the semiarid hilly-gully region on the Loess Plateau. After drying for 1 week outside in the sunlight, seeds were stored in a laboratory in a sealed container. An one-pot experiment was conducted from April to November 2012 in Yangling, Shaanxi Province, China (altitude of 530 m, 34°12'N, 108°7'E), which has a mean annual temperature of 12.9 °C, a maximum mean monthly temperature of 26.7 °C in July, a minimum temperature of –1 to –2 °C in January, and a mean annual rainfall of 637.6 mm.

The loessial soil used in the experiment was collected from the upper 20 cm of a cultivated field at ARS. The soil gravimetric moisture content at field capacity (FC) and wilting point (WP) was 20.0 and 4.0 %, respectively. The soil pH value was 8.77, and the soil organic matter content was 0.36 %. The soil total N, total P and total K contents were 0.025, 0.066 and 1.90 %, respectively, and the soil available N, P and K contents were 19.62, 50.78 and 101.55 mg kg⁻¹, respectively. As base fertilisers, 0.481 g CON₂H₄ and 3.949 g KH₂PO₄ were applied after mixing with 9.0 kg of air-dried soil, and the mixture was packed into each pot (20 cm in diameter and 30 cm in depth) on 1 April 2012. A vertical plastic pipe placed adjacent to the inner wall of each pot was used to supply water.

Species combination and water treatments

A replacement series design method was used at a density of 12 plants per pot, and seven sowing ratios of *B. ischaemum* to *L. davurica* (0:12, 2:10, 4:8, 6:6, 8:4, 10:2 and 12:0) were arranged. Seeds of two species were sown in 12 equally spaced dibbles in each pot on 3 April, 2012. The pots were initially well watered to ensure seedling establishment. When seedlings of *B. ischaemum* had five leaves and were approximately 0.10 m high, three water regimes [80 ± 5 % FC (HW), 60 ± 5 % FC (MW) and 40 ± 5 % FC (LW)] were initiated, on 28 May 2012. Before watering, a layer of perlite was spread on the soil surface of each pot (20 g, approximately 2.0 cm deep) to reduce evaporation from the soil surface. Daily evapo-transpiration was assessed at 18:00 h by weighing the pots, and the water losses were replaced via the plastic pipes to maintain the desired water regime. Each treatment was replicated three times, and all pots were distributed in a completely randomised design inside the rainfall shelter.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence kinetics parameters and rapid light curves of the two species were determined using a pulse amplitude modulated chlorophyll fluorescence

system (Imaging PAM, Walz, Effeltrich, Germany). The measurements were conducted during their three growth periods (based on the growth period of *B. ischaemum*): heading period (HP, 9–13 July), flowering period (FP, 11–15 August) and mature period (MP, 10–14 September). The corresponding growth periods for *L. davurica* were the budding period, flowering period and productive period.

In each pot, two newly expanded healthy leaves of each species were measured from 06:00 to 09:30 h every day. The selected leaves were dark adapted for 30 min prior to fluorescence kinetics measurement. Minimal fluorescence yield (F_o) was measured with relatively weak measuring light pulses (0.5 μmol m⁻² s⁻¹) at a low frequency (1 Hz). Maximal fluorescence yield (F_m) was determined by applying a pulse saturation light (duration 0.8 s, 1,580 μmol m⁻² s⁻¹). Following this, actinic light (200 μmol m⁻² s⁻¹) was switched on and saturating pulse was applied at 20-s intervals for 5 min to determine the maximum fluorescence yield of light adapted leaf (F_m'), and the steady fluorescence during the actinic illumination (F_s). For each interval, saturation pulse values of various chlorophyll fluorescence parameters were captured. Subsequently, the maximum PSII quantum yield [$F_v/F_m = (F_m - F_o)/F_m$], effective PSII quantum yield [$\Phi_{PSII} = (F_m' - F_s)/F_m'$], electron transport rate [ETR = $\Phi_{PSII} \times PAR \times 0.5 \times 0.84$], photochemical quenching [qP = $(F_m' - F_s)/(F_m' - F_o')$] and non-photochemical quenching [NPQ = $(F_m - F_m')/F_m'$] were obtained automatically using the ImagingWin software (Version 2.40, Walz). The two measured values for each species per pot were averaged as one replicate, and the average values of three replicates per treatment were used in the analysis.

Rapid light curves of the same leaves were obtained after the fluorescence kinetics measurement through the application of a series of saturation pulses with 10-s intervals between irradiances under increasing actinic irradiance (1, 27, 62, 87, 207, 337, 507, 717, 967, 1,257 and 1,537 μmol m⁻² s⁻¹). The relative electron transport rate (rETR) was calculated at each level of irradiance as rETR = $\Phi_{PSII} \times PAR$, where Φ_{PSII} is the effective quantum yield of PSII (Ralph et al. 2002). Data from the rapid light curves were fitted by the exponential equation of (Platt et al. 1982). The regression equation was expressed as:

$$P = P_s \times [1 - \exp(-\alpha \times E_d/P_s)] \times \exp(-\beta \times E_d/P_s) \quad (1)$$

P_s is a scaling parameter defined as the maximum potential rETR, α is measured by the initial slope of the rapid light curve before the onset of saturation, E_d is the downwelling irradiance (wavelength 400–700 nm), and β is the negative slope of the rapid light curve for high irradiances. The parameters rETR_{max} and I_k were estimated using the following equations (Ralph and Gademann 2005):

$$rETR_{\max} = P_s \times [\alpha/(\alpha + \beta)] \times [\beta/(\alpha + \beta)]\beta/\alpha \quad (2)$$

$$I_k = rETR_{\max}/\alpha \quad (3)$$

Curve fitting was achieved using the non-linear Levenberg–Marquardt regression algorithm in the *Origin* software program (Origin 6.0, Microcal software Inc., Northampton, MA, USA), and the fitted curves were good ($R^2 > 0.93$) in all cases.

Statistical analysis

Statistical analyses were performed using the SPSS statistical package (Version 16.0 for Windows, SPSS, Chicago, USA). Differences between the treatment means among

three water regimes, seven mixture ratios, three growth periods and two species were compared using Tukey's HSD (honestly significant difference) test at the 0.05 probability level.

Results

Maximum PSII quantum yield (F_v/F_m)

Water stress disproportionately decreased F_v/F_m values of each species in different growth periods (Fig. 1). Under the HW and MW regimes, there were no significant differences among the three growth periods for *B. ischaemum* in

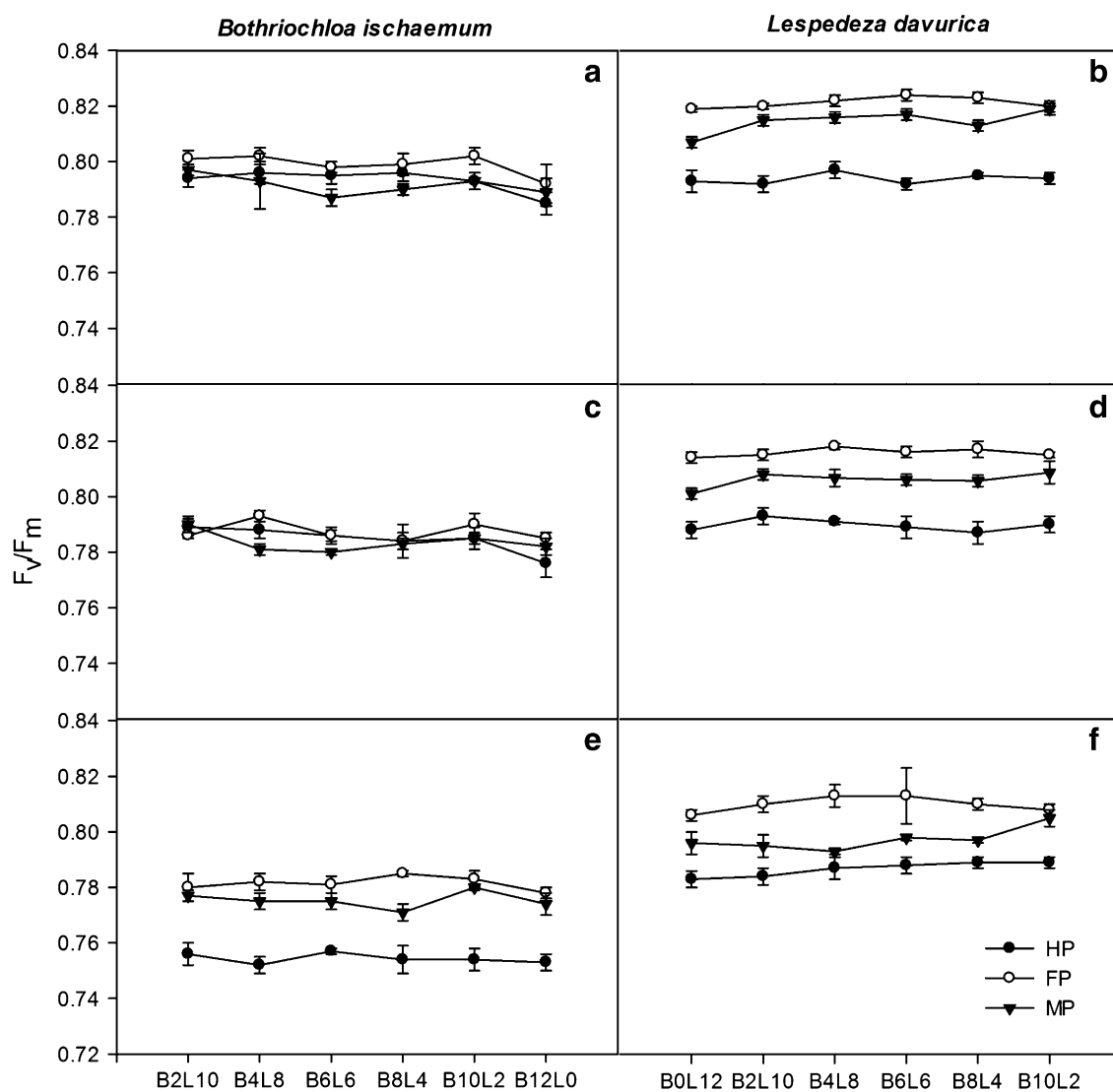


Fig. 1 Maximum photochemical efficiency (F_v/F_m) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP mature period) at different mixture ratios and for each water regime

[HW (a, b) $80 \pm 5\%$ field capacity, MW (c, d) $60 \pm 5\%$ field capacity, LW (e, f) $40 \pm 5\%$ field capacity]. Values are mean \pm SE ($n = 3$)

monoculture or mixtures, except the averaged F_v/F_m values in mixtures at the HP (0.795 and 0.786, respectively) were significantly ($P < 0.05$) higher than in monoculture (0.785 and 0.776, respectively) (Fig. 1a, c). Under the LW regime, no significant differences were observed between monoculture and mixtures under each growth period, and the F_v/F_m values of *B. ischaemum* in the HP were significantly lower than in the other two growth periods ($P < 0.05$) (Fig. 1e).

For *L. davurica* under each water regime, the lowest F_v/F_m values were found in the HP and the highest values were found in the FP (Fig. 1b, d, f). During the MP, the averaged value in mixtures (0.816) was significantly higher than in monoculture (0.807) under the HW regime ($P < 0.05$), and there were no significant differences between those values under the MW or LW regime (Fig. 1b, d, f).

In the same mixture ratio, the F_v/F_m values of *B. ischaemum* were significantly lower than those of *L. davurica* in the different growth periods under each water regime ($P < 0.05$), except in the HP under the HW and MW regimes (Fig. 1).

Non-photochemical quenching (NPQ)

There were no obvious changing trends in NPQ values of both species under different mixture ratios (Table 1). Compared with the averaged NPQ values of *B. ischaemum* under the HW regime, water stress (MW and LW) increased by approximately 15.7 and 30.9 % in the HP, 13.7 and 12.3 % in the FP, and 7.4 and 22.7 % in the MP, respectively (Table 1). In the same mixture ratio, there were no obvious variation trends among the three growth periods for *B. ischaemum* under each water regime, except that the NPQ values in the HP or MP were significantly higher than in the FP under the LW regime ($P < 0.05$), and there were no significant differences between the former two periods (Table 1).

Compared to the HW regime, MW and LW regimes increased the NPQ values of *L. davurica* by approximately 12.5 and 27.9 % in the HP, 26.1 and 104.1 % in the FP, and 7.3 and 22.0 % in the MP, respectively (Table 1). Under each water regime, the averaged NPQ value of *L. davurica* was significantly higher in the FP and lower in the MP ($P < 0.05$) (Table 1). NPQ values of *B. ischaemum*

Table 1 Non-photochemical quenching values (NPQ) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP

mature period) at different mixture ratios and for each water regime (HW 80 ± 5 % field capacity, MW 60 ± 5 % field capacity, LW 40 ± 5 % field capacity)

Water regime	B/L	<i>B. ischaemum</i>			<i>L. davurica</i>		
		HP	FP	MP	HP	FP	MP
HW	0/12				0.174 ± 0.006	0.164 ± 0.005	0.140 ± 0.005
	2/10	0.434 ± 0.005	0.444 ± 0.009	0.417 ± 0.002	0.156 ± 0.004	0.163 ± 0.006	0.134 ± 0.006
	4/8	0.462 ± 0.011	0.412 ± 0.008	0.415 ± 0.010	0.165 ± 0.005	0.166 ± 0.005	0.141 ± 0.002
	6/6	0.417 ± 0.008	0.406 ± 0.014	0.392 ± 0.008	0.164 ± 0.004	0.157 ± 0.003	0.131 ± 0.004
	8/4	0.404 ± 0.011	0.437 ± 0.013	0.510 ± 0.010	0.147 ± 0.005	0.176 ± 0.002	0.131 ± 0.004
	10/2	0.374 ± 0.008	0.433 ± 0.008	0.431 ± 0.008	0.136 ± 0.003	0.159 ± 0.004	0.132 ± 0.004
	12/0	0.436 ± 0.011	0.463 ± 0.007	0.476 ± 0.012			
MW	0/12				0.193 ± 0.007	0.181 ± 0.004	0.163 ± 0.005
	2/10	0.546 ± 0.013	0.430 ± 0.006	0.498 ± 0.016	0.191 ± 0.005	0.170 ± 0.006	0.137 ± 0.004
	4/8	0.522 ± 0.010	0.494 ± 0.019	0.463 ± 0.016	0.179 ± 0.006	0.183 ± 0.005	0.149 ± 0.002
	6/6	0.474 ± 0.010	0.462 ± 0.007	0.494 ± 0.006	0.174 ± 0.006	0.241 ± 0.007	0.163 ± 0.003
	8/4	0.478 ± 0.016	0.442 ± 0.011	0.510 ± 0.009	0.173 ± 0.006	0.241 ± 0.008	0.155 ± 0.005
	10/2	0.440 ± 0.015	0.517 ± 0.012	0.479 ± 0.013	0.178 ± 0.006	0.201 ± 0.005	0.149 ± 0.004
	12/0	0.496 ± 0.011	0.544 ± 0.009	0.485 ± 0.005			
LW	0/12				0.208 ± 0.005	0.321 ± 0.011	0.186 ± 0.006
	2/10	0.577 ± 0.016	0.482 ± 0.021	0.555 ± 0.009	0.211 ± 0.009	0.325 ± 0.007	0.159 ± 0.004
	4/8	0.542 ± 0.010	0.422 ± 0.001	0.559 ± 0.010	0.222 ± 0.009	0.316 ± 0.008	0.163 ± 0.004
	6/6	0.543 ± 0.012	0.470 ± 0.007	0.561 ± 0.013	0.204 ± 0.005	0.303 ± 0.007	0.170 ± 0.005
	8/4	0.554 ± 0.015	0.517 ± 0.008	0.550 ± 0.017	0.203 ± 0.005	0.324 ± 0.010	0.178 ± 0.004
	10/2	0.521 ± 0.013	0.476 ± 0.014	0.530 ± 0.010	0.208 ± 0.003	0.253 ± 0.008	0.187 ± 0.006
	12/0	0.571 ± 0.015	0.526 ± 0.006	0.562 ± 0.006			

Values are mean ± SE ($n = 3$)

were significantly higher than *L. davurica* under each water regime or mixture ratio treatment ($P < 0.05$) (Table 1).

Photochemical quenching (qP)

Water stress (MW and LW) decreased the averaged qP values of *B. ischaemum* by approximately 6.5 and 17.1 % in the HP, 7.5 and 7.4 % in the FP, 7.4 and 14.0 % in the MP, respectively, compared with the HW regime (Table 2). The averaged values in the HP (0.669) and MP (0.686) were significantly higher than in the FP (0.643) under the HW regime ($P < 0.05$), but the opposite trend occurred under the LW regime ($P < 0.05$), and there were no significant differences among the three periods under the MW regime (Table 2).

For *L. davurica*, the MW and LW regimes decreased by approximately 1.8 and 3.5 % in the HP, 3.6 and 6.6 % in the FP, and 3.1 and 5.3 % in the MP, respectively (Table 2). Under the HW, MW and LW regimes, the averaged qP values of *L. davurica* in the HP (0.667, 0.658 and 0.642, respectively) were significantly higher than in the FP (0.649, 0.630 and 0.621, respectively) or MP (0.646,

0.626 and 0.614, respectively) ($P < 0.05$), and there were no significant differences between the later two periods (Table 2).

In same mixture ratio, there was no obvious changing trend between the two species in different growth periods under each water regime, except in the case of the averaged qP values of *B. ischaemum* during the HP and MP (0.567 and 0.578, respectively), which were significantly lower than those of *L. davurica* under the LW regime ($P < 0.05$) (Table 2).

Maximum relative electron transport rate (rETR_{max})

The averaged rETR_{max} values of *B. ischaemum* decreased by 20 and 40 % in the HP, 20 and 30 % in the FP or MP under the MW and LW regimes, respectively, compared with those under the HW regime (Fig. 2a, c, e). In the HP period, the averaged values of *B. ischaemum* in mixtures (163.3 or 126.3) were significantly higher than in monoculture (145.6 or 106.2) under the HW or MW regime, respectively, while in FP, the corresponding averaged values in mixtures (170.6 or 132.5) were significantly higher than in monoculture (155.4 or 123.8) under the HW or MW

Table 2 Photochemical quenching (qP) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP mature period) at different

mixture ratios and for each water regime (HW 80 ± 5 % field capacity, MW 60 ± 5 % field capacity, LW 40 ± 5 % field capacity)

Water regime	B/L	<i>B. ischaemum</i>			<i>L. davurica</i>		
		HP	FP	MP	HP	FP	MP
HW	0/12				0.631 ± 0.008	0.676 ± 0.009	0.657 ± 0.014
	2/10	0.604 ± 0.010	0.626 ± 0.015	0.668 ± 0.002	0.666 ± 0.025	0.627 ± 0.022	0.659 ± 0.017
	4/8	0.631 ± 0.014	0.639 ± 0.014	0.699 ± 0.011	0.695 ± 0.012	0.656 ± 0.008	0.638 ± 0.012
	6/6	0.671 ± 0.014	0.629 ± 0.008	0.707 ± 0.012	0.711 ± 0.010	0.650 ± 0.017	0.632 ± 0.014
	8/4	0.680 ± 0.018	0.663 ± 0.021	0.662 ± 0.008	0.689 ± 0.010	0.671 ± 0.011	0.617 ± 0.015
	10/2	0.728 ± 0.023	0.651 ± 0.022	0.715 ± 0.005	0.667 ± 0.009	0.617 ± 0.016	0.673 ± 0.016
	12/0	0.697 ± 0.010	0.650 ± 0.021	0.667 ± 0.008			
MW	0/12				0.628 ± 0.012	0.646 ± 0.012	0.637 ± 0.015
	2/10	0.583 ± 0.016	0.593 ± 0.020	0.661 ± 0.018	0.648 ± 0.014	0.649 ± 0.020	0.635 ± 0.011
	4/8	0.601 ± 0.009	0.613 ± 0.010	0.596 ± 0.014	0.671 ± 0.004	0.642 ± 0.003	0.633 ± 0.006
	6/6	0.650 ± 0.008	0.594 ± 0.014	0.634 ± 0.016	0.680 ± 0.018	0.638 ± 0.008	0.621 ± 0.016
	8/4	0.633 ± 0.011	0.662 ± 0.013	0.626 ± 0.012	0.667 ± 0.008	0.640 ± 0.010	0.601 ± 0.014
	10/2	0.651 ± 0.017	0.628 ± 0.016	0.601 ± 0.012	0.655 ± 0.010	0.565 ± 0.007	0.630 ± 0.008
	12/0	0.647 ± 0.020	0.576 ± 0.013	0.632 ± 0.015			
LW	0/12				0.624 ± 0.020	0.609 ± 0.009	0.619 ± 0.015
	2/10	0.527 ± 0.014	0.607 ± 0.006	0.571 ± 0.006	0.643 ± 0.014	0.588 ± 0.015	0.647 ± 0.020
	4/8	0.591 ± 0.014	0.612 ± 0.007	0.586 ± 0.010	0.644 ± 0.016	0.593 ± 0.020	0.616 ± 0.004
	6/6	0.525 ± 0.004	0.616 ± 0.011	0.584 ± 0.011	0.638 ± 0.020	0.638 ± 0.019	0.620 ± 0.012
	8/4	0.577 ± 0.022	0.625 ± 0.022	0.570 ± 0.009	0.644 ± 0.005	0.645 ± 0.013	0.596 ± 0.011
	10/2	0.624 ± 0.021	0.613 ± 0.014	0.567 ± 0.008	0.659 ± 0.012	0.655 ± 0.009	0.587 ± 0.008
	12/0	0.557 ± 0.007	0.580 ± 0.012	0.591 ± 0.014			

Values are mean ± SE ($n = 3$)

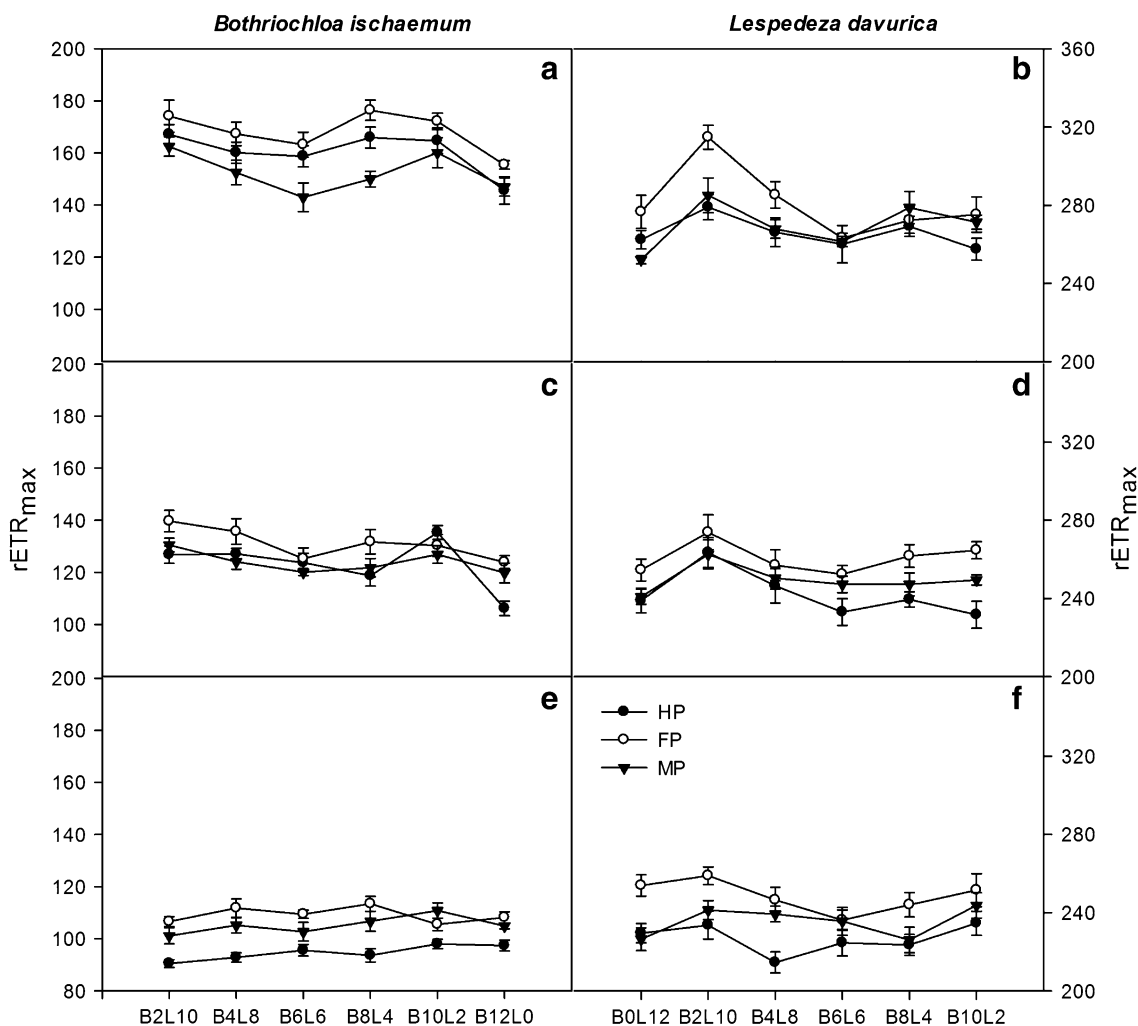


Fig. 2 Maximum relative electron transport rate (rETR_{max}) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP mature period) at different mixture ratios and for each water regime

[HW (a, b) 80 ± 5 % field capacity, MW (c, d) 60 ± 5 % field capacity, LW (e, f) 40 ± 5 % field capacity]. Values are mean ± SE ($n = 3$)

regime, respectively ($P < 0.05$) (Fig. 2a, c). Under the LW regime, the mean rETR_{max} values in the FP and MP were significantly higher than in the HP ($P < 0.05$) (Fig. 2e).

For *L. davurica*, the corresponding decreases were 10 % during each growth period under the MW or LW regime (Fig. 2d, f). The averaged rETR_{max} value of *L. davurica* in the FP was significantly higher than in the HP or MP, and there were no significant differences between the later two periods ($P < 0.05$) (Fig. 2b, d, f). Under the HW, MW or LW regimes, the averaged rETR_{max} values of *L. davurica* in mixture (272.9, 251.4 or 237.2) were significantly higher than in monoculture (253.1, 240.8 or 226.4, respectively) at the MP ($P < 0.05$), and the rETR_{max} values of *L. davurica* at the ratio of 2:10 were relatively higher than other mixture ratios under each water regime (Fig. 2b, d, f). The

rETR_{max} values of *B. ischaemum* were significantly lower than those of *L. davurica* under each water regime or mixture ratio ($P < 0.05$) (Fig. 2).

Minimum saturating irradiance (I_k)

There were no consistent changes in I_k values for both species in monoculture or for mixtures under each water regime (Table 3). Moderate (MW) and severe (LW) water stress had different effects on the I_k values of *B. ischaemum* during their growth periods in monoculture or mixtures; the MW regime increased the I_k values of *B. ischaemum* by approximately 20 % during the HP in the monoculture, whereas the averaged I_k values decreased by approximately 20 % in the FP (Table 3).

Table 3 Minimum saturating irradiance (I_k , $\mu\text{mol m}^{-2} \text{s}^{-1}$) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP mature period) at different mixture ratios and for each water regime (HW 80 ± 5 % field capacity, MW 60 ± 5 % field capacity, LW 40 ± 5 % field capacity)

Water regime	B/L	<i>B. ischaemum</i>			<i>L. davurica</i>		
		HP	FP	MP	HP	FP	MP
HW	0/12				411.9 ± 8.9	443.7 ± 7.0	411.7 ± 12.2
	2/10	176.8 ± 4.8	283.4 ± 7.0	309.5 ± 10.2	435.4 ± 10.7	465.2 ± 8.6	455.2 ± 11.4
	4/8	172.6 ± 1.6	266.1 ± 7.0	293.1 ± 7.8	405.4 ± 10.7	428.6 ± 11.4	434.2 ± 13.8
	6/6	183.1 ± 1.4	247.2 ± 5.4	285.9 ± 9.2	405.6 ± 9.6	403.4 ± 11.1	414.6 ± 7.7
	8/4	211.5 ± 6.7	263.1 ± 4.3	303.3 ± 11.6	425.8 ± 11.7	401.0 ± 14.2	408.2 ± 6.8
	10/2	198.4 ± 7.7	273.4 ± 9.0	286.0 ± 9.5	408.0 ± 9.2	398.6 ± 13.3	419.2 ± 5.6
	12/0	198.8 ± 6.4	266.3 ± 4.5	282.0 ± 8.1			
MW	0/12				376.0 ± 8.1	395.5 ± 13.1	397.5 ± 7.5
	2/10	209.3 ± 3.5	242.6 ± 6.8	293.2 ± 3.6	432.7 ± 11.7	436.2 ± 11.8	427.8 ± 11.7
	4/8	213.1 ± 4.2	249.6 ± 5.6	284.2 ± 6.9	403.0 ± 12.5	403.0 ± 9.8	408.5 ± 14.1
	6/6	193.7 ± 6.3	211.5 ± 2.9	277.6 ± 7.4	371.0 ± 9.1	407.7 ± 5.1	422.9 ± 2.4
	8/4	201.5 ± 4.4	230.8 ± 5.7	298.8 ± 3.0	372.3 ± 9.0	418.6 ± 7.5	399.4 ± 9.3
	10/2	202.2 ± 7.0	233.8 ± 8.5	257.6 ± 6.8	361.0 ± 9.4	403.4 ± 8.8	417.7 ± 3.1
	12/0	233.8 ± 11.6	211.8 ± 3.5	295.6 ± 7.8			
LW	0/12				359.5 ± 8.1	346.8 ± 3.8	383.1 ± 2.8
	2/10	191.4 ± 5.3	231.0 ± 4.6	224.9 ± 5.1	389.8 ± 9.9	395.6 ± 7.6	413.6 ± 4.2
	4/8	192.9 ± 7.0	232.5 ± 3.0	261.4 ± 8.9	357.1 ± 3.7	378.8 ± 11.3	402.1 ± 10.6
	6/6	200.6 ± 6.9	238.0 ± 7.5	273.6 ± 6.7	361.4 ± 10.6	377.2 ± 13.1	408.2 ± 14.2
	8/4	199.6 ± 5.6	229.0 ± 3.6	267.2 ± 8.4	370.1 ± 3.0	388.8 ± 10.9	375.6 ± 4.0
	10/2	215.0 ± 7.4	218.5 ± 6.6	283.3 ± 8.4	381.6 ± 10.0	389.0 ± 12.3	416.8 ± 10.1
	12/0	180.2 ± 3.0	217.8 ± 3.3	263.5 ± 8.1			

Values are mean ± SE ($n = 3$)

Compared to the HW regime, the LW regime on average decreased the I_k values by approximately 20 % in the FP or MP (Table 3). There were significant differences among the three growth periods of *B. ischaemum* under each water regime, with the highest values in the MP (288.8, 288.9 and 262.8 for the HW, MW and LW regimes, respectively) and the lowest values in the HP (193.6, 218.9 and 190.0 for the HW, MW and LW regimes, respectively) ($P < 0.05$) (Table 3).

For *L. davurica*, the MW and LW regimes decreased by approximately 10 % in the HP or FP, while the corresponding decreases were 10 % in the MP under the LW regime, compared with the HW regime (Table 3). There were no significant differences among the three growth periods of *L. davurica* under the HW regime, and the averaged I_k values in the HP (379.0) were significantly lower than in the FP (404.7) and MP (406.4) under the MW regime ($P < 0.05$), while those values in the HP (362.6) and FP (366.3) were significantly lower than those in the MP (393.2) ($P < 0.05$) (Table 3). In the same mixture ratio, the I_k values of *L. davurica* were significantly higher than those of *B. ischaemum* under each water regime ($P < 0.05$) (Table 3).

Initial slope of the curve (α)

Compared with the mean α value under the HW regime, MW and LW regimes decreased this value in *B. ischaemum* by approximately 20.4 and 19.9 % in the HP, 11.5 and 28.1 % in the FP, and 16.6 and 23.1 % in the MP, respectively. While for *L. davurica*, the corresponding decreases were 2.2 and 5.6 % in the HP, 5.3 and 4.5 % in the FP, 3.6 % in the FP and 6.1 % in the MP, respectively (Table 4). In the same mixture ratio, the averaged α value of *B. ischaemum* was lower than that of *L. davurica* under each water regime ($P < 0.05$), and this value in both species in the FP was higher than in the other two periods, except when *L. davurica* had ratios of 6:6 and 8:4 during the FP under the MW regime (Table 4).

Discussion

Species differences in response to water stress

Multi-species systems with plants in different life forms may affect their physiological response to lower water

Table 4 Initial slope of the curve (α , mol electrons mol photons⁻¹) of *Bothriochloa ischaemum* (B) and *Lespedeza davurica* (L) across their growing periods (HP heading period, FP flowering period, MP mature period) at different mixture ratios and for each water regime (HW 80 ± 5 % field capacity, MW 60 ± 5 % field capacity, LW 40 ± 5 % field capacity)

Water regime	B/L	<i>B. ischaemum</i>			<i>L. davurica</i>		
		HP	FP	MP	HP	FP	MP
HW	0/12				0.633 ± 0.006	0.654 ± 0.001	0.625 ± 0.005
	2/10	0.548 ± 0.008	0.615 ± 0.013	0.525 ± 0.006	0.641 ± 0.014	0.677 ± 0.016	0.626 ± 0.004
	4/8	0.569 ± 0.016	0.629 ± 0.005	0.521 ± 0.013	0.657 ± 0.019	0.666 ± 0.008	0.617 ± 0.011
	6/6	0.528 ± 0.011	0.660 ± 0.005	0.500 ± 0.009	0.643 ± 0.011	0.653 ± 0.023	0.631 ± 0.006
	8/4	0.499 ± 0.017	0.671 ± 0.019	0.495 ± 0.016	0.632 ± 0.009	0.679 ± 0.010	0.635 ± 0.013
	10/2	0.527 ± 0.008	0.630 ± 0.014	0.561 ± 0.010	0.628 ± 0.006	0.691 ± 0.019	0.647 ± 0.009
	12/0	0.511 ± 0.008	0.606 ± 0.006	0.512 ± 0.011			
MW	0/12				0.618 ± 0.006	0.623 ± 0.005	0.606 ± 0.003
	2/10	0.434 ± 0.008	0.576 ± 0.005	0.445 ± 0.004	0.609 ± 0.017	0.627 ± 0.009	0.614 ± 0.005
	4/8	0.410 ± 0.016	0.544 ± 0.002	0.437 ± 0.006	0.616 ± 0.012	0.638 ± 0.017	0.613 ± 0.007
	6/6	0.432 ± 0.012	0.587 ± 0.021	0.433 ± 0.009	0.628 ± 0.020	0.619 ± 0.012	0.585 ± 0.007
	8/4	0.411 ± 0.013	0.568 ± 0.011	0.407 ± 0.001	0.643 ± 0.012	0.625 ± 0.013	0.619 ± 0.005
	10/2	0.422 ± 0.012	0.558 ± 0.018	0.453 ± 0.013	0.642 ± 0.021	0.656 ± 0.010	0.597 ± 0.006
	12/0	0.410 ± 0.007	0.537 ± 0.006	0.426 ± 0.010			
LW	0/12				0.594 ± 0.009	0.627 ± 0.005	0.591 ± 0.008
	2/10	0.421 ± 0.010	0.461 ± 0.005	0.449 ± 0.004	0.600 ± 0.007	0.654 ± 0.004	0.583 ± 0.011
	4/8	0.430 ± 0.012	0.480 ± 0.014	0.403 ± 0.009	0.601 ± 0.012	0.651 ± 0.017	0.595 ± 0.018
	6/6	0.427 ± 0.009	0.459 ± 0.008	0.375 ± 0.012	0.621 ± 0.005	0.626 ± 0.006	0.577 ± 0.018
	8/4	0.419 ± 0.014	0.497 ± 0.006	0.399 ± 0.005	0.604 ± 0.011	0.628 ± 0.008	0.602 ± 0.018
	10/2	0.410 ± 0.008	0.483 ± 0.010	0.392 ± 0.005	0.615 ± 0.006	0.647 ± 0.006	0.585 ± 0.002
	12/0	0.416 ± 0.007	0.420 ± 0.007	0.390 ± 0.009			

Values are mean ± SE ($n = 3$)

availability (Cornic and Fresneau 2002; Grzesiak 2009), and can potentially lead to changes in structure and function of the communities (Porporato et al. 2004; Liu et al. 2011). Drought damage effects on plant photosynthetic apparatus depend on the degree of water deficit and the susceptibility of individual species (Griffiths and Parry 2002; Ashraf and Harris 2013). F_v/F_m was a parameter that is typically used in the monitoring of plant drought survival under water deficit conditions (Woo et al. 2008), and the values of F_v/F_m in the non-stressed plants were normally 0.75–0.85 (Bolhar-Nordenkamp et al. 1989). The results in this study showed that F_v/F_m values of both *B. ischaemum* and *L. davurica* in different growth periods were generally greater than 0.75, regardless of water regime and mixture ratio, which might be because the PSII of those species appears to be very resistant to drought stress, and the F_v/F_m measured in dark-adapted leaves did not change even in more severe drought conditions (Cornic and Fresneau 2002; Terzi et al. 2010), which demonstrated that the PSII of both *B. ischaemum* and *L. davurica* had strong drought resistance. This result is further supported by the fact that the primary photochemistry in PSII of the plants was hardly affected by water stress (Lu and Zhang 1999).

PSII photochemical efficiency has been used to clarify the involvement of regulation of photosynthesis in drought tolerance strategies for plants (Terzi et al. 2010). However, different species often show different photosynthetic performances or drought adaptation strategies in response to water availability due to their differences in morphology and physiology (Li and Wang 2003; Zhang et al. 2004; Lei et al. 2006; Sánchez-Rodríguez et al. 2012). The results in this study showed that water stress (MW and LW regimes) significantly decreased the F_v/F_m , qP and the rapid light curve-derived parameters (rETR_{max}, I_k or α) of both *B. ischaemum* and *L. davurica* during their growth periods, but the former species decreased much more than the later species, especially under the LW regime. This was consistent with previous studies that showed that *B. ischaemum* was more sensitive (and less stable) to soil water stress, compared with *L. davurica* (Xu et al. 2007). Additionally, the differences in the photosynthetic responses of two co-occurring species to lower water availability have also been reported in species of grasses, shrubs and trees (Szota et al. 2011; Ogaya et al. 2011; Maricle and Adler 2011), which indicate that *B. ischaemum* and *L. davurica* may possess different physiological strategies for coping with drought stress.

The rapid light curve measures the effective quantum yield as a function of irradiance, which provides detailed information on the saturation characteristics of electrons and is a powerful tool to assess photosynthetic activity (Ralph et al. 2002), and the decreases of $rETR_{max}$ and I_k also suggested the reduction in photosynthetic efficiency of plants under environmental stress (Song et al. 2013). In this study, *B. ischaemum* consistently showed significantly lower F_v/F_m and the rapid light curve-derived parameters ($rETR_{max}$ or I_k) than *L. davurica* under water stress, indicating that the photosynthetic activity and efficiency of *L. davurica* were higher than those of *B. ischaemum* (Figs. 1, 2), which may be attributed to the tap root system of *L. davurica* offering an advantage for soil water acquisition over the fibrous root system of *B. ischaemum*. Additionally, the PSII activity of C_4 species is always parallel to variations in the quantum yield of CO_2 fixation, whereas the C_3 species showed relatively higher PSII activity that typically partitioned between photosynthesis and photorespiration (Krall and Edwards 1992). Similar results were also reported by Throop et al. (2012), who demonstrated that the C_3 shrub (honey mesquite *Prosopis glandulosa*) consistently maintained higher physiological activity in leaves than the C_4 grass (black grama *Bouteloua eriopoda*) during the dry seasons in the Chihuahuan Desert natural grasslands.

The dissipation of excitation energy at the chloroplast level through NPQ under high light or water stress was thought to be an indicator of an essential regulation and photo-protection mechanism in photosynthetic organisms (Ruban and Murchie 2012; Lambrev et al. 2012). NPQ in *B. ischaemum* was significantly higher than in *L. davurica* among the three growth periods under each water regime and mixture ratio ($P < 0.05$), and the opposite trend occurred for the averaged qP values for all three growth periods between the two species under the MW and LW regimes, indicating that more light energy in *B. ischaemum* was dissipated in the form of heat, which may further explain the lower F_v/F_m values of *B. ischaemum* due to its relatively higher efficiency in NPQ and lower efficiency of qP (Tables 1, 2). On the other hand, it implies that *B. ischaemum* has stronger ability to dissipate excess light energy in PSII through NPQ to protect its photosynthetic organisms under water stress (Ruban and Murchie 2012).

Different responses in monoculture and mixtures

Ecological theory predicts that productivity will be higher in mixtures if species use environmental resources (light, water and nutrient) differently in time or space (Keltly 1992; Tilman 1997; Wilsey 2010). A previous study indicated that there were complementary effects to grow *B. ischaemum* and *L. davurica* together because of higher

relative yield total and transpiration water use efficiency (Xu et al. 2011a, b). Field experiments showed that the row ratios of *B. ischaemum* to *L. davurica* of 8:2 and 6:4 were beneficial in improving the photosynthesis and water use efficiencies of *B. ischaemum* (Wang et al. 2012). The results in the present study showed that the photosynthetic activity and efficiency of *B. ischaemum* in mixtures during the HP or FP were significantly higher than in monoculture under the HW and MW regimes ($P < 0.05$), whereas *L. davurica* in mixtures had significantly higher photosynthetic activity and efficiency in the MP under each water regime ($P < 0.05$) (Figs. 1, 2), which illustrated that mixture planting benefited the photosynthetic performance and may have enhanced the drought-resistant ability of both *B. ischaemum* and *L. davurica* under water stress.

However, the maximal photosynthetic performances of both species under each water regime in mixed culture depended on the developmental period of the individual plant, with the photosynthetic activity and efficiency of *B. ischaemum* in the HP and FP performing better than in the MP under sufficient water supply and moderate water stress conditions, whereas *L. davurica* showed the opposite trend under each water regime (Figs. 1, 2). According to previous studies, the coexistence of co-occurring species is determined by the balance between competition and resource partitioning (Barron-Gafford et al. 2013), and the ability of mixed species to compete for light, water and nutrient resources that are varied throughout the growing period (Percy et al. 1981; Yachi and Loreau 2007). In this study, there are differences in the photosynthetic activity and efficiency of *B. ischaemum* and *L. davurica* in mixtures across growth periods under each water regime. These potential explanations are that the ability of *B. ischaemum* to compete for resources decreases with the passing of the growth periods, and that it is a superior competitor in acquiring water or nutrient resources in the HP or FP, whereas *L. davurica* is more active in capturing resources in the MP. Furthermore, the competition ability of *B. ischaemum* in resource acquisition may be inhibited by the LW regime (Figs. 1, 2).

Photosynthetic performance differences of mixed species among each growth period are associated with their physiology and morphology and with environmental factors (Robledo and Freile-Pelegrín 2005; Sage and Kubien 2007). In the present study, the photosynthetic performance of both species obviously differed among their growth periods, and the *B. ischaemum* showed relatively higher photosynthetic activity and efficiency in the FP, while *L. davurica* showed relatively higher photosynthetic activity and efficiency in the FP and MP (Figs. 1, 2), which can be mainly attributed to the fact that the C_4 species are active in the higher temperature summer season while the C_3 species flourish in the cool autumn (Kemp and Williams 1980; Sage and Kubien 2007).

In summary, we contributed to identification of the physiological basis for differences in the photosynthetic responses of two co-occurring plant species. The results suggested that their maximal photosynthetic performances in mixed culture depend on the developmental stage of the individual plants. Under both sufficient water supply and water stress conditions, the application of mixture planting enhances the photosynthetic performance of *B. ischaemum* in HP and FP while that of *L. davurica* only in the MP.

Author contribution Bing-Cheng Xu, Xi-Ping Deng and Wei-Zhou Xu designed the entire experiments. Wei-Zhou Xu, Zhi-Juan Gao and Wen-Li Ding conducted the experiments, data collection and analysis. Wei-Zhou Xu and Bing-Cheng Xu wrote and edited the manuscript. Prof.s Bing-Cheng Xu and Xi-Ping Deng supervised the research as advisers. All authors have read and approved the final manuscript.

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References

- Ashraf M, Harris PJC (2013) Photosynthesis under stressful environments: an overview. *Photosynthetica* 51:163–190. doi:10.1007/s11099-013-0021-6
- Baker NR (1991) A possible role for photosystem II in environmental perturbations of photosynthesis. *Physiol Plantarum* 81:563–570. doi:10.1111/j.1399-3054.1991.tb05101.x
- Balaguer L, Pugnaire FI, Martínez-Ferri E, Armas C, Valladares F, Manrique E (2002) Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. *Plant Soil* 240:343–352. doi:10.1023/a:1015745118689
- Barker DH, Adams WW, Demmig-Adams B, Logan BA, Verhoeven AS, Smith SD (2002) Nocturnally retained zeaxanthin does not remain engaged in a state primed for energy dissipation during the summer in two *Yucca* species growing in the Mojave Desert. *Plant Cell Environ* 25:95–103. doi:10.1046/j.0016-8025.2001.00803.x
- Barron-Gafford GA, Angert AL, Venable DL, Tyler AP, Gerst KL, Huxman TE (2013) Photosynthetic temperature responses of co-occurring desert winter annuals with contrasting resource-use efficiencies and different temporal patterns of resource utilization may allow for species coexistence. *J Arid Environ* 91:95–103. doi:10.1016/j.jaridenv.2012.12.006
- Bolhar-Nordenkampf HR, Long SP, Baker NR, Oquist G, Schreiber U, Lechner EG (1989) Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: a review of current instrumentation. *Funct Ecol* 3:497–514. doi:10.1146/annurevpp45060194003221
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141:236–253. doi:10.1007/s00442-004-1551-1
- Christen D, Schönmann S, Jermini M, Strasser RJ, Défago G (2007) Characterization and early detection of grapevine (*Vitis vinifera*) stress responses to esca disease by in situ chlorophyll fluorescence and comparison with drought stress. *Environ Exp Bot* 60:504–514. doi:10.1016/j.envexpbot.2007.02.003
- Colom MR, Vazzana C (2003) Photosynthesis and PSII functionality of drought-resistant and drought-sensitive weeping lovegrass plants. *Environ Exp Bot* 49:135–144. doi:10.1016/s0098-8472(02)00065-5
- Cornic G, Fresneau C (2002) Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for photosystem II activity during a mild drought. *Ann Bot* 89:887–894. doi:10.1093/aob/mcf064
- Cornic G, Massacci A (2004) Leaf photosynthesis under drought stress. *Photosynthesis and the environment*. Springer, The Netherlands, pp 347–366
- Dijkstra FA, Blumenthal D, Morgan JA, LeCain DR, Follett RF (2010) Elevated CO₂ effects on semi-arid grassland plants in relation to water availability and competition. *Funct Ecol* 24:1152–1161. doi:10.1111/j.1365-2435.2010.01717.x
- Duan DP, Xu BC, Niu FR, Xu WZ (2012) Effects of water and phosphorus on chlorophyll fluorescence characteristics of different position leaves in *Lespedeza daurica*. *Pratac Sci* 29:422–428 (in Chinese)
- Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *BBA-Gen Subjects* 990:87–92. doi:10.1016/s0304-4165(89)80016-9
- Griffiths H, Parry MAJ (2002) Plant responses to water stress. *Ann Bot* 89:801–802. doi:10.1093/aob/mcf159
- Grzesiak MT (2009) Impact of soil compaction on root architecture, leaf water status, gas exchange and growth of maize and triticale seedlings. *Plant Root* 3:10–16. doi:10.3117/plantroot.3.10
- Kelty MJ (1992) Comparative productivity of monocultures and mixed-species stands. *The ecology and silviculture of mixed-species forests*. Springer, The Netherlands, pp 125–141
- Kemp PR, Williams GJ III (1980) A physiological basis for niche separation between *Agropyron Smithii* (C₃) and *Bouteloua Gracilis* (C₄). *Ecology* 61:846–858. doi:10.2307/1936755
- Krall JP, Edwards GE (1992) Relationship between photosystem II activity and CO₂ fixation in leaves. *Physiol Plantarum* 86:180–187. doi:10.1111/j.1399-3054.1992.tb01328.x
- Lambrev PH, Miloslavina Y, Jahns P, Holzwarth AR (2012) On the relationship between non-photochemical quenching and photo-protection of Photosystem II. *BBA-Bioenergetics* 1817:760–769. doi:10.1016/j.bbabi.2012.02.002
- Lei YB, Yin CY, Li CY (2006) Differences in some morphological, physiological, and biochemical responses to drought stress in two contrasting populations of *Populus przewalskii*. *Physiol Plantarum* 127:182–191. doi:10.1111/j.1399-3054.2006.00638.x
- Li CY, Wang KY (2003) Differences in drought responses of three contrasting *Eucalyptus microtheca* F Muell. populations. *For Ecol Manag* 179:377–385. doi:10.1016/s0378-1127(02)00552-2
- Liu WJ, Yuan S, Zhang NH, Lei T, Duan HG, Liang HG, Lin HH (2006) Effect of water stress on photosystem 2 in two wheat cultivars. *Biol Plantarum* 50:597–602. doi:10.1007/s10535-006-0094-1
- Liu CC, Liu YG, Guo K, Fan DY, Li GQ, Zheng YR, Yu LF, Yang R (2011) Effect of drought on pigments, osmotic adjustment and antioxidant enzymes in six woody plant species in karst habitats of southwestern China. *Environ Exp Bot* 71:174–183. doi:10.1016/j.envexpbot.2010.11.012
- Lu CM, Zhang JH (1999) Effects of water stress on photosystem II photochemistry and its thermostability in wheat plants. *J Exp Bot* 50:1199–1206. doi:10.1093/jxb/50.336.1199

- Maricle BR, Adler PB (2011) Effects of precipitation on photosynthesis and water potential in *Andropogon gerardii* and *Schizachyrium scoparium* in a southern mixed grass prairie. *Environ Exp Bot* 72:223–231. doi:10.1016/j.envexpbot.2011.03.011
- Ogaya R, Penuelas J, Asensio D, Llusà J (2011) Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change. *Environ Exp Bot* 73:89–93. doi:10.1016/j.envexpbot.2011.08.004
- Oukarroum A, Schansker G, Strasser RJ (2009) Drought stress effects on photosystem I content and photosystem II thermotolerance analyzed using Chl a fluorescence kinetics in barley varieties differing in their drought tolerance. *Physiol Plantarum* 137:188–199. doi:10.1111/j.1399-3054.2009.01273.x
- Pearcy RW, Tumosa N, Williams K (1981) Relationships between growth, photosynthesis and competitive interactions for a C₃ and C₄ plant. *Oecologia* 48:371–376. doi:10.1007/bf00346497
- Platt T, Harrison WG, Irwin B, Horne EP, Gallegos CL (1982) Photosynthesis and photoadaptation of marine phytoplankton in the Arctic. *Deep-Sea Res* 29:1159–1170. doi:10.1016/0198-0149(82)90087-5
- Porporato A, Daly E, Rodriguez-Iturbe I (2004) Soil water balance and ecosystem response to climate change. *Am Nat* 164:625–632. doi:10.1086/424970
- Ralph PJ, Gademann R (2005) Rapid light curves: a powerful tool to assess photosynthetic activity. *Aquat Bot* 82:222–237. doi:10.1016/j.aquabot.2005.02.006
- Ralph PJ, Polk SM, Moore KA, Orth RJ, Smith WO Jr (2002) Operation of the xanthophyll cycle in the seagrass *Zostera marina* in response to variable irradiance. *J Exp Mar Biol Ecol* 271:189–207. doi:10.1016/s0022-0981(02)00047-3
- Robledo D, Freile-Pelegrín Y (2005) Seasonal variation in photosynthesis and biochemical composition of *Caulerpa* spp. (Bryopsidales, Chlorophyta) from the Gulf of Mexico. *Phycologia* 44:312–319. doi:10.2216/0031-8884(2005)44[312:svipab]2.0.co;2
- Ruban AV, Murchie EH (2012) Assessing the photoprotective effectiveness of non-photochemical chlorophyll fluorescence quenching: a new approach. *BBA-Bioenergetics* 1817:977–982. doi:10.1016/j.bbabi.2012.03.026
- Sage RF, Kubien DS (2007) The temperature response of C₃ and C₄ photosynthesis. *Plant Cell Environ* 30:1086–1106. doi:10.1111/j.1365-3040.2007.01682.x
- Sánchez-Rodríguez E, Rubio-Wilhelmi MDM, Blasco B, Leyva R, Romero L, Ruiz JM (2012) Antioxidant response resides in the shoot in reciprocal grafts of drought-tolerant and drought-sensitive cultivars in tomato under water stress. *Plant Sci* 188:89–96. doi:10.1016/j.plantsci.2011.12.019
- Schreiber U (2004) Pulse-amplitude-modulation (PAM) fluorometry and saturation pulse method: an overview. *Chlorophyll a fluorescence*. Springer, The Netherlands, pp 279–319
- Schreiber U, Schliwa U, Bilger W (1986) Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosynth Res* 10:51–62. doi:10.1007/bf00024185
- Shan L, Deng XP, Su P, Huang ZB, Zhang SQ, Zhang ZB (2000) Excavating the potentiality of crop drought-resistance and water saving-the adaptability and adjustment of crop to highly variable and low water environment. *J Agri Sci Technol* 2:66–70 (in Chinese)
- Silvertown J (2004) Plant coexistence and the niche. *Trends Ecol Evol* 19:605–611. doi:10.1016/j.tree.2004.09.003
- Song R, Zhao CY, Liu J, Zhang J, Du YX, Li JZ, Sun HZ, Zhao HB, Zhao QZ (2013) Effect of sulphate nutrition on arsenic translocation and photosynthesis of rice seedlings. *Acta Physiol Plant* 35:3237–3243. doi:10.1007/s11738-013-1358-y
- Szota C, Farrell C, Koch JM, Lambers H, Veneklaas EJ (2011) Contrasting physiological responses of two co-occurring eucalypts to seasonal drought at restored bauxite mine sites. *Tree Physiol* 31:1052–1066. doi:10.1093/treephys/tpr085
- Terzi R, Saglam A, Kutlu N, Nar H, Kadioglu A (2010) Impact of soil drought stress on photochemical efficiency of photosystem II and antioxidant enzyme activities of *Phaseolus vulgaris* cultivars. *Turk J Bot* 34:1–10. doi:10.3906/bot-0905-20
- Throop HL, Reichmann LG, Sala OE, Archer SR (2012) Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland. *Oecologia* 169:373–383. doi:10.1007/s00442-011-2217-4
- Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92. doi:10.1890/12-1706.1
- Wang J, Xu BC, Gao ZJ, Duan DP, Niu FR, Xu WZ (2012) Photosynthetic diurnal changes of *Bothriochloa ischaemum* mixed sowing with *Lespedeza davurica* in loess hill-gully region. *Acta Agrestia Sin* 20:693–698 (in Chinese)
- Whitmarsh J (1999) The photosynthetic process. *Concepts in photobiology*. Springer, The Netherlands, pp 11–51
- Wilsey BJ (2010) Productivity and subordinate species response to dominant grass species and seed source during restoration. *Restor Ecol* 18:628–637. doi:10.1111/j.1526-100x.2008.00471.x
- Woo NS, Badger MR, Pogson BJ (2008) A rapid, non-invasive procedure for quantitative assessment of drought survival using chlorophyll fluorescence. *Plant Methods* 4:27–42. doi:10.1186/1746-4811-4-27
- Xu BC, Shan L, Li FM (2007) Comparison of ecophysiological characteristics of seven plant species in semiarid loess hilly-gully region. *Chin J Appl Ecol* 18:990–996 (in Chinese)
- Xu BC, Xu WZ, Huang J, Shan L, Li FM (2011a) Biomass allocation, relative competitive ability and water use efficiency of two dominant species in semiarid Loess Plateau under water stress. *Plant Sci* 181:644–665. doi:10.1016/j.plantsci.2011.03.005
- Xu BC, Xu WZ, Huang J, Shan L, Li FM (2011b) Biomass production and relative competitiveness of a C₃ legume and a C₄ grass co-dominant in the semiarid Loess Plateau of China. *Plant Soil* 347:25–39. doi:10.1007/s11104-011-0724-z
- Yachi S, Loreau M (2007) Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecol Lett* 10:54–62. doi:10.1111/j.1461-0248.2006.00994.x
- Zhang XL, Zang RG, Li CY (2004) Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress. *Plant Sci* 166:791–797. doi:10.1016/j.plantsci.2003.11.016