DOI: 10.1007/s11099-015-0108-3 PHOTOSYNTHETICA 53 (4): 489-498, 2015

Diurnal and seasonal variations in photosynthetic characteristics of switchgrass in semiarid region on the Loess Plateau of China

Z.J. GAO[*], B.C. XU[*,**,+], J. WANG[***], L.J. HUO[*], and S. LI[**]

State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, Shaanxi 712100, China[*]
Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, Shaanxi 712100, China[**]
Shaanxi Institute of Zoology, Xi'an, Shaanxi 710032, China[***]

Abstract

In order to use rationally switchgrass (*Panicum virgatum* L.) introduced in a large scale in semiarid regions on the Loess Plateau of China, we investigated and compared soil water storage dynamics, diurnal and seasonal changes in leaf photosynthetic characteristics, and biomass production of switchgrass grown under three different row spacing (20, 40, and 60 cm). Results indicated that photosynthetic parameters showed a pronounced seasonality. Diurnal course of net photosynthetic rate (P_N) was bimodal, showing obvious midday depression, which was mainly due to stomatal limitation in May and June, by nonstomatal limitation in August, and both stomatal and nonstomatal factors in September. Generally, P_N, stomatal conductance, instantaneous water-use efficiency, light-saturated net photosynthetic rate, saturation irradiance, and compensation irradiance increased with increasing row spacing. Plant height, leaf width, and a relative growth rate of biomass accumulation were significantly higher at the row spacing of 60 cm, while 20 cm spacing showed significantly higher aboveground biomass production and the biomass water-use efficiency. All these confirmed that soil water is the key limiting factor influencing switchgrass photosynthesis, and suggested that the wide row plantation (*i.e.*, 60 cm) was more beneficial to switchgrass growth, while narrow spacing was in favor of improving switchgrass productivity and water-use efficiency.

Additional key words: gas exchange; photosynthetically active radiation; plant productivity; soil water content.

Introduction

Water is a key limiting factor that affects plant growth and production in the semiarid region on the Loess Plateau of northwestern China. Beside relatively low and highly variable, the monthly distribution of annual rainfall is also very unreliable, thus water stored in soils is of great importance for plant growth (Shan and Chen 1993, Jia and Shao 2013). It has been proved that trees and established grassland is the most effective measure to increase rapidly vegetation coverage, and to control and reduce erosion in this region (Wang *et al.* 2012). However, the improper selection of plant species with high productivity, with high density and water-consuming capacity have induced deep soil desiccation, which affects further the vegetation growth (Xu *et al.* 2006). At the same time, problems, such as a sole grass variety, especially of the gramineous species, and a low survival rate, exist in grassland establishment in the region. Therefore, the rational introduction of eminent grass varieties with high adaptability is considered as effective measure to enrich cultivars for artificial grassland construction (Xu *et al.* 2006). Because rainfall and soil water were two main and basic sources for plant growth in the region, the productivity should be moderately developed to protect soil adjustment ability to keep water supply. The approaches

Received 1 July 2014, *accepted* 19 September 2014.
[+]Corresponding author; phone: +86-29-87016571, fax: +86-29-87012210, e-mail: Bcxu@ms.iswc.ac.cn
Abbreviations: AQE – apparent quantum efficiency; C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; I_c – compensation irradiance; I_s – saturation irradiance; L20 – row spacing of 20 cm; L40 – row spacing of 40 cm; L60 – row spacing of 60 cm; L_s – stomatal limitation value; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; R_D – dark respiration rate; RH – air relative humidity; SWS – soil water storage; T_{air} – air temperature; VPD – leaf to air vapor pressure deficit; WUE – instantaneous water-use efficiency; WUE_b – biomass water-use efficiency.
Acknowledgements: This work was financially supported by National Science Foundation of China (41371509), Programs for New Century Excellent Talents in University (NECT-11-0444) and Fundamental Research Funds for the Central Universities (ZD2013020).

include controlling perennial plant growth, reducing plantation intensity, and choosing plant types that have a certain biomass production (Shan and Chen 1993, Li 2002, Xu *et al*. 2006). Rational row spacing is one of the key measures to control density in crop production (Andrade *et al*. 2002). Studies have shown that row spacing significantly affects canopy architecture and micro-environment, such as sunlight, temperature, humidity, and CO_2, which ultimately affect canopy light energy utilization, plant photosynthetic efficiency, and the yield (Reta-Sánchez and Fowler 2002, Sharratt and McWilliams 2005).

Switchgrass (*Panicum virgatum* L.) is a perennial C_4, warm-season bunchgrass, native to North America with an excellent potential as a bioenergy crop (Saderson *et al*. 1996, Wright and Turhollow 2010). Compared to other perennial grasses, switchgrass shows many advantages, such as high energy production, low production costs and nutrient requirements, good environmental adaptability to marginal soils, and a potential for carbon storage in soil (Saderson *et al*. 1996). Research on switchgrass has been intensely carried out over the last decades, covering a variety selection, establishment method, nitrogen and water management, harvest time and frequency, and environmental impacts (Elbersen *et al.* 1999, Monti *et al.* 2001, 2007; McLauglin and Kszos 2005). Since early 1990s, switchgrass have been introduced and planted on the Loess Plateau of China, and exhibited great eco-adaptability to different habitats (Xu *et al.* 2008). Research showed that the mean gravimetric water content decreased below 6% in 0.6–2 m soil profile after growing for 3 years, implying that it is necessary to identify suitable density for rational use of switchgrass in this region (Jiang *et al.* 2007). Therefore, the objectives of this study were: (*1*) to compare the photosynthetic characteristics of switchgrass under different row spacings (densities) during growing season; (*2*) to determine the photosynthetic efficiency and its relations with growth and water use of switchgrass under different row spacings. Our final goal was to find optimum densities for planting switchgrass at a large scale, based on rational utilization of soil water and maintaining relatively high productivity in semiarid regions on the Loess Plateau.

Materials and methods

Site description: The study was conducted during growing season (April to October) in 2012 at the research farm of Ansai Research Station of Chinese Academy of Science in Shaanxi Province (36°51'30"N, 109°19'23"E; 1068 m a.s.l.). It is located in the semiarid region of northwestern China, with mean temperature of 8.8°C. Mean minimum temperature of the coldest month (January) is −6.9°C and mean maximum temperature of the hottest month (July) is 22.6°C. The active accumulated temperature (≥ 10°C) is about 3,119°C per year and the frost-free period is 159 d. The annual mean precipitation is 510 mm, of which about 60% falls from July to September. The loessial soil is characterized as silty loam.

Field experimental design: The field for this experiment was prepared in Autumn 2009. Switchgrass were sown at spacing of 20, 40, and 60 cm (L20, L40, and L60) among rows, respectively. Seeds were sown at 5 g(seed) m^{-1} of the row, or the equivalent rate of 255, 170, and 85 kg ha^{-1} for L20, L40, and L60 row spacing, respectively. The experiment used a randomized block design method with three replicates, and each plot was 12.0 m^2 (3 × 4 m). There was no irrigation or fertilization supplement after the experiment was established, and aboveground biomass was harvested every year at the end of the growing season by hand-held shears at a ground level.

Soil water content measurement: One aluminum tube (4 cm of diameter, 4 m in length) was installed at the center of each plot to measure soil water in April 2010. Soil volumetric water content was measured each month during April–October in 2012 using an intelligent water neutron meter (*CNC-503DR*, *Beijing Hean Nucleus Co. Ltd*., China). The measurements were taken at 10-cm intervals in 0–1.0 m of soil profile depth and 20-cm intervals in 1.0–3.8 m of soil profile depth. For this experiment, the soil water content was measured only at 3.0 m of soil depth. Thus, soil water storage (SWS) was calculated as:

$$\mathrm{SWS} = \sum_{i}^{20} \theta_v \times h_i \times 10$$

where θ_v is the soil volumetric water content at a specific soil depth [cm^3 cm^{-3}], and h_i is soil depth increment [cm].

Gas-exchange measurement: From May to September, the leaf net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), and the intercellular CO_2 concentration (C_i) were measured using a portable photosynthesis system (*CIRAS-2*, *PP Systems*, USA) at ambient environment. For each measurement, five newly expanded, healthy leaves of five plants were randomly chosen for each plot. Measurements were carried out at 2-h intervals from 8:00 to 18:00 h on three consecutive sunny days. Environmental factors, such as air temperature (T_{air}), PAR, vapor pressure deficit (VPD), and air relative humidity (RH) were obtained at the same time. Because of wind and heavy rain, no measurements were taken in July. Leaf instantaneous water-use efficiency (WUE) was calculated by dividing P_N by E (Fischer and Turner 1978), and stomatal limitation value (L_s) using the following formula: $L_s = 1 - C_i/C_a$ according to Berry and Downton (1982).

P_N-PAR response curves were measured at the same time with gas-exchange measurements, using *CIRAS-2* with a red-blue LED radiation source. The PAR was designed as follows: 2,000; 1,600; 1,200; 1,000; 800, 600, 400, 300, 200, 150, 100, 50, and 0 μmol(photon) m^{-2} s^{-1}. The response of P_N-PAR was modeled using a modified rectangular hyperbolic model (Ye and Yu 2008). The following parameters, such as the light-saturated net photosynthetic rate (P_{Nmax}), the dark respiration rate (R_D), compensation irradiance (I_c), and saturation irradiance (I_s) were also calculated directly.

The apparent quantum efficiency (AQE) was estimated from the linear part of the P_N-PAR curves, which was taken in the PAR range of 0–200 μmol(photon) m^{-2} s^{-1} (Singsaas *et al*. 2001).

Plant morphological traits: Plant height was measured every month during the growing season (May–October) from ten randomly selected plants in each plot from base to top of spike with a meter rod. Length and width of ten leaves selected at random from each plot was measured with a ruler.

Aboveground biomass production measurements were taken every month during the growing season; it was determined by manually harvesting three 50 cm long rows selected randomly from each plot. The aboveground biomass was first dried at 105°C for 30 min to stop any further metabolic processes of the plant material and then further dried at 80°C for 48 h to determine dry matter. Relative growth rate (RGR) according to Elberse *et al*. (2003) was calculated as follows: RGR = $(\ln W_{i+1} - \ln W_i)/(T_{i+1} - T_i)$, where W_{i+1} and W_i represent the aboveground dry matter yield at T_{i+1} and T_i, respectively; T_{i+1} and T_i represent the two harvest dates (18 and 128 d after turning green, respectively).

Biomass water-use efficiency (WUE_b) was calculated as the ratio of aboveground biomass production to water consumption. It was assumed that there were no runoff and subsurface drainage in terrace land, and thus water consumption was calculated as the total rainfall during switchgrass growing season plus the change in soil water storage between April and October (Shan and Chen 1993, Xu *et al*. 2006).

Statistical analysis: One-way analysis of variance (*ANOVA*) with the least significant differences (LSD) test was employed to compare leaf gas-exchange parameters across growth months and row spacing treatments at 0.05 probability level. All statistical tests were performed using *SPSS 16.0* (*SPSS*, Chicago, USA).

Results

Monthly precipitation and soil water storage: Total precipitation during the growing season (April–October) of switchgrass was 442.8 mm in 2012; it was lower than the long-term average (491.80 mm, 1971–2004). About 78.9% of the precipitation occurred between July and September; the highest precipitation occurred in September with 152.6 mm, while the lowest occurred in June with only 19.6 mm (Fig. 1*A*).

Soil water storage (SWS) at the profile (0–100 cm) under different row spacing changed with growth period and followed the same trend. It was gradually decreasing from the highest value in April to the lowest one in June, and then increased afterwards until September, while it finally decreased again in October (Fig. 1*B*). In April, SWS values at the 0–100 cm profile were 120.5, 129.8, and 129.3 mm at L20, L40, and L60, respectively. In June, it decreased sharply and reached the lowest values (75.5, 78.2, and 84.1 mm for L20, L40 and L60, respectively). Subsequently, because of high precipitation occurred between July and September, SWS increased significantly at each row spacing. At the end of the growing season (October), SWS was 115.0, 124.5, and 124.8 mm for L20, L40 and L60, respectively, and was lower than in April by 4.6, 4.1, and 3.5%. In average, SWS at L20 was significantly lower than that at L40 and L60 during the growing season, and there was no significant difference between the latter two.

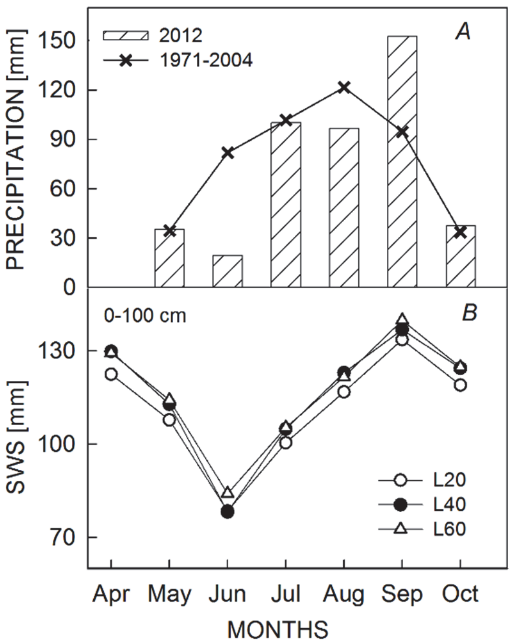

Fig. 1. Monthly precipitation in 2012 and the 34-year (1971–2004) average during May to October (*A*) and soil water storage of switchgrass (*B*) under different row spacing during the growing season (April to October) in 2012. L20, L40, and L60 indicate row spacing of 20, 40, and 60 cm, respectively.

Environmental factors: The diurnal changing trend of PAR showed a unimodal pattern and ranged from 1,700 to 2,400 μmol(photon) m^{-2} s^{-1} with the maximum values occurring between 10:00–14:00 h (Fig. 2*A*). T_{air} generally paralleled with PAR, which increased from a low value at 08:00 h (17–28°C) to a peak (25–35°C) between 12:00 and 14:00 h. The maximum mean air temperature occurred in June (32.1°C), whereas the minimum mean temperature was registered in September (22.05°C) (Fig. 2*B*). In all experimental days, diurnal patterns of VPD generally paralleled with PAR, increasing gradually in the morning and reaching maximum values at noon. VPD values were significantly higher in June than those during other months (Fig. 2*D*). Diurnal pattern of RH was opposite to that of VPD. The daily mean RH in June (30%) was the lowest RH during the growing season (Fig. 2*C*).

Gas-exchange parameters: The diurnal course of P_N was bimodal, showing the obvious midday depression (Fig. 3*A*–*D*). The first peaks occurred at 10:00 h in May,

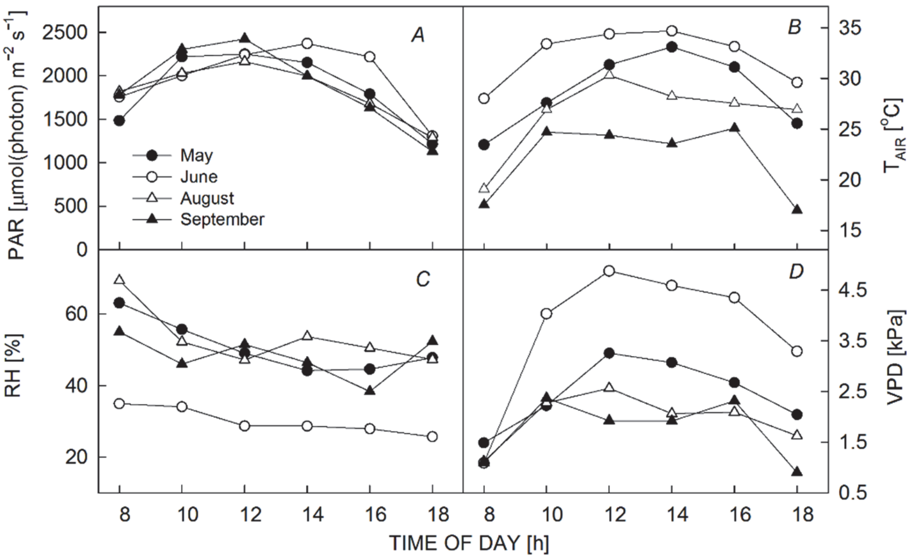

Fig. 2. Diurnal changes of photosynthetically active radiation (PAR) (*A*), air temperature (T_{air}) (*B*), air relative humidity (RH) (*C*), and leaf to air vapor pressure deficient (VPD) (*D*) during the experimental period in 2012.

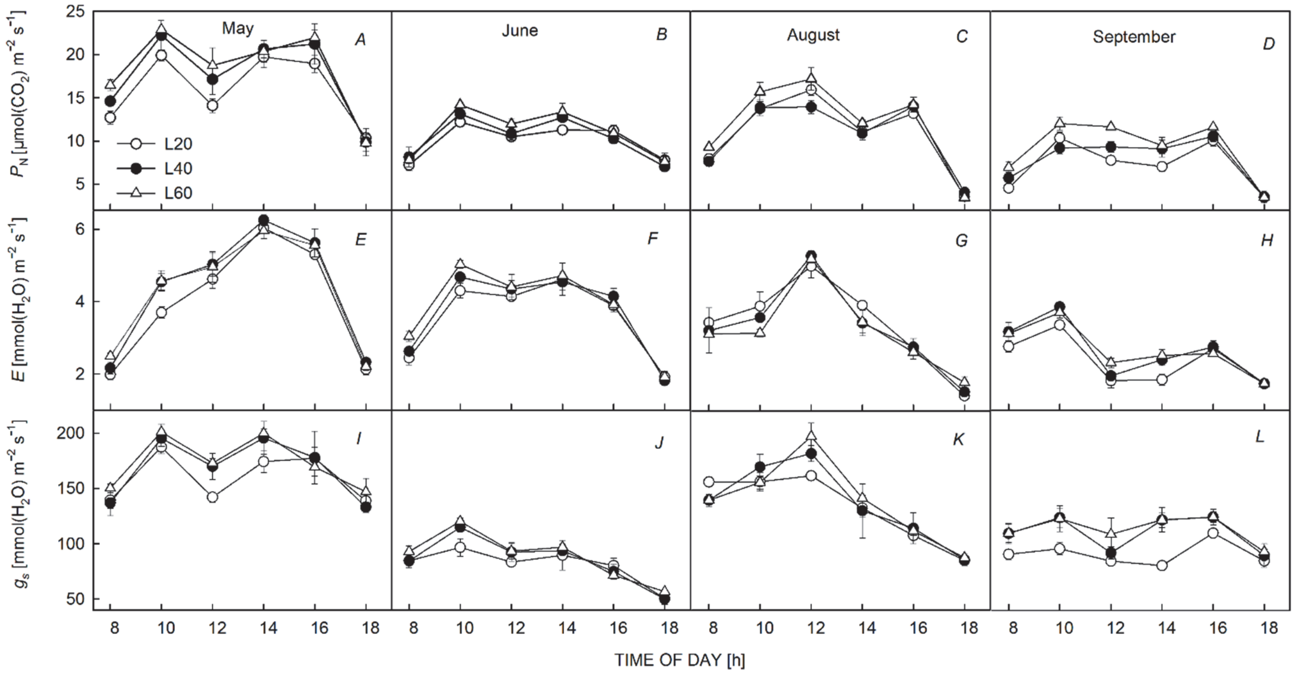

Fig. 3. Diurnal changes of the leaf photosynthetic rate (P_N) (*A*–*D*), transpiration rate (*E*) (*E*–H), stomatal conductance (g_s) (*I*–*L*) of switchgrass during the growing season under different row spacing in 2012. Bars indicate standard errors (*n* = 5). L20, L40, and L60 indicate row spacing of 20, 40, and 60 cm, respectively.

June, and September, while at 12:00 h in August. The second peaks occurred at 16:00 h in May, August, and September, whereas in June it occurred at 14:00 h. The values of the first peaks were higher than those of the second peaks.

The average P_N values of switchgrass in June and August were significantly lower than those in May, and all were significantly higher than those in September, but there were no significant difference between June and August (Table 1, Fig. 3*A–D*). The maximum daily P_N values [15.95, 17.60, and 18.35 μmol(CO_2) m^{-2} s^{-1}; May] were 54.8, 55.1, and 48.3% higher than the minimum values [7.21, 7.90, and 9.18 μmol(CO_2) m^{-2} s^{-1}; September] for L20, L40, and L60, respectively. Row spacing had significant effect on P_N values, and P_N of L60 was significantly higher than those of L20 and L40, except in May, when L60 and L40 exhibited similar values throughout the day (Table 1, Fig. 3*A–D*).

Diurnal variation of E in different growth months showed different changing trends (Fig. 3*E–H*). It presented a unimodal pattern in May and August, and the peak values occurred at 14:00 and 16:00 h, respectively. In June and September, the pattern was bimodal; the first peak values were observed at 10:00 h and the second occurred at 14:00 and 16:00 h, respectively. Daily mean E values under different row spacings showed a decreasing trend with growth month. The daily maximum E occurred in May; the values were 3.96, 4.32, and 4.29 mmol(H_2O) m^{-2} s^{-1} for L20, L40, and L60, respectively. Variance analysis showed that there were significant differences between months for all row spacing, except for L20 in May and June. L60 had significantly higher E value than L20 in May and September, but there was no significant difference between L40 and L60 (Table 1).

Diurnal changes in g_s showed a similar pattern during the growing season as for E (Fig. 3*I–L*). The diurnal variation of g_s was bimodal, and the first peaks occurred at about 10:00 h, while second peaks occurred at 14:00 h in May and June, whereas at 16:00 h in September. In August, it showed the unimodal pattern and reached the peak at 12:00 h. There were significant differences in g_s values between growing months and following the order as May > August > September > June (Table 1). Daily mean values of g_s ranked as: L60 > L40 > L20, but there were no substantial differences between row spacing, except in May and September, when L60 was significantly higher than L20.

Daily mean C_i values increased with growing season (Fig. 4*M–P*). During the day, C_i exhibited a similar trend for the three spacings, showing inverted-V shapes. There was no substantial difference between the row spacings, except in May and September, when L60 was significantly lower than L20 and L40. Diurnal variations in L_s followed the opposite trend to those of C_i (Fig. 4*Q–T*).

The diurnal course of WUE experienced seasonal fluctuations during the growing period, with the highest values recorded in May and the lowest values in September. The monthly mean WUE values were ranked as follows: May > August > September > June. In May, high WUE values showed in the early morning (8:00 h)

Table 1. Leaf net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), stomatal limitation value (L_s), and instantaneous water-use efficiency (WUE) of switchgrass under each row spacing during the growing season. Data are means ± SE (n = 5). Different *small letters* in parentheses within the same row indicate significant differences between months, whereas without parentheses indicate significant differences between row spacings according to LSD test (P<0.05).

Parameter	Row spacing [cm]	Month May	June	August	September
P_N [μmol(CO_2) $m^{-2}s^{-1}$]	20	15.95 ± 0.50$^{b(a)}$	10.05 ± 0.06$^{b(b)}$	10.68 ± 0.17$^{b(b)}$	7.21 ± 0.17$^{b(c)}$
	40	17.60 ± 0.49$^{a(a)}$	10.35 ± 0.06$^{b(b)}$	10.72 ± 0.31$^{b(b)}$	7.90 ± 0.11$^{b(c)}$
	60	18.35 ± 0.15$^{a(a)}$	10.97 ± 0.20$^{a(b)}$	12.01 ± 0.03$^{a(b)}$	9.18 ± 0.47$^{a(c)}$
E [mmol(H_2O) $m^{-2}s^{-1}$]	20	3.96 ± 0.07$^{b(a)}$	3.55 ± 0.04$^{a(b)}$	3.37 ± 0.10$^{a(b)}$	2.37 ± 0.03$^{b(c)}$
	40	4.32 ± 0.10$^{a(a)}$	3.69 ± 0.05$^{a(b)}$	3.28 ± 0.05$^{a(c)}$	2.64 ± 0.07$^{a(d)}$
	60	4.29 ± 0.09$^{a(a)}$	3.81 ± 0.11$^{a(b)}$	3.20 ± 0.06$^{a(c)}$	2.66 ± 0.05$^{a(d)}$
g_s [mmol(H_2O) $m^{-2}s^{-1}$]	20	157.31 ± 4.18$^{b(a)}$	80.83 ± 0.17$^{a(d)}$	133.08 ± 0.87$^{a(b)}$	90.85 ± 0.77$^{b(c)}$
	40	173.24 ± 2.74$^{a(a)}$	84.92 ± 1.32$^{a(d)}$	136.72 ± 2.70$^{a(b)}$	110.01 ± 5.29$^{a\ (c)}$
	60	172.84 ± 1.06$^{a(a)}$	88.63 ± 3.06$^{a(d)}$	138.71 ± 3.06$^{a(b)}$	113.21 ± 3.39$^{a(c)}$
C_i [μmol(CO_2) mol^{-1}]	20	147.77 ± 3.18$^{a(d)}$	173.42 ± 6.60$^{a(c)}$	223.72 ± 3.53$^{a(b)}$	250.78 ± 3.78$^{a(a)}$
	40	141.71 ± 0.56$^{ab(d)}$	161.08 ± 8.24$^{a(c)}$	216.85 ± 4.39$^{a(b)}$	243.56 ± 2.93$^{a(a)}$
	60	133.73 ± 3.58$^{b(c)}$	155.82 ± 6.62$^{a(b)}$	213.65 ± 4.36$^{a(a)}$	224.43 ± 3.07$^{b(a)}$
L_s	20	0.581 ± 0.020$^{b(a)}$	0.565 ± 0.021$^{b(a)}$	0.396 ± 0.008$^{a(b)}$	0.319 ± 0.011$^{b(c)}$
	40	0.593 ± 0.011$^{ab(a)}$	0.595 ± 0.021$^{a(a)}$	0.409 ± 0.012$^{a(b)}$	0.341 ± 0.015$^{b(c)}$
	60	0.613 ± 0.002$^{a(a)}$	0.610 ± 0.031$^{a(a)}$	0.418±0.012$^{a(b)}$	0.390 ± 0.010$^{a(b)}$
WUE [μmol(CO_2) $mmol^{-1}$(H_2O)]	20	4.46 ± 0.06$^{a(a)}$	2.95 ± 0.06$^{a(c)}$	3.22 ± 0.05$^{b(b)}$	3.08 ± 0.05$^{b(bc)}$
	40	4.46 ± 0.03$^{a(a)}$	2.92 ± 0.05$^{a(c)}$	3.32 ± 0.04$^{b(b)}$	3.07 ± 0.15$^{b(bc)}$
	60	4.52 ± 0.03$^{a(a)}$	2.96 ± 0.06$^{a(d)}$	3.70 ± 0.06$^{a(b)}$	3.46 ± 0.06$^{a(c)}$

Table 2. Parameters of P_N-PAR response curves for switchgrass under different row spacings during the growing season. Values for light-saturated net photosynthetic rate (P_{Nmax}), dark respiration rate (R_D), apparent quantum efficiency (AQE), compensation irradiance (I_c), and saturation irradiance (I_s) are mean ± SD (n = 5). Different *small letters* in parentheses within the same row indicate significant differences between months, whereas without parentheses indicate significant differences between row spacings according to LSD test (P<0.05).

Parameter	Row spacing [cm]	Month May	June	August
P_{Nmax} [μmol(CO_2) m^{-2} s^{-1}]	20	12.31 ± 0.58$^{c(a)}$	11.03 ± 0.05$^{b(b)}$	12.04 ± 0.56$^{b(a)}$
	40	15.29 ± 0.56$^{b(a)}$	11.49 ± 0.06$^{b(b)}$	14.69 ± 0.40$^{a(a)}$
	60	16.62 ± 0.67$^{a(a)}$	12.43 ± 0.0$^{a(c)}$	15.17 ± 0.63$^{a(b)}$
R_D [μmol(CO_2) m^{-2} s^{-1}]	20	1.49 ± 0.10$^{b(a)}$	1.16 ± 0.01$^{c(b)}$	1.27 ± 0.14$^{c(b)}$
	40	1.98 ± 0.06$^{a(a)}$	1.42 ± 0.04$^{b(b)}$	1.48 ± 0.09$^{b(b)}$
	60	2.05 ± 0.43$^{a(a)}$	1.64 ± 0.09$^{a(b)}$	1.71 ± 0.09$^{a(b)}$
AQE [μmol(CO_2) $μmol^{-1}$(photon)]	20	0.0423 ± 0.004$^{a(a)}$	0.0348 ± 0.002$^{a(b)}$	0.0411 ± 0.001$^{a(a)}$
	40	0.0408 ± 0.003$^{a(a)}$	0.0332 ± 0.001$^{a(b)}$	0.0398 ± 0.003$^{a(a)}$
	60	0.0402 ± 0.001$^{a(a)}$	0.0328 ± 0.003$^{a(b)}$	0.0401 ± 0.005$^{a(a)}$
I_c [μmol(photon) m^{-2} s^{-1}]	20	35.75 ± 2.03$^{b(a)}$	32.55 ± 1.46$^{b(a)}$	33.79 ± 4.96$^{b(a)}$
	40	46.39 ± 2.51$^{a(a)}$	41.09 ± 1.89$^{a(a)}$	43.10 ± 0.71$^{a(a)}$
	60	51.20 ± 3.20$^{a(a)}$	45.01 ± 1.61$^{a(b)}$	46.52 ± 3.20$^{a(b)}$
I_s [μmol(photon) m^{-2} s^{-1}]	20	1,398.7 ± 0.89$^{a(a)}$	1,249.5 ± 30.86$^{a(b)}$	1,418.7 ± 10.83$^{a(a)}$
	40	1,410.5 ± 24.76$^{a(a)}$	1,259.3 ± 14.56$^{a(b)}$	1,430.0 ± 22.13$^{a(a)}$
	60	1,442.3 ± 24.65$^{a(a)}$	1,265.7 ± 32.23$^{a(b)}$	1,453.3 ± 31.15$^{a(a)}$
R^2	20	0.997	0.992	0.997
	40	0.998	0.997	0.996
	60	0.996	0.992	0.994

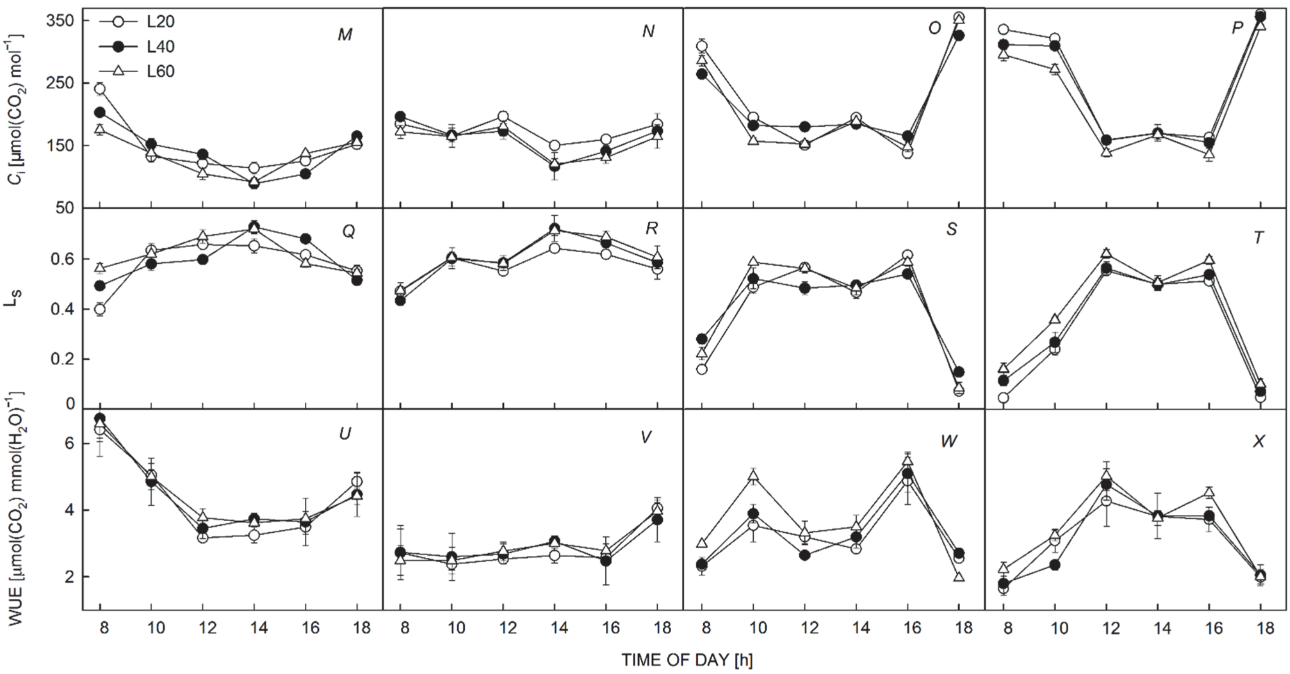

Fig. 4. Diurnal changes of intercellular CO_2 concentrations (C_i) (*M–P*), stomatal limitation value (L_s) (*Q–T*), and instantaneous water-use efficiency (WUE) (*U–X*) of switchgrass during the growing season under each row spacing in 2012. Bars indicate standard errors (n = 5). L20, L40, and L60 indicate row spacing of 20, 40, and 60 cm, respectively.

and later afternoon (18:00 h), and the daily mean values of WUE did not show significant differences between row spacings (Fig. 4*U*). With respect to June, the values of WUE under the three row spacings were maintained low and constant (2.5–3 µmol mmol^{-1}) during 8:00–16:00 h, and then slightly recovered at 18:00 h (Fig. 4*V*). The pattern was bimodal in August and September, the first peak values were observed at 10:00 and 12:00 h, respectively, the second peak values were both at 16:00 h (Fig. 4*W*,*X*). There was no significant difference between spacings, except in August and September, when WUE values in L60 were significantly higher.

P_N-PAR curves: The relation between P_N and PAR can be expressed as a rectangular hyperbolic model (Fig. 5*A*–*C*, Table 2). At low light intensities, P_N increased rapidly with increasing PAR, reaching a maximum rate of 12–16 µmol m^{-2} s^{-1} above 1,000 µmol(photon) m^{-2} s^{-1} PAR. No symptoms of photoinhibition were found in switchgrass even under PAR exceeding 2,000 µmol(photon) m^{-2} s^{-1} at noon.

Values of AQE, P_{Nmax}, R_D, and I_s were higher in May, then significantly declined in June, and finally reversed in August, whereas I_c values were constant under all row spacings. L60 showed significantly higher values of P_{Nmax} than that of L20 each month, whereas values of P_{Nmax} in L40 were significantly greater than in L20 in May and June. R_D values increased significantly as row spacing enlarged, except in May, when no significant difference was between L40 and L60. I_c values of L20 were significantly lower, whereas no significant differences were between L40 and L60. There were no significant differences in I_s values between row spacing each month (Table 2).

Switchgrass growth and biomass production: Plant height and leaf length were significantly higher under L60, while there were no significant differences between the three row spacings in leaf width (Table 3). Relative growth rate of switchgrass biomass accumulation was also significantly higher under L60, and there was no significant difference between L40 and L20 (Table 3). In 2011 and 2012, aboveground biomass production under

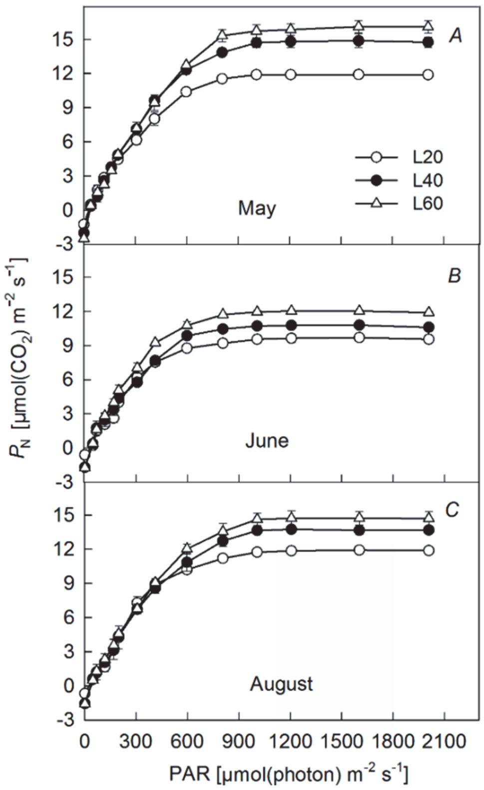

Fig. 5. Net photosynthetic rate (P_N)-PAR response curves for switchgrass under different row spacings. Bars indicate standard errors (*n* = 5). L20, L40, and L60 indicate row spacing of 20, 40, and 60 cm, respectively.

Table 3. Maximum plant height, leaf length, leaf width, and relative growth rate (RGR) of switchgrass under different row spacing. Values are means ± SE (*n* = 5), means followed by different *small letters* in the same column are significantly different at *P*<0.05 according to LSD test.

Row spacing [cm]	Plant height [cm]	Leaf length [cm]	Leaf width [cm]	RGR [kg ha^{-1} d^{-1}]
20	81.00 ± 1.73^c	32.33 ± 1.76^b	0.93 ± 0.02^a	0.048 ± 0.005^b
40	91.66 ± 2.03^b	37.60 ± 1.52^{ab}	1.06 ± 0.03^a	0.055 ± 0.007^b
60	110.02 ± 1.20^a	40.01 ± 1.73^a	1.10 ± 0.06^a	0.063 ± 0.004^a

Table 4. Biomass production, water consumption, and biomass water-use efficiency (WUE_b) of switchgrass under different row spacings in 2011 and 2012. Values are means ± SE (*n* = 5), means followed by different small letters in the same column are significantly different at *P*<0.05 according to LSD test.

Row spacing [cm]	2011 Biomass [kg ha^{-1}]	Water consumption [mm]	WUE_b [kg ha^{-1} mm^{-1}]	2012 Biomass [kg ha^{-1}]	Water consumption [mm]	WUE_b [kg ha^{-1} mm^{-1}]
20	4,815.7^a	511.6^a	9.41^a	7,771.8^a	468.7^a	16.58^a
40	3,940.3^b	499.8^a	7.88^b	6,976.8^b	472.1^a	14.78^b
60	3,733.3^b	492.5^a	7.58^b	6,609.2^b	477.8^a	13.83^b

L60 was significantly higher than those under L40 and L20, while there were no significant differences between the three row spacings in water consumption; it resulted in significantly higher water-use efficiency in L20 (Table 4). There were no significant differences between L40 and L60 in aboveground biomass production, water consumption, and water-use efficiency during the growing season in 2011 and 2012 (Table 4).

Discussion

Effects of row spacing on gas-exchange characteristics: Photosynthesis is an important biological process that directly influences plant growth and productivity (Guo *et al.* 2013). Plant spacing could affect the photosynthetic rate through affecting crop canopy structure and the growth environment, which is manifested in plant eco-physiological and growth performance (Andrade *et al.* 2002). Our results clearly showed that daily mean values of P_N, E, g_s, and WUE increased with increasing row spacing. Hou and Wang (2001) also reported that flag leaf P_N of spring wheat was significantly lower under high density (1,000 seedlings m^{-2}) than that under low density (100 seedlings m^{-2}) planting, and single plant biomass was also lower at high density under conditions of water deficit. Photosynthesis is also correlated with plant growing periods and environmental conditions (Berry and Downton 1982). It is believed that high temperature and low air humidity (*i.e.*, high VPD) were the basic factors causing the reduction of P_N in midday (Xu 1990). The significantly highest P_N values appeared in May, maybe not only due to favorable soil water availability, but also due to active vegetative development. The sharp reduction in maximal and mean daily gas exchange found at all row spacings in June could be attributed to the low soil water content, high VPD, and temperature (Matos *et al.* 1998, Bota *et al.* 2004, Zhang *et al.* 2008, Guo *et al.* 2013). Relatively lower P_N in August can not be only ascribed to the lower soil water content, but also to changes in the phenological stage of switchgrass, while in September, the daily mean P_N was the lowest (Fig. 3*D*) because of leaf senescence and lower carbohydrates demand (Matos *et al.* 1998).

Switchgrass showed obviously P_N midday depression. P_N midday depression can be attributed to stomatal or nonstomatal factor limitations, and their impacts vary with environmental conditions (Cai *et al.* 2012). According to Farquhar and Sharkey (1982), photosynthesis stomatal limitation occurs when g_s and C_i decrease and L_s increases simultaneously, otherwise nonstomatal limitation is responsible. Therefore, it can be concluded that P_N midday depression of switchgrass in May and June was mainly due to stomatal limitation, and due to nonstomatal limitation in August, while it was caused by both stomatal and nonstomatal factors in September.

WUE is the ratio of carbon gained in photosynthesis (P_N) in exchange for water used in transpiration (E), which mainly depends on environmental conditions, such as temperature, irradiance, relative humidity, and soil water. Xu *et al.* (2003) reported that maximum values of WUE of switchgrass occurred in the morning and then declined as the day progressed. In our study, similar trends were observed only in May, while they were significantly different in the other three months; such different trends occurred probably due to different habitat conditions and the growing period.

Effects of row spacing on P_N-PAR response curve: The P_N-PAR response curves can be fitted and described by many models and equations, such as nonrectangular hyperbola, rectangular hyperbola, and binomial regression models, of which the most extensively applied model is the nonrectangular hyperbola model, *i.e.*, Farquhar model (Farquhar and Sharkey 1982, Ye and Yu 2008). However, I_s and P_{Nmax} values cannot be calculated directly by non-rectangular hyperbola because the model is an asymptote, and calculated P_{Nmax} values were much higher, while calculated I_s values were far less lower than the measured using this model (Ye 2007, Xu *et al.* 2013). In the present study, the P_N-PAR curves of switchgrass were accurately fitted by the modified rectangular hyperbolic model, because the decision coefficient (R^2) were greater than 0.99.

I_s and I_c are two key traits reflecting plant sunlight-use efficiency. Normally, plants with higher I_s and lower I_c can use a wider irradiation range and have higher photo-synthetic capacity (Li *et al.* 2013). Results indicated that I_s, I_c, P_{Nmax}, and R_D decreased as row spacing was reduced, suggesting that the ability to use weak light increased, and radiation interception and radiation-use efficiency were improved under narrow spacing (Andrade *et al.* 2002, Miao *et al.* 2009). L20 had the lowest I_c value, which may be due to uneven light distribution, activating absorption and conversion efficiency of weak light (Cao *et al.* 2011). The lower R_D and I_c values could enable switchgrass under L20 to decrease respiratory carbon losses and to maintain a positive carbon balance under low light intensities (Craine and Reich 2005, Miao *et al.* 2009). Significantly lower values of P_{Nmax}, AQE, I_s, and R_D found in June coincided with severe water stress (the volumetric water content of 7.8%) (Li *et al.* 2013).

Effects of row spacing on growth and water use: In semiarid Loess Plateau, water is the primary and key factor affecting plant growth and production. To find sustainable and rational cropping patterns with high water-use efficiency is among the cardinal goals of research and extension systems (Shan and Chen 1993). Row spacing is an agronomical practice that affects plant spatial distribution, canopy structure, light interception and radiation-use efficiency, soil water use, and consequently, biomass production in cropping systems (Andrade *et al*. 2002, Mattera *et al*. 2013). Plant response can be studied both at the individual plant level (competition with other plants) and at the population level (effect on the total yield) (Fang *et al*. 2014). As we know, plant/crop production is a colony process rather than individual performance, because the ultimate goal for artificial population is to obtain higher biomass or economic yield (Zhao *et al*. 1997). In this research, switchgrass growth and ecophysiological performance did not show advantages in narrow spacing (*i.e*., 20 cm), as the lower plant height, leaf P_N, and WUE were found. It showed significantly higher aboveground biomass production and WUE_b, because switchgrass is an erect bunch-type grass; narrow spacing can increase the ground coverage and reduce soil evaporation (Sun *et al*. 2006, Chen *et al*. 2010).

In summary, row spacing and soil water exhibited significant effects on photosynthetic characteristics and plant morphology of switchgrass in terrace land at semiarid loess hilly-gully region on the Loess Plateau. The wider row spacing might be beneficial to individual plant development and growth, while narrower row spacing is in favor of improving biomass production per unit area and water-use efficiency for switchgrass in the region.

References

Andrade F.H., Calviño P., Cirilo A. *et al*.: Yield responses to narrow rows depend on increased radiation interception. – Agron. J. **94**: 975-980, 2002.

Berry J.A., Downton W.J.S.: Environmental regulation of photosynthesis. – In: Govindjee (ed.): Photosynthesis: Development, Carbon Metabolism, and Plant Productivity. Pp. 263-343. Academic Press, New York 1982.

Bota J., Medrano H., Flexas J.: Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? – New Phytol. **162**: 671-681, 2004.

Cai Q.S., Wang L.L., Yao W.H. *et al*.: Diallel analysis of photosynthetic traits in maize. – Crop Sci. **52**: 551-559, 2012.

Cao Y. H., Zhou B.Z., Chen S.L. *et al*.: The photosynthetic physiological properties of *Illicium lanceolatum* plants growing under different light intensity conditions. – Afr. J. Agric. Res. **6**: 5736-5741, 2011.

Chen S.Y., Zhang X.Y., Sun H.Y. *et al*.: Effects of winter wheat row spacing on evapotranspiration, grain yield and water use efficiency. – Agric. Water Manage. **97**: 1126-1132, 2010.

Craine J.M., Reich P.B.: Leaf-level light compensation points in shade-tolerant woody seedlings. – New Phytol. **166**: 710-713, 2005.

Elbersen H.W., Ocumpaugh W.R., Hussey M.A. *et al*.: Field evaluation of switchgrass seedlings divergently selected for crown node placement. – Crop Sci. **39**: 475-479, 1999.

Elberse I.A.M., Van Damme J.M.M., Van Tienderen P.H.: Plasticity of growth characteristics in wild barley (*Hordeum spontaneum*) in response to nutrient limitation. – J. Ecol. **91**: 371-382, 2003.

Fang Y., Xu B., Liu L. *et al*.: Does a mixture of old and modern winter wheat cultivars increase yield and water use efficiency in water-limited environments? – Field Crop. Res. **156**: 12-21, 2014.

Farquhar G.D., Sharkey T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant. Phys. **33**: 317-345, 1982.

Fischer R.A., Turner N.C.: Plant productivity in the arid and semiarid zones. – Annu. Rev. Plant. Phys. **29**: 277-314, 1978.

Guo C.Y., Li J.C., Yue J.Y. *et al*.: [Diurnal changes in the photosynthetic characteristics of two high yield and high quality grasses during different stages of growth and their response to changes in light intensity.] – Acta Ecol. Sin. **33**: 1751-1761, 2013. [In Chinese]

Hou Z.D., Wang G.X.: [Elementary study on net photosynthetic rate of spring wheat under different densities and soil water status.] – J. Desert Res. **21**: 236-239, 2001. [In Chinese]

Jia Y.H., Shao M.A.: Temporal stability of soil water storage under four types of revegetation on the northern Loess Plateau of China. – Agric. Water Manage. **117**: 33-42, 2013.

Jiang J., Li D.Q., Huang J.: [Growth of *Panicum virgatum* and soil moisture characteristics.] – Bull. Soil Water Conserv. **27**: 75-78, 2007. [In Chinese]

Li Y.S.: [Productivity dynamic of alfalfa and its effects on water eco-environment.] – Acta Pedol. Sin. **39**: 404-411, 2002. [In Chinese]

Li J.Y., Zhao C.Y., Li J. *et al*.: Growth and leaf gas exchange in *Populus euphratica* across soil water and salinity gradients. – Photosynthetica **51**: 321-329, 2013.

Matos M.C., Matos A.A., Mantas A. *et al*.: Diurnal and seasonal changes in *Prunus amygdalus* gas exchanges. – Photosynthetica **35**: 517-524, 1998.

Mattera J., Romero L.A., Cuatrín A.L. *et al*.: Yield components, light interception and radiation use efficiency of lucerne (*Medicago sativa* L.) in response to row spacing. – Eur. J. Agron. **45**: 87-95, 2013.

McLaughlin S.B., Kszos L.A.: Development of switchgrass (*Panicum virgatum*) as a bioenergy feedstock in the United States. – Biomass Bioenerg. **28**: 515-535, 2005.

Miao Z., Xu M., Lathrop R.G. *et al*.: Comparison of the A-Cc curve fitting methods in determining maximum ribulose 1.5-bisphosphatecarboxylase/oxygenase carboxylation rate, potential light saturated electron transport rate and leaf dark respiration. – Plant Cell Environ. **32**: 109-122, 2009.

Monti A., Fazio S., Lychnaras V. *et al*.: A full economic analysis of switchgrass under different scenarios in Italy estimated by BEE model. – Biomass Bioenerg. **31**: 177-185, 2007.

Monti A., Venturi P., Elbersen H.W.: Evaluation of the establishment of lowland and upland switchgrass (*Panicum virgatum* L.) varieties under different tillage and seedbed conditions in northern Italy. – Soil Till. Res. **63**: 75-83, 2001.

Reta-Sánchez D.G., Fowler J.L.: Canopy light environment and yield of narrow-row cotton as affected by canopy architecture. – Agron J. **94**: 1317-1323, 2002.

Saderson M.A., Reed R.L., McLaughlin S.B. *et al*.: Switchgrass as a sustainable bioenergy crop. – Bioresource Technol. **56**: 83-93, 1996.

Shan L., Chen G.L.: [Theory and practice of dryland farming on the Loess Plateau, Beijing.] Pp. 256-280. Chinese Science Press, Beijing 1993. [In Chinese]

Singsaas E.L., Ort D.R., DeLucia E.H.: Variation in measured values of photosynthetic quantum yield in ecophysiological studies. – Oecologia **128**: 15-23, 2001.

Sharratt B.S., McWilliams D.A.: Microclimatic and rooting

characteristics of narrow-row versus conventional-row corn. – Agron. J. **97**: 1129-1135, 2005.
Sun H.Y., Liu C.M., Zhang X.Y. *et al*.: [Effects of different row spacings on soil evaporation, evapotranspiration and yield of winter wheat.] – Trans. CSAE **22**: 22-26, 2006. [In Chinese]
Wang Y.Q., Shao M.A., Liu Z.P. *et al*.: Regional spatial pattern of deep soil water content and its influencing factors. – Hydrolog. Sci. J. **57**: 265-281, 2012.
Wright L., Turhollow A.: Switchgrass selection as a "model" bioenergy crop: a history of the process. – Biomass Bioenerg. **34**: 851-868, 2010.
Xu D.Q.: [Ecology, physiology and biochemistry of midday depression of photosynthesis.] – Plant Physiol. Commun. **6**: 5-10, 1990. [In Chinese]
Xu B.C., Li F.M., Shan L.: Switchgrass and milkvetch intercropping under 2:1 row-replacement in semiarid region, northwest China: Aboveground biomass and water use efficiency. – Eur. J. Agron. **28**: 485-492, 2008.
Xu B.C., Gichuki P., Shan L. *et al*.: Aboveground biomass production and soil water dynamics of four leguminous forages in semiarid region, northwest China. – S. Afr. J. Bot. **72**: 507-516, 2006.
Xu W.Z., Deng X.P., Xu B.C.: Effects of water stress and fertilization on leaf gas exchange and photosynthetic light-response curves of *Bothriochloa ischaemum* L. – Photosynthetica **51**: 603-612, 2013.
Xu B.C., Shan L., Huang Z.B. *et al*.: [Comparative of photosynthetic characteristics of old world bluestems (*Bothriochia ischaemum*) and switchgrass (*Panicum virgatum*) in Loess Hilly-gully Region of China.] – Grass. China **25**: 1-4, 2003. [in Chinese].
Ye Z.P., Yu Q.: A coupled model of stomatal conductance and photosynthesis for winter wheat. – Photosynthetica **46**: 637-640, 2008.
Ye Z.P.: A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*. – Photosynthetica **45**: 637-640, 2007.
Zhang J.L., Meng L.Z., Cao K.F.: Sustained diurnal photo-synthetic depression in uppermost-canopy leaves of four dipterocarp species in the rainy and dry seasons: does photo-respiration play a role in photoprotection? − Tree Physiol. **29**: 217-228, 2008.
Zhao S.L., Li F.M., Zhang D.Y. *et al*.: [Crop production is a population process.] – Acta Ecol. Sin. **17**: 100-104, 1997. [In Chinese]