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Full Length Research Paper

Soil carbon dioxide (CO₂) efflux of two shrubs in response to plant density in the northern Loess Plateau of China

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Although plant density should affect soil carbon dioxide (CO₂) efflux and carbon cycling in semi-arid regions, the effects of plant density on soil CO₂ efflux are not well known. This study was performed to investigate the responses of soil CO₂ efflux of two dominant shrubs (*Caragana korshinkii* and *Salix psammophila*) to plant density in the northern Loess Plateau of China. Two plant density treatments, low and high, were included for *C. korshinkii* (average 20,000 plants ha⁻¹ and average 66,667 plants ha⁻¹) and *S. psammophila* (average 9,583 plants ha⁻¹ and average 31,250 plants ha⁻¹). Soil CO₂ efflux was measured every other day with an Ultra-light portable photosynthesis system (CI-340, CID Inc., USA) from July to October 2009. Soil CO₂ efflux with high plant density was significantly larger than that with low plant density for both shrub species. Plant density did not change the temporal pattern of CO₂ efflux during the study period. Our results indicated that root biomass and aboveground biomass were the significant biotic factors mediating the response of soil CO₂ efflux to plant density for the two shrubs. Moreover, both soil water contents in the 0 - 6 cm soil layer and in deeper soil layer partly regulated the responses of soil CO₂ efflux to the shrub density treatments in the semi-arid region.

Key words: Plant density, semi-arid, shrub, soil CO₂ efflux.

INTRODUCTION

The wind and water erosion transitional belt located in the northern Loess Plateau is a typical semi-arid region. Soil respiration produces the second largest carbon flux from soil and plays a critical role in carbon cycling between terrestrial ecosystems and the atmosphere particularly in semi-arid ecosystems (Raich and Schlesinger, 1992; Conant et al., 2000; Schlesinger and Andrews, 2000; Luo and Zhou, 2006). The efflux of carbon dioxide (CO₂) in semi-arid ecosystems is highly sensitive to abiotic factors and biotic factors (Conant et al., 2000). Plant density that affects abiotic factors and biotic factors can alter the soil

CO₂ efflux during the growing season, with consequent impact on carbon cycling in semi-arid region (Conant et al., 2000; Cox et al., 2000; Raich and Tufekciogul, 2000).

Among the abiotic factors controlling soil CO₂ efflux, soil temperature and soil moisture are considered to be the dominant ones (Adachi et al., 2006). Efflux of CO₂ is highly sensitive to changes in temperature because of its effects on almost all aspects of CO₂ emission processes (Townsend et al., 1992; Boone et al., 1998; Davidson et al., 1998; Buchmann, 2000; Mikan et al., 2002; Luo and Zhou, 2006). Water availability is mainly dependent on precipitation, which affects soil dry-wet cycle and activates biological processes in semi-arid ecosystems; so it has a predominant effect on soil CO₂ efflux (Raich and Schlesinger, 1992; Conant et al., 1998; Huxman et al., 2004; Xu et al., 2004; Harper et al., 2005; Patrick et

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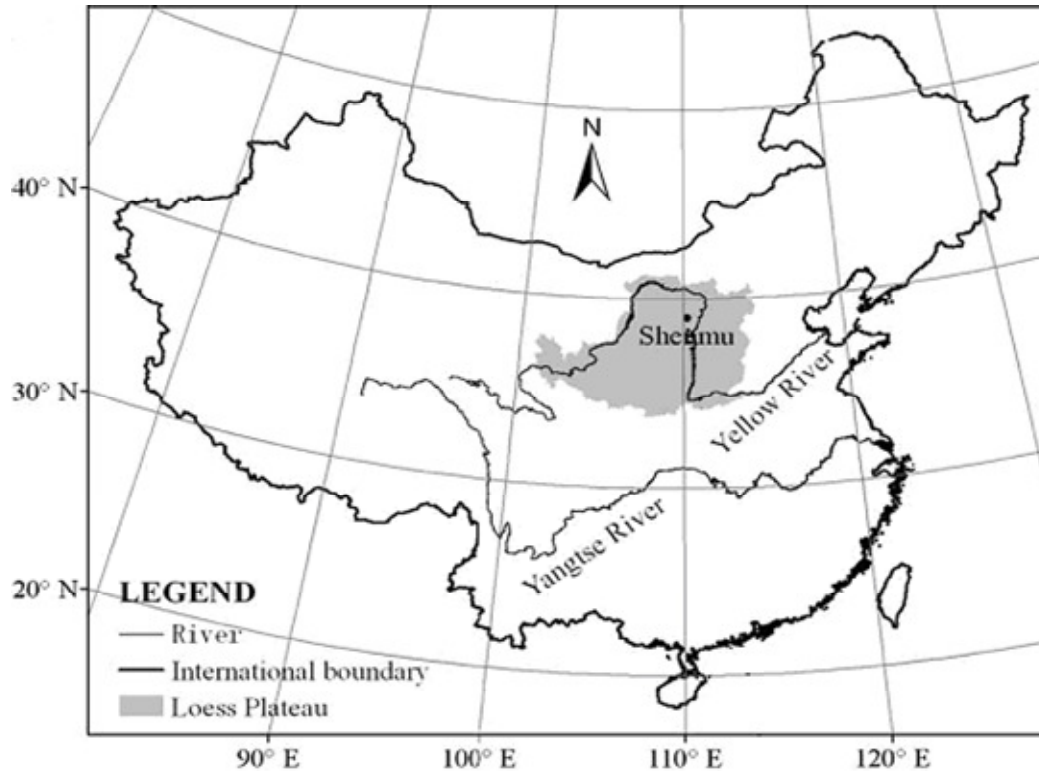


Figure 1. Location of the study site on the Loess Plateau (Wang et al., 2010).

et al., 2007). In the field, soil water content and soil temperature interact and together play a critical role in regulating the temporal variations of soil CO₂ efflux (Wildung et al., 1975; Raich and Tufekciogul, 2000; Joffre et al., 2003). Biotic factors such as plant root biomass and above-ground biomass potentially influence soil CO₂ efflux. Soil CO₂ efflux originates in part from root respiration and thus is associated with root biomass (Maier and Kress, 2000; Sørensen and Buchmann, 2005). Temporal and spatial variations in root respiration are connected with root biomass changes (Adachi et al., 2006; Jia et al., 2006; Zhu et al., 2009). Soil CO₂ efflux can also vary with aboveground plant biomass. There is some evidence that aboveground production is positively correlated with soil CO₂ efflux (Davidson et al., 2000; Flanagan and Johnson, 2005).

Plant density has direct effects on several biotic and abiotic factors controlling soil CO₂ efflux. For example, it is well documented that plant density causes variability in soil water content and soil temperature through altering plant water uptake and soil surface shading (Iverson and Hutchinson, 2002). Additionally, plant density is correlated with root biomass and aboveground biomass because of competition for resources and space (Bullard et al., 2002). Therefore, plant density can potentially affect soil respiration and carbon dioxide emissions at the soil-atmosphere interface (Raich and Tufekciogul, 2000; Zhu et al., 2008). However, how soil CO₂ efflux responds

to plant density in semi-arid environments is not well understood and further studies need to be conducted.

The wind and water erosion transitional belt suffers the most intensive soil erosion on the Loess Plateau, with fragile ecological environment and serious land desertification. In order to improve ecological and economic benefits and accelerate sustainable development in this region, vegetation construction is implemented by planting shrubs and grasses to reduce soil erosion and water and soil loss (Tang, 2000). *Caragana korshinskii* Kom and *Salix psammophila* are the two dominantly planted shrubs in the vegetation construction program. They are strongly drought tolerant with deep roots. The objectives of this study are to investigate the temporal responses of soil CO₂ efflux to plant density for two shrub species, and address the relative influence of abiotic and biotic factors involved with plant density effects on soil CO₂ efflux.

MATERIALS AND METHODS

Experimental site and design

The study was conducted at the Shenmu erosion and environmental experimental station, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, in Shaanxi Province, China (Figure 1). The study site is located in the wind-water erosion transitional belt of northern Loess Plateau (110° 21' E, 38° 47' N). Soil erosion and land desertification are very serious in this region. The climate is temperate zone semi-arid with

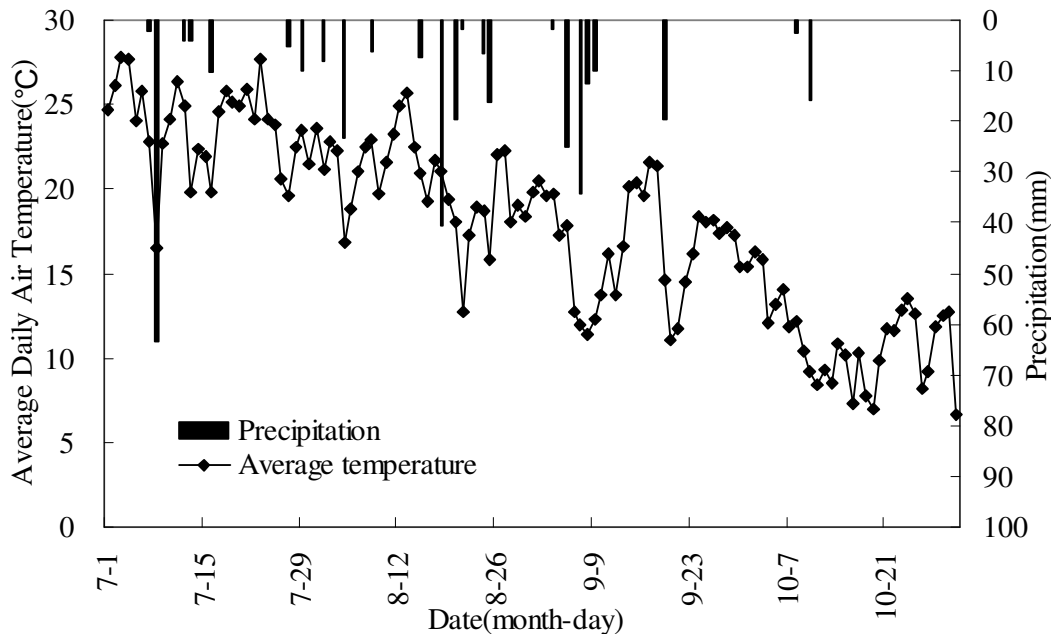


Figure 2. Average daily air temperature and precipitation at the study site from July to October in 2009.

mean annual temperature of about 8.4°C and an annual precipitation of about 437 mm, of which 77% falls from June to September (Figure 2). The soil texture of the site is silt loam with sand, 44.7%; silt, 53.2%; clay, 2.1% (according to the international system). The average bulk density and soil saturated hydraulic conductivity are 1.39 g/cm³ and 0.64 mm/min, respectively.

Two shrub species, *C. korshinkii* and *S. psammophila*, were used in this study. *C. korshinkii* is fabaceous and can fix nitrogen. Four 2 × 6 m plots (2 treatments × 2 replicates) were established for each shrub species on sloping land (12°) in 2006. Each shrub species was planted at two plant densities. The *C. korshinkii* plots included a low density treatment with average 20,000 plants ha⁻¹ and a high density treatment with average 66,667 plants ha⁻¹. The *S. psammophila* plots included a low density treatment with average 9,583 plants ha⁻¹ and a high density treatment with average 31,250 plants ha⁻¹.

Soil CO₂ efflux measurements

Soil CO₂ efflux was measured every other day with an ultra-light portable photosynthesis system (CI-340, CID Inc., USA) fitted with a soil respiration chamber (CI-301SR). All measurements were made between 9:00 and 11:00 am as suggested by Xu and Qi (2001). Measurements were made from July to October 2009, because vegetation growth and rainfall are highly coupled over this period. 5 days before initiating measurements, two polyvinyl chloride (PVC) collars (11 cm inside diameter, 9 cm in height) were pressed part way into the soil to a depth of about 5 cm at two randomly selected positions in each plot. Measurements were performed by placing the soil respiration chamber on the PVC collars in each plot. Soil temperature at a depth of 5 cm depth was measured using Digital Thermometer (Omega HH509R, Stamford, CT) adjacent to each PVC collar. Soil moisture in the 0 - 6 cm soil layer was measured using a frequency domain reflectometry (FDR) with a hand-held push probe (Theta probe type ML2X, Delta-T, UK). Two 2-m-long neutron probe access tubes were installed in each plot to measure soil water content profiles. Soil water content distribution were measured every 5 days to a depth of 2 m, at 0.1 m increments

between 0 and 1 m soil depth, and at 0.2 m increments between 1 and 2 m depths using a neutron probe (CNC-503B (DR), ChaoNeng, China).

Vegetation property measurements

Plant heights were measured monthly with a steel tape. Stem diameters were measured with vernier caliper every month. Vegetation cover was determined by a point-quarter method on three 100 cm² areas in each plot, photos of each designated area were analyzed with Image-J 1.36b software (National Institute of Health, USA) to determine the vegetation cover. Aboveground biomass was measured monthly by destructively sampling typical branches (n = 10) in each plot. Vegetation samples were oven-dried at 60°C for 48 h and then weighed. Total plant aboveground biomass was calculated by multiplying mean branch mass by the number of branches in a plot (Table 1).

At the end of the study, the root biomass was estimated by the sequential core method. Two soil profiles (0 - 100 cm) were sampled adjacent to each PVC collar from each plot using a soil corer (10 cm in diameter) at 10 cm depth increments. The roots in the samples were carefully separated by hand and washed with water over a 0.5 mm sieve. The washed roots were oven dried at 75°C until constant weight.

Statistical analysis

All statistical analysis was performed with the Statistical Analysis System (SAS) software (SAS Institute, Cary, NC, USA, 1999). The effects of plant density and growing period on soil CO₂ efflux were described using the general linear model procedure (GLM). If temporal effects showed significant differences (P < 0.05), the DUNCAN test (when equal variance occurred) was performed to separate the means. Likewise, the GLM procedure was used to determine the effects of plant species on soil CO₂ efflux. Paired T-Tests were used to test for differences in root biomass (at the same depth), soil water content and soil temperature of the same

Table 1. Plant growing indicators for *C. korshinkii* and *S. psammophila*.

Species	Density	Plant height (cm)	Canopy cover (%)	Above ground biomass (g/m ²)	Stem diameter (cm)
<i>C. korshinkii</i>	Low	115 ± 0.8	46	75 ± 22	0.72 ± 0.02
	High	99 ± 1.4	70	148 ± 31	0.65 ± 0.02
<i>S. psammophila</i>	Low	123 ± 3.9	25	22 ± 8	0.70 ± 0.02
	High	140 ± 0.8	50	51 ± 13	0.74 ± 0.02

Values are the means ± SE from May to September, 2009. n = 20 for aboveground biomass, 30 for plant height and stem diameter, respectively.

growing period between plant density treatments. Multiple regression analyses (REG procedure) using the stepwise method (R^2 and C_p criteria) were carried out to evaluate the possible effects of soil water content and soil temperature on soil CO₂ efflux.

RESULTS

Soil CO₂ efflux in different plant densities

Soil CO₂ efflux differed significantly between the low and high plant densities for shrub species (Figures 3 and 4). For both species, soil CO₂ efflux was always significantly greater at the high plant density than at the low plant density during the experimental period. Maximum CO₂ effluxes were 3.38 and 2.33 μmol/m²/s for *C. korshinkii* and *S. psammophila*, respectively ($P < 0.05$). There were significant differences in monthly soil CO₂ efflux ($P < 0.0001$), except between July and August in *S. psammophila* species (Table 2). Soil CO₂ efflux increased through July and peaked in August, followed by a gradual decrease during September and October (Figures 3 and 4). The efflux of soil CO₂ in the low plant density plots of *C. korshinkii* were significantly greater than those in the high plant density plots of *S. psammophila* from July to September (Table 2, Figure 5).

Abiotic factors in different plant densities

Soil water content and soil temperature are considered to be important abiotic factors regulating soil CO₂ efflux. Paired T-Tests showed that differences in soil water content for the two plant densities were generally insignificant for *C. korshinkii* with an exception of August ($P < 0.05$). Contrary to *C. korshinkii*, significant effects of plant density on soil water content were observed in the *S. psammophila* plots (Table 3). There were obvious temporal variations in the 5 cm depth soil temperatures, with temperature gradually decreasing from July to October. However, no significant differences in soil temperatures were observed between the plant densities treatments in both species (Table 3). Significant interactions of soil water content and soil temperature ($P < 0.0001$) were observed. The interaction could account for 65 - 73% of the total variation in soil CO₂ efflux for *C. korshinkii*, and for 52 - 69% of the variation in soil CO₂ efflux for *S.*

psammophila (Table 4).

Biotic factors in different plant densities

Root biomass in the high plant density was greater than in the low plant density with significant differences for the two shrubs ($P < 0.05$) (Figure 6). For *C. korshinkii*, high plant density plots had greater root biomass in the 60 - 70 cm layers, which accounted for more than 40% of the total root biomass. However, more than 50% of the root biomass in the low plant density plots of *C. korshinkii* occurred in the 20 - 40 cm soil layers. For *S. psammophila*, about 52 - 62% of the root biomass was concentrated in the 20 - 30 cm soil layers for both plant density treatments (Figure 6). In addition to belowground biomass, the effect of plant density on aboveground plant growth indicators was also observed in this study. Aboveground biomass and canopy cover of the two shrubs were larger in the high plant density plots than in the low plant density plots. Plant height and stem diameter of *S. psammophila* were larger in the high plant density plots than in the low plant density plots which was opposite to *C. korshinkii* (Table 1).

DISCUSSION

Anthropogenic activities have dramatically altered the vegetation cover of the terrestrial ecosystem. Such obvious changes have the potential to modify the global carbon cycle (Raich and Schlesinger, 2000). In this study, we observed greater soil CO₂ efflux in plots with high plant density than in plots with low plant density over the growing seasons for two shrub species. Experimental evidence indicated that plant density influenced soil CO₂ efflux indirectly by impacting abiotic and biotic factors in the semi-arid ecosystem.

The response of soil CO₂ efflux to abiotic factors in different plant densities

It is well known that soil water content and soil temperature are major abiotic factors controlling soil CO₂ efflux.

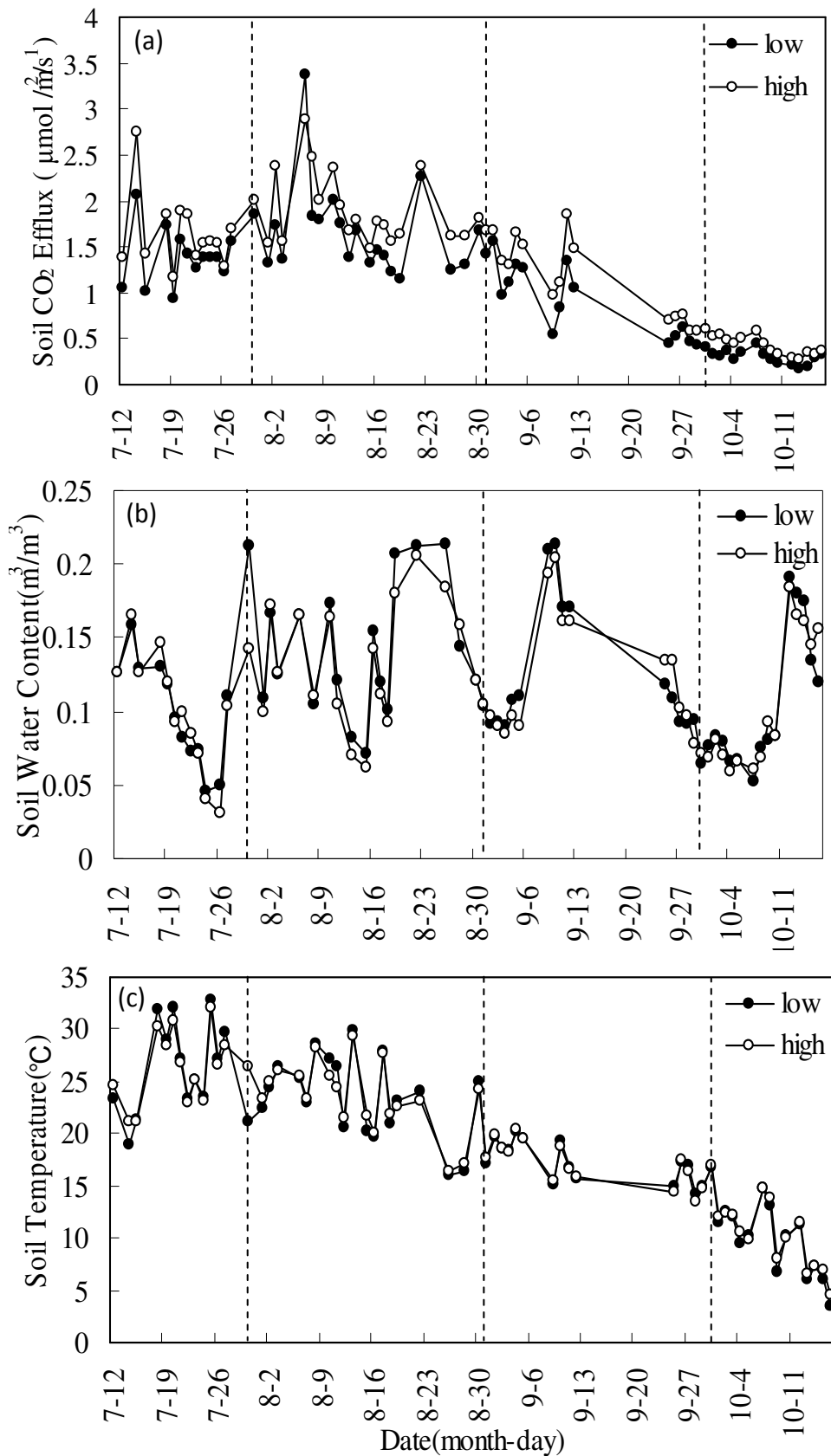


Figure 3. The variation of (a) Soil CO₂ efflux (b) soil water content (0-6 cm) (c) soil temperature (cm) for *C. korshinkii*.

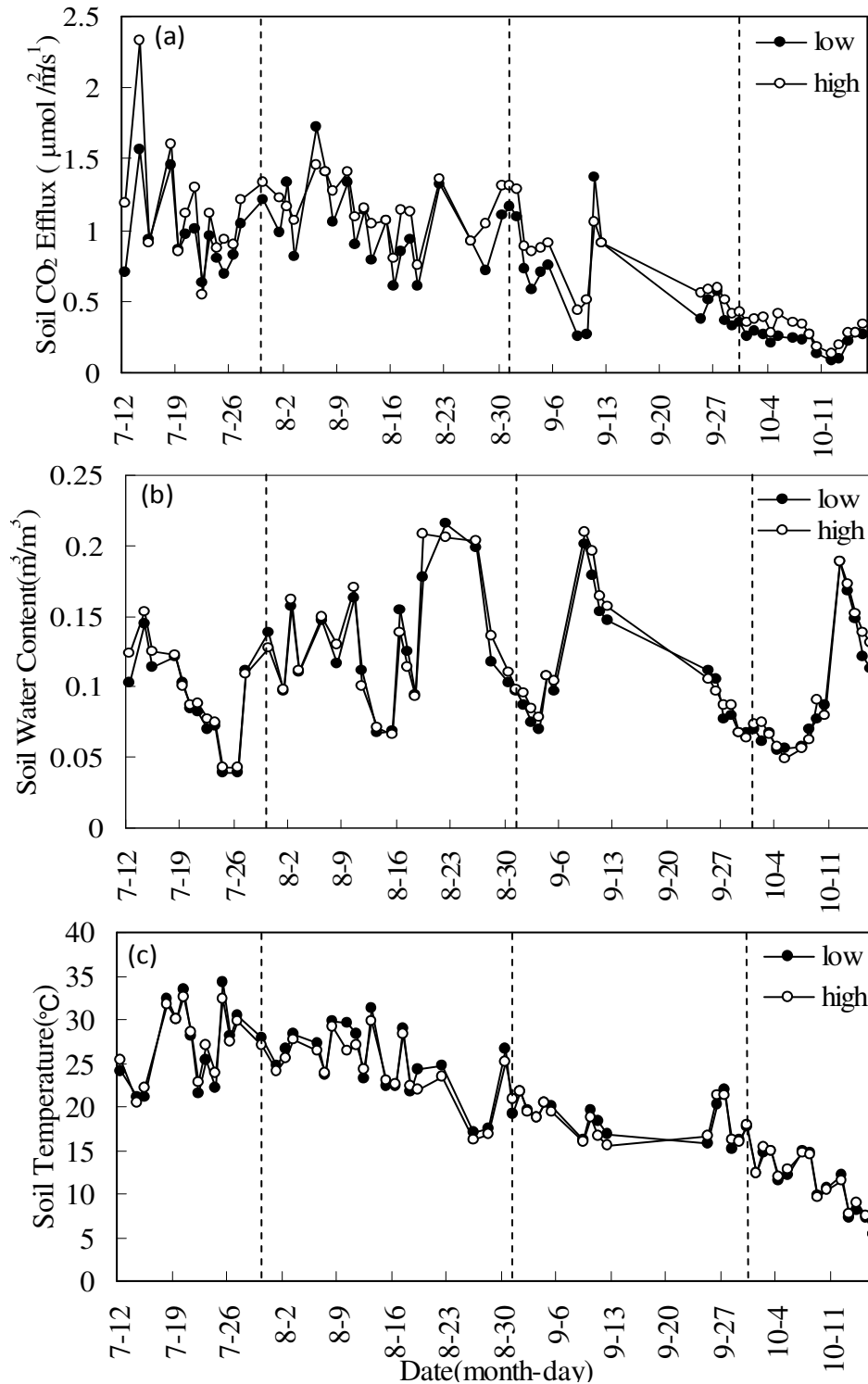


Figure 4. The variation of (a) soil CO₂ efflux (b) soil water content (0 - 6 cm) (c) soil temperature (5 cm) for *S. psammophila*.

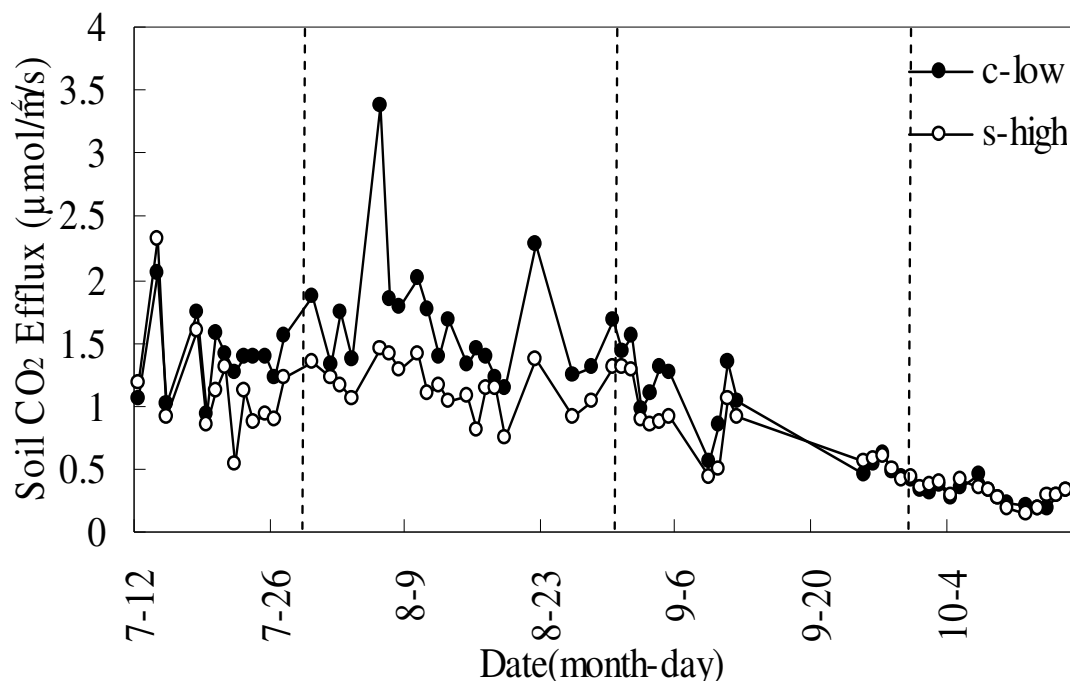
However, our results showed that there were no significant differences in soil temperature at a depth of 5 cm between low and high plant densities for the two shrubs (Table 3). These findings differ from those of

McCarthy and Brown (2006) indicating that microclimate conditions impact soil temperature. The finding shows that differences in soil water content (in the 0 - 6 cm soil layer) between low and high plant density were not

Table 2. Soil CO₂ efflux in *C. korshinkii* plots and *S. psammophila* plots.

Species	Variable	July (n=28)	August (n=40)	September (n=30)	October (n=28)
<i>C. korshinkii</i>	SCE (μmol/m ² /s)	1.54 ± 0.07b	1.77 ± 0.07 a	0.99 ± 0.08 c	0.36 ± 0.02 d
<i>S. psammophila</i>	SCE (μmol/m ² /s)	1.07 ± 0.07a	1.10 ± 0.04 a	0.67 ± 0.05 b	0.26 ± 0.02 c
F					
Species				100.73	
Month				148.25	
Species×Month				8.78	
P					
Species				< 0.0001	
Month				< 0.0001	
Species×Month				< 0.0001	

SCE, Soil CO₂ efflux (μmol/m²/s); P, probability. Values are the means ± SE. Different letters in a row denote differences at P < 0.05 as determined by the DUNCAN test.

**Figure 5.** The variation of soil CO₂ efflux for low plant density under *C. korshinkii* and high plant density under *S. psammophila*.**Table 3.** Paired T-Test (T-values) between low and high plant density among measured variables for the two shrubs.

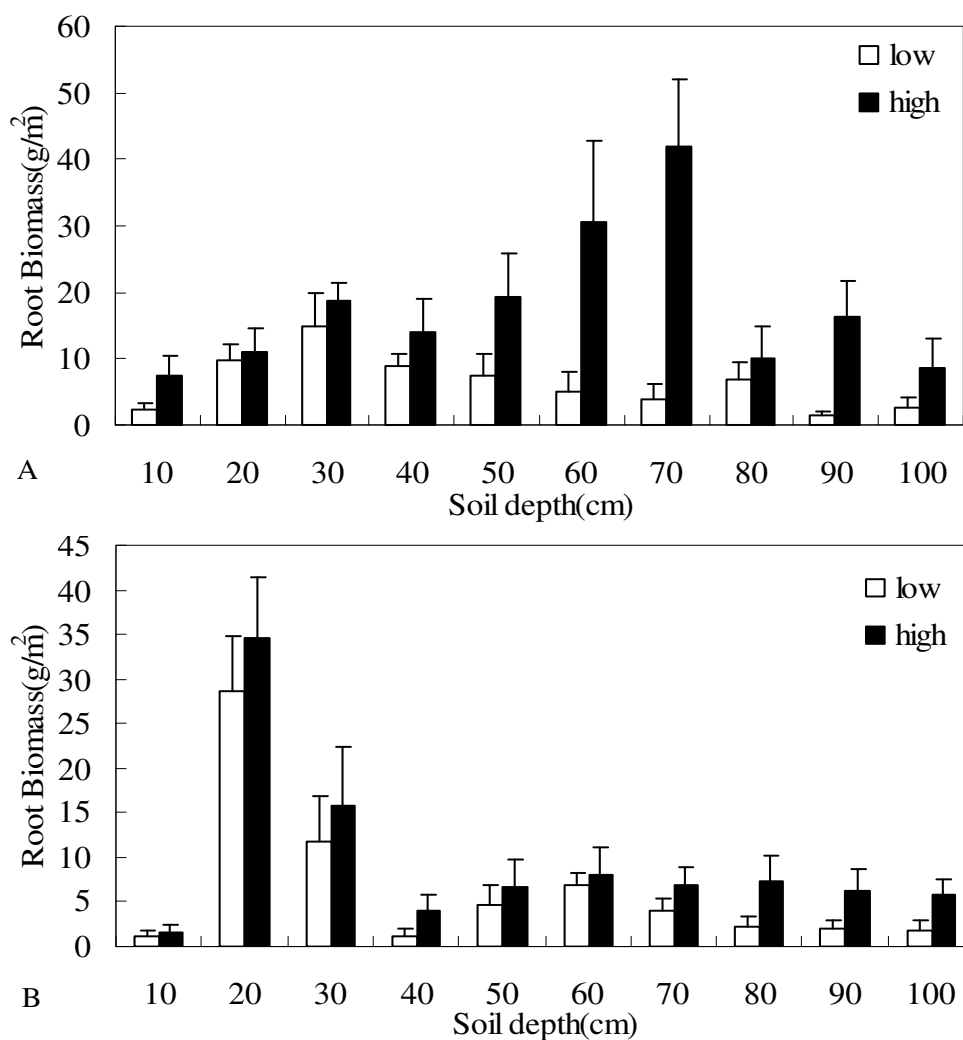
Species	Variables	July	August	September	October	Total
<i>C. korshinkii</i>	SCE	5.57(n = 14)**	5.05(n = 20)**	8.48(n = 15)**	8.56(n = 14)**	10.62(n = 63)**
	SWC	0.68 (n = 13)	2.56(n = 18)*	0.65(n = 15)	0.08(n = 14)	1.83(n = 60)
	ST	0.24(n = 14)	0.03(n = 20)	1.15(n = 15)	3.39(n = 14)*	0.78(n = 63)
<i>S. psammophila</i>	SCE	3.05(n = 14)*	3.35(n = 20)*	3.01(n = 15)*	6.33(n = 14)**	6.21(n = 63)**
	SWC	1.92(n = 13)	0.99(n = 18)	2.85(n = 15)*	1.58(n = 14)	3.38(n = 60)*
	ST	0.25(n = 14)	2.51(n = 20)*	1.03(n = 15)	1.04(n = 14)	1.67(n = 63)

SCE, Soil CO₂ efflux (μmol/m²/s); SWC= soil water content (m³/m³); ST, soil temperature (°C); * ** significant at P < 0.05 and 0.0001, respectively.

Table 4. Soil CO₂ efflux models based on selected variables: Soil water content and soil temperature using REG procedure with stepwise selection method.

Species	Density	Model	R ²	Cp	F	P
<i>C. korshinkii</i>	Low	SCE=-0.70 +0.04(SWC)+0.07(ST)	0.65	3.0	53.7	< 0.0001
	High	SCE=-0.80 + 0.05(SWC)+0.08(ST)	0.73	3.0	77.6	< 0.0001
<i>S. psammophila</i>	Low	SCE=-0.41 +0.02(SWC)+0.04(ST)	0.52	3.0	30.3	< 0.0001
	High	SCE=-0.39 + 0.02(SWC)+0.05(ST)	0.69	3.0	63.8	< 0.0001

SCE, Soil CO₂ efflux (μmol/m²/s); SWC, soil water content in 0-6 cm soil layer (m³/m³); ST = Soil temperature in 5 cm soil layer (°C); R² = coefficient of determination; Cp, Mallows' Cp; P, probability.

**Figure 6.** Root biomass in two plant densities for (A) *C. korshinkii* and (B) *S. psammophila* along the soil depth. Error bars represent SE.

observed for *C. korshinkii* but were observed for *S. psammophila* (Table 3). This can be explained by the root distributions observed in this study. In *S. psammophila* plots, the majority of the root biomass was in relatively shallow soil. Small differences in root biomass may result in large differences in soil water content (Figure 6). As for

C. korshinkii, while root biomass did not significantly affect soil water content in the 0 - 6 cm soil layer, there were significant differences in average soil water content in the soil profile between the plant density treatments (Figures 6 and 7). This showed that the deeper root distributions may exert notable effects on soil water

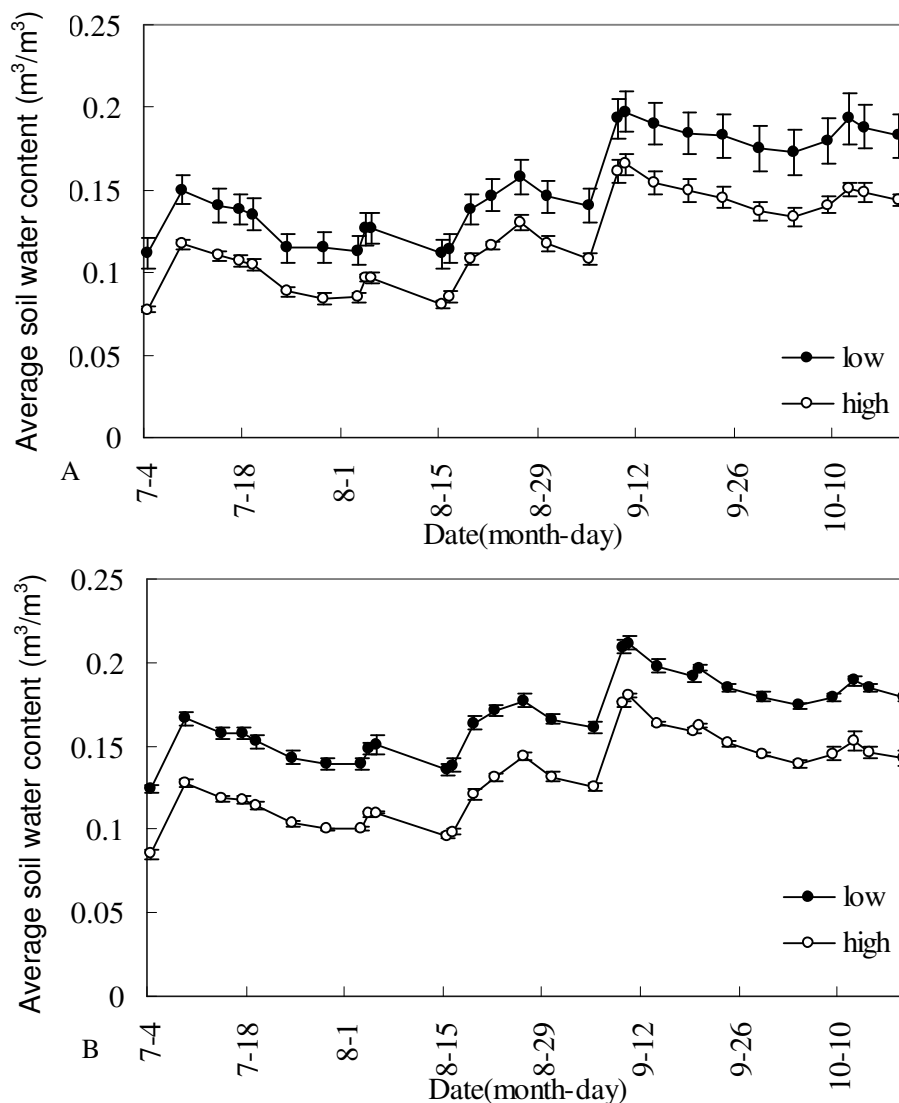


Figure 7. Average soil water content in the soil profile (0-2 m depth) during experiment for the two shrubs at two plant densities. (A) *C. korshinkii* and (B) *S. psammophila*. Error bars represent SE.

content in deeper soil layers. Consequently, the deeper soil water content affects soil CO₂ efflux in this region. This phenomenon is distinguished from humid and semi-humid regions (Davidson et al., 2000; Yuste et al., 2003; McCarthy and Brown, 2006). In this study soil temperature (5 cm depth) was not an overriding abiotic factor mediating the response of soil CO₂ efflux to plant density, but soil water content in the 0 - 6 cm layer in *S. psammophila* plots was responsible in part for mediating responses of soil CO₂ efflux to the plant densities. Additionally, soil water content in deeper soil may be an important abiotic factor regulating the effects of plant density on soil CO₂ efflux in this semi-arid region.

In agreement with the findings of Buchmann (2000), a trend of soil CO₂ efflux increasing from July to August, then decreasing in September and October, generally

coincided with temporal variations in soil temperature (Table 2, Figures 3 and 4). However, because soil water content and soil temperature were confounded statistically (Davidson et al., 2000), the temporal variation of soil CO₂ efflux was largely dependent upon a temperature-water interaction (Wildung et al., 1975; Singh and Gupta, 1977; Raich and Tufekciogul, 2000; Joffre et al., 2003). The mutual regulation of soil CO₂ efflux by soil water content and soil temperature was described by multiple regression models in this study (Table 4). It can be seen from the regression equations that soil temperatures were more closely correlated with soil CO₂ efflux than soil water content and the fraction accounting for the variability of soil CO₂ efflux were less than that reported by Wildung et al. (1975). In addition to soil water content and soil temperature, substrate supply, photosynthate

production and ecosystem productivity can also affect soil CO₂ efflux (Gaumont-Guay et al., 2006; Luo and Zhou, 2006).

The response of soil CO₂ efflux to biotic factors in different plant densities

In this study, root biomass was significantly larger in the high plant density plots than in the low plant density plots (Figure 6). This is probably due to high drought-tolerance of these two shrubs. When available water is limiting, water-competition can induce the shrubs at high plant density to develop more root biomass to enhance plant survival (Cheng et al., 2009). Furthermore, root distributions of *C. korshinkii* were deeper in the high plant density plots than in the low plant density plots. The different patterns of root distributions between plant densities could be explained by plant available water. In the high plant density plots, the available water in the upper soil layers was not enough to support water consumption of *C. korshinkii*, so it developed a deeper root system to extract soil water accordingly (Cheng et al., 2009). Evidence showed that root biomass could be primarily responsible for root respiration, and the effects of vegetation on soil CO₂ efflux may embody overall rate of root respiration (Raich and Tufekciogul, 2000). Therefore, these observations indicated that root biomass was an important biotic factor mediating the response of soil CO₂ efflux to plant density.

Plant aboveground biomass is a good proxy for estimating autotrophic and heterotrophic activity (Flanagan and Johnson, 2005). In our study, the aboveground biomass was larger in the high plant density plots than in the low plant density plots for both shrubs (Table 1). This provided good correspondence to the relationship between soil CO₂ efflux and plant densities. Consequently, our findings support the Raich (1998) conclusion that soil CO₂ efflux increased with increasing aboveground biomass. Given the well-documented inverse relationship of individual plant weight and plant density (Bullard et al., 2002), the low plant density *S. psammophila* plots were expected to have greater plant height and stem diameter than the high plant density plots. However, we found smaller plant height and stem diameter in the low plant density plots than in the high plant density plots (Table 1). This was probably connected to differences in morphology. There was less severe space competition for resources in the low plant density plots, leading to larger crown width and more branches, corresponding to lower plant heights and stem diameters. The observations indicated that the plant growth indicators may be another overriding biotic factor mediating the response of soil CO₂ efflux to plant density. Although the plant density in the high plant density plots of *S. psammophila* plots was more than 1.5 times that in the low plant density plots of *C. korshinkii*, soil CO₂ efflux of *S. psammophila* was significantly lower than *C.*

korshinkii. This is primarily because *C. korshinkii* fixes nitrogen, and root nitrogen uptake and assimilation is supported by energy derived from respiration (Luo and Zhou, 2006).

Conclusions

This study was conducted in the wind and water erosion transitional belt of the northern Loess Plateau to investigate the responses of soil CO₂ efflux of two dominant shrubs (*C. korshinkii* and *S. psammophila*) to planting density. Soil CO₂ efflux in high plant density plots was significantly larger than in low plant density for both shrub species. This was primarily attributed to the direct regulation of plant density on biotic factors and abiotic factors. Biotic factors (root biomass and aboveground biomass) were important factors mediating the response of soil CO₂ efflux to plant density, whereas abiotic factors (soil water content in the 0 - 6 cm) could partly regulate the response of soil CO₂ efflux to plant density in *S. psammophila* plots. Moreover, soil water content in deeper soil layer from both shrub plots may also be an important abiotic factor regulating the effects of plant density on soil CO₂ efflux in this semi-arid region.

Afforestation and reafforestation have been widely practiced in the Loess Plateau to restore vegetation cover and consequently, improve the environmental quality in this semi-arid region. However, optimal plant density is essential to maintain sustainable development in this region. The results from this study provide evidence for an indirect linkage between soil CO₂ efflux and plant density to understand mechanisms that soil CO₂ efflux responds to plant density in these widely distributed ecosystems. Therefore, further comparative studies need to address other vegetation types, such as grassland, grown on a range of soil types to enhance our understanding of the carbon cycling of these semi-arid ecosystems and their sensitivity to climate change.

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