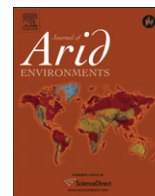




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## Significance of temperature and soil water content on soil respiration in three desert ecosystems in Northwest China

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## ABSTRACT

It is crucial to understand how abiotic factors influence soil respiration and to determine, in a quantitative manner, the site variation of abiotic regulators in desert ecosystems. In this study, soil respiration was measured using an automated CO<sub>2</sub> efflux system (LI-COR 8100) in 2005 and 2006. Additionally, the effects of soil temperature, moisture and a short-term precipitation manipulation on the rate of soil respiration were examined in *Haloxylon ammodendron*, *Anabasis aphylla* and *Halostachys caspica* in three distinct desert ecosystems. The difference in soil respiration among sites was significant. Air temperature explained 35–65% of the seasonal changes in soil respiration when an exponential equation was used. The effect of temperature on soil respiration and temperature sensitivity was stronger at sites with higher soil moisture. Soil respiration was significantly positively correlated with soil moisture. Amounts of variation in soil respiration explained by temperature and gravimetric water content were 41–44% in *H. ammodendron*, 62–65% in *A. aphylla* and 67–84% in *H. caspica* sites. Artificial rainfall treatments of 5 mm, 2.5 mm and 0 mm (control) were conducted. Soil respiration increased in a small pulse following rainfall. Temperature dominantly influenced soil respiration and soil water content enhanced the response of respiration to temperature.

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### 1. Introduction

Soil provides the second largest carbon (C) efflux to the atmosphere (Schlesinger and Andrews, 2000) and buffers atmospheric carbon dioxide (CO<sub>2</sub>) concentration against seasonal and inter-annual variations in plant growth (Raich et al., 2002). Slight modifications in the rate of soil respiration can result in significant changes to the global C cycle (Giardina and Ryan, 2000; Kirschbaum, 1995). Arid and semiarid areas occupy over 40% of the Earth's total surface (Reynolds, 2001) and soil respiration is one of the main methods of C loss from arid and semiarid soils (Conant et al., 2000). Soil temperature and water content are the key environmental factors responsible for variation in soil respiration (Davidson et al., 2000; Fang and Moncrieff, 2001; Joffre et al., 2003). Assessing the impacts of the changing climate on ecosystem C fluxes requires a quantification of the effects of temperature and moisture on soil respiration (Betts, 2000; Cox et al., 2000) and an understanding of the roles of substrate supply and plant

productivity in controlling respiration rates (Davidson and Janssens, 2006).

Temperature is the dominant factor in determining soil respiration rates at a forest stand scale or at smaller scales (Hanson et al., 2000; Jenkinson et al., 1991). However, respiratory processes in soil are also strongly influenced by soil moisture, with drier soils tending to yield lower effluxes of CO<sub>2</sub> (Davidson et al., 2000; Parker et al., 1984). Diurnal soil respiration variations are usually highly correlated with the temperature of surface soil layers (Drewitt et al., 2002; Jassal et al., 2005; Jia et al., 2006). A few studies, however, have found hysteresis-type behaviors and a decoupling between soil respiration and soil surface temperatures during drought conditions (Parkin and Kaspar, 2003; Subke et al., 2003; Xu and Qi, 2001a). Soil respiration is also highly correlated with changes in soil temperature when water is not limited at a seasonal time scale (Curiel-Yuste et al., 2003; Jassal et al., 2008; Palmroth et al., 2005). Jassal et al. (2008) found that soil respiration was positively correlated with soil temperature at 2 cm depth for soil water content at 4 cm depth ( $\theta$ ) > 0.11 m<sup>3</sup> m<sup>-3</sup> (corresponding to a soil water matric potential of –2 MPa). Below the value of  $\theta$ , soil respiration was unaffected by soil temperature. Soil respiration has

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been extensively studied in forest and grassland ecosystems. However, there are only a few studies on the influence of soil temperature and moisture on soil respiration and the site variations of abiotic regulators and soil respiration in desert ecosystems. McLain and Martens (2006) examined the influence of moisture on CO<sub>2</sub> flux in semiarid riparian soils. Fernandez et al. (2006) reported the thresholds of soil temperature and soil moisture that affected fluxes of CO<sub>2</sub> in a cold desert in southeast Utah. Xie et al. (2008) found that soil respiration in a saline desert was related to the air temperature 10 cm above the surface of the ground.

Desert habitats are characterized by a combination of extreme abiotic conditions, low and unpredictable amounts of moisture, low and heterogeneous distribution of nutrients and organic matter (Noy-Meir, 1980). Deserts, pulse driven ecosystems, are important to understand because of their high degree of responsiveness to global change (Smith et al., 2000). Soil respiration is the ecosystem property that is most sensitive to climatic change (West et al., 1994). Biological activity in deserts is driven primarily by discontinuous and discrete pulses of precipitation large enough to activate biota (Huxman et al., 2004; Noy-Meir, 1973; Sponseller, 2007). The timing of precipitation pulses is also important because biological activities, such as soil respiration, are temperature dependent (Fernandez et al., 2006).

To provide a more complete and quantitative understanding of how abiotic factors influence soil respiration in desert ecosystems, we conducted soil respiration measurements in three desert shrub communities of *Haloxylon ammodendron*, *Halostachys caspica* and *Anabasis aphylla* in the Junngar Basin, Northwestern China. The Junngar Basin is a temperate desert environment with little annual precipitation and strong temperature gradients. One of the main constructive species of central Asian desert vegetation is *H. ammodendron*, while *H. caspica* and *A. aphylla* are the major species in salinized deserts (Huang, 2002). The canopy cover and soil salinity differed among the study sites. The specific objectives of this research were: (1) to examine the temporal variability of soil respiration at three sites and to determine if there are any differences in soil respiration among the sites; (2) to analyze the influences of soil temperature and moisture on soil respiration, as well as its temperature sensitivity and the site variation of abiotic regulators; and (3) to characterize the effects of an artificial precipitation pulse on soil respiration.

## 2. Materials and methods

### 2.1. Site description

The study area is located at the periphery of a newly cultivated oasis in Kelamayi, in the western Junngar Basin. This area is adjacent to Zhayier Mountain in the north and the alluvion plain in the south. The altitude is 273–280 m in the southwest and 258–260 m in the northeast. The main soil types are relic bog soils, relic solonchaks and desert aeolian soils and the main texture is loamy soil (Qian et al., 2003, 2004). The area is characterized by a continental arid-desert climate and is hot in the summer, cold and without stable snow cover in the winter and windy in the spring. The mean annual temperature is 8 °C, the mean annual precipitation is 105.3 mm and the mean annual potential evaporation is 3545 mm (Wang et al., 2005).

Three desert shrub sites were each selected in a plant community. The three communities were representative communities of the local desert flora. The site in the *H. ammodendron* community was dominated by *H. ammodendron* but also had *A. aphylla*, *Nitraria sibirica* and *Lycium ruthenicum* shrubs, as well as *Peganum harmala*, *Halogeton glomeratus* and *Salsola spp.* grasses. *H. ammodendron* coverage was over 50%. The height of *H.*

*ammodendron* was between 100 and 250 cm. The site was located at 45°24'40"N, 84°50'29"E.

The site in the *A. aphylla* community was dominated by *A. aphylla*, with *Reaumuria soongorica* and *N. sibirica* shrubs, as well as *Aeluropus pungens* and *Limonium suffruticosum* grasses also present. *A. aphylla* coverage was 20%. The height of *A. aphylla* plants reached 50–70 cm. The site was located at 45°23'51"N, 84°51'26"E.

The site in the *H. caspica* community was dominated by *H. caspica*, with *R. soongorica*, *N. sibirica*, *Halocnemum strobilaceum*, *Kalidium foliatum* and *A. aphylla* shrubs, as well as *L. suffruticosum* and *Salsola foliosa* grasses. The site was located at 45°23'4"N, 84°51'25"E. The average plant height of *H. caspica* was 80 cm. *H. caspica* coverage was 25%. The distance between *H. ammodendron* and *A. aphylla* sites was 2 km, the distance between *A. aphylla* and *H. caspica* sites was 1.3 km and the straight-line distance between *H. ammodendron* and *H. caspica* sites was 3.2 km.

### 2.2. Field measurement

Each site was 30 m × 30 m. Five sampling points at each site were selected for soil respiration measurements. Soil collars with a height of 10 cm and diameter of 10 cm were inserted 7 cm into the soil at each sampling point three days prior to the first series of measurements. The soil collars were placed close to plants and the distances from plants were 10–110 cm. All soil collars were left on the sites during the entire study period. Soil respiration was measured by an automated soil CO<sub>2</sub> efflux measurement system (LI-8100, LI-COR, Lincoln, NE, USA).

The soil CO<sub>2</sub> efflux rate was computed using the following equation:

$$F_c = \frac{10VP_0(1 - \frac{W}{1000})}{RS(T_0 + 273.15)} \frac{\partial C}{\partial t} \quad (1)$$

where  $F_c$  is the soil CO<sub>2</sub> efflux rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $V$  is the volume ( $\text{cm}^3$ ),  $P_0$  is the initial pressure (kPa),  $W_0$  is the initial water vapor mole fraction ( $\text{mmol mol}^{-1}$ ),  $S$  is soil surface area ( $\text{cm}^2$ ),  $T_0$  is initial air temperature ( $^{\circ}\text{C}$ ) and  $\partial C/\partial t$  is the initial rate of change in water-corrected CO<sub>2</sub> mole fraction ( $\mu\text{mol}^{-1} \text{s}^{-1}$ ).

Soil respiration ( $R_s$ ) measurements were conducted once every month from May to October 2005–2006 around the 20th day of each month. Data was collected on one day at each site. The measurements were conducted every 2 h from 8:00 to 20:00. Each observation length was 120 s and the observation count was set to 2. It took 2 min for the chamber air to return to ambient conditions between the two observations. For each site, six to seven measurements were performed each day.

Air temperature ( $T_a$ ) (at 50 cm aboveground) and soil temperature ( $T_s$ ) (every 5 cm from 0 to 50 cm depth) were monitored at three points adjacent to the chamber using a digital thermometer (WMY-01C, Huachen Medical Instrument, Inc., Shanghai, China) at each site. Gravimetric soil water content ( $W_s$ ) was measured three times at 0–5 cm, 5–15 cm, 15–30 cm and 30–50 cm depths with the oven-drying method at 105 °C for 48 h. Soil samples from the three points at each depth were mixed as a single composite sample and were placed in Ziploc bags for soil properties measurement in June 2005. Soil nutrients (including soil organic matter, organic carbon, total and available N, P and K) and soil salts (including total salt, pH, electrical conductivity,  $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ,  $\text{CO}_3^{2-}$ ,  $\text{HCO}_3^-$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$  and  $\text{K}^+$ ) were measured using routine methods (Nanjing Institute of Petrology, 1978). The mean soil properties at 0–50 cm depth are shown in Table 1.

In 2007, artificial precipitation experiments were carried out in fixed *H. caspica* and *A. aphylla* sites on September 14 and 17, respectively. Water treatment was applied over an area of 2500  $\text{cm}^2$

**Table 1**  
Physical and chemical properties of the soil at the three study sites.

Site	Organic C	Organic matter	Total N	Total P	Total K	Available N	Available P	Available K	pH	EC
	g/kg					mg/kg			1:5	ms/cm
<i>H. ammodendron</i>	3.153	5.436	0.278	0.687	19.166	11.385	3.670	241.000	9.090	0.616
<i>A. aphylla</i>	3.037	5.236	0.290	0.663	19.218	11.183	2.039	132.900	8.341	0.784
<i>H. caspica</i>	3.361	5.795	0.326	0.758	20.692	9.869	5.901	129.100	8.125	1.923
	General salt	Total salinity	CO <sub>3</sub> <sup>2-</sup>	HCO <sub>3</sub> <sup>-</sup>	Cl <sup>-</sup>	SO <sub>4</sub> <sup>2-</sup>	Ca <sup>2+</sup>	Mg <sup>2+</sup>	Na <sup>+</sup>	K <sup>+</sup>
	g/kg									
<i>H. ammodendron</i>	2.247	2.157	0.070	0.530	0.536	0.287	0.026	0.010	0.679	0.018
<i>A. aphylla</i>	3.450	3.295	0.002	0.245	0.209	1.838	0.398	0.064	0.521	0.018
<i>H. caspica</i>	6.880	6.788	0.000	0.173	2.526	1.728	0.376	0.135	1.831	0.018

in two pulse sizes (2.5 and 5 mm) and a control (0 mm). Each treatment was conducted with three replicates at each location. Water was added using a plastic watering can to achieve a sprinkling effect. The rate of application was adjusted to prevent overland runoff. A soil collar, placed a distance of 50 cm from the plant stem, was installed in the center of the area receiving additional water.  $R_s$  was measured before wetting and then at 10, 60, 180, 300, 420 and 540 min after additional rainfall.  $W_s$  at depths of 0–10, 10–20 and 20–30 cm was determined gravimetrically by using a soil auger with a diameter of 4.2 cm at one point during each treatment at 60, 180, 300 and 540 min following additional rainfall.  $T_s$  was recorded every 5 cm from 0 to 25 cm depth and was measured at one point for each treatment using geothermometers. The same measuring frequency was used for soil respiration.  $T_a$  was measured with a psychrometer at a height of 150 cm.

### 2.3. Data analysis

Analysis of variance (ANOVA) and post-hoc test were used to test the differences in mean  $R_s$  and  $W_s$  among three sites.

A two-step analysis was used to quantify the influence of  $T$  (°C) and  $W_s$  (%) on  $R_s$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). We performed an exponential regression (Equation (2)) and nonlinear regression analysis of  $R_s$  against  $T$  (Equation (3)) (the Arrhenius function, Borken et al., 2002) and also performed linear, power and quadratic regression analyses of  $R_s$  against  $W_s$  using Equation (4) as follows:

$$R_s = ae^{bT} \text{ and } Q_{10} = e^{10b} \quad (2)$$

$$R_s = ae^{[-E/R(T+273.2)]} \quad (3)$$

$$R_s = a + bW_s, R_s = aW_s^b, \text{ or } R_s = a + bW_s + cW_s^2 \quad (4)$$

where  $a$  and  $b$  are fitted parameters,  $Q_{10}$  is the temperature sensitivity of  $R_s$ ,  $i$  is the fitted apparent activation energy ( $\text{kJ mol}^{-1}$ ) and  $R$  is the universal gas constant ( $\text{kJ mol}^{-1} \text{K}^{-1}$ ). Next, the following linear and nonlinear models (Equations (5)–(9)) were used to express the relationships among  $R_s$ ,  $T$  and  $W_s$ :

$$R_s = a + b(TW_s) \quad (5)$$

$$R_s = a + bT + cW_s \quad (6)$$

$$R_s = aT^bW_s^c \quad (7)$$

$$R_s = ae^{bT}W_s^c \quad (8)$$

$$R_s = a + bT + cW_s + dTW_s \quad (9)$$

where  $a$ ,  $b$  and  $c$  are fitted parameters. In Equation (5), a new variable of the product,  $T \times W_s$ , was introduced.

Statistical nonlinear regression analyses were performed using SPSS 11.5 (SPSS for Windows, Version 11.5, Chicago, IL). The Levenberg–Marquardt algorithm was used to determine the parameters that minimized the differences in the sum of squares of residuals between dependent variable values in the models and the observed values.

## 3. Results

### 3.1. Temporal variations of soil respiration, soil temperature and soil water content

#### 3.1.1. The daytime variation of soil respiration

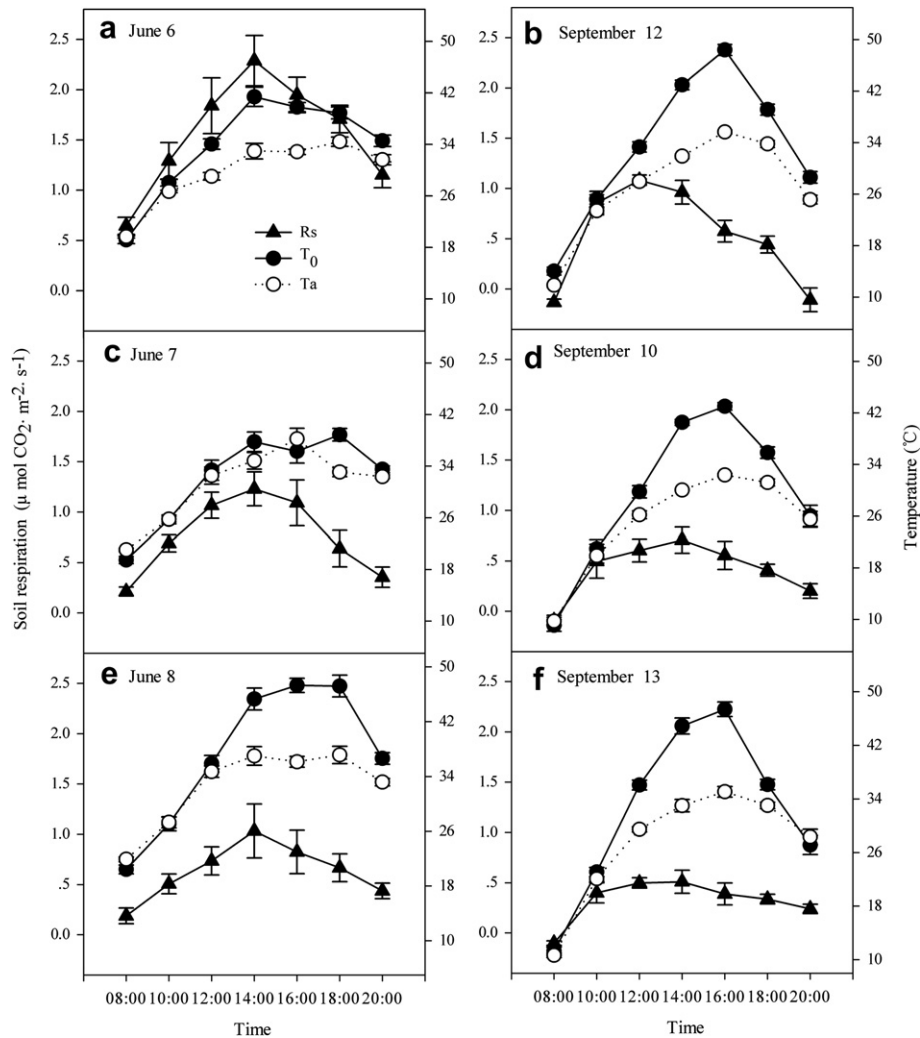
$R_s$  showed an asymmetric daytime pattern, with minimum respiration occurring at 8:00 h (Beijing time) and the maximum occurring around the middle of the day (12:00–14:00 h; Fig. 1). The daytime range was normally less than  $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , but was approximately 0.5–2 times more than the mean value.  $R_s$  followed the increasing trend of air temperature and soil temperature at 0 cm depth in the morning and decreased more quickly than the temperature in the afternoon. The maximum rate of  $R_s$  occurred earlier than the maximum rate of the  $T_a$  and soil temperature at 0 cm depth. Additionally,  $R_s$  at 8:00 h and 20:00 h in September and October was negative (approximately  $-0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and air and soil temperature at 0 cm depth were 5–14 °C.

#### 3.1.2. The seasonal variations of soil respiration

The temporal variation of  $R_s$  was characterized by having the lowest point in October (late growing season) and the highest point in June or July, which followed the temporal variation of  $T_a$  (Fig. 2c). However, there was a pulse of  $R_s$  during June in 2006 at the *H. ammodendron* site and  $R_s$  decreased, but  $T_a$  increased during June–July. The correlation of  $R_s$  among the three sites was significant (the minimum  $r$  was 0.60, between the *H. ammodendron* and *A. aphylla* sites,  $n = 12$ ; the maximum  $r$  was 0.86, between the *A. aphylla* and *H. caspica* sites,  $n = 12$ ).

Temporal variations of  $T_a$  among the three sites were similar and showed an asymmetrical “bell-shape” trend in one year (Fig. 2a). The low values were observed in autumn (October) and the maximum values occurred in the summer (July). The  $W_s$  at 0–50 cm depth had a dry–wet cycle over the season in 2005 but decreased from May to October in 2006 (Fig. 2b).  $W_s$  values at the *H. ammodendron* site were the lowest among the three sites, ranging from 5.23 to 10.34% with a mean value of 7.50%.  $W_s$  values at the *A. aphylla* site were the second lowest, ranging 10.38–23.13% with a mean value of 17.04%; while the largest ranged from 14.06 to 27.59% with a mean value of 19.60% at the *H. caspica* site.

The mean  $R_s$  of all recorded data (May to October) was  $0.76 \pm 0.33$  (mean  $\pm$  S.D.,  $n = 12$ ) in *H. ammodendron*,  $0.52 \pm 0.16$  in



**Fig. 1.** Daytime variation in soil respiration ( $R_s$ ) and temperature ( $T_0$ : soil temperature at 0 cm depth,  $T_a$ : air temperature) on June 6, June 7, June 8, September 10, September 12 and September 13 in 2006 at *H. ammodendron* (a, b), *A. aphylla* (c, d) and *H. caspica* (e, f) sites. Data are mean values and standard error on each sampling day ( $n = 5$  for soil respiration rate,  $n = 3$  for temperature).

*A. aphylla* and  $0.46 \pm 0.15$  in *H. caspica*, with an average of  $0.58 \pm 0.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  across the three sites. ANOVA showed that the differences in the  $R_s$  and  $W_s$  across sites were significant overall ( $F = 5.62$ ,  $df = 35$ ,  $p < 0.01$ ;  $F = 29.73$ ,  $df = 35$ ,  $p = 0.000$ ). Post-hoc tests indicated that the difference in  $R_s$  and  $W_s$  between the *H. ammodendron* and *A. aphylla* sites and between the *H. ammodendron* and *H. caspica* sites were significant, while the differences between the *A. aphylla* and *H. caspica* sites were not significant.

### 3.2. Relationships among soil respiration, temperature and soil water content

#### 3.2.1. Relationship between soil respiration and temperature

Among the temperature values measured at different soil depths, the fit between  $T_a$  and  $R_s$  was the best. Using an exponential equation,  $T_a$  explained 35–65% of the seasonal changes of  $R_s$  and it explained 24–60% of the seasonal change when an Arrhenius function was used (Table 2).  $R_s$  was more sensitive to  $T_a$  at the *A. aphylla* and *H. caspica* sites than at the *H. ammodendron* site (Fig. 3).

The temperature dependence of soil respiration is often described by the  $Q_{10}$  value, which is considered the temperature

sensitivity of  $R_s$ . The  $R_{10}$  is the respiration rate at a soil temperature of 10 °C, which is often used to compare the  $R_s$  characteristics of ecosystems. The  $Q_{10}$  values ranged from 1.35 to 1.52 with a value of 1.41 across the three sites with the exponential regression and ranged from 1.31 to 1.48 with a value of 1.36 across the sites with the Arrhenius function.  $Q_{10}$  was the mean value calculated for the temperature range of 20–30 °C using the Arrhenius function. Among the three sites, the  $R_{10}$  ranged from 0.22 to 0.45  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  with the exponential regression and 0.22–0.47  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  with the Arrhenius function (Table 2). The lowest  $Q_{10}$ , highest  $R_{10}$  and greatest  $R_s$  were found at the *H. ammodendron* site where the soil was the driest.

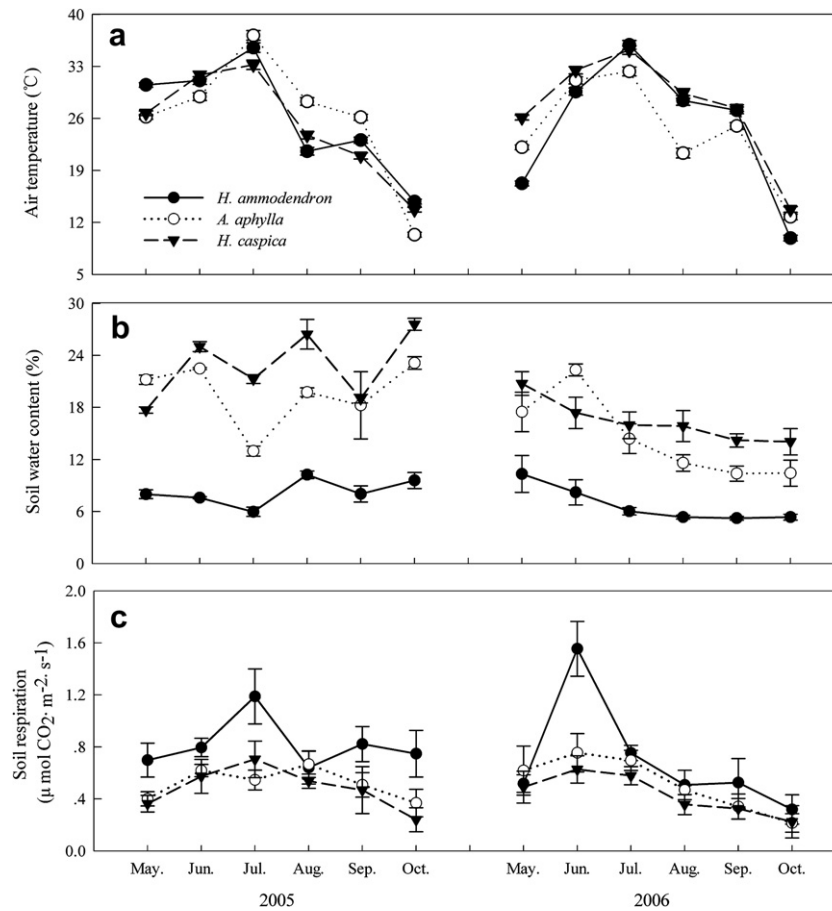
#### 3.2.2. Relationships between soil respiration and soil water content

In order to quantify the relationship between  $R_s$  and  $W_s$ , regression analyses were conducted using linear, power and quadratic models (Table 3). The correlation of  $R_s$  to  $W_s$  was significant at the 0.05 level only at the *H. caspica* site (quadratic model,  $R^2 = 0.51$ ).

In order to minimize the effect of high  $T_a$  values on  $R_s$ , we calculated the soil  $\text{CO}_2$  efflux at 10 °C ( $R_{S10}$ ) using the following equation:

$$R_S = R_{ST} e^{b(10-T)} \quad (10)$$





**Fig. 2.** Temporal variation of (a) air temperature ( $T_a$ ), (b) soil water content over 0–50 cm depth ( $W_s$ ) and (c) soil respiration rate ( $R_s$ ). Symbols represent the mean and standard error of  $T_a$ ,  $W_s$  and  $R_s$  on each sampling day ( $n = 7$ ).

where  $R_{st}$  is the measured  $\text{CO}_2$  efflux corresponding to  $T_a$  and  $b$  is the coefficient derived from the regression of  $R_s$  to  $T_a$  in Table 2 for all data from each site. We then analyzed the correlation between soil  $\text{CO}_2$  efflux at 10 °C and  $W_s$ . It is interesting that most of the fitted equations became significant at the 0.05 or 0.01 levels and  $R^2$  increased (Table 3). Most of the equations with large  $R^2$  and  $P$  values were power types. The effects of  $W_s$  on  $R_{s10}$  were different at the three sites and  $R^2$  was 0.32 at the *H. ammodendron* site, 0.41 at the *A. aphylla* site and 0.52 at the *H. caspica* site. Accordingly, the  $W_s$  for 0–50 cm depth at the *H. ammodendron* site was the lowest, while  $W_s$  values at the *H. caspica* site were the highest. The relationship between  $R_{s10}$  and  $W_s$  was positive at the *H. ammodendron* and *A. aphylla* sites and was positive at the *H. caspica* site when  $W_s < 21\%$  and negative when  $W_s > 21\%$  (Fig. 4).

As mentioned above, the significance and  $R^2$  of  $W_s$  to  $R_s$  increased when the measured  $R_s$  were normalized to 10 °C, which showed that the effect of  $W_s$  on  $R_s$  was clearer when the temperature was relatively low. However, the temporal changes of  $R_s$  at the

three sites were mainly controlled by  $T_a$  (Fig. 2). Furthermore, the  $R^2$  of  $R_s$  to  $T_a$  was larger than that of  $R_{s10}$  to  $W_s$  and greater scatter was found in the relationship between  $R_{s10}$  and  $W_s$  than between  $R_s$  and  $T_a$  (Figs. 3 and 4).

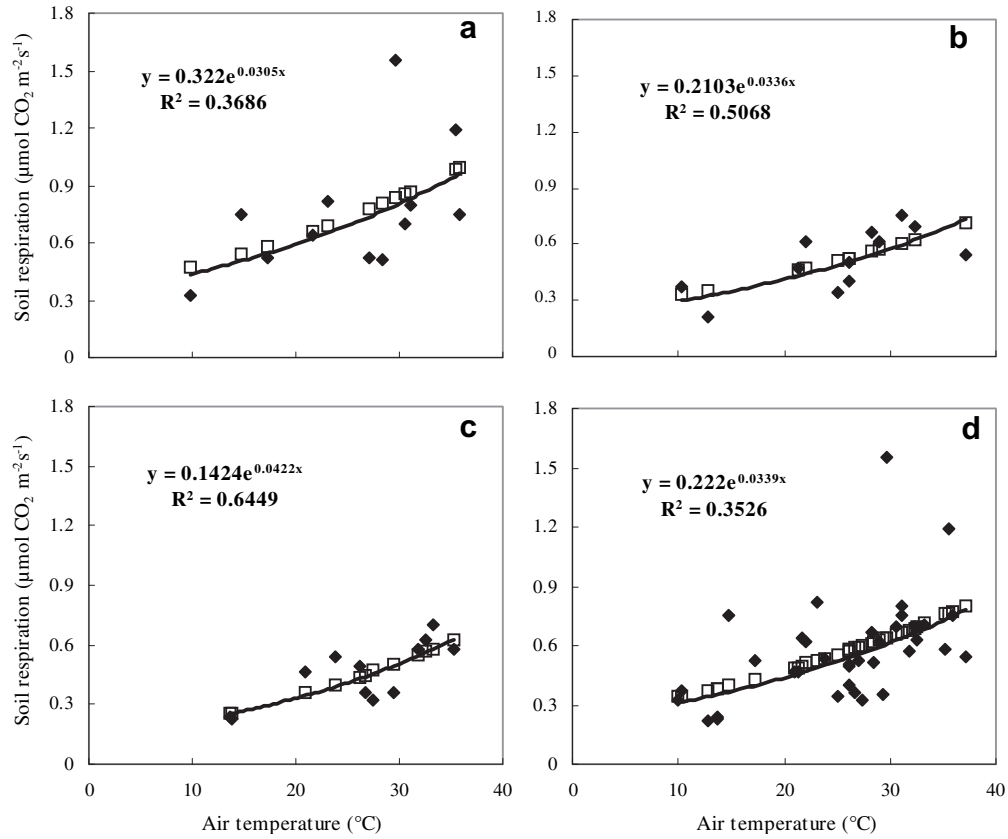
### 3.2.3. Combined relationships among soil respiration, temperature and soil water content

While the temperature-based model could be used to represent the relationship between  $R_s$  and  $T_s$ , the fitted equations did not account for  $W_s$  (Table 2). Since the  $R^2$  of the relationship between  $R_s$  and  $W_s$ , as well as the significance of the fitted equations, increased when  $R_s$  values were normalized to the  $R_s$  of 10 °C (Table 3), it was very clear that  $T_s$  and  $W_s$  played a complicated role in influencing  $R_s$  in this study.

In order to model the combined effect of  $T_s$  and  $W_s$  on  $R_s$  using all the measured data from the sites, we integrated both  $T_s$  and  $W_s$  into five equations (Eqs. 5–9). The modeling results are summarized in Table 4. Most of the equations were used to describe the

**Table 2**  
Parameters of the fitted function of  $R_s$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and  $T_a$  (°C) for all data.

Site	n	$R_s = ae^{bT_a}$					$R_s = ae^{(-E/R(T_a+273.2))}$					
		a	b	$R^2$	P	$R_{10}$	$Q_{10}$	a	E	$R^2$	$R_{10}$	$Q_{10}$
<i>H. ammodendron</i>	12	0.322	0.03	0.369	0.036	0.448	1.350	3796.515	21 200.55	0.267	0.467	1.320
<i>A. aphylla</i>	12	0.21	0.034	0.507	0.009	0.295	1.405	2248.805	20 817.8	0.463	0.325	1.313
<i>H. caspica</i>	12	0.142	0.042	0.645	0.002	0.216	1.522	74 042.548	29 932.56	0.602	0.223	1.480
All data	36	0.222	0.034	0.353	0.000	0.312	1.405	6416.267	23 193.9	0.243	0.338	1.355



**Fig. 3.** Relationships between soil respiration ( $R_s$ ) and air temperature ( $T_a$ ) when fitted with an exponential and Arrhenius model ( $a = H. ammodendron$  site,  $b = A. aphylla$  site,  $c = H. caspica$  site, and  $d =$  all data from the three sites). Each value in the plot represents the average value of each site on the sampling day. The solid symbol is the measured  $R_s$ , the open symbol is the value predicted by Arrhenius function and the solid line is the exponential regression line.

relationship of  $R_s$  to both  $T_s$  and  $W_s$  together and had  $R^2$  values ranging from 0.41 to 0.84. Most regressions were significant at the 0.05 level. In comparison with the one-dimensional equation above, the  $R^2$  of the two-dimensional equation increased at each site except when all three sites were analyzed together. The amount of variation explained by the five equations differed at each site: 41–44% at the *H. ammodendron* site, 62–65% at the *A. aphylla* site and 67–84% at the *H. caspica* site.

The  $R^2$  values were slightly different when each equation was applied to the same data set, indicating that each equation could be used to predict the  $R_s$  according to the measured  $T_s$  and  $W_s$  data. Among the five models, Eq. (5) was also the most parsimonious in explaining the  $R_s$  by  $T_s$  and  $W_s$  variations across seasons. The most

meaningful equation was Eq. (8), in which the exponential component was a  $Q_{10}$  function and the power component of the  $R_s$ - $W_s$  was in agreement with the relationship between the normalized  $R_s$  and  $W_s$  in Section 3.2.2.

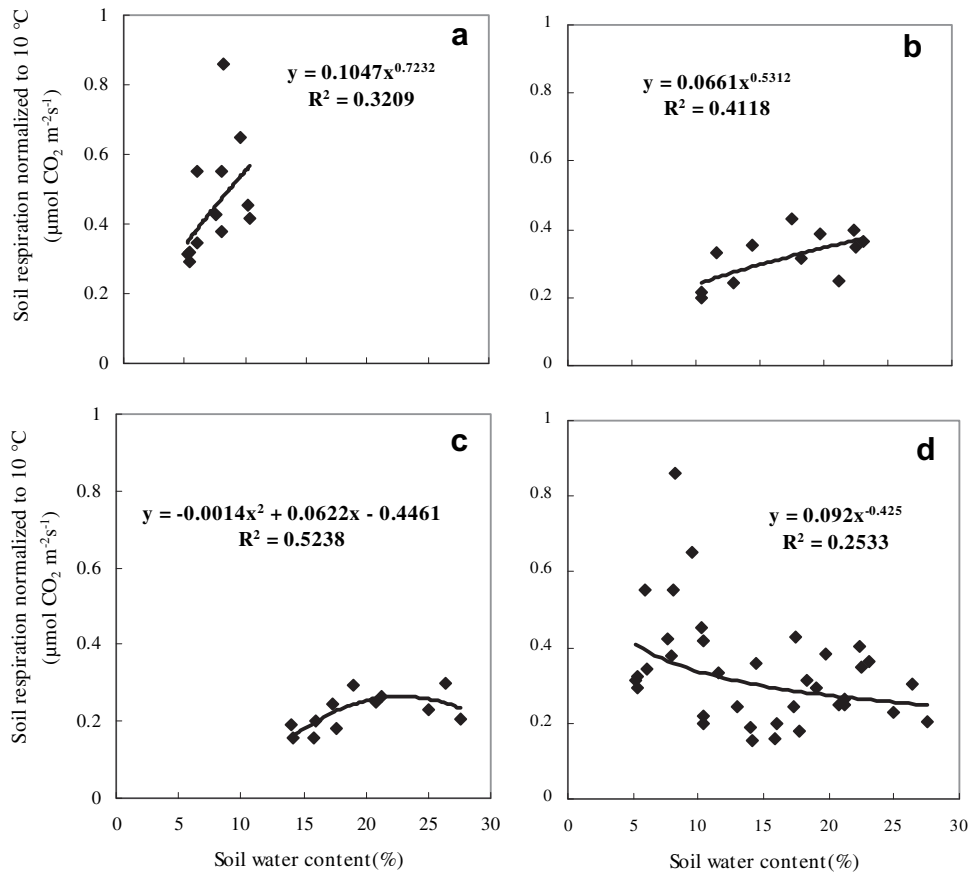
### 3.2.4. Effect of an artificial precipitation pulse on soil respiration

After wetting, the change of  $W_s$  at 0–10 cm depth was greater than the change at other soil depths (Fig. 5c,d). At 60 min, the  $W_s$  at 0–10 cm depth increased from 3.49% to 6.22% following 5 mm treatments and from 3.84% to 6.78% following 2.5 mm treatments at the *A. aphylla* site. At the *H. caspica* site, the  $W_s$  increased from 7.06% to 13.58% after 5 mm treatments and from 4.3% to 9.38% for 2.5 mm treatments in the *H. caspica* site.

**Table 3**

Fitted equations of  $R_s$  and  $R_{s10}$  (normalized soil respiration using the fit of  $Q_{10}$  function at 10 °C  $T_s$ ) against  $W_s$ .

Site	n	$R_s$ - $W_s$ (For all measured efflux)	$R^2$	P	$R_{s10}$ - $W_s$ (For efflux at 10 °C)	$R^2$	P
<i>H. ammodendron</i>	12	$R_s = 0.528 + 0.023W_s$	0.02	0.680	$R_s = 0.168 + 0.039W_s$	0.20	0.143
	12	$R_s = 0.291W_s^{0.441}$	0.08	0.388	$R_s = 0.105W_s^{0.723}$	<b>0.32</b>	0.055
	12	$R_s = -3.571 + 1.168W_s - 0.074W_s^2$	0.39	0.106	$R_s = -1.402 + 0.472W_s - 0.028W_s^2$	0.41	0.091
<i>A. aphylla</i>	12	$R_s = 0.276 + 0.014W_s$	0.18	0.171	$R_s = 0.152 + 0.009W_s$	<b>0.35</b>	0.044
	12	$R_s = 0.093W_s^{0.595}$	0.25	0.100	$R_s = 0.066W_s^{0.531}$	<b>0.41</b>	0.026
	12	$R_s = -1.166 + 0.202W_s - 0.006W_s^2$	0.46	0.063	$R_s = -0.207 + 0.056W_s - 0.001W_s^2$	0.44	0.076
<i>H. caspica</i>	12	$R_s = 0.007 + 0.325W_s$	0.04	0.525	$R_s = 0.111 + 0.006W_s$	0.30	0.067
	12	$R_s = 0.131W_s^{0.403}$	0.06	0.432	$R_s = 0.040W_s^{0.577}$	<b>0.36</b>	0.038
	12	$R_s = -2.180 + 0.261W_s - 0.006W_s^2$	<b>0.51</b>	0.041	$R_s = -0.446 + 0.062W_s - 0.001W_s^2$	<b>0.52</b>	0.036
All data	36	$R_s = 0.681 - 0.009W_s$	0.05	0.184	$R_s = 0.528 - 0.013W_s$	<b>0.22</b>	0.004
	36	$R_s = 0.733W_s^{-0.142}$	0.03	0.312	$R_s = 0.092W_s^{-0.425}$	<b>0.25</b>	0.002
	36	$R_s = 0.627 + 0.0003W_s - 0.0003W_s^2$	0.05	0.402	$R_s = 0.510 - 0.009W_s - 0.0001W_s^2$	<b>0.22</b>	0.018



**Fig. 4.** Relationships between the normalized soil respiration ( $R_{s10}$ ) at 10 °C Ts and soil water content (Ws) over the depth of 0–50 cm (a = *H. ammodendron* site, b = *A. aphylla* site, c = *H. caspica* site, and d = all data from the three sites). The solid line is the fitted regression line.

A cyclical pattern of  $R_s$  was observed after simulated rainfall. A decline in  $R_s$  was followed by a subsequent increase in  $R_s$  that was followed by yet another decline (Fig. 5). At the first post-wetting sample (10 min), respiration rates changed from 0.43 to 0.36  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for 5 mm additions at the *A. aphylla* site and from 0.19 to 0.17  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the *H. caspica* site. The decline in  $R_s$  was not apparent after the 2.5 mm addition (Fig. 5a,b). The maximum  $R_s$  after the water addition lagged behind that of the control: 300 min for the 5 mm treatment, 180 min for the 2.5 mm treatment and 60–180 min for the control. The maximum  $R_s$  rate and the declining respiration rate thereafter were higher after the 5 mm and 2.5 mm treatments than those in the 0 mm treatment. For all sites, the  $\text{CO}_2$  efflux returned to the pretreatment level over a 420 or 540 min period. The increases and decreases in  $R_s$  were consistent with changes in soil surface temperature.

Additionally, we observed a change in  $R_s$  after natural rainfalls. The measurement at 14:00 on May 10 in 2006 was made just after a sleet event that lasted for 20 min at the *H. ammodendron* site. The  $R_s$  decreased from 0.76  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at 12:00 h to 0.58  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at 14:00 h (Fig. 6a). Air temperature and soil temperature at the 0 cm depth also decreased markedly. However, the  $R_s$  measured at 16:00 and 18:00 h did not increase with increasing temperature. In addition, the  $R_s$  fluctuated at a low level due to the discontinuous rain before 16:00 h and changed along with temperature at 16:00, 18:00 and 20:00 h when it became sunny on August 17 in 2006 at the *A. aphylla* site (Fig. 6b). The  $R_s$  at 14:00 h decreased rapidly due to precipitation on October 19 in 2006 at the *A. aphylla* site (Fig. 6c). The  $R_s$  and temperature increased at 16:00 h to close to the pre-precipitation value found at 12:00 h and decreased at 18:00 and 20:00 h.

## 4. Discussion

### 4.1. Temporal variability of soil respiration

The mean soil respiration was  $0.58 \pm 0.26 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  across the three sites from May to October. These results are similar to a cold desert in southeast Utah in which soil respiration was 0.91  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the spring and 0.36  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the summer (Fernandez et al., 2006). In the current study, negative  $R_s$  were observed at 8:00 h and 20:00 h in September and October and became positive as the temperature increased. Xie et al. (2009) also found that monthly mean soil respiration was negative in September and October and suggested that inorganic  $\text{CO}_2$  absorption was a natural process found in all alkaline soils.  $\text{CO}_2$  contained in the atmosphere dissolves into soil water in saline/alkaline soil to form carbonic acid,  $\text{H}_2\text{CO}_3$ , which should partially neutralize the alkalinity of the soil water. Emmerich (2003) found large carbonate-related  $\text{CO}_2$  emissions after precipitation. Further studies are needed to understand the reason for negative soil  $\text{CO}_2$  efflux and to distinguish between the  $\text{CO}_2$  derived from these carbonates and soil organic matter decomposition or root respiration.

### 4.2. Relationships among soil respiration, temperature and soil moisture

The  $Q_{10}$  values were 1.35 at the *H. ammodendron* site, 1.41 at the *A. aphylla* site and 1.52 at the *H. caspica* site. The  $R_{10}$  values were 0.45  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the *H. ammodendron* site, 0.30  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the *A. aphylla* site and 0.22  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the

**Table 4**  
Regression equations for soil respiration ( $R_s$ ) against air temperature ( $T$ ) and soil water content ( $Ws$ ).

Site	n	$R_s = a + b(TW)$	$R^2$	$R_s = a + bT + cW$	$R^2$	$R_s = aT^bW^c$	$R^2$	$R_s = ae^{bT}W^c$	$R^2$	$R_s = a + bT + cW + dTW$	$R^2$
<i>H. ammodendron</i>	12	$R_s = 0.061 + 0.004 TW$	0.41*	$R_s = -0.362 + 0.026T + 0.061W$	0.38	$R_s = 0.005T^{1.035}W^{0.819}$	0.42*	$R_s = 0.037e^{0.045T}W^{0.919}$	0.44*	$R_s = 0.408 - 0.011T - 0.054W + 0.006 TW$	0.42
<i>A. aphylla</i>	12	$R_s = 0.207 + 0.001 TW$	0.62**	$R_s = -0.077 + 0.014T + 0.014W$	0.65**	$R_s = 0.019T^{0.644}W^{0.448}$	0.66*	$R_s = 0.064e^{0.029T}W^{0.475}$	0.65*	$R_s = 0.011 + 0.011T + 0.008W + 0.0002 TW$	0.65*
<i>H. caspica</i>	12	$R_s = 0.109 + 0.002 TW$	0.67**	$R_s = -0.257 + 0.018T + 0.012W$	0.73**	$R_s = 0.002T^{1.078}W^{0.640}$	0.77*	$R_s = 0.021e^{0.045T}W^{0.633}$	0.77*	$R_s = -0.141 + 0.012T + 0.004W + 0.0001 TW$	0.84**
All data	36	$R_s = 0.576 + 1.112 \times 10^{-6}TW$	0	$R_s = 0.241 + 0.017T - 0.008W$	0.29**	$R_s = 0.082T^{0.714}W^{-0.156}$	0.28*	$R_s = 0.361e^{0.030T}W^{-0.146}$	0.27*	$R_s = 0.156 + 0.020T + 0.0005W + 0.0003 TW$	0.29*

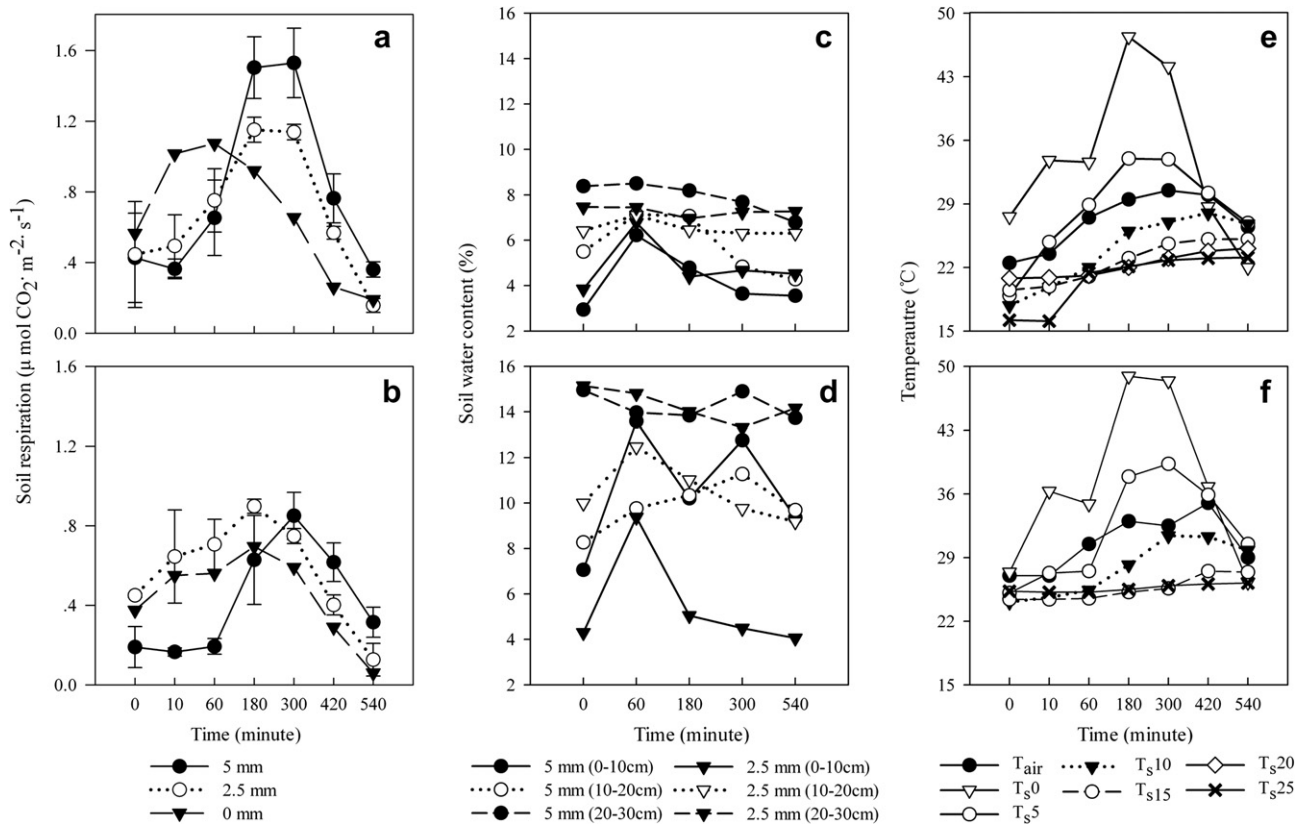
\*Significant at 0.05 confidence, \*\*Significant at 0.01 confidence.

*H. caspica* site. Soil water content increased gradually from the *H. ammodendron* site to the *A. aphylla* and *H. caspica* sites. The results support that the sensitivity of soil respiration to temperature appears to increase as soil water content increases (Borken et al., 2002; Curiel-Yuste et al., 2003; Gaumont-Guay et al., 2006; Jassal et al., 2008; Li et al., 2008; Xu and Qi, 2001a). However, Reichstein et al. (2005) did not find important changes in the direct sensitivity of soil respiration to temperature in response to soil moisture, soil horizon and incubation time in a laboratory experiment. They suggested that the dependency of  $Q_{10}$  on several factors was only at the ecosystem level and did not hold at lower organizational levels (Reichstein et al., 2005). In addition, the present study showed the highest  $R_{10}$  and smallest  $Q_{10}$  at the *H. ammodendron* site and the lowest  $R_{10}$  and largest  $Q_{10}$  at the *H. caspica* site. Davidson et al. (2006) also reported that the higher  $R_{10}$  found at an oak/rhododendron site resulted in a smaller  $Q_{10}$  ratio than might be expected, considering the similar seasonal amplitudes in temperature and larger seasonal amplitude of soil respiration. Basal rates of respiration increased and temperature sensitivity of respiration decreased across three sites along a decreasing soil water content gradient. Thus, the predominant factors influencing basal rates of respiration and temperature sensitivity were different.

In the present study, the decrease in  $R_{10}$  with an increase in  $Ws$  was unexpected. The basal rate of soil respiration was anticipated to be positively correlated to  $Ws$  as was previously shown by Li et al. (2008) in a Chinese mountain area. In the present study, the canopy cover was over 50% in the *H. ammodendron* community, 20% in the *A. aphylla* community and 25% in the *H. caspica* community. Larger canopy cover in desert vegetation usually corresponds to greater productivity of the aboveground vegetation which is proportional to root respiration and, therefore, to the increased efflux of  $CO_2$  (Davidson et al., 2000; Lulie et al., 2005). The *H. ammodendron* site had higher plant height and more canopy coverage than the other sites. Consequently, soil respiration rates at the *H. ammodendron* site were greater than those at other two sites. Small differences in soil organic matter content among the three sites could not contribute to the differences in soil respiration rates (Table 1). Nevertheless, the higher EC, salinity content and ion content (e.g.,  $Cl^-$ ,  $Mg^{2+}$  and  $Na^+$ ) might limit microbial biomass and ability and lead to lower  $R_s$  at the *H. caspica* site. Yuan et al. (2007) found that higher salinity resulted in a smaller and more stressed microbial community that was less metabolically efficient. Additionally, Chang et al. (2003) found that the soil water content decreased as vegetation coverage increased in the desert along the middle reaches of the Heihe River Basin. In our study,  $Ws$  was smallest at *H. ammodendron* site, where canopy cover was larger than the other two sites. The lower topography and smallest soil bulk density ( $1.45 \text{ g cm}^{-3}$ ) also contributed to the higher soil moisture at the *H. caspica* site. In addition to above-ground metabolism inducing changes in basal rate of  $R_s$  via differences in the below-ground supply of labile carbon, the high salt content is another factor that leads to difference in basal rates of  $R_s$ . Therefore, it is necessary to consider the differences in vegetation productivity and soil salt when using models to evaluate soil respiration in deserts due to large spatial variation of soil respiration at the ecosystem scale.

The two-variable model with both  $Ts$  and  $Ws$  as independent variables and  $R_s$  as the dependent variable has been extensively used in studies on the effects of  $Ts$  and  $Ws$  on  $R_s$  (Davidson et al., 1998; Jia et al., 2006; Kang et al., 2003; Li et al., 2008; Xu and Qi, 2001a, 2001b). In this study, however, the percent of the variance that was explained by the two-variable models was 41–44% at the *H. ammodendron* site and 27–29% for the three sites together. Therefore, there are still some unknown factors that impact  $R_s$ .





**Fig. 5.** Soil respiration, soil water content and soil temperature at different soil depths following rainfall additions at *A. aphylla* (a, c, e) and *H. caspica* sites (b, d, f). Data on soil respiration rates represents means  $\pm$  standard error ( $n = 3$ ).

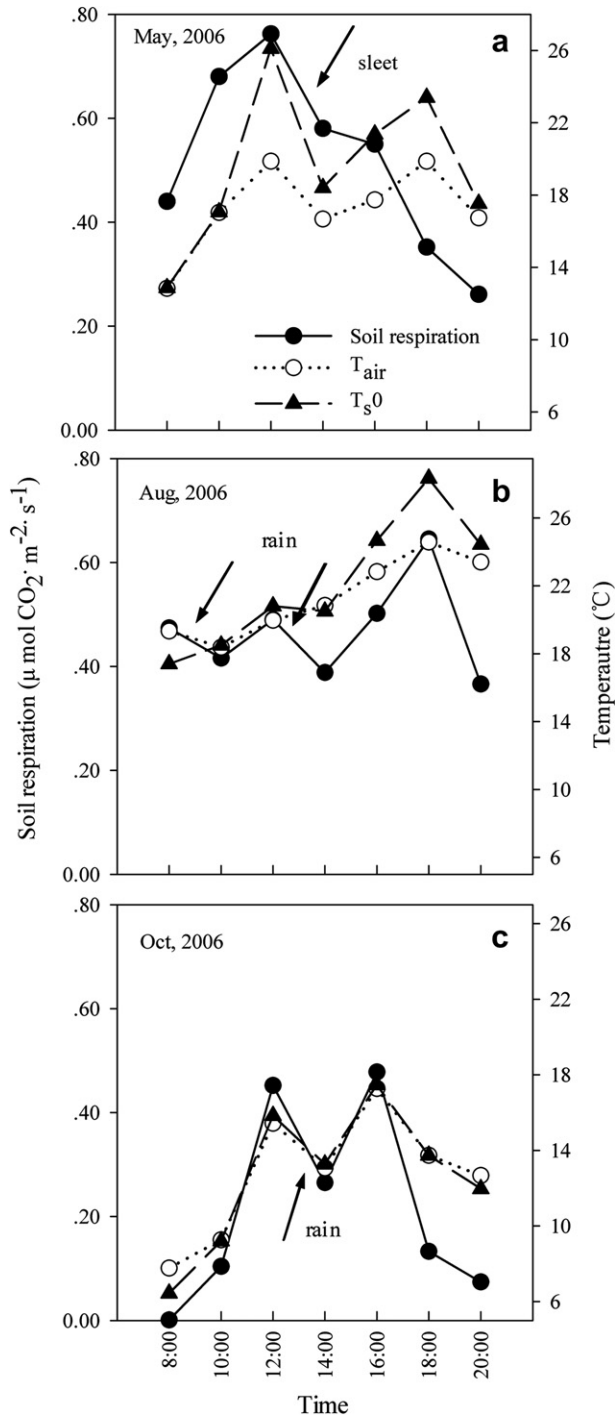
These unknown factors could include net primary productivity (NPP), root biomass, litter inputs, microbial populations, root nitrogen concentrations, substrate quantity and substrate quality (Buchmann, 2000; Curiel-Yuste et al., 2004; Dilustro et al., 2005; Fang and Moncrieff, 2001; Sánchez et al., 2003). Han et al. (2007) found that biotic factors (biomass and NPP) affected the response of soil respiration to soil temperature during the growing season in the maize agricultural ecosystem. Kirschbaum (2006) found that changes in substrate availability may confound the apparent temperature dependence of soil respiration. Therefore, it is necessary to incorporate additional factors (biotic factors or soil properties) into models of soil respiration. It is also important to determine the cause of the differences in the response of soil respiration to environmental factors. In this study, the variation explained by temperature, soil water content and two-variable models based on temperature and soil water content were lower for the three sites together than at each individual site. It is also important to enhance the precision of evaluating soil respiration at the ecosystem scale.

In this study, soil respiration decreased with increasing temperature from June to July of 2006 (maximum temperature). The synchronous occurrence of maximum respiration and temperature might suggest that soil respiration was inhibited by lower soil moisture during the hot summer (Fig. 2). Maestre and Cortina (2003) reported a decrease in soil  $\text{CO}_2$  efflux at the highest temperatures when soil moisture values were lowest in a semiarid prairie. The highest soil respiration occurred in spring when soil temperature was between 10.5 and 15.7  $^{\circ}\text{C}$  and volumetric soil moisture was greater than 9.5% in a cold desert (Fernandez et al., 2006). Based on these previous studies and the current study, the significant effect of temperature on soil

respiration is across a range of soil moisture measurements and high temperature combined with low soil water content may limit the increase of soil respiration.

#### 4.3. Effect of artificial precipitation pulse on soil respiration

Soil respiration increased with rainfall addition, with a peak flux larger than the control treatment. However, this peak but did not appear as a large pulse increase as was found by Sponseller (2007). Sponseller (2007) found that soil  $\text{CO}_2$  efflux increased by up to 30 times immediately following experimental rewetting in a Sonoran Desert ecosystem. The soil organic matter was 2.9% at 0–2 cm and 2.0% at 2–12 cm for interplant patches that were larger than the area of this study. Pulses of  $\text{CO}_2$  may be derived from the microbial oxidation and desorption of soil organic matter (SOM) and/or from the decomposition of death microorganisms accumulating during soil drought (Adu and Oades, 1978; Appel, 1998; Fierer and Schimel, 2003). The infiltration of rainwater may displace  $\text{CO}_2$  that accumulates in soil pore spaces during dry periods (Huxman et al., 2004). A rapid pulse of  $\text{CO}_2$  production following precipitation and rewetting of dry soil has been observed in several ecosystems (Austin et al., 2004; Borken et al., 2003; Franzluebbers et al., 2000). However, Degens and Sparling (1995) found no increase in organic C mineralization in a sandy loam soil subjected to six wet–dry cycles and contended that the organic C in this soil was stable and resistant to decomposition. Borken et al. (2002) also revealed that respiration in the mineral soil could still be limited by drought, while respiration in the O-horizon increased after small amounts of rainfall. In this study, the contents of soil organic matter at 0–5 cm depth were 0.73%, 0.78% and 1.05% at the *H. ammodendron*, *A. aphylla* and *H. caspica* sites, respectively. These values were lower



**Fig. 6.** Daytime variations in soil respiration, air temperature and soil temperature at 0 cm depth on rainy days in 2006 at the *H. ammodendron* site (a) and the *A. aphylla* site (b and c). Data are mean values for every sampling period ( $n = 5$  for soil respiration rate,  $n = 3$  for temperature).

than the values found by Sponseller (2007). Large pulses of  $\text{CO}_2$  were not observed in this study, which might be associated with the low soil organic matter content, decomposition rate and low microbial biomass (Gallardo and Schlesinger, 1992; Zhu et al., 2008) in the study area. Meanwhile, low water infiltration due to the fine texture of the soil, high temperature and intense evaporation led to a short duration of soil water content and thus affected the increase of soil  $\text{CO}_2$  efflux.

In this study, the maximum rate and the declining respiration rate thereafter were higher in the 5 mm and 2.5 mm rainfall treatments than in the 0 mm treatment, which supports previous studies that found that rainfall simulation significantly enhanced  $\text{CO}_2$  efflux (Casals et al., 2000; Fernandez et al., 2006; Maestre and Cortina, 2003). The decrease of soil respiration at 10 min after the addition of water may result from the increasing diffusion resistance due to decreasing soil permeability after precipitation, which in turn leads to a decline in measured soil respiration (Cavelier and Peñuela, 1990).

## 5. Conclusions

The mean soil respiration rates in the growing season were 0.76, 0.52 and 0.46  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the *H. ammodendron*, *A. aphylla* and *H. caspica* sites, respectively. The basal rate of soil respiration decreased and temperature sensitivity of respiration increased simultaneously across the three sites along an increasing soil water content gradient (*H. ammodendron* – *A. aphylla* – *H. caspica*). Canopy cover and soil salt were important factors that influenced the basal rate of soil respiration. The seasonal variation of soil respiration mainly was influenced by the air temperature at the three sites, whereas the increase of soil respiration appeared to be limited by high temperature with low soil water content in mid-summer. The response of soil respiration to air temperature was stronger at the site with higher soil water content. Soil respiration was significantly positively correlated with soil water content at the three sites. Overall amounts of variation explained by equations of soil respiration against temperature and gravimetric water content were better than one-dimensional equations. After the simulated rainfall treatments, soil respiration increased relative to the control group. However, the simulated rainfall treatments did not result in large pulses of  $\text{CO}_2$ . Soil respiration appeared to be influenced by temperature and soil moisture following both artificial and natural precipitation events.

Temperature was the dominant factor that influenced soil respiration. Soil water content was a limiting factor for soil respiration, especially at high temperatures. Greater soil water content enhanced the response intensity of soil respiration to temperature. The combination of temperature and soil water content improved the evaluation of soil respiration. The biotic factors such as micro-organism and root distribution should be considered in future research. Additionally, the soil salinity- important environment conditions like soil water content in study area cannot be ignored.

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