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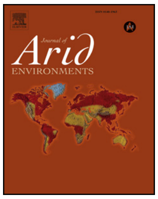

Changes and regulations of net ecosystem CO_2 exchange across temporal scales in the Alxa Desert

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ABSTRACT

Arid ecosystems are an important component of the global carbon cycle. In these ecosystems, plant functional types are particularly important in realizing many ecosystem processes such as the dynamics and regulations of net ecosystem exchange of CO_2 (NEE) to the changing environment. Here, we measured the diurnal dynamics of NEE in patches of succulent and non-succulent shrubs over two growing seasons (2012 and 2013) in the Alxa Desert, located in northern China. We find that the interannual difference of NEE was greater for the non-succulent shrub than that for he succulent shrub species. Diurnal NEE changes were similar for all species and were more strongly influenced by soil moisture than by temperature. Nonetheless, these environmental factors had a greater influence on non-succulent shrubs than succulent shrubs. Our findings highlight that species with different life history traits have different NEE dynamics and vary by time scales. These dynamics are strongly tied to water availability and plant type-specific water storage capacity, with plants possessing large water storage organs maintaining their physiological functioning better under stressful conditions. Our findings on the interaction between plant type and environment could be used to improve estimates of terrestrial carbon uptake in critical desert ecosystems.

1. Introduction

Dryland ecosystems cover 30–45% of the global terrestrial surface area (Emanuel et al., 1985; Schlesinger et al., 1990; Qi et al., 2017) and are an important component of the global carbon cycle (Ahlström et al., 2015; Chen et al., 2013; Maestre et al., 2016; Poulter et al., 2014). These ecosystems have high potentials for future CO_2 uptake (Emmerich, 2003; Houghton et al., 1999; Lal, 2004; Pacala et al., 2001), with their response to future conditions critical in determining future global carbon cycle trajectories (Baldocchi et al., 2018; Bates et al., 2006; Huxman et al., 2004; Niu et al., 2017; Smith et al., 2000). In these ecosystems, plant functional type is a particularly important variable for understanding many ecosystem processes, such as the dynamics and regulations of net ecosystem exchange of CO_2 (NEE), to the changing environment. However, it is not well known how plant type responses may influence ecosystem responses in dryland ecosystems.

Plant responses to environmental variation may differ among species because of their unique adaptive strategies to these changes (Baldocchi et al., 2004; Ellsworth et al., 2004; Enquist et al., 2007; Munson et al., 2012; Musavi et al., 2016). Desert environmental conditions (e.g., low rainfall & high temperature) favor species with traits that can effectively reduce water stress (e.g., high water storage, low transpiration) (Emanuel et al., 1985; Noy-Meir, 1973). These traits include succulent leaves and CAM photosynthesis (Borland et al., 2014; Owen and Griffiths, 2013; Sandquist, 2013; Yamori et al., 2014). Logically, there will be trade-offs between reduced water loss and a plant's ability to utilize water during times of high-water availability. As such, the community composition of different functional traits would have a strong influence on total ecosystem carbon exchange.

Circadian rhythm is a key driver of carbon exchange between plants and the atmosphere for many plant species (Resco de Dios and Gessler, 2017; Resco de Dios et al., 2012; McClung, 2006; Pittendrigh, 1954) in dryland ecosystems (Ahlström et al., 2015; Wohlfahrt et al., 2008). However, circadian rhythm may vary greatly among species with

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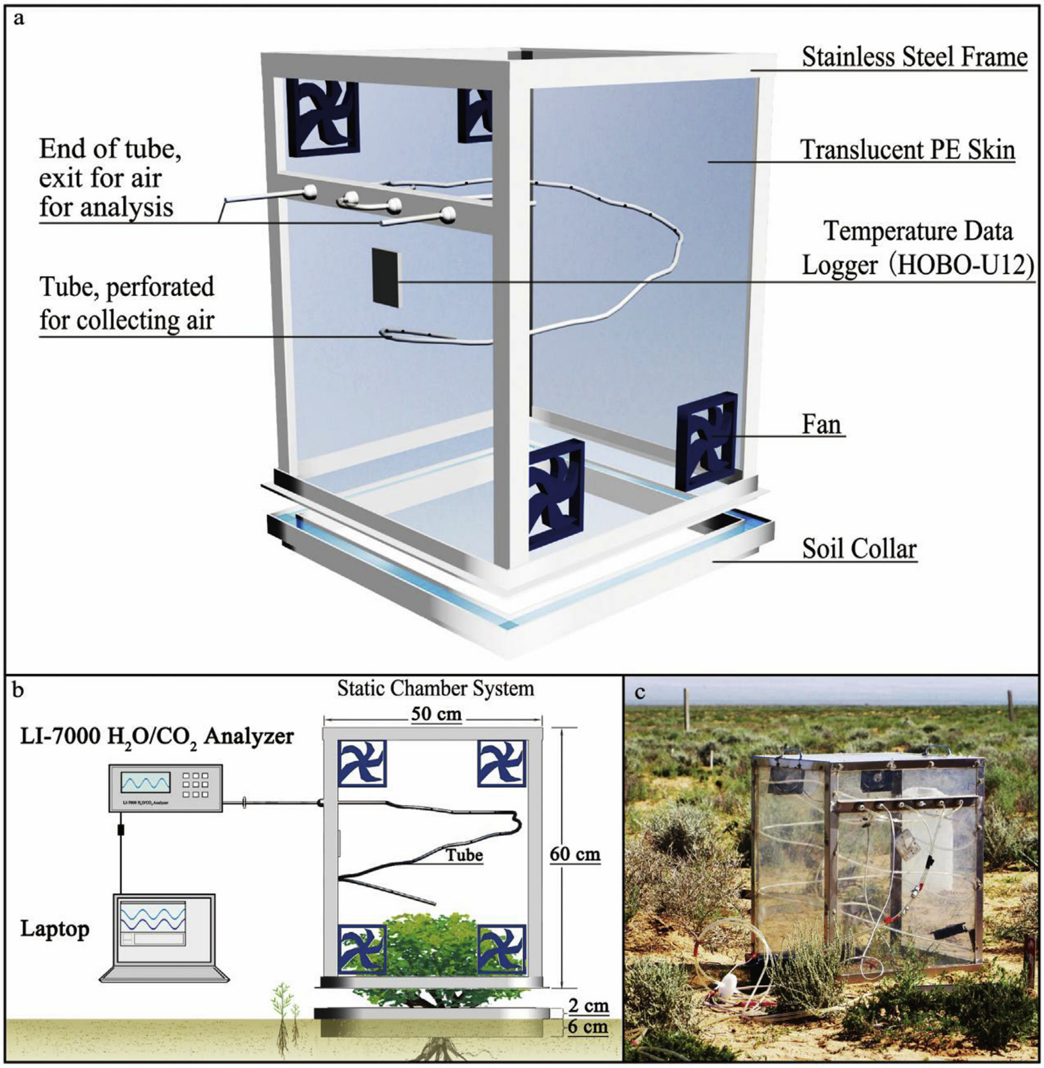

Fig. 1. The CO_2 flux measurement system by using a LI-7000 H_2O/CO_2 analyzer. (a) schematic illustration of the static chamber; (b) connection between the analyzer, laptop, and other facilities; and (c) an in-situ field photo of the system in the study area in Alxa Desert.

different adaptations (e.g., through water storage) in some dryland species. Plants may also regulate their strategies differently during the day when carbon assimilation dominates NEE, as opposed to at night when respiration dominates the NEE process. Clearly, our conceptual understanding of the changes in and regulations of NEE needs to be scale-specific.

To better understand the changes in and regulation of the NEE of major xeric shrubs at multiple time scales (e.g., diel, diurnal, seasonal and yearly), we conducted a two-year field study in a metacommunity located in the Alxa Desert using a static chamber method to measure NEE of three dominant xeric shrubs throughout the 24-h period, including a succulent leaf shrub (*Nitraria sphaerocarpa* Maxim.) and two non-succulent leaf shrubs (*Potaninia mongolica* Maxim. and *Krascheninnikovia ceratoides* Gueldenst). We hypothesize that the succulent and non-succulent shrub species have differing temporal NEE changes due to their unique avoidance strategies to drought. Specifically, we predict that the succulent shrubs have small variation in NEE in response to the changing environment (e.g., drought in particular) because of high water storage in the leaves, but lower maximum carbon uptake during wet periods than non-succulent shrubs. Similarly, we expect a lower diurnal variation in the succulent species than that in the non-succulent shrubs due to the greater water storage of the succulent shrubs.

2. Materials and methods

2.1. Study site

We conducted our study in the Alxa Plateau of northern China. The Alxa Plateau is on the eastern edge of the Eurasian desert and the southwestern edge of the Mongolian Plateau. The plateau is characterized by low rainfall and high temperatures. For the last 50 years, the average annual air temperature was 8.3 °C and the annual precipitation ranged between 33.2 mm and 209.0 mm (Chen et al., 2013). Shrub species distribution varies greatly across the plateau, with succulent shrubs being relatively more prevalent in the hyper arid regions in the west and non-succulents dominating in the east (He et al., 2007; Li et al., 2007). Our study site is located approximately 30 km south of Badain Jaran Town in Alxa Right Banner (38°57′N, 101°36′E, 1521 m a.s.l.) in the middle west of the Alxa Plateau. The experimental site was fenced and had not been grazed for more than 10 years (Fig. S1).

2.2. Static chamber system and sampling strategy

The net ecosystem CO_2 exchanges (NEE) of the patches dominated by three shrubs (*N. sphaerocarpa*, *P. mongolica*, and *K. ceratoides*) were measured using a static chamber system (Arnone III and Obrist, 2003;

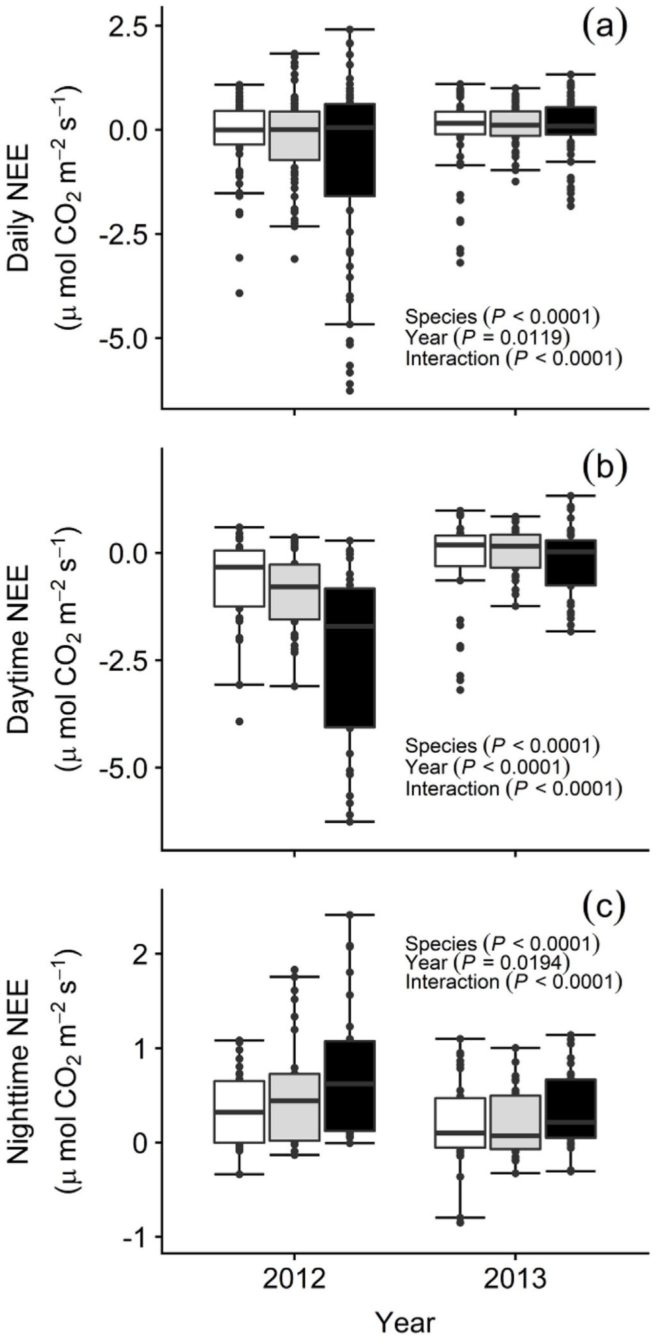

Fig. 2. The mean (± SE) net ecosystem CO_2 exchange (NEE) of three xeric shrubs three diurnal scales in the Alxa Desert. Inter-annual difference of the daily NEE (a), daytime NEE (b), and nighttime NEE (c) during the study period. White, grey, and black boxes represent *Nitraria sphaerocarpa*, *Potaninia mongolica*, and *Krascheninnikovia ceratoides*, respectively.

Jasoni et al., 2005). The system is comprised of a cube-shaped, open-bottomed chamber (volume 0.15 m^3) made of transparent acrylic with a steel frame and a square stainless-steel collar in a U-shaped profile sized to fit the lower edge of the chamber (Fig. 1a). We pushed the 8 cm high soil collar into the ground to a depth of 6 cm to ensure the enclosure and stability of the chamber (Fig. 1b). Prior to each measurement, the bottom edge of the chamber was inserted into the U-shaped collar to seal the bottom edge (Fig. 1c). Two diagonally positioned electric fans were mounted on the inner wall of the chamber and were turned on for 120 seconds prior to each measurement to mix the air inside the chamber. A loop of perforated tube fitted inside the chamber was connected to a CO_2 analyzer to extract air from the chamber for measurement (Fig. 1). The chamber was moved among the patches of 27 selected shrubs (i.e., 9 replicates for each of the three patches types). To reduce disturbance, each soil collar was secured into the soil at the start of each of the two growing seasons and was left in place throughout the season.

2.3. CO_2 measurement

Measurement of NEE in CO_2 was conducted using a LI-7000H_2O/CO_2 analyzer (LI-COR, Lincoln, NE, USA), a static chamber, and a laptop computer (Dell Inspiron 600 M, Dell Inc. Austin, TX, USA). We recorded CO_2 concentration (μmol mol^{-1}), atmospheric pressure (kPa), and water vapor density (mmol mol^{-1}) inside the chamber. For each measurement, data were recorded every second for 120 seconds to measure NEE. The daily observation period began at 7:00 a.m. and ended 24 hours later. Measurements were taken every two hours for all 27 patches, totaling 12 measurements per day. Daytime was defined as 6:00 a.m. to 6:00 p.m. and nighttime as 6:00 p.m. to 6:00 a.m. of the following day. Our intensive field measurements were conducted on 15th June, 15th July, 15th August, 5th September, 17th September, 5th October and 28th October in 2012, and 2nd May, 12th June, 12th July, 30th July, 25th August, 11th September, 30th September, and 30th October in 2013.

2.4. Measurements of the microclimate

HOBO-U12 temperature data loggers (HOBO, Onset Computer Corporation, MA, USA) were used to log continuous changes in temperature of the chamber during each measurement period. The loggers were positioned to record air temperature (T_a) and soil temperature at 5 cm (T_5), 10 cm (T_{10}), and 20 cm (T_{20}). Ten replicate soil samples were taken at 10 cm (W_{10}), 20 cm (W_{10}), 30 cm (W_{10}), and 50 cm (W_{10}) depth on each measurement day. Soil water content was determined by sampling in situ soil cores. The soil was sampled and stored in aluminum tins before shipping back to the lab for drying for 48 hours at 105 °C. Average precipitation and air temperature data for the study area were obtained from the nearest meteorological station located approximately 25 km from the study site (Alxa Right Banner, Inner Mongolia). Total annual precipitation was 54.5 mm in 2012 and 33.7 mm in 2013 (http://data.cma.cn).

Table 1
The mean (± SE) of net ecosystem CO_2 exchange (NEE) at daily, daytime, and nighttime scales of the three xeric shrubs in the Alxa Desert in 2012 and 2013. Lowercase letters denote a significant difference among the species in the same year based on the Tukey's-range test, and capital letters represent a significant difference between 2012 and 2013 in same species ($P < 0.05$).

Year	Species	Daily NEE (μmolCO_2·$m^{-2}s^{-1}$)	Daytime NEE (μmolCO_2·$m^{-2}s^{-1}$)	Nighttime NEE (μmolCO_2·$m^{-2}s^{-1}$)
2012	*N. sphaerocarpa*	−0.19 ± 0.06 aA	−0.70 ± 0.10 aA	0.31 ± 0.04bA
	P. mongolica	−0.18 ± 0.07 aB	−0.84 ± 0.10 aB	0.46 ± 0.05bA
	K. ceratoides	−0.89 ± 0.15bB	−2.51 ± 0.22bB	0.70 ± 0.07 aA
2013	*N. sphaerocarpa*	−0.17 ± 0.09bA	−0.57 ± 0.16bA	0.22 ± 0.06 aA
	P. mongolica	0.05 ± 0.05 aA	−0.10 ± 0.08 aA	0.20 ± 0.04 aB
	K. ceratoides	−0.05 ± 0.06abA	−0.43 ± 0.10abA	0.32 ± 0.05 aB

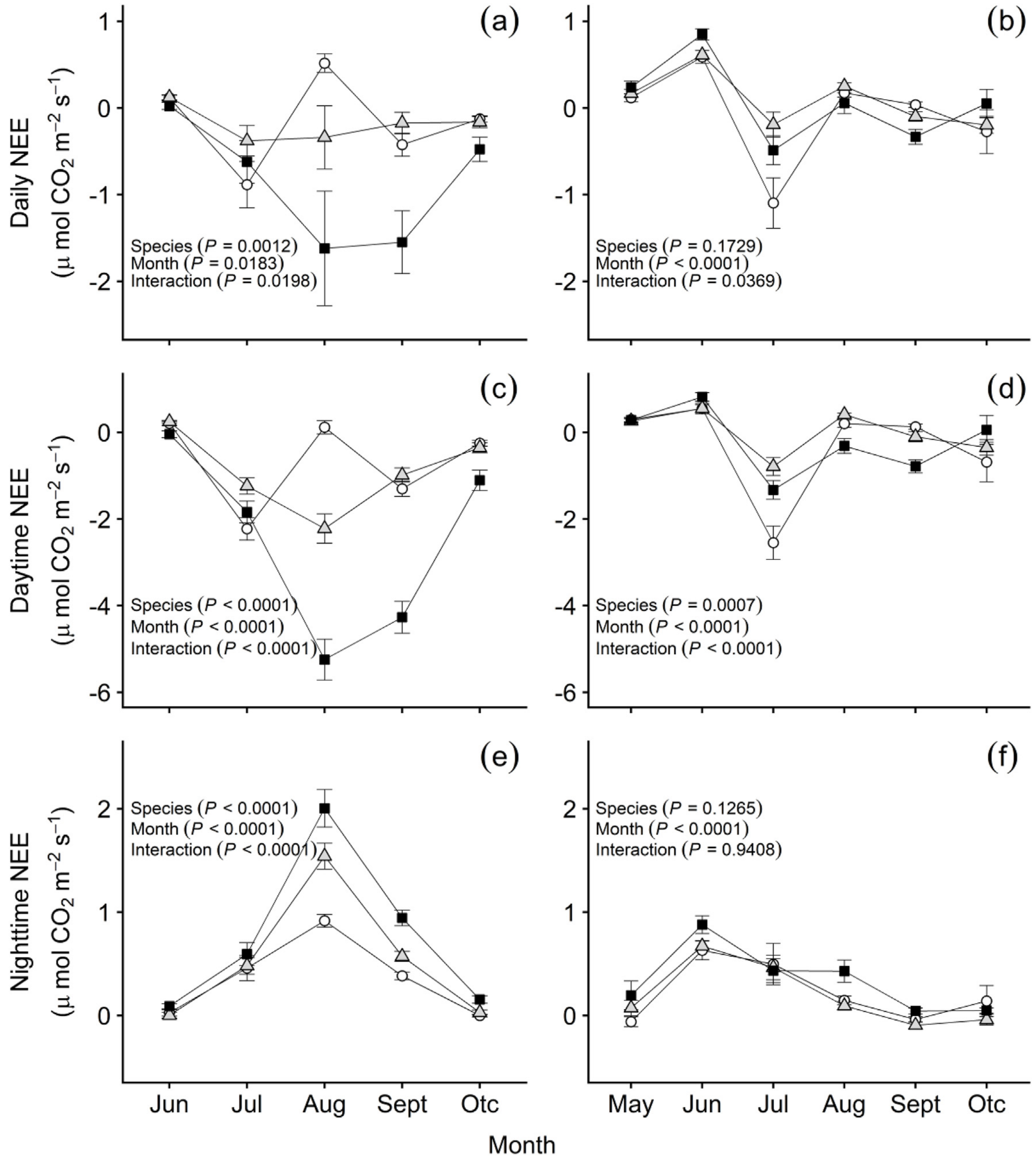

Fig. 3. Seasonal changes of net ecosystem CO_2 exchange (NEE) at three xeric shrubs in the Alxa Desert. Intra-annual variations of daily NEE for 2012 (a) and 2013 (b); daytime NEE for 2012 (c) and 2013 (d), and nighttime NEE for 2012 (e) and 2013 (f) during the study period. White circles, grey triangles, and black squares represent *Nitraria sphaerocarpa*, *Potaninia mongolica*, and *Krascheninnikovia ceratoides*, respectively.

2.5. Calculation of NEE

We calculated NEE of CO_2 for each measurement using Eq. (1):

$$\boldsymbol{NEE} = \frac{\boldsymbol{V} \times \boldsymbol{P_{av}} \times (1 - \frac{\boldsymbol{W_{av}}}{1000})}{\boldsymbol{R} \times \boldsymbol{S} \times (\boldsymbol{T_{av}} + 273.16)} \times \frac{\boldsymbol{dC'}}{\boldsymbol{dt}} \tag{1}$$

where *NEE* denotes the CO_2 flux (μmol·$m^{-2}s^{-1}$); *V* denotes the volume of the cube chamber (m^3); P_{av} denotes the mean value of atmosphere pressure (kPa) inside the chamber during the measurement period; W_{av} denotes the mean value of vapor density (mmol mol^{-1}); *R* denotes the gas constant value (8.314 J $mol^{-1}K^{-1}$); *S* denotes the surface area covered by the chamber (m^2); T_{av} denotes the mean value of inner-temperature (°C) during the measurement period; and *dC′/dt* denotes the change of the CO_2 concentration over time, which is the slope of a simple linear regression of CO_2 concentration over time (μmol $mol^{-1}s^{-1}$) (Jasoni et al., 2005).

2.6. Statistical analysis

To test for differences in NEE of CO_2 between the succulent and non-succulent species at multiple temporal scales (e.g., daily, daytime, nighttime, and seasonal) and their interactive effects, we ran three linear mixed-effects models (LMMs) using the *lmer* function in the lme4 library (Bates et al., 2015) in R v3.3.3 (R Core Team, 2017). First, we fit a model that included species, measurement year, and the interaction between species and year as fixed effects. We induced a hierarchical structure of diurnal intervals nested within month as a random factor. Secondly, we fit a model that included species, measurement month, and the interaction between species and month as fixed effects. We included diurnal time period as a random factor. Lastly, we fit a model

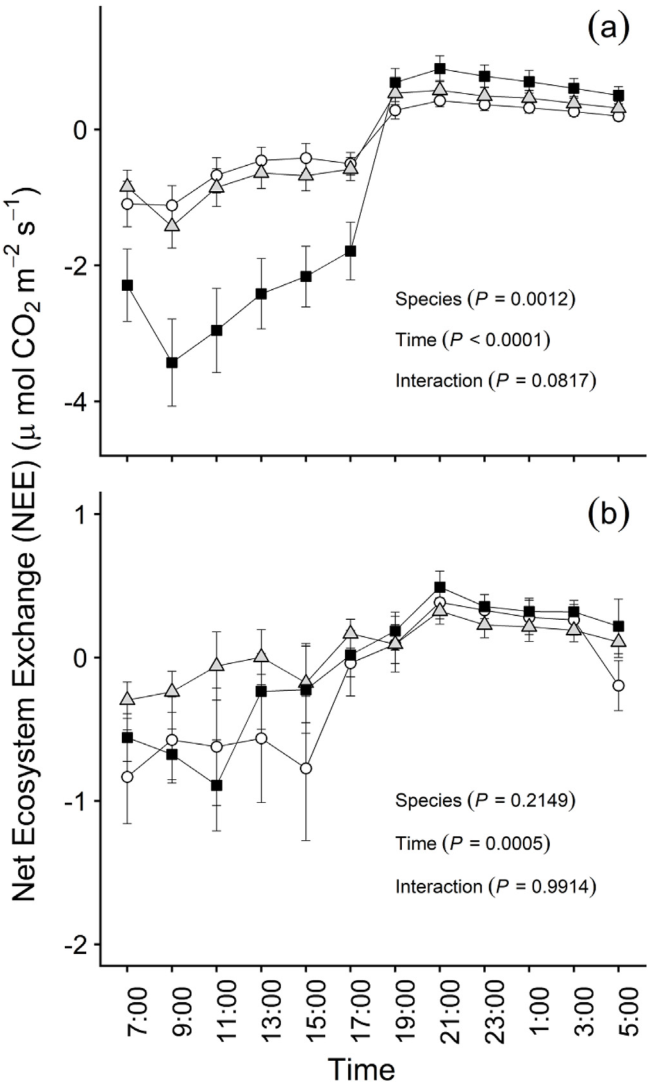

Fig. 4. Diurnal changes of net ecosystem CO_2 exchange (NEE) at three xeric shrubs in the Alxa Desert. Diurnal changes in NEE for 2012 (a) and 2013 (b) during the study period. White circles, grey triangles, and black squares represent *Nitraria sphaerocarpa*, *Potaninia mongolica*, and *Krascheninnikovia ceratoides*, respectively.

that included species, the diurnal time period, and the interaction between species and the diurnal time period as fixed effects. We included month as a random factor.

We performed the Tukey's multiple – range test to quantify the differences in NEE among the xeric shrubs between 2012 and 2013. We ran linear regression models to predict NEE from the significant environmental variables (i.e., temperature and soil water content) to explore the relationship between the environmental drivers and NEE.

3. Results

3.1. NEE of the xeric shrubs

Species, year, and their interactions significantly ($P < 0.05$) affected daily NEE, daytime NEE, and nighttime NEE (Fig. 2). However, the variations of daily NEE, daytime NEE, and nighttime NEE of the succulent shrub (*N. sphaerocarpa*) were not significant ($P > 0.05$ in all cases) between the two years. In comparison with 2012, daily NEE and daytime NEE of the non-succulent shrubs, *P. mongolica* and *K. ceratoides*, were 112% ($P < 0.05$) and 86% ($P < 0.05$) higher in 2013, respectively, while nighttime NEE was 57% ($P < 0.05$) and 54% ($P < 0.05$) lower than in 2013 (Table 1). Daily NEE and daytime NEE of *K. ceratoides* were lower than those of *N. sphaerocarpa* (368% and 258%, respectively) and *P. mongolica* (393% and 200%, respectively), whereas nighttime NEE of *K. ceratoides* was higher than those of *N. sphaerocarpa* (125%) and *P. mongolica* (51%) in 2012. Daily NEE and daytime NEE of *N. sphaerocarpa* were lower than those of *P. mongolica* (129% and 83%, respectively) and *K. ceratoides* (71% and 25%, respectively) in 2013 (Table 1, Fig. 2).

Species, month, and their interactions significantly ($P < 0.05$) affected daily NEE, daytime NEE, and nighttime NEE in 2012. In 2013, however, the month had a significant ($P < 0.05$) effect on daily NEE, daytime NEE, and nighttime NEE; species changed daytime NEE ($P = 0.0007$); their interactive effects appeared on daily NEE ($P = 0.0369$) (Fig. 3). Interestingly, there was a significant effect of diurnal time period on NEE both in 2012 ($P < 0.0001$) and 2013 ($P = 0.0005$), but we found no interactive effects with species (in 2012: $P = 0.0817$; in 2013: $P = 0.9914$) (Fig. 4).

3.2. Environmental drivers on NEE of the xeric shrubs

Daily NEE and daytime NEE of the succulent shrub (*N. sphaerocarpa*) were not affected by temperature ($P > 0.05$), whereas nighttime NEE of *N. sphaerocarpa* was positively correlated with both air temperature (T_a, $R^2 = 0.078$, $P = 0.011$) and soil temperature at 5 cm (T_5, $R^2 = 0.057$, $P = 0.034$), at 10 cm (T_{10}, $R^2 = 0.058$, $P = 0.032$), and at 20 cm (T_{20}, $R^2 = 0.117$, $P = 0.003$). For the non-succulent shrubs, T_{20}

Table 2
The linear relationships between net ecosystem CO_2 exchange (NEE) and temperature among three xeric shrubs in the Alxa Desert at daily (n = 168), daytime (n = 83), and nighttime (n = 85) scales. Correlation is significant at a 95% confidence level. *, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$.

	Air temperature (T_a)		Soil temperature at 5 cm (T_5)		Soil temperature at 10 cm (T_{10})		Soil temperature at 20 cm (T_{20})	
	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2
N. sphaerocarpa								
Daily NEE	−0.009	0.006	−0.001	0.000	0.008	0.003	0.011	0.005
Daytime NEE	0.018	0.017	0.015	0.014	0.007	0.002	−0.018	0.008
Nighttime NEE	0.016	0.078*	0.013	0.057*	0.015	0.058*	0.024	0.117**
P. mongolica								
Daily NEE	−0.0002	0.000	0.008	0.008	0.020	0.031*	0.025	0.036*
Daytime NEE	0.029	0.088*	0.027	0.100*	0.029	0.065*	0.010	0.005
Nighttime NEE	0.013	0.044	0.011	0.030	0.012	0.030	0.024	0.085*
K. ceratoides								
Daily NEE	−0.022	0.014	0.005	0.001	0.035	0.022	0.051	0.031*
Daytime NEE	0.050	0.056*	0.054	0.086*	0.061	0.062*	0.027	0.007
Nighttime NEE	0.014	0.034	0.011	0.020	0.013	0.024	0.028	0.080*

Table 3

The linear relationships between net ecosystem CO_2 exchange (NEE) and soil water content among three xeric shrubs in the Alxa Desert at daily, daytime, and nighttime scales (n = 15, in all scales). Correlation is significant at a 95% confidence level. *, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$.

	Soil water content at 0–10 cm (W_{10})		Soil water content at 10–20 cm (W_{20})		Soil water content at 20–30 cm (W_{30})		Soil water content at 30–50 cm (W_{50})	
	Slope	R^2	Slope	R^2	Slope	R^2	Slope	R^2
N. sphaerocarpa								
Daily NEE	−0.065	0.041	0.011	0.001	−0.069	0.027	−0.131	0.081
Daytime NEE	−0.268	0.158	−0.153	0.030	−0.291	0.111	−0.429	0.199
Nighttime NEE	0.144	0.676*	0.168	0.530*	0.156	0.464*	0.193	0.590*
P. mongolica								
Daily NEE	−0.045	0.078	−0.028	0.018	−0.127	0.376*	−0.135	0.352*
Daytime NEE	−0.296	0.459*	−0.328	0.325	−0.521	0.842***	−0.556	0.791**
Nightttime NEE	0.212	0.755**	0.271	0.717*	0.269	0.725**	0.298	0.736**
K. ceratoides								
Daily NEE	−0.206	0.256	−0.256	0.230	−0.399	0.570*	−0.366	0.397*
Daytime NEE	−0.630	0.402*	−0.814	0.389*	−1.091	0.714*	−1.022	0.517*
Nighttime NEE	0.239	0.695*	0.320	0.725**	0.314	0.723*	0.324	0.627*

positively influenced daily NEE (*P. mongolica*: $R^2 = 0.036$, $P = 0.021$; *K. ceratoides*: $R^2 = 0.031$, $P = 0.034$) and nighttime NEE (*P. mongolica*: $R^2 = 0.085$, $P = 0.012$; *K. ceratoides*: $R^2 = 0.080$, $P = 0.015$). T_{10} had a positive effect on the daily NEE of *P. mongolica* ($R^2 = 0.031$, $P = 0.027$). Daytime NEE was positively ($P < 0.05$) associated with T_a, T_5, and T_{10} (Table 2). Daily NEE and daytime NEE of *N. sphaerocarpa* were not correlated with soil water content at any depths ($P > 0.05$), whereas nighttime NEE of *N. sphaerocarpa* was positively associated with soil water content at 0–10 cm (W_{10}, $R^2 = 0.676$, $P = 0.001$), 10–20 cm (W_{20}, $R^2 = 0.530$, $P = 0.007$), 20–30 cm (W_{30}, $R^2 = 0.464$, $P = 0.015$), and 30–50 cm (W_{50}, $R^2 = 0.590$, $P = 0.004$). For the two non-succulent shrubs, daily NEE correlated significantly with soil water content at deep depths (i.e., W_{30} and W_{50}; $P < 0.05$ in both cases), but not at shallower depths (i.e. W_{10} and W_{20}; $P > 0.05$ in both cases). Daytime NEE was negatively correlated with soil water content at all depths, except W_{20} with *P. mongolica's* ($R^2 = 0.325$, $P = 0.053$). Nighttime NEE was positively correlated with soil water content at all depths ($P < 0.05$) (Table 3).

4. Discussion

4.1. Species-specific changes of xeric shrub NEE

Water has generally been recognized as an important force in directing CO_2 uptake of terrestrial ecosystems (Law et al., 2002; Wu et al., 2011), particularly in dryland regions (Ahlström et al., 2015; Poulter et al., 2014; Smith et al., 2000). The largest interannual variations in NEE (84% on average) were observed in the patches dominated by the non-succulent shrubs (*P. mongolica* and *K. ceratoides*), likely as a result of a large variability (162% higher in 2012 than in 2013) of total annual precipitation between 2012 (54.5 mm) and 2013 (33.7 mm). Interestingly, the variations in the daily NEE, daytime NEE, and nighttime NEE of the succulent shrub (*N. sphaerocarpa*) were not apparent between 2012 and 2013. This was likely because *N. sphaerocarpa* has succulent leaf water using and storing mechanisms (Chen et al., 2012; Li et al., 2007), which limits reductions in physiological performance under dry conditions (Sandquist, 2013).

Surprisingly, we did not find any differences in daily NEE at the diurnal scale among the species. This is likely because light may be the dominant driver of diurnal variability as an endogenous-generated and self-sustaining biological rhythm (McClung, 2006), allowing the plant physiological metabolisms (i.e. photosynthesis and respiration) to remain relatively ‘constant’ during the day/night cycle (Pittendrigh, 1954).

4.2. Environmental regulations of xeric shrub NEE

Differential responses of NEE to environmental drivers between succulent and non-succulent shrubs are most likely associated with their water storage mechanisms. Firstly, our results suggested that the daily NEE and daytime NEE of the patches of both *K. ceratoides* and *P. mongolica* (non-succulent) were affected by temperature and soil water content, whereas the *N. sphaerocarpa*'s (succulent) was not. In warm environments, increasing temperatures can reduce the net carbon gain of C3 plants (Sandquist, 2013; Yamori et al., 2014). Our findings are supported by eddy covariance studies of NEE in a desert community without succulent shrubs, which indicated that the NEE was negatively affected by temperature (Jia et al., 2014; Xie et al., 2015), whereas those from desert communities where succulent plants are dominant or sub-dominant suggested temperature has insignificant effect on NEE (Hastings et al., 2005; Jasoni et al., 2005; Wohlfahrt et al., 2008). Alternatively, we found that temperature was able to significantly predict the nighttime NEE of all shrub patches. This result highlights the similar effect of temperature on respiration in all of these xeric shrub species.

Our results showed that increases in soil water content promoted nighttime NEE of the shrub patches. Interestingly, these effects were 120%–150% greater for the non-succulent shrubs than the succulent shrub. Water is another important environmental driver influencing CO_2 uptake in dryland ecosystems (Ahlström et al., 2015; Arnone III and Obrist, 2003; Law et al., 2002; Poulter et al., 2014). However, in comparison to non-succulent plants, succulent plants can store more water in their tissues for the purpose of preventing water loss (Ellsworth et al., 2004; Munson et al., 2012; Owen and Griffiths, 2013) and have extremely high water-use efficiencies to defend against environmental stress (Borland et al., 2014; Sandquist, 2013). These advantages and mechanisms may serve to indirectly eliminate the responses of NEE of the succulent shrub to changes in soil water content.

5. Conclusions

Dynamics of NEE of major shrub patches in the Alxa Desert were similar by species at the diurnal scale, suggesting there are similar mechanisms at play. However, different responses were driven by plant functional type at the interannual scale, with a succulent shrub species (*N. sphaerocarpa*) showing less variability than the non-succulent shrub types (*P. mongolica* and *K. ceratoides*). This was likely due to the relatively high-water use strategies (i.e., increased water storage capacity) of the succulent shrub. We found evidence that the succulent shrubs had relatively low sensitivity to environmental factors, suggesting that these plant species might be presumably dominant in the succession of plant communities under warmer and drier climates. These results provide us with an avenue for including plant type-specific carbon uptake mechanisms in large-scale carbon cycle models, which will allow for better predictions of the response of these critical ecosystems to future global change.

Acknowledgments

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Appendix A. Supplementary data

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