Micro-topographic variation in soil respiration and its controlling factors vary with plant phenophases in a desert-shrub ecosystem

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Abstract

Soil respiration (R_s) and its biophysical controls were measured over a fixed sand dune in a desert-shrub ecosystem in northwest China in 2012 to explore the mechanisms controlling the spatial heterogeneity in R_s and to understand the plant effects on the spatial variation in R_s in different phenophases. The measurements were carried out on four slope orientations (i.e., windward, leeward, north- and south-face) and three height positions on each slope (i.e., lower, upper, and top) across the phenophases of the dominant shrub species (*Artemisia ordosica*). Coefficient of variation (i.e., standard deviation/mean) of R_s across the 11 microsites over our measurement period was 23.5%. Soil respiration was highest on the leeward slope, but lowest on the windward slope. Over the measurement period, plant-related factors, rather than micro-hydrometeorological factors, affected the micro-topographic variation in R_s. During the flower-bearing phase, root biomass affected R_s most, explaining 72% of the total variation. During the leaf coloration-defoliation phase, soil nitrogen content affected R_s the most, explaining 56% of the total variation. Our findings highlight that spatial pattern in R_s was dependent on plant distribution over a desert sand dune, and plant-related factors largely regulated topographic variation in R_s, and such regulations varied with plant phenology.

1 Introduction

Soil respiration (R_s) plays an important role in the global carbon (C) cycle (Bond-Lamberty and Thomson, 2010a). Even relatively small increases in R_s may have a profound impact on atmospheric CO_2 concentrations, exerting a positive feedback to global warming (Schlesinger and Andrews, 2000; Davidson and Janssens, 2006; Luo, 2007). However, estimating soil C release is usually difficult at large spatiotemporal scales, mainly due to the strong heterogeneity in R_s (Bond-Lamberty and Thomson, 2010b; Luo et al., 2012; Jia et al., 2013). Such heterogeneity depends strongly on the variability of substrate of respiration (e.g., soil organic matter and living biomass (Martin and Bolstad, 2009; Geng et al., 2012; Ngao et al., 2012)) and hydrometeorological factors (e.g., soil water content (SWC) and soil temperature (T_s); Marrin and Bolstad, 2009; Ngao et al., 2012).

Arid, semiarid and dry-subhumid ecosystems occupy 41% of the terrestrial surface (Safriel and Adeel, 2005). The C cycle in desert ecosystems cannot be ignored in the global C cycle (Austin, 2011; Poulter et al., 2014). R_s represents the second largest C flux between ecosystems and the atmosphere (Raich and Schlesinger, 1992; Raich et al., 2002), and exhibits high spatial variation in desert ecosystems (Mahall et al., 1992; Gold et al., 1995; Xie et al., 2001). In addition, active, semi-active aeolian, and fixed sand dunes are the primary features of desert landscapes. Since the greatest amount of living biomass occurs on fixed sand dunes (Roles et al., 2001), its R_s contributes significantly to C emissions to the atmosphere. Thus, for accurate regional C estimates, it is necessary to understand the mechanisms driving spatial pattern in R_s over fixed sand dunes.

Generally, topographic variation in R_s in arid and semi-arid areas can be explained by hydrometeorological factors alone, especially by SWC (Xu and Wan, 2008; and Liu et al., 2010). This is because T_s and SWC are reported to have a strong primary control on the spatiotemporal variation in R_s (Lloyd and Taylor, 1994; Davidson et al., 1998; Wang et al., 2014), as they both exhibit significant heterogeneity as a result of the influence of topography in governing the amount of solar radiation received and the re-distribution of surface and shallow subsurface water (Kang et al., 2003; Liu et al., 2010). Heterogeneity in micro-hydrometeorological factors also has an explicit role in defining the formation and patchy distribution of vegetation growing in an area (Richerson and Lum, 1980; Parker, 1991). Distribution of vegetation, in turn, constrains the spatial variation in R_s through its patchy supply of substrate to R_s. In desert ecosystems, such plant effects usually refer to a phenomenon called “fertility islands”. This phenomenon is observed by the enrichment of water, nutrient, and root biomass in vicinity of plant canopies (Hook et al., 1991, Schlesinger and Raikes, 1996), resulting from several plant-scale processes, including plant-facilitated entrapment of soil particles and organic matter propelled by wind or rain droplets, canopy shading, hydraulic lift, and accumulation and decomposition of litterfall (Schlesinger and Raikes, 1996; Stock et al., 1999; Thompson et al., 2005, Li et al., 2007). Consequently, plant controls on R_s could be nested within micro-hydrometeorological controls, leading to greater complexity in plant-soil interaction.

Moreover, both micro-hydrometeorological and plant control could vary with plant phenophases (Fu et al., 2002; Dungan et al., 2003; Kang et al., 2003; Yuste et al., 2004; Tang et al., 2005; Tamai, 2010; Asaeda and Rashid, 2014; Osono, 2014), as current photosynthate supply and decomposition and supplementation of litterfall changes over time. For example, root activity and rhizosphere processes could vary with plant phenophases (Fu et al., 2002), and potentially alter the relationship between R_s and T_s (Yuste et al., 2004; DeForest et al., 2006). Previous studies have focused on the influences of plant phenology on the temporal dynamics of R_s. However, understanding the temporal changes in effects of plants on the spatial variation in R_s is still an important gap in our knowledge concerning plant-soil interactions in desert environments.

We hypothesized that over a fixed sand dune: (1) topographic heterogeneity in R_s is controlled to a large measure by the distribution of substrate of respiration supplied by the annual casting of plant photosynthates and nitrogen compounds during leaf-fall; and (2) drivers of topographic variation in R_s vary with plant phenology. To test our hypothesis, R_s and associated micro-hydrometeorological and plant-related factors were measured over a fixed sand dune in a desert-shrub ecosystem in northwest China.

2 Materials and methods

2.1 Site description

The study was conducted on a fixed sand dune at Yanchi Research station of Beijing Forestry University, Ningxia, northwest China (107.20^o - 107.26^o E, 37.68^o - 37.73^o N, 1550 m a.s.l.). The site is located at the edge of the Mu Us desert in a transition zone between arid and semi-arid climatic conditions. Based on 51-years (1954 - 2004) of data from the meteorological station of Yanchi County, the mean annual temperature is 8.1 ^{o}C. The mean annual precipitation is 292 mm (with a range of 250 - 350 mm), of which 62% falls between July and September, and the mean annual total potential evaporation is 2024 mm (Wang et al., 2014). The sandy soil has a bulk density of 1.6 ± 0.02 g cm^{-3}. The water-filled pore space across all the microsites was 23.42 ± 0.92%. Soil organic matter and $CaCO_3$ content, and pH were 0.21 - 2.14 g kg^{-1}, 0.23 - 0.54 g kg^{-1}, and 7.76 - 9.08, respectively (Feng et al., 2013). The vegetation at our study site was regenerated since aerial seeding in 1998 and was dominated by semi-shrub species of is *Artemisia ordosica*, which averaged 50 cm tall with a canopy size of about 80 cm × 60 cm. The coverage percentage of plant in this area ranged from 30 - 60%.

2.2 Measurements of soil CO_2 efflux and micro-hydrometeorological factors

Soil CO_2 efflux (R_s, μmol CO_2 m^{-2} s^{-1}) was measured with 11 automated chambers from June to October 2012. The measurements were taken on different slope orientations (i.e., windward in the east, leeward in the west, and north- and south-facing slopes) and positions (i.e., lower, upper, and top positions) on a typical shrub-dominated sand dune. The sand dune was of typical size for the study area, with a (i) height of 2.9 m, (ii) 7.6 m long leeward slope, (iii) 15.6 m long windward slope, (iv) 13.3 m long north-facing slope, and (v) 13.4 m long south-facing slope. Soil respiration was measured *in situ* using an automated chamber system (model Li-8100A, equipped with Li-8150 multiplexer, LI-COR, Nebraska, USA). Measurements were made along two 26 m line transects that intersected at perpendicular angles at the centre of the sand dune (Fig. 1). The R_s system included the installation of 11 permanent opaque chambers set on PVC collars (model Li-104, LI-COR, Nebraska, USA). The collars, with a diameter of 20.3 cm and a height of 10 cm, were inserted into the soil at a 7 cm depth. The chambers were located at about 3 to 5 m apart along the line transects, each placement representing different sand-dune microsites: top (position 1); upper parts of both the windward (position 2) and leeward slopes (position 7); lower parts of both the windward (position 3) and leeward slopes (position 8); and the microsites from top to the bottom of both the south- (position 4, 5, 6) and north-facing slopes (position 9, 10, 11; Fig. 1).

Soil respiration measurement time for each chamber was 3 minutes and 15 seconds, including a 30 s pre-purge, a 45 s post-purge, and a 2 minute observation period. Any plant re-growth within the measurement collar was manually removed in a timely manner. Hourly soil temperature (T_s, ^{o}C) and volumetric soil water content (SWC, m^3 m^{-3}) were measured simultaneously at a 10 cm depth outside of each chamber using 8150-203 soil temperature and EC$_{H2O}$ soil moisture sensors (LI-COR, Nebraska, USA). For more details concerning measurement protocol for R_s, SWC, and T_s, see Wang et al. (2014).

2.3 Measurements of plant-related factors

Plant-related factors considered in this work were root biomass (kg m^{-3}), litterfall (kg m^{-2}), total soil nitrogen content (g kg^{-1}) within the first 25 cm of the soil, leaf area index (LAI, m^2 m^{-2}), and plant phenophases. Usually soil samples were collected near each R_s chamber on the 15th and 30th day of each month using a soil corer (25 cm in height and 5 cm in diameter). However, collection of soil samples was delayed for several days after rain events to avoid its effects on soil nitrogen content. Three soil replicates were taken near each collar (within 0.5 m), and mixed before they were air dried and sieved through 1, 0.5, 0.25 mm meshes. During sieving, roots and litterfall were first picked up manually, and scraps of litterfall remaining were separated from the sand by washing the sample with clean water. Dead and alive roots were sorted out by color. The black ones were dead roots and mixed with litterfall as the litterfall sample. The yellow ones were alive roots. Both alive roots and litterfall samples were oven dried at 70 ^{o}C to a constant weight. Then the soil samples were sieved through a 0.25 mm mesh for total soil nitrogen measurements. Total nitrogen in the soil was determined with a Kjeldahl Total Nitrogen Apparatus (FOSS 2200, Foss, Denmark).

LAI was measured near each chamber within one hour immediately after sunset using LI-COR 2000 (LI-COR, Nebraska, USA) with a 90^{o} view cap, twice or three times every month during the measurement period. At each measurement time, LAI was measured close to ground surface in eight directions, which were roughly uniformly distributed within a 0.5 m radius around the chamber, in order to well reflect the effect of vegetation around. Final output of LAI value was mean of the eight records of the eight directions. In addition, the phenological phases of *Artemisia ordosica* were observed and recorded over the growing season at weekly intervals. Three obvious phases identified were leaf expansion (phase I), flower-bearing (phase II), and leaf coloration-defoliation (phase III; Fig. 2).

2.4 Data analysis

Due to fewer measurements in Phase I, data analyses were mainly concentrated on Phase II and Phase III. Hourly R_s data were first screened and values beyond the range of -1 to 15 μmol CO_2 m^{-2} s^{-1} (mean ± 5 standard deviation) were removed from the dataset as spurious values (Wang et al., 2014). Instrument failure and quality control procedures resulted in the removal of about 3% of the data from 4 June to 22 October 2012. The days of rainfall were also excluded during our analyses. Daily mean values (total n = 92) of R_s, T_s and SWC were used in further analyses. We assumed these biweekly measurements of LAI (total n = 8), roots (total n = 7), litterfall (total n = 7) and soil nitrogen (total n = 7) represent or reflect the average variation over the defined time period, because those variables are slow responsive factors to environmental changes and remain relatively stable over two-week period. The point values in the regression for target variables represent the average characteristics over the defined time period. We calculated the daily coefficient of variation (CV, standard deviation/mean) in R_s across the 11 positions as a metric of spatial variability. CV for each of phenophases or whole measurement period was calculated as a mean of daily CV over the corresponding period.

Pearson correlation and regression analyses were used to examine the relationship between R_s and micro-hydrometeorological and plant-related factors. Class and Regression Tree analysis (CART) were used to explore the main factors controlling spatial variability in R_s (Breiman et al., 1984). We excluded measurements during rainfall events in both the correlation and CART analyses, due to the prevalence of CO_2 flux pulses during these events (Figure 5 in Wang et al., 2014). In CART analyses, we first set the split value to 1, and then used cost-complexity tree pruning based on a 10-fold cross-validation (Venables and Ripley, 2002). All statistical analyses were performed in Matlab (R2010b, Mathworks Inc., Natick MA, USA); the significance level was set at 0.05.

3 Results

3.1 Topographic heterogeneity in plant-related and micro-hydrometeorological factors, and in soil respiration

Plant-related factors (i.e., litterfall, root biomass, and soil nitrogen) except LAI, exhibited large spatial heterogeneity (Table 1, Fig. 3). The mean daily CVs of litterfall, root biomass, and soil nitrogen were 82.0, 64.7, and 49.1%, respectively (Table 1). In contrast, among the four slopes, the micro-hydrometeorological factors exhibited only minor spatial variation (Table 1, Fig. 3). The mean daily CVs of T_s and SWC were only 4.6 and 22.0%, respectively (Table 1). Among the four slopes, mean SWC changed very little (0.01 - 0.03 m^3 m^{-3}; Table 2). Soil temperature (T_s) differed among the four slopes ($p < 0.001$), with mean differences ranging from 0.5 to 2.4 ^{o}C (Table 2). Among the three height positions (lower, upper, and top positions), there were no consistent pattern in both plant-related and micro-hydrometeorological factors (Fig. 3).

Soil respiration on the four slopes exhibited obvious differences (Table 2). The lowest averaged R_s on the windward slope was 58% of the highest R_s on the leeward slope (Table 2). Mean daily CV for R_s across the 11 microsites was 23.5% over the entire measurement period (Table 1). Among the three height positions for all slopes, no consistent pattern existed in R_s (Fig. 3a).

3.2 Relationships between soil respiration, micro-hydrometeorological, and plant-related factors over the measurement period

Topographic heterogeneity in R_s was correlated positively with the plant-related factors, like root biomass (Table 3, Fig. 4a), litterfall (Table 3, Fig. 4b), and soil nitrogen over the measurement period (Table 3, Fig. 4c), but not with the micro-hydrometeorological factors (i.e., T_s and SWC, $p > 0.05$, Table 3). Aside from R_s, both root biomass and soil nitrogen were correlated positively with litterfall (Fig. 5a, b).

3.3 Relationship between micro-hydrometeorological factors, plant-related factors, and soil respiration for different phenophases

During phase II (Fig. 2), the spatial variation in R_s correlated with the spatial variation in root biomass, litterfall, and soil nitrogen (Table 3, Fig. 4d, e, f; Fig. 6d, f, g). Variation in root biomass, litterfall, and soil nitrogen explained the majority (> 61%) of the variation in R_s among the 11 microsites (Table 3, Fig 4). Regression slopes between R_s and root biomass, litterfall, and soil nitrogen were 0.94, 0.51 and 0.77, respectively (Table 3). Based on CART analysis, the root biomass was the most significant factor affecting the spatial variation in R_s during phase II (Fig. 7a).

During phase III (Fig. 2), spatial variation in R_s was strongly correlated to the spatial variation in root biomass and soil nitrogen content (Table 3, Fig. 4d, f; Fig. 6k, n). Variation in soil nitrogen content and root biomass explained 56 and 39% of the variation in R_s among the 11 microsites, respectively (Table 3, Fig. 4d, f). Regression slopes between R_s and root biomass and R_s and soil nitrogen content were 0.14 and 0.63 (Table 3). Based on CART analysis, soil nitrogen content affected the spatial variation in R_s the most during phase III (Fig. 7b).

4 Discussion

4.1 Spatial patterns in soil respiration with respect to plant patchiness

The observed pattern that R_s on the leeward slope was highest among the four slope orientations, was consistent with the findings of Chai et al. (2012), who found that R_s on leeward slopes was over two times greater than R_s on windward slopes of a sand dune. The greater R_s on leeward slopes may be explained by the presence of larger patches of vegetation, most likely supported by the better soil conditions induced by the “fertility island” effect, addressed earlier (Table 2). Associated with the “fertility island” effect is the enrichment of the soil near the plants by the annual casting of photosynthates and nitrogen compounds with annual litterfall. In contrast, on the windward slope the level of soil enrichment is limited as a result of smaller vegetation patches, leading to suppression of R_s. Higher supply of photosynthetic products and soil nitrogen in vicinity to the plants was reported in previous studies by Scott-Denton et al. (2003) and Tang et al. (2005).

However, we did not find consistent patterns in R_s between height positions. As a comparison, Chai et al., 2012 observed earlier that R_s was lower in the lower positions, whereas Xu and Wan (2008) and Liu et al. (2010) showed opposite result. The magnitude of R_s at a given slope position was consistent with those of plant-related factors (Table 3, Fig. 4), R_s being highest at positions closest to the plants regardless of height gradients along the slopes. It is therefore concluded that topographic position or height within the sand dune per se is a poor predictor of R_s.

4.2 Plant drivers of the topographic variation in soil respiration over the measurement period

Our present finding that plant-related factors drive the topographic variation in R_s over a sand dune (Table 3, Fig. 4) was consistent with those of Sponseller and Fisher (2008). They reported that spatial patterns in R_s in the Sonoran Desert were related to plant size and productivity, but unrelated to soil water. Desert ecosystems are generally limited with substrate supply due to their low living biomass and accumulated soil organic matter, but feature large spatial heterogeneity in respiration substrate due to the “fertility-island” effect (Gold et al., 1995; Xie et al., 2001). This can be supported by large CVs (49.1, 64.7 and 82.0%) in plant-related factors of our study. In contrast, CVs for the hydrometeorological factors were much smaller (4.6 and 22.0%). Positive relationship between plant-related factors (litterfall, soil nitrogen, and root biomass), together with their positive effects on R_s (Figs. 4, 6), emphasized that spatial variation in supply of respiration substrate regulated spatial variation in R_s. Current photosynthate is supplied for root and rhizosphere respiration (Högberg et al., 2001; Tang et al., 2005; Han et al., 2014). Litterfall is supplied for heterotrophic microbe respiration (Reichstein et al., 2002; Zhou et al., 2013). These processes are influenced by soil nitrogen content (Allison et al., 2008; Deng et al., 2010). These findings support our first hypothesis that topographic heterogeneity in R_s was controlled by the respiration substrate supply provided by plants.

In contrast, many studies in forests and grasslands report that topographic heterogeneity in R_s can be suitably explained by T_s and SWC (Kang et al., 2003; Liu et al., 2010). Spatial variation in T_s and

SWC is reported to contribute to the spatial variation in R_s in forest ecosystems. We suggested future studies on spatially scaling up soil respiration in desert ecosystems should consider the spatial variation in substrate supply more than temperature.

Our finding that plants controlled the topographic variation in R_s over a fixed sand dune, along with similar findings by other studies (Moyano et al., 2008; Kuzyakov and Gavrichkova, 2010; Han et al., 2014), challenge the legitimacy of empirical models of R_s at the sand-dune scale. As an alternative, we suggest that photosynthesis-related parameters (or variables, e.g. root biomass and litterfall) ought to be incorporated into these models for an improved characterization of soil-plant relationships in desert ecosystems.

4.3 Drivers of topographic heterogeneity in soil respiration as a function of plant phenology

In our study, topographic heterogeneity in R_s at the flower-bearing phase (phase II) was significantly related to root biomass, litterfall, and soil nitrogen content. But with consideration of interactions between these plant-related factors (Figure 6), only root biomass was identified as the most important driving factor. In contrast, topographic heterogeneity in R_s at the leaf coloration and defoliation phase (phase III) was significantly related to root biomass and soil nitrogen content, but only soil nitrogen content was identified as important. Our results support our second hypothesis that drivers of topographic variation in R_s varies with plant phenophases.

From phase II to III, photosynthetic pigments and leaf photosynthesis declined, and induced large decreases in current photosynthate supply for roots and rhizosphere microorganisms (Hanson et al., 2000; Fu et al., 2002; Sey et al., 2010). Decomposition of litterfall results in a high percentage of recalcitrant substrates during phase II, but addition of fresh litterfall during phase III increases the percentage of liable substrates (Lebret et al., 2001; Regina, 2001; Ochieng and Erftemeijer, 2002).

Thus, changes in substrate supply between the two phenophases could result in seasonal changes in the relative contribution of autotrophic and heterotrophic respiration to total R_s. Root respiration contributes largely to total R_s during the growing season, but heterotrophic respiration contributes largely during the senescence season (Fu et al., 2002; Sey et al., 2010; Mauritz and Lipson, 2013). Specifically, in our study, autotrophic respiration may contribute largely to the total R_s during the phase II, but heterotrophic respiration may contribute largely during the phase III. We could not test this inference directly due to lack of independent measurements of different R_s components. However, some of our results can indirectly confirm this inference.

In our study, R_s was sensitive to root biomass during the phase II, but less sensitive during the phase III, indicating a decrease in relative contribution of root respiration to R_s during the phase III. R_s was related to litterfall during the phase II, unlike during the phase III, indicating the switched substrate pool and disproportionate addition of fresh litterfall. However, the controlling factors of autotrophic and heterotrophic respiration can be quite different. Autotrophic respiration is shown in others studies be largely controlled by root biomass and soil nitrogen (Tu et al., 2013; Zhou et al., 2014), and heterotrophic respiration by the amount of litterfall and soil nitrogen (Yan et al., 2010; Sayer et al., 2011). Thus, the key factor controlling the variation in R_s can be different for the different plant phenophases.

There has been a clear lack of understanding on the effects of plant phenology on the driving forces of topographic heterogeneity in R_s (Janssens et al., 2004; Bahn et al., 2008; Talmon et al., 2011). In this sense, our work provides new knowledge of driving mechanisms of topographic heterogeneity in R_s as affected by plant phenology. Based on our work, we suggest that the influences of plant phenology on both current photosynthate and litterfall supply should not be neglected, and partitioning R_s is necessary for future studies on the spatial heterogeneity in R_s.

5 Conclusions

Soil respiration was the highest on the leeward slope, but the lowest on the windward slope. Topographic heterogeneity in R_s was related to the variation in supply of both recent photosynthetic products and litterfall, indicating that plants largely control the topographic heterogeneity in R_s over a sand dune. Due to the "fertility island" effect, spatial patterns of R_s on different slopes were related to the distance from plant patches, regardless of micro-topographic relief. Drivers of topographic heterogeneity in R_s varied with plant phenophases. Our findings highlight the importance of plants in controlling the spatial variation in R_s in desert ecosystems. We suggest that future studies on the spatial variation in R_s should consider both the spatial and the temporal effects of vegetation, especially in desert environments.

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Table 1. Average values (standard error in brackets) and CV (%) for micro-hydrometeorological factors and plant-related factors over the three plant phenophases and measurement period. The time scale for the means was showing in Fig. 2. R_s: soil respiration (μmol CO_2 m^{-2} s^{-1}); T_s: soil temperature at 10 cm depth (^oC); SWC: volumetric soil water content (m^3 m^{-3}); Litter: litterfall (kg m^{-2}); Root: root biomass (kg m^{-3}); LAI: leaf area index (m^2 m^{-2}); N: soil nitrogen content at 0 - 25 cm depth (g kg^{-1}); Phase I: leaf expansion; Phase II: flower-bearing; Phase III: coloration-defoliation..

Variale	Phase II		Phase III		Measurement period	
	mean (SE)	CV%	mean (SE)	CV%	mean (SE)	CV%
R_s	1.49 (0.11)	25.2	0.900 (0.06)	21.3	1.21 (0.09)	23.5
T_s	23.8 (0.24)	3.40	14.9 (0.33)	7.40	19.7 (0.27)	4.60
SWC	0.0897 (0.01)	20.8	0.0971 (0.01)	24.0	0.0931 (0.01)	22.0
Litter	0.737 (0.17)	78.5	0.262 (0.05)	67.7	0.629 (0.16)	82.0
Root	0.593 (0.15)	84.2	0.904 (0.25)	92.2	0.753 (0.14)	64.7
LAI	1.76 (0.12)	22.7	1.72 (0.12)	23.9	1.76 (0.12)	21.8
N	0.181 (0.02)	43.5	0.135 (0.02)	53.3	0.138 (0.02)	49.1

Table 2. Mean values (standard error in brackets) of micro-hydrometeorological and plant-related factors on different slope orientations over the measurement period. R_s: soil respiration (μmol CO_2 m^{-2} s^{-1}); T_s: soil temperature (^oC); SWC: volumetric soil water content (m^3 m^{-3}); Litter: litterfall (kg m^{-2}); Root: root biomass (kg m^{-3}); LAI: leaf area index (m^2 m^{-2}); N: soil nitrogen content at 0 - 25 cm soil depths (g kg^{-1}).

	Windward	Leeward	North-facing	South-facing
R_s	0.964 (0.05)	1.65 (0.03)	1.13 (0.27)	1.27 (0.19)
T_s	19.9 (0.60)	18.4 (0.08)	20.8 (0.23)	19.4 (0.09)
SWC	0.0964 (0.02)	0.107 (0.04)	0.0819 (0.02)	0.0918 (0.02)
Litter	0.487 (0.29)	1.53 (0.37)	0.231 (0.15)	0.671 (0.28)
Root	0.309 (0.13)	1.405 (0.02)	0.460 (0.03)	0.322 (0.17)
LAI	1.80 (0.48)	2.22 (0.43)	1.70 (0.05)	1.47 (0.25)
N	0.109 (0.03)	0.254 (0.04)	0.0848 (0.02)	0.141 (0.03)

Table 3. Regression equations between R_s (y) and different micro-hydrometeorological and plant-related factors (x) for the measurement period and flower-bearing (phase II) and leaf coloration-defoliation phase (phase III). T_s: soil temperature (^oC); SWC: volumetric soil water content ($m^3\ m^{-3}$); Litter: litterfall ($kg\ m^{-2}$); Root: root biomass ($kg\ m^{-3}$); LAI: leaf area index ($m^2\ m^{-2}$); N: soil nitrogen content at 0 - 25 cm soil depths ($g\ kg^{-1}$).

Phase	Factors	Equation	R^2	p
Whole period	Root biomass	$y = 0.51\ x + 0.93$	0.61	0.004
	Litterfall	$y = 0.43\ x + 0.95$	0.59	0.005
	T_s	$y = -0.18\ x + 4.84$	0.34	0.061
	SWC	$y = 0.89\ x + 1.13$	< 0.01	0.852
	LAI	$y = 0.28\ x + 0.73$	0.14	0.256
	N	$y = 3.48\ x + 0.74$	0.68	0.002
Phase II	Root biomass	$y = 0.64\ x + 1.11$	0.72	0.001
	Litterfall	$y = 0.51\ x + 1.11$	0.61	0.004
	T_s	$y = -0.23\ x + 7.00$	0.25	0.118
	SWC	$y = -0.27\ x + 1.51$	< 0.01	0.969
	LAI	$y = 0.48\ x + 0.64$	0.26	0.108
	N	$y = 5.04\ x + 0.77$	0.68	0.001
Phase III	Root biomass	$y = 0.14\ x + 0.77$	0.37	0.048
	Litterfall	$y = 0.55\ x + 0.76$	0.26	0.112
	T_s	$y = -0.09\ x + 2.24$	0.26	0.105
	SWC	$y = 0.39\ x + 0.86$	< 0.01	0.887
	LAI	$y = 0.11\ x + 0.71$	0.05	0.492
	N	$y = 1.99\ x + 0.63$	0.56	0.008

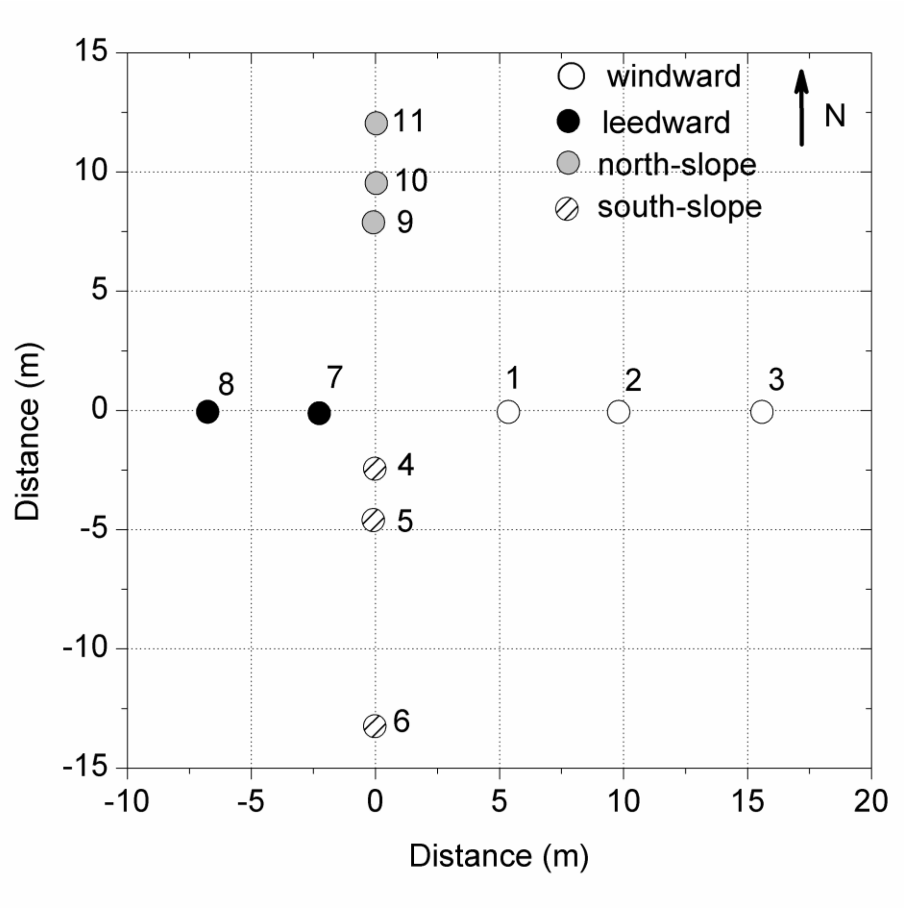

Figure 1. Schematic of measurement positions (11) distributed on four slopes (windward, leeward, north- and south-facing slope) over a fixed sand dune as well as plot positions and labels.

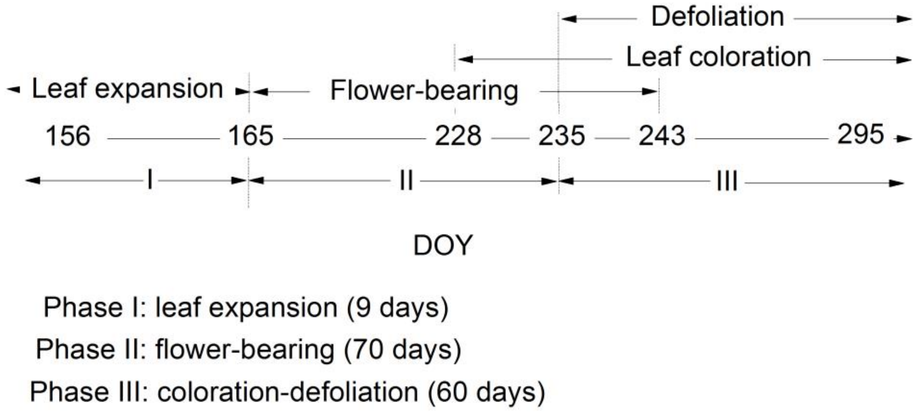

Figure 2. Phenophases of *Artemisia ordosica* over the measurement period. Three phases considered, included leaf expansion (phase I), flower-bearing (phase II), and leaf coloration-defoliation (phase III) phases.

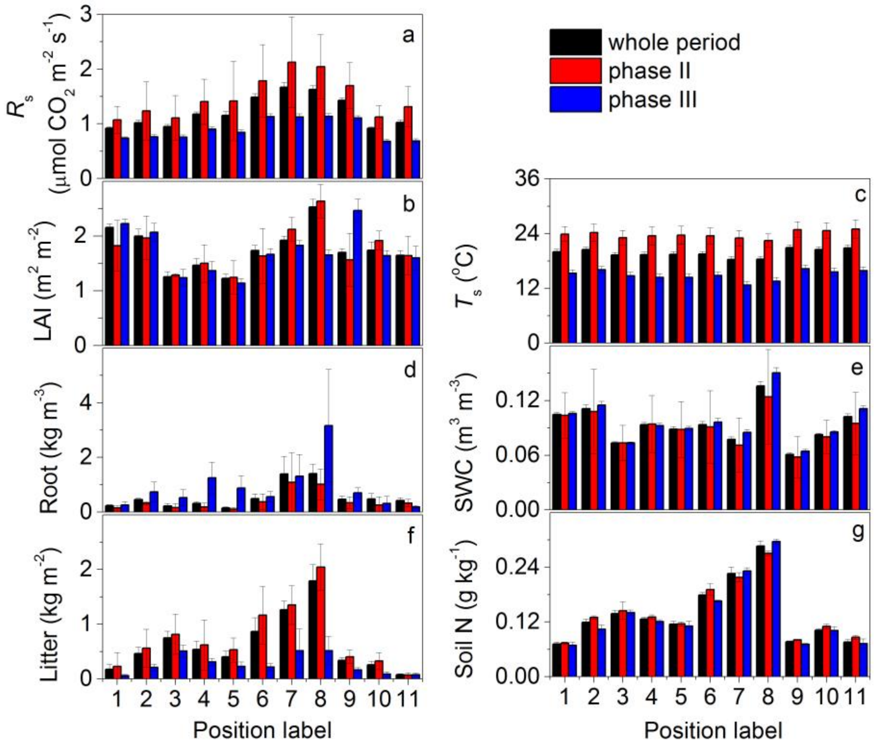

Figure 3. Mean values of soil respiration (R_s), micro-hydrometeorological (T_s and SWC) and plant-related factors (litter, root, soil N and LAI) at 11 positions over the measurement period (whole period), flower-bearing phase (phase II), and leaf coloration-defoliation phase (phase III) from June to October 2012. Time scales of each phenophases were shown in Figure 2. R_s: soil respiration (μmol CO$_2$ m^{-2} s^{-1}); T_s: soil temperature (^{o}C); SWC: volumetric soil water content (m^3 m^{-3}); Litter: litterfall (kg m^{-2}); Root: root biomass (kg m^{-3}); LAI: leaf area index (m^2 m^{-2}); Soil N: soil nitrogen content at 0 - 25 cm soil depths (g kg^{-1}). Error bar represents standard error. Black color represents for whole period.

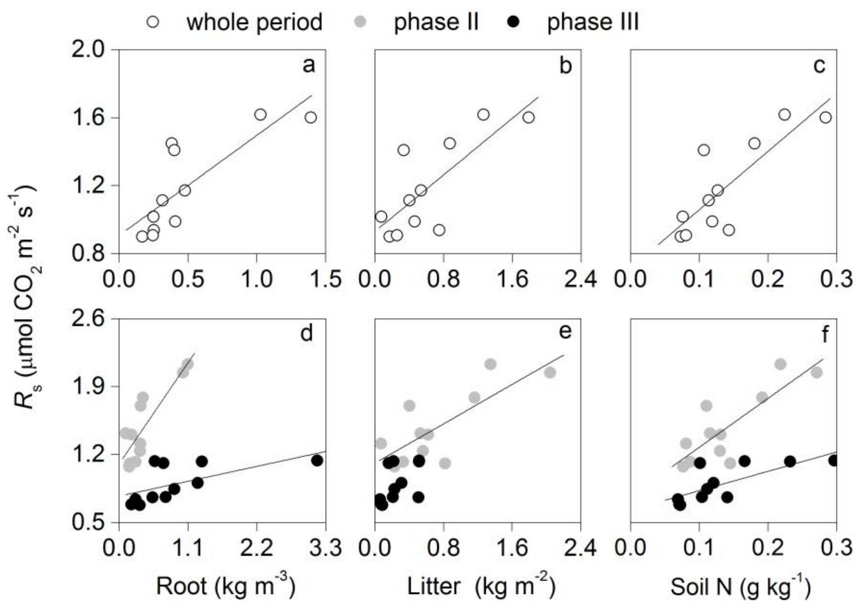

Figure 4. Relationships between soil respiration (R_s) and root biomass, and litterfall and soil nitrogen over the measurement period (open circles) and during flower-bearing (phase II; gray circles) and leaf coloration-defoliation (phase III; black circles) phase. Lines are linear regressions with $p < 0.05$. Equations, R^2, and p-values are given in Table 3.

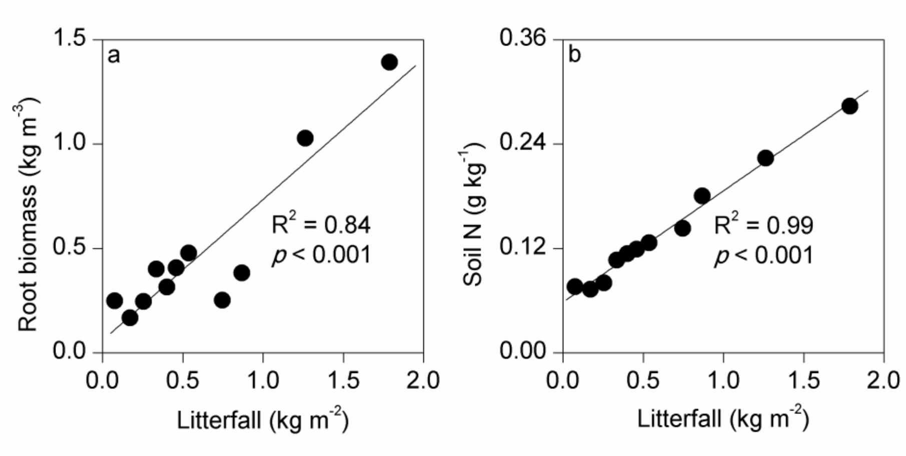

Figure 5. Relationships between litterfall and root (a), and soil nitrogen content (soil N) (b) over the measurement period.

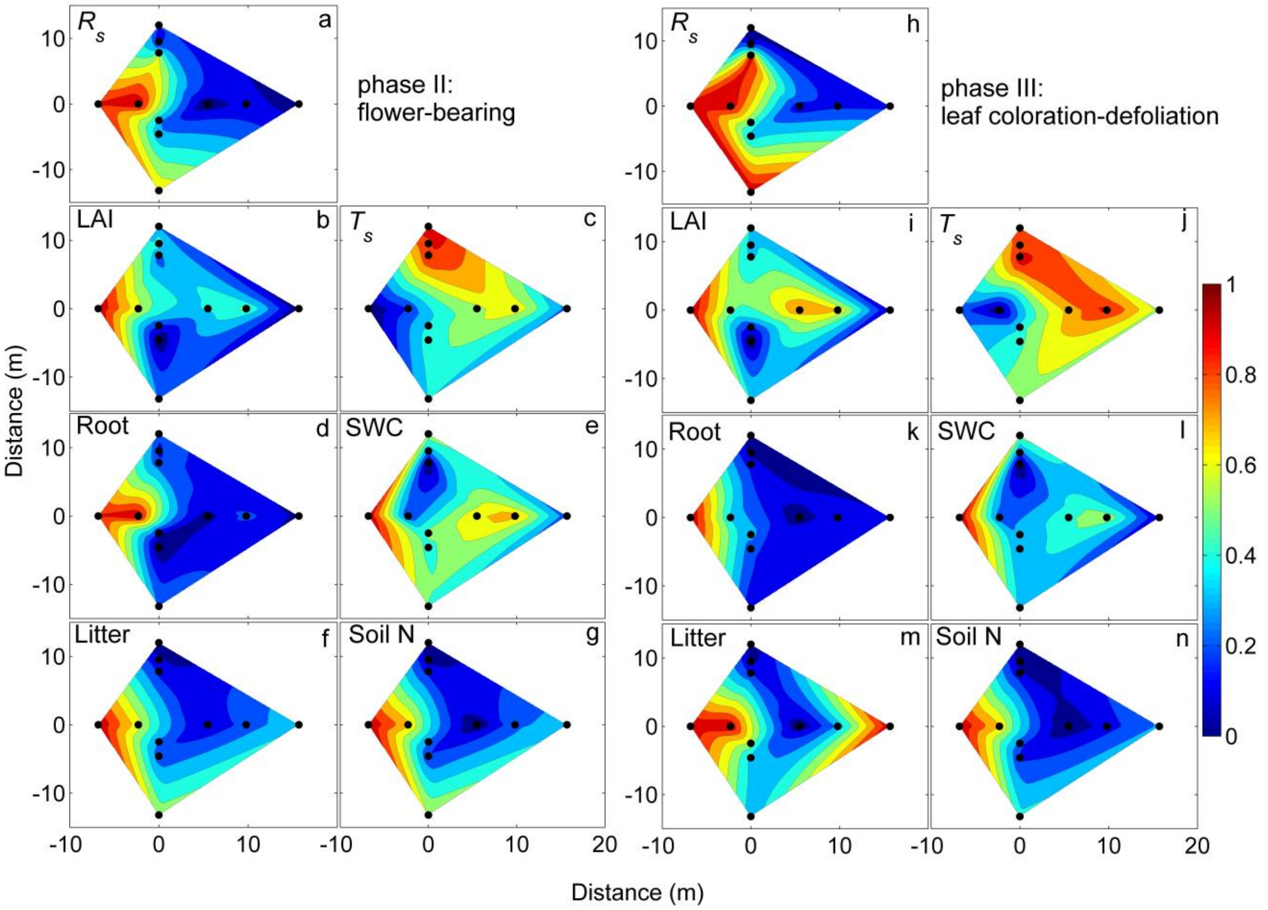

Figure 5. Spatial patterns of soil respiration (R_s), micro-hydro meteorological (T_s and SWC) and plant-related factors (Litter, Root, Soil N and LAI) over the sand dune in flower-bearing phase (phase II) and coloration-defoliation phase (phase III). Data values for all variables were normalized into the range of 0 - 1 using feature scaling method ($X_{\mathrm{normalized}} = (X - X_{\mathrm{min}}) / (X_{\mathrm{max}} - X_{\mathrm{min}})$). Black dots represent the measurement positions as showed in Fig. 1.

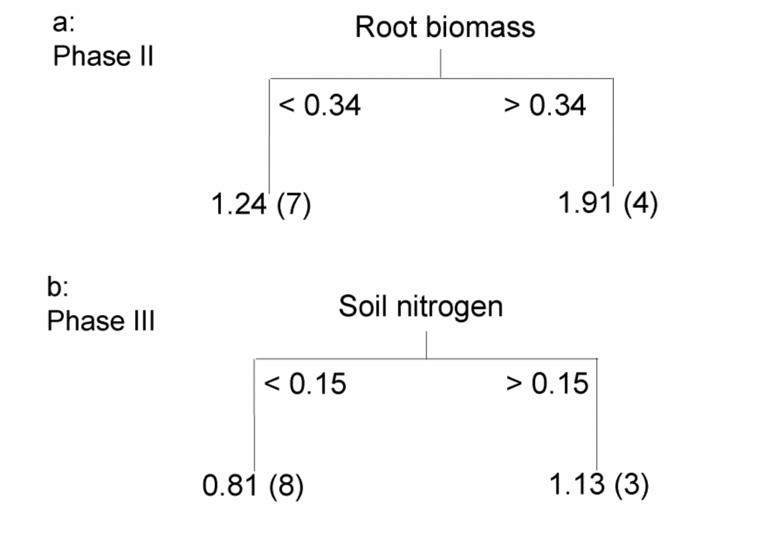

Figure 7. Results of CART analysis with key factors explaining spatial variability in soil respiration at the flower-bearing (a) and coloration-defoliation phases (b). Predictor variables are depicted at the top of each branch. Their critical values are shown at the side of each branch and the mean soil CO_2 efflux (including number of observations in parentheses) is reported below the terminal nodes.