

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

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16

17 **Abstract**

18 Soil respiration ( $R_s$ ) and its biophysical controls were measured over a fixed sand dune in a desert-  
19 shrub ecosystem in northwest China in 2012 to explore the mechanisms controlling the spatial  
20 heterogeneity in  $R_s$  and to understand the plant effects on the spatial variation in  $R_s$  in different

1 phenophases. The measurements were carried out on four slope orientations (i.e., windward,  
2 leeward, north- and south-face) and three height positions on each slope (i.e., lower, upper, and top)  
3 across the phenophases of the dominant shrub species (*Artemisia ordosica*). Coefficient of variation  
4 (i.e., standard deviation/mean) of  $R_s$  across the 11 microsites over our measurement period was  
5 23.5%. Soil respiration was highest on the leeward slope, but lowest on the windward slope. Over  
6 the measurement period, plant-related factors, rather than micro-hydrometeorological factors,  
7 affected the micro-topographic variation in  $R_s$ . During the flower-bearing phase, root biomass  
8 affected  $R_s$  most, explaining 72% of the total variation. During the leaf coloration-defoliation phase,  
9 soil nitrogen content affected  $R_s$  the most, explaining 56% of the total variation. Our findings  
10 highlight that spatial pattern in  $R_s$  was dependent on plant distribution over a desert sand dune, and  
11 plant-related factors largely regulated topographic variation in  $R_s$ , and such regulations varied with  
12 plant phenology.

13

## 14 **1 Introduction**

15 Soil respiration ( $R_s$ ) plays an important role in the global carbon (C) cycle (Bond-Lamberty and  
16 Thomson, 2010a). Even relatively small increases in  $R_s$  may have a profound impact on  
17 atmospheric CO<sub>2</sub> concentrations, exerting a positive feedback to global warming (Schlesinger and  
18 Andrews, 2000; Davidson and Janssens, 2006; Luo, 2007). However, estimating soil C release is  
19 usually difficult at large spatiotemporal scales, mainly due to the strong heterogeneity in  $R_s$  (Bond-  
20 Lamberty and Thomson, 2010b; Luo et al., 2012; Jia et al., 2013). Such heterogeneity depends  
21 strongly on the variability of substrate of respiration (e.g., soil organic matter and living biomass  
22 (Martin and Bolstad, 2009; Geng et al., 2012; Ngao et al., 2012)) and hydrometeorological factors

1 (e.g., soil water content (SWC) and soil temperature ( $T_s$ ); Marrin and Bolstad, 2009; Ngao et al.,  
2 2012).

3 Arid, semiarid and dry-subhumid ecosystems occupy 41% of the terrestrial surface (Safriel and  
4 Adeel, 2005). The C cycle in desert ecosystems cannot be ignored in the global C cycle (Austin,  
5 2011; Poulter et al., 2014).  $R_s$  represents the second largest C flux between ecosystems and the  
6 atmosphere (Raich and Schlesinger, 1992; Raich et al., 2002), and exhibits high spatial variation in  
7 desert ecosystems (Mahall et al., 1992; Gold et al., 1995; Xie et al., 2001). In addition, active, semi-  
8 active aeolian, and fixed sand dunes are the primary features of desert landscapes. Since the greatest  
9 amount of living biomass occurs on fixed sand dunes (Roles et al., 2001), its  $R_s$  contributes  
10 significantly to C emissions to the atmosphere. Thus, for accurate regional C estimates, it is  
11 necessary to understand the mechanisms driving spatial pattern in  $R_s$  over fixed sand dunes.

12 Generally, topographic variation in  $R_s$  in arid and semi-arid areas can be explained by  
13 hydrometeorological factors alone, especially by SWC (Xu and Wan, 2008; and Liu et al., 2010).  
14 This is because  $T_s$  and SWC are reported to have a strong primary control on the spatiotemporal  
15 variation in  $R_s$  (Lloyd and Taylor, 1994; Davidson et al., 1998; Wang et al., 2014), as they both  
16 exhibit significant heterogeneity as a result of the influence of topography in governing the amount  
17 of solar radiation received and the re-distribution of surface and shallow subsurface water (Kang et  
18 al., 2003; Liu et al., 2010). Heterogeneity in micro-hydrometeorological factors also has an explicit  
19 role in defining the formation and patchy distribution of vegetation growing in an area (Richerson  
20 and Lum, 1980; Parker, 1991). Distribution of vegetation, in turn, constrains the spatial variation in  
21  $R_s$  through its patchy supply of substrate to  $R_s$ . In desert ecosystems, such plant effects usually refer  
22 to a phenomenon called “fertility islands”. This phenomenon is observed by the enrichment of  
23 water, nutrient, and root biomass in vicinity of plant canopies (Hook et al., 1991, Schlesinger and  
24 Raikes, 1996), resulting from several plant-scale processes, including plant-facilitated entrapment

1 of soil particles and organic matter propelled by wind or rain droplets, canopy shading, hydraulic  
2 lift, and accumulation and decomposition of litterfall (Schlesinger and Raikes, 1996; Stock et al.,  
3 1999; Thompson et al., 2005, Li et al., 2007). Consequently, plant controls on  $R_s$  could be nested  
4 within micro-hydrometeorological controls, leading to greater complexity in plant-soil interaction.  
5 Moreover, both micro-hydrometeorological and plant control could vary with plant phenophases  
6 (Fu et al., 2002; Dungan et al., 2003; Kang et al., 2003; Yuste et al., 2004; Tang et al., 2005; Tamai,  
7 2010; Asaeda and Rashid, 2014; Osono, 2014), as current photosynthate supply and decomposition  
8 and supplementation of litterfall changes over time. For example, root activity and rhizosphere  
9 processes could vary with plant phenophases (Fu et al., 2002), and potentially alter the relationship  
10 between  $R_s$  and  $T_s$  (Yuste et al., 2004; DeForest et al., 2006). Previous studies have focused on the  
11 influences of plant phenology on the temporal dynamics of  $R_s$ . However, understanding the  
12 temporal changes in effects of plants on the spatial variation in  $R_s$  is still an important gap in our  
13 knowledge concerning plant-soil interactions in desert environments.

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

20

## 21 **2 Materials and methods**

### 22 **2.1 Site description**

1 The study was conducted on a fixed sand dune at Yanchi Research station of Beijing Forestry  
2 University, Ningxia, northwest China (107.20° - 107.26° E, 37.68° - 37.73° N, 1550 m a.s.l.). The  
3 site is located at the edge of the Mu Us desert in a transition zone between arid and semi-arid  
4 climatic conditions. Based on 51-years (1954 - 2004) of data from the meteorological station of  
5 Yanchi County, the mean annual temperature is 8.1 °C. The mean annual precipitation is 292 mm  
6 (with a range of 250 - 350 mm), of which 62% falls between July and September, and the mean  
7 annual total potential evaporation is 2024 mm (Wang et al., 2014). The sandy soil has a bulk density  
8 of  $1.6 \pm 0.02 \text{ g cm}^{-3}$ . The water-filled pore space across all the microsites was  $23.42 \pm 0.92\%$ . Soil  
9 organic matter and  $\text{CaCO}_3$  content, and pH were  $0.21 - 2.14 \text{ g kg}^{-1}$ ,  $0.23 - 0.54 \text{ g kg}^{-1}$ , and 7.76 -  
10 9.08, respectively (Feng et al., 2013). The vegetation at our study site was regenerated since aerial  
11 seeding in 1998 and was dominated by semi-shrub species of *Artemisia ordosica*, which averaged  
12 50 cm tall with a canopy size of about 80 cm  $\times$  60 cm. The coverage percentage of plant in this area  
13 ranged from 30 - 60%.

## 14 **2.2 Measurements of soil CO<sub>2</sub> efflux and micro-hydrometeorological factors**

15 Soil CO<sub>2</sub> efflux ( $R_s$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) was measured with 11 automated chambers from June to  
16 October 2012. The measurements were taken on different slope orientations (i.e., windward in the  
17 east, leeward in the west, and north- and south-facing slopes) and positions (i.e., lower, upper, and  
18 top positions) on a typical shrub-dominated sand dune. The sand dune was of typical size for the  
19 study area, with a (i) height of 2.9 m, (ii) 7.6 m long leeward slope, (iii) 15.6 m long windward  
20 slope, (iv) 13.3 m long north-facing slope, and (v) 13.4 m long south-facing slope. Soil respiration  
21 was measured *in situ* using an automated chamber system (model Li-8100A, equipped with Li-8150  
22 multiplexer, LI-COR, Nebraska, USA). Measurements were made along two 26 m line transects  
23 that intersected at perpendicular angles at the centre of the sand dune (Fig. 1). The  $R_s$  system

1 included the installation of 11 permanent opaque chambers set on PVC collars (model Li-104, LI-  
2 COR, Nebraska, USA). The collars, with a diameter of 20.3 cm and a height of 10 cm, were  
3 inserted into the soil at a 7 cm depth. The chambers were located at about 3 to 5 m apart along the  
4 line transects, each placement representing different sand-dune microsites: top (position 1); upper  
5 parts of both the windward (position 2) and leeward slopes (position 7); lower parts of both the  
6 windward (position 3) and leeward slopes (position 8); and the microsites from top to the bottom of  
7 both the south- (position 4, 5, 6) and north-facing slopes (position 9, 10, 11; Fig. 1).

8 Soil respiration measurement time for each chamber was 3 minutes and 15 seconds, including a 30 s  
9 pre-purge, a 45 s post-purge, and a 2 minute observation period. Any plant re-growth within the  
10 measurement collar was manually removed in a timely manner. Hourly soil temperature ( $T_s$ , °C) and  
11 volumetric soil water content (SWC,  $\text{m}^3 \text{m}^{-3}$ ) were measured simultaneously at a 10 cm depth  
12 outside of each chamber using 8150-203 soil temperature and  $\text{EC}_{\text{H}_2\text{O}}$  soil moisture sensors (LI-COR,  
13 Nebraska, USA). For more details concerning measurement protocol for  $R_s$ , SWC, and  $T_s$ , see Wang  
14 et al. (2014).

### 15 **2.3 Measurements of plant-related factors**

16 Plant-related factors considered in this work were root biomass ( $\text{kg m}^{-3}$ ), litterfall ( $\text{kg m}^{-2}$ ), total soil  
17 nitrogen content ( $\text{g kg}^{-1}$ ) within the first 25 cm of the soil, leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ), and plant  
18 phenophases. Usually soil samples were collected near each  $R_s$  chamber on the 15th and 30th day of  
19 each month using a soil corer (25 cm in height and 5 cm in diameter). However, collection of soil  
20 samples was delayed for several days after rain events to avoid its effects on soil nitrogen content.  
21 Three soil replicates were taken near each collar (within 0.5 m), and mixed before they were air  
22 dried and sieved through 1, 0.5, 0.25 mm meshes. During sieving, roots and litterfall were first  
23 picked up manually, and scraps of litterfall remaining were separated from the sand by washing the

1 sample with clean water. Dead and alive roots were sorted out by color. The black ones were dead  
2 roots and mixed with litterfall as the litterfall sample. The yellow ones were alive roots. Both alive  
3 roots and litterfall samples were oven dried at 70 °C to a constant weight. Then the soil samples  
4 were sieved through a 0.25 mm mesh for total soil nitrogen measurements. Total nitrogen in the soil  
5 was determined with a Kjeldahl Total Nitrogen Apparatus (FOSS 2200, Foss, Denmark).

6 LAI was measured near each chamber within one hour immediately after sunset using LI-COR  
7 2000 (LI-COR, Nebraska, USA) with a 90° view cap, twice or three times every month during the  
8 measurement period. At each measurement time, LAI was measured close to ground surface in  
9 eight directions, which were roughly uniformly distributed within a 0.5 m radius around the  
10 chamber, in order to well reflect the effect of vegetation around. Final output of LAI value was  
11 mean of the eight records of the eight directions. In addition, the phenological phases of *Artemisia*  
12 *ordosica* were observed and recorded over the growing season at weekly intervals. Three obvious  
13 phases identified were leaf expansion (phase I), flower-bearing (phase II), and leaf coloration-  
14 defoliation (phase III; Fig. 2).

## 15 **2.4 Data analysis**

16 Due to fewer measurements in Phase I, data analyses were mainly concentrated on Phase II and  
17 Phase III. Hourly  $R_s$  data were first screened and values beyond the range of -1 to 15  $\mu\text{mol CO}_2 \text{ m}^{-2}$   
18  $\text{s}^{-1}$  (mean  $\pm$  5 standard deviation) were removed from the dataset as spurious values (Wang et al.,  
19 2014). Instrument failure and quality control procedures resulted in the removal of about 3% of the  
20 data from 4 June to 22 October 2012. The days of rainfall were also excluded during our analyses.  
21 Daily mean values (total  $n = 92$ ) of  $R_s$ ,  $T_s$  and SWC were used in further analyses. We assumed  
22 these biweekly measurements of LAI (total  $n = 8$ ), roots (total  $n = 7$ ), litterfall (total  $n = 7$ ) and soil  
23 nitrogen (total  $n = 7$ ) represent or reflect the average variation over the defined time period, because

1 those variables are slow responsive factors to environmental changes and remain relatively stable  
2 over two-week period. The point values in the regression for target variables represent the average  
3 characteristics over the defined time period. We calculated the daily coefficient of variation (CV,  
4 standard deviation/mean) in  $R_s$  across the 11 positions as a metric of spatial variability. CV for each  
5 of phenophases or whole measurement period was calculated as a mean of daily CV over the  
6 corresponding period.

7 Pearson correlation and regression analyses were used to examine the relationship between  $R_s$  and  
8 micro-hydrometeorological and plant-related factors. Class and Regression Tree analysis (CART)  
9 were used to explore the main factors controlling spatial variability in  $R_s$  (Breiman et al., 1984). We  
10 excluded measurements during rainfall events in both the correlation and CART analyses, due to  
11 the prevalence of CO<sub>2</sub> flux pulses during these events (Figure 5 in Wang et al., 2014). In CART  
12 analyses, we first set the split value to 1, and then used cost-complexity tree pruning based on a 10-  
13 fold cross-validation (Venables and Ripley, 2002). All statistical analyses were performed in Matlab  
14 (R2010b, Mathworks Inc., Natick MA, USA); the significance level was set at 0.05.

### 15 **3 Results**

#### 16 **3.1 Topographic heterogeneity in plant-related and micro-hydrometeorological** 17 **factors, and in soil respiration**

18 Plant-related factors (i.e., litterfall, root biomass, and soil nitrogen) except LAI, exhibited large  
19 spatial heterogeneity (Table 1, Fig. 3). The mean daily CVs of litterfall, root biomass, and soil  
20 nitrogen were 82.0, 64.7, and 49.1%, respectively (Table 1). In contrast, among the four slopes, the  
21 micro-hydrometeorological factors exhibited only minor spatial variation (Table 1, Fig. 3). The  
22 mean daily CVs of  $T_s$  and SWC were only 4.6 and 22.0%, respectively (Table 1). Among the four  
23 slopes, mean SWC changed very little (0.01 - 0.03 m<sup>3</sup> m<sup>-3</sup>; Table 2). Soil temperature ( $T_s$ ) differed



1 among the four slopes ( $p < 0.001$ ), with mean differences ranging from 0.5 to 2.4 °C (Table 2).  
2 Among the three height positions (lower, upper, and top positions), there were no consistent pattern  
3 in both plant-related and micro-hydrometeorological factors (Fig. 3).

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

### 8 **3.2 Relationships between soil respiration, micro-hydrometeorological, and plant-** 9 **related factors over the measurement period**

10 Topographic heterogeneity in  $R_s$  was correlated positively with the plant-related factors, like root  
11 biomass (Table 3, Fig. 4a), litterfall (Table 3, Fig. 4b), and soil nitrogen over the measurement  
12 period (Table 3, Fig. 4c), but not with the micro-hydrometeorological factors (i.e.,  $T_s$  and SWC,  $p >$   
13 0.05, Table 3). Aside from  $R_s$ , both root biomass and soil nitrogen were correlated positively with  
14 litterfall (Fig. 5a, b).

### 15 **3.3 Relationship between micro-hydrometeorological factors, plant-related factors,** 16 **and soil respiration for different phenophases**

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

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

7

## 8 **4 Discussion**

### 9 **4.1 Spatial patterns in soil respiration with respect to plant patchiness**

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

20 However, we did not find consistent patterns in  $R_s$  between height positions. As a comparison, Chai  
21 et al., 2012 observed earlier that  $R_s$  was lower in the lower positions, whereas Xu and Wan (2008)  
22 and Liu et al. (2010) showed opposite result. The magnitude of  $R_s$  at a given slope position was

1 consistent with those of plant-related factors (Table 3, Fig. 4),  $R_s$  being highest at positions closest  
2 to the plants regardless of height gradients along the slopes. It is therefore concluded that  
3 topographic position or height within the sand dune per se is a poor predictor of  $R_s$ .

#### 4 **4.2 Plant drivers of the topographic variation in soil respiration over the** 5 **measurement period**

6 Our present finding that plant-related factors drive the topographic variation in  $R_s$  over a sand dune  
7 (Table 3, Fig. 4) was consistent with those of Sponseller and Fisher (2008). They reported that  
8 spatial patterns in  $R_s$  in the Sonoran Desert were related to plant size and productivity, but unrelated  
9 to soil water. Desert ecosystems are generally limited with substrate supply due to their low living  
10 biomass and accumulated soil organic matter, but feature large spatial heterogeneity in respiration  
11 substrate due to the “fertility-island” effect (Gold et al., 1995; Xie et al., 2001). This can be  
12 supported by large CVs (49.1, 64.7 and 82.0%) in plant-related factors of our study. In contrast,  
13 CVs for the hydrometeorological factors were much smaller (4.6 and 22.0%). Positive relationship  
14 between plant-related factors (litterfall, soil nitrogen, and root biomass), together with their positive  
15 effects on  $R_s$  (Figs. 4, 6), emphasized that spatial variation in supply of respiration substrate  
16 regulated spatial variation in  $R_s$ . Current photosynthate is supplied for root and rhizosphere  
17 respiration (Högberg et al., 2001; Tang et al., 2005; Han et al., 2014). Litterfall is supplied for  
18 heterotrophic microbe respiration (Reichstein et al., 2002; Zhou et al., 2013). These processes are  
19 influenced by soil nitrogen content (Allison et al., 2008; Deng et al., 2010). These findings support  
20 our first hypothesis that topographic heterogeneity in  $R_s$  was controlled by the respiration substrate  
21 supply provided by plants. In contrast, many studies in forests and grasslands report that  
22 topographic heterogeneity in  $R_s$  can be suitably explained by spatial heterogeneity in  $T_s$  and SWC  
23 (Kang et al., 2003; Liu et al., 2010). We suggested future studies on spatially scaling up soil

1 respiration in desert ecosystems should consider the spatial variation in substrate supply more than  
2 temperature.

3 Our finding that plants controlled the topographic variation in  $R_s$  over a fixed sand dune, along with  
4 similar findings by other studies (Moyano et al., 2008; Kuzyakov and Gavrichkova, 2010; Han et al.,  
5 2014), challenge the legitimacy of empirical models of  $R_s$  at the sand-dune scale. As an alternative,  
6 we suggest that photosynthesis-related parameters (or variables, e.g. root biomass and litterfall)  
7 ought to be incorporated into these models for an improved characterization of soil-plant  
8 relationships in desert ecosystems.

### 9 **4.3 Drivers of topographic heterogeneity in soil respiration as a function of plant** 10 **phenology**

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

18 From phase II to III, photosynthetic pigments and leaf photosynthesis declined, and induced large  
19 decreases in current photosynthate supply for roots and rhizosphere microorganisms (Hanson et al.,  
20 2000; Fu et al., 2002; Sey et al., 2010). Decomposition of litterfall results in a high percentage of  
21 recalcitrant substrates during phase II, but addition of fresh litterfall during phase III increases the  
22 percentage of liable substrates (Lebret et al., 2001; Regina, 2001; Ochieng and Erfemeijer, 2002).  
23 Thus, changes in substrate supply between the two phenophases could result in seasonal changes in

1 the relative contribution of autotrophic and heterotrophic respiration to total  $R_s$ . Root respiration  
2 contributes largely to total  $R_s$  during the growing season, but heterotrophic respiration contributes  
3 largely during the senescence season (Fu et al., 2002; Sey et al., 2010; Mauritz and Lipson, 2013).  
4 Specifically, in our study, autotrophic respiration may contribute largely to the total  $R_s$  during the  
5 phase II, but heterotrophic respiration may contribute largely during the phase III. We could not test  
6 this inference directly due to lack of independent measurements of different  $R_s$  components.  
7 However, some of our results can indirectly confirm this inference.

8 In our study,  $R_s$  was sensitive to root biomass during the phase II, but less sensitive during the phase  
9 III, indicating a decrease in relative contribution of root respiration to  $R_s$  during the phase III.  $R_s$   
10 was related to litterfall during the phase II, unlike during the phase III, indicating the switched  
11 substrate pool and disproportionate addition of fresh litterfall. However, the controlling factors of  
12 autotrophic and heterotrophic respiration can be quite different. Autotrophic respiration is shown in  
13 others studies be largely controlled by root biomass and soil nitrogen (Tu et al., 2013; Zhou et al.,  
14 2014), and heterotrophic respiration by the amount of litterfall and soil nitrogen (Yan et al., 2010;  
15 Sayer et al., 2011). Thus, the key factor controlling the variation in  $R_s$  can be different for the  
16 different plant phenophases.

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

23

## 1    **5 Conclusions**

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

## 11   **Acknowledgement**

12   We acknowledge the support obtained from National Natural Science Foundation of China (NSFC)  
13   (31270755 and 31361130340, 31200537), the Academy of Finland (proj. no. 14921), the Beijing  
14   Forestry University and University of Eastern Finland. This work is related to the ongoing Finnish-  
15   Chinese research collaboration project EXTREME, between Beijing Forestry University (BJFU)  
16   and University of Eastern Finland (UEF). Thanks to Dr. Graham Forbes for valuable comments and  
17   language revisions and to Huishu Shi, Yuming Zhang, Wei Feng, Sijing Li, Zhihao Chen, Siling  
18   Tang, Yajuan Wu and Yuan Li for their assistances with the field measurements and  
19   instrumentation maintenance.

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## 1 **References**

- 2 Allison, S. D., Czimczik, C. I., and Treseder, K. K.: Microbial activity and soil respiration under  
3 nitrogen addition in Alaskan boreal forest, *Glob. Change Biol.*, 14, 1-13, 2008.
- 4 Asaeda, T. and Rashid, M. H.: Nutrient retention associated with phenological features in  
5 *Sparganium erectum* stands in a lowland stream, *River Res. Appl.*, 31, 207-215, 2015..
- 6 Austin, A. T.: Has water limited our imagination for aridland biogeochemistry?, *Trends Ecol. Evol.*,  
7 26, 229-235, 2011.
- 8 Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drösler, M., Williams, M.,  
9 Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C.,  
10 Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., Wohlfahrt, G., and Gernusca, A.:  
11 Soil respiration in European grasslands in relation to climate and assimilate supply, *Ecosystems*, 11,  
12 1353-1367, 2008.
- 13 Bond-Lamberty, B. and Thomson, A.: Temperature-associated increases in the global soil  
14 respiration record, *Nature*, 464, 579-582, 2010a.
- 15 Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data, *Biogeosciences*, 7,  
16 1915-1926, 2010b.
- 17 Breimann L. Friedman, J. Stone, C.J. and Olshen, R. A.: Classification and regression trees,  
18 Chapman & Hall/CRC, Wadsworth, Belmont, California, 1984.
- 19 Chai, H., Feng, J., and Jing, Y.: Spatial distribution and change trait of soil respiration at the dunes  
20 in Hoqin Sand Land, *Arid Land Geography*, 3, 463-472, 2012.
- 21 Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and  
22 feedbacks to climate change, *Nature*, 440,165-173, 2006.

1 Davidson, E. A., Belk, E., and Boone, R. D.: Soil water content and temperature as independent or  
2 confounded factors controlling soil respiration in a temperate mixed hardwood forest, *Glob. Change*  
3 *Biol.*, 4, 217-227, 1998.

4 DeForest, J. L., Noormets, A., McNulty, S. G., Sun, G., Tenney, G., and Chen, J.: Phenophases alter  
5 the soil respiration-temperature relationship in an oak-dominated forest, *Int. J. Biometeorol.*, 51,  
6 135-144, 2006.

7 Deng, Q., Zhou, G., Liu, J., Liu, S., Duan, H., and Zhang, D.: Respiration of soil respiration to  
8 elevated carbon dioxide and nitrogen addition in subtropical forest ecosystems in China,  
9 *Biogeosciences*, 7, 315-328, doi:10.5194/bg-7-315-2010, 2010.

10 Dungan, R. J., Whitehead, D., and Duncan, R. P.: Seasonal and temperature dependence of  
11 photosynthesis and respiration for two co-occurring broad-leaved tree species with contrasting leaf  
12 phenology, *Tree Physiol.*, 23, 561-568, 2003.

13 Feng, W., Zhang, Y., Wu, B., Zha, T., Jia, X., Qin, S., Shao, C., Liu, J., Lai, Z., and Fa, K.:  
14 Influence of disturbance on soil respiration in biologically crusted soil during the dry season, *The*  
15 *Scientific World J.*, 2013, 408560, doi:10.1155/2013/408560, 2013.

16 Fu, S., Cheng, W., and Susfalk, R.: Rhizosphere respiration varies with plant species and phenology:  
17 a greenhouse pot experiment, *Plant and Soil*, 239, 133-140, 2002.

18 Geng, Y., Wang, Y., Yang, K., Wang, S., Zeng, H., Baumann, F., Kuehn, P., Scholten, T., and He,  
19 J.: Soil respiration in Tibetan Alpine Grasslands: Belowground biomass and soil moisture, but not  
20 soil temperature, best explain the large-scale patterns, *PLoS ONE*, 7, e34968.  
21 doi:10.1371/journal.pone.0034968, 2012.



1 Gold, W. G. and Bliss, L. C.: Water limitations and plant community development in a polar desert,  
2 Ecology, 76, 1558-1568, 1995.

3 Han, G., Luo, Y., Li, D., Xia, J., Xing, Q., and Yu, J.: Ecosystem photosynthesis regulates soil  
4 respiration on a diurnal scale with a short-term time lag in a coastal wetland, Soil Biol. Biochem.,  
5 68, 85-94, 2014.

6 Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial  
7 contributions to soil respiration: a review of methods and observations, Biogeochemistry, 48, 115-  
8 146, 2000.

9 Hook, P. B., Burke, I. C., and Lauenroth, W. K.: Heterogeneity of soil and plant N and C associated  
10 with individual plants and openings in North American short grass steppe, Plant Soil, 138, 247-256,  
11 1991.

12 Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg,  
13 G., Ottosson-Löfvenius, M., and Read, D. J.: Large-scale forest girdling shows that current  
14 photosynthesis drives soil respiration, Nature, 411, 789-792, 2001.

15 Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual  $Q_{10}$  of soil respiration reflects plant  
16 phenological patterns as well as temperature sensitivity, Glob. Change Biol., 10, 161-169, 2004.

17 Jia, X., Zhan, T., Wu, B., Zhang, Y., Chen, W., Wang, X., Yu, H., and He, G.: Temperature  
18 response of soil respiration in a Chinese pine plantation: hysteresis and seasonal vs. diel  $Q_{10}$ , PLoS  
19 ONE, 8, e57858. DOI:10.1371/journal.pone.0057858, 2013.

20 Kang, S., Doh, S., Lee, D. S., Lee, D., Jin, V. L., and Kimball, J. S.: Topographic and climatic  
21 controls on soil respiration in six temperate mixed-hardwood forest slopes, Korea, Glob. Change  
22 Biol., 9, 1427-1437, 2003.

- 1 Kuzyakov, Y. and Gavrichkova, O.: Time lag between photosynthesis and carbon dioxide efflux  
2 from soil: a review of mechanisms and controls, *Glob. Change Biol.*, 16, 3386-3406, 2010.
- 3 Lebret, M., Nys, C., and Forgeard, F.: Litter production in an Atlantic beech (*Fagus sylvatica* L.)  
4 time sequence, *Ann. For. Sci.*, 58, 755-768, 2001.
- 5 Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, *Funct. Ecol.*, 8, 315-  
6 323, 1994.
- 7 Li, J., Zhao, C., Zhu, H., Li, Y., and Wang, F.: Effect of plant species on shrub fertile island at an  
8 oasis-desert ecotone in the South Junggar Basin, China, *J. Arid Environ.*, 71, 350-361, 2007.
- 9 Li, P. X., Wang, N., He, W. M., Krüsi, B. O., Gao, S. Q., Zhang, S. M., Yu, F. H., and Dong, M.:  
10 Fertile islands under *Artemisia ordosica* in inland dunes of northern China: effects of habitats and  
11 plant developmental stages, *J. Arid Environ.*, 72, 953-963, 2008.
- 12 Liu, W., Xu, W., Hong, J., and Wan, S.: Interannual variability of soil microbial biomass and  
13 respiration in responses to topography, annual burning and N addition a semiarid temperature  
14 steppe, *Geoderma*, 158, 259-267, 2010.
- 15 Luo, J., Chen, Y., Wu, Y., Shi, P., She, J., and Zhou, P.: Temporal-spatial variation and controls of  
16 soil respiration in different primary succession stage on glacier forehead in Gongga Mountain,  
17 China, *PLoS ONE*, 7, e42354, doi:10.1371/journal.pone.0042354, 2012.
- 18 Luo, Y. Q.: Terrestrial carbon-cycle feedback to climate warming, *Annu. Rev. Ecol. Evol. S.*, 38,  
19 683-712, 2007.
- 20 Mahall, B. E. and Callaway, R. M.: Root communication mechanisms and intracommunity  
21 distributions of two Mojave Desert shrubs, *Ecology*, 73, 2145-2151, 1992.

- 1 Martin, J. G. and Bolstad, P. V.: Variation of soil respiration at three spatial scales: Components  
2 within measurements, intra-site variation and patterns on the landscape, *Soil Biol. Biochem.*, 41,  
3 530-543, 2009.
- 4 Mauritz, M. and Lipson, D. L.: Altered phenology and temperature sensitivity of invasive annual  
5 grasses and forbs changes autotrophic and heterotrophic respiration rates in a semi-arid shrub  
6 community, *Biogeosciences Discuss*, 10, 6335-6375, doi:10.5194/bgd-10-6335-2013, 2013.
- 7 Moyano, F. E., Kutsch, W. L., and Rebmann, C.: Soil respiration fluxes in relation to  
8 photosynthetic activity in broad-leaf and needle-leaf forest stands, *Agr. Forest Meteorol.*, 148, 135-  
9 143, 2008.
- 10 Ngao, J., Epron, D., Delpierre, N., Br éla, N., Granier, A., and Longdoz, B.: Spatial variability of  
11 soil CO<sub>2</sub> efflux linked to soil parameters and ecosystem characteristics in a temperate beech forest,  
12 *Agr. Forest Meteorol.*, 154, 136-146, 2012.
- 13 Ochieng, C. A. and Erfemeijer, P. L.: Phenology, litterfall and nutrient resorption in *Avicennia*  
14 *marina* (Forssk.) Vierh in Gazi Bay, Kenya, *Trees*, 16, 167-171, 2002.
- 15 Osono, T.: Diversity, resource utilization, and phenology of fruiting bodies of litter-decomposing  
16 macrofungi in subtropical, temperate, and subalpine forest, *J. Forest Res.-Jpn.*, 20, 60-68, 2014.
- 17 Parker, K. C.: Topography, substrate, and vegetation patterns in the northern Sonoran Desert, *J.*  
18 *Biogeogr.*, 18, 151-163, 1991.
- 19 Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G.,  
20 Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S., and Van der Werf, G. R.: Contribution of semi-  
21 arid ecosystems to interannual variability of the global carbon cycle, *Nature*, 509, 600-603, 2014.

- 1 Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its  
2 relationship to vegetation and climate, *Tellus B*, 44, 81–99, 1992.
- 3 Raich, J. W., Potter, C. S., and Bhagawati, D.: Interannual variability in global soil respiration,  
4 1980–94, *Glob. Change Biol.*, 8, 800–812, 2002.
- 5 Regina, I. S.: Litter fall, decomposition and nutrient release in three semi-arid forests of Duero  
6 basin, Spain, *Forestry*, 74, 347-358, 2001.
- 7 Reichstein, M., Tenhunen, J. D., Rouspard, O., Ourcival, J.-M., Rambal, S., Miglietta, F., Peressotti,  
8 A., Pecchiari, M., Tirone, G., and Valentini, R.: Severe drought effects on ecosystem CO<sub>2</sub> and H<sub>2</sub>O  
9 fluxes at three Mediterranean evergreen sites: revision of current hypotheses?, *Glob. Change Biol.*,  
10 8, 999-1017, 2002.
- 11 Richerson, P. J. and Lum, K.: Patterns of plant species diversity in California: relation to weather  
12 and topography, *Am. Nat.*, 116, 504-536, 1980.
- 13 Roles, B., Donders, S., Werger, M. J., and Dong, M.: Relation of wind-induced sand displacement  
14 to plant biomass and plant sand-binding capacity, *Acta Bot. Sin.*, 43, 979-982, 2001.
- 15 Safriel, U. and Adeel, Z.: Dryland ecosystems. II In: *Ecosystems and human well-being: current*  
16 *state and trends*, Vol 1 (eds by Hassan, R., Scholes, R., Neville, A.), pp. 623-662, Island Press,  
17 Washington, DC, 2005.
- 18 Sayer, E. J., Heard, M. S., Grant, H. K., Marthews, T. R., and Tanner, E. V. J.: Soil carbon release  
19 enhanced by increased tropical forest litterfall, *Nature Climate Change*, 1, 304-307, 2011.
- 20 Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle,  
21 *Biogeochemistry*, 48, 7-20, 2000.

- 1 Schlesinger, W. H. and Raikes, J. A.: On the spatial pattern of soil nutrients in desert ecosystems,  
2 *Ecology*, 77, 364-374, 1996.
- 3 Scott-Denton, L. E., Sparks, K. L., and Monson, R. K.: Spatial and temporal controls of soil  
4 respiration rate in a high-elevation, subalpine forest, *Soil Biol. Biochem.*, 35, 525-534, 2003.
- 5 Sey, B. K., Manceur, A. M., Whalen, J. K., Gregorich, E. G., and Rochette, P.: Root-derived  
6 respiration and nitrous oxide production as affected by crop phenology and nitrogen fertilization,  
7 *Plant Soil*, 326, 369-379, 2010.
- 8 Sponseller, R. A. and Fisher, S. G.: The influence of drainage networks on patterns of soil  
9 respiration in a desert catchment, *Ecology*, 89, 1089-1100, 2008.
- 10 Stock, W. D., Dlamini, T. S., and Cowling, R. M.: Plant induced fertile islands as possible  
11 indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa,  
12 *Plant Ecol.*, 142, 161-176, 1999.
- 13 Tamai, K.: Effects of environmental factors and soil properties on topographic variations of soil  
14 respiration, *Biogeosciences*, 7, 1133-1142, doi:10.5194/bg-7-1133-2010, 2010.
- 15 Tang, J., Baldocchi, D. D., and Xu, L.: Tree photosynthesis modulates soil respiration on a diurnal  
16 time scale, *Glob. Change Biol.* 11, 1298-1304, 2005.
- 17 Thompson, D. B., Walker, L. R., Landau, F. H., and Stark, L. R.: The influence of elevation, shrub  
18 species, and biological soil crust on fertile islands in the Mojave Desert, USA, *J. Arid Environ.*, 61,  
19 609-629, 2005.
- 20 Tu, L., Hu, X., Zhang, J., Li, X., Hu, H., Liu, L., and Xiao, Y.: Nitrogen addition simulates different  
21 components of soil respiration in a subtropical bamboo ecosystem, *Soil Biol. Biochem.*, 58, 255-  
22 264, 2013.

- 1 Venables, W. N. and Ripley, B. D.: Modern applied statistics with S-Plus. Springer Press, New York,  
2 2002.
- 3 Wang, B., Zha, T. S., Jia, X., Wu, B., Zhang, Y. Q., and Qin, S. G: Soil moisture modifies the  
4 response of soil respiration to temperature in a desert shrub ecosystem, *Biogeosciences*, 11, 259-268,  
5 doi:10.5194/bg-11-259-2014, 2014.
- 6 Xie, G. and Steinberger, Y.: Temporal patterns of C and N under shrub canopy in a loessial soil  
7 desert ecosystem, *Soil Biol. Biochem.*, 33, 1371-1379, 2001.
- 8 Xu, W. and Wan, S.: Water- and plant-mediated responses of soil respiration to topography, fire,  
9 and nitrogen fertilization in a semiarid grassland in north China, *Soil Biol. Biochem.*, 40, 679-687,  
10 2008.
- 11 Yan, L., Chen, S., Huang, J., and Lin, G.: Different responses of auto- and heterotrophic soil  
12 respiration to water and nitrogen addition in a semiarid temperate steppe, *Glob. Change Biol.*, 16,  
13 2345-2357, 2010.
- 14 Yuste, J. C., Janssens I. A., Carrara, A., and Ceulemans, R.: Annual  $Q_{10}$  of soil respiration reflects  
15 plant phenological patterns as well as temperature sensitivity, *Glob. Change Biol.*, 10, 161-169,  
16 2004.
- 17 Zhou, L., Zhou, X., Zhang, B., Lu, M., Luo, Y., Liu, L., and Li, B.: Different responses of soil  
18 respiration and its components to nitrogen addition among biomes: a meta-analysis, *Glob. Change*  
19 *Biol.*, 7, 2332-2343, 2014.
- 20 Zhou, Z., Zhang, Z., Zha, T., Luo, Z., Zheng, J., and Sun, J.: Predicting soil respiration using carbon  
21 stock in roots, litter and soil organic matter in forest of Loss Plateau in China, *Soil Biol. Biochem.*,  
22 57, 135-143, 2013.

1 Table 1. Average values (standard error in brackets) and CV (%) for micro-hydrometeorological  
 2 factors and plant-related factors over the three plant phenophases and measurement period. The  
 3 time scale for the means was showing in Fig. 2.  $R_s$ : soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ );  $T_s$ : soil  
 4 temperature at 10 cm depth ( $^{\circ}\text{C}$ ); SWC: volumetric soil water content ( $\text{m}^3 \text{ m}^{-3}$ ); Litter: litterfall ( $\text{kg}$   
 5  $\text{m}^{-2}$ ); Root: root biomass ( $\text{kg m}^{-3}$ ); LAI: leaf area index ( $\text{m}^2 \text{ m}^{-2}$ ); N: soil nitrogen content at 0 - 25  
 6 cm depth ( $\text{g kg}^{-1}$ ); Phase I: leaf expansion; Phase II: flower-bearing; Phase III: coloration-  
 7 defoliation..

8

Variabile	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

1 Table 2. Mean values (standard error in brackets) of micro-hydrometeorological and plant-related  
 2 factors on different slope orientations over the measurement period.  $R_s$ : soil respiration ( $\mu\text{mol CO}_2$   
 3  $\text{m}^{-2} \text{s}^{-1}$ );  $T_s$ : soil temperature ( $^{\circ}\text{C}$ ); SWC: volumetric soil water content ( $\text{m}^3 \text{m}^{-3}$ ); Litter: litterfall ( $\text{kg}$   
 4  $\text{m}^{-2}$ ); Root: root biomass ( $\text{kg m}^{-3}$ ); LAI: leaf area index ( $\text{m}^2 \text{m}^{-2}$ ); N: soil nitrogen content at 0 - 25  
 5 cm soil depths ( $\text{g kg}^{-1}$ ).

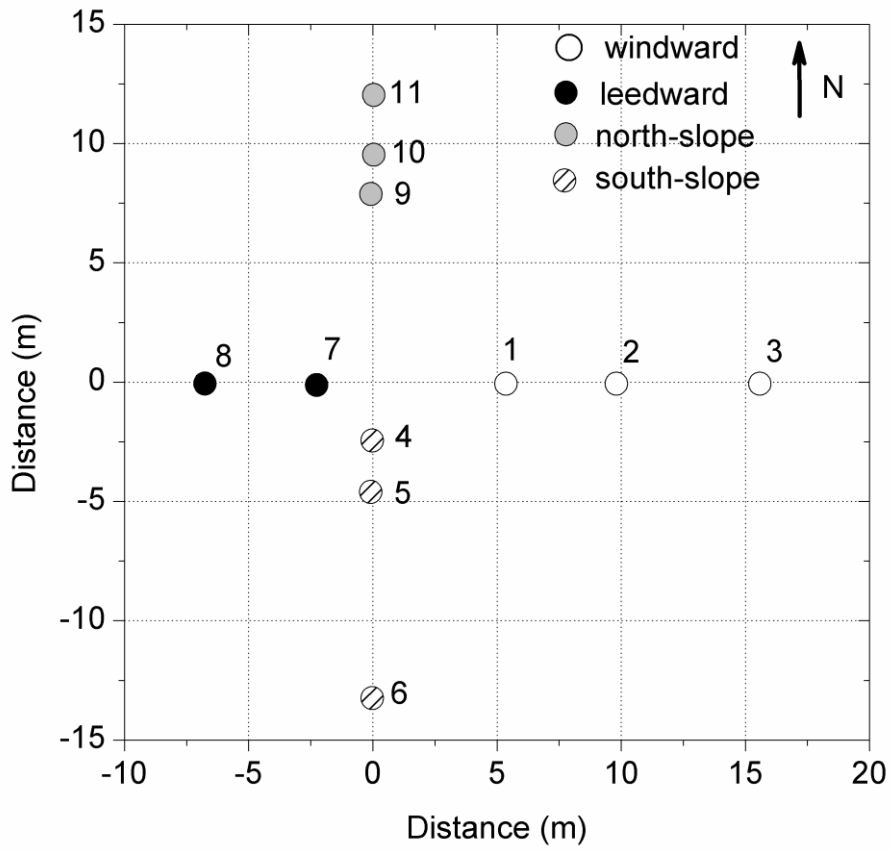
	Windward	Leeward	North-facing	South-facing
$R_s$	0.964 (0.05)	1.65 (0.03)	1.13 (0.27)	1.27 (0.19)
$T_s$	19.9 (0.60)	18.4 (0.08)	20.8 (0.23)	19.4 (0.09)
SWC	0.0964 (0.02)	0.107 (0.04)	0.0819 (0.02)	0.0918 (0.02)
Litter	0.487 (0.29)	1.53 (0.37)	0.231 (0.15)	0.671 (0.28)
Root	0.309 (0.13)	1.405 (0.02)	0.460 (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)

6



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

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



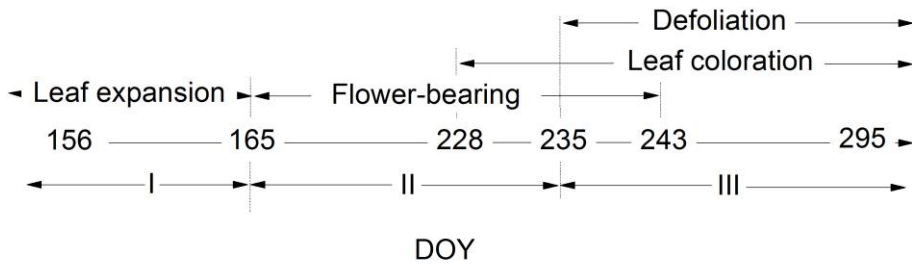
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3 Figure 1. Schematic of measurement positions (11) distributed on four slopes (windward, leeward,  
 4 north- and south-facing slope) over a fixed sand dune as well as plot positions and labels.

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Phase I: leaf expansion (9 days)

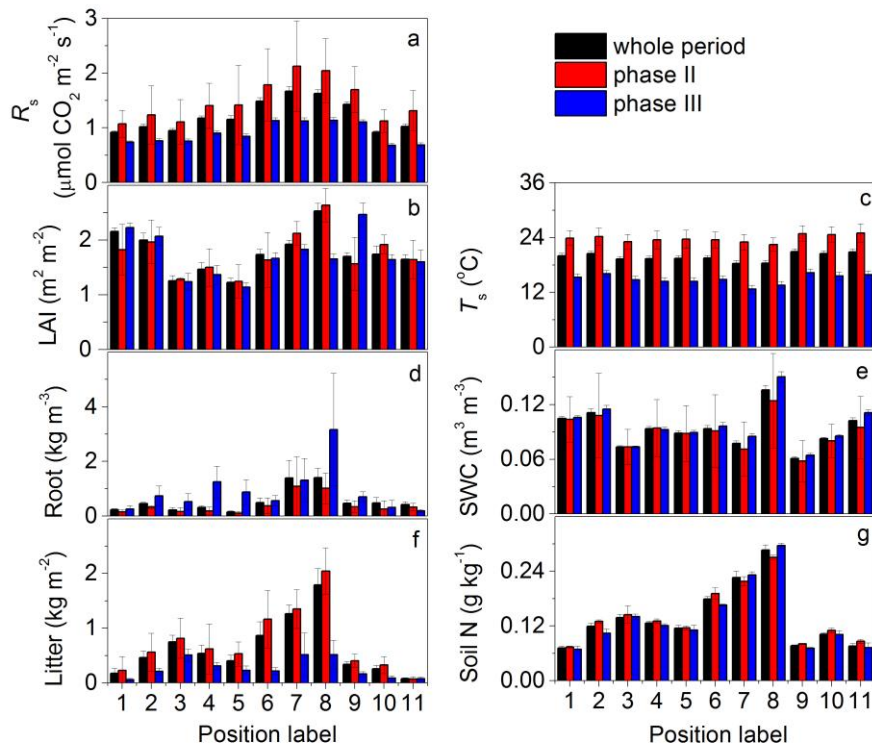
Phase II: flower-bearing (70 days)

Phase III: coloration-defoliation (60 days)

2

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

6

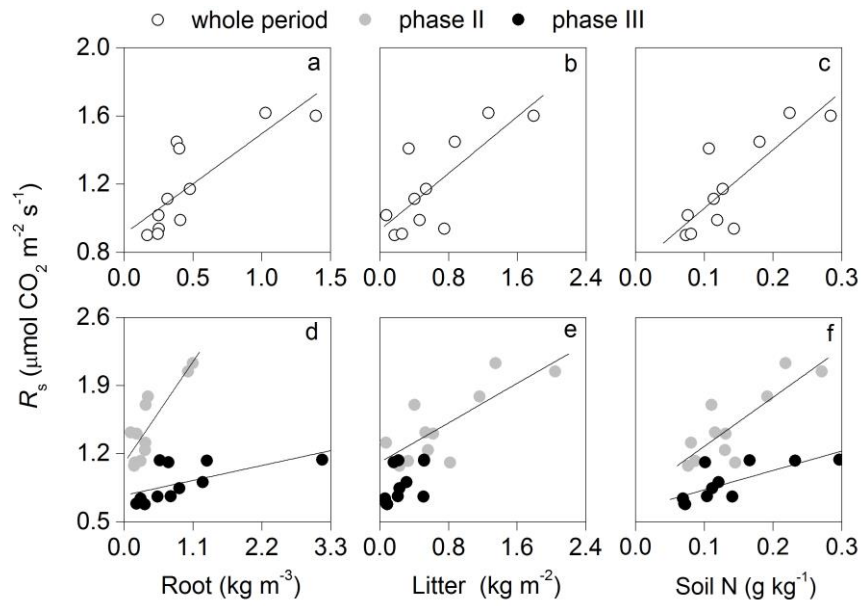


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3 Figure 3. Mean values of soil respiration ( $R_s$ ), micro-hydrometeorological ( $T_s$  and SWC) and plant-  
 4 related factors (litter, root, soil N and LAI) at 11 positions over the measurement period (whole  
 5 period), flower-bearing phase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

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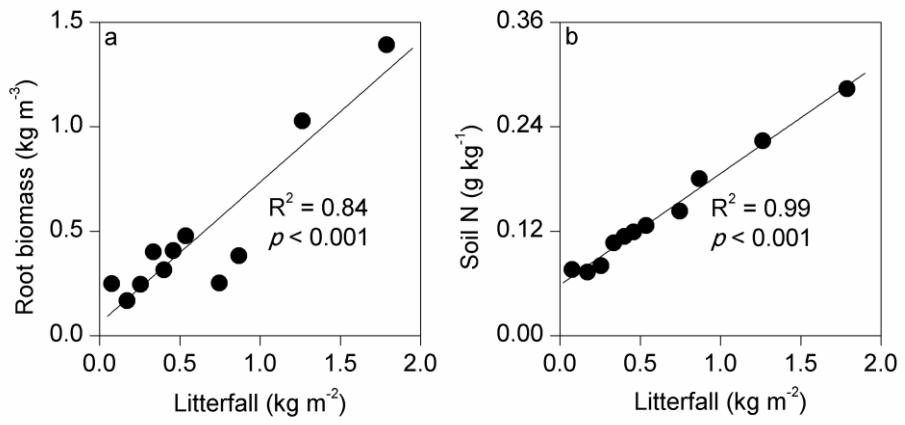


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3 Figure 4. Relationships between soil respiration ( $R_s$ ) and root biomass, and litterfall and soil  
 4 nitrogen over the measurement period (open circles) and during flower-bearing (phase II; gray  
 5 circles) and leaf coloration-defoliation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

7

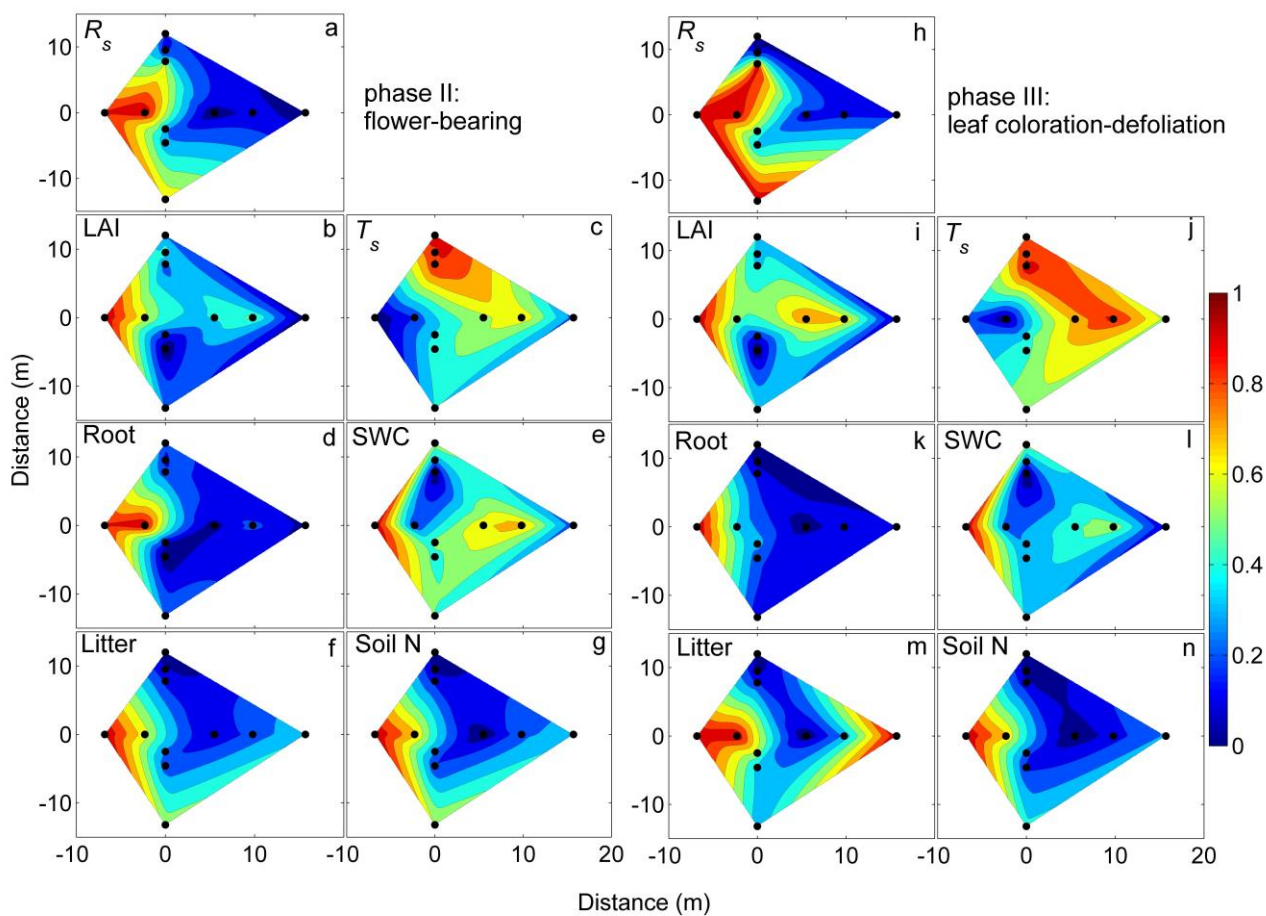


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3 Figure 5. Relationships between litterfall and root (a), and soil nitrogen content (soil N) (b) over the  
4 measurement period.

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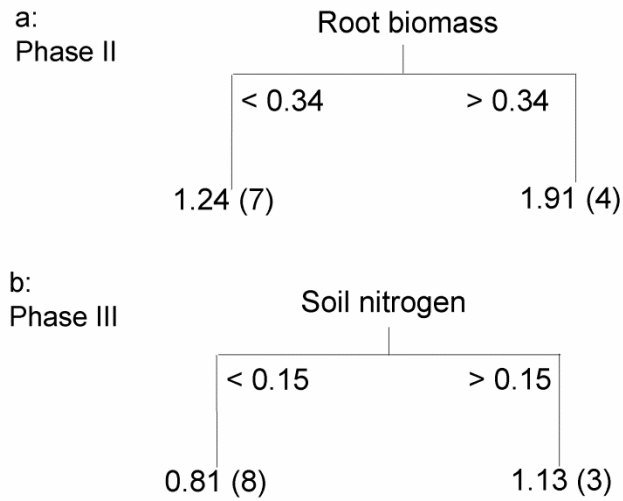
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3 Figure 6. Spatial patterns of soil respiration ( $R_s$ ), micro-hydro meteorological ( $T_s$  and SWC) and  
 4 plant-related factors (Litter, Root, Soil N and LAI) over the sand dune in flower-bearing phase  
 5 (phase II) and coloration-defoliation phase (phase III). Data values for all variables were normalized  
 6 into the range of 0 - 1 using feature scaling method ( $X_{\text{normalized}} = (X - X_{\text{min}}) / (X_{\text{max}} - X_{\text{min}})$ ). Black dots  
 7 represent the measurement positions as showed in Fig. 1.

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3 Figure 7. Results of CART analysis with key factors explaining spatial variability in soil respiration  
 4 at the flower-bearing (a) and coloration-defoliation phases (b). Predictor variables are depicted at  
 5 the top of each branch. Their critical values are shown at the side of each branch and the mean soil  
 6 CO<sub>2</sub> efflux (including number of observations in parentheses) is reported below the terminal nodes.