Dear Dr. Jens-Arne Subke,

Many thanks to you, all anonymous referees and public reviewer Dr. Ge, for your helpful and valuable comments which we appreciate and have been considered carefully in the revised manuscript. We here submit a revised manuscript that incorporates and highlights all reviewers' comments. The authors' detailed responses to those comments were listed below and italicized in blue color (please note that the page numbers in the response refer to those in the revised manuscript with changes marked-up).

With best regards,
Tianshan and all co-authors

Author response (bgd-12-9465-2015)
Response to Dr. Ge's comments (SC C3400):

General comments:

Wang B. and the co-authors do a good job with the high quality dataset of microtopographic variation in soil respiration in a desert-shrub ecosystem. This might be the first such study in terms of regulation of plant phenology in spatial variation in soil respiration. Accordingly, their findings are important to our understanding of biophysical control of soil respiration in the dune. Their results are robust, and the methods are well described.

I have only a few concerns for the manuscript. Firstly, I think it would be good to include in the introduction the references of Tamai (2010), Kang et al. (2003) and Yuste et al. (2004), whose reports showed the effects of environmental factors, soil properties and plant phenological patterns on topographic variations of soil respiration in different ecosystems. Secondly, I cannot understand why the dataset for Phase I was missing in some result sections, such as Fig. 3, Fig. 4, Fig 5, Fig. 6 and Fig. 8. Some related explanations are needed. I suggest combining Fig. 5 and Fig. 6 as a clear compared list. In Table 1, the Phases need to be defined. In Fig. 3, the unit of LAI is incorrect. In Fig. 7, the legend of (a) and (b) need to be defined.

References: Tamai K. 2010. Effects of environmental factors and soil properties on topographic variations of soil respiration. Biogeosciences, 7, 1133–1142. Kang S, Doh S, Lee D,L Dowon, Jin VL, Kimball JS. 2003. Topographic and climatic controls on soil respiration in six temperate mixed-hardwood forest slopes, Korea. Global Change Biology, 9, 1427–1437. Yuste JC, Janssens IA, Carrara A, Ceulemans R. 2004. Annual Q_{10} of soil respiration reïnˇC´ ects plant phenological patterns as well as temperature sensitivity. Global Change Biology, 10, 161–169.

Specific comments:

Firstly, I think it would be good to include in the introduction the references of Tamai (2010), Kang et al. (2003) and Yuste et al. (2004), whose reports showed the effects

of environmental factors, soil properties and plant phenological patterns on topographic variations of soil respiration in different ecosystems.
Answer: *We agree. We added the three references in Page 4, Line 7-8 in the revised manuscript.*

Secondly, I cannot understand why the dataset for Phase I was missing in some result sections, such as Fig. 3, Fig. 4, Fig 5, Fig. 6 and Fig. 8. Some related explanations are needed.
Answer: *Our measurements in Phase I were only 9 days, we think it cannot well represent for whole Phase I, thus we did not show dataset for phase I in our analyses. We added 'Due to fewer measurements in Phase I, data analyses were mainly concentrated on Phase II and Phase III.' in Page 7, Line 17-18 in the revised manuscript.*

I suggest combining Fig. 5 and Fig. 6 as a clear compared list.
Answer: *We agree. We combined Fig. 5 and Fig. 6. See Page 32 in the revised manuscript.*

In Table 1, the Phases need to be defined.
Answer: *We agree. We added the definition of Phases as 'Phase I: leaf expansion; Phase II: flowering-bearing; Phase III: coloration-defoliation' at the end of caption of Table 1. See Page 23, Line 6-7 in the revised manuscript.*

In Fig. 3, the unit of LAI is incorrect.
Answer: *We corrected it with '*m^2 m^{-2}*' in Fig.3b. See Page 29 in the revised manuscript.*

In Fig. 7, the legend of (a) and (b) need to be defined.
Answer: *We agree. We added legend (a) and (b) to caption of Fig.7. See Page 34 in the revised manuscript.*

Response to referee # 1's comments (RC C4050):

General comments:

The manuscript of Wang et al., titled "Micro-topographic variation in soil respiration and its controlling factors vary with plant phenophases in desert-shrub ecosystems": is an interesting observational study that investigated the spatial variability of Rs in desert ecosystem in relation to plants. While the sampling is limited, due to logistical constraints, the observations are still valuable. I agree with the other referee that the missing Phase I data should be excluded, it does not add much to your results and discussion, where you discuss only Phase II and III of the study. I would also suggest in the future to use portable IRGA system to sample and measure soil respiration in replicate dunes or increasing the sample points at this dune. The LI-8100 system is good for high frequency temporal data, but in this study you do not utilize that capacity you focus on spatial variability and relating fluxes to explanatory variables (ex. LAI, root biomass) that were measured on biweekly or longer timescales. So you

could’ve sampled Rs also on biweekly timescale using manual portable system to increase spatial area of study. It would’ve been nice to have a larger sample size in this study, not to take away from this one. The current study is still informative - a synthesis of multiple variables measured concurrently at the site, as the authors explore the causes of spacial variability in Rs.
Answer: *We agree with you. We excluded Phase I data in our study (see Page 23 in the revised manuscript). Thank you for your previous advices, you suggestions of how to increase sampling will be considered in our future field measurements.*

Response to referee # 3’s comments (RC C4554):

General comments:

It is a very written and concise paper, addressing micro-topographic variations in soil respiration and its controlling factors. This paper uses a well-designed and collected dataset to illustrate the variations caused by the plant biomass variation across sand dune. The information will be useful to the stabilization of the sand dune in the desert region. My minor suggestion to improve this paper is to ask the authors to further exemplify the potential application of this research in practical aspects. For example, how this study can be helpful in relating to the big issue - desertification.
In term of the microsite around a sand dune, the depression area around the sand dune is completely different from the sand dune slope. For example, there is a higher water level and different pH compared with sand slope. Soil texture is completely different. Therefore, the natural vegetation shows great variations across sand dune, which results from multiple processes (wind blowing, seed transportation, soil water movement during a year, and soil nutrient dynamics, soil crust formation, biological processes within the soil). In particular, the soil crust in the desert could change the gas release pattern of soil. The plant coverage can also have critical feedback impacts on the crust depth and structure. Therefore, the soil respiration difference could be a combined result of multiple processes. Do you have any finding which could illustrate the relationships between the crust depth and plant coverage or partitioning the component soil respiration.
A few other suggestions are attached in the supplement file.
Answer: *The main purpose of our study is to investigate the controls of micro-spatial variation in soil respiration across a sand dune, thus we exemplify the potential application of our results in C cycle models but not for desertification. However, our results showed much higher plant cover on leeward slope than other slopes, which potentially indicated a better condition for plant growth on this slope, and suggests revegetation in desert ecosystem may consider this specific slope of sand dunes.*
We agree with you that soil crust in the desert could change the gas release pattern of soil. However, the microsites we measured were with no crust, thus the influences of crust on soil respiration were not considered in our paper.

Specific comments (bgd-12-C4554-2015-supplement):

P9470 L9-12: This does not make any sense because only individual average size

without density does not tell the coverage. In the desert, the vegetation coverage has a critical impacts on the soil crust which has critical effects on the soil CO_2 efflux. I would convert a coverage percentage.
Answer: *We agree. We added 'The coverage percentage of plant in this area ranged from 30 - 60%.' next to this sentence. (see Page 5, Line 13-14 in the revised manuscript)*

P9471, L3: There is normally a depression area between sand dunes. There is a significant differences between the depression areas and sand dune slope. Do you have any measurement point(s) to address this?
Answer: *No, we did not have the measurements on depression area between sand dunes. This point will be considered in our future measurements at larger special scale, e.g. inter-dune variation in soil respiration.*

P 9473, L 10: Is the soil nitrogen plant related factor?
Answer: *In our study, we found good relationship between soil nitrogen and litter fall (Figure 7b), which suggested the decomposition processes of litterfall were the important sources of soil nitrogen. Therefore, we attributed the soil nitrogen to plant related factor in our site.*

P 9473, L 15: I would say locations instead of slopes.
Answer: *The slopes here represent for different orientations of the sand dune. Therefore, we prefer using word 'slopes'.*

P 9473, L 16: significant?
Answer: *Yes, it is statistically significant. We added the p value ($p < 0.001$) there. (see P 9473, L 16 in the revised manuscript)*

P 9475, L 17: space?
Answer: *We agree. We corrected 'earlierthat' to 'earlier that'. (see Page 9, Line 2 in the revised manuscript)*

P 9476, L 16-20: provide some justifications about why you have this comparison.
Answer: *Our results show the contributor to the spatial variation in soil variation in desert was different from that in forests and grassland. We suggested future studies on spatially scaling up soil respiration in desert ecosystems should consider the spatial variation in substrate supply more than temperature. This statement was added in the revised manuscript.(see Page 12, Line 5-6 in the revised manuscript)*

P 9476, L 25: What are they?
Answer: *Here, the photosynthesis-related parameters refer to root biomass and litterfall. We clarified the sentence (Page 12, Line 11) in the revised manuscript.*

P9477, L 10: Any concerns about the reason to cause the variations in plant distribution? To my knowledge, it is the soil water, nutrient and the microsite that has led to the distribution of plants along a sand dune.
Answer: *We agree that soil water, nutrient and the microsite that has led to the*

distribution of plants at earlier stage of plant formation on a sand dune, thus plants subsequently affecting spatial variation of soil respiration.

P 9478, L 3: ?
Answer: *We deleted 'to'. (see Page 13, Line 17 in the revised manuscript)*

P9485: what are the time scale for the means?
Answer: *The time scale for the means was showing in Figure 2 in our study. We added this statement (see Page 23, Line 2-3) in the revised manuscript.*

P9486: Time scale?
Answer: *we added time scale 'over the measurement period' at the end of this sentence. (see Page 24, Line 2 in the revised manuscript)*

P9486: Leeward has higher biomass and root mass, of course, higher soil respiration, even more soil biota activity as well because of the higher soil moisture, relatively lower soil temperature which are the critical factor in the desert ecosystem. It is the combination of relative.
Answer: *we agree with you.*

P9486: north-facing has a higher temperature than south-facing, any reason? What is the time scale for the mean?
Answer: *In our study, plant distribute sparsely in both north- and south-facing. However, litterfall in south-facing was about three times higher than that in north-facing, which may exert stronger shading effects in south-facing, thus resulting in lower soil temperature in south-facing. The time scale for the mean is the whole measurement period in our study.*

P9487: the "x" in the equation is not needed in my opinion.
Answer: *we agree. The "×" in the equation was excluded. (see Page 25 in the revised manuscript)*

P9488: Is there any site located in the depression area between sand dune?
Answer: *No, we don't have site in our study located in the depression area between sand dunes. The between-dune sites will be considered in our future measurements at larger special scale, e.g. inter-dune variation in soil respiration.*

P9490: Time scale?
Answer: *Time scales of each phenophases were showed in figure 2. We added this statement (see Page 29, Line 6) in the revised manuscript.*

P9490: represents?
Answer: *we agree. We changed 'represent' to 'represents'. (see Page 29, Line 9 in the revised manuscript)*

P9491: Table 3 can be combined into this figure, making the figure easy to understand.
Answer: *The relationships between soil respiration and other variables are also*

showing in Table 3, but no in Figure 4. Thus we would like to keep them both.

P9495:’ thresholds’
Answer: we changed ‘thresholds’ into ‘critical values’. (see Page 35, Line 5 in the revised manuscript).

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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 topographic variation in R_s. During the flowering-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).

Desert ecosystems cover up to 45 % of the global terrestrial surface (Asner et al., 2003). 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, there is an urgent need 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 strong topographic 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; Tang et al., 2005; Asaeda and Rashid, 2015; 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 (107.20–107.26° E, 37.68–37.73° 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 °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 $1.6 \pm 0.02\,\mathrm{g\,cm^{-3}}$. The water-filled pore space across all the microsites was $23.42 \pm 0.92\,\%$. Soil organic matter and $CaCO_3$ content, and pH were 0.21–2.14, 0.23–0.54 $\mathrm{g\,kg^{-1}}$, 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.

2.2 Measurements of soil CO_2 efflux and micro-hydrometeorological factors

Soil CO_2 efflux (R_s, $\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) was measured with 11 automated chambers from June to October 2012. The measurements were taken on different slope orientations (i.e., windward, leeward, 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 gas 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 min and 15 s, including a 30 s pre-purge, a 45 s post-purge, and a 2 min observation period. Any plant re-growth within the measurement collar was manually removed in a timely manner. Hourly soil temperature (T_s, °C) and volumetric soil water content (SWC, $\mathrm{m^3\,m^{-3}}$) were measured simultaneously at a 10 cm depth outside of each chamber using 8150–203 soil temperature and $\mathrm{EC_{H_2O}}$ 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 ($\mathrm{kg\,m^{-3}}$), litterfall ($\mathrm{kg\,m^{-2}}$), total soil nitrogen content ($\mathrm{g\,kg^{-1}}$) within the first 25 cm of the soil, leaf area index (LAI, ~~$\mathrm{m^3\,m^{-3}}$~~), 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 °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° 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), flowering-bearing (phase II), and leaf coloration-defoliation (phase III; Fig. 2).

2.4 Data analysis

Hourly R_s data were first screened using limit checking, in which 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 $n =$ ~~92~~) 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 (Fig. 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 nominal 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, with mean differences ranging from 0.5 to 2.4 °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; $p = 0.061$; Table 3 and SWC; $p = 0.852$; Table 3). Aside from R_s, both root biomass and soil nitrogen were correlated positively with litterfall (Fig. ~~7a and 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, Figs. 4d–f and 5d, 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. ~~8a~~).

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, Figs. 4d, f and ~~6d, g~~). 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 and 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. ~~8b~~).

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. Thus, we could not draw the conclusion that R_s at the top position was higher than that at low positions or vice versa. As a comparison, Chai et al., 2012 observed ~~earlierthat~~ 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.

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 and 7), 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). These forests and grasslands are generally not limited by substrate supply, thus more litterfall and heterotrophic respiration. Spatial variation in T_s and SWC is reported to contribute to the spatial variation in R_s in forest ecosystems.

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 based on inputs of T_s and VWC at the sand-dune scale. As an alternative, we suggest that photosynthesis-related parameters (or variables) ought to be incorporated into these models for an improved characterization of soil–plant relationships in desert ecosystems.

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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 flowering and 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 (Fig. 7), 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 ~~to~~ 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 downed photosynthetic products, 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. R_s: soil respiration (µmol CO_2 m^{-2} s^{-1}); T_s: soil temperature at 10 cm depth (°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}); N: soil nitrogen content at 0–25 cm depth (g kg^{-1}).

Variale	~~Phase I~~		Phase II		Phase III		Measurement period	
	~~mean (SE)~~	~~CV%~~	mean (SE)	CV%	mean (SE)	CV%	mean (SE)	CV%
R_s	~~0.94 (0.22)~~	~~23.6~~	1.49 (0.11)	25.2	0.90 (0.06)	21.3	1.21 (0.09)	23.5
T_s	~~21.73 (0.92)~~	~~4.2~~	23.82 (0.24)	3.4	14.90 (0.33)	7.4	19.74 (0.27)	4.6
SWC	~~0.07 (0.01)~~	~~14.3~~	0.09 (0.01)	20.8	0.10 (0.01)	24.0	0.09 (0.01)	22.0
Litter			0.74 (0.17)	78.5	0.26 (0.05)	67.7	0.63 (0.16)	82.0
Root			0.59 (0.15)	84.2	0.90 (0.25)	92.2	0.75 (0.14)	64.7
LAI			1.76 (0.12)	22.7	1.72 (0.12)	23.9	1.76 (0.12)	21.8
N			0.18 (0.02)	43.5	0.13 (0.02)	53.3	0.14 (0.02)	49.1

Table 2. Mean values (standard error in brackets) of micro-hydrometeorological and plant-related factors on different slope orientations. R_s: soil respiration (µmol CO_2 m^{-2} s^{-1}); T_s: soil temperature (°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}); N: soil nitrogen content at 0–25 cm soil depths (g kg^{-1}).

	Windward	Leeward	North-facing	South-facing
R_s	0.96 (0.05)	1.65 (0.03)	1.13 (0.27)	1.27 (0.19)
T_s	19.94 (0.60)	18.36 (0.08)	20.77 (0.23)	19.44 (0.09)
SWC	0.10 (0.02)	0.11 (0.04)	0.08 (0.02)	0.09 (0.02)
Litter	0.49 (0.29)	1.53 (0.37)	0.23 (0.15)	0.67 (0.28)
Root	0.31 (0.13)	1.41 (0.02)	0.46 (0.03)	0.32 (0.17)
LAI	1.80 (0.48)	2.22 (0.43)	1.70 (0.05)	1.47 (0.25)
N	0.11 (0.03)	0.25 (0.04)	0.09 0.02	0.14 (0.03)

Table 3. Regression equations between R_s (y) and different micro-hydrometeorological and plant-related factors (x) for the measurement period and flowering-bearing (phase II) and leaf coloration-defoliation phase (phase III). T_s: soil temperature (°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 ($m^2\,m^{-2}$); N: soil nitrogen content at 0–25 cm soil depths ($g\,kg^{-1}$).

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

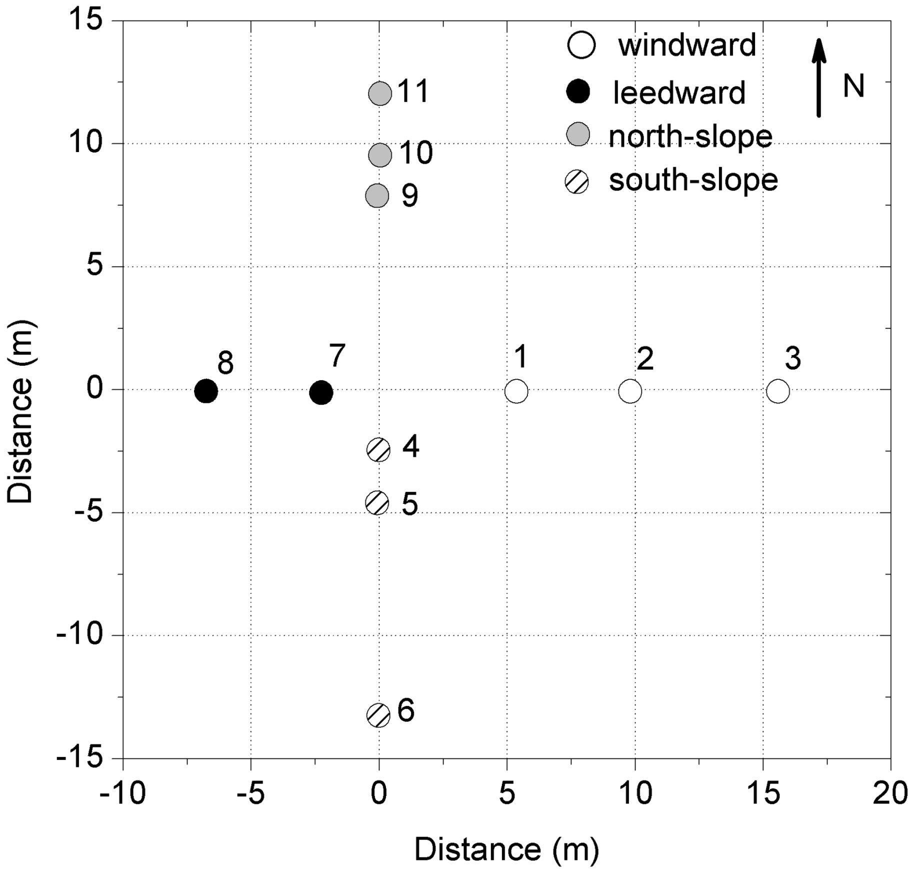

Figure 1. Schematic of measurement positions (11) distributed on four slopes (windward, leeward, north- and south-facing slope) over a fixed sand dune as well as plot positions and labels.

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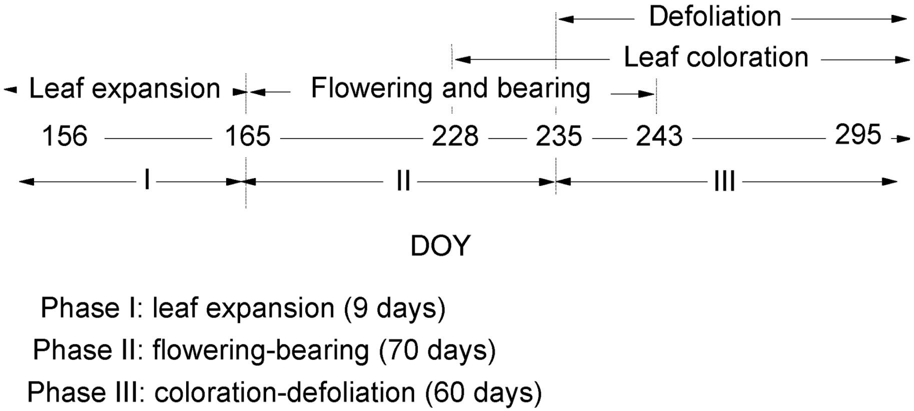

Figure 2. Phenophases of *Artemisia ordosica* over the measurement period. Three phases considered, included leaf expansion (phase I), flowering-bearing (phase II), and leaf coloration-defoliation (phase III) phases.

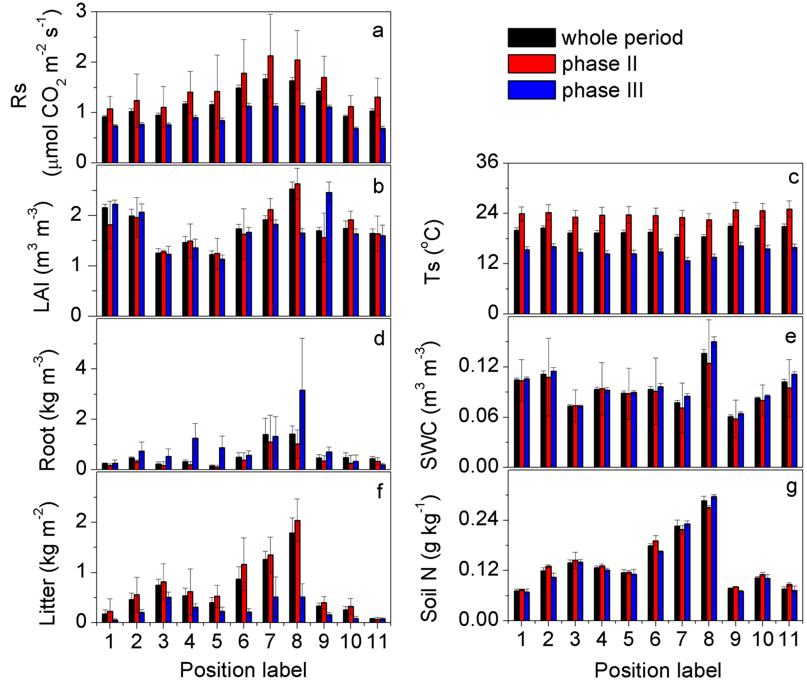

Figure 3. Mean values of soil respiration (R_s), micro-hydrometeorological (T_s and SWC) and plant-related factors (litter, root, soil N and LAI) at 11 positions over the measurement period (whole period), flowering-bearing phase (phase II), and leaf coloration-defoliation phase (phase III) from June to October 2012. R_s: soil respiration (μmol CO$_2$ m^{-2} s^{-1}); T_s: soil temperature (°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 ~~represent~~ standard error. Black color represents for whole period. Red color represents for flowering-bearing phase. Bule color represents for leaf coloration-defoliation phase.

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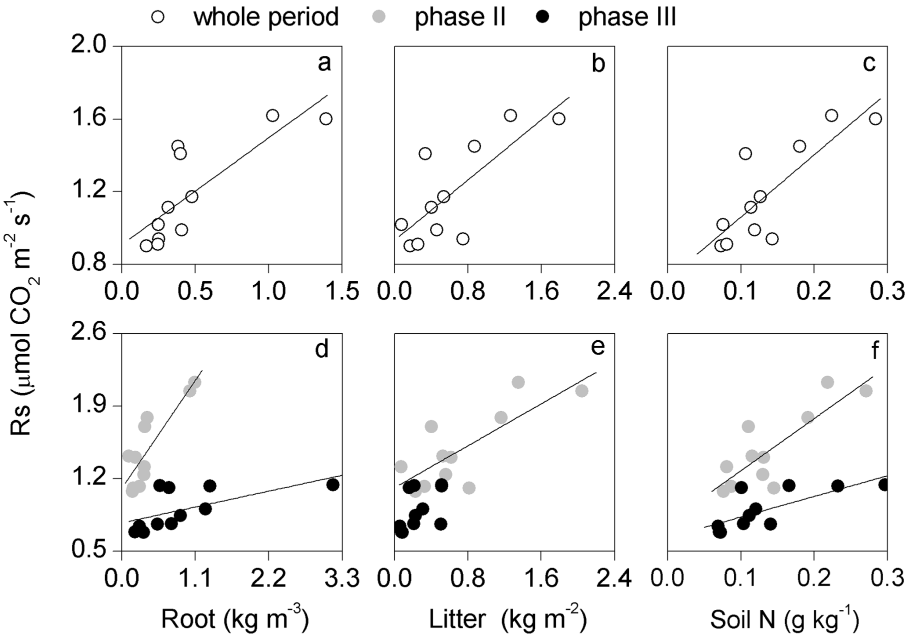

Figure 4. Relationships between soil respiration (R_s) and root biomass, and litterfall and soil nitrogen over the measurement period (open circles) and during flowering-bearing (phase II; gray circles) and leaf coloration-defoliation (phase III; black circles) phase. Equations, R^2, and *p* values are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

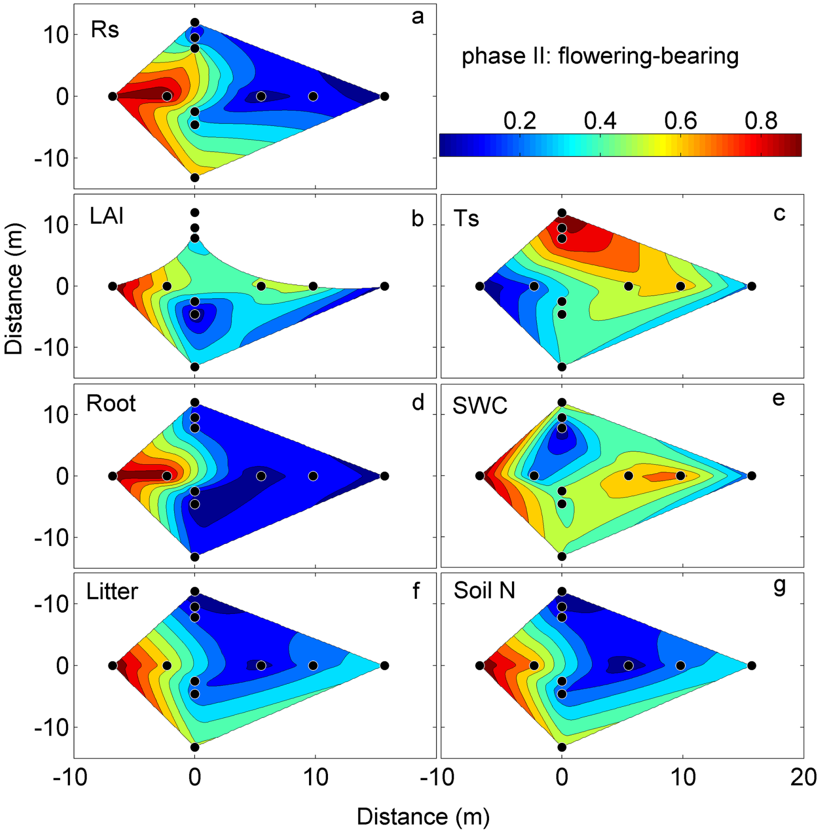

Figure 5. Spatial patterns of soil respiration (R_s), micro-hydro meteorological (T_s and SWC) and plant-related factors (Litter, Root, Soil N and LAI) over the sand dune in flowering-bearing phase. Data values for all variables were normalized into the range of 0–1 using feature scaling method ($X_{\text{normalized}}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

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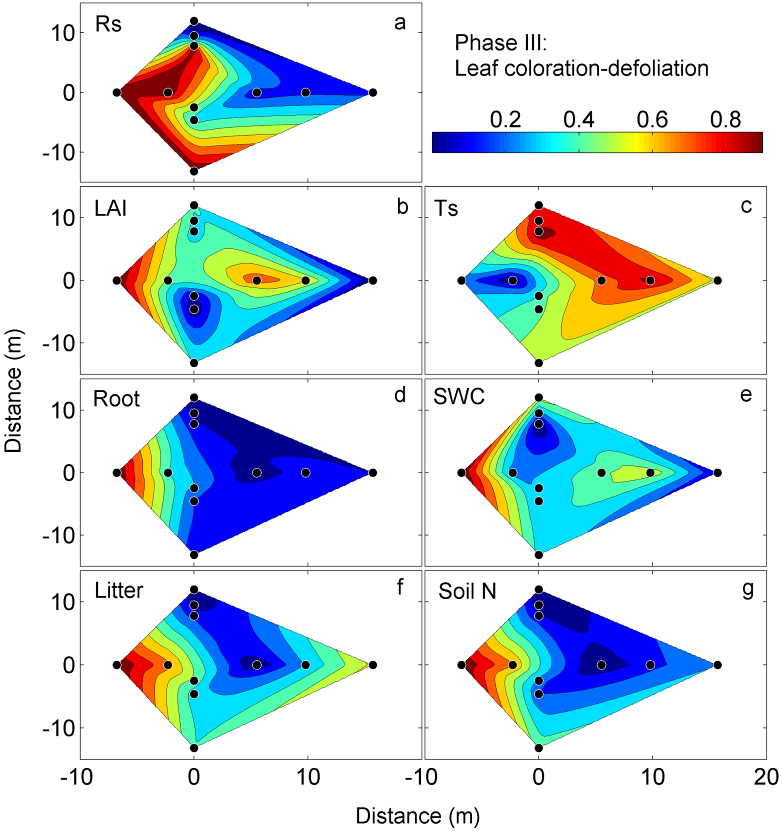

~~**Figure 6.** Spatial patterns of soil respiration (R_s), micro-hydro meteorological (T_s and SWC) and plant-related factors (Litter, Root, Soil N and LAI) over the sand dune in coloration-defoliation phase. Data values for all variables were normalized into the range of 0–1 using feature scaling method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

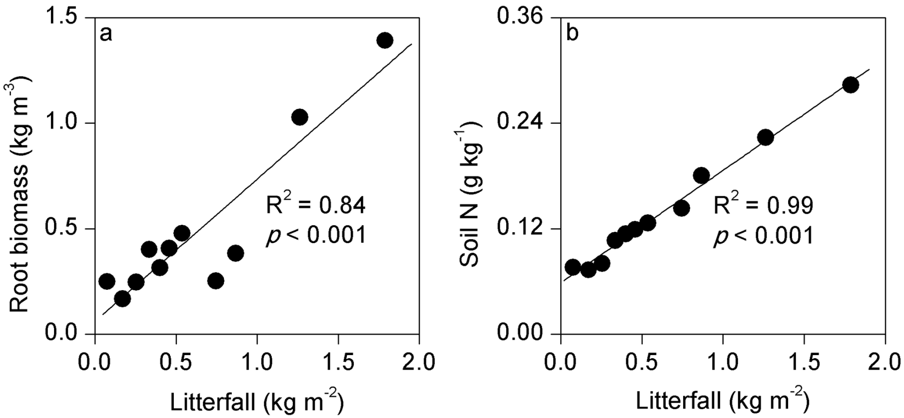

Figure 7. Relationships between litterfall and root, and soil nitrogen content (soil N) over the measurement period.

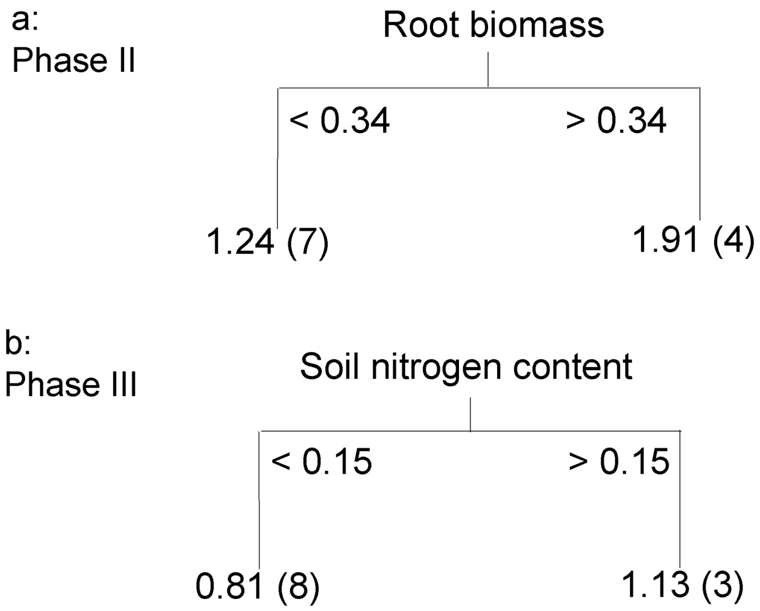

Figure ~~8~~. Results of CART analysis with key factors explaining spatial variability in soil respiration at the flowering-bearing **(a)** and coloration-defoliation phases **(b)**. Predictor variables are depicted at the top of each branch. Their ~~thresholds~~ are shown at the side of each branch and the mean soil CO_2 efflux (including number of observations in parentheses) is reported below the terminal nodes.

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