Soil Respiration May Overestimate or Underestimate in Forest Ecosystems

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Abstract: The inappropriate selection of measurement points and measurement times in an ecosystem may easily lead to the underestimation or overestimation of soil respiration due to spatial and temporal heterogeneity. To assess the law of spatial and temporal heterogeneity and more accurately determine the soil respiration rate, we measured the soil respiration rate of a forest in the plant growing season from 2011 to 2013 on Changbai Mountain in 8 directions and 7 distances from each tree trunk. Neglecting the direction of the measuring point may overestimate or underestimate the soil respiration rate by 29.81% and 26.09%, respectively; neglecting the distance may overestimate or underestimate the soil respiration rate by 41.36% and 20.28%, respectively; and ignoring the measurement time may overestimate and underestimate the soil respiration rate by 41.71% and 57.64%, respectively. In addition, choosing a measurement point in the eastern direction at a 1.8 m distance and conducting the measurement in September may relatively accurately reflect the soil respiration rate of the ecosystem. These findings can deepen our understanding of soil respiration rate heterogeneity and may provide new ideas for improving the measurement method of soil respiration.

Keywords: soil respiration rate in forest ecosystem; spatial and temporal heterogeneity; measurement points and measurement times; soil respiration accuracy

1. Introduction

Carbon dioxide emissions have increased with industrial production and human activities [1]. As an important greenhouse gas, increases in carbon dioxide emissions can cause major changes in global temperature and determine the climate change phenomenon. [2–4]. Soil respiration is one of the main natural pathways for carbon dioxide release into the atmosphere in terrestrial ecosystems, and studying soil respiration can more fully recognize the global carbon cycle [3]. Globally, soil respiration is as high as 80.4 Pg C a⁻¹, just lower than that of marine ecosystems, which play a key role in the biosphere and atmospheric C exchange [5]. Small changes in the respiration rate may lead to significant changes in atmospheric CO₂, which has large impacts on the global carbon cycle and budget [6]. Therefore, measuring the soil respiration rate accurately has become particularly important. To accurately measure soil respiration, the method of determination is critical [7]. The measurement of soil respiration has been formulated based on mature methodology after decades of continuous research and development [8]. The measurement point is also important for the assessment of the accuracy of soil respiration, but few current
studies have explored how to determine the measurement point of soil respiration. Most studies consider that environmental and biological factors are decisive components of soil respiration, and small spatial changes may cause great changes in the decisive factors, further driving soil respiration rate changes [9,10]. Therefore, the soil respiration rate may differ depending on the measurement points in natural ecosystems. At present, most studies on the spatial heterogeneity of soil respiration are carried out on large scales or in different ecosystems [11,12], but how soil respiration changes in small spaces has received little attention.

To reveal the effects of small spatial changes on soil respiration, it is necessary to understand the driving mechanism of soil respiration [13,14]. The mechanism of environmental and biological factors on soil respiration has been continuously explored and discussed in recent decades [15]. Soil temperature, soil water content, precipitation and soil carbon and nitrogen are the main environmental factors affecting soil respiration [6]. There is a significant correlation between soil respiration and soil temperature that has been indicated with linear, quadratic, exponential and Arrhenius relationships [16]. There is also a threshold limit on the correlation between soil respiration and soil temperature; microbial activity may be suppressed or destroyed when the soil temperature is at the high temperature limit, and soil microbes may appear to be dormant at low temperatures [14]. Linear, quadratic, and hyperbolic relationships have been described between the soil moisture content and soil respiration, but the general trend is consistent: the soil respiration rate will decrease sharply when the soil moisture content is unsuitable, such as during droughts or disasters [11,13]. The driving mechanism is that a low soil water content cannot provide the living environment necessary for the roots and microorganisms, and a high soil water content may change the ratio between the two phase states of soil [11]. The oxygen required for breathing is limited, and the carbon dioxide venting channel is also blocked. Precipitation can affect the soil respiration rate by affecting the amount of water required for biological activities and root growth in the soil, soil moisture, and soil temperature [11,17]. The direct cause is that precipitation activates the activities of soil microbes and increases the population of microbes, enhancing decomposition activities [18]. Precipitation may also cause a decrease in soil respiration that is attributed to a decrease in soil temperature; alternatively, channels fill with water and impede the emission rate of carbon dioxide, thereby reducing the rate of soil respiration [11,13]. The effect of soil nutrients on soil respiration is also evident. Soil organic matter is the material basis for the decomposition of microorganisms and is the largest carbon pool of terrestrial ecosystems, which directly affects soil respiration [19,20]. Many studies have found a positive correlation between the soil organic matter content and soil respiration rate, which can predict the soil respiration rate [19–21]. The effect of soil nitrogen on the soil respiration rate is highly controversial [20]. Some researchers have suggested that an increase in nitrogen content may increase the activities of microorganisms and thus have a positive effect on soil respiration [22]. However, some studies have suggested that a high nitrogen content will reduce the utilization efficiency of carbon, thereby hindering the metabolic activities of microorganisms [23].

The biological factors affecting soil respiration changes mainly include vegetation type, root biomass, and litter [24]. The vegetation type affects the litter quality and reserves and the cellulose content, which affects the decomposition time of carbon by microbes and fungi [25]. The vegetation type also affects the proportion of roots to the total biomass, and root respiration is usually positively correlated with root biomass [26]. In addition, plant roots can also affect soil respiration by affecting the physical and chemical properties of the soil [27]. As a unique structural level in the ecosystem, the litter layer has a certain shaping effect on the environment, soil and vegetation of an ecosystem, thus affecting the temperature and soil water content and driving soil respiration [28]. Overall, changes in either environmental or biological factors can result in soil respiration changes. Therefore, in order to obtain reliable data from a field experiment several replicates are needed.
Environmental and biological factors change with spatial change, which may cause spatial heterogeneity in soil respiration rates [28]. In this study, spatial change refers to changes in the measuring point, including changes in direction or distance from the tree trunk. Phototropism and the spatial competitiveness of tree growth determine the heterogeneity in the spatial distribution of the canopy and branch length [29]. The combination of the canopy with external factors such as light and precipitation may drive changes in environmental and biological factors [30]. The canopy has the ability to intercept rainfall, and a thick canopy results in more rainfall interception [29,30]. Generally, distances closer to the tree trunk have a thicker canopy and a greater ability to intercept rainfall [31]. The greater the rainfall interception rate is, the lower the soil moisture below the canopy; the lower the interception rate is, the higher the soil moisture [30]. In addition, the lengths and widths of branches affect the intercepted rainfall area, which also has the ability to regulate soil moisture [29]. There is a significant negative correlation between the thickness and area of the canopy and the ground light intensity below the canopy, affecting the soil temperature and soil water evaporation rate. Spatial heterogeneity in the canopy may also affect soil nutrients [32]. Spatial differences in the canopy interception rate may cause heterogeneity in the soil nutrient leaching capacity space [28,31]. Moreover, canopy spatial heterogeneity also affects the microbial community structure and activity through regulating soil moisture and temperature, which will inevitably lead to the heterogeneity of soil biochemical reactions, thus impacting nutrient cycling and nutrient content [28]. The soil moisture content, temperature and nutrient spatial heterogeneity due to canopy heterogeneity may also affect the growth of shrubs and herbs in the underlying trees, which may affect plant species changes and the spatial distribution of plant roots [28]. The heterogeneity of these environmental and biological factors may result in spatial heterogeneity in soil respiration [15–17,28–32]. However, the degree to which soil respiration is affected by spatial changes (changes in direction or distance from the tree trunk) is unclear, and the mechanism by which soil respiration heterogeneity is affected by spatial changes urgently needs to be determined.

Environmental and biological factors change with temporal change, which may cause temporal heterogeneity in soil respiration rates [33,34]. There is clear seasonal variation in solar radiation and precipitation that affects soil moisture, temperature and nutrients [34]. The physiological processes of plant growth also change with changes in solar radiation and precipitation, which also lead to obvious seasonal changes in the structure and function of the canopy [35]. These differences may cause the soil temperature to exhibit temporal heterogeneity, which is affected not only by solar radiation but also by seasonal changes in the canopy. In addition, many studies have shown that the microbial community structure and activity also respond significantly to seasonal changes, which may be attributed to soil temperature, soil moisture and soil basic nutrients [36,37]. Therefore, it can be inferred that temporal changes may also cause temporal heterogeneity of soil respiration. However, the degree to which soil respiration heterogeneity is caused by temporal changes is unclear, and the mechanism remains unknown. In addition, in previous studies, when measuring the soil respiration of an ecosystem, the selection of measurement points and measurement times was mostly random [33–35]. For this reason, the soil respiration rate can be easily overestimated or underestimated. Therefore, fully accounting for the effects of space and time on soil respiration may be more accurate for assessing the soil respiration rate of an ecosystem.

Here, we measured the soil respiration rate of a *Pinus koraiensis* forest once a month in the plant growing season from 2011 to 2013 in Changbai Mountain, China, and measurement points were established in 8 directions and 7 distances from each tree trunk to study the effect of temporal and spatial changes on the soil respiration rates in forest ecosystems. This study had three objectives: (1) to quantitatively analyse how much of the heterogeneity in the soil respiration rate is caused by spatial variation; (2) to quantitatively analyse how much of the heterogeneity in the soil respiration rate is caused by temporal variation; and (3) to determine how to choose the measurement point and measurement
time to accurately assess the soil respiration rates of forest ecosystems. If this study were to demonstrate spatial and temporal heterogeneity in soil respiration rates, then the soil respiration rates of forest ecosystems may overestimate or underestimate by random selection of measurement points and measurement times; this study also provides important information for accurately measuring soil respiration.

2. Materials and Methods

2.1. Experiment Site

The study area was located on the northern slope of the National Natural Conservation Park of Changbai Mountain in eastern Jilin Province in Northeast China. This site is situated at 42° 24′ 09″–42° 19′ 82″ N, 128° 05′ 45″–128° 06′ 20″ E and has an elevation of 738 m [38]. The climate is characterized as temperate continental and is influenced by monsoons; the growing season is warm and wet (June–September), and the non-growing season is dry and cold. The annual rainfall average is approximately 695.3 mm based on 22 years of meteorological records. More than 80% of the annual precipitation occurs during the growing season. The mean air temperature is 3.6 °C, ranging from winter temperatures below −30 °C to summer temperatures approaching 33 °C. The snowy season lasts approximately 5 months, from November to March each year. On average, the area is covered by a 200-year-old multi-storied uneven-aged multi-species mixed forest consisting of Pinus koraiensis, Tilia amurensis, Acer mono, Fraxinus mandshurica, Quercus mongolica and 135 other species. The standard density was 560 stems ha⁻¹ (stem diameter > 8 cm), and the forest consisted of multiple broad-leaved shrub species that had a height of 0.5–2 m. The soil is classified as dark brown forest soil.

2.2. Experimental Design

We selected 3 Pinus koraiensis trees in the forest with canopy closures of 0.7, diameter at breast heights of 45.3, 44.7, and 44.9 cm and tree heights of 23.5, 22.9, 23.0 m where we measured soil respiration below their canopies. The soil respiration rate was measured in the plant growing season (three times a month) from 2011 to 2013, and the measurement points of soil respiration rate were intentionally set in 8 directions (N, E-N, E, E-S, S, W-S, W, and W-N) and at 7 distances (distances from the trunk were 0.6, 1.2, 1.8, 2.4, 3.0, 3.6, 4.2, and 4.8 m) (Figure 1).

![Figure 1. A schematic of the arrangement of soil collars in the study. The collars were placed on the cross points of 7 concentric circles (0.6 m away from each other) and in 8 direction lines around the trees. The black dots represent the respiration collars.](image-url)
Buried collars (with a height of 4.5 cm and a diameter of 10 cm at each measurement point) were used for the soil respiration measurements, and a soil chamber (LI-6400-09, Li-Cor, Inc., Lincoln, NE, USA) connected to a portable infrared gas analyser (IRGA, LI-6400, Li-Cor, Inc.) was used to measure the soil respiration rates on sunny mornings (from 8:00 to 11:00 am). The soil temperature was measured simultaneously with the soil respiration using a thermocouple penetration probe (LI-6400-013, Li-Cor, Inc.) inserted to a soil depth of 5 cm in the vicinity of the soil collars. The soil moisture was also measured in the same locations with a hand-held time-domain reflectometer (Type ML2x, Delta-T Devices Ltd., Cambridge, UK).

The root biomass and soil nutrient content were determined at the end of the growing season. Soil and root were collected in 0–100 cm soil layer by soil auger in all measure points. After handpicking out stones and litters, the roots were separated from the soil by soaking them in water followed by gentle washing with a 2.0 mm mesh. The roots were sorted into fine roots and coarse roots with a threshold of 2 mm in diameter, air-dried, placed in suitable paper bags and oven-dried to a constant weight at 80 °C. The Walkley–Black acid digestion method [39] was used to measure the soil carbon. The semi-micro Kjeldahl method and molybdenum blue colorimetry [40] were used to measure the soil total nitrogen (TN) and total phosphorus (TP), respectively.

2.3. Data Analysis

One-way analysis of variance (ANOVA) was used to analyse the differences in soil respiration rates in different spaces (directions and distances) and times (years or months). The least significant difference (LSD) test at the 5% level was also used to analyse the differences in environmental factors and biological factors in different directions and distances. Linear regression equations were used to analyse the relationships between the soil respiration rate and observed distance in different directions or at different distances, environmental factors, and correlations with the biological factors. All statistical analyses were conducted using SPSS (version 19.0) software and Office 2010 was used to create all of the figures.

3. Results
3.1. Spatial Heterogeneity in the Soil Respiration Rate

Soil respiration rates significantly differ among sampling directions; the lowest soil respiration rate (5.552 µmol m⁻² s⁻¹) was north of the trees, and the highest soil respiration rate (9.750 µmol m⁻² s⁻¹) was west of the trees (Figure 2A). There was a significant difference (p < 0.05) in the soil respiration rates between the north and west directions, and the soil respiration rate in the west was 75.60% larger than that in the north. The relative deviations of soil respiration rates in different directions were also heterogeneous. The minimum relative deviation was in the north (−0.261), and the largest was in the west (0.298). In addition, the soil respiration rates in the E-S, E, W-S, and W directions were greater than the mean soil respiration rate, while the soil respiration rates in the other four directions were less than the mean value (Figure 2B).

There was a significant linear negative correlation between the soil respiration rate and distances (p < 0.001); the maximum mean respiration rate was 10.616 µmol m⁻² s⁻¹ for the 0.6 m measuring points, and the minimum mean respiration rate was 5.987 µmol m⁻² s⁻¹ for the 3.6 m measuring points (Figure 2C). The relative deviations in the soil respiration rates differed with the measurement distance. The minimum relative deviation in the different measurement distances was −0.203 for the 3.6 m measuring points, and the maximum relative deviation was 0.414 for the 0.6 m measuring points. Moreover, when the distances were less than 1.2 m, the soil respiration rates were greater than the mean soil respiration rate, while the soil respiration rates were less than the mean value when the distance was greater than 1.8 m (Figure 2D).
Figure 2. Cont.
Distance/m

Figure 2. Soil respiration rates in different directions (A) and different distances (C) and the relative deviations in different directions (B) and distances (D). The vertical bars represent the standard deviations, different lowercase letters indicate significant differences at the $p < 0.05$ level. The same below.

3.2. Temporal Heterogeneity in the Soil Respiration Rate

There was no significant difference ($p > 0.05$) in the soil respiration rate among years, but there was obvious heterogeneity ($p < 0.05$) among months (Figure 3A,B). In the plant growing season, the soil respiration rate showed a single peak trend in overall performance; the maximum soil respiration rate was in August (10.644 µmol m$^{-2}$ s$^{-1}$), and the minimum was in October (3.182 µmol m$^{-2}$ s$^{-1}$). The relative deviation in the soil respiration rate on a monthly scale also differed (Figure 3C). The maximum relative deviation was 0.417 in August, and the minimum relative deviation was −0.576 in October.

Figure 3. Cont.
3.3. Correlation between Soil Respiration and the Driving Factors

There were significant differences in the soil temperature in different directions ($p < 0.05$), which had a similar trend as the soil respiration rate in different directions. However, there was no significant difference in the soil moisture content in different directions ($p > 0.05$) (Figure 4A). In addition, there was a significant linear positive correlation between the soil temperature and soil respiration rate in different directions ($p = 0.038$) and a significant linear negative correlation between the soil moisture content and soil respiration rate ($p = 0.045$) (Figure 4C). There were no significant differences in the soil temperature at different distances ($p > 0.05$), while the soil moisture content increased with increasing distance (Figure 4B). Furthermore, there was no significant linear relationship between the soil temperature and soil respiration rate at different distances ($p = 0.154$), and there was a significant linear negative correlation between the soil water content and soil temperature ($p = 0.003$) (Figure 4D). There was a significant linear positive correlation between soil organic carbon (SOC), TN and the soil respiration rate in different directions and at different distances ($p < 0.05$). However, there was no significant linear relationship between TP and the soil respiration rates (Figure 5).
Figure 4. The soil temperatures and soil moisture contents in different directions (A) and distances (B); the relationships between the soil respiration rate and soil temperature and soil moisture content in different directions (C) and distances (D).
There was heterogeneity in the root biomass (fine roots, coarse roots and total root biomass) in different directions and distances, and there was a difference in the regression between the direction and distance (Figure 6A,B). Regarding direction, there was no significant correlation between the fine roots, coarse roots and total root biomass and the soil respiration rate, while there was a significant linear positive correlation between the fine roots, total root biomass and soil respiration rate at different distances (Figure 6C,D).

Figure 5. The relationships between the soil respiration rate and nutrient contents in different directions (A) and at different distances (B).
Figure 6. Root distributions in different directions (A) and distances (B); the relationship between the soil respiration rate and root biomass in different directions (C) and distances (D).
4. Discussion

Small changes in respiration rates may lead to significant changes in atmospheric CO₂, which has a large impact on the global carbon cycle and budget [1,2]. Therefore, the accurate determination of the soil respiration rate is also a matter of great concern. The choice of soil respiration measurement points is also very important because spatial variation is likely to cause heterogeneity in soil respiration measurements [3,13]. Previous research has proven that the soil respiration rate is easily affected by the conversion of regional scale space [21,35], although there is a lack of evidence regarding whether small-scale conversions would cause changes in the soil respiration rate. The study of the heterogeneity in soil respiration in different directions and distances would help reveal how small scale variation causes soil respiration rate changes. The selection of the measuring points for the determining the soil respiration rate has mostly been random in forest ecosystems [27]. If there is heterogeneity over small areas in forest ecosystems, the soil respiration rate may be overestimated or underestimated. We found that ignoring the direction or distance where the measurement is taken might cause the overestimation or underestimation of the soil respiration rate in forest ecosystems. Therefore, scientifically selecting soil respiration measurement points is necessary, which can reflect the actual soil respiration rate of an ecosystem more accurately. We found that the minimum relative deviation in the soil respiration rate was in the east and at 1.8 m from the trunk, which may suggest that the soil respiration rate at this point may be more accurate for expressing the soil respiration rate in this forest ecosystem.

Many studies have found that soil respiration rates are driven by environmental and biological factors [23]. The main environmental factors in this study included soil temperature, soil moisture and the nutrient contents, which were significantly affected by spatial and temporal heterogeneity. Previous studies indicated that soil respiration remains high at high levels of spatial heterogeneity [13,18,23]. This study also found that soil temperature showed heterogeneity in different directions, although this factor was not affected by distance. The illumination intensity is different at different time periods during a whole day, and the direction of sunlight and shade changes over time [32,33], which may cause heterogeneity in the soil temperature in different directions. The canopy density of the forest was 0.7 in the study, and the light intensity was relatively uniform at the different measuring distances; therefore, there was no difference in the soil temperature at different distances. We also found that the soil temperature significantly affected the soil respiration rate in different directions, although the soil temperature did not significantly drive the soil respiration changes at different distances. This result may prove that the heterogeneity in soil respiration was driven by soil temperature heterogeneity. In addition, the study revealed that there was no significant difference in the soil moisture content in different directions, but there were significant differences at different distances. This result may be due to the fact that the thickness of the canopy was not significantly heterogeneous in different directions; however, there were differences at different distances that affected the redistribution of precipitation and thus had different effects on the soil water content in different directions and distances. An interesting phenomenon was that the soil moisture content inhibited the soil respiration rate in different directions and at different distances. Previous studies found that the soil moisture content promotes soil respiration when the soil moisture content is less than 12% [34]. However, the average soil moisture content was always higher than 14% in this study, which may have reduced the supply of oxygen to microorganisms and obstructed the discharge channel of carbon dioxide, thus causing the soil moisture content to restrict the soil respiration rate.
Studies on the effect of the soil nutrient content on the soil respiration rate have received extensive attention [17,19,36], but the relationships between soil nutrients and the soil respiration rate in different directions and at different distances have rarely been reported. Previous studies showed that SOC and TN were expected to affect soil respiration by altering microclimatic conditions, carbon chemistry and the microbial biomass in the soil [20,23]. In addition, the soil microbial quantity and activity were closely related to SOC and TN, and the soil microbial biomass and soil TP content had a significant linear positive correlation, which may be an effective mechanism for soil nutrients to drive soil respiration changes [22,26]. There was no significant correlation between TP and soil respiration in this study, which may be because phosphorus was not a limiting element, with an average TP concentration of 0.85 g kg\(^{-1}\) in this area. The other reason may be that TP had more spatial heterogeneity, and the heterogeneity was not consistent with the soil respiration rate heterogeneity.

Plant roots are biological factors that drive soil respiration and can directly affect the total respiration rate of soil through their own respiration [26,28]. Plant roots may also indirectly affect the soil respiration rate by regulating the soil nutrient contents. We found that the root biomass showed heterogeneity in different directions and distances. In different directions, the root biomasses of each diameter were not significantly correlated with the soil respiration rate. At different distances, the fine root biomass and total root biomass drove the change in the soil respiration rate, while coarse roots and soil respiration rate were not significantly linearly correlated. Martin and Bolstad indicated that the spatial variability in soil respiration was mainly driven by the root biomass [41]. However, our results demonstrated that the root biomass may only drive soil respiration rate changes at different distances, while there was insufficient evidence to prove whether the root biomass drove the soil respiration rate changes in different directions. Although coarse roots had the highest root biomass, the respiration rate of the roots was relatively low, and its contribution to the total respiratory rate of the soil was weak [42]. Therefore, the correlation between the soil respiration rate and coarse root biomass was not significant in either direction or distance. Although fine root biomass was significantly lower than coarse root biomass, its metabolic intensity was large [43]. Furthermore, the respiration rate of the fine roots was much higher than that of the coarse roots, which contributes greatly to the ecosystem carbon cycle [44]. In different directions, there was a difference in the roots, but there was no significant linear regression relationship between the roots and the soil respiration rate. This result may suggest that the intrinsic mechanism of how root biomass drives soil respiration rate change may be incomprehensible, while the soil respiration rate was more susceptible to the soil temperature, water moisture content and soil nutrients.

Soil temperature, moisture, nutrients and root biomass are all significantly affected by seasonal changes, and therefore, we inferred that the soil respiration rate may show heterogeneity over time [3,13,27,42–44]. In this study, both annual and monthly scales were assessed. There was no significant difference in the soil respiration rate on the interannual scale, which may be attributed to the stable forest ecosystem [45]; thus, the driving factor may not have an interannual influence. In the plant growing season, the soil respiration rate showed a unimodal trend that was consistent with the trends in the monthly mean soil temperature and monthly mean soil moisture content (Figure 7A). Previous research found that soil moisture content was the dominant factor driving soil respiration changes over time [34], while we found that both the soil moisture content and soil temperature significantly drove changes in the soil respiration rate (Figure 7B). In addition, the results showed that the soil respiration rate in September was closest to the mean soil respiration rate and, therefore, it may be more accurate to estimate the soil respiration rate throughout the year in this forest system.
5. Conclusions

This study evaluated the effects of temporal and spatial changes (different directions, distances, and time) on the soil respiration rate in a forest ecosystem. Furthermore, the intrinsic mechanisms of temporal and spatial heterogeneity in the soil respiration rate were revealed by analysing the correlations between the environmental factors and biological factors and the soil respiration rate. Our results demonstrated that the soil respiration rate in the forest ecosystem had spatial and temporal heterogeneity. Neglecting the direction of the measuring point may overestimate or underestimate the soil respiration rate by 29.81% and 26.09%, respectively; neglecting the distance may overestimate or underestimate the soil respiration rate by 41.36% and 20.28%, respectively; and ignoring the measurement time may overestimate and underestimate the soil respiration rate by 41.71% and 57.64%, respectively, on a monthly scale. In particular, our study proved that a measuring point selected at a distance 1.8 m from the tree and in the eastern direction in September may accurately measure the soil respiration rate. This finding suggests that a more accurate assessment of the soil respiration rate takes the measurement point and the measurement time in an ecosystem into account. This study also demonstrated that spatial and temporal heterogeneity in the soil temperature, soil moisture content, nutrient content and root biomass may be the intrinsic mechanisms that drive soil respiration rate heterogeneity. These findings can deepen our understanding of soil respiration rate heterogeneity and may provide new ideas for improving the measurement method of soil respiration.
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