Characteristics of soil respiration in upper and lower slope positions with different aboveground biomass: a case study in a Japanese cypress forest

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Abstract

Differences in aboveground biomass along a slope position are often overserved because of varying levels of nutrient availability. Such differences can affect the spatial variation in soil respiration (Rs) via changes in biological factors (e.g., fine root biomass and litter mass), in addition to environmental factors. This study clarified the differences in Rs and the factors affecting Rs between the upper and lower slope positions with contrasting aboveground biomass, within a small watershed covered by a Japanese cypress forest.

The soil water content (SWC) was lower, whereas the soil temperature (Ts) and fine root biomass were higher in the upper plot (UP) than in the lower plot (LP). Rs was negatively correlated with SWC, but positively correlated with Ts and fine root biomass. These results gave rise to a positive effect of Rs on the UP. However, Rs was comparable between the plots. The results from a multiple linear regression model indicated that factors other than SWC, Ts, and fine root biomass increased Rs in the LP. We speculate that high litterfall could enhance Rs in the LP, as litterfall is an important source of decomposed respiration. The higher aboveground net primary production and lower fine root biomass in the LP suggest that more carbon was allocated aboveground and less carbon was allocated belowground, resulting in comparable Rs but different contribution of aboveground and belowground sources on Rs between the plots. It is considered that differences in phosphorus availability between the plots caused the different carbon allocation patterns, even at a small spatial scale of less than 100 m.

Key words: Carbon allocation, Chamaecyparis obtusa, Slope, Soil CO2 efflux, Spatial variation

1. Introduction

Soil respiration (Rs), which is the carbon released from soil surface, is the primary component of the total carbon released from forest ecosystems. Although Rs estimates at stand scale are necessary to understand the carbon cycling in forest ecosystems, the spatial variation in Rs is considerably high (e.g., Ohashi and Gyokusen, 2007; Katayama et al., 2009), which makes it difficult to estimate Rs at a stand scale. Therefore, it is important to examine the spatial variation in Rs and gather knowledge on how to upscale Rs at a stand scale. Rs is strongly affected by environmental factors, such as soil water content (SWC, m3m-3) and soil temperature (Ts, °C, Davidson et al., 1998; Stoyan et al., 2000). It is also well known that Rs is influenced by biological factors such as fine root biomass (Hanson et al., 1993; Shibistova et al., 2002), litter amount (Fang et al., 1998), and microbial biomass (Scott-Denton et al., 2003). These factors, which are potential determinants of Rs, often differ with topography such as slope position (e.g., McCarthy and Brown, 2006; Tamai, 2010), slope aspects (e.g., Hanson et al., 1993), and slope degree (e.g., Creed et al., 2013). Thus, it is necessary to examine how these factors affect the spatial variation in Rs under different topographic conditions, particularly for the forests in mountainous regions.

It is often observed that environmental factors vary with topography, especially with the slope position. For example, lower SWC in upper slopes results in higher Rs (Davidson et al., 1998; Piñol et al., 1995), because Rs is often negatively correlated with SWC, except under very dry soil conditions. Under low SWC conditions, diffusion of O2 accelerates the CO2 production, resulting in high Rs (Davidson et al., 1998). On the other hand, in some studies, Rs did not differ along a slope, despite the differences in SWC and Ts (McCarty and Brown, 2006; Sotta et al., 2006). Tamai (2010) found that Rs covaried with environmental factors, but the environmental factors alone were not enough to explain the variation in Rs along the slope of an evergreen coniferous forest. These results suggest that it is insufficient to consider only the environmental factors for explaining the variation in Rs in mountainous forests.

It is well known that aboveground biomass also differs along a slope, because of variation in nutrient availability. For example, it has been shown that the nitrogen availability decreases upslope, and the aboveground biomass decreases and fine root biomass increases upslope, owing to a shift in carbon allocation from aboveground to belowground sources (Enoki et al., 1996; Tateno et al., 2004). High fine root biomass often facilitates root respiration and dead root decomposition, resulting in high Rs (Katayama et al., 2009; Shibistova et al., 2002). These studies imply that higher fine root biomass might result in higher Rs in the upper slopes, where the aboveground biomass is typically low. Accordingly, Hanson et al., (1993) found that Rs values in the valley-bottom locations were lower than those at the ridge-top, where the fine root biomass values were much higher.
compared with the valley-bottom. Although aboveground biomass might affect the spatial variation in $R_{soil}$ through a change in biological factors, especially in complex mountainous forests, only a few studies to date have examined $R_{soil}$ along a slope while focusing on biomass allocation in forest ecosystems.

The relationships of $R_{soil}$ with environmental and biological factors are often examined to understand the factors of spatial variation in $R_{soil}$ at a stand scale (e.g., Soe and Buchmann, 2005; ArchMiller et al., 2016). Such knowledge is useful for spatial upscaling from point-measurements to stand-level $R_{soil}$ patterns (Katayama et al., 2009). Recently, tower-based flux measurements were taken in a forest with complex topography (Takanashi et al., 2005). In such forests, topographical variations in environmental and biological factors might explain the spatial variation in $R_{soil}$ and discovering the relationship of $R_{soil}$ with environmental and biological factors might enable scaling at a whole stand scale, including upper and lower slope positions. On the other hand, Suchewaboripont et al., (2015) found that the relationships of $R_{soil}$ with SWC and $T_{soil}$ should be constructed separately in areas with different forest structures (i.e., dense canopy cover and canopy gap). There is little existing knowledge as to how the relationship of $R_{soil}$ with environmental and biological factors can be consistent across slope regions with different aboveground biomass.

The objective of this study was to clarify the differences in $R_{soil}$ and the factors affecting $R_{soil}$, between the upper and lower slope positions with different aboveground biomass within a watershed covered by a Japanese cypress forest. In this stand, 42% larger diameter at breast height (DBH, cm) and 36% taller trees were found at the lower slope position compared with the higher slope position (Kume et al., 2016). By using data obtained in the two contrasting plots, we first examined the differences in $R_{soil}$, environmental factors (i.e., SWC and $T_{soil}$), and biological factors (fine root biomass and litter mass) between the two plots. Second, we examined the relationship of $R_{soil}$ with the environmental and biological factors and quantified the differences in the effects of each factor on $R_{soil}$ between the upper slope plot (UP) and a lower slope plot (LP), using a multiple linear regression model.

### 2. Materials and Methods

#### 2.1 Study Site

This study was conducted in the Ochozu experimental watershed (OEW) of the Kasuya Research Forest (33° 38’ N, 130° 32’ E), Kyushu, western Japan. The OEW is a suburban forested area, located 15 km west of the Fukuoka metropolitan area (33° 38’ N, 130° 32’ E; Fig 1), with an elevation range of 160–300 m asl. The watershed area is 9.5 ha. The annual mean air temperature and precipitation at the OEW were 15.7 °C and 1,834 mm, respectively, during the years 2009–2012. Mean (± standard deviation (S.D.)) of the carbon (C) : nitrogen (N) ratio and phosphorus (P) content of surface soil in the OEW were 19 ± 2.1 and 10.1 ± 2.9 mg kg⁻¹, respectively (Chiwa et al., 2016).

Approximately 50% of the OEW ground area is covered with a Japanese cypress (Chamaecyparis obtusa Sieb. et Zucc.) plantation planted in 1957, their age being more than 50 years at the time of study. The continuous canopy layer is at a height of approximately 15 m and the stand density is 1,371 trees ha⁻¹ (Katayama et al., 2014). The forest floor has scarce vegetation cover, particularly in the riparian area (Ide et al., 2009). The soil is yellow-brown soil with medium porosity (40%–50%), originating from serpentinite and chlorite schist, and the soil texture is clay loam with a depth of 0.4–0.5 m (Kume et al., 2008). Two 10 m × 10 m plots, UP and LP, were used and compared in the present study. The UP and the LP were located 70 m apart horizontally and 26 m apart vertically on a 20° slope, facing toward southwest (Kume et al., 2016). LP is in a riparian area with a relatively gentle (<10°) and concave slope, whereas UP is close to a ridge in a convex slope (>20°). The tree DBH in the UP (14.9 cm) was lower than that in the LP (21.2 cm), and the stand density in both plots was 1700 trees ha⁻¹ four years before our measurements (Kume et al., 2016).

#### 2.2 Measurements

##### 2.2.1 $R_{soil}$ and environmental measurements

$R_{soil}$ values were measured using a commercial respirometer (LI-6400, LI-COR Inc., Lincoln, NE, USA), consisting of an infrared gas analyzer (IRGA) and a small soil chamber (LI-6400-09) of volume 962 cm³ (diameter 9.5 cm). $R_{soil}$ was measured in a closed and dynamic system. Before each cycle of flux measurement, the air in the chamber headspace was scrubbed down to about 320 ppm, and then allowed to rise as a consequence of CO2 efflux. The CO2 concentration inside the IRGA headspace was calculated at the end of 20-ppm increase. Measurements were replicated three times at each sampling point, spanning several minutes, and averaged. Polyvinyl chloride (PVC) collars (diameter 10.4 cm and height 5.0 cm) were inserted into the forest floor to a depth of 2 cm at nine points for each plot, which were located on the grids at an interval of 5 m. All the collars were left at each point for the entire study period. Litter was left in the collars and there was no grass in the collars. Measurements at the nine points for each plot were conducted from November 2010 to November 2011 at 1–3 month intervals. In total, 10 measurement campaigns were conducted. Each measurement campaign was conducted between 10:30 am and 02:00 pm.
except for measurements between 7:30 am and 9:30 am during November 2010 and measurements between 03:00 pm and 05:00 pm during December 2011. The SWC and \( T_{\text{soil}} \) at 10-cm depth were measured simultaneously during each measurement campaign using hand-held sensors (ML2x, Delta-T Devices Inc., UK and LI-6400, LI-COR Inc., Lincoln, NE). The average values and standard deviations of \( R_{\text{soil}} \), SWC, and \( T_{\text{soil}} \) in the UP and LP for the entire measurements period were calculated using the average at each measurement point.

Dry bulk density of the topsoil (g cm\(^{-3}\)) was measured using the same samples as for fine root biomass (see next subsection). Soil samples at the depth of 0–5 cm (volume 100 cm\(^3\)) were collected near the \( R_{\text{soil}} \) measurement point in UP and LP during March, 2011. After the fine roots were removed, the soil was oven-dried for 72 h at 105 °C. After drying, the soil was weighed and the dry bulk density was obtained and averaged for each plot.

### 2.2.2 Biological measurements

The aboveground biomass, aboveground net primary production (ANPP, Mg C ha\(^{-1}\) year\(^{-1}\)), and fine root biomass were measured in each plot. The ANPP was estimated as the sum of aboveground biomass increment (ABI, Mg C ha\(^{-1}\) year\(^{-1}\)) and annual litterfall-C (LF, Mg C ha\(^{-1}\) year\(^{-1}\)).

Aboveground biomass, which is the sum of stem, branch, and foliage biomass, was estimated by allometric equations using DBH and tree height (Forestry and Forest Products Research Institute, 2004). DBH values for all trees in each plot were measured during September 2006 in the LP, September 2007 in the UP, and October 2010 in both plots. Tree heights were measured using a laser rangefinder (TruPulse 200, Laser Technology Inc., USA) during March 2011. ABI was calculated as the sum of differences in aboveground biomass between the periods. Litterfall was collected during 2011 using 0.5 m\(^2\) litter traps at four locations in each plot. The traps were made of 1-mm nylon mesh and were placed 1 m above the ground. Litterfall was collected from the traps at intervals of 1–2 months. The litterfall was separated into fine litter, including leaves, twigs, and cones of Japanese cypress and broad-leaved trees, oven-dried for 72 h at 50 °C, and weighed. LF was estimated by summing the litterfall in each sampling for only Japanese cypress. Note that the litterfall for broad-leaved trees accounted for only 2% and 5% of the total for the UP and the LP, respectively. We assumed that the C content of the dried biomass was 50%, similar to a previous study on Japanese cypress forests (Fukuda et al., 2003).

The plant area index (PAI; the one-sided plant area per unit ground area, m\(^2\) m\(^{-2}\)) was measured during August 2012 at the nine \( R_{\text{soil}} \) measurement points in each plot using digital nonspherical color photographs (Nikon COOLPIX990). The photographs were taken with the camera pointing upward 1 m above the ground on a cloudy day to avoid the effect of direct sunlight, and the PAI was determined from the photographs using Gap Light Analyzer software (Frazer et al., 1999). The fine root biomass (g m\(^{-2}\)) was measured using soil samples from a depth of 0–5 cm (volume 100 cm\(^3\)), collected near the \( R_{\text{soil}} \) measurement points in the UP and the LP during March 2011. Fine roots (diameter < 2 mm), including both live and dead roots, were collected by hand from the soil samples. Litter mass (g m\(^{-2}\)), which accumulated on the soil surface, was collected in an area of 20 cm \( \times \) 20 cm near the \( R_{\text{soil}} \) measurement points in the UP and the LP during February 2011. The fine roots and litter were oven-dried for 72 h at 50 °C, and weighed.

Chemical analyses of fresh leaves were conducted to determine the spatial variation in leaf C, N, P contents and C:N and N:P ratios, as follows. In each plot, eight trees were cut down, and one leaf sample at the canopy top of each tree was collected. The leaves were dried at 70 °C for 48 h. Total N in the leaves was determined by the combustion method (CN corder MT-700, Yanaco Co., Ltd., Tokyo, Japan); for P, the dried samples were burned at 550 °C for 2 h, following which they were digested using potassium peroxodisulfate (K\(_2\)S\(_2\)O\(_8\)). P content was measured using molybdenum blue (ascorbic acid) absorptiometry (UV mini-1240, Shimadzu, Kyoto, Japan). A standard reference material (NIST Apple Leaves 1515, National Institute of Standards and Technology, Gaithersburg, MD, USA) was analyzed alongside the leaf samples.

### 2.3 Statistical analysis

The differences in environmental factors (i.e., SWC and \( T_{\text{soil}} \)), biological factors (i.e., DBH, tree height, fine root biomass, and litter mass), and \( R_{\text{soil}} \) between the plots were analyzed using analysis of variance (ANOVA). Explanatory factors for SWC, \( T_{\text{soil}} \), and \( R_{\text{soil}} \) were plot, measurements date, and interaction effect. For biological factors, only plot was set as an explanatory factor.

Multiple linear regression models were constructed to determine the factors explaining spatial variation in \( R_{\text{soil}} \), and to quantify the contribution of each explanatory factor and a plot effect on \( R_{\text{soil}} \). The plot effect behaves as a different intercept between UP and LP and it is determined as the difference of LP from UP. To examine the necessity of interaction effects between the plots and each explanatory factor and of the plot effect in the multiple linear regression models, generalized linear mixed models (GLMMs) were examined. GLMMs were constructed using the maximum-likelihood method, following a normal distribution. GLMMs were separately constructed for each environmental (i.e., SWC and \( T_{\text{soil}} \)) and biological factor (i.e., fine root biomass, litter mass). The plot effect was also set as a fixed effect for each model. The measurement date was set as a random intercept in all models. The four kinds of GLMMs were constructed for each explanatory factor, that is, (1) different slope between the plots with the plot effect, (2) different slope between the plots without the plot effect, (3) the same slope between the plots with the plot effect, and (4) the same slope between the plot without the plot effect. The best-fit model was determined from the four GLMMs using the lowest Akaike information criterion (AIC). When a significant difference in the slope between the plots and/or the significant plot effect were observed in the best-fit models of each GLMM, interaction effects and/or the plot effect were set in the multiple linear regression models.

Possible explanatory factors of the multiple linear regression models were SWC, \( T_{\text{soil}} \), fine root biomass, and litter mass. In the multiple linear regression models, interaction effects on each explanatory factor were not considered, whereas the plot effects
were considered because of the results of GLMM analyses (see Results). All possible models with the combinations of explanatory factors were constructed; the total number of models was 31, with each model numbered from Model 1 to Model 31. AIC values for all the models were calculated and the best-fit model was determined according to the lowest AIC. The potential difference in \( R_{\text{soil}} \) between the plots due to each factor was independently assessed by applying differences in the average SWC, \( T_{\text{soil}} \), and fine root biomass between the plots to the best-fit model. In the calculation, other factors and intercept were set as zero. All statistical analyses were conducted using R ver. 3.1.3.

### 3. Results

#### 3.1 Differences in \( R_{\text{soil}} \), and environmental and biological factors

\( R_{\text{soil}} \) increased in the growing season and decreased in the dormant season, and this trend corresponded to seasonal variation in \( T_{\text{soil}} \) (Fig. 2). SWC was not correlated with \( T_{\text{soil}} \). The average \( R_{\text{soil}} \) in the UP and the LP was 2.49 ± 0.93 and 2.32 ± 0.68 µmol m\(^{-2}\) s\(^{-1}\), respectively. \( R_{\text{soil}} \) was not significantly different between the plots (\( P = 0.27 \)). SWC in the UP (0.19 ± 0.14 m\(^{3}\) m\(^{-3}\)) was significantly lower than that in the LP (0.32 ± 0.07 m\(^{3}\) m\(^{-3}\), \( P < 0.001 \)), and the difference was 0.13 ± 0.16 m\(^{3}\) m\(^{-3}\). \( T_{\text{soil}} \) in the UP (15.88 ± 0.32 °C) was significantly higher than that in the LP (15.18 ± 0.16 °C, \( P < 0.001 \)), and the difference was 0.70 ± 0.35 °C.

DBH and tree height were significantly lower in the UP compared with the LP (\( P < 0.05 \), Table 1). As a result, AGB was lower in the UP than in the LP. ABI in the UP was also much lower than that in the LP, whereas the annual LF in the UP was also lower compared with the LP. Accordingly, ANPP was lower in the UP than that in the LP. In contrast to the aboveground biomass, fine root biomass in the UP was significantly higher than that in the LP (\( P < 0.05 \)), and the difference was 178.6 g m\(^{-2}\). Litter mass on the soil and PAI were not significantly different between the plots (Table 1).

#### 3.2 Relationships of \( R_{\text{soil}} \) with environmental and biological factors

The best-fit models for each factor in the GLMMs are shown in Table 2. SWC was negatively correlated with \( R_{\text{soil}} \) (\( P < 0.01 \), Fig. 3a). The slope of the relationship was not different between the plots, whereas the plot effect was observed, which was a significant positive effect on LP (\( P < 0.05 \), Table 2, Fig. 3a). \( T_{\text{soil}} \) positively affected \( R_{\text{soil}} \) (\( P < 0.01 \)), and there were no differences in the slope between the plots and the plot effect was not observed (Table 2, Fig. 3b). Fine root biomass positively affected \( R_{\text{soil}} \) (\( P < 0.01 \)). Although different slopes between the plots were selected, the significant difference between the plots was not observed (\( P > 0.1 \)). The plot effect was also observed, implying a significantly positive effect of LP (\( P < 0.05 \), Table 2, Fig. 3c). Litter mass was not significantly correlated with \( R_{\text{soil}} \) (\( P = 0.84 \)). Thus, SWC, \( T_{\text{soil}} \), and fine root biomass significantly affected \( R_{\text{soil}} \) and the interaction effect of plots were not

### Table 1. Mean ± S.D. of biological factors and aboveground productivity in the upper plot (UP) and the lower plot (LP).

| Factor          | UP             | LP             |
|-----------------|----------------|----------------|
| DBH (cm)        | 15.5 ± 5.4 *   | 21.4 ± 6.0 *   |
| Height (m)      | 11.5 ± 2.0 *   | 15.6 ± 1.3 *   |
| Fine root biomass (g m\(^{-2}\)) | 391.6 ± 165.2 * | 213.1 ± 199.4 * |
| Litter mass (g m\(^{-2}\)) | 922.0 ± 281.2 | 1056.6 ± 417.8 |
| PAI (m\(^{3}\) m\(^{-2}\)) | 1.41 ± 0.12 | 1.37 ± 0.11 |
| AGB (MgC ha\(^{-1}\)) | 48.0 | 105.6 |
| ABI (MgC ha\(^{-1}\) year\(^{-1}\)) | 1.23 | 2.28 |
| LF (MgC ha\(^{-1}\) year\(^{-1}\)) | 1.59 | 1.99 |
| ANPP (MgC ha\(^{-1}\) year\(^{-1}\)) | 2.92 | 4.27 |

Abbreviations: DBH, diameter at breast height; PAI, plant area index; AGB, aboveground biomass; ABI, Aboveground biomass increment; LF, litterfall carbon; ANPP, aboveground net primary production.
observed, whereas the significant plot effects in the relationships of $R_{\text{soil}}$ with SWC and fine root biomass were observed, which enhanced $R_{\text{soil}}$ in the LP.

Because slopes in the GLMMs were not significantly different (Table 2), interactions of the plots with each environmental and biological factor were not considered in the multiple linear regression models. On the other hand, the plot effects were examined in the models because the significant plot effects in the models with SWC and fine root biomass were observed (Table 2). The top eight multiple linear regression models determined by AIC are shown in Table 3. The results showed that the best-fit model was Model 2, in which $T_{\text{soil}}$, SWC, fine root biomass, and the plot effects were set as explanatory variables. All the factors of Model 2 significantly affected $R_{\text{soil}}$ ($P < 0.05$). The plot effect enhanced $R_{\text{soil}}$ in the LP. The effect of litter mass was not important because the AIC of Model 1, in which all the factors were set as explanatory factors, was similar to that of Model 2. On the other hand, the AICs of the other models, in which neither of SWC, $T_{\text{soil}}$, fine root biomass, and the plot effect was set as an explanatory factor, were higher than that of the best-fit model.

By applying mean difference in SWC, $T_{\text{soil}}$, and fine root biomass to Model 2, the difference in SWC and fine root biomass between the plots resulted in a relatively large difference in $R_{\text{soil}}$.

Table 2. Summary of the results of GLMMs for $R_{\text{soil}}$ with fixed effects of each of the environmental and biological factors. The estimated values of slope, the plot effect and intercept for the best-fit models are shown. Bold values show a significant effect in the relationships ($P < 0.05$). Plot effect implies the difference of the lower plot (LP) from the upper plot (UP). Significant differences between the plots in each slope were not observed ($P > 0.1$).

| Explanatory factors | Slope UP | Plot effect | Intercept |
|---------------------|----------|-------------|-----------|
| SWC                 | -4.276   | 0.364       | 3.302     |
| $T_{\text{soil}}$   | 0.152    | --          | 0.048     |
| Fine root biomass   | 0.003    | 0.002       | 0.734     | 1.227     |
| Litter mass         | 0.002    | 0.002       | 0.625     | 2.410     |

Abbreviations: $T_{\text{soil}}$, soil temperature; SWC, soil water content.

Fig. 3. Relationships of soil respiration ($R_{\text{soil}}$) with (a) soil water content (SWC), (b) soil temperature ($T_{\text{soil}}$), and (c) fine root biomass in the upper plot (UP) (closed circles) and the lower plot (LP) (open circles). The results of fixed effects of the best-fit models of generalized mixed linear models (GLMMs) are shown for UP (solid line) and LP (dotted line). Significant differences in slope and the plot effect are shown; n.s. denotes no significance, and * denotes significant difference at $P < 0.05$. The intercepts in the figures show fixed effect and the results of random effect are not shown.

4. Discussion

4.1 Differences in environmental and biological factors between the plots

We observed significant differences in the environmental factors between the plots. SWC was significantly lower in the UP than in the LP. Lower SWC was also observed in upper slope in previous studies (Enoki et al., 1996; Tamai 2010). Generally, the soil water content decreases upslope because of hydrological processes. In addition, the lower dry soil bulk density, which was probably caused by the root mat in the UP, might be attributed to lower SWC in the present study. This might result in higher permeability, lower water storage ability, and therefore, lower SWC. $T_{\text{soil}}$ was also significantly different between the plots, but the difference was small. This might be because comparable PAI (Table 1) resulted in comparable solar radiation on the forest floor. These suggest that the difference in aboveground biomass partly affected the environmental factors.

ANPP and AGB were lower but the fine root biomass was higher in the UP than in the LP (Table 1). This result was similar to the results of previous studies, which found that limitation of N resources in upper slope positions resulted in high biomass allocation to belowground parts to increase the nutrient uptake (e.g., Tateno et al., 2004). In the present study, significantly lower P content and higher N:P ratio in the foliage were observed in the UP, whereas the N content and C:N ratio in the foliage were not different between the plots. The N:P ratio of the UP (18.10 ± 3.01) was higher than the criterion (i.e., 16), which indicates P limitation (Koerselman and Meuleman, 1996).

Accordingly, Chiwa et al. (2016) showed that P availability affected aboveground biomass productivity in this forest. In this forest, P availability might be more important for biomass
productivity rather than N because the bedrock in the present study site is serpentine, which is known to have a low P availability and high N deposition (e.g., Kitayama et al., 2000). Thus, difference in P availability could be one of the reasons that caused the differences in ANPP, AGB, and fine root biomass between the plots.

4.2 Effect of environmental and biological factors on \( R_{\text{soil}} \)

SWC was negatively correlated with \( R_{\text{soil}} \) in the multiple linear regression model. Previous studies have reported the relationship between \( R_{\text{soil}} \) and SWC as negative (e.g., Kosugi et al., 2007; Atkins et al., 2015; Piñol et al., 1995), positive (e.g., Sotta et al., 2004; Shi et al., 2011), or both (e.g., Davidson et al., 1998; Kang et al., 2003; Xu and Qi, 2001). Generally, \( R_{\text{soil}} \) correlates negatively with SWC in high SWC conditions, because SWC could impede O\(_2\) diffusion, thereby reducing rates of decomposition and microbial production of CO\(_2\), whereas \( R_{\text{soil}} \) correlates positively with SWC in low SWC conditions, because the activity of microorganism and root respiration could increase with SWC (Davidson et al., 1998). The difference in the relationships might be attributed to site-specific characteristics such as rainfall seasonality or soil properties. In our study site, higher CO\(_2\) production and diffusion under low SWC enhanced \( R_{\text{soil}} \) because the rainfall is distributed across a whole year and there is no dry period in the growing season. On the other hand, Ohashi and Gyokusen (2007) examined the spatial variation in \( R_{\text{soil}} \) on a slope in a Japanese cypress forest every season and found that soil hardness affected the spatial variation in \( R_{\text{soil}} \). They considered that soil hardness affected gas diffusivity, and therefore spatial variation in \( R_{\text{soil}} \). Although they did not measure biological factors, soil physical factors in addition to biological factors such as fine root biomass might mask the effect of SWC on \( R_{\text{soil}} \).

\( T_{\text{soil}} \) significantly affected \( R_{\text{soil}} \), similar to previous studies, and the relationship was consistent with the plots (Fig. 3). In addition to the environmental factors, fine root biomass significantly affected \( R_{\text{soil}} \) (Fig. 3). The multiple linear regression results showed that fine root biomass accounted for the additional spatial variation in \( R_{\text{soil}} \) that was not explained by SWC and \( T_{\text{soil}} \), because AIC and \( R^2 \) of the best-fit model including fine root biomass as an explanatory factor was better for other models without fine root biomass. Fine root biomass often determines the heterogeneity in \( R_{\text{soil}} \) (Katayama et al., 2009; Shibistova et al., 2002), and fine root biomass often differs with slope position (Enoki et al., 1996; Tateno et al., 2004). Thus, fine root biomass played an important role in understanding the heterogeneity in \( R_{\text{soil}} \) on a slope. Therefore, the inclusion of fine root biomass in the multiple linear regression model improved the accuracy of \( R_{\text{soil}} \) in the present study (Table 3).

4.3 Differences in relationship of \( R_{\text{soil}} \) with factors between the plots

Lower SWC, higher \( T_{\text{soil}} \), and larger amount of fine root biomass resulted in an increase in \( R_{\text{soil}} \) in the UP than LP, resulting from the negative relationships between \( R_{\text{soil}} \) and SWC and the positive relationships of \( R_{\text{soil}} \) with \( T_{\text{soil}} \) and fine root biomass (Table 4). On the other hand, we found the plot effect which enhanced \( R_{\text{soil}} \) in the LP in the multiple linear regression model. The plot effect canceled out the increase in \( R_{\text{soil}} \) caused by lower SWC, higher \( T_{\text{soil}} \), and fine root biomass, resulting in comparable \( R_{\text{soil}} \) between the plots with different aboveground biomass in the present study.

The plot effect in the multiple linear regression model suggests that other factors, different from SWC, \( T_{\text{soil}} \), and fine root biomass, might enhance \( R_{\text{soil}} \) in the LP. One of the possible causes is higher LF in the LP (Table 1). The origin of \( R_{\text{soil}} \) is divided into two components: belowground and aboveground. A belowground source translates to carbon from rhizosphere respiration and the decomposition of rhizosphere litter. The aboveground litter is an important source of decomposition.

Table 3. Summary of the results of multiple linear regression models for \( R_{\text{soil}} \). Bold values indicate a significant effect in the relationships (P < 0.05). The top eight models as determined by AIC are shown. Model 2, for which the explanatory factors were SWC, \( T_{\text{soil}} \), and fine root biomass with the plot effect, was selected as the best-fit model. Plot effect implies the difference of the lower plot (LP) from the upper plot (UP).

| Coefficients | SWC | Fine root biomass | Litter mass | Plot effect | Intercepts | Adjusted \( R^2 \) | AIC | \( \Delta \) AIC |
|--------------|-----|-------------------|-------------|-------------|------------|----------------|-----|--------------|
| Model 2      | -2.254 | 0.137            | 0.0017      | -0.004      | 0.510      | 0.079          | 0.480 | 496.6        |
| Model 1      | -2.165 | 0.137            | 0.0017      | -0.004      | 0.521      | 0.223          | 0.479 | 497.9        |
| Model 7      | -1.791 | 0.137            | 0.0012      | -0.003      | 0.631      | 0.922          | 0.438 | 509.6        |
| Model 3      | -1.723 | 0.137            | 0.0012      | -0.003      | 0.461      | 0.453          | 0.507 | 9.1          |
| Model 8      | -2.964 | 0.134            | --          | 0.008       | 0.366      | 0.382          | 0.440 | 509.9        |
| Model 6      | --     | 0.146            | 0.0022      | -0.008      | 0.332      | 0.710          | 0.436 | 510.2        |
| Model 10     | --     | 0.146            | 0.0022      | --          | 0.306      | 1.080          | 0.437 | 510.8        |

Abbreviations: \( T_{\text{soil}} \), soil temperature; SWC, soil water content; AIC, Akaike information criterion.
Table 4. Differences in the average soil water content (SWC), soil temperature \((T_{soil})\), and fine root biomass between the lower plot (LP) and upper plot (UP), along with the slope for each explanatory factor (Table 3) and the difference in \(R_{soil}\) caused by the difference in each factor between the plots, based on Model 2. The difference in \(R_{soil}\) was calculated individually by applying the differences in SWC, \(T_{soil}\), and fine root biomass to Model 2. The differences are calculated as LP minus UP, that is, negative values mean that LP is lower than UP.

| Differences in each factor \((LP - UP)\) | Slope | Difference in \(R_{soil}\) \((LP - UP)\) |
|-------------------------------|-----------------|----------------------------------|
| SWC \(0.13 \text{ (m}^2\text{ m}^{-3}\) | \(-2.254\) | \(-0.28 \text{ µmol m}^{-2} \text{s}^{-1}\) |
| \(T_{soil}\) \(-0.70 \text{ (°C)}\) | \(0.137\) | \(-0.10 \text{ µmol m}^{-2} \text{s}^{-1}\) |
| Fine root biomass \(-178.6 \text{ (g m}^{-2}\) | \(0.0017\) | \(-0.30 \text{ µmol m}^{-2} \text{s}^{-1}\) |
| Plot effect \(-6.5\) | \(-5.1\) | \(0.51 \text{ µmol m}^{-2} \text{s}^{-1}\) |
| Total \(-11.1\) | \(-8.6\) | \(-0.17 \text{ µmol m}^{-2} \text{s}^{-1}\) |

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