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The effect of landform on soil microbial activity and biomass in a Hyrcanian Oriental Beech stand

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Abstract:

Beech stands in Hyrcanian forests cover a hilly landscape with many topographical ridge–valley gradients or catenas. This study aims at providing important insights regarding the role of landscape shape and position on the drivers of soil microbial biomass and activity in these forest ecosystems. Variations in the depth profiles (0-15, 15-30 and 30-45 cm) of soil organic carbon (OC), total nitrogen (TN), soil water content (SWC), soil microbial respiration (SR), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and metabolic coefficient (qCO_2) were evaluated at different slope positions (the summit, shoulder, back slope, foot slope and toe slope) along both concave (C-shaped) and convex-shaped (V-shaped) catenas. The results of our study evidenced that catena shape and slope position significantly influenced most of the parameters evaluated, confirming the importance of topography in creating heterogeneity in soil properties. In general, the significantly greater soil microbial biomass and activities observed in C-shaped with respect to V-shaped catenas, and in lower with respect to upper slope positions was related to higher SWC, OC and TN contents. We concluded that spatial variability in water and substrate availabilities are important components in determining microbial activities and the cycling of limiting nutrients for plant growth in different microsite ecosystems present in catenas.

Key words: Carbon, Catena, Soil water content, Slope position, Respiration.

1. Introduction

Soil properties are a product of soil-forming factors including topography, vegetation, climatic factors and ecosystem management. Soil biological and biochemical properties may respond more rapidly than physical and chemical properties to management activities and perturbations. The biological component of soil is responsible for many soil functions, including the decomposition of organic debris, nutrient cycling, stabilization of organic matter, and soil-atmosphere gas exchange (Paz-Ferreiro and Fu, 2016). Variations in microbial activity pose one of the greatest current uncertainties, and are particularly poorly understood in forest soils (McCarthy and Brown, 2006). The important role that soil microorganisms play in the nutrient and energy-flow relationships of natural, as well as anthropogenically influenced ecosystems, has given rise to the need for easily measured biological indicators of ecosystem development and disturbance. Microorganisms are involved in the mineralization of soil organic matter leading to carbon (C) loss by respiration, and incorporation into the soil microbial biomass pool. As the second largest C flux between terrestrial ecosystems and the atmosphere (Kuzyakov, 2006; Raich and Tufekcioglu, 2000), soil respiration plays an important role in regulating soil C pools and cycling in terrestrial ecosystems such as forests (Luo et al., 2001; McCarthy and Brown, 2006; Saiz et al., 2006). Representing CO_2 release from the soil surface combined by metabolic activity of roots and free living and symbiotic heterotrophs (Hogberg et al., 2001; Wan and Luo, 2003), soil respiration is influenced by soil temperature (Rustad et al., 2001), soil water content (SWC) status (Liu et al., 2002), plant growth (Curiel Yuste et al., 2004), and soil C and nitrogen (N) availability (Franzluebbers et al., 2002). Soil microbial biomass is considered as an important indicator of soil biological fertility (Powlson et al., 1987), and holds important implications on the biogeochemical cycling of C and N in terrestrial ecosystems (Jenkinson, 1988).

More recently, it has been demonstrated that at large scales the spatial variability of soil respiration and microbial activity is organized by topographic factors such as altitude, landscape morphology and structure (Riveros-Iregui and McGlynn, 2009), and influenced by changing patterns of precipitation, temperature and humidity (Paz-Ferreiro et al., 2010). Environmental perturbations that affect these biotic and abiotic factors can alter soil respiration and microbial activity, with consequent impact on terrestrial C cycling and feedbacks to climate change (Cox et al., 2000). Spatial heterogeneity is an intrinsic characteristic in terrestrial ecosystems (Hook and Burke, 2000). Topography is well documented to cause variability of soil temperature, SWC, plant growth, and soil C and N contents (Hook and Burke, 2000; Liu et al., 2007), and consequent variations in soil respiration and microbial activity with slope directions (Kang et al., 2006) or even with positions in the same slope (Ohashi and Gyokusen, 2007). Ridge-Hilly structures are two dominant landscape elements in catchments and generally have different SWC and groundwater table regimes, leading to differences in soil properties and vegetation characteristics (McGlynn and Seibert, 2003).

Numerous studies have evaluated the effect of landscape position and land management on physical, chemical and biological soil properties (Yimer et al., 2006; Udawatta et al., 2008; Paz-Ferreiro et al., 2009; Paz-Ferreiro et al., 2010; Abrishamkesh et al., 2011). Past research has examined the spatial variability of soil microbial activity across landscapes and has revealed important spatial differences in CO_2 emissions. For example, altitude was found to be a significant factor that affected most soil biochemical properties (Yimer et al., 2006; Paz-Ferreiro et al., 2010), and microbial activity decreased with altitude (Margesin et al., 2009; Miralles et al., 2007). Soil water content is known to limit biological processes in soils (Li and Sarah, 2003), and also suppress the relative activity of certain groups of fungi, leading to a decrease in enzymatic activities and soil respiration (Allison and Treseder, 2008). Significant differences in soil respiration have been found between north- and south-facing slopes in the northern hemisphere (Kang et al., 2006), across wet and dry landscape positions

(Pacific et al., 2009; Riveros-Iregui et al. 2008; Webster et al., 2008), and as a result of the distribution, quantity, and quality of organic matter (Webster et al., 2008).

While progress has been made in understanding the key factors controlling soil microbial activity, our understanding of the changes in soil microbial properties in different catena shapes and positions is still limited. Hyrcanian forests are ridge valley structures with combined topographic convergence and divergence, contrasting aspects, multiple landscape elements, variable groundwater dynamics (Fazlollahi Mohammadi et al., 2016b) and, this heterogeneity in topography results in a heterogeneous land cover. This study therefore aims at providing important insights regarding the role of landscape shape and position on the drivers of soil microbial biomass and activity in these forest ecosystems. We tested the hypothesis that topography, in particular catena shape and slope position, may influence SWC, soil organic C (OC) and total N (TN) contents, consequently regulating soil microbial biomass and activity.

2. Material and methods
2.1. Study area

This research was carried out within the TMU (Tarbiat Modares University) Experimental Forest Station located in a temperate forest of the Mazandaran province in northern Iran, between 36°31′56″ N and 36°32′11″ N latitude and 51°47′49″ E and 51°47′56″ E longitude. The region has a humid-temperate climate based on Köppen classification, with mean annual temperature, rainfall and relative humidity of 10.5 °C, 858 mm and 75.2 %, respectively. The parent material is limestone and dolomite limestone (Sagheb Talebi et al., 2014), which belongs to the upper Jurassic and lower Cretaceous periods. Soils in the site were classified as Typic Endoaqualfs (Soil Survey Staff, 2014). Average cation exchange capacity of topsoils ranged from 10-12 $cmol_{(+)}kg^{-1}$, pH ranged from 6.0-7.5, and soil textures varied from silty clay loam to loam. Solum depths ranged from 87 to 150 cm depending on slope position. Although all soil profiles were generally characterized by O, A and B (Bt or Bht) horizons, those at the lower slope positions were more developed. Detailed soil profile descriptions for the site were provided elsewhere (Fazlollahi Mohammadi et al., 2016a).
Vegetation cover is characterized by a multistoried, multi-aged beech stand, dominated by *Fagus orientalis* Lipsky., *Carpinus betulus* L., *Alnus subcordata* C.A.Mey., and to a lesser extent, *Acer velutinum* Boiss. and *Tilia platyphyllos* Scop. Other tree species present in the area include *Quercus castaneifolia* C.A.Mey., *Cerasusavium* Moench., *Fraxinus excelsior* Bovéex. and *Acer cappadocicum* Gled. The density of the three dominant tree species was highest at lower slope positions and tended to decrease upslope (Fazlollahi Mohammadi et al., 2016b).

2.2. Data and sample collection

In the summer of 2013, we established a total of 30 quadrats at the site that encompassed two catena shapes and five catena positions. First we selected six catenas, three with a concave slope (called C-shaped hereafter) and three with a convex slope (called V-shaped hereafter). For each catena, five slope positions were located (the summit, shoulder, back slope, foot slope and toe slope), along a transect 20 m in width (Fig. 1). Aspect values were assigned to one category: north-east, in order to standardize aspect direction. At each of the five positions, a central point was delineated using a Garmin GPS model. Once transects were established, the elevation and slope of each position were recorded to verify field observations. From each slope position we collected composite soil samples from three depths (0-15, 15-30 and 30-45 cm). Samples were mixed completely, and roots and organic debris removed by hand. An aliquot was air dried and ground to < 2 mm for the determination of physical and chemical properties.

2.3. Soil analyses

Soil water content was determined on fresh soils by measuring weight loss after drying at 105°C for 24 h. Soil OC was determined on air dried samples using the Walkley-Black method (Allison, 1975), while TN was determined using a semi-Micro-Kjeldahl technique (Bremner and Mulvaney, 1982). For the determination of soil respiration, soil microbial biomass C and N the collected fresh soils were kept at 4˚C until analysis. Soil microbial respiration (SR) was determined by trapping the CO_2 evolved over a 3 day incubation at 25°C in a 0.05 M NaOH solution, and titrating against 0.1 M HCl (Alef, 1995). Soil microbial biomass C and N (MBC and MBN respectively) were determined using the chloroform fumigation-extraction method (Brookes et al., 1985). Soil microbial respiration and MBC were used to calculate the metabolic quotient (qCO_2), which is the amount of CO_2–C produced per unit of microbial biomass carbon (Anderson and Domsch, 1986).

2.4. Data processing

Prior to statistical analyses, normality and equality of variances were assessed for the calculated dependent variables using the Kolmogrov-Smirnov and Levene tests. The effects of catena shape and slope position on measured parameters were analyzed with three-way ANOVA utilizing a split-plot design using the F-test in SPSS Ver. 20 software. The Duncan's test at $P < 0.05$ was used to compare means of the dependent variables significantly affected by slope position. Correlations between soil characteristics were determined by calculating Pearson's correlation.

3. Results

3.1. Statistical analysis

The results of our study indicated that catena shape, slope position and soil depth generally influenced most of the soil characteristics analyzed. Mean and range of values obtained are reported in Table 1. All soil characteristics evaluated (SWC, OC, TN, SR, MBC and MBN) except qCO_2 showed significant differences with catena shape, catena position and soil depth (Table 2). Moreover, for all soil parameters except qCO_2 there was a significant interaction between catena shape and slope position. Significant interaction between catena shape and soil depth was observed for SWC and N. In addition, the variations in TN, MBN and MBC were influenced by the interaction between slope position and soil depth. Finally, OC and TN also showed a significant interaction between catena shape, slope position and soil depth varied (Table 2).

3.2. Catena shape, slope position and soil depth

SWC was significantly greater in C-shaped compared to V-shaped catena (mean values of 38.42 and 22.04%, respectively; Fig. 2). Moreover, SWC tended to increase along the catena with lowest contents at the summit and highest contents in the toe slope (26.82 and 37.78% average values, respectively). SWC generally decreased with soil depth however, the significant interaction between catena shape and soil depth suggested that this decrease only significant in C-shaped catena (Fig. 3).

Organic C contents were significantly greater in C-shaped compared to V-shaped catena (1.24 and 1.05% average values, respectively). Moreover, OC tended to increase along the catena with lowest contents at the summit (mean of 1.05%) and highest contents in the toe slope (mean of 1.32%; Fig. 2). However, the significant interaction between catena shape and slope position suggested that this increasing trend was limited to C-shaped catena, while no differences were observed in OC contents of soils in different positions along the V-shaped catena (Fig. 3). Soil OC contents generally

decreased with soil depth in both catena shapes and at all positions except for foot slope and toe slope positions in the C-shaped catena where OC contents were relatively high throughout the soil profile with no significant differences with depth (Fig. 3).

Total N contents were influenced by catena shape and tended to increase along the catena in a similar way for both C- and V-shaped catenas (0.11 and 0.09% average values, respectively). In fact, TN was significantly higher in toe slope (mean 0.15%) and foot slope (mean 0.12%) position with respect to the summit, shoulder, and back slope (0.07-0.09% average values; Fig. 2). However, the significant interaction between catena shape and slope position suggested that this increasing trend was seen along both C-shaped and V-shaped catenas (Fig. 4). As for OC, soil TN contents generally decreased with soil depth in both catena shapes and at all positions especially for foot slope and toe slope positions with significant differences with depth (Fig. 4).

Both MBC and MBN were significantly higher in C-shaped with respect to V-shaped catena (Fig. 5). However, both variables showed a significant interaction between catena shape and position. In fact, significant differences in MBC and MBN were observed between different positions of the V-shaped catena, with mean values of 318.05 mg C kg^{-1} and 47.26 mg N kg^{-1}, respectively. On the other hand, C-shaped catena showed significantly higher MBC and MBN in the toe slope (mean values of 757.15 mg C kg^{-1} and 113.07 mg N kg^{-1}), and higher MBN in the foot and toe slope, with respect to the other positions in the catena that, in contrast, showed relatively low values similar to those obtained for the V-shaped catena. In all cases both MBC and MBN decreased with soil depth with highest mean values of 712.1 mg C kg^{-1} and 96.89 mg N kg^{-1} in correspondence with the 0-15 cm depth.

Soil respiration was significantly greater in C-shaped compared with V-shaped catenas (0.58 and 0.3 mg CO_2-C g^{-1} d^{-1} average values, respectively), and like OC tended to increase along the catena (Fig. 2). However, the significant interaction between catena shape and position for this variable showed that this increase in SR was only significant for the C-shaped catena with mean values ranging from 0.25 to 0.61 mg CO_2-C g^{-1} d^{-1} at the shoulder and toe slope positions, respectively (Fig. 5). As expected, SR decreased rapidly with soil depth or was significantly higher at 0-15 cm (0.63 mg CO_2-C g^{-1} d^{-1}) than in 15-30 cm (0.36 mg CO_2-C g^{-1} d^{-1}) and 30-45 cm (0.31 mg CO_2-C g^{-1} d^{-1}).

The metabolic quotient was not significantly influenced by catena shape, slope position and soil depth. The results of correlations between soil characteristics by calculating Pearson's correlation indicated that all soil characteristics were generally inter related except for qCO_2 that seemed to be only correlated to MBC and MBN (Table 3).

4. Discussion

Topographically induced microclimates can affect soil microbial activity by constraining microsite factors, such as soil temperature and soil water contents, but also the availability of organic C. Consequently, the influence of topography on microclimatic conditions introduces a level of uncertainty in forecasting soil microbial activity at landscape and larger regional scales (Kang et al., 2000). Because most Hyrcanian forests are distributed across ridge and valley montane areas, and regional climates vary considerably, interaction between local topography and climate are likely to have a strong influence on local and regional estimates of soil microbial activity rates (Fazlollahi Mohammadi et al., 2016b). This study has highlighted the importance of topography in creating heterogeneity in soil properties in line with previous studies (Pacific et al., 2009; Sotta et al., 2006; Webster et al., 2008). Soils develop in response to three-dimensional processes along the hillslope catena connected by the flow of water, and particulate and dissolved materials (Sotta et al., 2006).

There is evidence for the movement of matter within small watersheds due to soil erosion occurring in the back slope and shoulder, and soil deposition in the foot slope and toe slope positions (Moorman et al., 2004). This was confirmed by our results that showed significantly lower OC and TN contents for the back slope, summit and shoulder with respect to foot slope and toe slope elements.

Overall, we observed that position in the landscape affects the accumulation and redistribution of water, nutrients, sediments and organic matter. Apart from their influence on soil processes on the small scale, soil water content (Xu and Qi, 2001), soil substrate quality, vegetation (Raich & Tufekcioglu, 2000), and disturbance regime has been also shown to affect soil microbial activity in forested ecosystems at larger geographic scales, perhaps even more than soil temperatures alone. Because a variety of factors can influence landscape and latitudinal-level variations in soil microbial activity rates, estimates of soil microbial activity at larger spatial and temporal scales require a better understanding of these factors to increase the reliability of regional estimates and improve the understanding of global terrestrial carbon fluxes (Rustad et al., 2000; Savin et al., 2001).

We found higher SR, MBC and MBN in the lower than upper slope positions (Fig. 2). These findings are consistent with the results of Liu et al. (2007). Several possible reasons could explain the response pattern of soil microbial activity to topography observed in this study. Typically higher soil microbial biomass at lower slope positions has been associated to the transfer and deposition of organic matter from steeply sloping soils (Chen and Chiu, 2000). Soils on ridges and upper slopes will tend to loose soil particles and organic matter that will tend to accumulate on lower slopes and in depressions. This is consistent with the more developed soils observed at the base of the slopes with higher solum depth and more horizons (Fazlollahi Mohammadi et al., 2016a), as well as the strong positive correlation between SR, MBC and MBN, and OC and TN (Table 3).

In forest ecosystems, SWC represents the primary limiting factor for plant growth, net primary productivity, and microbial activities (Liu et al., 2007). We observed a significant correlation between soil microbial activities and SWC (Table 3), indicating that significant differences in the drivers of soil microbial activities can exist as a function of landscape shape and position. Generally, soils in lower-slope positions will tend to have a wetter SWC regime for a longer period (Murphy et al., 2010). Higher SWC, and higher and more persistent ground-water tables are often observed in convergent (McGlynn and Seibert, 2003), depressional (Parkin et al., 2005), lower slope positions (Sotta et al., 2006; Pacific et al., 2009; Xu and Wan, 2008) with respect to high upslope areas (Jencso et al., 2009; Pacific et al., 2010). This can result in greater plant growth, belowground C allocation as well as litter decomposition (Wan et al., 2007), providing more C substrate for the activities and respiration of soil microorganisms (Franzluebbers et al., 2002; Saiz et al., 2006; Liu et al., 2007). This was consistent with the presence of a more productive plant community observed at the base of the hill (Fazlollahi Mohammadi, 2016b), and the microbial biomass may has been influenced by vegetation patterns. In addition, greater water availability in the lower slope can also directly stimulate auto- and heterotrophic activities and respiration. This variability in SWC can in turn affect the microbial biomass and activity and consequently organic C and N cycling (Moldrup et al., 2001; Schwendenmann et al., 2003; Sjogersten et al., 2006; Sotta et al., 2007).

Soil microbial activity, OC and TN were greater in the C-shaped with respect to V-shaped catena. These results indicate that relatively wet, nitrogen-rich conditions promote higher soil microbial activities confirmed by the significant correlation between these parameters (Table 3). These results are consistent with the observations reported by Raich et al. (2002). SWC was greater at C-shaped with respect to V-shaped catena, and this characteristic can directly influence microbial activities and respiration (Table 3). These results are consistent with the findings of Rustad et al.

(2001) and Scott-Denton et al. (2006) and/or indirectly via altering plant growth and belowground C allocation as well as litter decomposition (Wan et al., 2007), which determine the availability of C substrate for soil microorganisms. Soil microbial communities are often limited by C or N (Broughton and Gross, 2000). On the other hand, soil microbial activity spatial patterns were better explained by SWC (Table 3). Kang et al. (2003) concluded that a convex-type function better describes topography-driven heterogeneity in soil respiration rates where topography produces spatially heterogeneous SWC. Both of their incubation and field measurements suggested a convex-type function relating soil respiration to SWC (Raich et al., 2002) that attains maximum levels near soil field saturation capacity as discussed by Davidson et al. (2000). Our results suggest that slope-specific micro-climates generate heterogeneous distributions of SWC, and thus soil respiration and microbial activities within and between slopes (Kang et al. 2003) as simulated by Kang (2001).

Despite the above findings, the mechanism causing the spatial variability was not clear because physical and topographical factors are not related to soil microbial activities directly, but rather indirectly through their effect on direct factors such as soil gas diffusivity, root biomass (Hanson et al., 1993; Fang et al., 1998) nutrient and OC availability (Scott-Denton et al., 2003; Adachi et al., 2006). In general, landform (catena shape, slope position) and soil depth can affect soil microbial biomass and activities, by influencing soil SWC, OC and TN contents. Because local topography influences incident solar radiation (Kang et al., 2002), evapotranspiration (Kang, 2001), and subsurface water redistribution (White et al., 1998), the spatial distribution of SWC is subsequently controlled by slope-specific microclimates created by local topography.

5. Conclusion

Our study on the effect of landform and soil depth on soil microbial biomass and activity and their dependence on SWC, OC and TN showed that catena shape, slope position and soil depth were important in determining the spatial variability of these parameters in the virgin forest in northern Iran. Due to its greater SWC, C-shaped catena had significantly higher OC, SR, MBC, and MBN than the V-shaped one. On the other hand, the lower slope position had greater soil microbial activity than the upper slope and the soil microbial activities decreased with increasing soil depth. We concluded that spatial variability in SWC and OC are important components in determining microbial activities and the cycling of limiting nutrients for plant growth in different microsite ecosystems present in catenas.

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FIGURES
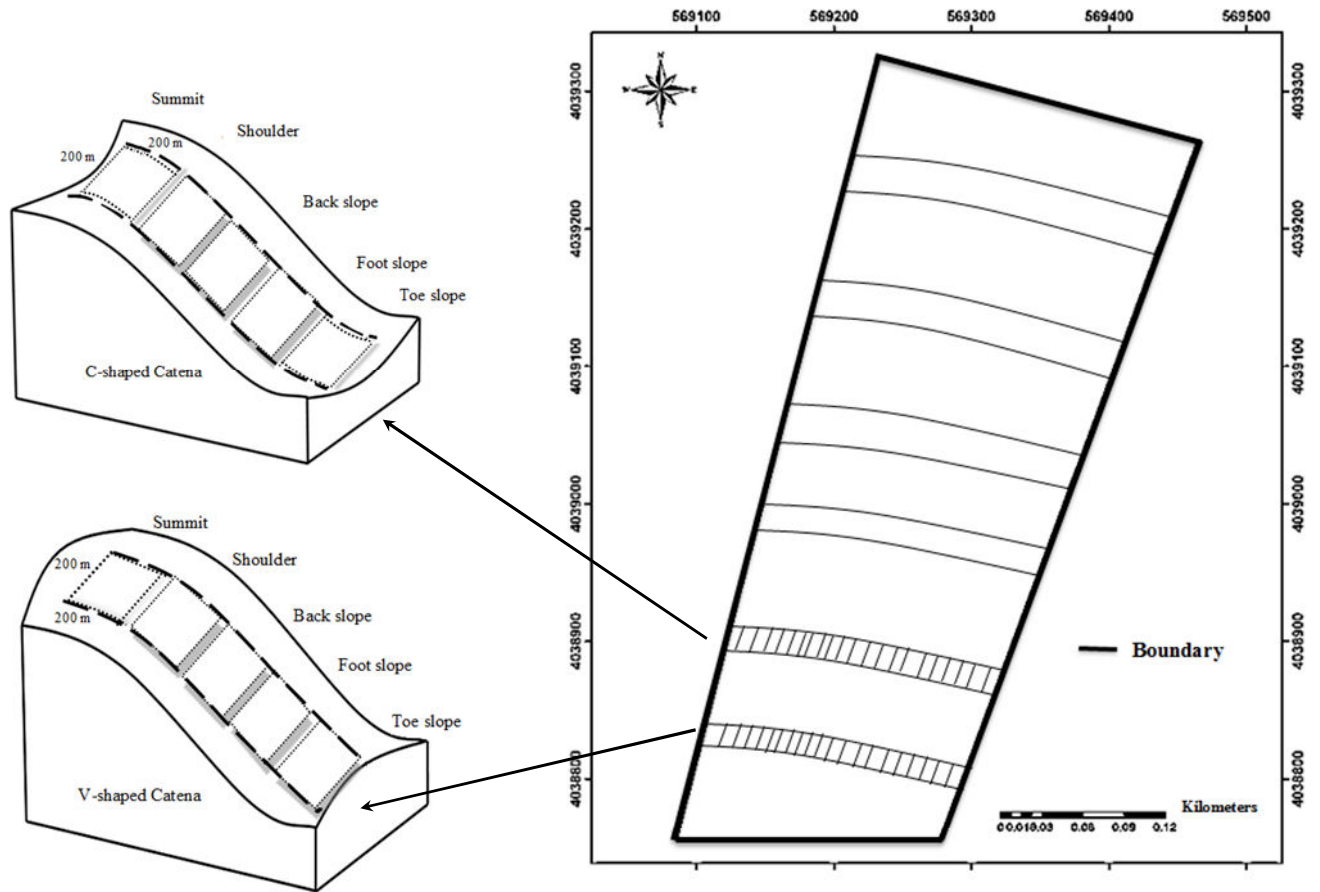
Fig. 1 Soil sampling scheme in the Experimental Forest Station of Tarbiat Modares University (TMU) in Mazandaran Province, Northern Iran.
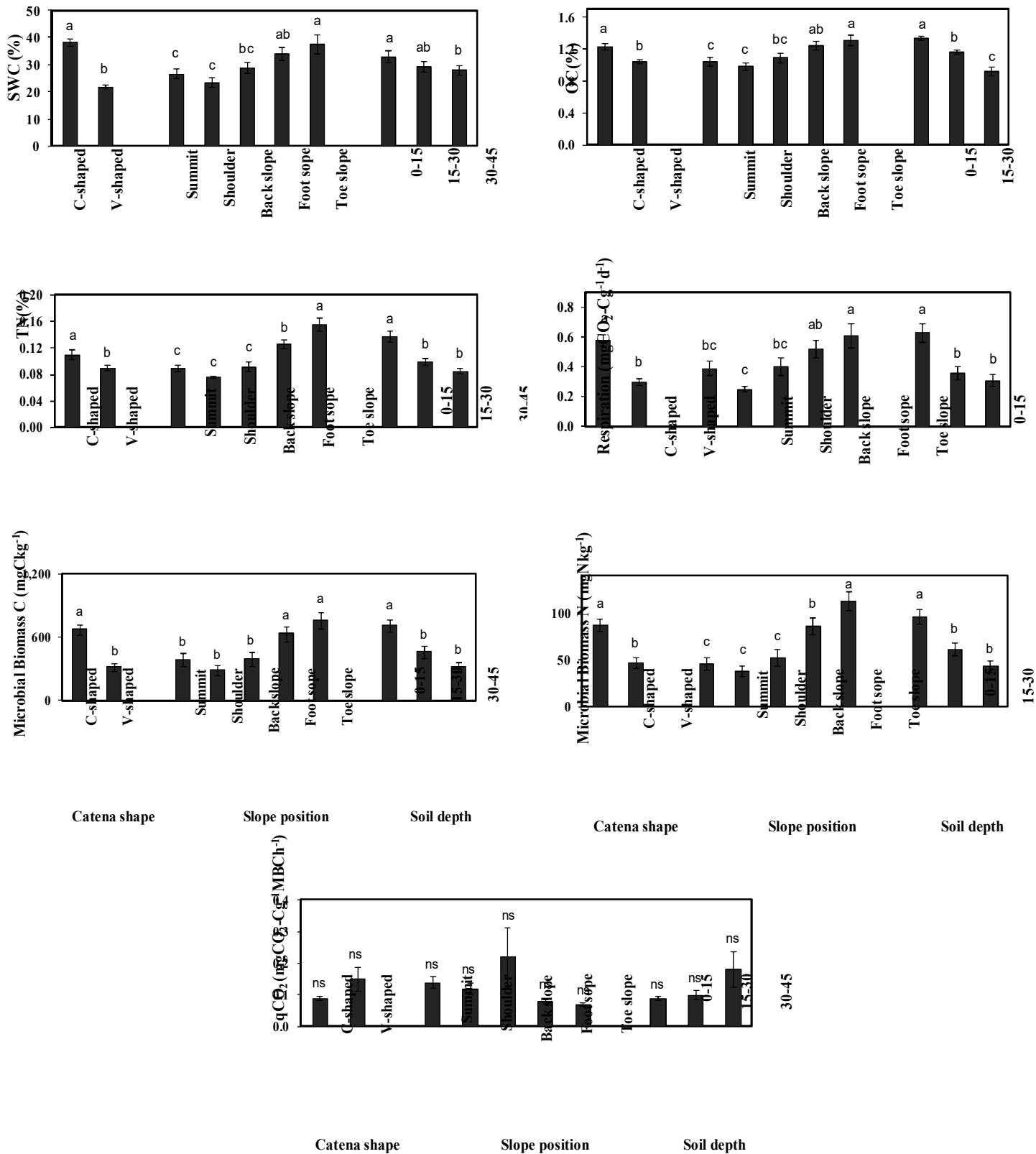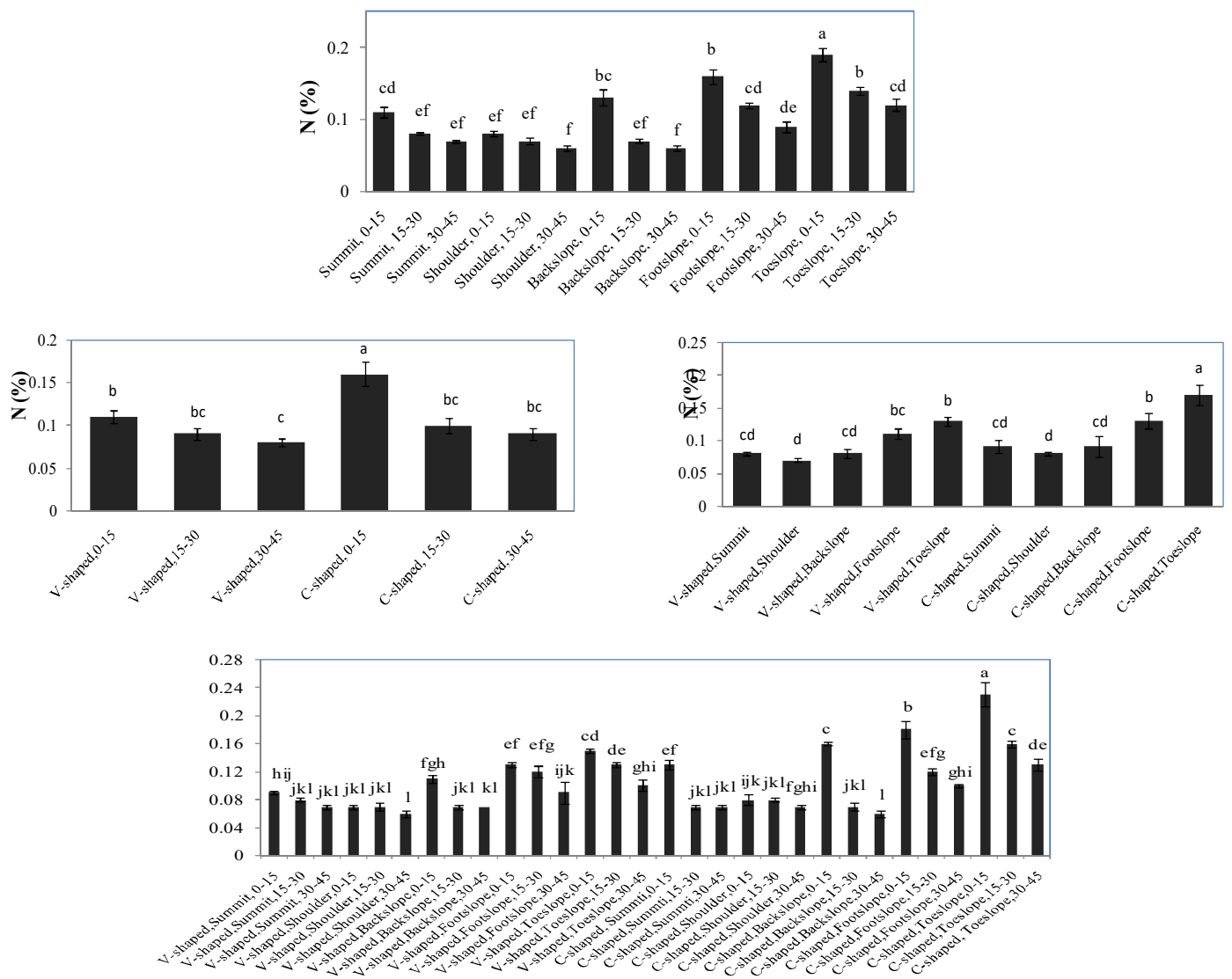
Fig. 2 Mean values of soil characteristics across different catena shapes, slope positions and soil depths. Different letters indicate significant differences between catena shapes, slope position or soil depths while ns indicate no significant differences.
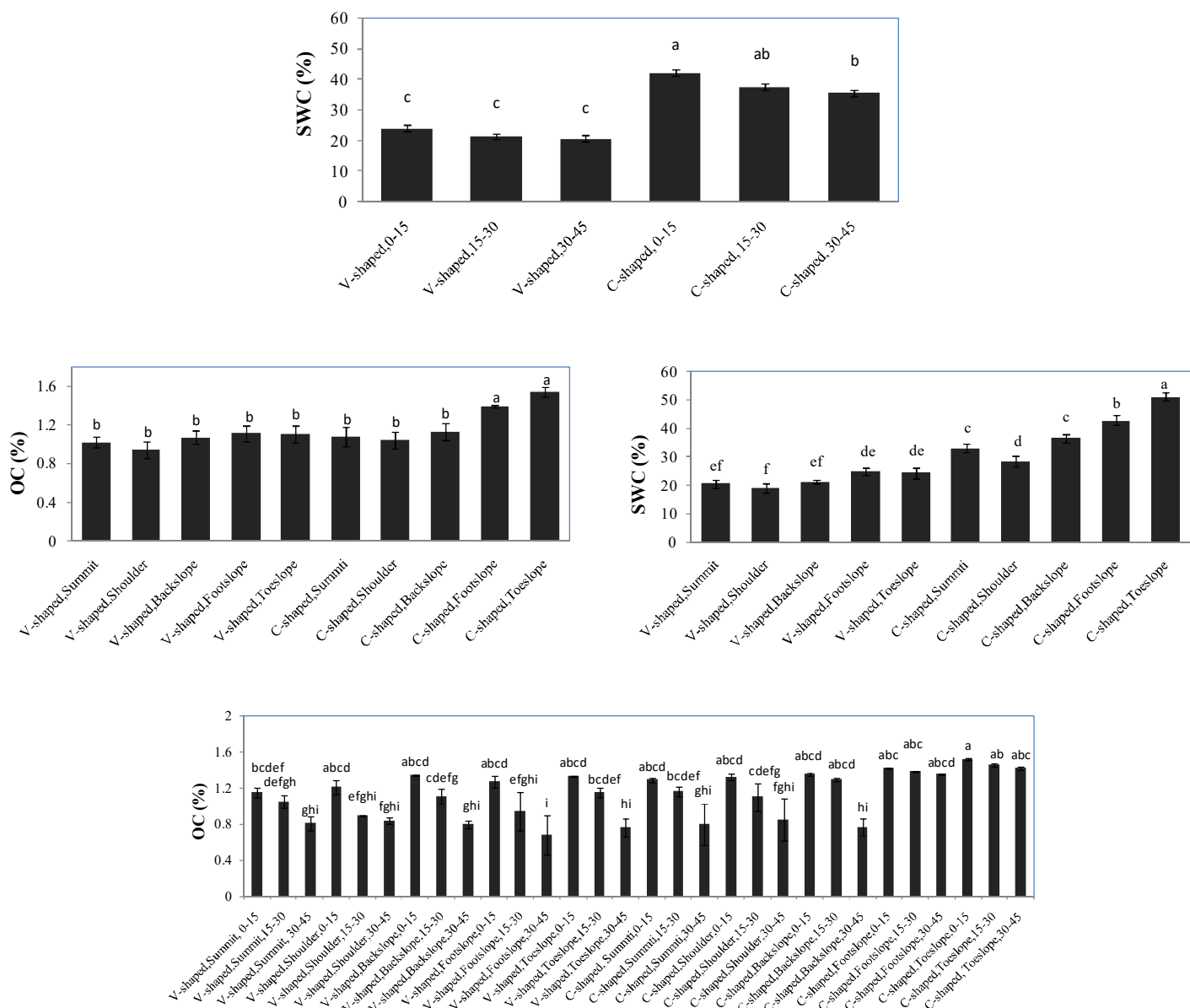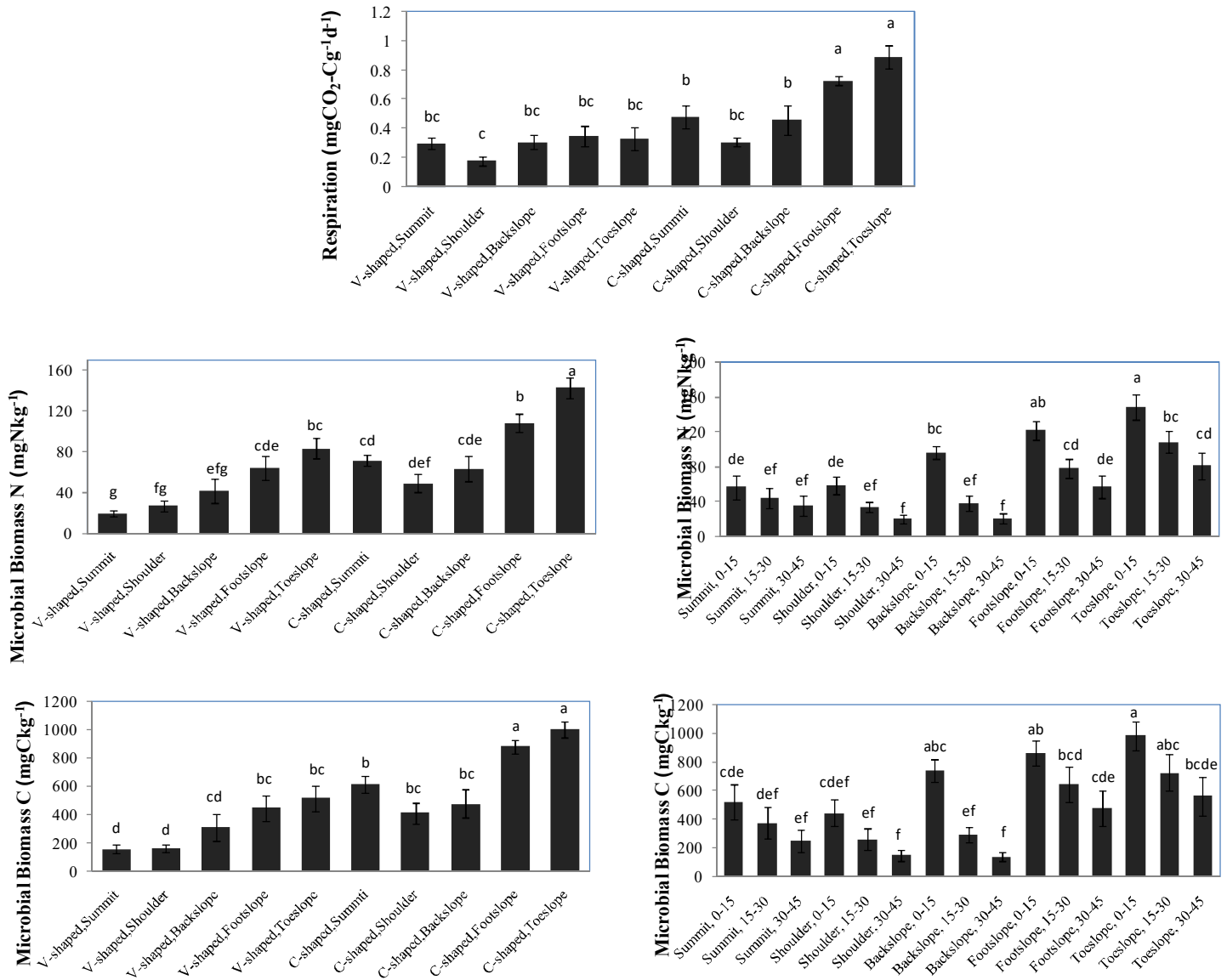
Fig. 3 Interactions between catena shape, slope position and soil depth on SWC and OC. Different letters indicate significant differences between mean values.

Fig. 4 Interactions between catena shape, slope position and soil depth on TN. Different letters indicate significant differences between mean values.

Fig. 5 Interactions between catena shape, slope position and soil depth on SR, MBN and MBC. Different letters indicate significant differences between mean values.

Table 1. Range of values for soil characteristics

	SWC (%)	OC (%)	TN (%)	SR (mg CO_2-C g^{-1} d^{-1})	MBC (mg C kg^{-1})	MBN (mg N kg^{-1})	qCO_2 (mg CO_2-C g^{-1} MBC h^{-1})
Minimum	12.2	0.35	0.05	0.07	60	10	0.01
Average	30.2	1.14	0.10	0.44	497	67	0.12
Maximum	57.3	1.83	0.27	1.50	1234	199	0.37

SWC, soil water content; OC, organic carbon; TN, total nitrogen; SR, soil microbial respiration; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; qCO_2, metabolic quotient.

Table 2. Results of multivariate ANOVA for soil characteristics at the different catena shapes, slope positions and soil depth.

Sources	SWC	OC	TN	SR	MBC	MBN	qCO_2
Repeat	ns	ns	ns	ns	ns	ns	ns
Shape of catena (A)	45.65*	47.23*	22.50*	37.53*	87.06*	315.40**	ns
Catena positions (B)	13.87*	34.50**	180.00**	29.08**	43.56**	92.59**	ns
Interaction (A × B)	4.85**	12.80**	10.00**	14.58**	5.28*	6.84**	ns
Soil Depth (C)	72.98**	64.67**	244.91**	41.61**	99.97**	132.44**	ns
Interaction (A×C)	6.19**	ns	41.93**	ns	ns	ns	ns
Interaction (B×C)	ns	ns	13.60**	ns	2.66*	5.09**	ns
Interaction (A×B×C)	ns	2.19*	3.61**	ns	ns	ns	ns

Values represent F values based on split-plot design. *P(F) < 0.05; **P(F) < 0.01; ns: not significant (P(F) > 0.05). SWC, soil water content; OC, organic carbon; TN, total nitrogen; SR, soil microbial respiration; MBC, soil microbial biomass carbon; MBN, soil microbial biomass nitrogen; qCO_2, metabolic quotient.

Table 3. Pearson's correlation coefficients between the soil characteristics

	SWC	OC	TN	Respiration	MBC	MBN
SWC	1	-	-	-	-	-
OC	0.608**	1	-	-	-	-
TN	0.640**	0.724**	1	-	-	-
SR	0.734**	0.721**	0.738**	1	-	-
MBC	0.756**	0.745**	0.786**	0.844**	1	-
MBN	O.753**	0.722**	0.862**	0.800**	0.931**	1
qCO$_2$	-0.161	-0.194	-0.187	-0.104	-0.314**	-0.311**

Values represent the Pearson's correlation coefficients; *$P < 0.05$; **$P < 0.01$.