

# Effect of land-use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems



Holger Pabst<sup>a,\*</sup>, Anna Kühnel<sup>b</sup>, Yakov Kuzyakov<sup>a,c</sup>

<sup>a</sup> Department of Soil Science of Temperate Ecosystems, University of Göttingen, Germany

<sup>b</sup> Department of Soil Physics, University of Bayreuth, Germany

<sup>c</sup> Department of Agropedology, University of Göttingen, Germany

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## ABSTRACT

Microbial biomass carbon (MBC) and water-extractable organic carbon (WOC) – as sensitive and important parameters for soil fertility and C turnover – are strongly affected by land-use changes all over the world. These effects are particularly distinct upon conversion of natural to agricultural ecosystems due to very fast carbon (C) and nutrient cycles and high vulnerability, especially in the tropics. The objective of this study was to use the unique advantage of Mt. Kilimanjaro – altitudinal gradient leading to different tropical ecosystems but developed all on the same soil parent material – to investigate the effects of land-use change and elevation on MBC and WOC contents during a transition phase from dry to wet season. Down to a soil depth of 50 cm, we compared MBC and WOC contents of 2 natural (*Ocotea* and *Podocarpus* forest), 3 seminatural (lower montane forest, grassland, savannah), 1 sustainably used (homegarden) and 2 intensively used (maize field, coffee plantation) ecosystems on an elevation gradient from 950 to 2850 m a.s.l. Independent of land-use, both MBC and WOC strongly increased with elevation on Mt. Kilimanjaro corresponding to ecosystem productivity and biodiversity. Through the agricultural use of ecosystems MBC and WOC contents decreased – especially in surface layers – on average by 765 mg kg<sup>-1</sup> for MBC and 916 mg kg<sup>-1</sup> for WOC, compared to the respective natural ecosystems. The decrease with depth was highest for forests > grasslands > agroecosystems and also was positively correlated with elevation. We conclude that MBC and WOC contents in soils of Mt. Kilimanjaro ecosystems are highly sensitive to land-use changes, especially in topsoil. The MBC and WOC contents were considerably reduced even in sustainable agricultural systems. Since MBC and WOC are very fast reacting and sensitive C pools, we expect a decrease in other soil C pools accompanied by a strong decrease in fertility and productivity due to changes in land use from natural to agricultural ecosystems.

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## 1. Introduction

Land-use and climate change, habitat destruction as well as other human perturbations strongly alter natural ecosystems. Understanding these responses is crucial to forecast the sustainability of environmental services. Tropical ecosystems are known for high biodiversity and for important effects on global climate and biogeochemical cycles, especially on C turnover and sequestration (Detwiler and Hall, 1988; Gascon et al., 1999; Katovai et al., 2012; Malhi and Phillips, 2004). Due to faster transformation processes during litter decomposition, tropical soils have higher turnover rates than soils in colder climates (Zech et al., 1997). Therefore, tropical ecosystems are in special focus in recent studies concerning anthropogenic disturbances and C budgets (Don et al., 2011; Houghton and Goodale, 2004). Conversion from natural to

agricultural ecosystems led to an average decrease in C stocks of 25–30% (Don et al., 2011; Houghton and Goodale, 2004). Organic carbon contents in both moist and dry soils in tropical ecosystems are especially altered by land-use change (Ogle et al., 2005).

Several studies have been conducted on soil microbial biomass in tropical ecosystems. For example, Sanginga et al. (1992) described the importance of soil microorganisms for sustainability of agricultural soils in tropical ecosystems. Management practices, such as tillage, also influence soil microbial activity (Calderón et al., 2000). Singh and Yadava (2006) investigated the dynamic of microbial biomass in soils in north-east India and found a decrease of 16% in microbial biomass within four years after the conversion from grassland into an agroecosystem.

The increasing demand for agricultural land directly accelerates deforestation and a decrease of up to 75% in both soil organic carbon C and microbial biomass was recorded for the conversion from forest to agricultural ecosystems (Lemenih et al., 2005; Houghton and Goodale, 2004; Waldrop et al., 2000). Although deforestation is a common practice for the conversion of natural to agricultural

\* Corresponding author. Tel.: +49 551 39 33505.

E-mail address: [hpabst@gwdg.de](mailto:hpabst@gwdg.de) (H. Pabst).

managed land-use systems, afforestation has become a much discussed topic in recent years. In a few years after abandoning agriculture, soil microbial biomass contents are nearly as high as in the natural forests (Maithani et al., 1996; Templer et al., 2005). Consequently, microbial biomass is a sensitive C (and N) pool responding to land-use changes much faster than total organic matter and the most other C pools in soils (Hu et al., 1997; Powlson et al., 1987; Trumbore et al., 1996).

Most studies on land-use change effects on tropical ecosystems were conducted on the Southern American or Asian continent. Processes, nutrient stocks and biological diversity during land-use change in the tropical part of Africa remain widely unknown. This is despite the fact that East Africa's forest area has an annual decrease rate of 1.01% (2000–2010) (FAO, 2011), which is amongst the highest in the world. Due to its unique topographical conditions as an isolated high mountain, Mt. Kilimanjaro offers outstanding potential to investigate land-use changes in African tropical habitats along an elevation gradient. This reflects with at least two facts. First, tropical ecosystems from dry savannah to montane rainforest are present at different elevations of Mt. Kilimanjaro (Hemp, 2006a). Second, most soils originated from similar parent material (volcanic ash) and have similar age (<400 ky) (Schrumppf, 2004). Consequently, according to the soil forming factors concept (Jenny, 1994), the main differences in soil properties are connected with climate and vegetation (which is a function of climate) as well as land-use. Dry and rainy seasons are two extrema in tropical ecosystems which have a major influence on productivity, nutrient cycling and microbial biomass. Several studies report seasonal variability of microbial biomass, but depending on ecosystem, the highest contents of soil microbial biomass were found in both, dry (Maithani et al., 1996; Montaña et al., 2007) and wet seasons (Devi and Yadava, 2006). This was mostly explained by the general effect of soil moisture on microbial biomass (Wardle and Parkinson, 1990). Nonetheless, the processes and dynamics during the transition seasons remain mostly unknown. Eaton (2001) detected a fast and significant effect of wet-to-dry and dry-to-wet transitions on microbial activity and nutrient cycling in Belize, Central America. Apparently, no attempt has been made to investigate the soil microbial properties during a climatic transition phase in Eastern Africa.

The occurrence of each, two pronounced dry and wet seasons, contributes to the high soil fertility in the Kilimanjaro region. Kaihura et al. (1999) found higher SOC contents and nutrient use efficiency in Kilimanjaro soils compared to other regions in Tanzania. Investigations of the montane rainforest of Mt. Kilimanjaro by Schrumppf et al. (2006, 2007) showed low inputs of nutrients through rainfall and due to the combination of low nutrient availability and high plant uptake, small to no losses of base cations by leaching were assumed. Despite the studies above, little is known about the biogeochemical – especially the microbial – properties of the soils of Africa's highest mountain.

Today, 1.4 Mio. people inhabit the Kilimanjaro region, with 79% of them living in rural areas (103 persons km<sup>-2</sup>) (National Bureau of Statistics, 2006). This has a strong influence on the ecosystems, including land-use change due to a higher demand of agricultural land, anthropogenically induced fires, illegal logging and the introduction of new plant species through tourism (Hemp, 2008, 2009; Lambrechts et al., 2002; Soini, 2005; Torbick et al., 2009). The agricultural productivity in the East African region varies enormously during the year and is strongly affected by climatic change (Thornton et al., 2009). Due to the slow plant growth and nutrient uptake during dry seasons, the reported high amounts of microbial biomass retain nutrients (Singh et al., 1989). In the rainy seasons fast plant growth and root activity as well as drastic changes in soil moisture stimulate fast turnover of microbes (Fierer and Schimel, 2003). This leads to lower microbial biomass contents and

increasing CO<sub>2</sub> efflux rates (Otieno et al., 2010; Singh et al., 1989; Sugihara et al., 2010). Hence, it is assumed that in tropical ecosystems with a bimodal climatic pattern soil microbes represent both a sink and source of nutrients (Srivastava, 1992).

We therefore used the advantages of Mt. Kilimanjaro to simultaneously observe several natural and anthropogenically affected ecosystems. In the present study we analyzed microbial biomass carbon (MBC) and water extractable organic carbon (WOC) in eight ecosystems at increasing altitudes on Mt. Kilimanjaro on a monthly basis during the transition phase from March to May (dry-to-wet). We assumed that the increasing precipitation during the transition from dry to wet season affects soil microbial biomass.

This study focused on three hypotheses: (1) land-use changes from natural to agricultural ecosystems strongly affect the contents of MBC and WOC. (2) Temporal changes of MBC and WOC contents during the transition phase from dry-to-wet season are affected by elevation as the temperature and precipitation patterns change with altitude. (3) Stronger changes in MBC and WOC during the transition from dry to wet seasons are expected in the topsoil as compared to deeper soil layers.

Our objectives within this study at Mt. Kilimanjaro were (1) to assess the dynamics of soil MBC and WOC during the transition from dry to wet season; (2) to assess the effect of land-use on soil microbial biomass and WOC; and (3) to obtain an overview of the effect of altitude and climate on soil microbial biomass and WOC.

## 2. Materials and methods

### 2.1. Study area

This study was conducted at the southern slopes of Mt. Kilimanjaro (3°4'33"S 37°21'12"E), located in the northeastern region of Tanzania. Soil sampling was performed in the Machame area of Kilimanjaro National Park, as well as in the southern areas Kibosho and Kilema and in the southeastern region of Lake Chala from March to May 2012. This time period of three months marked the transition period from dry to wet season. Eight sites in eight different natural and anthropogenically affected ecosystems were investigated, i.e., savannah, Chagga homegardens, coffee plantation, maize field, grassland, lower montane forest, *Ocotea* forest and *Podocarpus* forest. The elevation of the investigation sites varied between 950 m and 2850 m above sea level (Table 1). The respective vegetation was described in detail by Axmacher (2003) and Hemp (2006a,b,c) and approximations for net primary production (NPP) in tropical ecosystems were presented by Clark et al. (2001) and Schuur (2003). The investigated sites were classified in land-use classes, i.e. natural, seminatural, sustainably and intensively used (Table 1). Natural ecosystems did not show considerable disturbances, whereas seminatural plots were altered through collection of firewood and occasional mowing. Intensively used ecosystems were characterized by mechanical cultivation, the use of pesticides and relatively frequent fertilization. Fernandes et al. (1985), Fernandes and Nair (1986) and Hemp (2006b) described the sustainably used agroecosystem referred to as homegarden, which mostly developed through anthropogenic influence on the lower montane forests of Mt. Kilimanjaro. To satisfy the demand of building material, firewood and farmland, lower montane forests are often also converted to grasslands which subsequently could be used to establish coffee plantations. The rising demand for farmland leads also to the clear cutting of *Acacia* trees in the savannah and to ground suitable for maize cultivation. Soils from the Kilimanjaro area are described as Andosols and the pH of the investigated ecosystems was between 3.5 and 5.8 (Table 1). The bulk density and soil organic carbon contents in the surface layer were in the range of 0.26–1.21 g cm<sup>-3</sup> and 14.54–214.57 mg g<sup>-1</sup>, respectively (Table 1).

**Table 1**  
Land-use, abiotic and physico-chemical properties of the investigated ecosystems on the southern slope of Mt. Kilimanjaro at 0–10 cm depth.

Ecosystem	Elevation (m a.s.l.)	Precipitation <sup>a</sup> (mm yr <sup>-1</sup> )	Temperature <sup>b</sup> (°C)	Land-use type	pH (1:2.5 KCl)	Organic C (mg g <sup>-1</sup> )	Total N (mg g <sup>-1</sup> )	C/N	Bulk density (g cm <sup>-3</sup> )
<i>Podocarpus</i> forest	2850	1250	10.5	Natural	3.83	205.91	10.01	20.56	0.26 ± 0.03
<i>Ocotea</i> forest	2120	1850	14.0	Natural	3.49	214.57	12.37	17.35	0.26 ± 0.03
Forest lower montane	1920	1800	15.5	Semi-natural	4.34	134.84	9.22	14.63	0.34 ± 0.09
Grassland	1660	1650	16.5	Semi-natural	4.59	148.56	10.05	14.79	0.51 ± 0.01
Coffee plantation	1300	1250	19.0	Agricultural	4.28	18.89	1.85	10.24	1.02 ± 0.06
Homegarden	1260	1200	19.0	Sustainably used	5.79	32.05	2.78	11.55	0.77 ± 0.04
Maize field	1020	775	20.5	Agricultural	4.56	14.54	1.25	11.67	1.21 ± 0.03
Savannah	950	770	21.0	Semi-natural	5.38	27.53	1.99	13.84	0.83 ± 0.05

<sup>a</sup> From Røhr and Killingtveit (2003).

<sup>b</sup> From Hemp (2006a).

Using the climate classification system of Köppen–Geiger, the Mt. Kilimanjaro region is characterized by a seasonal tropical wet and dry climate (Hess and McKnight, 2011; Peel et al., 2007) and an equatorial rainfall regime with rainy seasons from March to May and around November (Hemp, 2006a; Sarmiento, 1986). The annual precipitation in the research areas is strongly dependent on elevation (Basist et al., 1994) and differs between 700 and 2000 mm, with a maximum at an altitude of approximately 2100–2200 m (Hemp, 2006a; Røhr and Killingtveit, 2003). The mean annual temperature of the investigation sites varied between 10 and 21 °C (Table 1).

## 2.2. Soil sampling

Soils of natural, semi-natural and anthropologically changed ecosystems were sampled on a monthly basis in March, April and May 2012 – during the transition phase from dry to wet season. Within the exploratory design of this study, one slope-parallel experimental plot of 50 m × 50 m was established in each of the ecosystems and to retrieve the exact position at a later sampling, ground nails (length: 0.5 m) were used to mark the corners. Using a soil auger (2 cm diameter × 60 cm depth), samples were taken in four corners and in the center of each plot, giving a total of five positions per sampling. For the May sampling of grassland and savannah soils, only four positions were used, since at that the same time vegetation was recorded (Hemp, unpublished) and the middle position could not be accessed. To obtain composite samples per depth and position, four augers were taken per position, subdivided into depths of 0–10, 10–20, 20–30 and 30–50 cm and mixed, respectively. At one sampling this lead to a total of 20 samples per ecosystem and to 472 samples overall. Since the O horizon in montane rainforests is often densely rooted (Schrumpp, 2004), only the litter layer was removed. After removing visible plant debris, replicates were sieved through a 2-mm mesh screen and stored under field moist conditions at 4–6 °C until analysis.

## 2.3. Soil analysis

All samples were analyzed for microbial biomass carbon (MBC), water extractable organic carbon (WOC) and soil moisture. The concentration of inorganic carbon in the investigated soils is negligible and consequently no correction was conducted. MBC was analyzed by the fumigation–extraction method (Vance et al., 1987). Summarily, ethanol-free CHCl<sub>3</sub> was used to fumigate 7–8 g of each field-moist soil sample for 24 h in an exsiccator at room temperature. After fumigation, CHCl<sub>3</sub> was removed and soluble C from fumigated and non-fumigated samples was extracted with 60 ml of 0.5 M K<sub>2</sub>SO<sub>4</sub> by shaking on an orbital shaker (60 min, 120 rotations min<sup>-1</sup>). C content in K<sub>2</sub>SO<sub>4</sub> extracts from respective soil samples without CHCl<sub>3</sub> fumigation was accepted as WOC (Beck et al., 1997; Blagodatskaya et al., 2009). Solute organic C in fumigated and non-fumigated extracts was determined. Since not all

of the soil carbon can be extracted by K<sub>2</sub>SO<sub>4</sub>, a *k*<sub>EC</sub> factor of 0.45 (Joergensen, 1996) was used to convert microbial C flush (difference between extractable C from fumigated and non-fumigated samples) into MBC.

## 2.4. Statistical analysis

The investigated ecosystems are affected differently by the start of the wet season, which is due to the fact that the independent variable of sampling date in this study represents a change in climatic conditions, which on the other hand varies with topographic location. Therefore, temporal changes in MBC, WOC and soil water contents were detected using ANOVA for each ecosystem, respectively. Using data from all three samplings, a second ANOVA was calculated to detect the effects of ecosystems (vegetation) and soil depth on MBC and WOC. For the investigation of land-use changes, pairs of semi-natural and its respective anthropogenically used ecosystem were compared by using another, third, ANOVA. All ANOVAs were coupled with *Bonferroni* outlier and *Tukey's* post hoc tests. All statistical analyzes were performed with R v2.15.1. All results expressed in the text for MBC and WOC are on a dry-weight basis as the mean over sampling dates ± standard deviation.

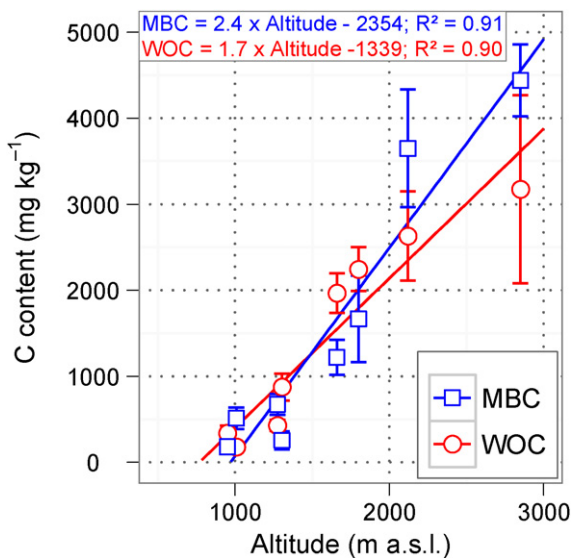
## 3. Results

### 3.1. Microbial biomass carbon

Microbial biomass carbon (MBC) varied between sampling dates (Supplementary Table 1) and also between investigation sites and soil depth (Supplementary Table 2). It correlated positively with altitude and therefore was generally higher in the upper ecosystems (Fig. 1). The highest portion of MBC in the 0–10 cm layer were observed in *Podocarpus* forest, 2850 m a.s.l. (4440 ± 416 mg kg<sup>-1</sup>), and the lowest values (179 ± 53 mg kg<sup>-1</sup>) were under the maize field, 1009 m a.s.l. (Fig. 2).

The investigated ecosystems homegarden, lower montane forest, maize field and savannah showed significantly lower (*p* < .05) microbial C contents in the wet (May 2012) compared to dry season (March 2012). Contrary to the before mentioned ecosystems, the higher altitude ecosystems of *Ocotea* and *Podocarpus* forest showed significant (*p* < .05) differences between April and May, but not between March and May. This temporal effect was bigger on lower plots (e.g. savannah) than in ecosystems at high elevation (e.g. *Ocotea* forest), probably because of the lesser contrast between dry and wet season. For the grassland and coffee plantation the portion of microbial C in soil did not vary noticeably between sampling dates (*p* > .05).

The ANOVA, comparing all ecosystems during the whole three-month sampling campaign, showed significant differences (*p* < .01) in MBC contents (Supplementary Table 2). Based on



**Fig. 1.** Regression between altitude and MBC (squares, blue) or WOC (circles, red) in the 0–10 cm layer of soils at the southern slope of Mt. Kilimanjaro. Displayed values are means of the three-month sampling campaign. Standard errors are shown as vertical bars. (For interpretation of the references to color in this artwork, the reader is referred to the web version of the article.)

pairwise comparisons of the Tukey HSD-test, *Podocarpus* forest, *Ocotea* forest and homegarden were different from any other investigated ecosystem. Based on the same ANOVA, the remaining ecosystems could be categorized into intrinsically indistinguishable groups, such as grassland and lower montane forest as well as coffee plantation, maize field and savannah.

As expected, land-use had a strong effect on the MBC. This was revealed by analysis of factor-related variance (Supplementary Table 3). The MBC contents ( $p < .01$ ) were much higher in all semi-natural compared to the respective anthropogenically used ecosystems, whereas the highest decrease was observed in the surface soil layer (Fig. 2). In the upper 10 cm, the semi-natural ecosystems lower montane forest and savannah ( $1668 \pm 506 \text{ mg kg}^{-1}$  and  $512 \pm 125 \text{ mg kg}^{-1}$ ) contained 2.5-fold higher portions of MBC than the agriculturally used ecosystems homegarden and maize field ( $672 \pm 121 \text{ mg kg}^{-1}$  and  $179 \pm 53 \text{ mg kg}^{-1}$ ). In contrast, MBC in grassland at 0–10 cm ( $1221 \pm 203 \text{ mg kg}^{-1}$ ) is 5-fold higher than in the corresponding coffee plantation ( $256 \pm 107 \text{ mg kg}^{-1}$ ). Except for the coffee plantation, a significant decrease in the microbial C content with increasing depth was observed and ratios of contents found in the 0–10 cm to 30–50 cm layer showed clear contrasts between the semi-natural and anthropogenically used ecosystems. The natural ecosystem *Ocotea* forest showed the strongest negative trend with depth from  $3648 \pm 684 \text{ mg kg}^{-1}$  at 0–10 cm to  $426 \pm 360 \text{ mg kg}^{-1}$  at 30–50 cm, whereas the smallest decrease of microbial C content with depth was found at the sustainably used homegarden site ( $672 \pm 121 \text{ mg kg}^{-1}$  at 0–10 cm to  $339 \pm 83 \text{ mg kg}^{-1}$  at 30–50 cm).

### 3.2. Water extractable organic carbon (WOC)

Significant differences of WOC contents were discovered between investigation sites and soil depth (Supplementary Table 2) and also between sampling dates (Supplementary Table 1). In six of the eight investigated ecosystems the water extractable organic C was several-fold higher than the respective portion of MBC. Likewise to MBC, WOC followed a linear increase with altitude,

although this trend with elevation was less distinct than for MBC (Fig. 1). WOC contents were the smallest at low altitudes receiving lowest precipitation, e.g. savannah ( $180 \pm 29 \text{ mg kg}^{-1}$ , 951 m a.s.l.), and highest ( $3175 \pm 1094 \text{ mg kg}^{-1}$ ) in the *Podocarpus* forest (2850 m a.s.l.) (Fig. 3). In the ecosystems *Ocotea* forest, homegarden, coffee plantation and savannah, WOC levels were highest at the second sampling (April 2012), indicating dissolution of organic C and eventually redistribution within the soil profile with start of the wet season. For these ecosystems a comparison with other sampling dates revealed a specific WOC dynamic (Fig. 3): from March to April 2012, WOC increased ( $p < .05$ ), followed by a subsequent decrease ( $p < .05$ ) with ongoing rains (May 2012). This pattern was more distinct in low-elevation ecosystems. Lower montane forest had its highest WOC level in May 2012 and its lowest in March 2012 – whereas significant differences ( $p < .05$ ) could only be observed regarding March but not April and May. *Podocarpus* forest, grassland and maize field showed no significant temporal changes in WOC contents.

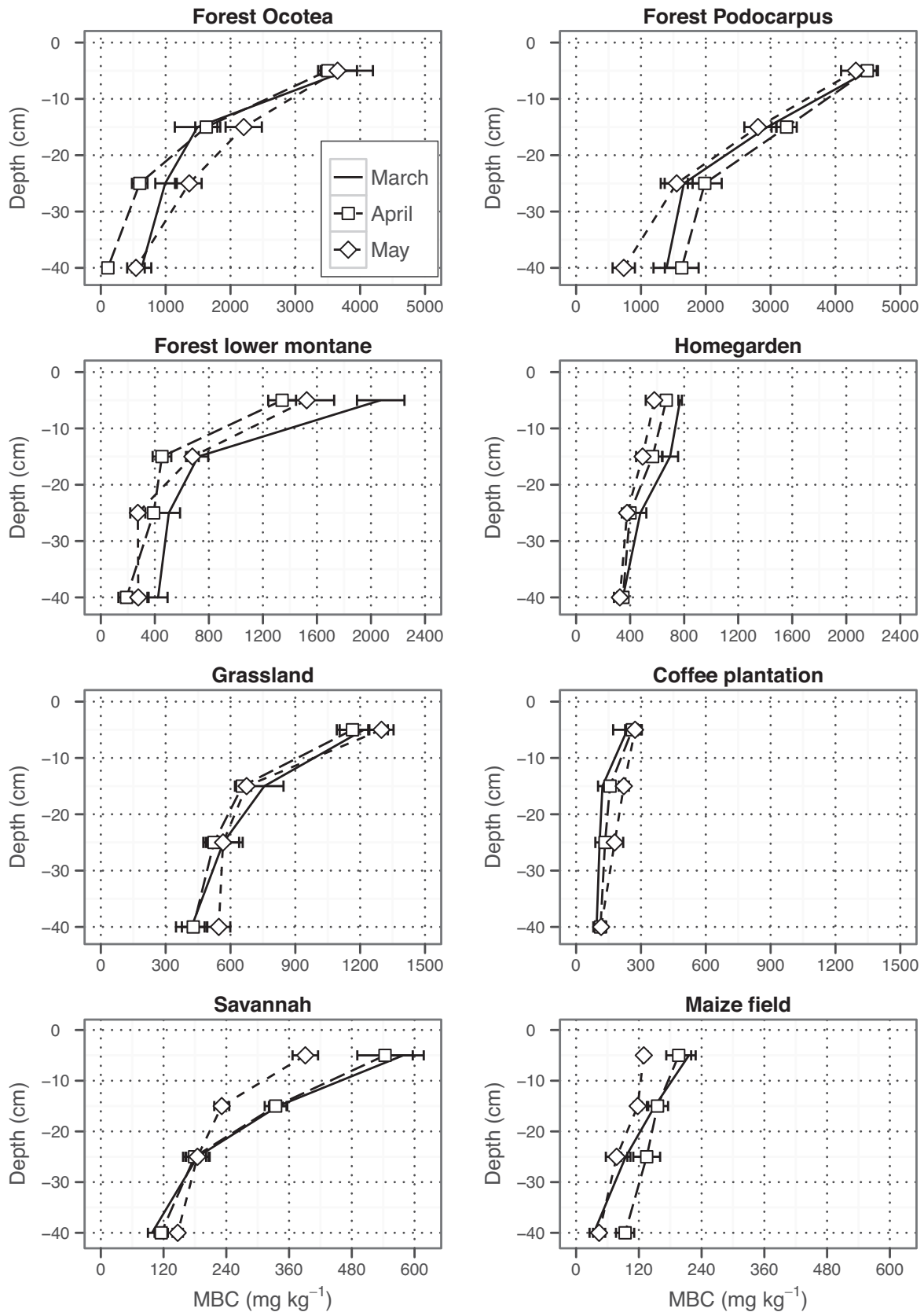
In contrast to MBC, for WOC the pairwise comparisons of ecosystems revealed only one intrinsically indistinguishable group ( $p > .05$ ) – this group consisted of maize field, homegarden and savannah. All other ecosystems showed no similarities to any other investigated ecosystem.

Both, the variation of WOC with soil depth and total contents of water-extractable organic C in the semi-natural and agricultural ecosystems were influenced by land-use. Similar to MBC, significantly higher portions of WOC ( $p < .05$ ) were found in semi-natural ecosystems of lower montane forest and grassland ( $2245 \pm 257 \text{ mg kg}^{-1}$  and  $1966 \pm 232 \text{ mg kg}^{-1}$  in the 0–10 cm layer), whereas the corresponding agriculturally used homegarden and coffee plantation were strongly depleted in WOC ( $430 \pm 66 \text{ mg kg}^{-1}$  and  $875 \pm 160 \text{ mg kg}^{-1}$  in the 0–10 cm layer). In contrast, the maize field exhibited higher WOC contents ( $339 \pm 87 \text{ mg kg}^{-1}$ ) than its respective natural ecosystem of savannah ( $180 \pm 29 \text{ mg kg}^{-1}$ ) (Fig. 3). The ratio of WOC contents in semi-natural and agroecosystems increased with elevation from  $\sim 0.5$  at the savannah/maize field, over  $\sim 2$  at the grassland/coffee plantation, to  $\sim 5$  at the lower montane forest/homegarden. In contrast to the negative MBC trend with depth, no significant decrease could be observed for WOC contents – except for the coffee plantation and homegarden site (data not shown).

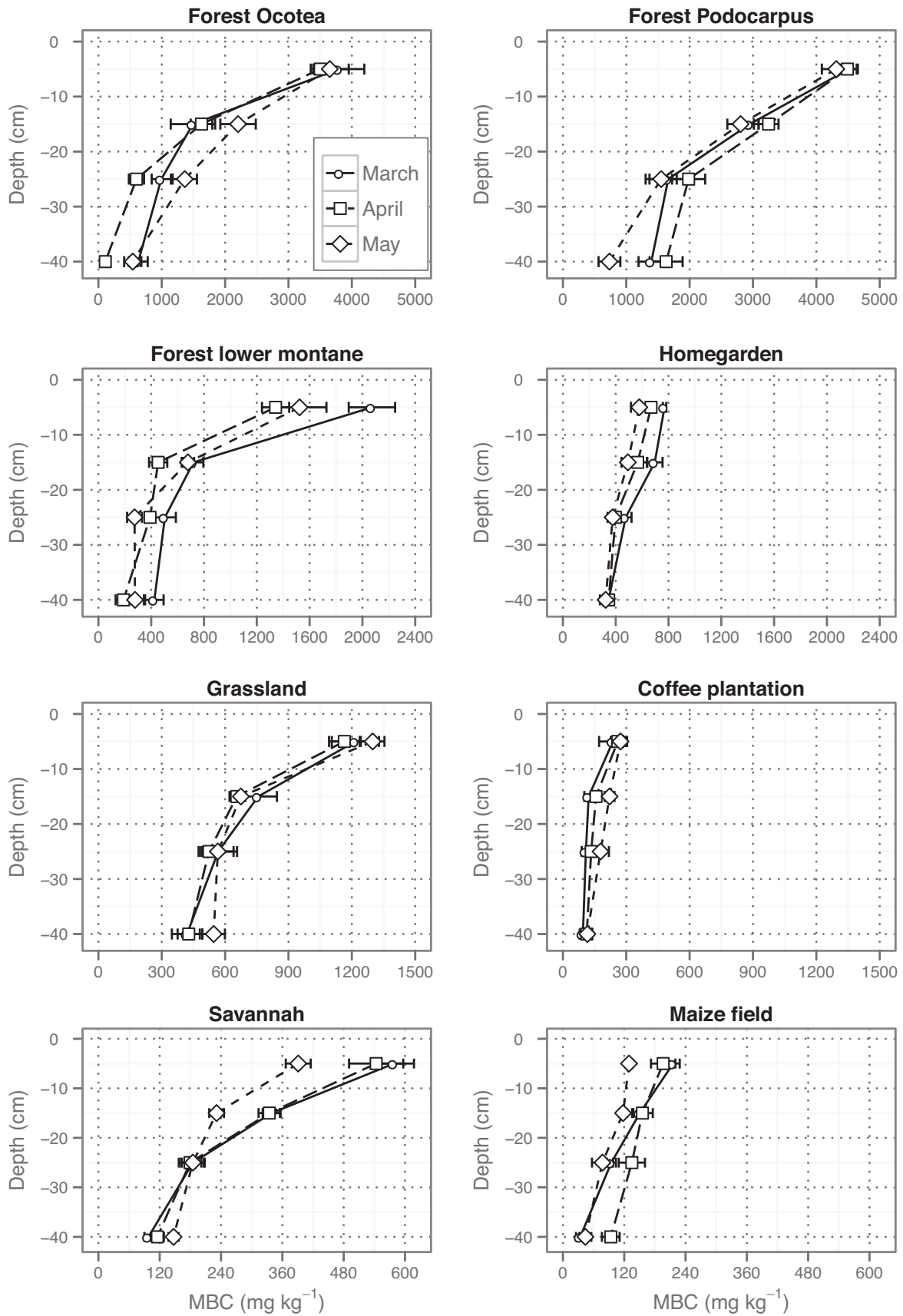
### 3.3. Soil water content

The effect of temporal change in precipitation and temperature on soil water content was investigated and varied in all of the investigated ecosystems during the three-month sampling campaign (Supplementary Table 1). Four ecosystems (savannah, maize field, coffee plantation, grassland) showed significantly increasing ( $p < .05$ ) soil water contents between March and April as well as April and May 2012. Lower montane and *Podocarpus* forest showed increases, which were significant ( $p < 0.05$ ) between April and May 2012 but not between March and April. For the above mentioned six ecosystems, soil water contents were positively correlated with elevation and ranged between 3.2–13.2%, 5.4–14.7% and 7.5–18.8%, for the three months respectively. Surprisingly, the homegarden and *Ocotea* forest sites exhibited different temporal regimes of soil water contents, whereas all changes were significantly different ( $p < .05$ ). For the high-altitude *Ocotea* forest, soil water contents decreased from initially  $15.9 \pm 2.6\%$  to  $9.9 \pm 1.9\%$  and increased back to  $18.7 \pm 2.7\%$ . Soil water contents in the homegarden on the other hand, strongly increased from  $6.4 \pm 0.9\%$  to  $17.1 \pm 2.4\%$  and decreased to  $13.5 \pm 2.7\%$ . Some differences in soil water depth distributions were discovered, but not further investigated since this was not part of this study.





**Fig. 2.** MBC in Mt. Kilimanjaro ecosystems depending on soil depth and sampling date. *Ocotea* and *Podocarpus* forests represent natural ecosystems without a corresponding agroecosystem. Left-hand side semi-natural ecosystems (lower montane forest, grassland and savannah) are compared with the respective right-hand side agriculturally used ecosystems (homegarden, coffee plantation and maize field). Standard errors as black lines. Note different X scales for ecosystems at different elevation.



**Fig. 3.** WOC contents in Mt. Kilimanjaro ecosystems depending on soil depth and sampling date. *Ocotea* and *Podocarpus* forests represent natural ecosystems without a corresponding agroecosystem. Left-hand side semi-natural ecosystems (lower montane forest, grassland and savannah) are compared with the respective right-hand side agriculturally used ecosystems (homegarden, coffee plantation and maize field). Standard errors as black lines. Note different X scales for ecosystems at different elevation.

## 4. Discussion

### 4.1. Effect of elevation

Elevation was one of the two main factors affecting MBC and WOC. Both parameters and SOC (which is source of both, MBC and WOC) strongly increased with elevation in (semi-)natural and anthropogenically affected ecosystems. *Schrumpf (2004)* reported high contents of C in organic (O) horizons as well as densely rooted humus layers in the montane rainforests at Mt. Kilimanjaro, which correlates with this study (Table 1). Depending on changing altitudes from 100 to 2700 m in Costa Rica, an increasing litter layer is combined with a decreasing amount of annual litter fall (*Heaney and Proctor, 1989*). Moreover, the decrease in temperature with increasing altitude has a strong effect on soil microbial biomass. In a study by *Blume et al. (2002)*, hot summer temperatures increased microbial activity by more than 80%. They also postulated that low temperature seasons negatively affect the metabolism of soil microorganisms but not the content of MBC. In addition, the productivity of tropical montane cloud forests, which is connected to the activity of soil microbial biomass, is known to be lower than in lowland tropical rainforests (*Bruijnzeel and Veneklaas, 1998*). Therefore, the very high contents of MBC and WOC we found in the surface layer of the high-altitude *Podocarpus* forest ecosystem (Figs. 2 and 3) are very likely due to the high availability of substrate coming with above- and below-ground litter input. Based on the vegetation records of *Hemp (2006a)* and the already mentioned effects of altitude on annual litter fall and productivity (*Clark et al., 2001*), we further assume a decrease of MBC and WOC in the higher sub-alpine heathland and lower alpine zone of Mt. Kilimanjaro. In the subnival zone of the Peruvian Andes at 5000 m a.s.l., portion of MBC decreased to 200–250 mg kg<sup>-1</sup>, because of a strong decrease in productivity and partial absence of vegetation due to the extreme climatic and abiotic conditions (*King et al., 2008*).

### 4.2. Effect of land-use

Confirming our hypothesis that human-induced land-use change strongly decreases MBC and WOC, the investigated semi-natural ecosystems had on average 3-fold higher contents of MBC and WOC and 4-fold higher contents of SOC in the 0–10 cm layer than their respective agroecosystems. A decline in SOC after deforestation and cultivation also reduces MBC and DOC (*Dinesh et al., 2003*). Several land-use change types in the tropics and their SOC losses were reviewed by *Don et al. (2011)*. They reported SOC losses from primary forest to cropland or perennial crops (–25% and –30%, respectively) and grassland to cropland (–10%). The same land-use changes occur at Mt. Kilimanjaro, e.g. lower montane forest to homegarden and grassland to coffee plantation. These losses of relative SOC reviewed by *Don et al. (2011)* are several-fold smaller than SOC losses in the investigated Mt. Kilimanjaro ecosystems (in the 0–10 cm layer; –76% and –87%, respectively). But in the southern highlands of Ethiopia at an elevation of 2100 m a.s.l., similar high decrease in SOC were observed after deforestation (*Lemenih et al., 2005*). The MBC and WOC contents on the other hand, decreased by 57% and 79%, which equals the values reported by *Waldrop et al. (2000)*. Based on the assumptions of *Clark et al. (2001)* and *Schuur (2003)*, at 2100 m a.s.l. at Mt. Kilimanjaro the ecosystems with the highest net primary production (NPP) occur (lower montane and *Ocotea* forest). Due to the effect of elevation on ecosystem productivity, decomposition and climate, the more elevated forest ecosystems at Mt. Kilimanjaro have more soluble organics in soil (*Bruijnzeel and Veneklaas, 1998*; *Heaney and Proctor, 1989*). This is reflected in the increasing difference in WOC contents between semi-natural and agriculturally used ecosystems with higher elevations at Mt. Kilimanjaro. Therefore

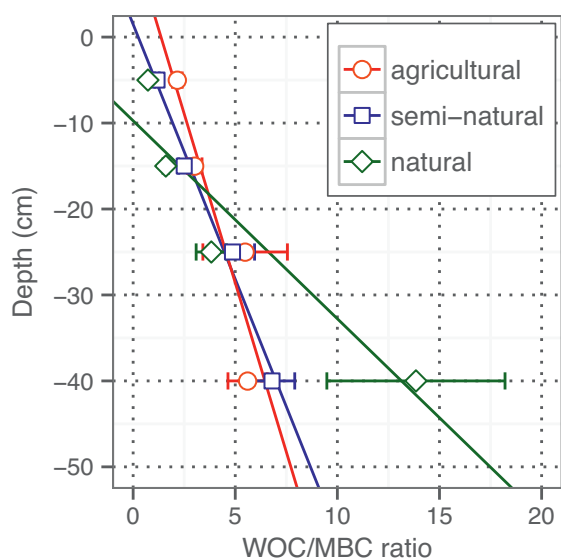
we concluded that SOC, MBC and WOC contents in this mountains' ecosystems with high NPP are more affected by land-use change than ecosystems with comparably low NPP. Conclusively, elevation, topography and climate indirectly influence the magnitude of the land-use change effect.

In mineral soils of tropical and temperate regions, dissolved organic C leaching from O horizons is an important substrate source for microbial biomass (*Fujii et al., 2009*). The investigated agroecosystems have presumably much lower C input by litter and consequently much less WOC since in coffee plantations as well as maize fields the available litter is normally removed. Hence, less WOC in the investigated agricultural ecosystems are due to the absence of the litter layer and O horizons. The very strong decrease in MBC after the mid-altitudinal conversion from grassland to coffee plantation probably reflects the intensive use of pesticides and herbicides for coffee production. In coffee plantations at Mt. Kilimanjaro plant debris is removed after pruning of coffee bushes, which results in a decrease of SOC and low availability of substrate for microbial decomposition. MBC under grassland and savannah ecosystems is mostly attributed to the dense root system of the grass cover (*Fall et al., 2012*; *Blume et al., 2002*). In the maize field, however, this permanent dense root system is missing and the above ground litter input is strongly reduced since the whole plant is harvested. As a result of the before mentioned, MBC in the 0–10 cm layer (Fig. 2) is reduced. In contrast, the higher WOC content in soil under maize vs. savannah (Fig. 3) is very likely due to organic animal manure, which is applied by local farmers. *Tessier et al. (1998)* found several-fold higher DOC contents throughout the soil profile on manure-treated compared to unfertilized sites. Accordingly, MBC and WOC contents are influenced not only by the land-use change itself, but also by agricultural management practices (*Emmerling et al., 2001*; *Friedel et al., 1996*).

### 4.3. Effect of depth

The highest contents of MBC and WOC were found in the 0–10 cm layer. This is common in most ecosystems because much of the organic input is localized on and close to the soil surface. In Senegal, MBC in a savannah ecosystem was most abundant close to the surface and near *Acacia* trees (*Fall et al., 2012*). According to *Blume et al. (2002)* the upper 0–20 cm in semiarid forest soils of Spain show a much higher microbial population than lower layers. For the humid subtropical climate in southern Brazil, *Babujia et al. (2010)* reported more MBC in surface than in subsoil samples – independent of management practice. In homegardens, the substrate input by plant residues such as roots and exudates decreases with depth, which is directly reflected by MBC contents (*Wichern et al., 2003*). Forest ecosystems feature the strongest decrease in SOC with depth, followed by grass- and shrublands (*Jobbágy and Jackson, 2000*). This agrees with the correlation between depth and SOC, MBC or DOC found in our study. *Jobbágy and Jackson (2000)* also reported that SOC contents are influenced by temperature and precipitation (which corresponds to elevation in our study), whereas this effect is bigger in the surface soil layers. In their review, higher precipitation and lower temperatures lead to a stronger decline of SOC with depth, which is reflected in shallower SOC distribution – the same was observed in our study for SOC, MBC and water-extractable organic C contents. On the other hand, it should be noticed that this effect is eventually more due to changing vegetation along precipitation gradients than the precipitation itself (*Jobbágy and Jackson, 2000*).

Due to the advanced stage of weathering of Mt. Kilimanjaro soils (*Schrumpf, 2004*), the mountain's ecosystems are especially prone to nutrient and C losses through leaching. Strong rains – which also occur at Mt. Kilimanjaro – favor leaching and litter decomposition because more precipitation leads to higher DOC contents



**Fig. 4.** WOC/MBC ratio in agriculturally used (circles, red,  $R^2 = 0.77$ ), semi-natural (squares, blue,  $R^2 = 0.98$ ) and natural (diamonds, green,  $R^2 = 0.80$ ) ecosystems. Agricultural ecosystems represent homegarden, coffee plantation and maize field, whereas semi-natural stands for lower montane forest, grassland and savannah, *Podocarpus* and *Ocotea* forest are indicated as natural. Means over all three sampling dates, standard errors as horizontal bars. (For interpretation of the references to color in this artwork, the reader is referred to the web version of the article.)

(Salamanca et al., 2003). Like MCB, DOC normally decreases with depth (Babujia et al., 2010; Fall et al., 2012; Goberna et al., 2006). In all of the investigated ecosystems, no organic fertilizer was manually mixed into the soil; in maize fields, manuring is done solely by surface application. Nevertheless, we observed more or less equal contents of WOC in all soil depths down to 50 cm. In contrast to the upper soil layers, sorption at minerals but not microbial decomposition controls DOC dynamics in deeper horizons of tropical ecosystems (Schwendenmann and Veldkamp, 2005). This supports the assumption that abundant WOC at greater depths originates from litter or surface layer. The excess of dissolved organic C at the surface, translocated into deeper horizons, will be partly adsorbed at minerals and hence is less available for the decreasing contents of microbial biomass—especially in dry seasons with low soil water contents (Schwendenmann and Veldkamp, 2005). As the WOC/MBC ratios increase with depth (Fig. 4), substrate shortage cannot be a limiting factor for microbial growth at greater depths. Therefore, we assume the possibility of C leaching in the investigated, especially in the natural, ecosystems.

#### 4.4. Effect of season

Our results on the season-transitional pattern of MBC (decreasing contents with start of the rains) are supported by Maithani et al. (1996) and Montañó et al. (2007). They found a similar MBC pattern between the wet and dry season in a wet subtropical forest in north-east India and a tropical deciduous forest in Mexico. Ecosystem productivity and soil  $\text{CO}_2$  fluxes – which also reflect microbial activity – are closely linked to precipitation and therefore to soil moisture contents as well. A decline in soil water content during the dry season in a Kenyan savannah reduced  $\text{CO}_2$  fluxes from soil and lowered biomass productivity (Otieno et al., 2010). Following re-wetting of soils at the beginning of the wet season, tropical rain forests often show higher  $\text{CO}_2$  effluxes, mainly due to briefly increased microbial activity. During the ongoing wet season, high soil moisture contents lead to oxygen limitation, which may decrease the microbial activity and the  $\text{CO}_2$  efflux rates from soil (Schwendenmann et al., 2003).

For a deciduous forest in north-east India, Devi and Yadava (2006), in contrast, reported the highest contents of MBC during the rainy season and the lowest contents during the dry winter period. In subtropical soils of China as well, more MBC was present in the hot-humid than in the cold-dry season (Iqbal et al., 2010). Based on their successional stage, primary and secondary forests in a seasonally dry tropical region of Mexico are variously affected by the increased precipitation during the wet season (Saynes et al., 2005). The vast range of results found in these studies implies that seasonal variability of MBC in tropical ecosystems is strongly influenced not only by climate, but also by soil type, land-use, vegetation and indirectly by topography.

During the three-month sampling campaign, WOC levels were highest in April 2012, indicating dissolving of C in soil water and relocation within the soil profile with the onset of the rains rather than in the wet season itself. The partly mineralized litter layer formed during the past dry season represents a source of soluble C: during strong rains at the beginning of the wet season, high contents of WOC leached downward.

Ecosystems located at lower elevation were more strongly affected by the increased rainfalls during the wet season than the *Ocotea* and *Podocarpus* forests at higher locations. In tropical montane ecosystems, seasonal variability in temperature and precipitation is low due to cloud cover, high humidity, frequency of fog and a more or less constant level of solar radiance throughout the year (Buytaert et al., 2011). Sarmiento (1986) described precipitation patterns in tropical high mountains, including rain belts. These rain belts have only slight climatic variability, and rainfalls occur in varying frequencies during the whole year. Additionally, the closed canopy cover in forest ecosystems provides further protection against inter-annual climatic variations and microclimatic extremes at the soil surface (Martius et al., 2004). This, and the fact that *Ocotea* and *Podocarpus* forest sites are located in the rain belt of Mt. Kilimanjaro, reduce the influence of increasing rains on the portions of MBC and WOC in soils. The result is an insignificant effect of the transition from dry to wet season on C contents in the forest ecosystems of Mt. Kilimanjaro.

## 5. Conclusions

At Mt. Kilimanjaro the effect of climatic changes during transition periods on MBC and WOC is more distinct in lower elevated than higher elevated ecosystems. From 900 to 2900 m a.s.l. and through different ecosystems, MBC and WOC contents in soils of Mt. Kilimanjaro increase linearly. The mountains ecosystems are strongly affected by land-use: especially in the upper soil layers, soil microbial biomass and water-extractable C are decreased approximately three times compared to semi-natural ecosystems. Additionally, the magnitudes of the land-use change induced differences in the C balance are further influenced depending on net primary production and agricultural management practice, as well as elevation, climate and topography of the ecosystems.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.apsoil.2013.02.006>.

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