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Vertical distribution and pools of microbial residues in tropical forest soils formed from distinct parent materials

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Abstract The contribution of soil microbial residues to stable carbon pools may be of particular importance in the tropics where carbon residence times are short and any available carbon is rapidly utilized. In this study we investigated the vertical distribution of microbially-derived amino sugars in two tropical forests on contrasting meta-sedimentary and serpentinite parent materials in the lowlands of Mt. Kinabalu, Borneo. Despite their similar climate, vegetative cover, and general microbial community structure, the two soils were chemically and physically distinct. We found that both parent material and depth significantly influenced the pool sizes of microbial residues in the two soils. In particular, the soil derived from sedimentary parent material had greater amino sugar contents, glucosamine to galactosamine ratios, and percentage of total soil carbon that is amino sugar derived, than the soil derived from serpentinite substrate. We speculate that residue stabilization was linked to soil iron oxide content, with significant difference in amino sugars contribution to total soil carbon at depth in the serpentinite-derived soil versus that derived from sedimentary parent material. Based on observed patterns of amino sugar content and relative abundance we suggest that near the surface of both soils vegetation and litter input determines the composition and quantity of microbial residues. With increasing depth the influence of vegetation declines and production and stabilization of microbial amino sugars becomes driven by soil matrix characteristics. These differences in stabilization mechanism and carbon dynamics with depth may be particularly critical in deep weathered tropical soils.

Keywords Amino sugars · Carbon stabilization · Microbial biomarkers · Soil depth profiles · Tropical forest soil · Ultrabasic soil

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Introduction

Soils constitute the largest terrestrial reservoir of organic carbon on earth and the soil matrix represents a complex balance of organic matter additions, losses, transformations, and translocations (Jobbágy and Jackson 2000). More specifically, the dynamic cycling of soil organic matter (SOM) is constrained by intricate interrelationships among quality and quantity of carbon (C) inputs and C mineralization, residence time and stabilization, in addition to climatic and edaphic factors (Feller and Beare 1997; Zech et al. 1997). The primary carbon inputs in terrestrial systems are plant material, including litter and exudates, and secondary potentially stable carbon comes from microbial residues, including

extant and decomposing biomass (Zech et al. 1997; Guggenberger et al. 1999; Kögel-Knabner 2002). Carbon additions from plant and microbial residues exhibit varying degrees of stability in soil over time, with carbon pools ranging in turnover times from rapid (labile C) to intermediate/slow (stable, humified, or recalcitrant C) (Zech et al. 1997; Lützow et al. 2006). Microbial residues in particular have been shown to persist in soil over time and represent an important constituent of the intermediate residence time carbon pool (Parsons 1981; Chantigny et al. 1997; Zech et al. 1997; Guggenberger et al. 1999; Kögel-Knabner 2002; Glaser et al. 2004; Liang and Balser 2008).

The stabilization of microbially derived organic matter in soils can be investigated using amino sugar biomarker analysis (Benzing-Purdie 1981, 1984; Stevenson 1982; Amelung 2001; Liang et al. 2007a, b, c). Amino sugars are contained in the cell walls of living and decomposing soil microorganisms and are a common constituent of bacterial extracellular polysaccharides as well as fungal chitin/chitosan (Parsons 1981). They are almost exclusively synthesized by soil microorganisms and are not found in higher plants, making them an effective marker for examining microbial (rather than plant) inputs into SOM (Parsons 1981; Stevenson 1982; Amelung 2001; Glaser et al. 2004). Some amino sugars are produced primarily by particular taxonomic groups and thus amino sugar information can be further used to determine whether SOM is derived from fungi or bacteria (Chantigny et al. 1997; Guggenberger et al. 1999; Amelung 2001). Glucosamine (GluN) is often the most abundant amino sugar found in soils and is a constituent of chitin, found in fungi and arthropods, and peptidoglycan, found primarily in Gram positive (Gm+) bacteria (Stevenson and Braids 1968; Parsons 1981; Stevenson 1982; Guggenberger 1999; Zhang et al. 1998; Amelung et al. 1999; Amelung 2001; Kögel-Knabner 2002). Muramic acid (MurA) is a less abundant amino sugar in soils, but it is particularly relevant because it is unique to bacteria in terrestrial systems and present in the same proportion as GluN in peptidoglycan (i.e., 1:1) (Parsons 1981; Brock and Madigan 1988; Zhang and Amelung 1996; Amelung 2001; Kögel-Knabner 2002). Because the GluN/MurA ratio in soils is commonly larger than one, GluN is considered to be a fungal marker, and thus the ratio of GluN/MurA may be used to assess the relative bacterial versus fungal contribution to the microbially derived SOM pool (Chantigny et al. 1997; Amelung et al. 1999; Solomon et al. 2001). However, care must be used with MurA, as this amino sugar contrasts with the hexosamines (such as GluN) in that it is stabilized only when bound in soil and thus has a lower inherent resistance to microbial degradation (Zhang et al. 1998). Galactosamine (GalN) is another significant amino sugar that is largely confined to bacterial production and accordingly the ratio of GluN/GalN is often used to indicate the relative contribution of fungal residues to SOM (Parsons 1981; Kögel and Bochter 1985; Amelung et al. 1999; Solomon et al. 2001). Finally, mannosamine (ManN) is extracted and quantified during amino sugar analysis, but is only used in total amino sugar counts, as its origin (bacterial or fungal) is uncertain (Coelho et al. 1997; Amelung 2001; Liang et al. 2007c).

Considerable research has been done on amino sugar contents of surface soils (up to 20 cm) in grassland and agricultural systems (Chantigny et al. 1997; Guggenberger et al. 1999; Amelung et al. 1999; Solomon et al. 2001; Six et al. 2006), with much of the literature focusing on allocation in particle size fractions (Benzing-Purdie 1981, 1984; Zhang et al. 1998, 1999; Six et al. 2001; Turrión et al. 2002). Recently, several studies have concentrated on the influence of vegetative species on amino sugar production using in situ and laboratory experiments (Liang et al. 2007a, b, c).

The distribution of amino sugars with depth has received substantially less attention (Stevenson and Braids 1968; Möller et al. 2002), despite the fact that 50–65% of the organic carbon contained in the top 1 m of soil is distributed below 30 cm (Jobbágy and Jackson 2000). In addition, few studies of amino sugars have been conducted outside of temperate regions (and particularly in forested systems) (Solomon et al. 2001; Möller et al. 2002). In tropical rainforests, where C residence times are brief and competition is high for any available soil nutrients in the nutrient poor, highly weathered soils, the contribution of microbially derived organic matter may be a particularly critical component of SOM cycling (Feller and Beare 1997; Zech et al. 1997; Amundson 2001). Further, because of the depth of profile development, the importance of C dynamics and mineralogy with depth may be critical in tropical soils.

In this study, we investigated the vertical distribution of amino sugars in two tropical forests in Sabah, Malaysia (Borneo). The work is part of a larger effort to investigate microbial and carbon dynamics in tropical ecosystems, and here we report on the accumulation/stabilization of microbially-derived amino sugars with depth in soils formed from sedimentary and ultrabasic parent material.

Materials and methods

Field sites

Soils were sampled from two lowland hill dipterocarp forests established on contrasting parent materials of meta-sedimentary (Sed) and ultrabasic (UB; serpentinite) origin of similar Tertiary age, located on the lower eastern slope of Mt. Kinabalu (4095 m, 6°05′N, 160°33′E) in Sabah, Malaysia (Borneo) in Mt. Kinabalu National Park (Fig. 1) (Jacobson 1970; Aiba and Kitayama 1999). Both sites support pristine, intact primary rainforest, and have no prior land use history. The two forests had similar basal areas and stem densities and were located at 700 m elevation on slopes ranging from 11–19%, each with northeasterly aspects (Aiba and Kitayama 1999; Table 1). The climate is generally aseasonal, with a mean annual temperature of approximately 23.8 °C and precipitation ranging from 2300–2500 mm year^{-1} (Aiba and Kitayama 1999; Table 1). Therefore, the two forests have similar vegetation, climate, topography, and time of soil pedogenesis, allowing the investigation of the effects of parent material on amino sugar accumulation with depth in an otherwise uniform ecological setting.

One hectare study plots were established on the two parent materials in 1995 (Aiba and Kitayama 1999). In August 2006 soil pits on each substrate were either re-excavated to approximately 120 cm, or dug new, for a total of three individual pits per substrate type, Existing soil pits were initially excavated in 2002, to a depth of approximately 60 cm. In order to avoid artifacts from the use of older pits we widened and deepened the pits, then cut the sampling face back 25–30 cm. The meta-sedimentary-derived soils (Sed) are tentatively classified as Typic Kandiudults whereas the ultrabasic soils (UB) are tentatively considered Rhodic Acroperoxes (Soil Survey Staff 2006). Soil samples were taken at seven depth intervals: 0–5, 5–15, 15–30, 30–50, 50–75, 75–105 cm (110 cm for the ultrabasic site), and at 105 and 110+ cm (ultrabasic site). Samples were homogenized and roots removed using a 4 mm sieve and pH determinations were made in 0.01 M $CaCl_2$ on field-moist soil (1:2 soil:solution).

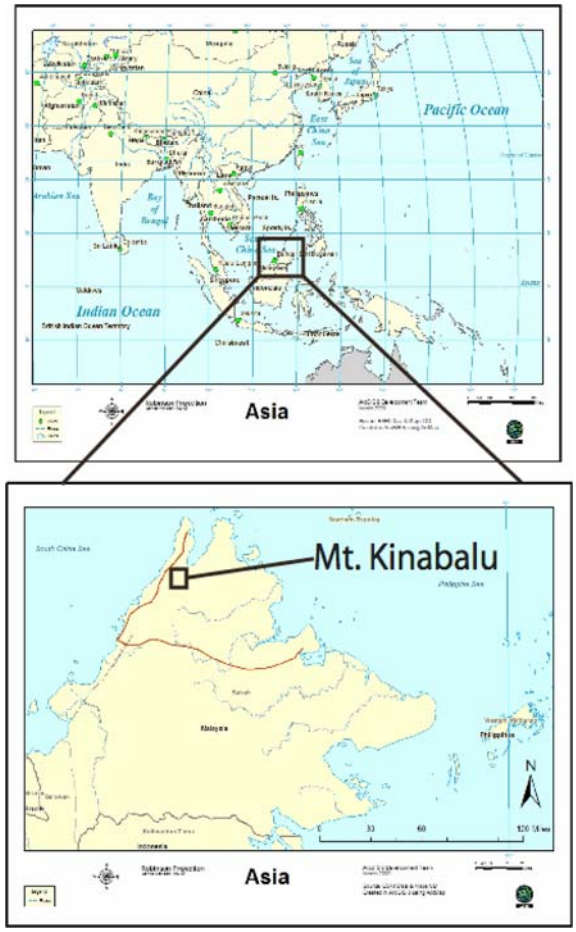

Fig. 1 Map of world showing the Pacific island of Borneo in Southeast Asia with detailed inset showing location of Mt. Kinabalu Park and study area

Laboratory assays

After sieving, sub-samples were frozen at −20 °C and freeze-dried over the following six weeks during August and September of 2006. Freeze-dried samples were used for particle size determination and other assays. Particle size determinations were made using the pipette method (Kilmer and Alexander 1949; Gee and Bauder 1986). Iron oxide contents were quantified by X-ray fluoroscopy using fused glass borate disks (Karathanasis and Hajek 1996). Soil total C and

Table 1 Site characteristics of Sedimentary and Ultrabasic sites on Mount Kinabalu, Borneo. From Aiba and Kitayama (1999)

Site	Abbreviation	Exact altitude (m)	Slope (°)	Aspect	Mean annual temp (°C)	Mean annual precip (mm)	Basal area (m^2 ha^{-1})	Stem density (m^2 ha^{-1})
Sedimentary	Sed	650	19	N85E	23.9	2509	36.2	1,064
Ultrabasic	UB	700	11	N80E	23.7	2509	40.7	1,175

N were determined by combustion on samples ground to pass through a 120-mesh sieve (125 μm opening) using a LECO CNS-2000 elemental analyzer (LECO Corporation, St. Joseph, Michigan, USA). Because of the absence of carbonates in these soils, total C is equal to organic C and hereafter shall be referred to as soil organic carbon (SOC).

The four amino sugars (GluN, MurA, GalN, and ManN) were quantified using the procedure outlined in Zhang and Amelung (1996), with the derivatization step as described by Guerrant and Moss (1984). Briefly, freeze-dried soil samples were hydrolyzed for 8 h in 6 M HCl at 105°C and the liquid phase was filtered and neutralized (Liang et al. 2007a, b, c). The supernatant was freeze-dried and the residues rinsed with methanol to recover the amino sugars. The amino sugars were subsequently transformed into aldonitrile derivatives and analyzed using a Hewlett-Packard 6890 Gas Chromatograph equipped with a flame ionization detector and Ultra 2 capillary column (Agilent Technologies, Wilmington, Delaware, USA). The peaks were identified by comparing sample retention times to those of pure standards using Chemstation software and manual integration. Myo-inositol was added as an internal standard prior to the neutralization (purification) step and amino sugars were quantified relative to this surrogate. Methylglucamine was utilized as a recovery standard prior to derivatization to monitor recovery efficiency (Liang et al. 2007a, b).

Statistical analysis

Data were analyzed using one-way analysis of variance (ANOVA), followed by Tukey's HSD test as a post hoc to assess differences between sites and among depths within each site (Tables 2, 3). We further analyzed data using two-way ANOVA to test overall site by depth differences (Table 4). Individual amino sugars (GluN, GalN, MurA, and ManN) were summed for total amino sugars, and the ratios of GluN/GalN and GluN/MurA were calculated. Total amino sugar C and total amino sugar N were calculated and subsequently divided by total SOC and N to give a conservative estimate of the microbial contribution to the C and N pools of soil SOM (Turrión et al. 2002; Glaser et al. 2004; Liang et al. 2007a, b). Finally, we calculated pairwise correlations between site variables and amino sugar characteristics. One sample was removed from all amino sugar statistical analyses because the extraction failed to yield measurable amino sugars and contained a barely detectable level of myo-inositol internal standard, suggesting laboratory error during the procedure (UB site, Pit 3, 30–50 cm).

Results

General soil physical and chemical properties

Select physical and chemical properties of each site are given in Tables 1 and 2 while Table 3 details the distribution of amino sugars contents between sites and among depths. All soil physical, chemical, and amino sugar characteristics were significantly different between the two sites ($p < 0.1$) with the exception of soil organic nitrogen (SON), GalN and the GluN/MurA ratio (Tables 2, 3, 4). Soil pH, iron oxide content, carbon to nitrogen (C/N) ratios, and percent clay were consistently lower at the sedimentary (Sed) site than the ultrabasic (UB) site ($p < 0.05$; Table 2). Bulk density was typically lower at the UB site (Table 2), while the Sed site generally had greater total soil nitrogen (N) at each sampling interval, particularly from 30–105 cm ($p < 0.05$; Table 2). With depth, soil pH, bulk density, and iron oxide content increased and silicon oxides decreased (Table 2). Clay contents were typically highest at intermediate depths (approximately 50–105 cm), suggesting a zone of clay accumulation within the Sed and UB soil profiles. Soil organic C, N, and C/N ratios generally decreased with depth, indicating a decline in microbial metabolic resources with progression towards the subsoil

Table 2 Selected soil properties of Sed and UB sites at Mount Kinabalu, Borneo

Depth Interval (cm)	pH 0.01 M $CaCl_2$		Bulk density (g cm^{-3})		Soil organic carbon (g kg^{-1})		Total N (g kg^{-1})		C:N ratio		wt% Fe Oxides		wt% Si Oxides		Soil texture	
	Sed	UB	Sed	UB	Sed	UB	Sed	UB	Sed	UB	Sed	UB	Sed	UB	Sed	UB
0–5	3.70a	4.05a	0.64a	0.87a	28.9a	32.7a	1.89a	1.77a	15.1a	18.5a	4.48a**	58.2a	73.6a**	12.5a	CL	C
5–15	3.89b*	4.76ab	1.08b	0.99ab	15.1b	19.6b	1.22b	1.27ab	12.4ab*	15.3ab	4.84a**	60.3a	74.3a**	11.8a	CL	C
15–30	3.94b**	5.37bc	1.16b*	0.85a	11.6bc	13.3bc	1.05bc	0.942bc	11.0b**	14.1abc	4.99a**	62.1a	75.5a**	10.4a	CL	C
30–50	3.97bc**	5.89c	1.25b*	1.05ab	8.04bc	8.25c	0.820cd*	0.685cd	9.82bc*	12.0bcd	5.51a**	65.1a	73.8a**	7.56a	CL	C
50–75	4.05bc**	6.06c	1.30b*	1.14ab	5.72bc	4.54c	0.728cd**	0.461 cd	7.86 cd*	9.86 cd	5.78a**	67.9a	73.4a**	5.54a	CL	C
75–105	4.12c**	5.96c	1.21b	1.27b	4.90c*	3.28c	0.705d**	0.377d	6.95cd	8.80d	6.45a**	69.8a	71.8a**	4.84a	C	C
105+	4.13c*	5.92c	1.32b	1.06ab	3.97c	7.61c	0.587d	0.645 cd	6.76d	10.4bcd	6.58a**	70.3a	71.6a**	5.00a	CL	C

Ratio of 1:2 (soil:solution)

CL clay loam, *C* clay

Asterisks indicate significant difference between sites at a given depth * $p < 0.05$; ** $p<0.01$. Letters within each column indicate differences among depths within a given site using Tukey's HSD post-hoc; shared letters among depths indicate no significant difference. $N = 3$ for each sampling depth per site

(Table 2). The lowest sampling interval at the UB site was the single exception, as here we observed an increase in SOC, N, and C/N. Although we did not quantify fine root biomass, we attribute this increase to the greater proportion of fine roots we observed at depth in the UB profiles.

Amino sugars and biomarker ratios

Amino sugars were quantified per unit soil weight (Table 3; Fig. 2), and on an areal basis (Fig. 4). At each site, the amount each amino sugar contributed to the total amino sugar pool followed the order GluN > GalN > MurA > ManN. At the Sed site, total amino sugar contents ranged from 750 μg g^{-1} soil at the surface to 334 μg g^{-1} soil at the deepest sampling interval, while concentrations at the UB site were 927 μg g^{-1} soil at the surface and declined to 97 μg g^{-1} soil at the bottom of the soil profile. Overall, total amino sugar contents were significantly different between the Sed and UB sites (Table 4), particularly below 50 cm (Table 3). All three hexosamines and MurA had greater concentrations at the Sed site below 5 cm. Ratios of GluN/MurA were greater at the Sed site (Fig. 2; significant at 0–5, 50–75, and 75–105 cm; $p < 0.05$), suggesting that fungi contributed a greater proportion of amino sugars in Sed soils, while bacteria contributed relatively more amino sugars at the UB site. Both the percentage of total soil carbon (SOC) derived from amino sugar carbon and that of total soil nitrogen derived from amino sugar nitrogen were higher at the Sed site from 5–120 cm (Fig. 3), and percentage of SOC derived from amino sugar carbon also increased with depth in Sed soils. The difference in percentage SOC from amino sugars between sites was significant from 75–120 cm ($p < 0.01$), while amino sugar percentage of soil N was significant at only the deepest sampling interval ($p < 0.05$) (Fig. 3). Total profile (to a meter depth) amino sugar content was substantially greater at the Sed site than the UB (Fig. 4). At the Sed site surface (0–30 cm) content of amino sugars was 30% of the total, whereas at the UB site it was 42%.

Discussion

The analysis of amino sugar biomarkers in soil may help provide insight into SOM dynamics and stabil-

Table 3 Amino sugar biomarkers for Sed and UB sites on Mount Kinabalu, Borneo

Depth interval (cm)	GluN μg g^{-1} soil		ManN μg g^{-1} soil		GalN μg g^{-1} soil		MurA μg g^{-1} soil		Total amino sugars	
	Sed	UB	Sed	UB	Sed	UB	Sed	UB	Sed	UB
0–5	524a	618a	16.5a*	2.38a	157a	205a	53.4ab	101.6a	750ab	927a
5–15	487ab	357ab	21.2a*	0a	263a	149a	66.5a	47.1ab	838a	554ab
15–30	254bc	192bc	12.8a	0a	136a	76.6a	63.1ab*	12.5b	466abc	282b
30–50	277bc	251bc	8.26a	14.5a	155a	125a	53.2ab	38.3ab	494abc	429ab
50–75	260bc**	46.5c	16.8a*	0a	137a	114a	42.4abc**	5.00b	456abc*	165b
75–105	208c*	48.6c	15.5a	1.46a	122a**	21.6a	37.0bc	15.3b	382bc*	86.9b
105–120	204c*	55.7c	8.97a	0a	102a*	23.0a	19.3c	18.2b	334c*	97.0b

Asterisks indicate significant difference between sites at a given depth * $p < 0.05$; ** $p < 0.01$. Letters within each column indicate differences among depths within a given site using Tukey's HSD post-hoc; shared letters among depths indicate no significant difference. $N = 3$ for each sampling depth per site and $N = 3$ for UB site, 30–50 cm

Table 4 Repeated measures ANOVA results for chemical, physical, and amino sugar characteristics

Variable	Depth	Site	Depth × site interaction
pH $CaCl_2$	20.1***	103***	16.87***
Bulk density	12.59***	14.42**	4.01**
wt% Fe_2O_3	13.61**	669***	6.93*
wt% SiO_2	19.09***	1259***	6.07**
% Sand	13.27***	24.77***	9.24***
% Clay	1.81***	57.62***	NS
Total C	194***	NS	NS
Total N	70.8***	NS	NS
C/N	84.73***	17.63**	NS
GluN	13.44***	451**	6.5**
GalN	NS	NS	NS
MurA	3.2**	6.13*	3.04**
Total AS	4.92***	6.14*	NS
AS-C % of SOC	5.52***	66.35***	2.09*
AS-N % of soil N	2.25*	9.72*	NS
GluN/MurA	3.54**	NS	NS
GluN/GalN	NS	14.92**	2.18*

F-ratio statistic is shown in parenthesis to indicate strength of *p*-value

* $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$, *NS* not significant

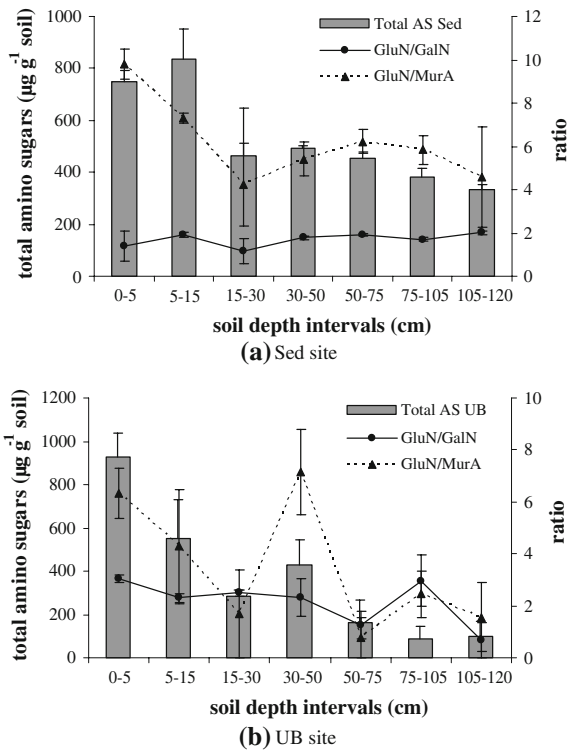

Fig. 2 **a** Total amino sugars (Total AS) and biomarker ratios at different soil depths in Sed site. **b** Total AS and biomarker ratios at different sampling depths in UB site. Total amino sugars (Total AS) on the left-hand y-axis and GluN/GalN and GluN/MurA ratios on the right-hand y-axis. Error bars are ±1 standard error of the mean and $n = 3$

ization (Benzing-Purdie 1981, 1984; Stevenson 1982; Amelung 2001, 2003; Liang et al. 2007a, b, c). Here we found that amino sugar contents and distribution patterns differed significantly between parent materials of contrasting meta-sedimentary and serpentinite origin. Given that the vegetation, soil organic carbon, climate, topography, time of soil pedogenesis, and microbial communities (biomass and structure) are nearly identical between sites (Moritz 2008), we suggest that the inherent physical and chemical characteristics of the soil derived from the parent material

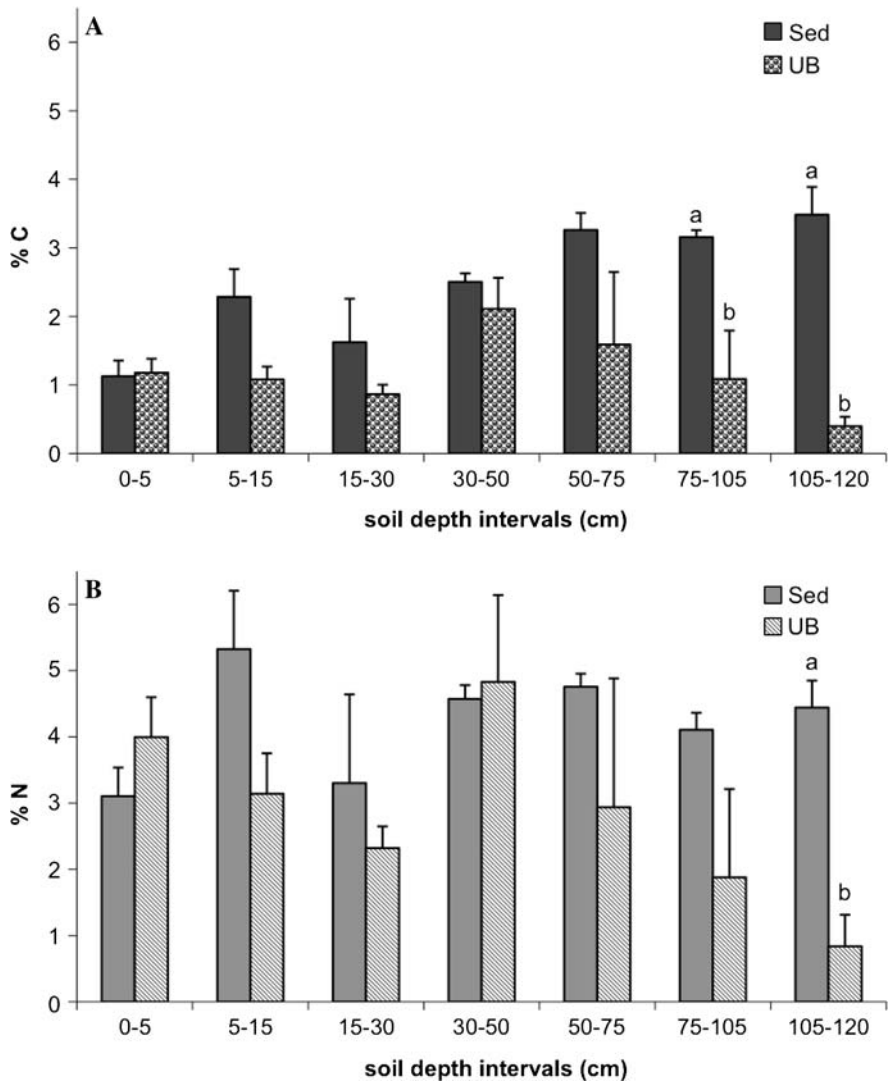

Fig. 3 Depth profiles showing percent of total soil organic carbon (**a**) or nitrogen (**b**) that is amino-sugar derived. **a** Percent of total soil organic carbon that is amino sugar derived at Sed and UB sites. **b** Percent of total soil nitrogen that is amino sugar nitrogen derived at Sed and UB sites. Letters indicate significant difference ($p < 0.05$) between Sed and UB sites. Error bars are ± 1 standard error of the mean and $n = 3$

are responsible for the observed amino sugar differences between sites. Specifically, iron oxides may play a critical role in the smaller amino sugars quantities at the UB site by either preventing stabilization or interfering with production of amino sugars, while the lower pH of the Sed site may provide a competitive advantage for fungi.

Total amino sugars

At both sites on Mt. Kinabalu, amino sugars (AS) contributed to the total AS pool in the order GluN > GalN > MurA > ManN, which is consistent with a number of other amino sugar studies across a range of biomes (Amelung et al. 1999; Zhang et al. 1999; Guggenberger et al. 1999; Solomon et al. 2001; Turrión et al. 2002; Liang et al. 2007c). The total amount of amino sugars measured at each site was low when compared to a study in agricultural North American soils (Guggenberger et al. 1999), yet similar to studies in surface soils of an old-growth forest in upper Michigan (Liang et al. 2007c) and a semi-arid tropical woodland (Solomon et al. 2001). In a study of amino sugars across a North American climosequence Amelung et al. (1999) found that the highest amino sugar production occurred with a mean annual temperature (MAT) of 12–15 °C, above which amino sugar contents decreased with increasing MAT and below which amino sugars decreased with decreasing MAT. Because of the rapid cycling of SOM in tropical

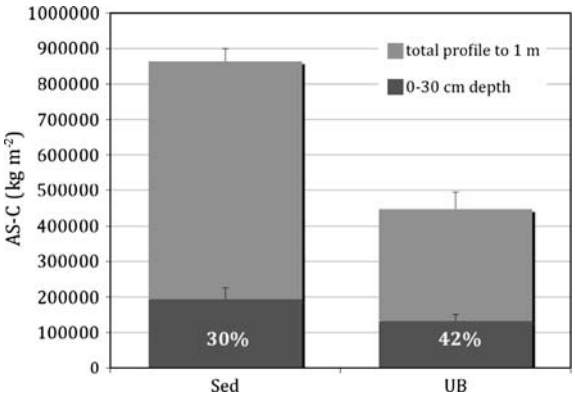

Fig. 4 Total amino sugar content on a kg m^{-2} basis at Sed and UB sites. Taller lighter bars are the AS content in the total soil profile to a meter depth. The darker bars represent AS content in the top 30 cm. Numbers in parentheses are the percent of the total profile AS accounted for by AS in the top 30 cm. Error bars are ±1 standard error of the mean and $n = 3$

climates and the depletion of organic matter that is typical of highly weathered tropical soils, it is not surprising that amino sugar contents are lower in the Mt. Kinabalu lowlands (with a MAT ~ 24 °C). Because of the rapid utilization of any organic carbon entering into tropical systems, SOM pools are low when compared to temperate or boreal systems (where organic matter decomposes at a slower rate) (Zech et al. 1997; Davidson and Janssens 2006). Indeed, Amelung et al. (1999) concluded that when MAT exceeds 15 °C, soil microorganisms begin to decompose their own amino sugar products more rapidly and suggested this is related to a lack of sufficient organic substrate in warmer climates. When preferable substrates have been utilized, soil microorganisms may turn to what would ordinarily be considered a less desirable substrate (Amelung et al. 1999; Zak et al. 1999). Thus, at Mt. Kinabalu we speculate that SOM dynamics, in particular the persistence of amino sugars, may be determined by the presence or absence of other suitable substrate (such as glucose or cellulose) for the soil microbial community to metabolize.

Influence of depth

It is well known that soil texture acts as a strong control over SOC concentrations in soils and particle sizes contain pools of different SOM quality and turnover rates (Feller and Beare 1997; Zech et al. 1997; Amelung et al. 1998; Zinn et al. 2007), and studies have shown that amino sugar contents are often highest in the silt and clay fractions (Guggenberger et al. 1999; Zhang et al. 1998, 1999; Solomon et al. 2001; Turrión et al. 2002). In this study, amino sugar contents generally declined with depth, albeit with some irregular decreases at intermediate depths (Table 3; Fig. 2). We suggest the subtle increases we observed in some amino sugars at intermediate depths may be related to observed zones of clay accumulation and the capacity of high surface area clays to physically protect and stabilize amino sugars in soil (Parsons 1981; Feller and Beare 1997; Zech et al. 1997). In addition, some amino sugars may move through the soil profile as dissolved organic carbon and accumulate in subsurface soils, causing irregularities in amino sugar depth profiles (Kaiser et al. 2004).

The ratios of GluN/MurA at both sites had a linear decline to 30 cm, suggesting that (not unexpectedly) the relative contribution of fungi to SOM decreases with distance from the surface (Fig. 2). Therefore, with increasing depth, bacteria constitute a greater relative proportion of the microbially derived SOM pool. A similar result was reported in a depth study of amino sugars in Thailand by Möller et al. (2002). Fungi are aerobic organisms that typically utilize fresh litter as their preferred carbon source and generally successfully out-compete bacteria in surface soils, particularly under acidic conditions, such as were present in the surface soils of both Sed and UB sites (Paul and Clark 1996; Turrión et al. 2002). With increasing depth, studies typically report a decrease in the relative abundance of fungi, as was observed in the upper 30 cm of this study (Möller et al. 2002; Taylor et al. 2002; Fierer et al. 2003). Below 30 cm, GluN/MurA ratios show a smooth parabolic curve at the Sed site while the UB site has irregular patterns, and this may again be linked to the sorptive capacity of clays for amino sugar retention (Fig. 2). The presence of silts and clay as retentive sorption surfaces is especially important for MurA, as this amino sugar contrasts with the hexosamines in that it is stabilized only when bound in soil (Zhang et al. 1998). In contrast, the ratios of GluN/GalN at both sites were generally consistent at each sampling interval, suggesting comparable relative contributions of these fungal and bacterially-derived amino sugars to SOM throughout the soil profiles at each site (Table 4; Fig. 2). This difference between the two ratio types (GluN/MurA and GluN/GalN) could be due to different relative

retention times of the various amino sugars, or it could be that GluN/MurA and GluN/GalN indicate different aspects of relative fungal to bacterial contribution (Liang et al. 2007b).

The percentage of total soil organic carbon (SOC) or nitrogen (soil N) derived from amino sugars had different vertical distribution patterns at each site (Fig. 3). At the Sed site, the percent of SOC derived from AS increased with depth and thus microbial residues contributed an increasing proportion to SOC with depth in the profile. This result at the Sed site is similar to that reported in an amino sugar depth study in a primary tropical forest in Thailand by Möller et al. (2002), who suggested the increasing contribution of amino sugars to SOC with depth may be attributed to amino sugar stabilization by clay and subsequent accumulation over time. In contrast, the proportion of SOC from AS was steady throughout the profile at the UB site, indicating that amino sugars contribute a consistent percentage of C to SOC throughout all sampling depths. At the Sed site, the AS percent of soil N remained steady throughout the profile, suggesting amino sugars contribute a consistent proportion of N to soil N pools with depth. Conversely, the AS percent of soil N generally declined with increasing depth below 50 cm in the profile at the UB site, indicating a potential decrease in the microbial contribution to soil N pools with depth. Although pool sizes do not indicate flux rates, these distinct trends with depth may indicate that the UB site has less capacity to protect amino sugars from microbial degradation than the soils of the Sed site, and thus has a lower overall stabilization of residues. Generally, there are few depth studies of amino sugars in the literature and more research is needed to elucidate trends of microbially-derived SOM throughout the soil profile, particularly in ultrabasic soils with different sorption capacities and mineralogy. Further study of amino sugars and their stabilization in various clay minerals is desirable to understand the persistence of amino sugars in soil and the microbial contribution to SOM cycling.

Importance of parent material

Both the Sed and UB sites support forests of similar species composition, structure, and stocking density, and both soil profiles have comparable SOC contents (Table 2). Moritz et al. (in preparation) used lipid biomarker analysis in these soils to assess microbial community composition and found that generally microbial biomass and community structure were similar between the sites. The two sites also share similar climate, topography, and time of soil pedogenesis, and thus four of Jenny's (1941) soil forming factors remain consistent between sites and the effect of parent material may be isolated (Aiba and Kitayama 1999). Taken together these observations suggest that there are carbon additions of similar quality and quantity being metabolized by a similar microbial community, and therefore, we might expect similar amino sugar production at each site. While we did not specifically measure production, we do generally see greater amino sugar contents, GluN/MurA ratios, and microbial contribution to SOC and N pools at the Sed site, with significant differences at increasing depths in the profile below 50 cm ($p < 0.05$; Table 3; Figs. 2, 3). We suggest the observed similarities in the upper profile might be attributed to the similar aboveground vegetation and C inputs, as recent studies have shown that plant species influence the composition of microbial residues (Liang et al. 2007c) and that quantity and composition of C affect microbial transformation of C and N into amino sugars (Liang et al. 2007b). With increasing depth, there are diminished vegetation effects and the production and retention of amino sugars may be primarily dictated by the soil matrix as constructed by the parent material. Perhaps the most striking difference between the two sites is their strongly contrasting elemental compositions, with iron oxides dominating at the UB site and silicon oxides at the Sed site (Table 2). Amelung et al. (2001) investigated the effects of minerals on organic matter cycling and found that iron oxides inhibited bacterial amino sugar synthesis (MurA and GalN) in a litter decomposition study, resulting in lower contributions of bacterially-derived amino sugars to the SOC pool. The iron oxides did not, however, affect GluN contents and the fungal production of amino sugars actually appeared to increase, rendering the total amino sugars concentrations equivalent between control and Fe-amended litter. Amelung et al. (2001) postulated that there was either an inhibition of bacterial production of amino sugars in the Fe oxide amended litter that may have resulted from sorptive losses of labile C, i.e. a lack of substrate for bacterial metabolism and subsequent amino sugar production, or that high metal concentrations may have adversely affected bacteria.

In this study, we found fewer bacterial amino sugars in the Fe oxide-rich profiles of the UB site, and also found lower *total* amino sugar contents as well (Fig. 4). The role of iron oxides in the stabilization of organic matter is well known (Zech et al. 1997; Mikutta et al. 2006; Kaiser and Guggenberger 2007; Wagai and Mayer 2007; Zinn et al. 2007). When Fe binds with organic matter, the resulting complex is extremely stable, making it relatively unavailable to microorganisms for use as C substrate (Zech et al. 1997). While it is true that the microbial communities in studies using Fe addition may not be adapted to conditions of elevated iron, Wagai and Mayer (2007) studied the sorptive stabilization of organic matter by iron oxides at the same Sed and UB sites as in this study and found over half of the total organic carbon (OC) of the soil was released as reductively soluble OC upon Fe reduction at the UB site, while less than 25% of the total OC was released at the Sed site after dithionite extraction. Therefore we speculate that a substantial proportion of the OC present at the UB site may be sorbed onto iron oxides and this pool is largely protected from microbial degradation (Zech et al. 1997). We propose that while overall SOC contents are similar between the Sed and UB sites, the SOC is stabilized differently in each soil because of the different elemental compositions and subsequent mineralogy inherited from the contrasting parent materials and suggest that the amount of SOC accessible to soil microorganisms is lower at the UB site perhaps because of the relative insolubility of Fe and organic matter complexes. As a result, soil microorganisms degrade their own products (i.e. amino sugars) in response to the limited amount of labile C substrates (Amelung et al. 1999). This is demonstrated in Fig. 4; the total amount of Amino sugars at the UB site is half that of the Sed site, despite comparable microbial biomass pool sizes and comparable total carbon (Table 2). The potential relationship between iron oxides and amino sugar characteristics is further supported by significant negative correlations between iron oxide contents and total amino sugars, GluN/MurA, AS-C/SOC, and AS-N/soil N (Table 5). Accordingly, we suggest that differences in amino sugar contents, GluN/MurA, and AS-C/SOC and AS-N/soil N at the Sed and UB sites become more pronounced with depth as the vegetative influence begins to weaken and the inherent characteristics of the parent material, including iron oxide contents and pH, become the dominant factor affecting amino sugar production and retention. Parent material, through its impact on the accessibility of OC to the microbial community can thus alter the retention or stabilization of amino sugar residues. This in turn can influence the capacity of a soil to sequester carbon and its resilience to release carbon upon perturbations, such as land use conversion, which is of great concern in the tropics, or global warming.

Conclusions

This study is one of the first to characterize microbial biomarkers with depth in soils of contrasting parent materials in a tropical forest soil. In particular, to the best of our knowledge, there have been no prior studies of amino sugars in ultrabasic soils and no studies have explicitly examined the effects of parent material on amino sugar pool sizes in situ. We found (as might be expected) that soil characteristics differed

Table 5 Correlations among soil site variables, amino sugar contents, amino sugar ratios, and relative carbon and nitrogen proportions

	pH 0.01 M $CaCl_2$	C:N ratio	wt% Fe_20_3	wt% SiO_2	% Sand	% Clay
GluN	0.65***	0.64***	−0.34*		0.53**	−0.52**
GalN	0.43**		−0.36*	0.33*	0.39*	−0.31*
MurA	0.52**	0.50**	−0.31*		0.54**	−0.51**
Total AS	0.64***	0.55**	−0.39*	0.36*	0.55**	−0.51**
GluN/MurA	0.69***		−0.53***	0.51**	0.51**	−0.50**
GluN/GalN						
AS-C/SOC		−0.51**	−0.60***	0.59***	0.44**	
AS-N/soil N	0.33*		−0.48**	0.46**	0.43*	

$N = 41$

* $p < .05$, ** $p < .005$, *** $p < .0001$

markedly between the two sites studied. Further, soil parent material influenced microbial residue accumulation with depth despite similarities in microbial community structure and biomass in the surface soil. The importance of including soil depth in carbon cycle studies cannot be underestimated, particularly in tropical latitudes where carbon cycling is particularly intense.

We suggest that additional research is needed across a range of biomes to confirm the role of iron oxides in the persistence of microbial residues in soil, and to explore the mechanisms by which minerals affect microbial access to carbon substrates and whether this influences the stabilization versus degradation of their cellular products.

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References

Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. Plant Ecol 140:139–157. doi:10.1023/A:1009710618040

Amelung W (2001) Methods using amino sugars as markers for microbial residues in soil. In: Lal R, Kimble JM, Follett RF, Stewart BA (eds) Assessment methods for soil carbon pools. Advances in soil science. CRC/Lewis, Boca Raton, pp 233–270

Amelung W (2003) Nitrogen biomarkers and their fate in soil. J Plant Nutr Soil Sci 166:677–686. doi:10.1002/jpln.200321274

Amelung W, Zech W, Zhang X, Follett RF, Tiessen H, Knox E, Flach K-W (1998) Carbon, nitrogen and sulfur pools in particle-size fractions as influenced by climate. Soil Sci Soc Am J 62:172–181

Amelung W, Zhang X, Flach KW, Zech W (1999) Amino sugars in native grassland soils along a climosequence in North America. Soil Sci Soc Am J 63:86–92

Amelung W, Miltner A, Zhang X, Zech W (2001) Fate of microbial residues during litter decomposition as affected by minerals. Soil Sci 166:598–606. doi:10.1097/00010694-200109000-00003

Amundson R (2001) The carbon budget in soils. Annu Rev Earth Planet Sci 29:535–562. doi:10.1146/annurev.earth.29.1.535

Benzing-Purdie L (1981) Glucosamine and galactosamine distribution in a soil as determined by gas-liquid-chromatography of soil hydrolysates—effect of acid strength and cations. Soil Sci Soc Am J 45:66–70

Benzing-Purdie L (1984) Amino sugar distribution in 4 soils as determined by high-resolution gas-chromatography. Soil Sci Soc Am J 48:219–222

Brock TD, Madigan MT (1988) Biology of microorganisms, 5th edn. Prentice-Hall, Englewood Cliffs

Chantigny MH, Angers DA, Prévost D, Vézin L-P, Chalifour FP (1997) Soil aggregation and fungal and bacterial biomass under annual and perennial cropping systems. Soil Sci Soc Am J 61:262–267

Coelho RRR, Sacramento DR, Linhares LF (1997) Amino sugars in fungal melanins and soil humic acids. Eur J Soil Sci 48:425–429. doi:10.1046/j.1365-2389.1997.00094.x

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173. doi:10.1038/nature04514

Feller C, Beare MH (1997) Physical control of soil organic matter dynamics in the tropics. Geoderma 79:69–116. doi:10.1016/S0016-7061(97)00039-6

Fierer N, Schimel JP, Holden PA (2003) Variations in microbial community composition through two soil depth profiles. Soil Biol Biochem 35:167–176. doi:10.1016/S0038-0717(02)00251-1

Gee GW, Bauder JW (1986) Particle-size analysis. In: Klute A (ed) Methods of soil analysis, Pt. 1. Physical and mineral methods, 2nd edn. American Society of Agronomy-Soil Science Society of America, Madison, pp 383–411

Glaser B, Turrión MB, Alef K (2004) Amino sugars and muramic acid—biomarkers for soil microbial community structure analysis. Soil Biol Biochem 36:399–407. doi:10.1016/j.soilbio.2003.10.013

Guerrant GO, Moss CW (1984) Determination of monosaccharides as aldononitrile, *o*-methyloxime, alditol, and cyclitol acetate derivatives by gas-chromatography. Anal Chem 56:633–638. doi:10.1021/ac00268a010

Guggenberger G, Frey SD, Six J, Paustian K, Elliott ET (1999) Bacterial and fungal cell-wall residues in conventional and no-tillage agroecosystems. Soil Sci Soc Am J 63:1188–1198

Jacobson G (1970) Gunong Kinabalu Area, Sabah, Malaysia. 8: Geological Survey Malaysia, Kuching, Sarawak

Jenny H (1941) Factors of soil formation. McGraw Hill, New York

Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic matter and its relation to climate and vegetation. Ecol Appl 10:423–436. doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2

Kaiser K, Guggenberger G (2007) Sorptive stabilization of organic matter by microporous goethite: sorption into small pores vs. surface complexation. Eur J Soil Sci 58:45–59. doi:10.1111/j.1365-2389.2006.00799.x

Kaiser K, Guggenberger G, Haumaier L (2004) Changes in dissolved lignin-derived phenols, neutral sugars, uronic acids, and amino sugars with depth in forested haplic arenosols and rendzic leptosols. Biogeochemistry 70:135–151. doi:10.1023/B:BIOG.0000049340.77963.18

Karathanasis AD, Hajek BF (1996) Elemental analysis by X-ray fluorescence spectroscopy. In: Sparks DL (ed) Methods of soil analysis, pt. 3. Chemical methods, 1st edn. Soil Science Society of America and American Society of Agronomy, Madison, pp 161–218

Kilmer VJ, Alexander LT (1949) Methods of making mechanical analysis of soils. Soil Sci 68:15–24. doi:10.1097/00010694-194907000-00003

Kögel I, Bochter R (1985) Amino sugar determination in organic soils by capillary gas-chromatography using a nitrogen-selective detector. Z Pflanzen Bodenk 148:260–267. doi:10.1002/jpln.19851480306

Kögel-Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol Biochem 34:139–162. doi:10.1016/S0038-0717(01)00158-4

Liang C, Balser TC (2008) Preferential sequestration of microbial carbon in subsoils of a glacial-landscape toposequence, Dane County, WI, USA. Geoderma 148:113–119. doi:10.1016/j.geoderma.2008.09.012

Liang C, Fujinuma R, Wei L, Balser TC (2007a) Tree species-specific effects on soil microbial residues in an upper Michigan old-growth forest system. Forestry 80:65–72. doi:10.1093/forestry/cpl035

Liang C, Zhang X, Balser TC (2007b) Net microbial amino sugar accumulation process in soil as influenced by different plant material inputs. Biol Fertil Soils 44:1–7. doi:10.1007/s00374-007-0170-5

Liang C, Zhang X, Rubert KF, Balser TC (2007c) Effect of plant materials on microbial transformation of amino sugars in three soil microcosms. Biol Fertil Soils 43:631–639. doi:10.1007/s00374-006-0142-1

Lützow M, Kögel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. Eur J Soil Sci 57:426–445. doi:10.1111/j.1365-2389.2006.00809.x

Mikutta R, Kleber M, Torn MS, Jahn R (2006) Stabilization of soil oganic matter: association with minerals or chemical recalcitrance? Biogeochemistry 77:25–56. doi:10.1007/s10533-005-0712-6

Möller A, Kaiser K, Zech W (2002) Lignin, carbohydrate, and amino sugar distribution and transformation in the tropical highland soils of northern Thailand under cabbage cultivation, Pinus reforestation, secondary forest, and primary forest. Aust J Soil Res 40:977–998. doi:10.1071/SR01030

Moritz LK (2008) Soil habitat and microbial communities on Mount Kinabalu, Borneo. Master's Thesis, Department of Soil Science, University of Wisconsin, Madison.

Parsons JW (1981) Chemistry and distribution of amino sugars in soils and soil organisms. In: Paul EA, Ladd JN (eds) Soil biochemistry, vol 5. Marcel Dekker, Inc., New York, pp 197–227

Paul E, Clark F (1996) Soil microbiology and biochemistry. Academic Press, San Diego

Six J, Guggenberger G, Paustian K, Haumaier L, Elliott ET, Zech W (2001) Sources and composition of soil organic matter fractions between and within soil aggregates. Eur J Soil Sci 52:607–618. doi:10.1046/j.1365-2389.2001.00406.x

Six J, Frey SD, Thiet RK, Batten KM (2006) Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci Soc Am J 70:555–569. doi:10.2136/sssaj2004.0347

Soil Survey Staff (2006) Keys to soil taxonomy, 10th edn. United States Department of Agriculture Natural Resources Conservation Service, USA

Solomon D, Lehmann J, Zech W (2001) Land use effects on amino sugar signature of chromic luvisol in the semi-arid part of northern Tanzania. Biol Fertil Soils 33:33–40. doi:10.1007/s003740000287

Stevenson FJ (1982) Organic forms of soil nitrogen. In: Stevenson FJ (ed) Nitrogen in agricultural soils. American Society of Agronomy, Madison, pp 101–104

Stevenson FJ, Braids OC (1968) Variation in relative distribution of amino sugars with depth in some soil profiles. Soil Sci Soc Am Proc 32:590–598

Taylor JP, Wilson B, Mills MS, Burns RG (2002) Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. Soil Biol Biochem 34:387–401

Turrión MB, Glaser B, Zech W (2002) Effects of deforestation on contents and distribution of amino sugars within particle-size fractions of mountain soils. Biol Fertil Soils 35:49–53. doi:10.1007/s00374-001-0440-6

Wagai R, Mayer LM (2007) Sorptive stabilization of organic matter in soils by hydrous iron oxides. Geochimica 71:25–35. doi:10.1016/j.gca.2006.08.047

Zak DR, Holmes WE, MacDonald NW, Pregitzer KS (1999) Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. Soil Sci Soc Am J 63:575–584

Zech W, Senesi N, Guggenberger G, Kaiser K, Lehmann J, Miano TM, Miltner A, Schroth G (1997) Factors controlling humification and mineralization of soil organic matter in the tropics. Geoderma 79:117–161. doi:10.1016/S0016-7061(97)00040-2

Zhang X, Amelung W (1996) Gas chromatographic determination of muramic acid, glucosamine, mannosamine, and galactosamine in soils. Soil Biol Biochem 28:1201–1206. doi:10.1016/0038-0717(96)00117-4

Zhang X, Amelung W, Yuan Y, Zech W (1998) Amino sugar signature of particle-size fractions in soils of the native prairie as affected by climate. Soil Sci 163:220–229. doi:10.1097/00010694-199803000-00007

Zhang X, Amelung W, Yuan Y, Samson-Liebig S, Brown L, Zech W (1999) Land-use effects on amino sugars in particle size fractions of an Argiudoll. Appl Soil Ecol 11:271–275. doi:10.1016/S0929-1393(98)00136-X

Zinn YL, Lal R, Bigham JM, Resck DVS (2007) Edaphic controls on soil organic carbon retention in the Brazilian Cerrado: Texture and mineralogy. Soil Sci Soc Am J 71:1204–1214. doi:10.2136/sssaj2006.0014