

Stabilization of recent soil carbon in the humid tropics following land use changes: evidence from aggregate fractionation and stable isotope analyses

Sonja Paul · Heiner Flessa · Edzo Veldkamp ·
Magdalena López-Ulloa

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Abstract Quantitative knowledge of stabilization- and decomposition processes is necessary to understand, assess and predict effects of land use changes on storage and stability of soil organic carbon (soil C) in the tropics. Although it is well documented that different soil types have different soil C stocks, it is presently unknown how different soil types affect the stability of recently formed soil C. Here, we analyze the main controls of soil C storage in the top 0.1 m of soils developed on Tertiary sediments and soils developed on volcanic ashes. Using a combination of fractionation techniques with ^{13}C isotopes analyses we had the opportunity to trace origin and stability of soil carbon in different aggregate fractions under pasture and secondary forest. Soil C contents were higher in volcanic ash soils ($47\text{--}130\text{ g kg}^{-1}$) than in sedimentary soils ($19\text{--}50\text{ g kg}^{-1}$). Mean residence time (MRT) of forest-derived carbon in pastures increased from 37 to 57 years with increasing silt + clay content in sedimentary soils, but was independent from soil properties in volcanic ash soils. MRTs

of pasture-derived carbon in secondary forests were considerably shorter, especially in volcanic ash soils, where no pasture-derived carbon could be detected in any of the four studied secondary forests. The implications of these results are that the MRT of recently incorporated organic carbon depends on clay mineralogy and is longer in soils dominated by smectite than non-crystalline minerals. Our results show that the presence of soil C stabilization processes, does not necessarily mean that recent incorporated soil C will also be effectively stabilized.

Keywords Carbon sequestration · Ecuador · Mean residence time · Pasture · Secondary forest · Soil type · Texture · Water-stable aggregates

Introduction

Globally, soils contain about 75% of the terrestrial organic carbon pool (Post et al. 1982). About 1,500 Gt of organic carbon are stored in the top meter of soils, of which 32% are located in tropical soils (Jobbagy and Jackson 2000). Presently, about one fourth of anthropogenic CO_2 emissions are attributed to deforestation in the tropics (Denman et al. 2007). Although these CO_2 emissions are mainly caused by the loss of above ground carbon stocks, mineralization of soil organic matter also contributes significantly (Detwiller 1986). Conversion of tropical forests and

S. Paul (✉) · E. Veldkamp · M. López-Ulloa
Büsgen Institute, Soil Science of Tropical and Subtropical
Ecosystems, Georg-August University Göttingen,
Büsgenweg 2, 37077 Göttingen, Germany
e-mail: spaul1@gwdg.de

H. Flessa
Büsgen Institute, Soil Science of Temperate and Boreal
Ecosystems, Georg-August University Göttingen,
Büsgenweg 2, 37077 Göttingen, Germany

pastures to cropland typically decreases soil organic carbon (soil C) stocks by 40–60% (van Noordwijk et al. 1997; Guo and Gifford 2002) with coarse textured soils being more susceptible to soil C losses than soils with finer textures (Zinn et al. 2005). In contrast, conversion of forests to pastures can result in both gains and losses of soil C, depending on soil properties, climate, and pasture management (Detwiler 1986; Lugo and Brown 1993; Powers and Veldkamp 2005). Forest regrowth on former pastures was found to be associated either with increases or decreases in soil carbon stocks depending on land use history and soil properties (de Koning et al. 2003).

Quantitative knowledge of stabilization and decomposition processes of organic matter in different soils is necessary in order to understand, assess and predict effects of land use changes on the storage and stability of soil C. Several mechanisms can contribute to stabilization of carbon in soils, which can be broadly divided into three groups: recalcitrance, interactions and accessibility (Sollins et al. 1996; von Lützow et al. 2006). Aggregation reduces accessibility of microbial biomass to substrate and thus contributes to the physical protection of soil C (Sollins et al. 1996). In 1982, Tisdall and Oades formulated the hypothesis that stable microaggregates (<250 μm) are bound together to larger units (macroaggregates) by labile organic material. This concept, which they called “soil aggregate hierarchy,” was supported by subsequent studies which showed that macroaggregates had higher carbon contents, contained less decomposed organic material, and had faster soil C turnover compared to microaggregates (Six et al. 2002; John et al. 2005). However, the concept of aggregate hierarchy, that relies on organic matter as main binding agent, may not be suitable for heavily weathered tropical soils with 1:1 clays nor for volcanic ash soils, as in these soils, rich in iron and aluminum oxides, formation of aggregates by mineral–mineral bindings is more important (Oades and Waters 1991; Hoyos and Comerford 2005; Schwendenmann and Pendall 2006).

Changes in $\delta^{13}\text{C}$ of soil C following conversion from tropical forests to grassland or cropland have been used widely to determine soil C stability in tropical soils (e.g., Veldkamp 1994; Desjardins et al. 1994). A review of available data on soil C turnover times calculated from C_3/C_4 vegetation changes

showed that the mean soil C turnover time was considerably shorter for tropical soils (36 years) than for temperate soils (63 years; Six et al. 2002). The higher turnover in tropical soils was related to faster decomposition rates due to high temperatures in connection with high precipitation in the tropics. However, the review also revealed a substantial overlap in estimated turnover times (13–108 years for tropical soils versus 14–141 years for temperate soils; Six et al. 2002), indicating no simple relationship between climate and carbon stabilization. In addition to climatic conditions, soil C turnover may vary considerably depending on soil mineralogy and related chemical and physical interactions of soil C with mineral soil particles (Torn et al. 1997), which may differ in tropical and temperate soils. It was found that soil C associated with smectite had considerably longer mean residence time (MRT) than soil C associated with kaolinite (Wattel-Koek et al. 2003). Current knowledge is very limited how soil properties influence soil C turnover rates (Desjardins et al. 2004). Even less is known about the differences in stabilization processes of recently incorporated carbon compared to older carbon in different soil types.

In the humid tropics of Northwest Ecuador, both forest clearing for pasture and pasture abandonment followed by forest regrowth have occurred during the past few decades. In this area, de Koning et al. (2003) analyzed the potential to increase soil C stocks after forest regrowth on abandoned pastures. Forest regrowth led to a yearly increase of soil C stocks in the upper 50 cm of about $1.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ if the secondary forest had at least 20 years to grow (de Koning et al. 2003). In a correlative study on a selection of these sites, long-term stabilization of soil C in volcanic ash soils was associated with the formation of metal-humus complexes and allophanes, whereas in soils with smectitic clay minerals soil C was stabilized primarily through sorption to clay (López-Ulloa et al. 2005). In the present study, our objectives were: (i) to determine how important aggregation is for the stabilization of soil C in the topsoil of different soil types in natural forests, pastures and secondary forests of the humid tropics of Ecuador and (ii) to determine the stability of forest-derived soil C in pastures and of pasture-derived soil C in secondary forests in different aggregate fractions.

Materials and methods

Site description

We selected a subset of eight sites used by de Koning et al. (2003) and López-Ulloa et al. (2005). In addition to the sites which consisted of paired secondary forest (or tree plantation) and pasture we selected an additional natural forest site with similar overall environmental characteristics of pasture and secondary forest plots as close as possible. In most cases, the natural forests plots (nf) were well protected and showed no evidence of human activity. However, in a few cases (Chonta Duro), individual trees had been extracted in the past from the natural forest plot. Pasture plots had been established after cutting and burning natural forest. Pastures (ps) were dominated by C₄ grasses [*Paspalum dilatatum* Poir., *Panicum maximum* Jacq., *Cynodon plectostachyus* (K. Schum.) Pilger]. Secondary forests formed on abandoned pastures due to natural succession without management, whereas the plantations were established on former pastures by planting trees. As there were no differences in soil C contents between secondary forests and plantations (de Koning et al. 2003), these sites were grouped and analyzed together [we call these sites ‘secondary forest’ (sf)].

Our sites were located in the Northwest of Ecuador (Table 1). Four sites had soils developed in volcanic ashes and differed in silt + clay content and were classified as Hapludands. The mineralogy was characterized by the presence of allophane (de Koning et al. 2003). Soils of the other four sites were developed in marine Tertiary sediments and covered a gradient in clay content. These soils were classified as Haplustepts and Paleudalfs (Soil Survey Staff 1998). X-ray diffraction of clay fraction of sedimentary soils revealed that sedimentary soils were dominated by smectite with only marginal contribution of illite, chlorite, and kaolinite. In the following, soils developed in marine Tertiary sediments we call ‘sedimentary soils’ and soils developed in volcanic ashes ‘volcanic ash soils’.

At all sites, we combined fractionation of water-stable aggregates with ¹³C isotope analyses, which gave us the opportunity to trace origin and stability of soil C pools in different aggregate fractions and to calculate mean apparent residence times of soil C under different land use types in the humid tropics of northwest Ecuador. At each plot, we sampled and described one soil profile and we selected four additional sampling points along a 50 m transect. At each sampling point fine root samples were taken using a root corer. We only sampled the upper 0.1 m since we expected that effects of land use changes on soil

Table 1 Location, general site characteristics and land use history

Site	N (°)	W (°)	Elevation (m)	Annual average precipitation (mm year ⁻¹)	Annual average air temperature (°C)	Age of current pasture ^a (year)	Age of secondary forest ^b (year)	Age of former pasture ^c (year)
Sedimentary soils								
Tazonas	00°43.24	079°50.09	95	1,800	26	35	14	21
Penas	01°04.37	079°08.09	45	2,500	27	30	10	20
Chonta duro	00°55.26	079°25.30	30	1,800	27	35	17	20
Minas	00°51.86	079°34.24	191	1,300	27	33	10	20
Volcanic ash soils								
Mindo	00°01.45	078°46.16	1,665	3,500	18	20	23	5
Maquipucuna	00°07.21	078°37.55	1,359	2,300	19	50	20	30
Pedro Vicente	00°05.65	079°01.51	690	4,900	22	13	15	8
Pitzara	00°16.22	079°09.74	294	3,500	23	20	10	10

^a Pastures were established after clearing of natural forest

^b Secondary forests were established on former pastures

^c Duration of pasture before the site was changed to secondary forest

aggregation and soil C stocks of different origin and stability are most pronounced in the top soil (Desjardins et al. 1994; Bashkin and Binkley 1998). History of land use and site management was obtained by interviewing current and former landowners (Table 1).

General soil and vegetation analyses

For all individual sampling points of sedimentary soils particle size distribution was analyzed using sieving and the pipette method with sodiumpyrophosphate as a dispersing agent (König and Fortmann 1996). As the determination of clay content for the volcanic ash soils reveals ambiguous results due to incomplete dispersion (Nanzyo et al. 1993), we did not determine the clay content of these volcanic ash soils. The silt + clay content was determined by difference from sand. Bulk soil density was determined gravimetrically at each sampling point from undisturbed soil cores (300 cm³) after drying at 105°C. Soil pH_{H2O} and effective cation exchange capacity (ECEC) were determined using composite samples from the A horizon of the soil profiles. ECEC was determined by leaching soil samples with 100 ml of unbuffered 1 M ammonium chloride (NH₄Cl) for 4–5 h. Cations in extracts were quantified by atomic absorption spectroscopy (König and Fortmann 1996). Total C and N were measured with an automated C and N analyzer (Elementaranalysator CNS, Vario EL, Elementar, Hanau, Germany) after milling the samples.

All soil samples were characterized using selective dissolution techniques. Selective dissolution was done using acid ammonium-oxalate extraction of aluminum (Al_o) and iron (Fe_o); dithionite-citrate extraction of iron (Fe_d) and pyrophosphate extraction of aluminum (Al_p) (Buurman et al. 1996). Fe and Al concentrations in these extracts were measured by inductively coupled plasma emission spectroscopy (Flame-ICP, Spectro Analytical Instruments, Kleve, Germany). Acid ammonium-oxalate extracts Al in allophane and imogolite; Al and Fe in organic complexes and Fe and Al in non-crystalline hydrous oxides (Wada 1989). Dithionite-citrate solution extracts Al and Fe in organic complexes; Al from non-crystalline hydrous oxides and Fe from crystalline and non-crystalline hydrous oxides. Finally, pyrophosphate extracts Al and Fe from organic complexes only (Wada 1989). The ratio of Al_p/Al_o indicates the proportion of Al humus complexes versus allophane content. Soils

dominated by humus complexes are characterized by a ratio near 1, while soils dominated by allophane have ratios <0.5 (allophanic soils; Nanzyo et al. 1993). The difference between Al_o and Al_p gives a measure of non-crystalline compounds.

Samples of fine roots (down to 0.1 m depth) were dried at 60°C, weighed, milled and analyzed for total carbon and nitrogen contents by an automated C and N analyzer (Heraeus Elementar Vario EL, Hanau, Germany).

Fractionation of water-stable aggregates

Fractionation of water-stable aggregates was modified from the method described by Elliott (1986). The main difference with his method was that we used moist soil, which was adjusted to 70% of its maximum water holding capacity. We did not use air-dried soil samples for aggregate fractionation because volcanic ash soils display irreversible flocculation and changes in aggregate distribution upon drying (Wells and Theng 1988). Other studies that did aggregate fractionations in volcanic ash soils also used moist soil samples (Churchman and Tate 1986; Parfitt et al. 2002). For a comparison of the effect of aggregate fractionation on dry versus moist soil samples, see Paul et al. (in press a).

Soil samples were first gently broken by hand and passed through a 8,000 µm sieve. This sample (equivalent to 100 g dry soil) was submersed in distilled water for 5 min on top of a 2,000 µm sieve and the sieve was manually moved 3 cm up and down, 50 times within 2 min. Aggregates of 8,000–2,000 µm were collected and sieving was repeated with sieves of 250 µm and 53 µm. The fraction <53 µm was precipitated using a 1 M CaCl₂ solution and the supernatant was discarded. All fractions were oven-dried at 40°C. Roots were hand-picked and samples were milled using a ball mill. At one site (pasture of Minas) we found carbonates in the C horizons. Therefore, aggregate fractions of the site Minas were leached with liquid HCl (10%) prior to analyses. Sand content was determined in sub-samples of all aggregate classes >53 µm and organic carbon content of aggregates was expressed as soil C in sand-free aggregates (Elliott et al. 1991). Mean Weight Diameter (MWD) of water-stable aggregates was calculated as: $MWD = \sum (\text{Weight \% sample on sieve} \times \text{mean inter-sieve size}/100)$, where the upper limit was 8,000 µm (Kemper and Rosenau 1986).

Isotope analyses

The $^{13}\text{C}/^{12}\text{C}$ isotope ratio was measured using an isotope ratio mass spectrometer (IRMS, Finnigan MAT, DELTA^{plus}, Bremen, Germany) at the Center for Stable Isotopes Research and Analysis, University of Göttingen. The C isotope ratios are expressed as $\delta^{13}\text{C}$ (V-PDB). Standard deviation of measurements was $<0.1\%$. The proportion of soil C derived from pasture vegetation (= soil $\text{C}_4\text{-C}$) was calculated according to Balesdent and Mariotti (1996):

$$f = (\delta_{\text{sam}} - \delta_{\text{ref}}) / (\delta_{\text{pasture}} - \delta_{\text{forest}}), \quad (1)$$

where f is the proportion of pasture-derived C in the sample, δ_{sam} is the measured $\delta^{13}\text{C}$ -value of the topsoil sample, δ_{ref} is the $\delta^{13}\text{C}$ -value of the corresponding sample from the natural forest as C_3 reference soil, and δ_{pasture} and δ_{forest} are the $\delta^{13}\text{C}$ -values of fine roots collected from the topsoil of the pastures and forests, respectively. The standard deviation S_f of the pasture-derived proportions was calculated from the standard deviations of δ_{ref} , δ_{sam} , δ_{pasture} , and δ_{forest} using a first-order Taylor series approximation.

Calculation of mean apparent residence time of soil C

The mean apparent residence time of forest-derived soil C was calculated from the decrease of the proportion of soil C derived from forest (= soil $\text{C}_3\text{-C}$) in pasture under the assumptions that soil C fractions are homogeneous and that decomposition can be described with a single pool model. Describing soil C decomposition with a single pool model is a rough simplification (Davidson and Janssens 2006). Studies of chronosequences with different land use ages show that soil C pools of different stability exist (Veldkamp 1994; Feigl et al. 1995) which is also reflected in most soil C models which assume the existence of several soil C pools with different turnover times. Nevertheless, the single pool approach can be useful to obtain a first impression of soil C stability. The MRT is an inverse function of the turnover rate k (1 years^{-1}) and defined as:

$$\text{MRT} = 1/k = -(t - t_0) / \ln(C_t/C_{t_0}), \quad (2)$$

where k = rate constant of first-order decay, t = year of sampling (in our case 2004), t_0 = the year of

vegetation change (conversion from natural forest to pasture), C_t = soil $\text{C}_3\text{-C}$ (g kg^{-1} , corrected for the sand content of the sample) in the pasture soil at time of sampling, and C_{t_0} = initial soil $\text{C}_3\text{-C}$ (g kg^{-1} ; corrected for the sand content of the sample) at t_0 in the soil of the natural forest. We calculated sand-free soil C concentrations because the sand content of some of our experimental plots (natural forest, pasture, and secondary forest) within the same site differed slightly (Table 2). The sand-free soil C concentration was calculated:

$$\begin{aligned} \text{Soil C} (\text{g kg}^{-1} \text{ sand free soil}) \\ = \text{Soil C} (\text{g kg}^{-1}) 1000 / [1000 - \text{Sand} (\text{g kg}^{-1})], \end{aligned} \quad (3)$$

where soil C is the soil organic carbon concentration (g kg^{-1}) and Sand is the sand concentration (g kg^{-1}).

We also calculated mean apparent residence times for C_4 -derived soil C found in secondary forest soils. This soil C pool was built up under the former pasture. In this case also equation 2 was used with the following variables: C_t = soil $\text{C}_4\text{-C}$ (g kg^{-1} corrected for the sand content of the sample) in the secondary forest soil at the time of sampling, C_{t_0} = soil $\text{C}_4\text{-C}$ (g kg^{-1} corrected for the sand content of the sample) in the pasture soil before the secondary forest was established, t = duration of the former pasture period (Table 1) and the observed accumulation of soil $\text{C}_4\text{-C}$ in the existing pasture plot:

$$C_{t_0} = C_{\text{tps}} - C_{\text{tnf}} e^{(-k \cdot t)}, \quad (4)$$

where C_{tps} = carbon concentration in the pasture soil at the time of vegetation change (it is assumed that C_{tps} was the same as the measured soil C concentration in the existing pasture soil and that the term $C_{\text{tnf}} e^{(-k \cdot t)}$ that is remaining concentration of soil $\text{C}_3\text{-C}$ in the former pasture at the time of pasture abandonment), C_{tnf} = carbon concentration in the natural forest soil, t is the duration of the former pasture period, k is the decay constant of the soil $\text{C}_3\text{-C}$ pool in the existing pasture.

Statistical analyses

At each site and land use, four soil samples (replicates) were taken at equal distances along a 50 m transect. As is typically the case with soil C, normal

Table 2 Soil organic carbon (soil C), total nitrogen (N_t), soil bulk density (BD), effective cation exchange capacity (ECEC), pH, clay, and sand content, Aluminum extracted by pyrophosphate (Al_p) and acid-oxalate (Al_o), Iron extracted by acid-oxalate (Fe_o), and dithionite (Fe_d) of the different sites

Site	Land use	Soil C (g kg ⁻¹)	N _t (g kg ⁻¹)	BD (g cm ⁻³)	ECEC ^a (cmol _c kg ⁻¹)	pH ^a	Clay (g kg ⁻¹)	Sand (g kg ⁻¹)	Al _p (g kg ⁻¹)	Al _o (g kg ⁻¹)	Fe _o (g kg ⁻¹)	Fe _d (g kg ⁻¹)
Sedimentary soils												
Tazonas	nf	30.8 (6.4)	3.3 (0.5)	0.96 (0.14)	35	7.1	287 (45)	269 (64)	0.2 (0.0)	1.3 (0.1)	1.0 (0.1)	2.9 (1.0)
	ps	20.2 (1.7)	2.1 (0.2)	1.30 (0.06)	25	6.2	324 (54)	377 (29)	0.3 (0.1)	0.8 (0.0)	2.5 (0.4)	5.4 (0.3)
	sf	21.7 (7.2)	2.4 (0.6)	1.19 (0.12)	25	6.5	360 (79)	266 (86)	0.2 (0.1)	0.9 (0.1)	1.9 (0.2)	5.5 (1.5)
Penas	nf	28.7 (7.0)	3.0 (0.6)	1.00 (0.12)	27	6.0	369 (30)	190 (51)	0.2 (0.1)	1.1 (0.1)	1.9 (0.1)	6.8 (2.7)
	ps	19.3 (4.2)	2.0 (0.4)	1.44 (0.10)	27	6.4	293 (35)	340 (32)	0.3 (0.2)	0.5 (0.0)	1.7 (0.3)	2.7 (0.2)
Chonta duro	sf	34.4 (3.2)	3.6 (0.3)	0.93 (0.09)	47	5.6	532 (26)	40 (9)	0.5 (0.2)	1.6 (0.1)	3.2 (0.5)	10.9 (1.3)
	nf	35.1 (10.9)	3.4 (0.7)	0.89 (0.07)	46	6.0	592 (30)	37 (3)	0.3 (0.1)	1.4 (0.1)	3.7 (0.5)	10.5 (1.5)
	ps	33.0 (3.8)	3.4 (0.4)	0.93 (0.07)	nd	5.7	607 (58)	27 (1)	1.1 (0.9)	1.3 (0.3)	4.7 (0.6)	6.5 (0.9)
Minas	sf	30.4 (5.4)	3.3 (0.3)	0.96 (0.05)	45	5.8	603 (17)	35 (2)	0.5 (0.3)	1.1 (0.1)	3.1 (0.5)	7.5 (0.8)
	nf	49.6 (2.9)	4.4 (0.1)	0.69 (0.11)	48	6.9	622 (33)	33 (5)	0.3 (0.1)	1.5 (0.1)	2.8 (0.4)	11.1 (0.9)
Volcanic ash soils	ps	44.0 (3.2)	4.4 (0.2)	0.85 (0.02)	47	7.4	619 (37)	39 (17)	0.6 (0.4)	1.6 (0.1)	3.5 (0.7)	7.7 (2.0)
	sf	48.2 (4.5)	4.3 (0.2)	0.79 (0.03)	61	6.9	639 (22)	17 (6)	0.5 (0.2)	1.6 (0.1)	1.5 (0.3)	5.4 (1.1)
Mindo	nf	62.3 (12.5)	4.5 (0.8)	0.57 (0.12)	7.6	5.1	nd ^b	655 (38)	4.9 (0.9)	5.5 (1.0)	3.6 (0.7)	3.8 (0.8)
	ps	60.5 (16.3)	5.0 (1.7)	0.81 (0.07)	5.9	5.0	nd	624 (61)	3.3 (0.5)	4.4 (0.7)	3.8 (0.6)	4.9 (1.3)
	sf	59.0 (4.7)	4.2 (0.5)	0.63 (0.13)	6.7	5.0	nd	664 (30)	4.3 (0.4)	5.0 (0.4)	4.2 (1.7)	4.7 (2.0)
Maquipucuna	nf	60.9 (12.5)	4.2 (0.5)	0.64 (0.10)	9.7	5.3	nd	597 (32)	4.7 (0.6)	8.2 (0.4)	4.5 (0.6)	5.6 (0.2)
	ps	63.3 (11.2)	5.0 (1.0)	0.62 (0.06)	6.9	5.4	nd	560 (134)	4.4 (0.5)	7.3 (0.9)	5.4 (1.0)	6.1 (0.9)
Pedro viciente	sf	46.5 (10.0)	3.7 (0.8)	0.78 (0.10)	7.1	5.3	nd	622 (47)	4.4 (0.3)	8.3 (1.1)	5.1 (0.4)	5.4 (0.7)
	nf	114.7 (5.9)	7.5 (0.3)	0.46 (0.04)	6.0	4.7	nd	323 (26)	7.3 (0.4)	10.1 (1.3)	5.9 (0.9)	6.6 (0.8)
	ps	73.7 (8.0)	6.1 (0.6)	0.61 (0.07)	4.4	5.6	nd	383 (30)	6.3 (0.8)	16.4 (3.0)	6.5 (0.3)	7.0 (0.4)
Pitzara	Sf	86.6 (8.5)	6.2 (1.0)	0.57 (0.02)	3.8	5.1	nd	372 (24)	8.4 (1.1)	17.3 (3.3)	6.5 (0.7)	7.2 (0.7)
	nf	129.8 (35.3)	9.2 (1.9)	0.48 (0.06)	9.8	4.7	nd	262 (75)	10.8 (1.5)	19.0 (2.4)	6.8 (0.4)	7.7 (0.4)
sf	ps	106.2 (11.8)	8.0 (0.0)	0.50 (0.05)	7.1	5.3	nd	219 (38)	8.6 (2.2)	21.7 (1.4)	6.7 (0.3)	7.8 (0.7)
	sf	116.2 (6.3)	8.6 (0.1)	0.45 (0.05)	9.7	5.3	nd	217 (11)	8.4 (0.6)	26.7 (1.6)	6.2 (0.1)	8.3 (0.3)

nf, natural forest; ps, pasture; sf, secondary forest

^a Based on the soil profile ($n = 1$), all other values were expressed as mean ($n = 4$) and SD in parentheses

^b nd, not determined

distribution was assumed. Analyses were carried out using ANOVA; multiple comparisons of dry matter yield, soil C, C/N ratio, bulk density among land use types and soil types were conducted using Tukey's post hoc test. Multiple comparison of pasture-derived carbon was analyzed among sites and clay content, and MRT of sedimentary soils was analyzed among sites and land use. Pearson correlation was used to assess the relationships of soil C with MWD, silt + clay content, Al_p , Al_o , Fe_o , $Al_o + 0.5 Fe_o$, $Al_o - Al_p$, and Al_p/Al_o . Multiple regression with stepwise variable selection was used to relate MWD to clay + silt content and to soil C content. All statistical analyses were carried out using the STATISTICA 6.1 software package (StatSoft Inc., Tulsa, OK, USA).

Results

Soil organic matter influenced by soil type and land use

Soil C concentrations in volcanic ash soils were 1.5–3 times higher than in sedimentary soils ($P < 0.001$; Table 2). In both soil types, soil C content increased with increasing silt + clay content ($P < 0.001$; Fig. 1a). However, the amount of soil C stored per unit silt + clay was about four times higher in volcanic ash soils than in sedimentary soils ($P < 0.001$). In volcanic ash soils, soil C concentrations were positively correlated with the contents of silt + clay ($r = 0.88$; $P < 0.001$), Al_p ($r = 0.83$; $P < 0.001$), Al_o ($r = 0.66$; $P < 0.001$) Fe_o ($r = 0.58$; $P < 0.001$), and with $Al_o + 0.5 Fe_o$ ($r = 0.67$; $P < 0.001$), and $Al_o - Al_p$ ($r = 0.50$; $P < 0.001$). Natural forest soils showed higher carbon storage than pasture soils ($P < 0.01$). This effect was more pronounced at sites with high Al_p content ($>6 \text{ g kg}^{-1}$; Pedro Vicente and Pitzara). The C/N ratio of volcanic soils was influenced by the type of land use with pastures having a lower C/N (12.6 ± 1.2) than natural forests ($14.4 \pm .3$; $P < 0.01$). In sedimentary soils, soil C content was higher in natural forest soils ($36.4 \pm 1.0 \text{ g kg}^{-1}$) than in pastures (29.1 ± 11.0 ; $P < 0.01$). The mean C/N ratio of the sedimentary soils was $9.9 (\pm 0)$ and independent of land use. Soil C was positively correlated with Al_o ($r = 0.83$; $P < 0.001$) and with

$Al_o + 0.5 Fe_o$ ($r = 0.50$; $P < 0.001$), and $Al_o - Al_p$ ($r = 0.55$; $P < 0.001$) under all land uses. In the pasture soils, soil C correlated with Al_p ($r = 0.55$; $P < 0.05$) and Fe_o ($r = 0.56$; $P < 0.05$).

Water-stable aggregates influenced by soil type and land use

Mean Weight Diameter of water-stable aggregates was higher in sedimentary ($3.6 \pm .4 \text{ mm}$) soils than in volcanic ash soils ($2.4 \pm .4 \text{ mm}$; $P < 0.001$; see also Fig. 2). Silt + clay content was positively correlated with MWD ($r = 0.86$; $P < 0.001$) for the whole dataset but also separately for each soil type (Fig. 2a). In sedimentary soils, soil C was not correlated with MWD of natural forest ($P < 0.05$) but in secondary forest ($r = 0.83$; $P < 0.001$) and in pastures ($r = 0.89$, $P < 0.001$; Fig. 2b), soil C did correlate with MWD. In volcanic ash soils MWD was correlated with soil C under all land uses ($r = 0.59$; $P < 0.001$). Using multiple regression, soil C could not explain additional variation in MWD in addition to silt + clay content.

In sedimentary soils, macroaggregates of 2,000–8,000 μm were the largest fraction containing between 60 and 79% of total soil mass and between 58 and 74% of total soil carbon. Microaggregates (53–250 μm) contained only between 1 and 12% of soil mass and between 3 and 9% of soil carbon. Yield of macroaggregates increased with soil carbon content independent of land use ($P < 0.05$; see Appendix A, Table A1). Natural forest soils contained more small macroaggregates (2,000–250 μm) than the corresponding pasture soils ($P < 0.001$). In sedimentary soils mean soil C concentration (corrected for sand content) was highest in microaggregates (52 g kg^{-1}), followed by small macroaggregates (42 g kg^{-1}), and then by large macroaggregates (36 g kg^{-1}), and the $<53 \mu\text{m}$ fraction (34 g kg^{-1} , all at $P < 0.001$ means calculated from Appendix A, Table A1). Mean C/N ratio of aggregates from the sedimentary soils increased in the order: fraction $<53 \mu\text{m}$ ($C/N = 9.4$) $<$ large macroaggregates (10.0) \leq small macroaggregates (10.5) \leq microaggregates (10.9 ; $P < 0.05$ means calculated from Appendix A, Table A1). The general pattern of the distribution of soil C among the aggregate fractions was similar under all land use types.

Fig. 1 (a) Relation of the silt + clay content with soil C in volcanic ash soils (circles) and sedimentary soils (triangles) and (b) Al_p content with soil C in volcanic ash soils and sedimentary soils of different land use types (white = pasture, grey = secondary forest, black = natural forest)

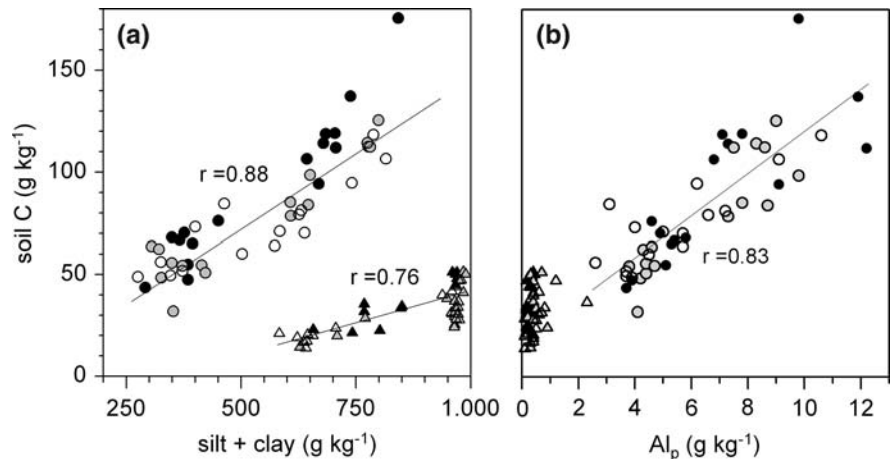
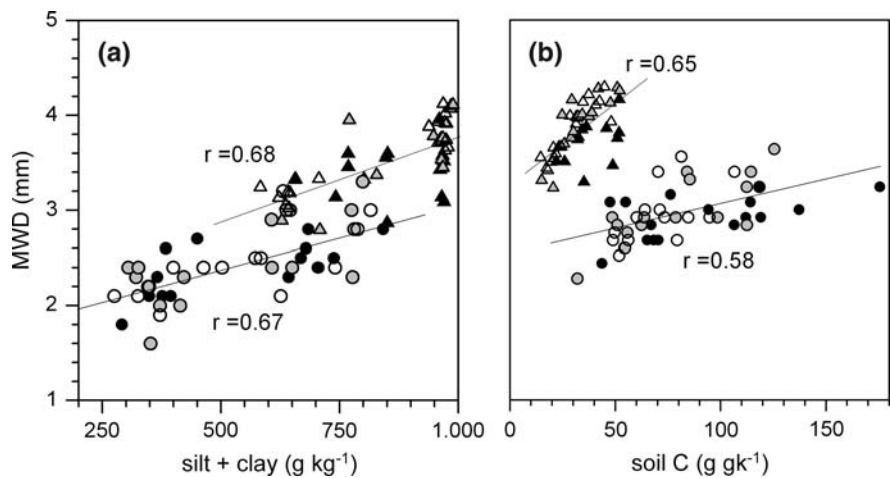


Fig. 2 Relation of Mean Weight Diameter (MWD) of water stable aggregates with (a) silt + clay content in volcanic ash soils (circles) and sedimentary soils (triangles) and (b) MWD with soil C in volcanic ash soils and sedimentary soils of the different types of land use (white = pasture, grey = secondary forest, black = natural forest)



Land use did not influence aggregate size distribution of volcanic ash soils. In this soil type both macroaggregate fractions (2,000–8,000 μm and 250–2,000 μm) contained most of the soil mass (41 and 34%) and soil C (44 and 30%, see Appendix A, Table A2). The size class $<53 \mu\text{m}$ contained the smallest amount of soil (6–17%) and contributed only 8–25% of soil C. With the exception of the fraction $<53 \mu\text{m}$ which had less soil C and a lower C/N ratio, soil C concentration and C/N ratio were similar in all aggregate size fractions ($P < 0.001$; see Appendix A, Table A1).

$\delta^{13}\text{C}$ -values and mean apparent residence time of soil C

Mean $\delta^{13}\text{C}$ -values ($n = 32$) of above ground vegetation/litter layer was $-1.8 (\pm 0.6)\text{‰}$ / $-14.8\text{‰} (\pm 0.6\text{‰})$

for pastures, $-30.1\text{‰} (\pm 0.0\text{‰})$ / $-29.3\text{‰} (\pm 0.8\text{‰})$ for secondary forests, and $-29.9\text{‰} (\pm 0.3\text{‰})$ / $-29.4\text{‰} (\pm 0.8\text{‰})$ in natural forests. Mean $\delta^{13}\text{C}$ -values ($n = 32$) of fine roots were $-13.4\text{‰} (\pm 0.7\text{‰})$ in pastures, $-28.8\text{‰} (\pm 0.8\text{‰})$ in secondary forests and $-29.1\text{‰} (\pm 0.7\text{‰})$ in natural forests.

After 30–35 years of pasture three of four sedimentary sites contained about 50% pasture-derived soil C (Table 3) whereas at the site Minas this was only 38%. The corresponding MRTs of forest-derived soil C varied between 37 and 57 years (Fig. 3). MRT of soil $\text{C}_3\text{--C}$ tended to increase with silt + clay content and was significantly higher at Minas compared to Tazones and Penas ($P < 0.05$; Fig. 3). All secondary forest plots on sedimentary soils had a pasture history of about 20 years (Table 1). After 10–17 years of secondary forest between 5 and 18% of soil C was pasture-derived (this was equal to

Table 3 $\delta^{13}\text{C}$ of soil C in soils of natural forest, pasture, and secondary forest and pasture-derived C (soil $\text{C}_4\text{-C}$) in pasture and secondary forest soils of the different sites

Site	$\delta^{13}\text{C}$ (‰ V-PDB) ^a			Soil $\text{C}_4\text{-C}$ (%) ^a	
	Natural forest	Pasture	Secondary forest	Pasture	Secondary forest
Sedimentary soils					
Tazones	−26.9 (0.4)	−19.4 (0.6)	−24.2 (0.4)	50 (6)	18 (4)
Penas	−26.9 (0.2)	−20.0 (0.6)	−24.5 (0.7)	47 (7)	16 (6)
Chonta Duro	−26.5 (0.4)	−18.9 (0.8)	−25.9 (0.4)	48 (7)	5 (4)
Minas	−25.9 (0.3)	−20.3 (0.4)	−23.8 (0.8)	38 (4)	14 (6)
Volcanic ash soils					
Mindo	−27.1 (0.3)	−18.2 (1.2)	−27.7 (0.5)	50 (7)	nd ^b
Maquipucuna	−27.3 (0.6)	−16.5 (1.9)	−27.1 (0.4)	62 (12)	nd
Pedro Vicente	−28.6 (0.5)	−26.0 (0.7)	−28.3 (0.3)	19 (6)	nd
Pitzara	−27.9 (0.2)	−23.5 (0.3)	−27.7 (0.2)	31 (7)	nd

^a Values are given as mean and SD ($n = 4$)

^b nd, not determined; pasture-derived carbon could not be calculated due to lack of difference in $\delta^{13}\text{C}$ -values between natural and secondary forest soils

13–65% of the former soil $\text{C}_4\text{-C}$; Table 3). The resulting MRT of C_4 -derived carbon in the secondary forests were considerably shorter (between 8 and 25 years) than the corresponding MRT of soil $\text{C}_3\text{-C}$ in the pastures at all sites except for Penas ($P < 0.01$; Fig. 3).

In volcanic ash soils MRT of forest-derived soil C ranged from 24 to 56 years (Fig. 3). At Maquipucuna MRT was higher (56 years) than at Mindo

even though both sites are characterized by low Al_p and carbon content. At Pitzara and Pedro Vicente, both with high Al_p and carbon contents, MRT did not differ (36 and 24 years). No pasture-derived soil C could be detected in any of the secondary forests on volcanic ash soils. In Maquipucuna, no C_4 carbon was found in a 20 years old secondary forest even though the period with pasture lasted for 30 years.

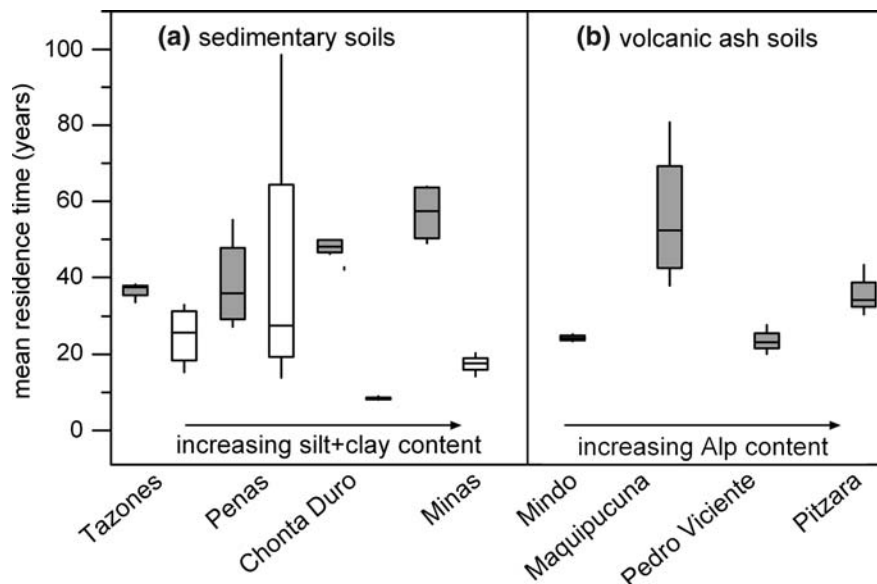


Fig. 3 Box-plot of the mean residence time of soil organic carbon of the different sites calculated for the C_3 -derived soil C pool in the pasture soils (grey) and for the C_4 -derived soil C pool in the secondary forests soils (white) (Minas, Chonta: $n = 3$; Penas: C_4 -turnover times in secondary forest soils were

overestimated due to differences in clay content and consequently carbon content in the secondary forest soil compared to the pasture soil). C_4 -derived mean residence time could not be calculated for volcanic ash soils as no C_4 -derived soil C could be detected at all secondary forests on volcanic ash soils

In volcanic soils under pasture, pasture-derived soil C was homogeneously distributed among aggregates whereas in sedimentary soils different aggregate fractions had different percentages of soil C₄-C (Table 4). In sedimentary soils under pasture, the proportion of pasture-derived carbon was highest in microaggregates and decreased further from small to big macroaggregates ($P < 0.001$). In secondary forests, we detected no differences in C₄-derived soil C among aggregate fractions (Table 4).

Discussion

Effects of soil type and land use on C storage

Texture strongly influenced soil C storage in both soil types: increasing silt + clay contents were associated with higher soil C storage (Fig. 1), as has been reported by other studies (e.g., Feller and Beare 1997). Even more important for carbon storage was mineralogy. In agreement with Feller and Beare (1997) we found that volcanic ash soils have higher

soil C storage per unit silt + clay compared to the sedimentary soils. Normally this is explained by the high specific surface area of allophane in combination with large amounts of non-crystalline compounds which cause the higher carbon storage per unit silt + clay in volcanic ash soils (Saggar et al. 1996; Six et al. 2002).

Strong correlations of soil C with Al_p were reported for volcanic ash soils (e.g., Percival et al. 2000; de Koning et al. 2003) and in a range of other soil types (Percival et al. 2000) and were explained with stabilization of soil C through Al-humus complexes and non-crystalline hydroxides (Torn et al. 1997; Masiello et al. 2004). This has also been shown in laboratory experiments in which non-crystalline Al-hydroxides, Al-complexes, and allophane were efficient in retarding decomposition of citric acid (Boudot 1992).

Soil C storage is expected to be higher under wetter and cooler conditions than in warmer and drier soils (Admundson 2001). However, within the volcanic ash soils we measured higher soil C storage at the warmer and less wet soils. Furthermore, the

Table 4 Pasture-derived soil organic carbon (soil C₄-C) in pasture and secondary forests in aggregates of different size (8,000–2,000 μm, 2,000–250 μm, 250–53 μm, <53 μm)

Site	Soil C ₄ -C (%) ^a							
	Aggregate size							
	Pasture				Secondary forest			
	8,000– 2,000 μm	2,000– 250 μm	250– 53 μm	<53 μm	8,000– 2,000 μm	2,000– 250 μm	250– 53 μm	<53 μm
Sedimentary soils								
Tazonos	47 (7)	51 (7)	59 (7)	48 (6)	17 (7)	14 (4)	11 (6)	19 (6)
Penas	48 (8)	50 (8)	55 (12)	45 (6)	20 (6)	14 (7)	10 (nd) ^b	16 (5)
Chonta Duro	43 (5)	48 (6)	57 (nd) ^b	45 (6)	4 (2)	3 (3)	4 (nd) ^b	1 (3)
Minas	36 (5)	50 (16)	60 (nd) ^b	42 (9)	13 (5)	13 (16)	7 (nd) ^b	15 (5)
Volcanic ash soils								
Mindo	52 (7)	51 (6)	50 (6)	45 (7)	nd ^c	nd ^c	nd ^c	nd ^c
Maquipucuna	59 (11)	61 (14)	64 (11)	59 (10)	nd ^c	nd ^c	nd ^c	nd ^c
Pedro Vicente	17 (6)	18 (6)	18 (5)	16 (5)	nd ^c	nd ^c	nd ^c	nd ^c
Pitzara	26 (5)	31 (5)	31 (6)	25 (5)	nd ^c	nd ^c	nd ^c	nd ^c

^a Values are given as mean and SD ($n = 4$)

^b nd, not determined; due to insufficient sample size

^c nd, not determined pasture-derived; carbon could not be calculated due to lack of difference in $\delta^{13}\text{C}$ -values between natural and secondary forest soils

relatively small differences in temperature are not enough to explain why there is three times more soil C in the volcanic ash soils compared to the sedimentary soils. Thus, the results indicate that soil C storage was dominated by soil properties rather than by climatic differences between sites.

Changes on soil C storage induced by land use change were influenced by soil properties within volcanic ash soils: at sites with high Al_p and Al_o content (Pitzara and Pedro Vicente) natural forest soils contained more soil C per unit silt + clay than corresponding pasture soils. This may indicate that soils with high Al_p and Al_o were more sensitive to changes in land use than soils containing less Al_p and Al_o .

The influence of aggregation on soil C storage in different soil types and land use

Normally texture strongly influences aggregation: higher clay content leads to increased aggregate stability (Edwards and Bremner 1967). In other studies, a positive correlation has also been found between MWD and both clay and soil C content (Franzluebbers and Arshad 1996) or between MWD and soil C only (Koutika et al. 1997) suggesting that both texture and soil C may influence aggregation. Our results suggest that texture played the dominant role in formation and stabilization of aggregates.

For the sedimentary soils we found an “inverse” aggregate hierarchy (decreasing soil C concentration and proportion of pasture-derived carbon with increasing aggregate sizes) which may be a result of the sample treatment before aggregate fractionation. Wet-sieving of air-dry soil led to increasing soil C concentration with increasing aggregate sizes (Puget et al. 1995). During slaking of air-dried soil, unstable macroaggregates (with low soil C content) disintegrated into smaller particles and were recovered in the microaggregate class. In contrast, the moist pretreatment that was applied in this study, resulted in fewer broken macroaggregates recovered in the microaggregate fraction and resulted in decreasing soil C content with increasing aggregate size (Paul et al. *in press*, a).

In our volcanic ash soils, aggregate distribution was not affected by land use. Huygens et al. (2005)

found no differences in the aggregate distribution of natural forest, grassland, and a pine plantation. The absence of an aggregate hierarchy suggests that in volcanic ash soils aggregates are not predominantly stabilized by particulate organic matter. Formation and stabilization of aggregates is more likely to occur by electrostatic attractions among amorphous Al components and clay minerals in addition to metal-humus complexes acting as binding agents through ligand exchange between functional groups of soil C and Al (Nanzyo et al. 1993; Huygens et al. 2005). Comparable results have been reported in Chile, where no aggregate hierarchy was found in a volcanic ash soil.

Mean residence time of pasture- and forest-derived carbon

Our results suggest a trend of longer MRT of forest-derived carbon associated with higher silt + clay content for sedimentary soils. A study in Brazil also reported a more rapid increase of pasture-derived carbon in a coarse textured soil than in a clay soil (Desjardins et al. 2004). However, other field studies do not support this observation (Desjardins et al. 1994, 2004; Feigl et al. 1995; Koutika et al. 1997; Powers and Veldkamp 2005; Schwendenman and Pendall 2006). Texture effects are often masked by other effects like clay mineralogy, land use history, or management (Saggar et al. 1996; de Koning et al. 2003; Powers and Veldkamp 2005). In the volcanic soils, we found no evidence that the amount of non-crystalline compounds contribute to stabilization of recently incorporated soil C. In contrast, the mean ^{14}C age of total soil C was related to non-crystalline compounds in soils of volcanic parent material (Torn et al. 1997) and to the chelation of Al and Fe by organic ligands in temperate Inceptisols, Mollisols and Alfisols (Masiello et al. 2004).

Published data on MRT derived from forest-to-pasture conversions show that MRT does not only depend on soil properties but also on pasture age (Fig. 4). This shows the limitation of the single pool model in calculation of MRT and is probably responsible for the high estimate of MRT in Maquipucuna compared to Mindo.

Our finding that recently formed pasture-derived soil C was less stable than the old forest soil C

Appendix A

Table A1 Total dry matter yield, soil C storage (g kg^{-1}), soil C concentration (g kg^{-1} sandfree aggregates), C/N, and $\delta^{13}\text{C}$ (‰) of water stable aggregates in sedimentary soils of natural forest (nf), pasture (ps), and secondary forest (sf) soils

Site	Use	Aggregates (μm)	Yield (%)	Soil C (g kg^{-1} soil)	Soil C (g kg^{-1} sandfree aggregates)	C/N	$\delta^{13}\text{C}$ (‰)
Tazonas	nf	8,000–2,000	65 (1.8)	17.6 (4.0)	36.8 (4.6)	9.0 (0.4)	−26.6 (0.4)
		2,000–250	19 (4.3)	6.6 (3.1)	48.7 (8.7)	10.0 (0.4)	−27.2 (0.4)
		250–53	5 (1.9)	1.0 (0.1)	53.9 (2.8)	11.3 (1.2)	−27.9 (0.3)
		<53	11 (4.2)	4.0 (1.3)	38.7 (3.5)	9.4 (0.6)	−26.9 (0.4)
	ps	8,000–2,000	60 (1.9)	11.0 (1.6)	30.3 (4.7)	9.8 (1.1)	−19.7 (0.8)
		2,000–250	11 (2.6)	1.8 (0.4)	28.5 (5.3)	10.9 (0.8)	−19.5 (0.7)
		250–53	12 (1.2)	1.2 (0.2)	53.6 (8.5)	11.2 (0.7)	−19.4 (0.8)
		<53	16 (1.4)	4.7 (0.3)	28.8 (0.8)	9.1 (0.5)	−19.8 (0.5)
	sf	8,000–2,000	62 (10.9)	13.3 (5.6)	27.7 (4.8)	9.6 (1.1)	−24.2 (0.9)
		2,000–250	11 (2.2)	2.7 (1.3)	38.6 (14.8)	9.7 (0.7)	−25.0 (0.5)
		250–53	9 (5.4)	1.1 (0.2)	36.6 (9.0)	9.8 (1.5)	−26.3 (0.8)
		<53	17 (6.5)	4.6 (1.6)	27.5 (4.4)	9.2 (1.0)	−24.3 (0.8)
Penas	nf	8,000–2,000	60 (6.9)	13.3 (10.0)	36.8 (7.0)	10.0 (0.4)	−27.0 (0.3)
		2,000–250	20 (10.1)	6.7 (3.9)	41.7 (5.6)	10.3 (0.7)	−27.0 (0.5)
		250–53	7 (2.1)	1.7 (0.8)	46.2 (2.0)	10.0 (1.0)	−27.7 (1.4)
		<53	12 (6.9)	3.5 (1.2)	31.0 (6.3)	9.2 (0.5)	−26.8 (0.2)
	ps	8,000–2,000	62 (3.6)	11.5 (3.0)	28.3 (5.1)	9.9 (0.3)	−20.0 (0.8)
		2,000–250	11 (0.5)	1.7 (0.8)	31.8 (15.8)	10.5 (0.7)	−19.7 (0.8)
		250–53	8 (1.3)	1.0 (0.1)	57.3 (11.4)	12.4 (0.9)	−19.6 (0.4)
		<53	19 (1.6)	4.2 (0.7)	22.7 (3.8)	9.5 (0.7)	−20.3 (0.5)
	sf	8,000–2,000	67 (1.7)	21.0 (2.3)	32.8 (2.9)	9.4 (0.2)	−24.0 (0.7)
		2,000–250	20 (1.8)	7.8 (1.1)	41.2 (8.1)	10.5 (1.0)	−25.0 (0.8)
		250–53	2 (0.4)	1.0 (0.2)	51.4 (nd)	10.0 (nd)	−26.3 (nd)
		<53	6 (0.8)	1.9 (0.4)	32.4 (4.8)	9.3 (0.0)	−24.5 (0.6)
Chonta Duro	nf	8,000–2,000	65 (5.5)	22.8 (6.6)	36.3 (10.4)	10.7 (1.9)	−26.4 (0.1)
		2,000–250	16 (6.1)	6.2 (3.9)	38.3 (9.3)	10.7 (1.4)	−26.6 (0.4)
		250–53	3 (0.6)	1.0 (0.2)	36.7 (nd)	11.2 (nd)	−27.5 (nd)
		<53	15 (4.5)	4.3 (0.4)	30.3 (9.1)	9.2 (1.4)	−26.2 (0.4)
	ps	8,000–2,000	74 (4.0)	23.3 (5.3)	32.3 (6.0)	9.7 (0.8)	−19.6 (0.6)
		2,000–250	10 (1.6)	3.5 (0.9)	35.5 (3.7)	9.7 (1.0)	−19.0 (0.6)
		250–53	2 (0.5)	0.9 (0.2)	43.2 (nd)	9.7 (nd)	−18.5 (nd)
		<53	13 (3.2)	3.5 (0.6)	27.7 (3.0)	8.3 (1.0)	−19.2 (0.7)
	sf	8,000–2,000	68 (4.3)	20.2 (4.2)	30.7 (4.9)	9.2 (0.9)	−25.9 (0.3)
		2,000–250	17 (1.4)	5.7 (0.6)	35.0 (4.3)	9.6 (0.6)	−26.2 (0.3)
		250–53	3 (0.3)	1.0 (0.1)	42.7 (nd)	10.3 (nd)	−26.8 (nd)
		<53	11 (2.6)	3.3 (0.8)	30.0 (4.3)	9.2 (0.5)	−25.9 (0.2)
Minas	nf	8,000–2,000	65 (9.0)	31.8 (5.3)	48.0 (3.5)	11.1 (0.9)	−26.0 (0.3)
		2,000–250	27 (7.7)	12.2 (2.6)	53.2 (4.5)	11.8 (1.3)	−27.2 (2.2)
		250–53	3 (0.6)	1.4 (0.3)	62.2 (nd)	10.8 (nd)	−26.9 (nd)
		<53	6 (0.6)	2.7 (0.3)	49.9 (1.8)	11.1 (0.7)	−26.0 (0.2)

Table A1 continued

Site	Use	Aggregates (μm)	Yield (%)	Soil C (g kg^{-1} soil)	Soil C (g kg^{-1} sandfree aggregates)	C/N	$\delta^{13}\text{C}$ (‰)
	ps	8,000–2,000	74 (5.1)	30.6 (3.8)	42.8 (2.4)	10.2 (0.9)	−20.5 (0.6)
		2,000–250	16 (3.3)	8.2 (1.9)	51.8 (4.9)	10.4 (1.0)	−19.7 (0.9)
		250–53	2 (0.4)	1.5 (0.3)	79.2 (nd)	11.4 (nd)	−17.8 (nd)
		<53	7 (2.3)	3.5 (0.5)	44.7 (3.2)	10.1 (0.5)	−19.7 (1.3)
	sf	8,000–2,000	79 (3.8)	35.2 (3.5)	45.6 (3.0)	11.4 (0.7)	−24.0 (0.7)
		2,000–250	15 (3.8)	7.5 (2.2)	51.1 (6.3)	11.8 (1.0)	−24.2 (1.0)
		250–53	1 (0.1)	0.7 (nd)	68.2 (nd)	12.0 (nd)	−28.8 (nd)
		<53	6 (1.5)	2.7 (0.5)	42.9 (4.7)	10.6 (0.9)	−23.7 (0.8)

Values are given as mean and SD ($n = 4$)

nd, not determined

Table A2 Total dry matter yield, soil C storage (g kg^{-1} soil), soil C concentration (g kg^{-1} sandfree aggregates), C/N, and $\delta^{13}\text{C}$ (‰) of water stable aggregates in volcanic ash soils of natural forest (nf), pasture (ps), and secondary forest (sf) soils. Values are given as mean and SD ($n = 4$)

Site	Use	Aggregates (μm)	Yield (%)	Soil C (g kg^{-1} soil)	Soil C (g kg^{-1} sandfree aggregates)	C/N	$\delta^{13}\text{C}$ (‰)
Mindo	nf	8,000–2,000	31 (4.4)	19.9 (5.8)	183.4 (20.6)	13.8 (0.7)	−27.1 (0.3)
		2,000–250	44 (1.5)	21.3 (5.7)	199.7 (3.4)	14.1 (0.7)	−27.3 (0.3)
		250–53	17 (2.9)	8.3 (2.1)	190.6 (25.4)	14.6 (1.0)	−27.5 (0.4)
		<53	7 (1.2)	11.6 (0.7)	159.0 (14.9)	13.9 (0.9)	−27.0 (0.2)
	ps	8,000–2,000	33 (4.5)	22.6 (5.9)	152.4 (3.2)	12.6 (1.5)	−17.7 (1.1)
		2,000–250	42 (4.3)	16.3 (4.3)	167.0 (34.0)	12.0 (0.5)	−18.0 (1.0)
		250–53	17 (2.3)	7.2 (1.4)	155.7 (46.2)	13.8 (1.6)	−18.5 (1.0)
		<53	7 (1.1)	10.8 (1.2)	149.6 (9.7)	12.1 (0.5)	−19.0 (1.2)
	sf	8,000–2,000	34 (3.9)	24.6 (7.7)	199.8 (38.9)	14.4 (0.6)	−27.7 (0.6)
		2,000–250	43 (1.7)	16.9 (1.9)	184.2 (54.0)	14.6 (0.8)	−27.6 (0.4)
		250–53	16 (1.9)	8.0 (1.1)	198.1 (13.7)	14.1 (0.8)	−27.8 (0.4)
		<53	6 (1.1)	10.3 (1.5)	164.7 (17.3)	13.5 (0.6)	−27.4 (0.5)
Maquipucuna	nf	8,000–2,000	41 (5.1)	25.7 (6.9)	150.5 (17.9)	14.6 (1.9)	−27.2 (0.5)
		2,000–250	38 (2.0)	16.2 (5.0)	138.8 (27.7)	14.3 (2.7)	−27.4 (0.6)
		250–53	13 (3.7)	5.9 (1.8)	159.4 (30.0)	13.9 (1.5)	−27.7 (0.5)
		<53	8 (2.5)	10.6 (4.4)	131.6 (20.8)	12.5 (1.0)	−27.2 (0.4)
	ps	8,000–2,000	40 (2.5)	25.2 (6.0)	137.9 (14.9)	12.8 (1.7)	−16.9 (1.9)
		2,000–250	36 (2.3)	16.6 (6.5)	160.8 (48.5)	12.6 (2.0)	−16.8 (2.3)
		250–53	19 (4.8)	8.4 (2.2)	133.5 (34.5)	12.7 (1.2)	−16.5 (1.8)
		<53	10 (3.3)	11.8 (3.9)	112.4 (6.1)	11.8 (0.6)	−16.8 (1.7)
	sf	8,000–2,000	32 (7.1)	16.3 (4.1)	130.8 (9.9)	13.0 (0.9)	−27.1 (0.2)
		2,000–250	34 (1.8)	12.4 (2.1)	152.6 (44.1)	13.1 (0.7)	−27.2 (0.1)
		250–53	21 (4.3)	7.6 (1.0)	139.1 (11.6)	12.3 (0.1)	−27.4 (0.1)
		<53	11 (2.4)	11.9 (2.5)	112.5 (3.4)	11.8 (1.0)	−27.1 (0.3)

Table A2 continued

Site	Use	Aggregates (μm)	Yield (%)	Soil C (g kg^{-1} soil)	Soil C (g kg^{-1} sandfree aggregates)	C/N	$\delta^{13}\text{C}$ (‰)
Pedro Vicente	nf	8,000–2,000	45 (5.0)	51.3 (7.6)	169.1 (5.5)	15.4 (1.1)	–28.3 (0.3)
		2,000–250	22 (2.9)	27.3 (2.2)	187.3 (12.6)	15.8 (1.3)	–28.4 (0.4)
		250–53	16 (2.7)	9.9 (1.2)	184.1 (12.6)	16.4 (1.0)	–28.7 (0.2)
		<53	17 (1.9)	22.8 (2.7)	136.7 (7.9)	15.0 (1.0)	–28.3 (0.4)
	ps	8,000–2,000	48 (9.1)	35.3 (9.0)	120.4 (10.7)	12.2 (0.1)	–25.8 (0.8)
		2,000–250	24 (3.2)	17.0 (3.4)	119.0 (24.3)	12.5 (0.4)	–25.9 (0.7)
		250–53	15 (6.2)	5.6 (1.9)	104.2 (8.9)	12.7 (0.5)	–26.1 (0.7)
		<53	12 (6.1)	12.8 (8.3)	105.0 (14.1)	12.6 (1.6)	–26.1 (0.5)
	sf	8,000–2,000	47 (6.7)	40.5 (6.6)	138.1 (15.9)	14.2 (1.0)	–28.1 (0.1)
		2,000–250	26 (3.0)	24.0 (4.2)	152.8 (22.0)	14.8 (1.1)	–28.4 (0.4)
		250–53	15 (1.9)	7.0 (1.7)	152.8 (15.6)	15.2 (0.6)	–28.6 (0.2)
		<53	14 (1.1)	15.3 (4.8)	124.3 (8.9)	13.1 (0.3)	–28.0 (0.3)
Pitzara	nf	8,000–2,000	44 (4.0)	56.4 (20.0)	171.2 (29.2)	14.3 (0.6)	–27.8 (0.2)
		2,000–250	31 (3.9)	44.3 (11.5)	185.5 (39.5)	14.5 (0.9)	–28.0 (0.1)
		250–53	13 (2.6)	10.9 (1.9)	180.7 (32.6)	15.4 (0.8)	–28.2 (0.3)
		<53	12 (0.3)	18.7 (3.2)	160.7 (31.3)	14.6 (0.7)	–27.8 (0.3)
	ps	8,000–2,000	45 (4.9)	48.1 (10.6)	134.7 (9.1)	13.3 (1.0)	–23.6 (0.7)
		2,000–250	35 (3.4)	41.1 (6.1)	151.9 (17.7)	13.6 (1.2)	–23.1 (0.5)
		250–53	11 (2.9)	8.5 (2.4)	132.7 (4.0)	13.8 (1.2)	–23.2 (0.7)
		<53	6 (3.5)	6.9 (3.5)	108.2 (5.0)	12.6 (1.4)	–23.8 (0.6)
	sf	8,000–2,000	50 (9.6)	53.8 (13.5)	136.5 (8.8)	13.4 (1.3)	–27.7 (0.2)
		2,000–250	30 (5.1)	37.7 (4.4)	155.2 (7.9)	14.2 (1.2)	–27.6 (0.2)
		250–53	11 (3.0)	9.1 (1.7)	163.0 (8.1)	14.7 (0.9)	–28.0 (0.1)
		<53	9 (3.0)	11.9 (3.2)	126.8 (9.5)	12.4 (0.6)	–27.5 (0.2)

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