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ABSTRACT

Volcanic soils contain a large stock of soil organic carbon (SOC) which is highly vulnerable to changes in land use and climate warming. In this study we examine the changes of SOC stocks along a tropical elevation gradient (100 m-700 m; +437 mm yr^{-1} of rainfall and –0.7°C every 100 m), which is subject to two intensive agricultural systems (banana monoculture and vegetable crops) characterised by the heavy use of fertilisers and pesticides. We hypothesise that in these systems SOC is mainly controlled by soil mineralogy, climatic factors and soil tillage. We used a process-based approach to determine soil C inputs and outputs along the elevation gradient. The banana monoculture systems (198 plots) are characterised by a temporal steady-state of SOC, and the vegetable crop systems (55 plots) present high annual SOC losses. The banana systems were used to determine for the first time the altitudinal change in the in situ rate constant of SOC mineralisation (k_{SOC}). Under banana monoculture, SOC stock increased by 218%, C input from crop residues decreased by 44%, and k_{SOC} decreased by 570% across the altitudinal gradient. These results indicated that the SOC gradient was mainly induced by changes in C outputs. Allophane content increased with altitude (R^2 = 0.61; 8 g kg^{-1} every 100 m) and was positively correlated with SOC content (R^2 = 0.51) and negatively correlated with k_{SOC} (R^2 = 0.53). We hypothesise that the physical protection of SOC within amorphous allophanic minerals was the main factor responsible for the k_{SOC} and SOC stock gradients. Strictly, the effects of allophane content and rainfall cannot be separated because soil mineralogy in the studied area is mainly determined by the level of rainfall. Our process-based analysis indicated that changes in temperature along the elevation gradient could only explain 22% of the observed change in k_{SOC}. SOC stocks under vegetable crops also increased with altitude; they were 57% lower than under banana at low altitude but only 9% lower at high altitude. This reflected simultaneously the higher C outputs under vegetable crops due to more intensive soil tillage, and the greater resilience to soil disturbance of protected SOC in altitude. The results suggested that neither soil nutrient content nor soil biological properties contributed to the SOC and k_{SOC} gradients under the intensive cropping systems analysed during this study. Overall, we conclude that SOC might be more vulnerable to soil tillage and warming in low-altitude soils.

Keywords: allophane; banana; SOC decomposition; soil tillage; temperature sensitivity; vegetable crops

1. Introduction

Although volcanic soils account for less than 1% of Earth's land area, they store about 5% of the global stock of soil organic carbon (SOC) (Dahlgren et al., 2004). These soils have peculiar physical (e.g. very high water content at field capacity, high resilience to compaction and erosion), chemical (e.g. high SOC and basic cations contents), and physico-chemical properties (e.g. high P fixation, high anion exchange capacity), which are controlled by soil mineralogy, characterised by the presence of amorphous minerals such as allophane (Clermont-Dauphin et al., 2004). These soils are mostly found on the flanks of volcanic mountains and are occupied by forests and agricultural land, the latter mainly in the inter-tropical zone where altitude moderates climate (Legros, 2012). Volcanic soils have high agricultural productivity and are easy to work, but aluminium toxicity and P deficiency may occur in those that are more acidic (Dahlgren et al., 2004). Because of the high SOC stocks in these soils, conversion of the natural vegetation into farmland frequently induces SOC losses that can reach 2%-3% per year (e.g. Lemenih and Itanna, 2004; Sierra et al., 2015). However, some authors have reported that the proper management of cropping systems, including diversified production and reduced soil tillage, can be useful to preserving SOC stocks in volcanic soils (Segnini et al., 2011; Sierra et al., 2017). This is of crucial concern in tropical mountain systems where warming is likely to be particularly marked during coming decades and could contribute to increasing SOC losses (Nottingham et al., 2016).

Most worldwide studies dealing with the dynamics of SOC in natural mountain systems have observed positive correlations between SOC stocks and altitude (Tashi et al., 2016, for a meta-analysis on this topic). A few exceptions did not demonstrate any such relationship (e.g. Tan and Wang, 2016) or an increase up to a given altitude and then a decrease (e.g. Djukic et al., 2010). Generally as altitude increases so does annual rainfall, while air temperature decreases, thus causing marked changes in vegetation, soil type and soil microbial activity across the elevation gradient, which in turn may affect the C cycle. Numerous factors and mechanisms have been proposed to explain the increase of SOC in line with elevation in each particular system; e.g. an improved physical protection of SOC because of the increase in the soil aggregate rate (Li et al., 2016), a reduction in

SOC decomposition linked to the decline of soil temperature (Dieleman et al., 2013), or the increase of C humification associated with changes in vegetation and litter quality (Wang et al., 2016). This general pattern of increasing SOC with altitude is frequently masked in areas where forests have been replaced by agricultural systems which cause local decline in SOC stocks (Ozalp et al., 2016).

The high SOC stocks in mountain systems dominated by volcanic soils have generally been attributed to the physical protection of organic matter provided by allophanic minerals, together with a reduction in microbial activity breaking down SOC due to soil acidity, poor P availability and low soil temperature (Lemenih and Itanna, 2004; Naafs et al., 2004). As these factors co-vary with altitude, confounding effects may occur when the relationship between them and SOC is evaluated using correlation analysis (Körner, 2007). In this sense, although some authors have proposed that mountain areas – with their elevation gradients of temperature and rainfall – may be useful to assess the impact of climate changes similar to those observed across latitudes (Klimek et al., 2016; Wang et al., 2016), Nottingham et al. (2015) pointed out that careful consideration should be given to the effects of other soil and plant factors varying concomitantly with elevation. Undoubtedly, knowledge of the interactions between the factors that induce changes in SOC is necessary to assess the impact of projected warming in mountain areas. For example, if falling temperatures at higher altitudes is the main factor that controls rises in SOC, then studies addressing the temperature sensitivity of SOC decomposition (e.g. evaluation of the Q_{10} coefficient) are essential to predict the impact of warming. Indeed, several studies have focused on this topic (e.g. Zimmermann et al., 2009; Zimmermann and Bird, 2012). By contrast, more complex studies will be necessary if warming simultaneously affects C outputs (e.g. SOC decomposition) and C inputs (i.e. changes in vegetation and litter quality) (Nottingham et al., 2016), or if SOC changes are primarily controlled by the physical protection provided by soil structure, whose characteristics vary with altitude (Kramer and Chadwick, 2016).

The flanks of volcanic islands in tropical regions where the elevation gradient of climate is one of the strongest in the world present a wide range of soil types, with andosols on the summit and ferralsols, luvisols and nitisols on the footslopes (Legros, 2012). These regions therefore represent an interesting edaphic and climatic setting to determine the effects of the factors impacting SOC stocks. In this study we examine the changes of SOC stocks in an altitudinal gradient of a tropical volcanic island where the land is subject to two intensive agricultural systems (banana monoculture and vegetable crops), which are characterised by the heavy use of fertilisers and pesticides. We hypothesise that in these systems SOC is mainly controlled by soil mineralogy, climatic factors and soil tillage. We consider that the effects of other factors such as soil nutrient content and soil biological properties are of minor importance in our intensive agricultural systems. The aim of this study was therefore to assess the underlying mechanisms controlling SOC by focusing on the effect of the gradients of soil mineralogy (e.g. allophanic mineral content), climate (e.g. temperature and rainfall), and the intensity of soil tillage (low under banana, high under vegetable crops). The banana cropping systems are characterised by a temporal steady-state of SOC stocks and the vegetable crop systems present high annual SOC losses (Sierra et al., 2015). To reduce the impact of confounding effects caused by factors that co-vary with altitude, we used a process-based approach to estimate C outputs and C inputs and to assess their effects on the SOC balance along the elevation gradient. The study was carried out in Guadeloupe (French West Indies), which exhibits within a small area nearly every physical landscape and cropping system found in the Caribbean region. This study formed part of a larger project devoted to quantifying the impact of cropping systems, the pedoclimate and warming on SOC stocks, using Guadeloupe as a case study of the Caribbean (Sierra et al., 2017).

2. Materials and methods

2.1. Study location, soils and climate

The study was carried out in the uplands of south Basse-Terre, the main island of the Guadeloupe archipelago located in the eastern Caribbean (16° 05’ N, 61° 40’ W) (Fig. 1). Basse-Terre Island is dominated by a mountain chain oriented northwest to southeast where the crest standing at 1456 m.a.s.l. (La Soufrière volcano). Although the land west of the crest slopes steeply toward the Caribbean Sea (slopes of 20-30%), the eastern side of the chain slopes more gently toward the Atlantic Ocean (slopes of 10%). On both slopes, deep valleys trending at right angles to the mountain chain are separated by sharp ridges. During the present study we focused on the land areas dominated by andosols (FAO classification) (Fig. 1), which had developed on volcanic ash deposited directly by successive volcanic eruptions throughout the Late Glacial and Holocene (Legros, 2012). Because of the increase in the allophanic clay content with altitude, the hydrated microporous structure of the soil, responsible for its high water content at field capacity, progressively expands with increasing altitude, whereas bulk density decreases (Colmet-Daage and Lagache, 1965). The zone of transition between the upland andosols and rich halloysite nitisols of the lowlands is placed between 100 m and 200 m on the eastern slopes, and between 200 m and 300 m on the western slopes (Fig. 1). In the studied area, the mean air temperature drops by 0.7°C and annual rainfall increases by 437 mm yr^{-1} per every 100 m (Fig. 2). The level of rainfall is lower from December to May, which is slightly more pronounced in the lowlands (38% of the annual rainfall takes place in this 6-month period; an average of 170 mm per month) than in the uplands (45% of the annual rainfall; an average of 380 mm per month).

2.2. Land use and farming practices

The agricultural land in the studied area is oriented toward the production of bananas for the European market and vegetable crops for the local market (Sierra et al., 2015). Farms devoted to banana production are situated from 100 m to 700 m and average 10 ha, while those focused on vegetable crops are located from 100 m to 900 m and average 4 ha. The land above an altitude of 900 m is occupied by tropical rainforest; this is a protected area where agriculture and deforestation have been banned. Only the agricultural land was included in the present study (Fig. 1). Sierra et al. (2015) had previously reported that the SOC stored under banana cropping systems in this region is likely to be close to, or at, a steady-state when crop residues are the only C input to the soil (i.e. when no organic amendments are applied). By contrast, SOC stocks decrease by 2.0 ± 1.1 Mg C ha^{-1} yr^{-1} in soils cultivated with vegetable crops (Sierra et al., 2017).

Banana is managed mainly as a pluriannual system and its cycle is 5-6 years. The growth season is 9-12 months and varies among plants in the same plot; so, the initially homogeneous plant population becoming heterogeneous after few years. This is important to the time of harvest because each plant is harvested separately (Raphael et al., 2012). Harvesting is performed manually and residues (leaves and stems) are cut and placed on the soil. During growth, each plant (mother plant) produces a sucker (daughter plant) which grows after harvest of the mother plant. For this reason, soil tillage is only applied before planting every 5-6 years. In plots with steep slopes where mechanised tillage is not possible, the soil is not ploughed and replanting is ensured gradually by hand as the old plants die. Such a system can be considered as being perennial (Clermont-Dauphin et al., 2004).

The principal vegetable crops in the studied area are tomato, cabbage, salad, eggplant and pepper. They are cultivated under monoculture systems; some farmers apply one year of fallow after 5-6 years of cultivation. Soil tillage is highly intensive with at least six tillage operations per year. Harvesting is manual and the residues (leaves and stems) are placed on the soil or buried at a depth of 0.1–0.2 m.

Most banana and vegetable crop systems are based on the heavy use of synthetic fertilisers and pesticides. For example, N fertilisers are applied at a rate of 400-600 kg N ha^{-1} yr^{-1} in banana and 150-200 kg N ha^{-1} yr^{-1} in vegetable crops. For K, the rates are 120 kg K ha^{-1} yr^{-1} for banana and 80 kg K ha^{-1} yr^{-1} for vegetables. For P, the rates are 50 kg P ha^{-1} yr^{-1} for banana and 80 kg P ha^{-1} yr^{-1} for vegetables. For banana, P and K fertilisers are applied after harvest of the mother plant, and N fertiliser is split into 8-12 applications along the growth cycle. For vegetables, all the fertilisers are applied at planting. No irrigation is applied in these cropping systems. In fact, the water requirement for banana crops in the studied area is 120-150 mm per month (Lassoudière, 2007), which is fully supplied by rainfall even during the drier season in the lowlands. About 50% of the plots under banana and vegetable crop systems are limed every 5-10 years to raise soil pH and to reduce the impact of aluminium toxicity on plant growth on the more acidic soils.

2.3. Soil and plant data

SOC stocks were evaluated using the soil database developed for the TropEmis Project performed in Guadeloupe (Sierra et al., 2015). This database contains information on soils and farm characteristics covering all agro-ecological regions of the archipelago. For the present study we selected data corresponding to the studied area, which included 198 plots under banana monoculture since about 1980, and 55 plots cultivated with vegetable crops since about 1990. These plots had never received organic amendments. Information on the farms included their size, the number and size of plots, location, altitude, soil type, cropping systems, and the management of fertilizers, organic amendments, crop residues and soil tillage. The soil characteristics of the selected plots included SOC (determined with a C analyser), organic N (Kjeldahl method), extractable P (Truog method), cation exchangeable capacity and exchangeable cations (ammonium acetate method) and pH (soil-water ratio of 1:5). Soil bulk density (core method; NRCS, 2014) was available for 89 plots (53 under banana monoculture and 36 under vegetable crops). Allophane content was available for 28 plots under banana monoculture and was estimated as proposed by Buurman et al. (2007):

$$\text{Allophane} = Si_o/0.14 \quad (1)$$

where Si_o (g kg^{-1}) is Si in allophane determined using the ammonium oxalate-oxalic acid method (Matus et al., 2008). We selected allophane content to assess soil mineralogy because it was well correlated with SOC content in several studies carried out on volcanic soils (e.g. Matus et al., 2008; Garrido and Matus, 2012).

Soil analyses were performed on the 0-0.25 m soil layer and all soil samples were collected by the same team. Soil sampling was carried out on a systematic grid using a 0.06-m diameter auger and collecting the equivalent of 30 sub-samples per hectare. Chemical analyses were performed on a composite sample (~1 kg dry matter) at the SADEF Soil Testing Laboratory in France. Bulk density was determined with five replications per plot. No significant differences between the two cropping systems were observed for bulk density for plots located at the same altitude (Sierra et al., 2015). Only yields that concern export crops are available in Guadeloupe. Banana yields in the studied area were obtained from the Banana Producer Group of Guadeloupe and corresponded to the yields observed in 2015 for 90 plots included in the soil database. It is important to point out that the groups of banana plots with available information concerning bulk density, allophane content and yields were not fully identical, but they were within the selected 198 plots under banana monoculture.

2.4. Analytical approach

In this study, most of the factors affecting SOC present a high level of collinearity (e.g. Fig. 2), which prevents them from being including together in a multiple regression model to predict SOC content (de Oliveira Aparecido et al., 2017). We therefore adopted a mechanistic approach by applying a process-based analysis to estimate C fluxes and SOC balance along the elevation gradient. The analysis involved two steps. In the first step, we determined C inputs and outputs in order to assess their relative influence on the SOC balance along the elevation gradient. Although C input was represented by the humified crop residue C, C output corresponded to the in situ rate constant of SOC mineralisation. This step was based on the results obtained in this study. In the second step we investigated the relationships between these C fluxes and the soil (e.g. allophane and nutrient contents, C/N ratio, microbial biomass, abundance of detritivore mesofauna) and climatic factors (e.g. temperature and rainfall) affecting SOC turnover. This step was based on our results as well as on those obtained in previous studies performed in the same area analysed here. The analysis was applied to the plots under banana monoculture and calculations were made under the hypothesis of a temporal steady-state of SOC stock. As cited above, this hypothesis was supported by the results reported by Sierra et al. (2015), and also by the long period under banana monoculture without any application of organic amendments. Because this hypothesis could not be applied to the plots cultivated with vegetable crops (i.e. SOC stocks decrease over time), the rate constant of SOC mineralisation was not calculated for these systems. SOC stocks under vegetable crop systems were used to compare them with the altitudinal trend of SOC stocks observed for the banana systems.

We considered that in situ SOC mineralisation follows a first order kinetic (Saffih-Hdadi and Mary, 2008). Therefore, under the hypothesis of a temporal steady-state of SOC stock at the plot scale it may be established that:

$$dSOC_{stock} / dt = 0 = (C_{res} \times h_{res}) - (SOC_{stock} \times k_{SOC}) \quad (2)$$

and then:

$$k_{SOC} = (C_{res} \times h_{res}) / SOC_{stock} \quad (3)$$

where SOC_{stock} (Mg C ha^{-1}) is the SOC stock and $dSOC_{stock} / dt$ is the annual change in SOC stock (Mg C ha^{-1} yr^{-1}), C_{res} (Mg C ha^{-1} yr^{-1}) is the annual C input from crop residues (aboveground and roots), h_{res} (unitless) is the humification coefficient of crop residues, and k_{SOC} (yr^{-1}) is the rate constant of mineralisation of SOC_{stock}.

The characteristics of crop residues analysed in this study and the equations used to calculate SOC_{stock}, C input from crop residues and the temperature sensitivity of k_{SOC} (the Q_{10} coefficient) are presented as Supplementary Information in Appendix A (Table A.1 and Eqs. (A), respectively). Bulk density was used to calculate SOC_{stock} (Eq. (A.1)), banana yields were used to calculate C inputs from crop residues (Eqs. (A.2) and (A.3)), and temperature was used to calculate the Q_{10} coefficient as proposed by Hamdi et al. (2013) (Eqs. (A.4) and (A.5)). Although bulk density, banana yields and temperature varied with altitude (see section 3 and Fig. 2), as mentioned above, these data were not available for all of the selected banana plots. We therefore used the equations fitted to quantify the altitudinal gradient of these three variables in order to estimate their values for each selected plot based on knowledge of its altitude. All the fits were performed using the Newton solution of the Excel™ solver.

3. Results

To simplify the presentation of the results, the altitudinal pattern of some soil properties are provided as Supplementary Information in Appendix A (Figs. A).

Only 15% of the selected banana plots were managed as perennial systems. These plots were present from an altitude of about 300 m, and their SOC stocks were similar to those observed for the plots managed as pluriannual systems located at the same altitude (Fig. A.1). In this way, all the banana plots could be analysed as a single population regardless of their management. The SOC content increased with altitude under both banana monoculture and vegetable crop systems (Fig. 3). The intercept and the slope of the linear regression fitted to SOC data differed significantly between the two cropping systems ($P < 0.05$); e.g. the intercept was higher and the slope was lower for the banana monoculture. At an altitude of 100 m, the estimated SOC content was about 35 g C kg^{-1} under banana monoculture and 25 g C kg^{-1} under vegetable crops; these values were respectively 75 g C kg^{-1} and 65 g C kg^{-1} at 700 m. Soil bulk density decreased with altitude from about 0.82 Mg m^{-3} at 100 m to about 0.67 Mg m^{-3} at 700 m (Fig. 4a). Allophane content increased with altitude from about 25 g kg^{-1} at 100 m to 75 g kg^{-1} at 700 m (Fig. 4b). SOC stocks were calculated from the SOC content of each selected plot and the soil bulk density data obtained using the equation shown in Fig. 4a. The SOC stocks displayed the same trend as that observed for SOC content (Fig. A.2). The differences between cropping systems in terms of SOC stocks, in absolute and in relative terms, were higher at low altitude (e.g. at 100 m, 55 Mg C ha^{-1} for banana and 35 Mg C ha^{-1} for vegetable crops; i.e. 57% higher for banana) than at high altitude (e.g. at 700 m, 120 Mg C ha^{-1} for banana and 110 Mg C ha^{-1} for vegetable crops; i.e. 9% higher for banana).

For both banana and vegetable crop systems, no changes with altitude were observed for cation exchangeable capacity (Figs. 5a and 5b) and soil pH (Figs. 5c and 5d). The same was observed for the C/N ratio (Fig. A.3), cations and base saturation (Fig. A.4), and extractable P (Fig. A.5). The average values of these soil properties are presented in Table 1. No differences were observed between the two cropping systems except for extractable P (higher under vegetable crops) and exchangeable K (higher under banana) ($P < 0.05$) (Table 1).

As the C/N ratio did not display any trend with altitude, the altitudinal gradient of organic N was very similar to that presented in Fig. 3 for SOC (Fig. A.6). Under banana monoculture, organic N increased from 2.7 g N kg^{-1} at 100 m (5.6 Mg N ha^{-1}) to 7.3 g N kg^{-1} at 700 m (12.3 Mg N ha^{-1}). For vegetable crops, organic N increased from 1.7 g N kg^{-1} at 100 m (3.8 Mg N ha^{-1}) to 6.6 mg N kg^{-1} at 700 m (10.9 Mg N ha^{-1}).

Banana yields decreased with altitude from about 45 Mg ha^{-1} at 100 m to 20 Mg ha^{-1} at 700 m (Fig. 6a). Yields displayed a relatively high variability throughout the altitudinal gradient. Using these yield values, banana residues estimated from Eqs. (A.2) and (A.3) decreased from 15 Mg ha^{-1} at 100 m to 7 Mg ha^{-1} at 700 m. Therefore, the input of humified C derived from banana residues ($C_{res} \times h_{res}$, in Eq. (2)) decreased 2.2-fold between 100 m (1.6 Mg C ha^{-1} yr^{-1}) and 700 m (0.7 Mg C ha^{-1} yr^{-1}).

The in situ k_{SOC} estimated from Eq. (3) for the selected plots of banana monoculture are presented in Fig. 6b. k_{SOC} decreased 6.7-fold between 100 m (3.0×10^{-2} yr^{-1}) and 700 m of altitude (4.4×10^{-3} yr^{-1}). With such a steep change, the Q_{10} temperature coefficient estimated from Eq. (A.5) was as great as 31, which is highly unrealistic, as will be discussed in section 4.2.2. For the 28 banana plots used to determine allophane content, SOC content correlated positively and k_{SOC} correlated negatively with allophane content ($P < 0.05$) (Fig. 7).

4. Discussion

4.1. Relative impact of C inputs and outputs on the SOC balance under banana monoculture

Our results confirmed that tropical volcanic soils under agriculture can store amounts of organic matter equivalent to those observed in natural forest systems. For example, the SOC stocks observed under banana monoculture were similar to those reported by Powers and Schlesinger (2002) for a tropical rainforest in Costa Rica on volcanic soils, with comparable altitudinal gradient (e.g. 50 Mg C ha^{-1} at 50 m to 140 Mg C ha^{-1} at 800 m) and climatic conditions (e.g. temperature ranging from 25°C to 20°C and rainfall ranging from 3500 mm yr^{-1} to 4700 mm yr^{-1}). In addition, the rise in SOC levels with altitude in our study tended to be linear as had previously been found by other authors in natural ecosystems (e.g. Zimmermann et al., 2009; Dieleman et al., 2013). However, it is likely that altitude did not exert a direct impact on the SOC gradient, but an indirect effect involving soil (e.g. mineralogy), climatic (e.g. temperature and rainfall) and vegetation factors (e.g. amount of crop residues) that varied across the elevation gradient. Because SOC stocks result from a balance of

C inputs and outputs, such factors might induce the SOC gradient due to their impacts on C input and output fluxes.

In our agricultural systems, C input was dependent on the quantity of crop residues and the humification coefficient (Eq. (2)). In fact, the plots included in this study were selected because no organic amendments were applied so that C from crop residues was the only C input into the soil. The decline of banana yields at increasing altitudes, and consequently the reduction of the amount of crop residues, revealed that changes in C input could not be responsible for the increase in SOC with altitude, but might weaken it. Banana yields drop with altitude because lower temperatures reduce the growth rate and extend the growing season, which together diminish plant biomass and annual fruit production (Brisson et al., 1998). In contrast with this finding in our agricultural systems, several authors have found that in natural forest systems, C inputs rise with altitude because of an increase in the amount of litter associated with marked changes in the composition and density of vegetation (e.g. Powers and Schlesinger, 2002; Tashi et al., 2016).

Although the temperature gradient may also affect the decomposition rate of crop residues, the humification coefficient of crop residues is generally considered to be dependent solely on residue quality (e.g. Justes et al., 2009). We thus considered that h_{res} in Eq. (2) was not affected by the temperature gradient, in which case C input only varied as a function of the amount of crop residues (i.e. Eqs. (A.2) and (A.3)). Some authors have reported that the humification coefficient in natural forest systems varies in line with changes in vegetation and litter quality along the altitudinal gradient; e.g. humification of litter C increased in an elevation gradient in Taiwan (Wang et al., 2016) and decreased in an elevation gradient in Peru (Segnini et al., 2011). This was not the case during the present study because vegetation and crop residue quality were the same across the altitudinal gradient. This is consistent with the results obtained in a recent study carried out in the same area analysed here, which indicated that nutrient content of banana plants and residues was not affected by the elevation gradient (G. Loranger-Merciris, unpublished).

On the basis of our results it appears that the increase in SOC stocks with altitude was primarily controlled by the reduction of C outputs, as suggested by the steep decline of k_{SOC} with altitude. Indeed, the banana monoculture systems are characterised by a steady-state of SOC stock at each altitude, where the level of SOC at equilibrium increases with altitude because C outputs decrease faster than C inputs. Therefore, the assessment of the underlying mechanisms that induce the SOC gradient should be based on the evaluation of the most important factors affecting the gradient of k_{SOC}.

4.2. Factors affecting the altitudinal gradient of k_{SOC}

In our process-based approach, k_{SOC} represents the soil biological activity linked to SOC mineralisation and integrates the impact of the climatic and soil factors that affect mineralisation in the field. On the basis of our results, we hypothesise that the k_{SOC} gradient was firstly controlled by soil mineralogy and rainfall and secondly by temperature. We consider that other factors such as soil nutrient content, soil C/N ratio and soil biological properties (e.g. microbial biomass and abundance of detritivore mesofauna) were of minor importance in this study. These factors are analysed below.

4.2.1. Soil mineralogy and rainfall

These factors cannot be analysed separately because soil mineralogy in the studied area is mainly determined by the level of rainfall, which controls the intensity of the weathering processes (Colmet-Daage and Lagache, 1965; Legros, 2012). In this way, soils located in the wet uplands are characterised by chemically reactive allophanic materials, which incorporate organic compounds to develop amorphous gels (Clermont-Dauphin et al., 2004). The content in allophanic materials diminishes as the altitude and rainfall decrease, and some gel minerals reorganise progressively into crystalline 1:1 clay minerals (e.g. halloysite) and aluminium and iron hydrous oxides, which adsorb organic matter on their surfaces but do not incorporate it into the mineral matrix (Kramer and Chadwick, 2016). The crystallisation of 1:1 minerals occurs during the drier season and is then more rapid in lowlands with a lower level of rainfall in that season (Sedov et al., 2003). The increase of allophane content and the decrease of bulk density with altitude observed in the present study reflected this change in soil mineralogy, which was in line with the results reported by other studies on volcanic soils (Powers and Schlesinger, 2002; Li et al., 2016).

Several authors reported that SOC content was positively correlated with allophane content in elevation gradients of volcanic soils (e.g. Powers and Schlesinger, 2002; Matus et al., 2008), and the same was observed in the present study (Fig. 7a). Moreover, the range of values of allophane content observed in this study was similar to that reported by Matus et al. (2008) and Garrido and Matus (2012) for volcanic soils in Chile. Buurman et al. (2007) proposed that high rainfall in the uplands favours the presence of anoxic conditions inside the micropores of the allophanic gels, reducing SOC decay and inducing the increase in SOC content with altitude. On the other hand, Garrido and Matus (2012) proposed that SOC stabilisation in andosols is associated with the low physical accessibility for microbial decomposers of SOC inside the micropores of allophanic clay minerals. Although the mechanisms of SOC stabilisation in andosols are not fully elucidated at this time (Filimonova et al., 2016), it appears that this stabilisation would be the major responsible for the increase in the mean residence time and the content of SOC with altitude in elevation gradients of volcanic soils (Kramer and Chadwick, 2016). We hypothesise that the steep drop observed in k_{SOC} along the altitudinal gradient reflected the increase in the mean residence time of SOC. This hypothesis is supported by the negative correlation observed between k_{SOC} and allophane content, which indicated that allophane content explained about 53% of the variability of k_{SOC}. (Fig. 7b). Since SOC is more protected against microbial degradation within allophanic materials than on the surfaces of secondary minerals, k_{SOC} decreases and SOC stocks increase with altitude.

It is interesting to point out that k_{SOC} was higher at low altitudes despite a lower level of rainfall, mainly in the drier season. However, an effect of rainfall on k_{SOC} in lowlands cannot be discarded because it could affect the activity of SOC decomposers. Although under the prevailing rainfall regime in the uplands the soils are at field capacity much of the year (Clermont-Dauphin et al., 2004), a modelling study carried out in the lowlands of the studied area indicated that water content in the top soil layer can be lower than that at field capacity during a part of the drier season (Brisson et al., 1998). Therefore, rainfall could weaken the k_{SOC} gradient by reducing the k_{SOC} values in the lowlands. While it is difficult to separate the influence of rainfall on microbial activity and on soil mineralogy in lowlands, it seems clear that the latter was a key factor explaining the decrease of k_{SOC} with increasing altitude.

4.2.2. Temperature

The decrease of temperature with altitude is frequently cited as the main factor inducing an increase in SOC content in elevation gradients under natural forest systems. For example, Luo et al. (2014) found that in situ soil respiration decreased by 35% in the altitudinal gradient of a subalpine secondary forest in China, which was attributed to a drop in soil temperature from 11°C to 8°C along the elevation gradient. Using Eqs. (A.4) and (A.5), we calculated that the Q_{10} coefficient of soil respiration corresponding to the results of Luo et al. (2014) would be 2.7, which is within the range of values cited by several authors (e.g. Nottingham et al., 2015). In our study, k_{SOC} decayed 6.7-fold from 100 m to 700 m for a temperature gradient of only 4.4°C. Indeed, this sharp decay of k_{SOC} gave rise to a highly unrealistic Q_{10} value (31). The kinetic theory on which the estimate of Q_{10} is based predicts a value of around 2 for typical ambient temperatures of 0°C-20°C (Davidson and Janssens, 2006), which increases for the low ranges of temperature and for organic compounds of greater chemical complexity (Nottingham et al., 2015). For example, in laboratory studies carried out on soils collected from altitudinal gradients, the Q_{10} of SOC mineralisation was about 1.5 in the Changbai Mountains of China (Wang et al., 2016), and ranged from 2 to 3 in the Western Carpathians of Poland (Klimek et al., 2016). Nottingham et al. (2015) pointed out that the higher Q_{10} values frequently observed in situ experiments (e.g. up to 7 in their study), when compared with the lower values obtained from laboratory studies, might be associated with complex interactions between factors varying simultaneously with elevation. We think this was also the case in our study, where the unrealistic Q_{10} might have been an artefact induced by other factors changing with altitude such as soil mineralogy.

Using Eqs. (A.4) and (A.5), we calculated that for the temperature gradient observed in the present study, k_{SOC} would decrease 1.4-fold from 100 m to 700 m for a Q_{10} value of 2. The decrease would be 1.6-fold for a Q_{10} of 3. This implies that changes in temperature in our elevation gradient only could explain between 21% and 24% (i.e. 1.4/6.7 and 1.6/6.7, respectively) of the observed change in k_{SOC} in the studied area.

4.2.3. Soil nutrient content and C/N ratio

Natural systems in tropical uplands are frequently characterised by gradients of nutrient limitation that affect plants, microbial activity and SOC decomposition, mainly with respect to N and P (Buurman et al., 2007; Nottingham et al., 2015). This does not appear to be the case in our study because of the heavy use of NPK fertilisers and lime in banana cropping systems, which could explain the lack of altitudinal gradients for P and cation contents. In a study carried out on tropical forest soils in Costa Rica, Cleveland et al. (2004) reported that available soil P was a limiting factor for SOC and litter decomposition. However, the contents of extractable P found by these authors were 10-15 times smaller than those observed under banana monoculture in the present study (Table 1). Similarly, the contents of exchangeable Ca, Mg and K observed in our soils were about two-fold higher than the values reported for other elevation gradients of volcanic soils under natural vegetation (e.g. Kramer and Chadwick, 2016).

Concerning N availability, even if organic N content was lower in the lowlands than in the uplands (Fig. A.6), it is unlikely that N could limit k_{SOC} at low altitudes because of the high rates of N fertiliser applied in banana monoculture along the growth cycle (400-600 kg N ha^{-1} yr^{-1}, split into several applications). Moreover, Dorel et al. (2005) found that the amount of mineralisable N measured in a laboratory experiment using andosols of the same area analysed here was much higher than that observed in other tropical soils and was not correlated with either altitude or SOC content. For an elevation gradient in the Western Carpathians, Klimek et al. (2016) observed a reduction in the soil C/N ratio that was associated with an increase at high altitudes of the more chemically recalcitrant fraction of SOC, which could decrease the rate of SOC decomposition in the uplands. In contrast to this, our results showed that the C/N ratio did not exhibit any trend with altitude; i.e. there was no evidence of a change in SOC recalcitrance with altitude. Overall, these results suggest that neither soil nutrient content nor soil C/N ratio contributed to the SOC and k_{SOC} gradients.

4.2.4. Microbial biomass and detritivore mesofauna

Several authors observed that microbial biomass and the structure of bacterial and fungal communities change with altitude, which may affect SOC turnover. For example, Pabst et al. (2013) found that microbial biomass increased in an elevation gradient of Mount Kilimanjaro (Tanzania) under natural forest and savannah ecosystems. Similar results were obtained by Chang et al. (2016) for an elevation gradient in Taiwan dominated by bamboo plantations. In addition, these authors reported that the fungi-bacteria ratio also increased with altitude, which was related to the increase in SOC content, mainly in the amount of the labile SOC fraction.

In the present study, we did not focus on the biological properties of the soils because previous studies performed in the same area indicated that they were affected by the management of the banana cropping system but not by altitude. For example, Clermont-Dauphin et al. (2004) and Dorel et al. (2005) found that microbial biomass was higher in less intensive cropping systems, regardless of their altitude. These systems included low rates of fertilisers and pesticides and the use of organic amendments. In addition, the number and the biomass of earthworms were higher under these less intensive systems (Clermont-Dauphin et al., 2004), and the same was found for the abundance of detritivore mesofauna such as ants and termites (G. Loranger-Merciris, unpublished). These studies indicated that microbial biomass and the abundance of mesofauna did not display any trend with altitude in the more intensive systems involved in the present study. As discussed above, banana systems including the use of organic amendments were not analysed in our study because the hypothesis of a steady-state of SOC could not be applied to these systems (Sierra et al., 2015). On the basis of these results, we consider that the SOC and k_{SOC} gradients observed in our intensive banana systems cannot be attributed to changes in microbial biomass or in the size of the mesofauna population with altitude.

4.3. Differences in SOC stocks between banana and vegetable cropping systems

Several authors reported that SOC stocks decreased dramatically following the conversion of natural vegetation into arable land in elevation gradients (e.g. Lemenih and Itanna, 2004; Pabst et al., 2013). In our long-term agricultural systems, where deforestation had not been applied during the past five decades, SOC stocks were lower under vegetable crop systems than under banana monoculture throughout the elevation gradient. This could be due to two factors: a lower C input because of smaller quantities of crop residues from vegetable crops, and a higher C output because of the more intensive soil tillage applied in these systems. Crop residues from vegetable crops vary from 10.3 Mg dry matter ha^{-1} yr^{-1} for eggplant to 2.2 Mg ha^{-1} yr^{-1} for salad (Table A.1). The coefficient of humification for vegetable crop residues averaged 0.34, which is close to that of banana residues (i.e. 0.31; Table A.1), which suggests that residue humification was of minor importance when trying to explain the differences between the two cropping systems. By considering the mean quantity of residues from vegetable crops (i.e. 6 Mg ha^{-1} yr^{-1}) and the mean humification coefficient (Table A.1), the mean input of humified C derived from vegetable crop residues would be about 0.9 Mg C ha^{-1} yr^{-1}, which is 45% lower than that observed for banana monoculture at 100 m (i.e. 1.6 Mg C ha^{-1} yr^{-1}) and 30% higher than that observed at 700 m (i.e. 0.7 Mg C ha^{-1} yr^{-1}) . Although in Guadeloupe there are not data on the changes of vegetable crop yields and their crop residues with altitude, it seems that on average the C input from crop residues was probably lower under vegetable crops than under banana monoculture, which may partially explain their lower SOC stocks. Concerning C outputs, Sierra et al. (2015) found that SOC mineralisation in the region studied during this work was about 110% higher in soils under vegetable crops compared to those under banana monoculture, linked to differences between the systems in terms of the intensity of soil tillage. It therefore seems that differences between the two cropping systems in C outputs were much higher than their differences in C inputs. We concluded that differences in SOC stocks between the two cropping systems along the elevation gradient were mainly associated with C outputs and secondarily with C inputs. Although differences between the two systems regarding extractable P (higher under vegetable crops) and exchangeable K (higher under banana) contents reflected the specific fertiliser practices of each cropping system, the level of most soil properties was similar in both cropping systems (Table 1). We therefore consider that these properties were of minor importance to explain the differences in SOC stocks between vegetable and banana cropping systems.

A more interesting finding from this study was that the differences in SOC stocks between the two cropping systems decreased with altitude. This was consistent with the hypothesis that changes in soil mineralogy played a major role in SOC protection and decomposition. Thus SOC occluded within allophanic minerals at high altitude would be less responsive to differences in soil tillage between the cropping systems, and its vulnerability would increase in line with the reduction of allophane content at lower altitudes. This is consistent with the kinetic theory of SOC decomposition (Nottingham et al., 2016), and agrees with the results reported by Nottingham et al. (2015) concerning the greater sensitivity of unprotected SOC to environmental changes along an elevation gradient in the Peruvian Andes.

The results of this study may provide some insights concerning the impact of climate warming on SOC stocks in our tropical altitudinal gradient. Climate models predict that the mean temperature in the Guadeloupe archipelago will rise 0.7°C in the next three decades (Sierra et al., 2010). Assuming a Q_{10} value of 2 for SOC mineralisation, this rise in temperature would induce a 5% increase in the current k_{SOC} values. The increase would be 8% for a Q_{10} of 3. Even though warming and Q_{10} may vary along the altitudinal gradient, it appears that the magnitude of the change in k_{SOC} due to warming might be much smaller than that observed for k_{SOC} between the lowlands and uplands in this study (i.e. 570%). It follows that SOC decomposition and C emissions will continue to be higher in lowlands under a climate warming scenario, mainly under vegetable cropping systems.

Indeed, this hypothesis needs to be tested during future laboratory and field studies designed to determine Q_{10} values across the gradient of soil mineralogy.

5. Conclusions

Our results confirm that any assessment of the underlying mechanisms controlling SOC changes in altitudinal gradients needs to consider the confounding influence of the various edaphic, climatic and vegetation factors that co-vary with elevation. For this, the process-based approach applied in this study to analyse the banana cropping systems, characterised by a steady-state of SOC stock, was useful to assess the factors affecting the SOC gradient. This approach made it possible to establish that the level of SOC at the steady-state increases with altitude because C outputs decrease faster than C inputs. In other words, the increase in SOC with altitude was primarily controlled by the reduction in C outputs, represented by the in situ rate constant of SOC mineralisation (k_{SOC}). Changes in allophane content with altitude explained 53% of the observed variability of k_{SOC}, which probably reflected the effect of the physical protection of SOC within amorphous allophanic minerals. Although changes in temperature only could explain 22% of such variability, the unrealistic Q_{10} value of k_{SOC} estimated for the entire altitudinal gradient suggests that the temperature sensitivity of SOC needs to be determined at a local level (e.g. for each soil mineralogical type defined by the allophane content).

In contrast to reports on altitudinal gradients under natural ecosystems, it appears that neither soil nutrient content nor biological soil properties contributed to the SOC and k_{SOC} gradients under our agricultural systems characterised by a heavy use of fertilisers and pesticides. In addition, SOC vulnerability to climate warming would be less in uplands because of the physical protection provided by allophanic amorphous minerals. These results suggest that SOC under vegetable crop systems may be more vulnerable to warming than that under banana monoculture, which would be linked to an increase in the content of unprotected SOC following the intensive soil tillage applied in the former case. Further work is now necessary to assess the combined effects of warming and soil mineralogy on SOC stocks under contrasting tropical agricultural systems.

Acknowledgements

This study formed part of the TropEmis Project funded by the Reacctif Programme of the French Agency for the Environment and Energy Management (ADEME) (Grant 410-00159), the European Regional Development Fund (FEDER) (Grant 410-00160) and the Regional Council of

Guadeloupe (Grant 410-00161), and of the RIVAGE Project funded by the FEDER (Grant 410-00242) and the Regional Council of Guadeloupe (Grant 410-00325). We are grateful to Marcus Hery of the Banana Producer Group of Guadeloupe for providing us with the database on banana yield, and to the 253 farmers who were interviewed for this study. We would like to Victoria Hawken for reviewing the English manuscript. We thank the anonymous reviewers for their constructive comments, which helped us to improve the manuscript.

Appendix A. Supplementary Information

Supplementary information linked to this article can be found at:

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Figure captions

Fig. 1. Location of the studied area in the southern part of Basse-Terre Island in the Guadeloupe archipelago. The land occupied by andosols out of the area included in this study corresponds to the rainforest.

Fig. 2. Mean air temperature and rainfall across the altitudinal gradient. Vertical bars indicate the standard deviation.

Fig. 3. Soil organic C content across the altitudinal gradient under (a) banana monoculture and (b) vegetable cropping systems.

Fig. 4. Altitudinal gradient of (a) soil bulk density and (b) allophane content.

Fig. 5. Changes across the altitudinal gradient in (a)(b) cation exchangeable capacity, and (c)(d) soil pH, for banana monoculture and vegetable crops, respectively.

Fig. 6. Altitudinal gradients of (a) banana yields and (b) the in situ rate constant of soil organic C mineralisation (k_{SOC}). k_{SOC} was estimated for plots under banana monoculture.

Fig. 7. Relationships between allophane content and (a) soil organic C and (b) the in situ rate constant of soil organic C mineralisation (k_{SOC}).

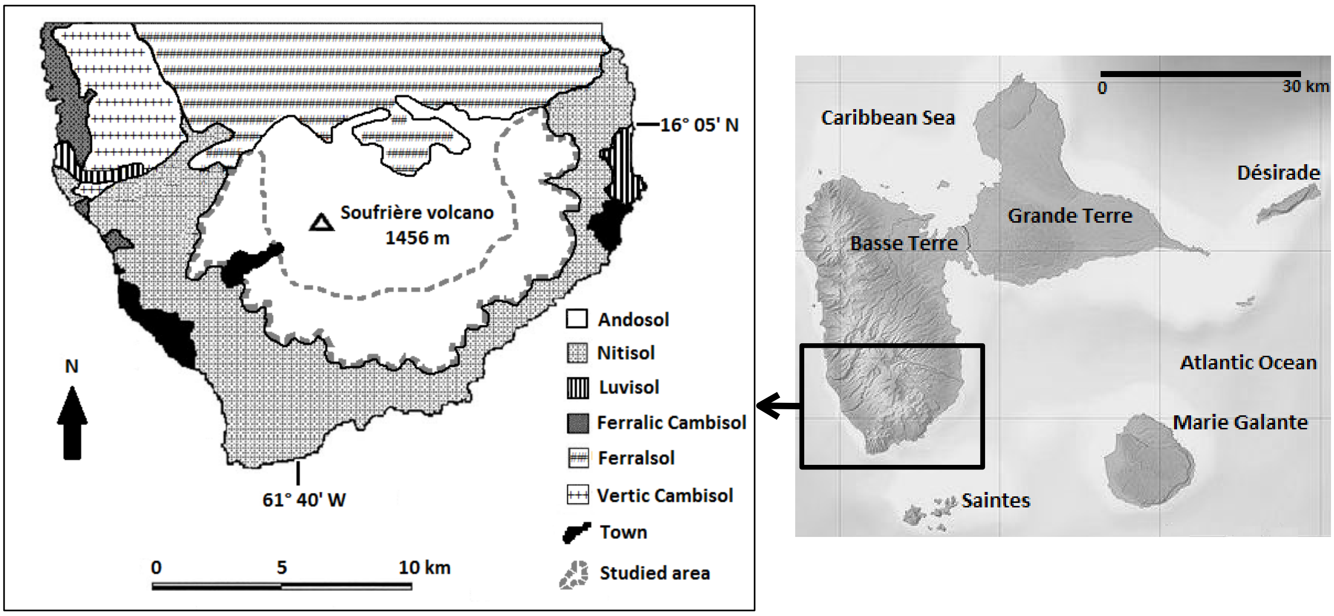

16° 05' N
Soufrière volcano
1456 m
Andosol
Nitisol
Luvisol
Ferralic Cambisol
Ferralsol
Vertic Cambisol
Town
Studied area
N
61° 40' W
0
5
10 km
Caribbean Sea
0
30 km
Désirade
Grande Terre
Basse Terre
Atlantic Ocean
Marie Galante
Saintes

Fig. 1.

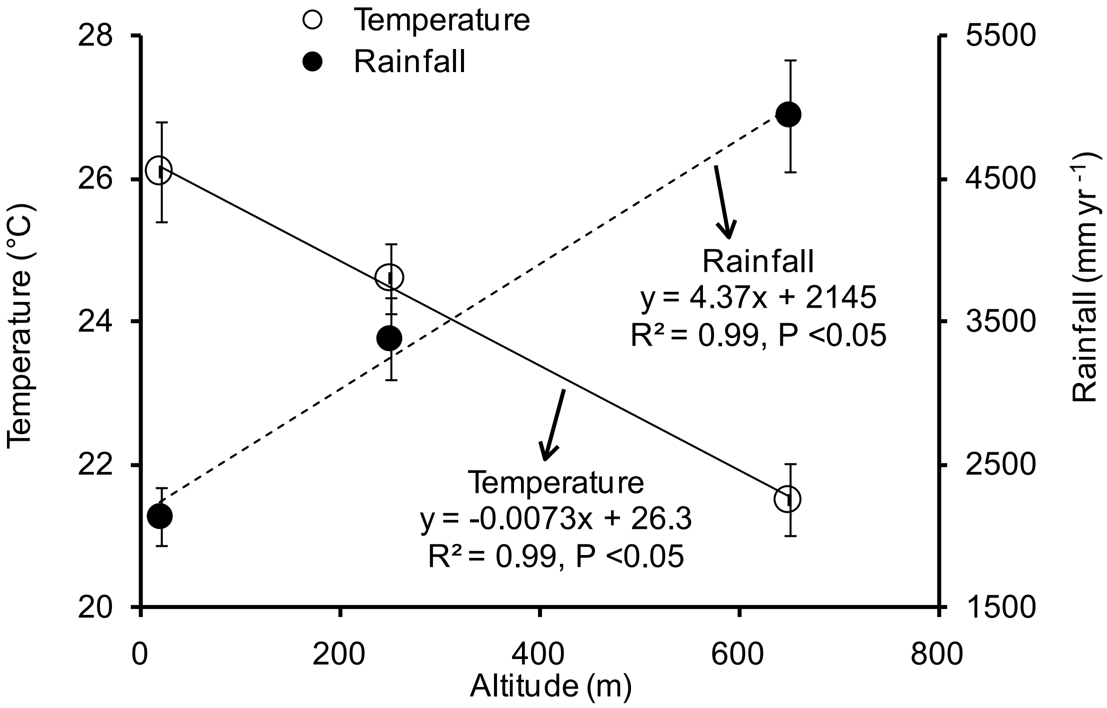

Temperature
Rainfall
28
26
24
22
20
5500
4500
3500
2500
1500
Temperature (°C)
Rainfall (mm yr⁻¹)
Rainfall
y = 4.37x + 2145
R² = 0.99, P <0.05
Temperature
y = -0.0073x + 26.3
R² = 0.99, P <0.05
0
200
400
600
800
Altitude (m)

Fig. 2.

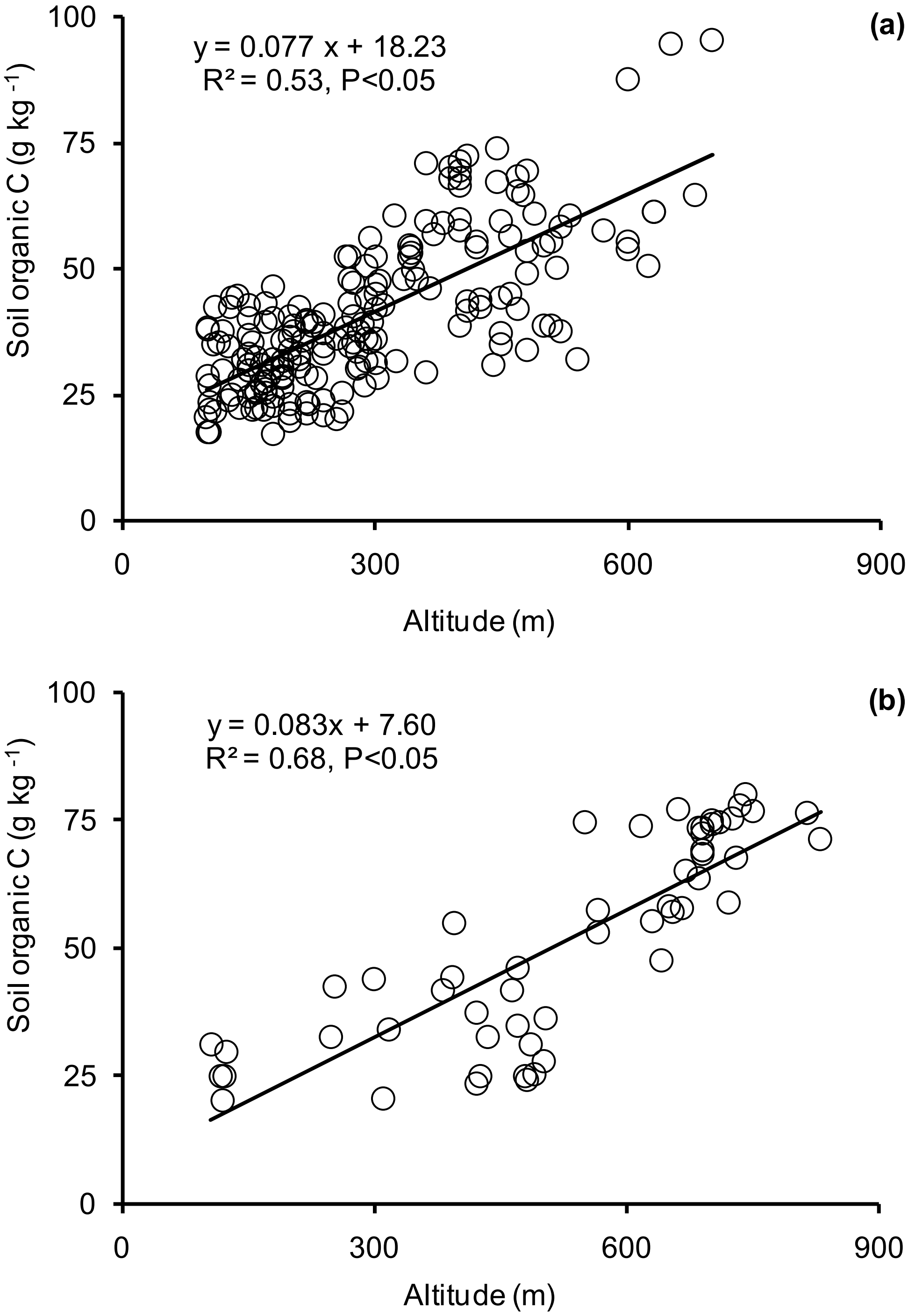

(a)
y = 0.077 x + 18.23
R² = 0.53, P<0.05
Soil organic C (g kg -1)
100
75
50
25
0
0
300
600
900
Altitude (m)
(b)
y = 0.083x + 7.60
R² = 0.68, P<0.05
Soil organic C (g kg -1)
100
75
50
25
0
0
300
600
900
Altitude (m)

Fig. 3.

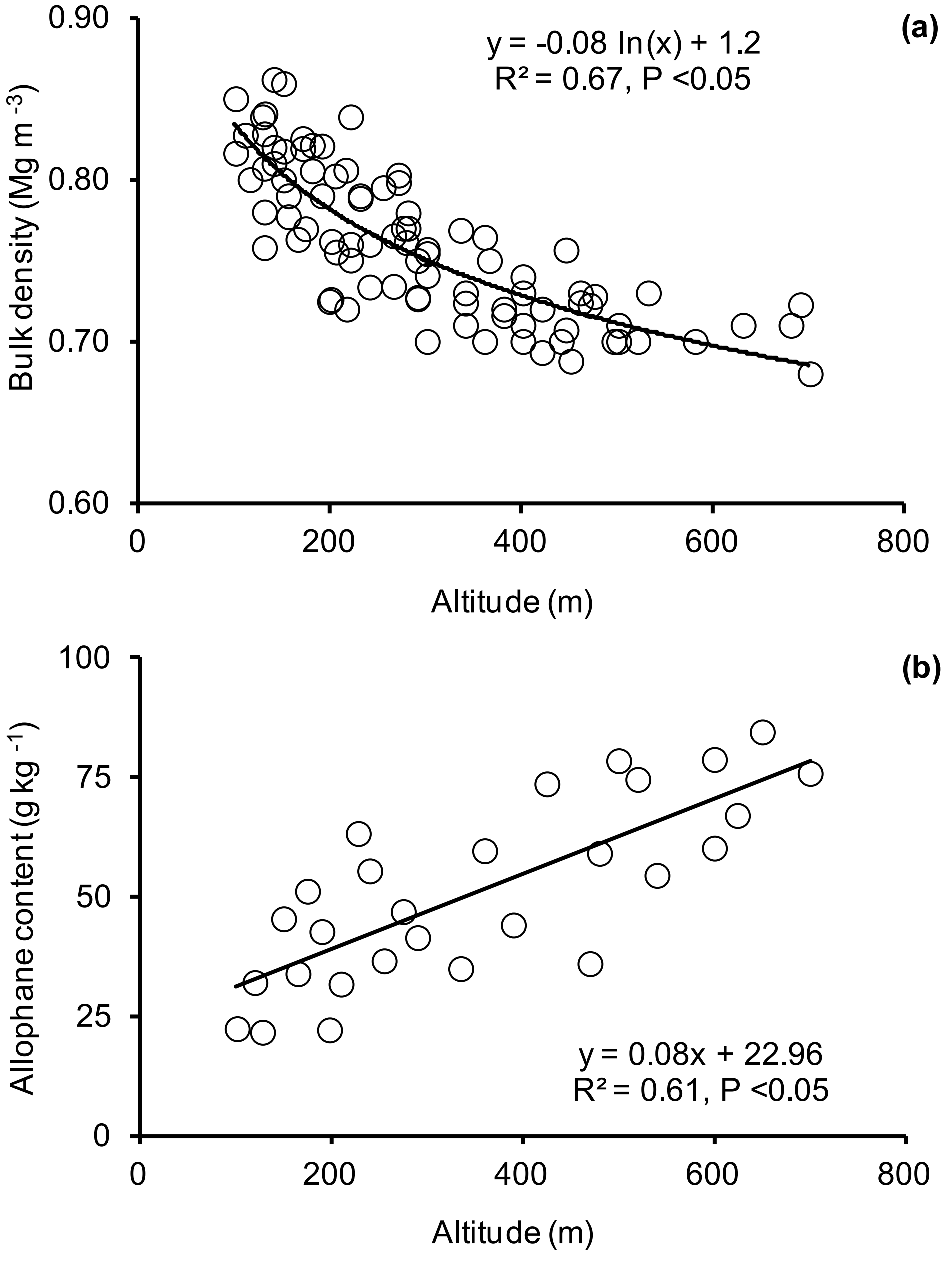
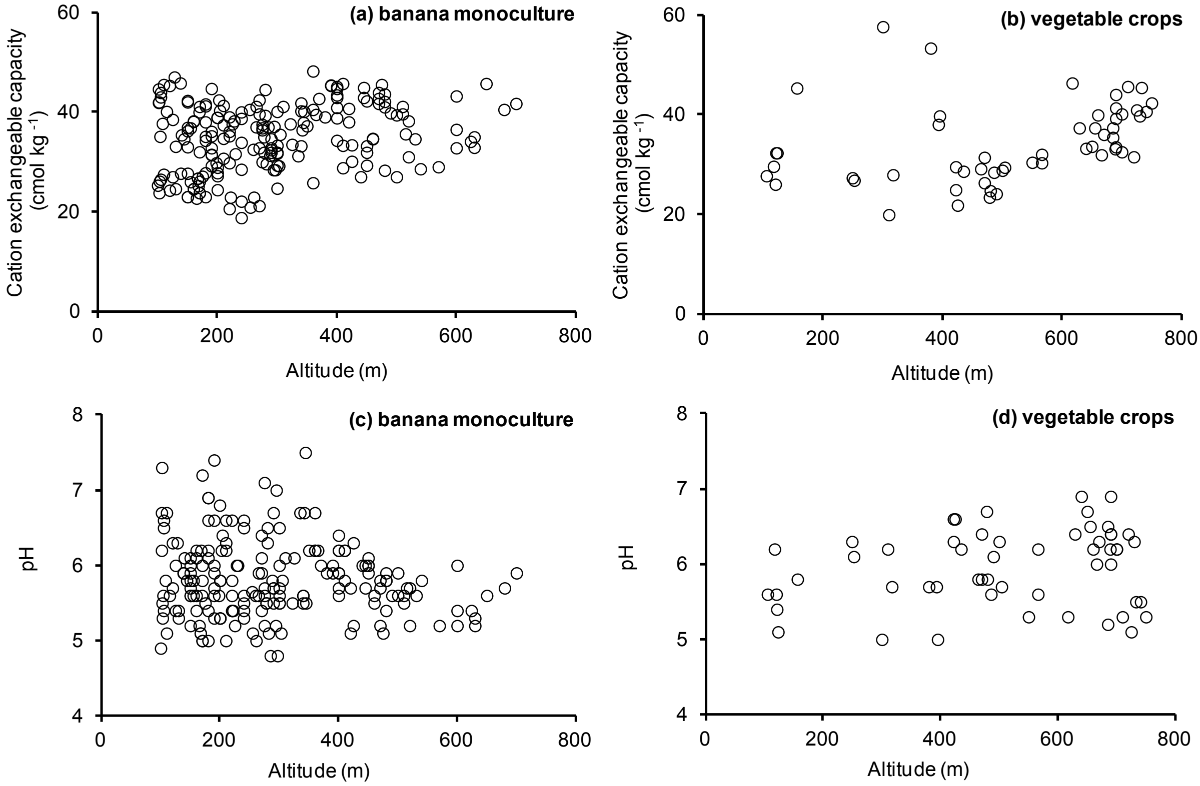
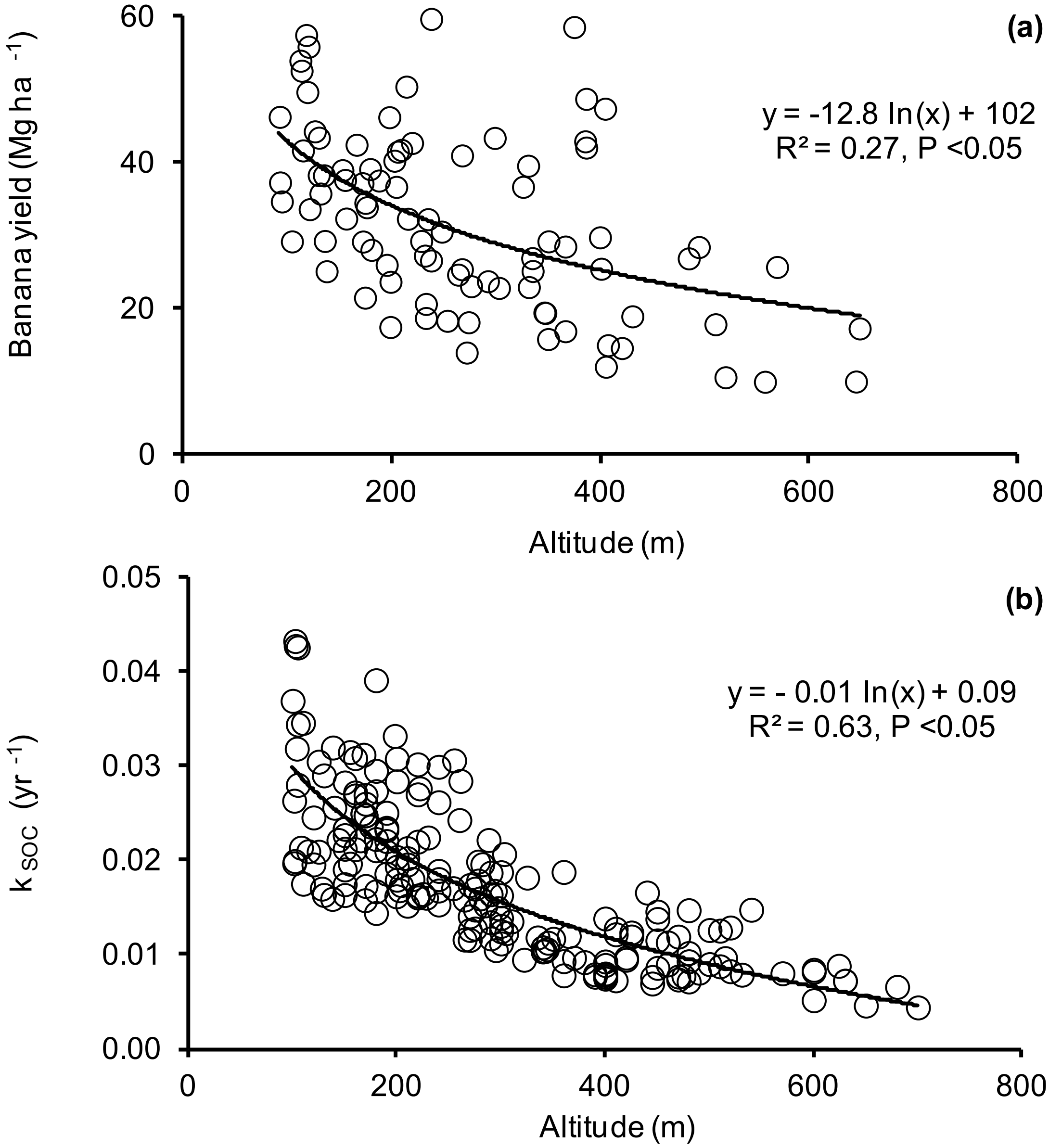

0.90
0.80
0.70
0.60
Bulk density (Mg m -3)
y = -0.08 ln(x) + 1.2
R² = 0.67, P <0.05
(a)
0
200
400
600
800
Altitude (m)
100
75
50
25
0
Allophane content (g kg -1)
(b)
y = 0.08x + 22.96
R² = 0.61, P <0.05
0
200
400
600
800
Altitude (m)

Fig. 4.



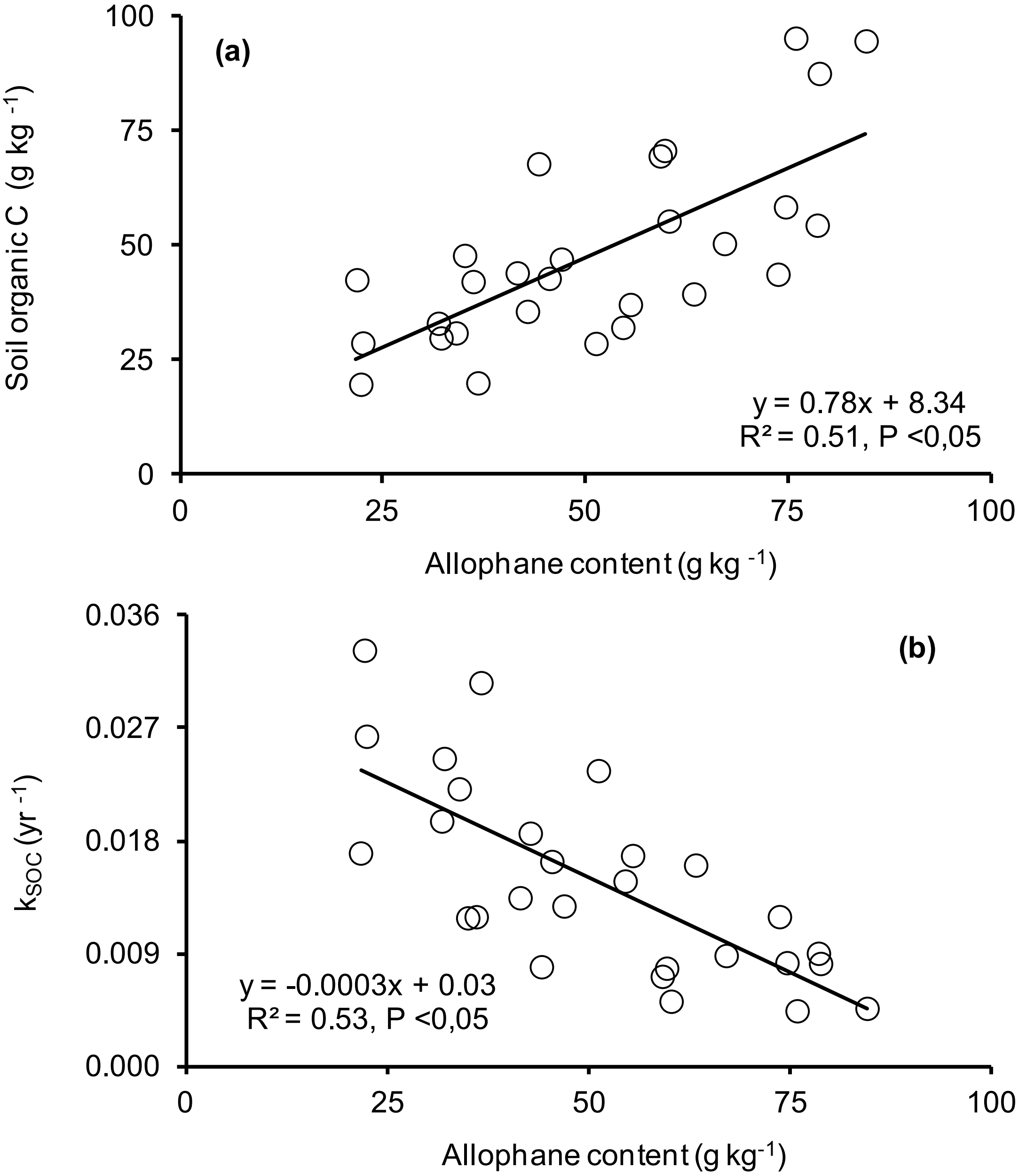
(a) banana monoculture
Cation exchangeable capacity (cmol kg-1)
0
20
40
60
0
200
400
600
800
Altitude (m)
(b) vegetable crops
Cation exchangeable capacity (cmol kg-1)
0
20
40
60
0
200
400
600
800
Altitude (m)
(c) banana monoculture
pH
4
5
6
7
8
0
200
400
600
800
Altitude (m)
(d) vegetable crops
pH
4
5
6
7
8
0
200
400
600
800
Altitude (m)

Fig. 5.



(a)
y = -12.8 ln(x) + 102
R² = 0.27, P <0.05
Banana yield (Mg ha -1)
60
40
20
0
0
200
400
600
800
Altitude (m)
(b)
y = - 0.01 ln(x) + 0.09
R² = 0.63, P <0.05
k SOC (yr -1)
0.05
0.04
0.03
0.02
0.01
0.00
0
200
400
600
800
Altitude (m)

Fig. 6.



(a)
Soil organic C (g kg -1)
100
75
50
25
0
0
25
50
75
100
Allophane content (g kg -1)
y = 0.78x + 8.34
R² = 0.51, P <0,05
(b)
kSOC (yr -1)
0.036
0.027
0.018
0.009
0.000
0
25
50
75
100
Allophane content (g kg-1)
y = -0.0003x + 0.03
R² = 0.53, P <0,05

Fig. 7.

Table 1

Mean values of the soil properties displaying no trend across the altitudinal gradient. CEC: cation exchangeable capacity. The values in brackets refer to the coefficient of variation expressed in %. For each property, mean values followed by different letters are significantly different at P <0.05.

Cropping system	pH	C/N	Extractable P	Exchangeable				CEC	Base saturation
				Ca	Mg	K	Na		
			mg kg^{-1}	cmol kg^{-1}					%
Banana monoculture	5.8 (9)a	9.7 (10)a	30 (128)a	7.2 (72)a	1.9 (46)a	1.9 (61)b	0.1 (8)a	35 (20)a	32 (51)a
Vegetable crops	6.0 (9)a	9.9 (9)a	51 (52)b	8.4 (52)a	1.8 (47)a	1.1 (78)a	0.1 (6)a	34 (23)a	35 (47)a