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1 **Changes in soil carbon inputs and outputs along a tropical altitudinal gradient of volcanic soils**
2 **under intensive agriculture**

3
4 Jorge Sierra*, François Causeret

5
6 ASTRO Agrosystèmes Tropicaux, INRA, 97170, Petit-Bourg, Guadeloupe, France.

7 * Corresponding author at: ASTRO Agrosystèmes Tropicaux, INRA, 97170, Petit-Bourg, Guadeloupe,
8 France.

9 E-mail address: jorge.sierra@inra.fr (J. Sierra).

10

11

12 **ABSTRACT**

13

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

37 soil biological properties contributed to the SOC and k_{SOC} gradients under the intensive cropping
38 systems analysed during this study. Overall, we conclude that SOC might be more vulnerable to soil
39 tillage and warming in low-altitude soils.

40

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

43

44

45 **1. Introduction**

46

47 Although volcanic soils account for less than 1% of Earth's land area, they store about 5% of
48 the global stock of soil organic carbon (SOC) (Dahlgren et al., 2004). These soils have peculiar physical
49 (e.g. very high water content at field capacity, high resilience to compaction and erosion), chemical
50 (e.g. high SOC and basic cations contents), and physico-chemical properties (e.g. high P fixation, high
51 anion exchange capacity), which are controlled by soil mineralogy, characterised by the presence of
52 amorphous minerals such as allophane (Clermont-Dauphin et al., 2004). These soils are mostly found
53 on the flanks of volcanic mountains and are occupied by forests and agricultural land, the latter
54 mainly in the inter-tropical zone where altitude moderates climate (Legros, 2012). Volcanic soils have
55 high agricultural productivity and are easy to work, but aluminium toxicity and P deficiency may
56 occur in those that are more acidic (Dahlgren et al., 2004). Because of the high SOC stocks in these
57 soils, conversion of the natural vegetation into farmland frequently induces SOC losses that can reach
58 2%-3% per year (e.g. Lemenih and Itanna, 2004; Sierra et al., 2015). However, some authors have
59 reported that the proper management of cropping systems, including diversified production and
60 reduced soil tillage, can be useful to preserving SOC stocks in volcanic soils (Segnini et al., 2011;
61 Sierra et al., 2017). This is of crucial concern in tropical mountain systems where warming is likely to
62 be particularly marked during coming decades and could contribute to increasing SOC losses
63 (Nottingham et al., 2016).

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

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

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

96 The flanks of volcanic islands in tropical regions where the elevation gradient of climate is
97 one of the strongest in the world present a wide range of soil types, with andosols on the summit
98 and ferralsols, luvisols and nitisols on the footslopes (Legros, 2012). These regions therefore
99 represent an interesting edaphic and climatic setting to determine the effects of the factors
100 impacting SOC stocks. In this study we examine the changes of SOC stocks in an altitudinal gradient
101 of a tropical volcanic island where the land is subject to two intensive agricultural systems (banana
102 monoculture and vegetable crops), which are characterised by the heavy use of fertilisers and
103 pesticides. We hypothesise that in these systems SOC is mainly controlled by soil mineralogy, climatic
104 factors and soil tillage. We consider that the effects of other factors such as soil nutrient content and
105 soil biological properties are of minor importance in our intensive agricultural systems. The aim of
106 this study was therefore to assess the underlying mechanisms controlling SOC by focusing on the
107 effect of the gradients of soil mineralogy (e.g. allophanic mineral content), climate (e.g. temperature
108 and rainfall), and the intensity of soil tillage (low under banana, high under vegetable crops). The

109 banana cropping systems are characterised by a temporal steady-state of SOC stocks and the
110 vegetable crop systems present high annual SOC losses (Sierra et al., 2015). To reduce the impact of
111 confounding effects caused by factors that co-vary with altitude, we used a process-based approach
112 to estimate C outputs and C inputs and to assess their effects on the SOC balance along the elevation
113 gradient. The study was carried out in Guadeloupe (French West Indies), which exhibits within a
114 small area nearly every physical landscape and cropping system found in the Caribbean region. This
115 study formed part of a larger project devoted to quantifying the impact of cropping systems, the
116 pedoclimate and warming on SOC stocks, using Guadeloupe as a case study of the Caribbean (Sierra
117 et al., 2017).

118
119

120 **2. Materials and methods**

121

122 *2.1. Study location, soils and climate*

123

124 The study was carried out in the uplands of south Basse-Terre, the main island of the
125 Guadeloupe archipelago located in the eastern Caribbean (16° 05' N, 61° 40' W) (Fig. 1). Basse-Terre
126 Island is dominated by a mountain chain oriented northwest to southeast where the crest standing at
127 1456 m.a.s.l. (La Soufrière volcano). Although the land west of the crest slopes steeply toward the
128 Caribbean Sea (slopes of 20-30%), the eastern side of the chain slopes more gently toward the
129 Atlantic Ocean (slopes of 10%). On both slopes, deep valleys trending at right angles to the mountain
130 chain are separated by sharp ridges. During the present study we focused on the land areas
131 dominated by andosols (FAO classification) (Fig. 1), which had developed on volcanic ash deposited
132 directly by successive volcanic eruptions throughout the Late Glacial and Holocene (Legros, 2012).
133 Because of the increase in the allophanic clay content with altitude, the hydrated microporous
134 structure of the soil, responsible for its high water content at field capacity, progressively expands
135 with increasing altitude, whereas bulk density decreases (Colmet-Daage and Lagache, 1965). The
136 zone of transition between the upland andosols and rich halloysite nitosols of the lowlands is placed
137 between 100 m and 200 m on the eastern slopes, and between 200 m and 300 m on the western
138 slopes (Fig. 1). In the studied area, the mean air temperature drops by 0.7°C and annual rainfall
139 increases by 437 mm yr⁻¹ per every 100 m (Fig. 2). The level of rainfall is lower from December to
140 May, which is slightly more pronounced in the lowlands (38% of the annual rainfall takes place in this
141 6-month period; an average of 170 mm per month) than in the uplands (45% of the annual rainfall;
142 an average of 380 mm per month).

143

144 *2.2. Land use and farming practices*

145

146 The agricultural land in the studied area is oriented toward the production of bananas for the
147 European market and vegetable crops for the local market (Sierra et al., 2015). Farms devoted to
148 banana production are situated from 100 m to 700 m and average 10 ha, while those focused on
149 vegetable crops are located from 100 m to 900 m and average 4 ha. The land above an altitude of
150 900 m is occupied by tropical rainforest; this is a protected area where agriculture and deforestation
151 have been banned. Only the agricultural land was included in the present study (Fig. 1). Sierra et al.
152 (2015) had previously reported that the SOC stored under banana cropping systems in this region is
153 likely to be close to, or at, a steady-state when crop residues are the only C input to the soil (i.e.
154 when no organic amendments are applied). By contrast, SOC stocks decrease by $2.0 \pm 1.1 \text{ Mg C ha}^{-1}$
155 yr^{-1} in soils cultivated with vegetable crops (Sierra et al., 2017).

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

166 The principal vegetable crops in the studied area are tomato, cabbage, salad, eggplant and
167 pepper. They are cultivated under monoculture systems; some farmers apply one year of fallow after
168 5-6 years of cultivation. Soil tillage is highly intensive with at least six tillage operations per year.
169 Harvesting is manual and the residues (leaves and stems) are placed on the soil or buried at a depth
170 of 0.1-0.2 m.

171 Most banana and vegetable crop systems are based on the heavy use of synthetic fertilisers
172 and pesticides. For example, N fertilisers are applied at a rate of $400\text{-}600 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in banana and
173 $150\text{-}200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in vegetable crops. For K, the rates are $120 \text{ kg K ha}^{-1} \text{ yr}^{-1}$ for banana and 80 kg K
174 $\text{ha}^{-1} \text{ yr}^{-1}$ for vegetables. For P, the rates are $50 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ for banana and $80 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ for
175 vegetables. For banana, P and K fertilisers are applied after harvest of the mother plant, and N
176 fertiliser is split into 8-12 applications along the growth cycle. For vegetables, all the fertilisers are
177 applied at planting. No irrigation is applied in these cropping systems. In fact, the water requirement
178 for banana crops in the studied area is 120-150 mm per month (Lassoudière, 2007), which is fully
179 supplied by rainfall even during the drier season in the lowlands. About 50% of the plots under

180 banana and vegetable crop systems are limed every 5-10 years to raise soil pH and to reduce the
181 impact of aluminium toxicity on plant growth on the more acidic soils.

182

183 2.3. Soil and plant data

184

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

$$198 \text{ Allophane} = \text{Si}_o / 0.14 \quad (1)$$

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

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

215

216 2.4. Analytical approach

217

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

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

$$240 \quad dSOC_{stock} / dt = 0 = (C_{res} \times h_{res}) - (SOC_{stock} \times k_{SOC}) \quad (2)$$

241 and then:

$$242 \quad k_{SOC} = (C_{res} \times h_{res}) / SOC_{stock} \quad (3)$$

243 where SOC_{stock} ($Mg \text{ C ha}^{-1}$) is the SOC stock and $dSOC_{stock} / dt$ is the annual change in SOC stock ($Mg \text{ C}$
 244 $\text{ha}^{-1} \text{ yr}^{-1}$), C_{res} ($Mg \text{ C ha}^{-1} \text{ yr}^{-1}$) is the annual C input from crop residues (aboveground and roots), h_{res}
 245 (unitless) is the humification coefficient of crop residues, and k_{SOC} (yr^{-1}) is the rate constant of
 246 mineralisation of SOC_{stock} .

247 The characteristics of crop residues analysed in this study and the equations used to calculate
 248 SOC_{stock} , C input from crop residues and the temperature sensitivity of k_{SOC} (the Q_{10} coefficient) are

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

258

259

260 3. Results

261

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

264 Only 15% of the selected banana plots were managed as perennial systems. These plots were
265 present from an altitude of about 300 m, and their SOC stocks were similar to those observed for the
266 plots managed as pluriannual systems located at the same altitude (Fig. A.1). In this way, all the
267 banana plots could be analysed as a single population regardless of their management. The SOC
268 content increased with altitude under both banana monoculture and vegetable crop systems (Fig. 3).
269 The intercept and the slope of the linear regression fitted to SOC data differed significantly between
270 the two cropping systems ($P < 0.05$); e.g. the intercept was higher and the slope was lower for the
271 banana monoculture. At an altitude of 100 m, the estimated SOC content was about 35 g C kg^{-1} under
272 banana monoculture and 25 g C kg^{-1} under vegetable crops; these values were respectively 75 g C kg^{-1}
273 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
274 to about 0.67 Mg m^{-3} at 700 m (Fig. 4a). Allophane content increased with altitude from about 25 g
275 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
276 selected plot and the soil bulk density data obtained using the equation shown in Fig. 4a. The SOC
277 stocks displayed the same trend as that observed for SOC content (Fig. A.2). The differences between
278 cropping systems in terms of SOC stocks, in absolute and in relative terms, were higher at low
279 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
280 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
281 vegetable crops; i.e. 9% higher for banana).

282 For both banana and vegetable crop systems, no changes with altitude were observed for
283 cation exchangeable capacity (Figs. 5a and 5b) and soil pH (Figs. 5c and 5d). The same was observed
284 for the C/N ratio (Fig. A.3), cations and base saturation (Fig. A.4), and extractable P (Fig. A.5). The

285 average values of these soil properties are presented in Table 1. No differences were observed
 286 between the two cropping systems except for extractable P (higher under vegetable crops) and
 287 exchangeable K (higher under banana) ($P < 0.05$) (Table 1).

288 As the C/N ratio did not display any trend with altitude, the altitudinal gradient of organic N
 289 was very similar to that presented in Fig. 3 for SOC (Fig. A.6). Under banana monoculture, organic N
 290 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
 291 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
 292 700 m (10.9 Mg N ha⁻¹).

293 Banana yields decreased with altitude from about 45 Mg ha⁻¹ at 100 m to 20 Mg ha⁻¹ at 700
 294 m (Fig. 6a). Yields displayed a relatively high variability throughout the altitudinal gradient. Using
 295 these yield values, banana residues estimated from Eqs. (A.2) and (A.3) decreased from 15 Mg ha⁻¹ at
 296 100 m to 7 Mg ha⁻¹ at 700 m. Therefore, the input of humified C derived from banana residues ($C_{res} \times$
 297 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).

298 The in situ k_{SOC} estimated from Eq. (3) for the selected plots of banana monoculture are
 299 presented in Fig. 6b. k_{SOC} decreased 6.7-fold between 100 m (3.0×10^{-2} yr⁻¹) and 700 m of altitude
 300 (4.4×10^{-3} yr⁻¹). With such a steep change, the Q_{10} temperature coefficient estimated from Eq. (A.5)
 301 was as great as 31, which is highly unrealistic, as will be discussed in section 4.2.2. For the 28 banana
 302 plots used to determine allophane content, SOC content correlated positively and k_{SOC} correlated
 303 negatively with allophane content ($P < 0.05$) (Fig. 7).

304

305

306 4. Discussion

307

308 4.1. Relative impact of C inputs and outputs on the SOC balance under banana monoculture

309

310 Our results confirmed that tropical volcanic soils under agriculture can store amounts of
 311 organic matter equivalent to those observed in natural forest systems. For example, the SOC stocks
 312 observed under banana monoculture were similar to those reported by Powers and Schlesinger
 313 (2002) for a tropical rainforest in Costa Rica on volcanic soils, with comparable altitudinal gradient
 314 (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
 315 ranging from 25°C to 20°C and rainfall ranging from 3500 mm yr⁻¹ to 4700 mm yr⁻¹). In addition, the
 316 rise in SOC levels with altitude in our study tended to be linear as had previously been found by other
 317 authors in natural ecosystems (e.g. Zimmermann et al., 2009; Dieleman et al., 2013). However, it is
 318 likely that altitude did not exert a direct impact on the SOC gradient, but an indirect effect involving
 319 soil (e.g. mineralogy), climatic (e.g. temperature and rainfall) and vegetation factors (e.g. amount of
 320 crop residues) that varied across the elevation gradient. Because SOC stocks result from a balance of

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

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

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

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

353

354 *4.2. Factors affecting the altitudinal gradient of k_{SOC}*

355

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

362

363 4.2.1. Soil mineralogy and rainfall

364

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

378 Several authors reported that SOC content was positively correlated with allophane content
379 in elevation gradients of volcanic soils (e.g. Powers and Schlesinger, 2002; Matus et al., 2008), and
380 the same was observed in the present study (Fig. 7a). Moreover, the range of values of allophane
381 content observed in this study was similar to that reported by Matus et al. (2008) and Garrido and
382 Matus (2012) for volcanic soils in Chile. Buurman et al. (2007) proposed that high rainfall in the
383 uplands favours the presence of anoxic conditions inside the micropores of the allophanic gels,
384 reducing SOC decay and inducing the increase in SOC content with altitude. On the other hand,
385 Garrido and Matus (2012) proposed that SOC stabilisation in andosols is associated with the low
386 physical accessibility for microbial decomposers of SOC inside the micropores of allophanic clay
387 minerals. Although the mechanisms of SOC stabilisation in andosols are not fully elucidated at this
388 time (Filimonova et al., 2016), it appears that this stabilisation would be the major responsible for
389 the increase in the mean residence time and the content of SOC with altitude in elevation gradients
390 of volcanic soils (Kramer and Chadwick, 2016). We hypothesise that the steep drop observed in k_{SOC}
391 along the altitudinal gradient reflected the increase in the mean residence time of SOC. This

392 hypothesis is supported by the negative correlation observed between k_{SOC} and allophane content,
393 which indicated that allophane content explained about 53% of the variability of k_{SOC} . (Fig. 7b). Since
394 SOC is more protected against microbial degradation within allophanic materials than on the surfaces
395 of secondary minerals, k_{SOC} decreases and SOC stocks increase with altitude.

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

406

407 4.2.2. Temperature

408

409 The decrease of temperature with altitude is frequently cited as the main factor inducing an
410 increase in SOC content in elevation gradients under natural forest systems. For example, Luo et al.
411 (2014) found that in situ soil respiration decreased by 35% in the altitudinal gradient of a subalpine
412 secondary forest in China, which was attributed to a drop in soil temperature from 11°C to 8°C along
413 the elevation gradient. Using Eqs. (A.4) and (A.5), we calculated that the Q_{10} coefficient of soil
414 respiration corresponding to the results of Luo et al. (2014) would be 2.7, which is within the range of
415 values cited by several authors (e.g. Nottingham et al., 2015). In our study, k_{SOC} decayed 6.7-fold from
416 100 m to 700 m for a temperature gradient of only 4.4°C. Indeed, this sharp decay of k_{SOC} gave rise to
417 a highly unrealistic Q_{10} value (31). The kinetic theory on which the estimate of Q_{10} is based predicts a
418 value of around 2 for typical ambient temperatures of 0°C-20°C (Davidson and Janssens, 2006), which
419 increases for the low ranges of temperature and for organic compounds of greater chemical
420 complexity (Nottingham et al., 2015). For example, in laboratory studies carried out on soils collected
421 from altitudinal gradients, the Q_{10} of SOC mineralisation was about 1.5 in the Changbai Mountains of
422 China (Wang et al., 2016), and ranged from 2 to 3 in the Western Carpathians of Poland (Klimek et
423 al., 2016). Nottingham et al. (2015) pointed out that the higher Q_{10} values frequently observed in situ
424 experiments (e.g. up to 7 in their study), when compared with the lower values obtained from
425 laboratory studies, might be associated with complex interactions between factors varying
426 simultaneously with elevation. We think this was also the case in our study, where the unrealistic Q_{10}
427 might have been an artefact induced by other factors changing with altitude such as soil mineralogy.

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

433

434 4.2.3. Soil nutrient content and C/N ratio

435

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

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

460

461 4.2.4. Microbial biomass and detritivore mesofauna

462

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

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

485

486 *4.3. Differences in SOC stocks between banana and vegetable cropping systems*

487

488 Several authors reported that SOC stocks decreased dramatically following the conversion of
489 natural vegetation into arable land in elevation gradients (e.g. Lemenih and Itanna, 2004; Pabst et al.,
490 2013). In our long-term agricultural systems, where deforestation had not been applied during the
491 past five decades, SOC stocks were lower under vegetable crop systems than under banana
492 monoculture throughout the elevation gradient. This could be due to two factors: a lower C input
493 because of smaller quantities of crop residues from vegetable crops, and a higher C output because
494 of the more intensive soil tillage applied in these systems. Crop residues from vegetable crops vary
495 from 10.3 Mg dry matter $\text{ha}^{-1} \text{yr}^{-1}$ for eggplant to 2.2 Mg $\text{ha}^{-1} \text{yr}^{-1}$ for salad (Table A.1). The coefficient
496 of humification for vegetable crop residues averaged 0.34, which is close to that of banana residues
497 (i.e. 0.31; Table A.1), which suggests that residue humification was of minor importance when trying
498 to explain the differences between the two cropping systems. By considering the mean quantity of

499 residues from vegetable crops (i.e. $6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and the mean humification coefficient (Table A.1),
500 the mean input of humified C derived from vegetable crop residues would be about $0.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$
501 ¹, which is 45% lower than that observed for banana monoculture at 100 m (i.e. $1.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$)
502 and 30% higher than that observed at 700 m (i.e. $0.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Although in Guadeloupe there
503 are not data on the changes of vegetable crop yields and their crop residues with altitude, it seems
504 that on average the C input from crop residues was probably lower under vegetable crops than under
505 banana monoculture, which may partially explain their lower SOC stocks. Concerning C outputs,
506 Sierra et al. (2015) found that SOC mineralisation in the region studied during this work was about
507 110% higher in soils under vegetable crops compared to those under banana monoculture, linked to
508 differences between the systems in terms of the intensity of soil tillage. It therefore seems that
509 differences between the two cropping systems in C outputs were much higher than their differences
510 in C inputs. We concluded that differences in SOC stocks between the two cropping systems along
511 the elevation gradient were mainly associated with C outputs and secondarily with C inputs.
512 Although differences between the two systems regarding extractable P (higher under vegetable
513 crops) and exchangeable K (higher under banana) contents reflected the specific fertiliser practices of
514 each cropping system, the level of most soil properties was similar in both cropping systems (Table
515 1). We therefore consider that these properties were of minor importance to explain the differences
516 in SOC stocks between vegetable and banana cropping systems.

517 A more interesting finding from this study was that the differences in SOC stocks between
518 the two cropping systems decreased with altitude. This was consistent with the hypothesis that
519 changes in soil mineralogy played a major role in SOC protection and decomposition. Thus SOC
520 occluded within allophanic minerals at high altitude would be less responsive to differences in soil
521 tillage between the cropping systems, and its vulnerability would increase in line with the reduction
522 of allophane content at lower altitudes. This is consistent with the kinetic theory of SOC
523 decomposition (Nottingham et al., 2016), and agrees with the results reported by Nottingham et al.
524 (2015) concerning the greater sensitivity of unprotected SOC to environmental changes along an
525 elevation gradient in the Peruvian Andes.

526 The results of this study may provide some insights concerning the impact of climate
527 warming on SOC stocks in our tropical altitudinal gradient. Climate models predict that the mean
528 temperature in the Guadeloupe archipelago will rise 0.7°C in the next three decades (Sierra et al.,
529 2010). Assuming a Q_{10} value of 2 for SOC mineralisation, this rise in temperature would induce a 5%
530 increase in the current k_{SOC} values. The increase would be 8% for a Q_{10} of 3. Even though warming
531 and Q_{10} may vary along the altitudinal gradient, it appears that the magnitude of the change in k_{SOC}
532 due to warming might be much smaller than that observed for k_{SOC} between the lowlands and
533 uplands in this study (i.e. 570%). It follows that SOC decomposition and C emissions will continue to
534 be higher in lowlands under a climate warming scenario, mainly under vegetable cropping systems.

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

537

538

539 **5. Conclusions**

540

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

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

564

565

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567

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577

578

579 **Appendix A. Supplementary Information**

580

581 Supplementary information linked to this article can be found at:

582

583

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- 696
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- 698

699 **Figure captions**

700

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

704

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

707

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

710

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

712

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

715

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

718

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

721

722

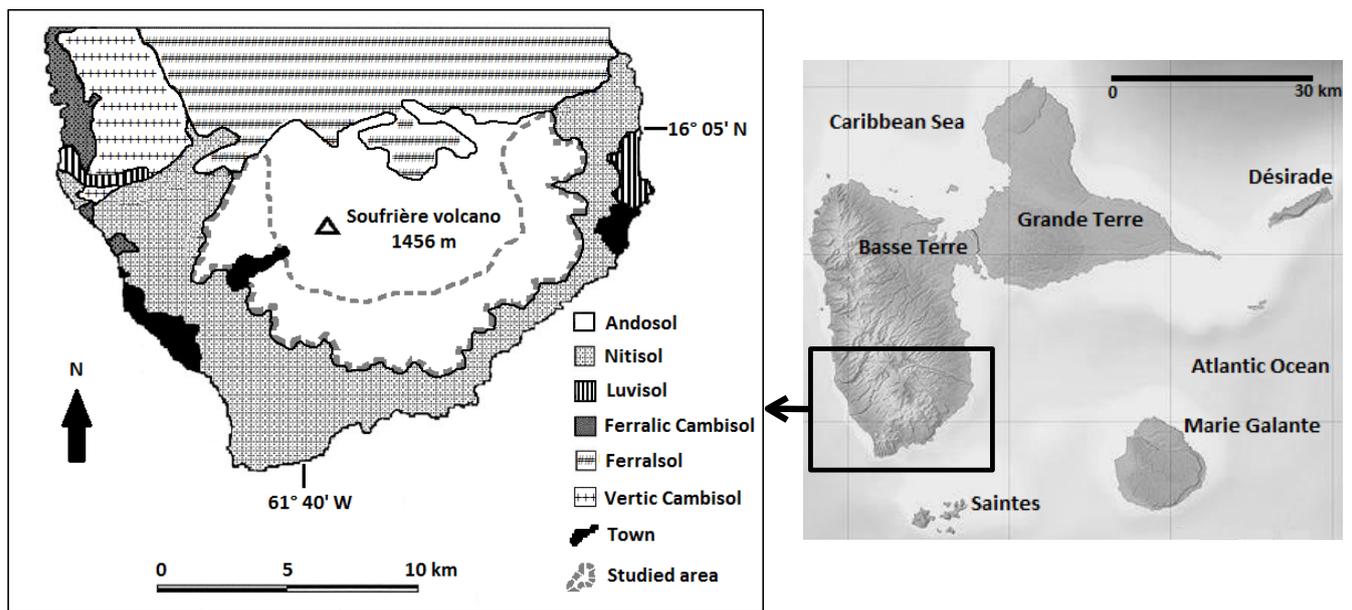


Fig. 1.

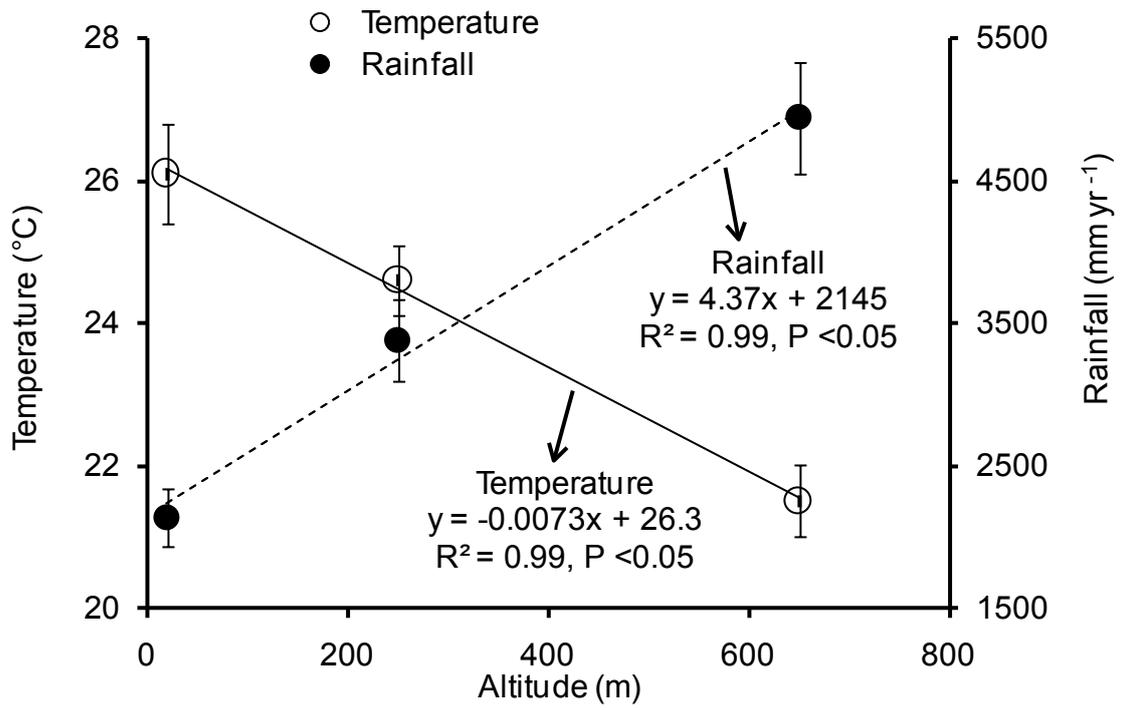


Fig. 2.

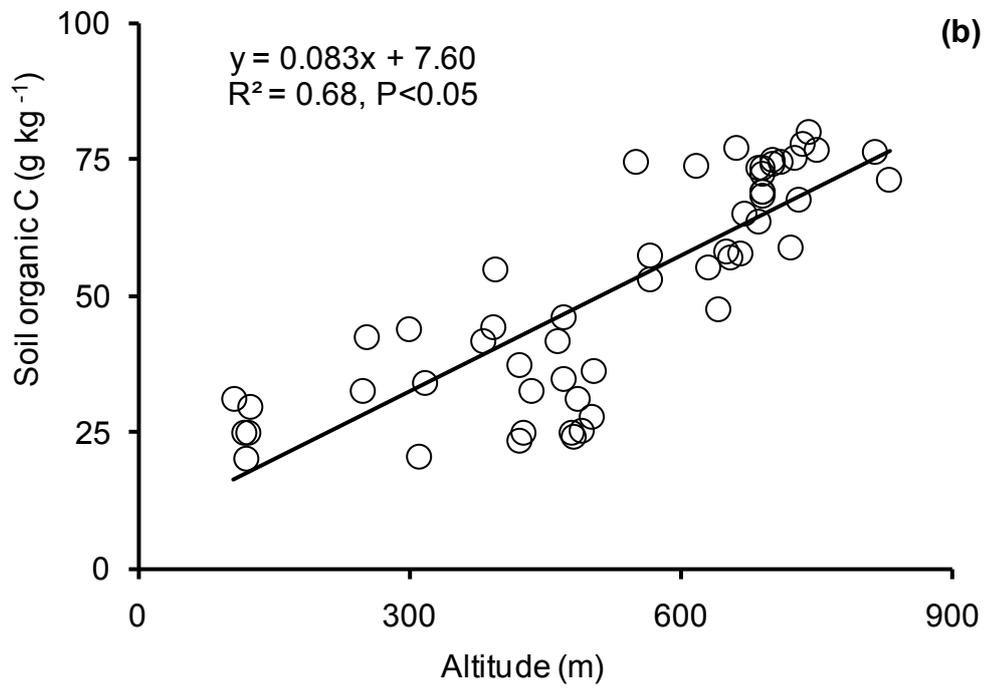
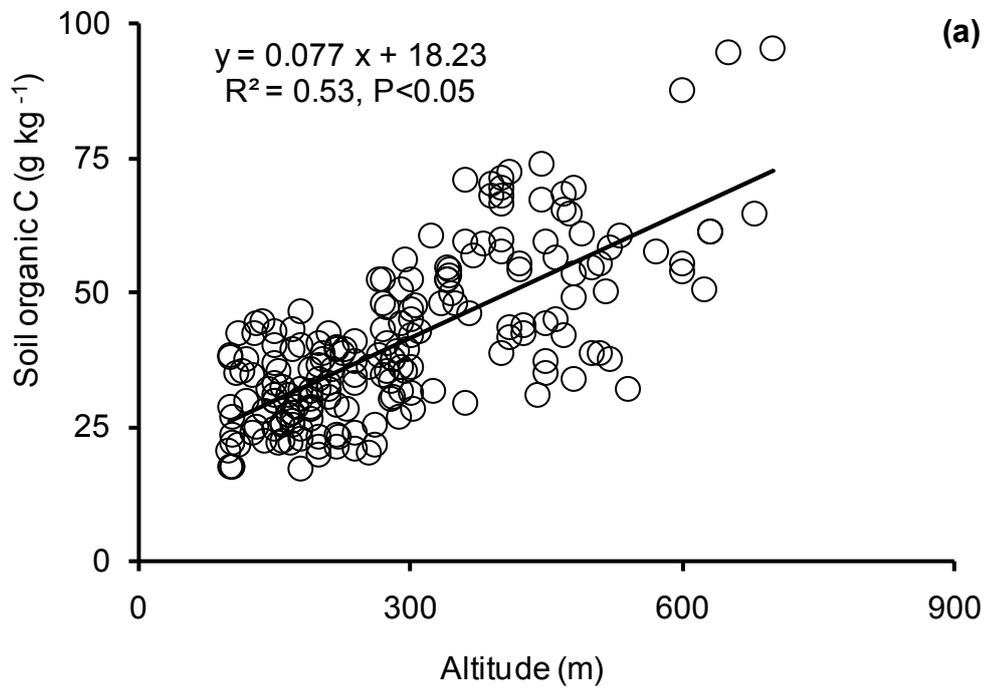


Fig. 3.

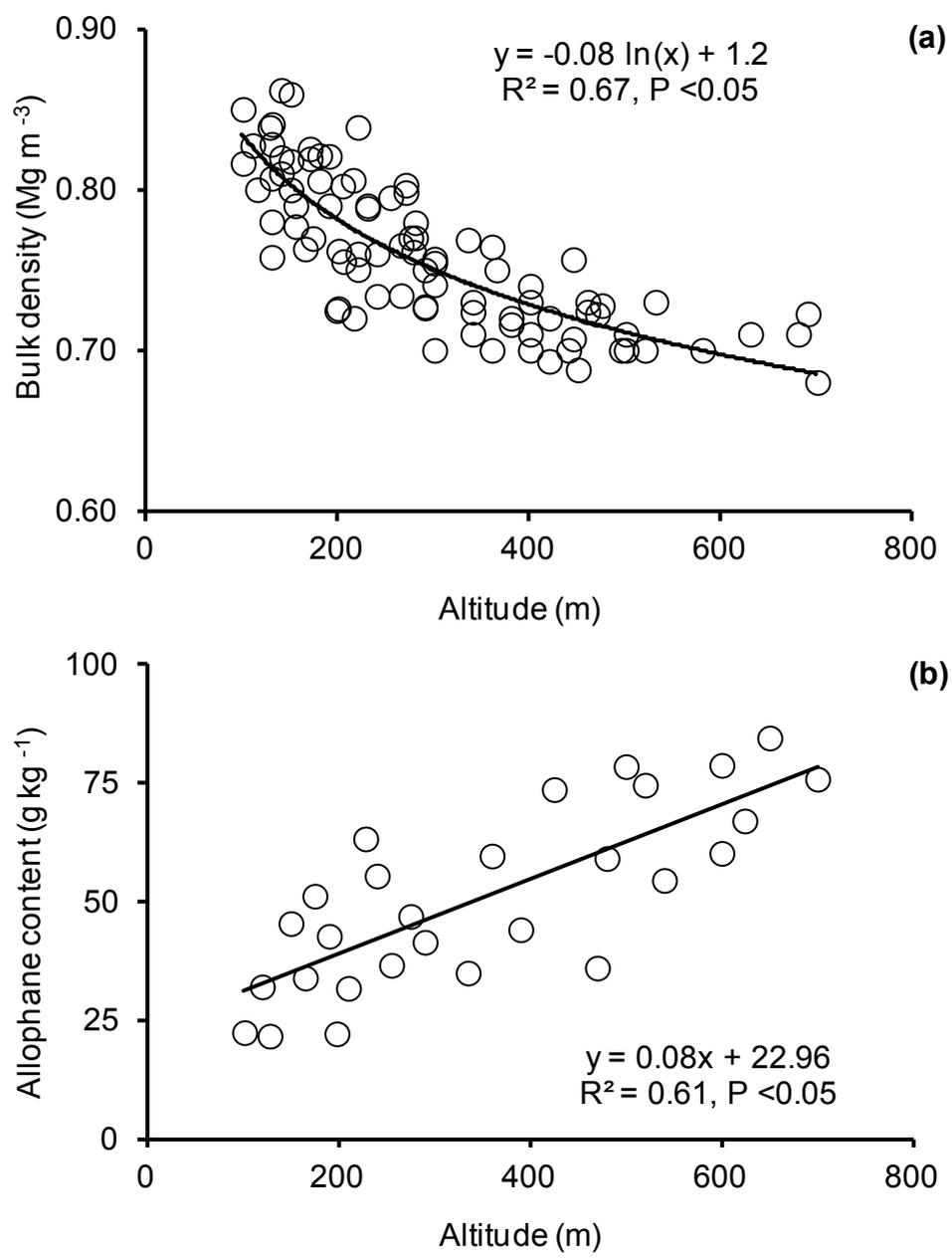


Fig. 4.

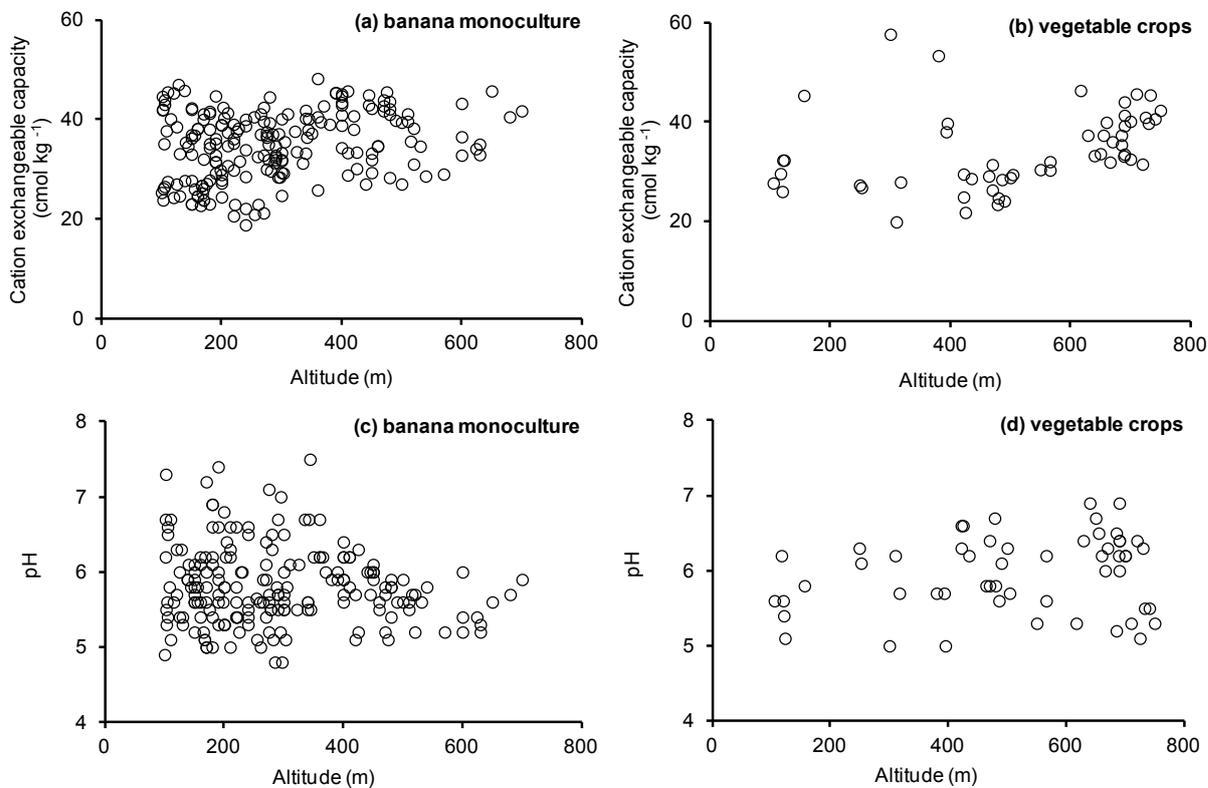


Fig. 5.

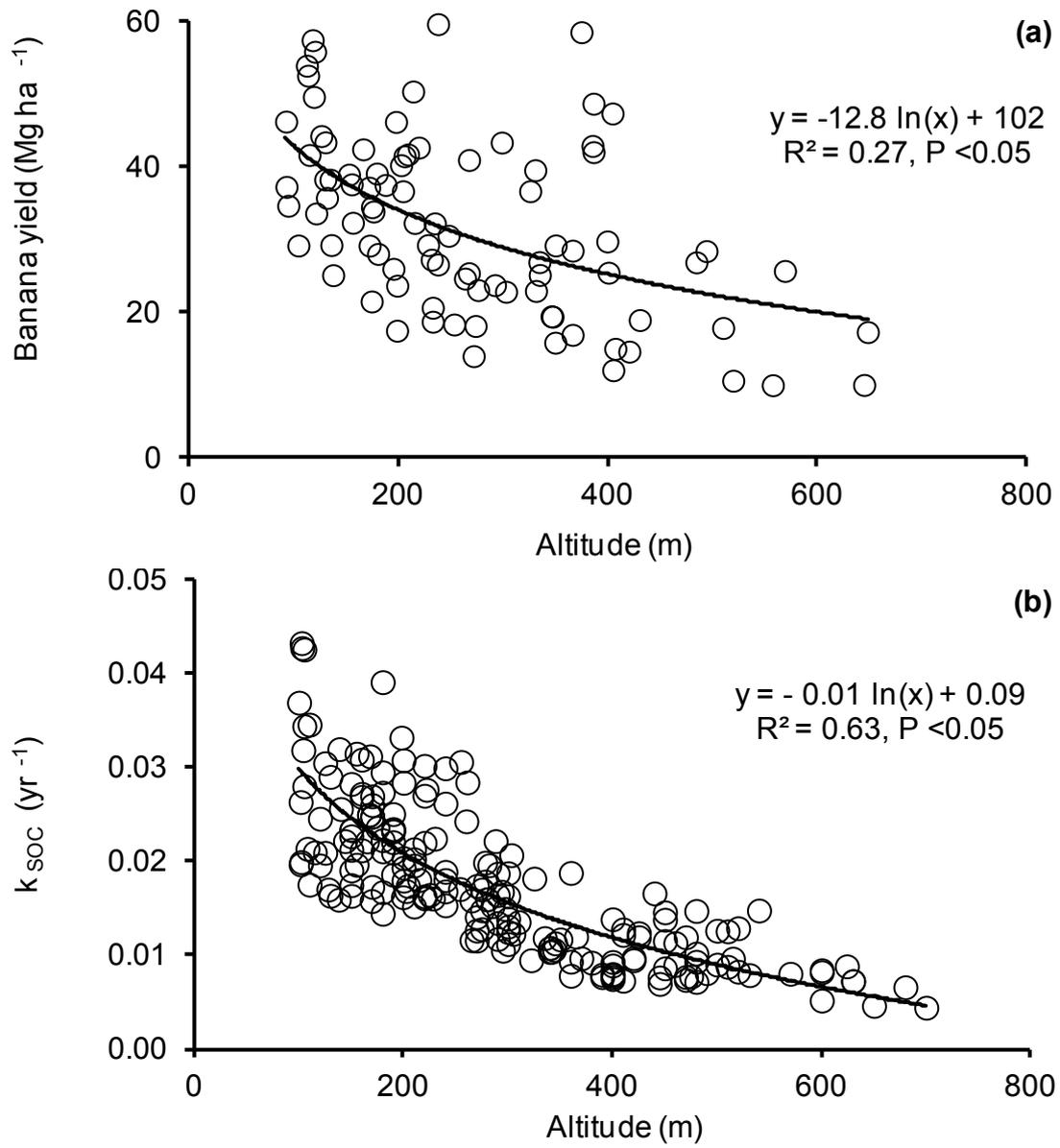


Fig. 6.

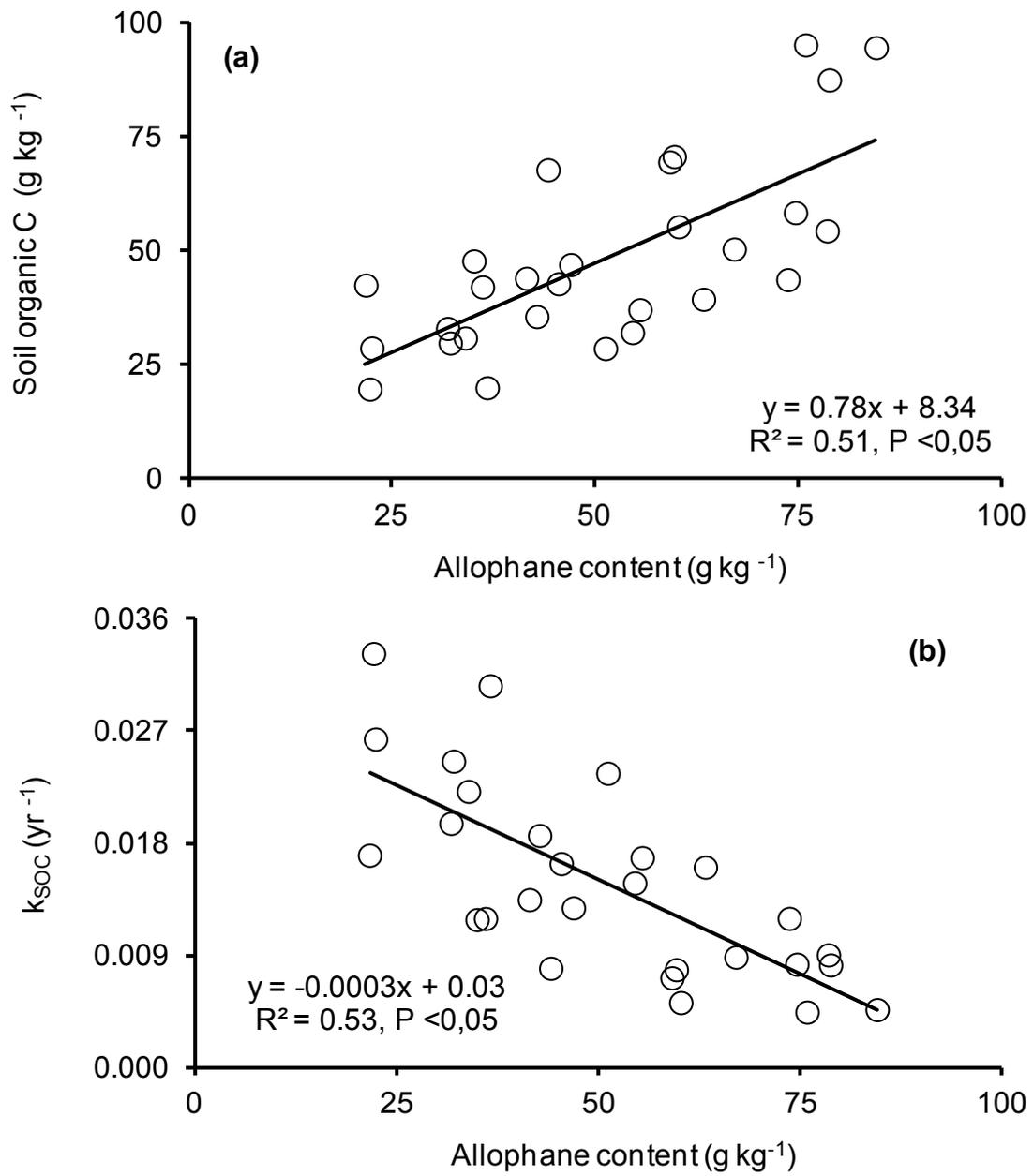


Fig. 7.

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 mg kg ⁻¹	Exchangeable				CEC	Base saturation %
				Ca	Mg	K	Na		
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