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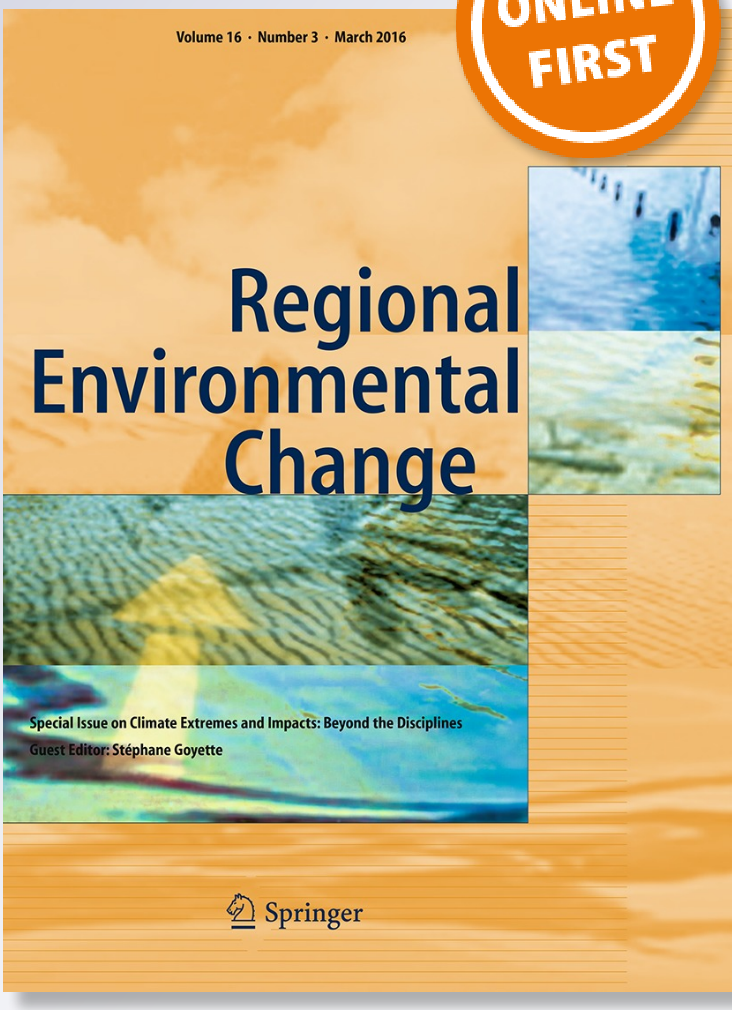

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ORIGINAL ARTICLE

Soil carbon stocks after conversion of Amazonian tropical forest to grazed pasture: importance of deep soil layers

Clément Stahl[1,2] · Vincent Freycon[3] · Sébastien Fontaine[4] · Camille Dezécache[1,5] · Lise Ponchant[1,5] · Catherine Picon-Cochard[4] · Katja Klumpp[4] · Jean-François Soussana[4] · Vincent Blanfort[1,5]

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Abstract Recent studies suggest that carbon (C) is stored in the topsoil of pastures established after deforestation. However, little is known about the long-term capacity of tropical pastures to sequester C in different soil layers after deforestation. Deep soil layers are generally not taken into consideration or are underestimated when C storage is calculated. Here we show that in French Guiana, the C stored in the deep soil layers contributes significantly to C stocks down to a depth of 100 cm and that C is sequestered in recalcitrant soil organic matter in the soil below a depth of 20 cm. The contribution of the 50–100 cm soil layer increased from 22 to 31 % with the age of the pasture. We show that long-term C sequestration in C4 tropical pastures is linked to the development of C3 species (legumes and shrubs), which increase both inputs of N into the ecosystem and the C:N ratio of soil organic matter. The deep soil under old pastures contained more C3 carbon than the native forest. If C sequestration in the deep soil is taken into account, our results suggest that the soil C stock in pastures in Amazonia would be higher with sustainable pasture management, in particular by promoting the development of legumes already in place and by introducing new species.

Keywords C3 contribution · Deep soil C · Native forest · Old pasture · Mixed-grass pasture

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Introduction

Some authors have argued that the world's permanent pastures (30 % of total land) could offset up to 4 % of global GHG emissions, as they have a carbon (C) storage potential equal to 0.5 Mg C ha^{-1} year^{-1} (Lal 2004). According to this hypothesis, pastures are good candidates to increase soil C stock in the soil while simultaneously producing basic fodder for livestock. In parallel, interest in soil carbon stocks in tropical deforested areas has increased in recent decades. Two recent meta-analyses described different ways in which the soil stores C, mostly depending on land use, on land management (Don et al. 2011; Eclesia et al. 2012), and on the length of time since deforestation. In Amazonia, more than 15 % of the forest has been converted into pasture (46 M ha in Brazilian Amazonia, INPE 2010) and this land can play a major role in mitigating the effects of climate change by sequestering C in the soil.

Despite the extent of the areas concerned, little information is available on possible long-term carbon sequestration in pastures, or on their capacity to store C in the intermediate (20–50 cm) to deep soil (50–100 cm) layers. Recently, a meta-analysis by McSherry and Ritchie (2013) underlined the need for more studies on soil carbon stock in tropical grasslands. Such data are indispensable to determine the carbon cycle of the Amazon basin, and to adjust land-use management accordingly. Most existing studies have been limited to stocks of C in the topsoil (0–20 cm soil layer) and revealed different patterns (Smith 2014). Referring to the first two decades after conversion to pasture, most studies showed an increase in stocks of C in the topsoil (Bonde et al. 1992; Fisher et al. 1994; Trumbore et al. 1995; Moraes et al. 1996; Guo and Gifford 2002; Cerri et al. 2004; Desjardins et al. 2004; Powers and Veldkamp 2005; Don et al. 2011; Eclesia et al. 2012), while others, although far fewer, showed a decrease (Falesi 1976; Asner et al. 2004; Don et al. 2011) depending on the site concerned. Some of these differences could be due to the type of native vegetation, environmental conditions, and pasture management (Jobbagy and Jackson 2000; Cerri et al. 2004; Lopez-Ulloa et al. 2005; Laganière et al. 2010; McSherry and Ritchie 2013; Smith 2014). Smith (2014) emphasises that having a grassland does not inevitably result in a carbon sink and that judicious management of previously poorly managed grasslands can increase their sink capacity. Other authors reported that pasture management had no significant effect on soil organic carbon (SOC), but huge variability was observed between pasture management systems (Fujisaki et al. 2015). These results suggest that this current classification of pasture (degraded, nominal and improved) is not sufficient to understand the dynamics of SOC.

On the other hand, soils below a depth of 20 cm are generally not included in calculations of C storage. Although deep soil layers are likely to have lower C contents and higher bulk densities than topsoil, C sequestration can nevertheless contribute considerably when the whole soil profile is included in the calculations (Koutika et al. 1997; Jobbagy and Jackson 2000). Jobbagy and Jackson (2000) considered carbon stocks in the top and deep soil layers of natural «tropical grassland/savanna» ecosystems but unfortunately not in grazed pastures. In addition, deeper soil layers often contain recalcitrant C (humified C), whose residence time can range from several centuries to thousands of years (Fontaine et al. 2007; Rumpel and Kögel-Knabner 2011). A better understanding of the role of deep soil layers in C sequestration is thus needed for the calculation of the exact contribution of pastures to the Amazonia carbon cycle.

The capacity of pastures to sequester carbon is often linked to the nitrogen content of the topsoil (Cerri et al. 2004; Eclesia et al. 2012). A reduction in available N may thus reduce soil N content and limit carbon accumulation in the soil due to competition between plant and soil microbes (Fontaine et al. 2004; Kirschbaum et al. 2008; Piñeiro et al. 2009). The capacity of a given soil to sequester C is thus often limited by its capacity to fix N (Hagedorn et al. 2003; Bowden et al. 2004; Fontaine et al. 2004). Eclesia et al. (2012) reported a constant C:N ratio along the soil profile (0–90 cm) in pasture, suggesting that carbon and nitrogen have the same pattern in different soil layers. But here again, little is known about the role of N in deep soil layers.

The origin of C stocks in soil under pasture is ascribed to the accumulation of C4 plants (grasses) in the topsoil rather than to C3 plants (i.e., forest residues) (Cerri et al. 2004; Desjardins et al. 2004). During the first decade of pasture, the topsoil consists of more than 80 % of carbon originating from C3 residues of the former forest (Trumbore et al. 1995; Koutika et al. 1997; Cerri et al. 2004; Desjardins et al. 2004), whereas in old pastures (>20 years), the top soil contains up to 89.5 % of C originating from C4 plant residues (Cerri et al. 2004). However, Koutika et al. (1997) showed that the proportion of C3 carbon in the deep soil layers can remain unchanged (>90 %) during the first decades following deforestation. Despite this knowledge, the contribution of C3 carbon to total C stocks in deep soil under old pasture (>20 years) is still largely unknown. The transfer of C from the topsoil to deeper soil layers is the direct result of the turnover of grass roots (Salimon et al. 2004). Processes which take place in deep soil layers are more complex and depend on the root/shoot ratio of the vegetation cover as well as on the contribution of different plant functional groups (shrubs, grasses, and legumes). As a result, the soil below a depth of 20 cm only receives small quantities of fresh C, which limits the mineralisation of recalcitrant compounds and enables the long-term accumulation of carbon (Fontaine et al. 2007).

The aims of the present study were to (1) assess the contribution of C stored in the intermediate and deep soil layers (0–100 cm soil layer) to total C stocks in pastures aged from 0.5 to 36 years, and (2) to identify the origin of the carbon in the deep soil layers of these pastures.

Our two hypotheses are (1) the carbon of the deep soil layers is responsible for a substantial increase in the soil carbon stocks of pastures over time; (2) these "deep" carbon stocks are mainly composed of carbon originating from C3 herbaceous plants, at least during the first decade after establishment of the pasture, whereas carbon stocks in the topsoil are mainly composed of C originating from C4 plants, i.e. the forage grasses planted after deforestation.

Materials and methods

Site description

The study was conducted in French Guiana, South America (5°16′54″N, 52°54′44″W), along a 200 km stretch of coastline which hosts almost the entire human population of the country as well as agricultural areas including areas dedicated to livestock raising [32 % of Useable Agricultural

Area (UAA)] (Fig. 1). Mean annual rainfall is 3041 mm, and the mean air temperature is 25.7 °C (Gourlet-Fleury et al. 2004). The climate in French Guiana is affected by the north/south movements of the inter-tropical convergence zone, which cause major seasonal variations in rainfall. The region receives around 500–800 mm of rain in May and in June, whereas during the long dry season from mid-August to the end of November, less than 100 mm of rain falls each month (Bonal et al. 2008; Stahl et al. 2010). We focused our study on the hilltop zones of granite hills where the clayey soils are classified as Ferralsols or Acrisols according to the IUSS Working Group WRB (2006). Widespread deforestation of this coastal region began in the 1970s with the “Green Plan” (Huguenin et al. 2010). The area is the site of current and future expansion of pasture systems. For the study, we selected 24 pastures established after deforestation of native rainforest between 1976 and 2010, which belonged to eight farms. These pastures are distributed in four geographical coastal areas where deforestation occurred, with one representative native forest site in each geographical area (Fig. 1). The eight farmers were interviewed to determine the history of land use after deforestation and agricultural management (see Supplementary Table 1).

The conditions required for a site to be included in the chronosequence study were that, with the exception of time, all soil-forming factors had remained constant since deforestation (Huggett, 1998). The following criteria were chosen to ensure the sites were comparable: (1) the parent material had to be the same (precambrian metamorphic formation), which we checked on geological outcrops along nearby roads; (2) the sites had to be situated in a hilltop zone with a slight slope to avoid major transport of sediments in riverbeds; (3) no crop rotation or land-use change since forest conversion, nor fertilisation prior to sampling, which was checked by identifying the land-use history in interviews with the farmer; and (4) soils had to be comparable in terms of texture and pH, which was checked by soil analysis. The topsoil had a CEC of 2.6 $\pm$ 0.2, a CEC saturation rate of 55.2 $\pm$ 5.8 and a pH of 5.2 $\pm$ 0.1. These values are in the same range as those of productive pastures in Brazil (Koutika et al. 1997; Neill and Melillo 1997).

According to the farmers, the pastures were established by slash-and-burn but had not been burned since. They were managed with a rotational grazing plan at an animal stocking rate of $\sim$1 LSU ha^{-1} (Livestock Standard Unit).

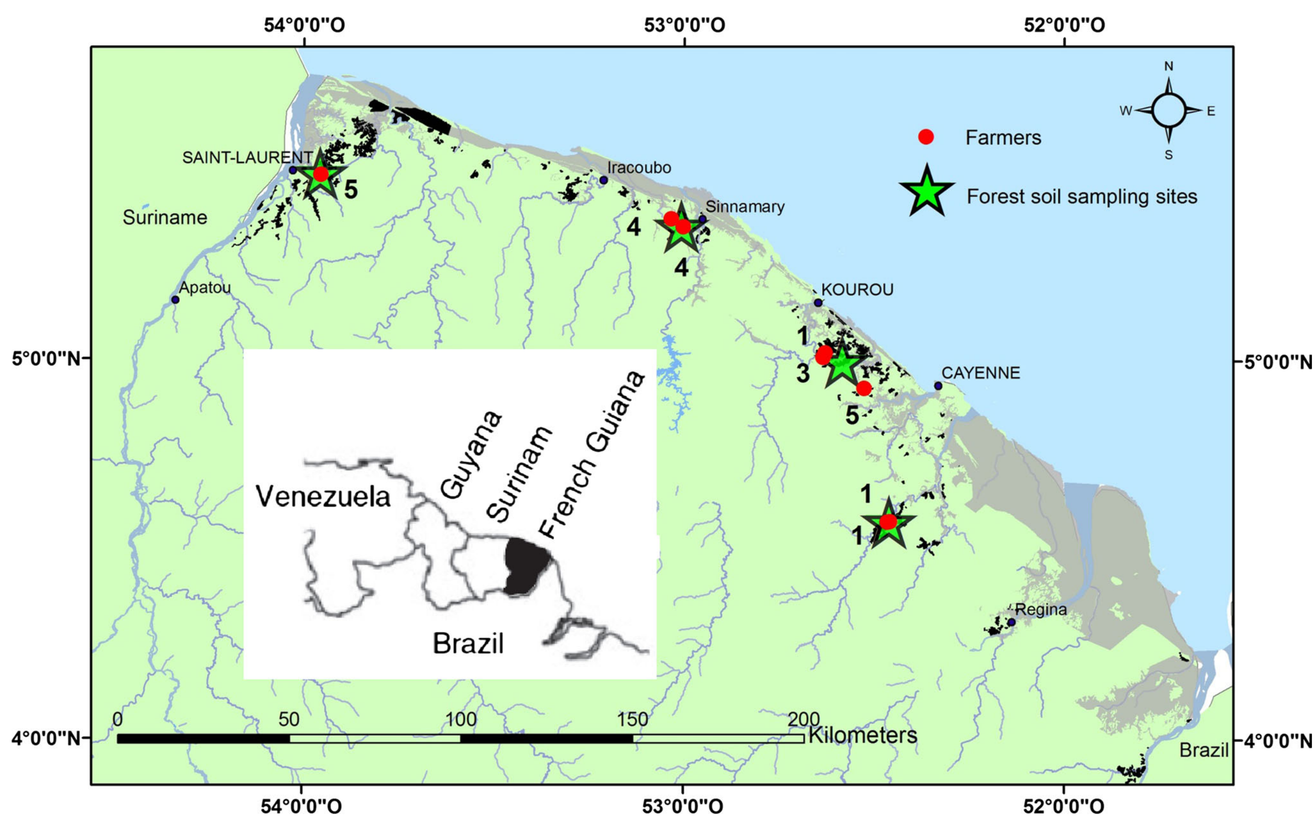

Fig. 1 Map of study sites. The study comprised 24 pastures belonging to eight farms (*red circles*). The *numbers* indicate the number of pastures sampled in each farm. The four reference forest sites are indicated by a *green star*. The area in *light green* is the tropical forest; the *grey area* is swamp, and the *black area* is agricultural area. The *inset* shows the location French Guiana in South America (colour figure online)

They were grazed by cattle, except for four of the pastures, which were grazed by goats ($\sim$10 goats ha^{-1}) (Supplementary Table 1). In accordance with general grazing systems in French Guiana, the vegetation in the pastures was dominated by a C4 species: the grass *Brachiaria humidicola*, which is one of the most widely sown exotic C_4 species in the Amazon basin (Table 3).

Soil sampling and physical analysis

Soil was sampled in the wet season in 2011 and in 2012. In each pasture and forest plot, we extracted eight soil cores to a depth of 100 cm. The cores were sampled using a jackhammer equipped with a drill gauge (Cobra TT, Eijkelkamp, The Netherlands). The litter layer was removed before the soil was sampled. Eight samples were taken from four cores spaced 10 m apart along two 30-m parallel transects (eight sampling points in a 30 × 10-m matrix). Each core was split into three layers: 0–20; 20–50; 50–100 cm, dried (for 48 h at 60 °C to constant mass) and sieved at 2 mm. Each layer of the eight cores was pooled proportionally to its mass to obtain a composite sample for each site. The mass of fine soil (<2 mm), and of coarse particulate organic matter (>200 µm) and the soil texture, were determined in each layer.

Chemical analyses

Powdered soil samples were combusted, and the concentration of elemental C and N in each layer was measured (IsotopeCube, Elementar, Hanau). The isotopic signatures of the fine soil and shoot and root biomass were measured with a $\delta^{13}C$ Finnigan continuous flow isotope ratio mass spectrometer (Delta S, Finnigan MAT, Bremen, Germany) at the stable isotope facility at INRA Nancy, France. Carbon isotope composition ($\delta^{13}C$) was calculated as:

$$\delta^{13}C(‰) = [(R_{sa}/R_{st}) - 1] \times 1000 \quad (1)$$

where R_{sa} and R_{st} are the ^{13}C:^{12}C ratio in the sample and in the conventional Pee Dee Belemnite standard, respectively. Carbon isotope composition ($\delta^{13}C$, ‰) was expressed with an analytical precision of 0.19 ‰ (standard deviation).

The isotopic signature of the vegetation present in the sampled pastures was measured on samples of the shoots and roots of the four commons species (*B. humidicola*, *Desmodium ovalifolium*, *Mimosa pudica*, and *Spermacoce verticillata*) using the same isotopic method.

Determination of soil carbon stocks and origin of C

The C stock in each soil layer was corrected to an equivalent soil mass. This correction is appropriate to standardise the different sites sampled in our chronosequence approach. First, we standardised the soil C stock in each plot by applying the average fine soil mass (<2 mm) for all plots (0–100 cm, native forests and pastures, $n = 28$) (Ellert et al. 2002; Gifford and Roderick 2003; Don et al. 2011; Mosquera et al. 2012; Bahr et al. 2014). Second, we corrected soil C stock using the same method of equivalent soil mass for each soil layer. After correcting for fine soil, we added a correction for clay content (Powers and Schlesinger 2002; de Koning et al. 2003; Zinn et al. 2005) to account for the close relationship between clay and C content. We standardised C stocks using the mean clay content in each soil layer for all plots (native forests and pastures, $n = 28$). These corrections were applied in order to reduce the variance in each sites due to the soil characteristics (fine soil, clay content, Supplementary Fig. 1) which have an already known effect.

To determine the contribution of C derived from C3 plants (forest and pasture species) and C4 plants (pasture grasses), we applied two mass balances equations (Balesdent et al. 1988):

$$C_{toti} = C3_i + C4_i \quad (2)$$

$$C4_i = C_{toti} \times \frac{(\delta soil_{C4i} - \delta soil_{C3i})}{(\delta root_{C4i} - \delta soil_{C3i})} \quad (3)$$

where C_{toti} is the C stock in the soil layer i, $C3_i$ is the C stock originating from the forest and C3 pasture species in the soil layer i and $C4_i$ is the C stock originating from grasses in the pasture, present in the soil layer i, $\delta soil_{C4i}$ is the $\delta^{13}C$ isotopic composition in the pasture in the soil layer i and $\delta soil_{C3i}$ is the $\delta^{13}C$ isotopic composition in the native forests and in the C3 pasture species in the soil layer i, and $\delta root_{C4i}$ is the $\delta^{13}C$ isotopic composition of the roots of C4 grass in the soil layer i.

Statistical analysis

A Student's t test was conducted to compare total C stocks in the 0–100 cm soil layer according to the age of the pasture and native forest and to test the contribution of each of the three soil layers in each age class. A t test was also conducted to compare: (1) soil C stocks, soil N stocks and the C:N ratio among the soil layers and the age classes; (2) aboveground and belowground C content, N content, the C:N ratio and $\delta^{13}C$ in the four main species; (3) the difference between the soil C stocks in native forest (only C3 plants) and soil C3 stock in the pasture in each age class and in each soil layer along with the proportion of C3 plants among each age class and each soil layer; (4) soil C3 stocks, soil C4 stocks among the soil layers and the age classes. All statistical analyses were conducted with R software (R Development core Team 2010).

Results

Effect of age on soil C stocks in the 0–100 cm soil layer

Soil analyses showed higher soil C stocks in the one metre soil layer in old pastures (31–36 years old; 135.1 ± 11.3 tC ha^{-1}, $n = 6$) than in the three age classes of younger pastures (0–9, 10–20 and 21–30 years old, 91.8 ± 8.6 tC ha^{-1}, $n = 7$; 78.3 ± 6.2 tC ha^{-1}, $n = 6$; and 96.8 ± 11.0 tC ha^{-1}, $n = 5$, respectively). Soil C stocks in old pastures were 1.5-fold higher than in the native forest (99.6 ± 7.4 tC ha^{-1}, $n = 4$) (Table 1).

Effect of age on soil C stock as a function of the soil layer

Soil C stocks in the topsoil (0–20 cm soil layer) represented 47.1 % in the young pasture (0.5–30 years old) of the total soil C stock, 39.8 % in old pastures, but 53.8 % in the native forest. Soil C stocks in the intermediate soil layer (20–50 cm) decreased slightly (from 30.9 to 21.4 %) until 30 years of age but increased notably (29.2 %) in the last age class. Finally, C stocks in the deep soil layer (50–100 cm) increased from 22.6 to 31.0 % with the age of the pasture (Table 1). We observed a different pattern in each soil layer. In the topsoil, soil C stocks decreased over the first 20 years after deforestation, before reaching the same value as in native forest (Fig. 2; Table 2). Stocks in the two deep soil layers remained stable until 30 years old and increased thereafter. The oldest pasture (31–36 years old) had high soil C stocks in all three soil layers, and the values in each layer were similar. In this pasture, the middle soil layer had higher C stocks than in the young pasture, except for pastures between 0 and 9 years old. The deep soil layers had the highest stocks compared to the plots in pastures and native forest. In old pastures, the two deep soil layers had higher C stocks than the same layers in the younger pastures and native forests, except in pastures between 0 and 20 years old, where the middle layers had similar stocks (Fig. 2; Table 2).

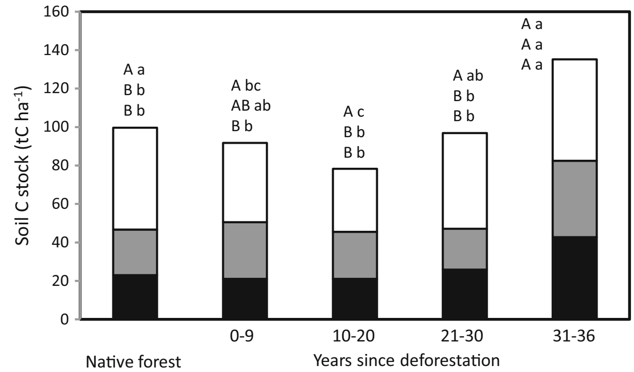

Fig. 2 Soil carbon stocks in each layer in native forest and in pastures established after deforestation (0–9, 10–20, 21–30, 31–36 years). *White bars* represent the topsoil layer (0–20 cm), *grey bars* the middle layer (20–50 cm) and *black bars* the deep layer (50–100 cm). For a given age class, mean values followed by the same *upper case letter* did not differ significantly among soil layers according to a Student's *t* test ($p < 0.05$). For a given soil layer, mean values followed by the same *lower case letter* did not differ significantly among age classes according to a Student's *t* test ($p < 0.05$)

Soil N stock and C:N pattern

We found no difference in soil N stocks in any of the soil layers between the native forest and pastures in the different age classes. Pastures more than 10 years old had higher nitrogen stocks in the topsoil than in the deep soil layers (Table 2). The C:N ratio (mean of 14) remained stable throughout the soil profile and no difference was found between young pastures and native forest. In the old

Table 1 Mean soil C stocks in native forest and pasture, and the difference between pasture and the original native forests in each age class

	Native forest	Years since deforestation			
	–	0–9	10–20	21–30	31–36
N	4	7	6	5	6
Soil C stocks (tC ha^{-1})	99.6 ± 7.4b	91.8 ± 8.6b	78.3 ± 6.2b	96.8 ± 11.0b	135.1 ± 11.3a
Difference between forest and pasture (%)	–	−19.5 ± 9.7b	−10.6 ± 6.1b	−15.4 ± 14.7b	+40.8 ± 13.4a
Contribution of topsoil (0–20 cm) to 1 m (%)	53.8 ± 3.5a	46.8 ± 5.1ab	42.0 ± 0.6ab	52.6 ± 3.7a	39.8 ± 3.7b
Contribution of deep soil (20–50 cm) to 1 m (%)	23.6 ± 6.0ab	30.9 ± 4.3a	31.5 ± 1.5a	21.4 ± 2.4b	29.2 ± 0.7ab
Contribution of deep soil (50–100 cm) to 1 m (%)	22.6 ± 3.3ab	22.3 ± 2.5b	26.6 ± 2.7ab	26.0 ± 2.9ab	31.0 ± 2.7a

Differences between carbon stocks in the topsoil and at a depth of 1 m and the percentage contribution of the deep soil layers to total C stocks in the whole 1 m soil layer

Mean values followed by the same lower case letter did not differ significantly among age classes according to Student's *t* test ($p < 0.05$)

Table 2 Soil C stocks, N stocks and the C:N ratio of forest and pasture according to the soil horizon (mean ± standard error)

Soil horizon	Native forest	Years since deforestation			
	–	0–9	10–20	21–30	31–36
C (t ha^{-1})					
0–20	53.0 ± 1.9aA	41.3 ± 3.4bcA	32.7 ± 2.3cA	49.7 ± 4.4abA	52.7 ± 4.5aA
20–50	23.6 ± 5.0bB	29.4 ± 5.3abAB	24.5 ± 1.7bB	21.3 ± 3.8bB	39.7 ± 4.4aA
50–100	23.0 ± 4.0bB	21.1 ± 3.6bB	21.1 ± 2.7bB	25.8 ± 4.7bB	42.7 ± 6.8aA
N (t ha^{-1})					
0–20	2.9 ± 0.2abA	2.2 ± 0.3aA	2.9 ± 0.1aA	3.0 ± 0.2aA	3.5 ± 0.3aA
20–50	2.0 ± 0.2aAB	1.9 ± 0.2aA	1.6 ± 0.1aB	1.5 ± 0.2aB	1.9 ± 0.4aB
50–100	1.8 ± 0.2aB	1.5 ± 0.1aA	1.5 ± 0.1aB	1.4 ± 0.2aB	1.9 ± 0.3aB
C/N					
0–20	13.9 ± 0.3aA	14.6 ± 0.6aA	13.9 ± 0.1aA	13.5 ± 1.0aA	15.2 ± 0.5aB
20–50	14.4 ± 1.0bA	14.8 ± 1.1bA	12.5 ± 1.2bA	17.7 ± 3.0abA	20.9 ± 2.0aA
50–100	14.6 ± 0.9bA	14.5 ± 1.4bA	15.1 ± 1.4bA	17.7 ± 1.7abA	20.9 ± 1.8aA

For a specific soil layer, mean values followed by the same lower case letter did not differ significantly among age classes according to a Student's *t* test ($p < 0.05$). For a specific age class, mean values followed by the same upper case letter did not differ significantly among soil layers according to a Student's *t* test ($p < 0.05$)

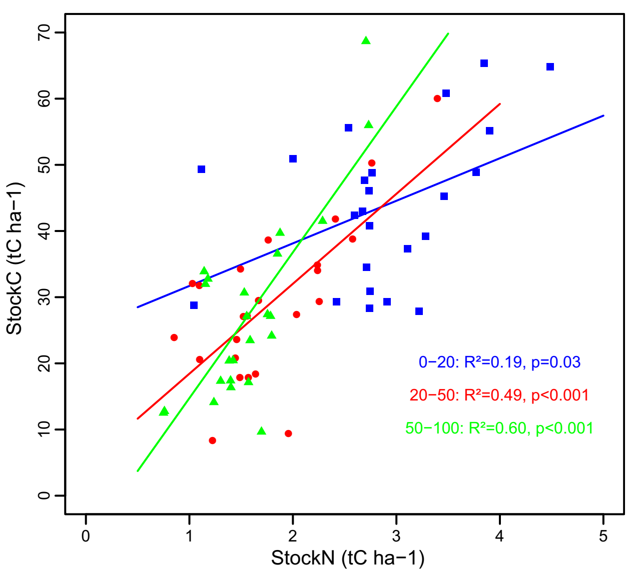

Fig. 3 Relationship between C and N stocks in each soil layer. *Blue squares* represent the topsoil layer (0–20 cm), *red circles* the middle layer (20–50 cm) and *green triangles* the deep layer (50–100 cm). The *solid line* shows significant relationships ($p < 0.05$) (colour figure online)

pastures, the ratio increased to 21 in the deep soil layers (Table 2). The pattern resembled that of soil C stocks, and this was confirmed by the positive relation between C and N stocks in all three soil layers (Fig. 3). The slope of the regression between the C stock and the N stock was stronger in the deep soil (50–100 cm) than in the topsoil (Fig. 3).

Chemical characteristics of common species

The N content of the aboveground parts of *B. humidicola* was lower than the N content of the legume *D. ovalifolium* but the same as that of *M. pudica* and *S. verticillata* (Table 3). The isotopic composition of the C4 species had a higher δ^{13}C value (−12.5 ‰) than the main C3 species (∼−30 ‰). The N and C contents of the belowground (0–20 cm) parts of the C4 species were also lower than those of the C3 plants, except for the N content of *S. verticillata*. Among C3 species, *S. verticillata* had the highest C:N ratio in both underground and above grounds parts of the plant (Table 3).

Contribution of soil C3 stock to soil C stock as a function of the soil layer

The contributions of C3 (legumes and shrubs) to C stocks in the topsoil decreased with an increase in the age of the pasture. The topsoil of young pastures (0–9 years old) and of old pastures (31–36 years old) had, respectively, 34.5 ± 3.6 and 50.5 ± 4.9 tC ha^{-1} less carbon originating from C3 species than their native forests (Table 4a). The pattern differed in the deep soil layer (50–100 cm): young pastures had 30.5 ± 2.7 tC ha^{-1} less carbon originating from C3 species than the native forest, but the old pastures had 86.1 ± 43.4 tC ha^{-1} more than the native forest. In the topsoil, the proportion of "C3 carbon" was higher in the young pasture (81.2 %) than in the pastures in the other age groups (Table 4b). The proportion of C3

Table 3 Aboveground and belowground chemical characteristics and $\delta^{13}C$ of the four main plant species growing in the pastures sampled in our experiment

Species Origins and functional group	*Brachiaria humidicola* Sown C_4 grass	*Desmodium ovalifolium* Sown C_3 legume	*Mimosa pudica* Native C_3 legume	*Spermacoce verticillata* Native C_3 shrub
N	4	4	3	3
Aboveground				
C (gC kg^{-1})	45.3 ± 0.6b	47.9 ± 0.5a	46.9 ± 0.2ab	47.4 ± 0.5a
N (gN kg^{-1})	0.7 ± 0.1b	1.6 ± 0.1a	1.0 ± 0.1b	0.9 ± 0.1b
C:N	63.7 ± 2.7a	30.7 ± 2.8c	48.6 ± 5.3b	54.8 ± 6.2ab
$\delta^{13}C$ (‰)	−12.5 ± 0.1a	−31.1 ± 0.3c	−30.4 ± 0.1bc	−30.3 ± 0.2b
Belowground 0–20 cm				
C (gC kg^{-1})	25.8 ± 1.3b	41.1 ± 2.6a	43.1 ± 2.0a	42.53 ± 1.24a
N (gN kg^{-1})	0.7 ± 0.1b	1.3 ± 0.1a	1.1 ± 0.1a	0.54 ± 0.03b
C:N	38.3 ± 4.9b	31.7 ± 4.2b	38.5 ± 4.9b	79.11 ± 6.24a
$\delta^{13}C$ (‰)	−14.7 ± 0.1a	−29.8 ± 0.6b	−29.4 ± 0.2b	−29.04 ± 0.32b
Belowground 20–50 cm				
C (gC kg^{-1})			44.9 ± 0.0a	38.9 ± 3.5a
N (gN kg^{-1})			1.2 ± 0.0a	0.4 ± 0.1b
C:N			38.5 ± 0.8a	89.3 ± 19.1a
$\delta^{13}C$ (‰)			−29.0 ± 0.1b	−28.1 ± 0.2a

Mean values followed by the same lower case letter did not differ significantly among species according to a Student's *t* test ($p < 0.05$)

Table 4 (a) Differences between soil C3 stocks in pastures and in nearby native forest (only C3 stock) according to the age class, (b) percentage of soil C3 stocks in each soil layer according to the age class

	Native forest	Years since deforestation			
	–	0–9	10–20	21–30	31–36
N	4	7	6	5	6
(a) ΔC3 plant (tC ha^{-1})					
0–20	–	−34.5 ± 3.6^{a}	−57.8 ± 4.3^{b}	−56.0 ± 6.4^{b}	−50.5 ± 4.9^{b}
20–50	–	−27.7 ± 5.9^{a}	−31.7 ± 4.9^{a}	+28.3 ± 70.6^{a}	−14.5 ± 12.9^{a}
50–100	–	−30.5 ± 2.7^{b}	−8.9 ± 9.5^{b}	−44.8 ± 12.9^{b}	+86.1 ± 43.4^{a}
(b) %C3 plant					
0–20	100	81.2 ± 3.9^{a}	65.4 ± 7.0^{b}	48.8 ± 5.2^{c}	46.5 ± 3.3^{c}
20–50	100	77.1 ± 3.5^{a}	70.0 ± 3.6^{ab}	57.3 ± 7.5^{b}	59.7 ± 1.9^{b}
50–100	100	65.0 ± 5.7^{a}	62.9 ± 5.5^{a}	64.8 ± 8.2^{a}	60.1 ± 4.3^{a}
0–100		74	65	56	55

For a specific soil layer, mean values followed by the same lower case letter did not differ significantly among age classes according to a Student's *t* test ($p < 0.05$)

carbon in the intermediate soil layers decreased from 77.1 % in the young pasture to 59.7 % in the old pasture. The proportion in the deep soil layers remained stable at around 63 % of C3 stocks in the pastures in all the age classes (Table 4b).

Pattern of soil C3/C4 stocks among soil layers and age classes

We found no significant difference in soil C3 stocks among soil layers in each age class after deforestation (Fig. 4). Soil C3 stocks in the topsoil decreased over the first 20 years after deforestation but then increased. In the oldest pastures (31–36 years old), the soil C3 stock in the intermediate (20–50 cm) and deep soil layers (50–100 cm) was higher than in the previous age class. These pastures had a higher soil C3 stock in the 50–100 cm layer than in the other layers. Soil C4 stock was higher in the topsoil in the age classes “0–9”, “21–30” and “31–36” than in the two deeper soil layers (20–50 and 50–100 cm) (Fig. 4). The soil C4 stock increased with age since deforestation in all the soil layers (Fig. 4).

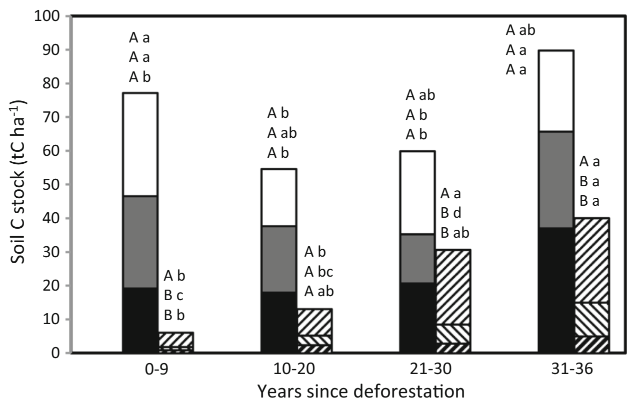

Fig. 4 Soil C3 and C4 stocks in each layer in native forest and pastures established after deforestation (0–9, 10–20, 21–30, 31–36 years). For C3 stocks (*left bars*), *white bars* represent the topsoil layer (0–20 cm), *grey bars* the middle layer (20–50 cm) and *black bars* the deep layer (50–100 cm). For C4 stocks (*right bars*) *white with black stripes* represent the topsoil layer (0–20 cm), *white with inverse black stripes the middle layer* (20–50 cm) and *black with white stripes* the deep layer (50–100 cm). For a given age class, mean values followed by the same *upper case letter* did not differ significantly among soil layers according to a Student's *t* test ($p < 0.05$). For a given soil layer, mean values followed by the same *lower case letter* did not differ significantly among age classes according to a Student's *t* test ($p < 0.05$)

Discussion

Contribution of deep soil layers to carbon stocks

Our study highlights the fact that in pastures in all age classes, the intermediate (28 %) and deep (26 %) soil layers contributed significantly to total C stocks in the whole 0–100 cm soil profile (Fig. 2; Table 1). Consequently, if only carbon stocks in the topsoil layer are analysed, total soil C stocks will be considerably underestimated, as reported by Jobbagy and Jackson (2000). Furthermore, in our study, the contribution of the deep soil layer to total C stocks increased from 22 to 31 % with an increase in the age of the pasture (Table 1), emphasising that C transfer and storage in the deep soil layers is a slow process, and may only be measurable after several decades. We observed a marked decline in C stocks in the topsoil over time, thereby confirming our hypothesis. The high C stocks observed in old pastures are thus the result of an almost equal contribution of the three layers, while in younger pastures, topsoil is the main contributor. The review by Jobbagy and Jackson (2000) also provided evidence that C stocks in tropical pastures are likely to increase in even deeper soil layers (e.g. 100–200 cm and 200–300 cm). But sampling soil below a depth of 1 metre is difficult and mainly provides information on the origin of the soil rather than on the effect of land-use change.

Contribution of N stocks to C stocks

Regardless of the age of the pasture, soil C stocks were significantly correlated with soil N stocks (Fig. 3), suggesting a direct effect of available N on C stocks (Schipper et al. 2010). This correlation was much stronger in the deep soil layer (50–100 cm) than in the intermediate and top soil layers, suggesting a slowdown in decomposition and an increase in recalcitrant C compounds (with low N content) in the deep soil layers (Fontaine and Barot 2005). Indeed, the proportion of legumes and shrubs in the vegetation cover increased from 1.3 to 5.0 % in the older age classes (data not shown), which may explain the recalcitrant compounds of plant origin with a high C:N ratio (Table 3).

Marked differences in the C:N ratio in old pastures and in native forest (20 vs. 14 in native forest) confirmed our hypothesis (Table 2). Some authors have reported relatively stable C:N ratios throughout the soil profile (from 0 to 100 cm) in tropical pastures less than 20 years old (Koutika et al. 1997; Eclesia et al. 2012). Others (Krull and Skjemstad 2003) reported either a rapid decrease in the C:N ratio, or an increase in the C:N ratio with depth (up to a value of 15) linked to the presence of oxisol. In our study, all the soils are ferralsols and the increase in the C:N ratio in old pastures was thus not explained by the type of soil. Another possible explanation for a higher C:N ratio may be the presence of burned plant material dating from the establishment of the pasture (Dümig et al. 2009). However, to our knowledge, all the pastures sampled in our study (with or without stumping) were burned on only one occasion, i.e. during their establishment. We rarely came across charcoal in the top and deep soil layers in the forest and pastures plots we sampled, which is consistent with the type of forest in this part of French Guiana. These forests were not subject to major climatic disturbances during the Holocene, as dry climatic conditions prevailed in the Amazon Basin and the Guiana Shield (the past 10,000 years); i.e. they were not replaced by C4 savannahs or C4 forest savannahs for long periods (Freycon et al. 2010).

Origin of the C stock in each soil layer

Our experiment revealed a significant contribution by carbon of two different origins (C4 plants and C3 plants), with a specific pattern along the chronosequence (Fig. 4).

During the first 20 years after the pasture was established, we observed a decrease in C3 stocks and an increase in C4 stocks in all three soil layers. A comparable pattern has been reported in topsoils in pastures in Brazil and Costa Rica (Neill et al. 1996; Neill and Melillo 1997; Cerri et al. 2004; Powers and Veldkamp 2005). This initial decrease in C stocks in young pastures can be explained by the fact that pasture-derived C4-carbon increased more slowly than forest-derived C3 carbon was lost. This is in contrast to the hypothesis of Neill et al. (1996). Low rates of C storage is evidence that new inputs of C4-carbon (grasses) and C3-carbon (legumes and weeds) in deep soils occur more slowly than C is lost after conversion from forest to pasture through leaching. In our study, the fraction of C3 carbon remained dominant in all the soil layers (>60 %; Table 4b) in the first 20 years. The slow C4 storage in the 50–100 cm soil layer is explained by the fact that the root system of *B. humidicola* is mainly present in the topsoil. The gradual change in isotopic composition with an increase in the age of the pasture is in agreement with the results of Powers and Veldkamp (2005). However, in our experiment, we found no pure C4 plant communities. The proportion of C4 species (native and sown) exceeded 90 % in only six pastures (unpublished data).

After 20 years, and especially in the 31–36 age class, the pattern of C3 shifted, with a major increase mainly in the intermediate and deep soil layers, leading to marked differences in the three soil layers under old pastures. To our knowledge, this pattern has never previously been reported. The higher total C stocks in old pasture than in native forests in our study can be explained by additional C3 carbon from C3 pasture vegetation such as legumes and weeds (shrubs or herbaceous). However, locally, the roots of old trees could also contribute this amount of organic carbon to the deep soil layer. 20 years after pasture establishment, we observed some naturally established species (the legume *M. pudica*, the shrub *S. verticillata*) and also sown C3 species (the legumes *Calopogonium mucunoïdes* and *Desmodium sp.*) (Table 3), which contributed to carbon inputs in different soil layers. The increase in C4 stocks mainly in the topsoil, but also in the intermediate soil layer, suggests that the limited quantities of deep-rooted grasses were able to sequester a significant amount of organic carbon in the deep soil layer (Trumbore et al. 1995). Deep-rootedness is considered to be a major factor in adaptation to low-fertility soils; this is particularly true of *Andropgon gayanus*, which plays a significant role in carbon sequestration in deep soil layers (Fisher et al. 1994).

Several studies reported degradation of pasture and of their quality with the establishment of C3 weeds in pastures. However, in our study, biomass production (data not shown) suggests that the presence of both weeds and shrubs in old pastures did not affect soil quality and productivity (which was the same as in young pastures) but, quite the contrary, improved soil C stocks, as also reported by Müller et al. (2004) and Mosquera et al. (2012). Moreover, in some studies, the period during which such pastures (considered as degraded) were managed was not long enough to observe an increase in soil C stocks in comparison with native vegetation (Maia et al. 2009). In our study, apparent degradation by weeds and shrubs led to an increase in C storage without loss of pasture productivity. The abundance of unappetizing weeds and shrubs (<6 %) remained at a level that is compatible with the basic function of grasslands: the provision of forage for livestock, i.e. grasses and legumes remained dominant.

Conclusion

Our study shows that pastures grazed by cattle can be maintained for several decades and provide high soil carbon storage throughout the 0–100 cm soil layer. According to our results, the intermediate and deep soil layers contribute substantially to total carbon stocks in the soil under pastures, which underlining the need to include these stocks in the carbon budget of the ecosystem to avoid underestimating soil C stocks. The change in soil C stocks over time was explained by the significant contribution of the C3 pasture species including legumes and shrubs, mainly to C stocks in the deep soil layers. In old pastures, the increase in C4 and C3 stocks suggests that C from both origins plays a synergistic role in the development of high soil C stocks. This increase is not accompanied by agronomic degradation and highlights the possible cohabitation of the two functional groups. Long-term management practices promoting high grass and legume production and an acceptable shrub cover lead to greater inputs of C to soils under pastures. Our results also suggest that sowing an appropriate mixture of C3 and C4 plants could trigger the same high rate of C storage in young pastures as observed in old pastures in French Guiana. Carbon storage in old pastures could be improved through a better balance between C4 and C3 species by promoting the development of legumes already in place and their sustainability. Finally, there is a need for more studies to identify appropriate pasture management practices in order to improve the ecosystem services (e.g. carbon sequestration, soil fertility, and the quality and quantity of forage for livestock).

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