Insight

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Impact Of Tropical Forest Succession On Soil Organic Carbon Storage In The Lopé National Park, Gabon

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ABSTRACT

This study quantifies the soil organic carbon (SOC) stock changes occurring during different phases of forest colonization on savannahs. SOC stock changes occur below 30 cm depth, indicating the subsoil as the principal compartment contributing to SOC sequestration, and suggesting the need to consider the entire profile (0-100 cm) to thoroughly assess the effect of woody encroachment on SOC stock.

Key words: Marantaceae forests; Natural succession; Savannahs; Soil carbon stock; Tropical forests

WOODY PLANT ENCROACHMENT INTO SAVANNAHS AND GRASSLANDS REPRESENTS A SIGNIFICANT GLOBAL CHANGE PHENOMENON (Archer *et al.* 2001), and is commonplace on the African continent, with a considerable impact on carbon (C) dynamics at an ecosystem level (Mitchard *et al.* 2013, Buitenwerf *et al.* 2012, Angassa *et al.* 2010, Mitchard *et al.* 2009, Spichiger & Pamard 1973). Trees and shrubs influence the spatial distribution and cycling of nutrients by altering soil respiration rates (Raich & Schlesinger 1992), hydrology (Wilcox 2002), microclimate (Hoffman & Jackson 2000) and by concentrating soil organic carbon (SOC) beneath their canopies (Binkley & Giardina 1998). Understanding SOC changes in relation to woody encroachment is becoming increasingly important, given the worldwide occurrence of this phenomenon and the growing interest in the C balance of the tropics (Aragão *et al.* 2014, Grace *et al.* 2014, Valentini *et al.* 2014).

In this study, we aimed to quantify SOC levels in different soil layers down to 1 m depth across the different phases of a natural succession from savannah to forest. We hypothesized that SOC levels increase during the transition from savannah to forest due to both the increase in C inputs to soil via litter deposition and the presence of herbaceous vegetation during the different phases of natural succession. Evaluating SOC changes at different depths, down to 1 m, is of outmost importance since often SOC changes are reported only for the upper soil layers, those where the changes should be easily detectable (e.g. 0-30 cm depth), while below 30 cm depth changes are often considered to be negligible.

The Lopé National Park in central Gabon (00° 12′ 04″ S; 11° 36′ 05″ E), offers a unique opportunity for investigating SOC variations as a result of the natural expansion of forests into savannahs. The park is part of the Congo Basin lowland forests and it is principally covered by closed canopy rainforests with savannah systems in the north and east that are interspersed with natural forest fragments, marshes and gallery forests (Fig. S1). The main forest formations resulting from woody encroachment are the Marantaceae forests, characterized by a thick layer of herbaceous plants of the Marantaceae and Zingiberaceae families that dominates the understory. The landscape is characterized by hills with an average elevation of 500 m. The geological substrate is represented by rocks of the Metamorphic series of the Ogooué river from the Proterozoic era (Schulter 2008), and the typical soils of the area are comprised within the order of the Oxisols (Martin *et al.* 1981).

Soil samples were collected in five successional phases of forest colonization, as defined in White (2001): 1) savannah (S); 2) colonising forest (CF); 3) monodominant forest (MF); 4) young Marantaceae forest (YMF) and 5) mixed Marantaceae forest (MMF). Five 1-hectare plots in each of the five phases were investigated. Basic characteristics of the vegetation of each plot, together with site features and locations are reported in Table S1. In each of the plots five sampling points were randomly selected and soil samples were collected at multiple depths. In the topsoil (0-30 cm depth) the samples were collected at 0-5, 5-10, 10-20 and 20-30 cm depth using a cylinder of known volume (diameter = 5 cm; height = 5 cm) to also determine the bulk density (BD), while for the subsoil (30-100 cm depth) samples were collected within two intervals, 30-50 cm and 50-100 cm depth, using an auger. The SOC data were reported for the topsoil, and subsoil according to IPCC guidelines requirements (IPCC 2006). Five samples of the organic horizon, namely the litter layer, were collected randomly in each plot using a 20 cm x 20 cm frame.

All samples were oven-dried (60 °C) and sieved at 2 mm, while the litter layer was ground in a ball mill. All the analyses were performed on the fine soil fraction (< 2 mm). A single composite sample per layer (n=5) was analysed for particle size distribution (Mikutta *et al.* 2005) and pH. All samples were individually (n=5 per layer) measured for total C and N by dry combustion (ThermoFinnigan Flash EA112 CHN). Since the auger did not allow for a precise measure of the BD for the 30-50 and 50-100 cm depths, BD was determined using the clod method (Blake & Hartge 1986) on three soil peds from each subsoil layer at each site. The SOC stocks were calculated considering the C concentration, the BD, the rock fragment content and the depth of each layer (Boone *et al.* 1999). Differences in C concentrations and stocks were determined among all the phases of the succession and within each phase using analysis of variance (ANOVA) with depth treated as a repeated measure using R software. When significant interaction effects were observed a multiple comparisons test (Tukey HSD) was completed. Statistical significance for ANOVA were tested at $p < 0.001$.

Bulk density did not differ among the phases of the natural succession in the topsoil and subsoil, clustering around 1.3 Mg/m^3, and 1.4-1.5 Mg/m^3, respectively (Table S2). The similarity of the particle size distribution and pH between the phases supports sites comparability indicating similar soil conditions in the different plots (Table S2), with the soil always classified as Inceptic Hapludox (Soil Survey Staff 2014). Within each soil depth there was very little SOC variation among plots within successional phases, but significant differences were observed between successional phases (Table 1; Table S3). Particularly, in the 0-5 cm depth the SOC concentration increases progressively from 12.5±0.7 g C kg^{-1} in the S to 24.8±0.2 g C kg^{-1} in the MMF (Table 1). In the other layers, a SOC decline is evident below 30 cm depth in the S sites, 2.8±0.2 g C kg^{-1}, compared to all the other phases, ~3.8-4.8 g C kg^{-1} (Table 1).

The SOC stock variations can be entirely attributable to variations in SOC concentration, due to the non-significant variations in BD between the successional phases, and the absence of rock fragments in these soils (Table S2). In the topsoil, the SOC stocks do not show a significant increase in the different phases of the natural succession, with values around 30 Mg/ha, and only in the last phase the SOC stock is significantly higher than all the other phases (MMF = 38.6±1.7 Mg/ha; Fig. 1). In the subsoil SOC stock increases significant in the first phase (CF = 39.5±2.2 Mg/ha), then it remains stable to increases again in the last phase (Fig. 1). The C stock of the litter layer, absent in the savannah plots, increases across the succession: 3.6±1.5 Mg/ha in the CF, 4.8±1.9 Mg/ha in the MF, 4.8±1.7 Mg/ha in the YMF and 6.8.1±3.4 Mg/ha in the MMF.

The rate or direction of the SOC changes occurring after woody plant establishment are not consistent in the scientific literature. Some studies indicate SOC increases as a consequence of the increase in the soil nutrient pool (Scholes & Archer 1997, Archer 1995), while other studies indicate a significant SOC decline with increasing in precipitation (Jackson *et al.* 2002, Scott *et al.* 1999). After woody plant invasion on herbaceous vegetation a negative relationship between precipitation and SOC changes was shown by Jackson *et al.* (2002) and Guo & Gifford (2002), with the SOC levels decreasing in areas of high precipitation (>1200 mm), and increasing in areas with low precipitation. Accordingly, in the Lopè National park, with an average annual precipitation of about 1500 mm, woody encroachment should cause a decline in SOC levels. Nevertheless, in the topsoil of all the phases SOC levels are stable and increase only in the last phase, while in the subsoil the changes in SOC levels occur already in the first phase.

The main driver of the SOC increases in the topsoil of the last phase is possibly the increase in litter inputs, leading to a progressive C accumulation in the 0-5 cm layer of the different phases. In forests litter production is a significant fraction of the net primary productivity, rather than stemwood biomass production, hence representing an important C input to soil (Brown & Lugo 1990). However, despite an increases in litter C should cause an increases in topsoil C (Guo & Gifford 2002), the increasing litter inputs along the succession do not affect consistently the change in topsoil C, apart in the last phase where the SOC concentration and stock increase of about 1 percent and 8.5 Mg/ha compared to savannahs. This fact suggests that in the long term there is a positive impact of litter inputs on SOC sequestration and can help to explain the increase in SOC levels only in the last phase of the succession. The effect of the litter in increasing the SOC concentration is the result of a higher recalcitrance of the C inputs from woody species rather than herbaceous vegetation (Marín-Spiotta *et al.* 2008). Woody plants produce lipids, such as waxes, suberin, cutin, and terpenoids, that are resistant to oxidation and consumption, as protection against herbivory and parasitism (Gleixner *et al.* 2001). The production of these and other plant secondary compounds is thought to increase during tropical forest succession (Coley & Barone 1996).

Contrarily, compared to savannah the SOC levels in the subsoil increase significantly in the first phase of succession (+ 16.4 Mg/ha) and again in the last phase (+ 29.9 Mg/ha) leading to hypothesize a significant role of the root apparatus in the translocation of the SOC in deeper layers. In fact, while herbaceous vegetation has the root apparatus concentrated in the topsoil, roots from woody vegetation can go much deeper. The SOC increases in the subsoil could be also related to the increases in soil cover due to the increased number of trees that protect the soil from heavy rains and reduce the loss of SOC as dissolved organic carbon.

Considering the whole soil profile, the SOC stock in the last phase of the succession increases by 43 percent compared to the savannah, and increases to 52 percent if we also account for the C stored in the litter layer. In Amazonia San Jose et al. (1988) observed a similar trend during woody encroachment on savannah, with significant SOC increases only when the forest became established, while in the intermediate phases the SOC was rather stable. On the other hand, other studies report a decline in SOC following encroachment (Don *et al.* 2011). These contrasting results support the evidence that SOC can react differently to the events depending on the geographic locations of the investigated area, suggesting that no general rules can be derived for extrapolating general data that describe the effect of this natural land use change (Powers *et al.* 2011).The impact of the secondary forest vegetation in increasing the SOC levels is observable immediately only in the subsoil, while in the topsoil the changes are evident only on the long term. Different mechanisms are possibly responsible for this different behaviour between the phases, with increasing litter inputs influencing the SOC accumulation in the topsoil and a different roots distribution being responsible for the SOC accumulation in the subsoil. Finally, a crucial point is the time needed for the natural transition to occur. The process of natural succession can be relatively fast in the initial stages (e.g. years or few decades) but can take several centuries to reach forest maturity, as suggested by Saldarriaga *et al.* (1988) in a study across a range of soil types.

In conclusion, this study points out the importance of measuring the SOC along the whole profile (0-100 cm depth) to avoid overlooking the great amount of C that can accumulate in the subsoil during natural succession to forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. a) Map of the Lopé National Park. The sampling area where the different plots are located is represented by the square; b) the position of the Park within Gabon and; c) Gabon in the African continent.

TABLE S1. *Location, altitude and dominant vegetation of each of the investigated plots.*

TABLE S2. *Bulk density, particle size distribution and pH for the topsoil (0-30 cm) and subsoil (30-100 cm) of the twenty-five plots describing the natural succession. * S = Savannah; CF = colonizing forest; MF = Monodominant forest; YMF = Young Marantaceae forest; MMF = Mixed Marantaceae forest.*

TABLE S3. *Soil organic carbon concentration along the soil profile of all plots from each phase of the chronosequence. Within each column, different letters indicate significant differences ($p<0.001$) only for the same phase of the natural succession, while no letters indicate no any significant difference within the same layer of phase.*

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TABLE 1. *SOC concentrations in the mineral soil for the different phases of the natural succession. Within each column, means followed by the same letters are not significantly different (ANOVA; $p < 0.001$; $n = 25$ per layer).*

* S = Savannah; CF = colonizing forest; MF = Monodominant forest; YMF = Young Marantaceae forest; MMF = Mixed Marantaceae forest.

Vegetation type *	0-5 cm	5-10 cm	10-20 cm	20-30 cm	30-50 cm	50-100 cm
	g/kg	g/kg	g/kg	g/kg	g/kg	g/kg
S	12.5±0.7a	9.6±1.6ab	7.5±1.4a	5.1±0.9a	2.8±0.2a	2.8±0.2a
CF	13.2±0.6ab	8.8±0.3a	7.9±0.6a	6.4±0.4a	4.6±0.3b	3.8±0.2b
MF	14.7±0.5b	8.5±0.5a	6.9±0.6a	5.7±0.3a	5.4±0.9b	4.2±0.4b
YMF	18.5±1.3c	10.3±0.4b	7.2±0.9a	5.4±0.4a	4.7±0.6b	4.5±0.4bc
MMF	24.8±0.2d	10.7±0.1b	7.5±0.1a	6.3±0.1a	5.6±0.1b	4.8±0.1c

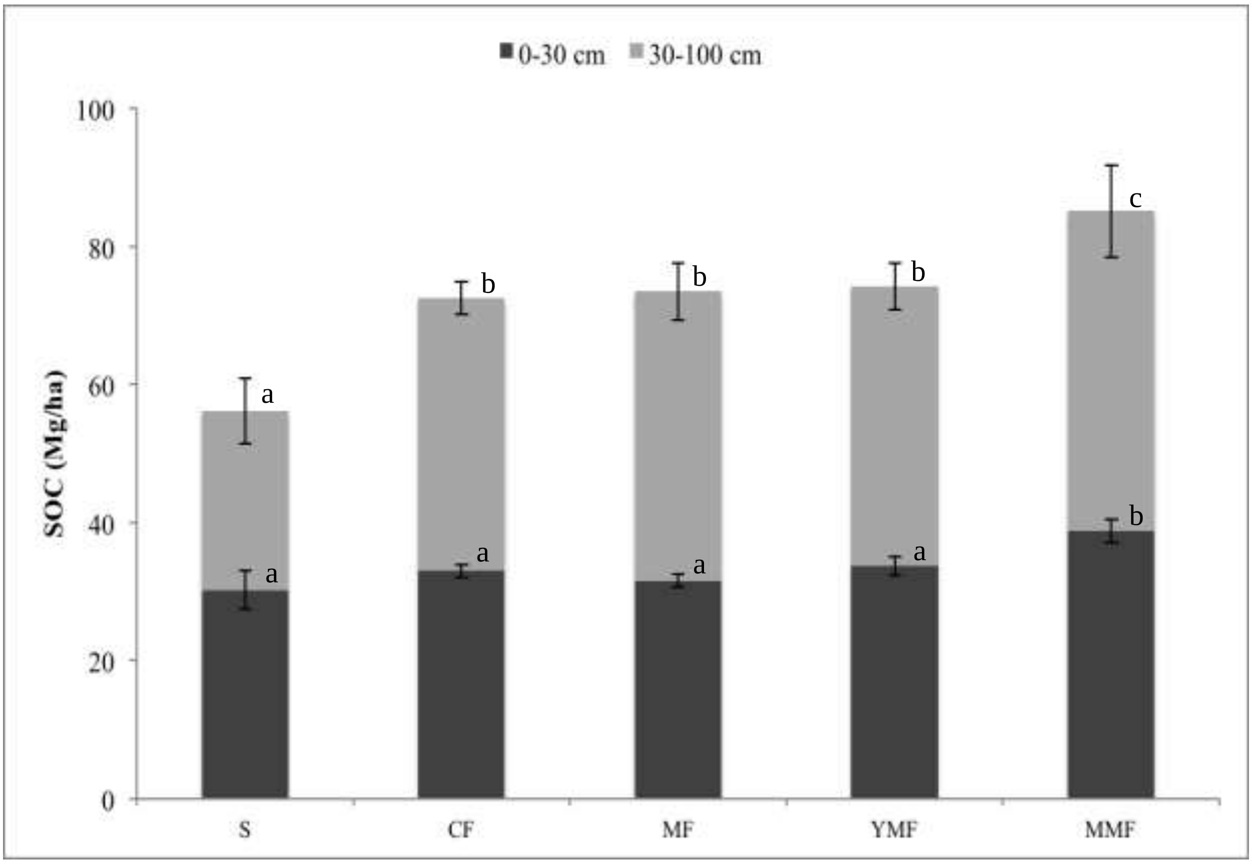

FIGURE 1. Mean SOC stock for the 0-30 cm and 30-100 cm depth of mineral soil under the different vegetation types across the natural succession. Different letters indicate significant differences (ANOVA; $p < 0.001$; $n = 25$ per vegetation type both in the topsoil and subsoil) only within the same compartment. S = Savannah; CF = colonizing forest; MF = Monodominant forest; YMF = Young Marantaceae forest; MMF = Mixed Marantaceae forest.