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INSIGHTS

# Impact of woody encroachment on soil organic carbon storage in the Lopé National Park, Gabon

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## ABSTRACT

This study quantifies changes in soil organic carbon (SOC) stock as a result of woody encroachment on savannas. Changes in SOC stocks 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 stocks.

*Key words*: Marantaceae forests; savannas; soil carbon stocks; tropical forests; woody encroachment.

Woody plant encroachment into savannas 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 (Spichiger & Pamard 1973, Mitchard *et al.* 2009, Angassa & Oba 2010, Buitenwerf *et al.* 2012, Mitchard & Flintrop 2013). 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 (Aragao *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 different stages of woody encroachment on savanna. We hypothesized that SOC levels increase during the transition from savanna to forest due to both, the increase in C inputs to soil via litter deposition and the presence of herbaceous vegetation during the different stages of woody encroachment. Most studies typically quantify SOC changes down to 30-cm depth because changes below this depth are often considered to be negligible. However, it is of utmost importance to verify this assumption, and thus we measured SOC stocks to 1-m depth.

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 savannas. The park is part of the Congo Basin lowland forests and it is principally covered by closed canopy rainforests with savanna 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 (Schlüter 2008), and the typical soils of the area are classified as Oxisols (Martin *et al.* 1981).

Soil samples were collected in five successive stages of forest colonization, as defined in White (2001): (1) savanna (S); (2) colonizing forest (CF); (3) monodominant forest (MF); (4) young Marantaceae forest (YMF); and (5) mixed Marantaceae forest (MMF). Five 1-ha plots in each of the five stages were investigated. Basic characteristics of the vegetation of each plot, together with site features and locations are reported in

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TABLE 1. *SOC concentrations in the mineral soil of the different stages. Within each column, means followed by the same letters are not significantly different (ANOVA; P < 0.001; N =* 25 per layer).

| Vegetation type* | 0–5 cm g/kg | 5–10 cm g/kg | 10–20 cm g/kg | 20–30 cm g/kg | 30–50 cm g/kg | 50–100 cm 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 |

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

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 × 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 analyzed 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. SOC stocks were calculated considering C concentration, BD, rock fragment content, and depth of each layer (Boone *et al.* 1999). Differences in C concentrations and stocks were determined among all the stages of woody encroachment and within each stage 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 used. Statistical significance for ANOVA were tested at $P < 0.001$.

Bulk density did not differ among the different stages 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 stages 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 the same stage, but significant differences were observed between different stages (Table 1; Table S3). Particularly, in the 0–5 cm depth the SOC concentration increased 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 was evident below 30 cm depth in the S sites, 2.8 ± 0.2 g C kg$^{-1}$, compared to all the other stages, ~3.8–4.8 g C kg$^{-1}$ (Table 1).

The SOC stock variations can be entirely attributable to variations in SOC concentration, given that BD did not differ between the different stages and the absence of rock fragments in these soils (Table S2). In the topsoil, the SOC stocks did not show a significant increase in the different stages of the woody encroachment, with values around 30 Mg/ha, and only in the last stage the SOC stock was significantly higher than all the other stages (MMF = 38.6 ± 1.7 Mg/ha; Fig. 1). In the subsoil, SOC stock increased significantly in the first stage (CF = 39.5 ± 2.2 Mg/ha), then remained stable and increased again in the last stage (Fig. 1). The C stock of the litter layer, absent in the savanna plots, increased across the different stages: 3.6 ± 1.5 Mg/ha in the CF, 4.8 ± 1.9 Mg/ha in the MF,

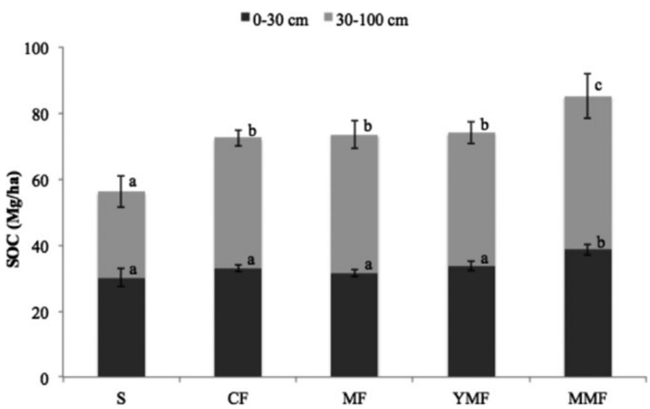


FIGURE 1. Mean SOC stock for the 0–30 cm and 30–100-cm depth of mineral soil under the different vegetation types across the woody encroachment stages. Different letters indicate significant differences (*ANOVA*; $P < 0.001$; $N = 25$ per vegetation type both in the topsoil and subsoil) only within the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

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 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 (Archer 1995, Scholes & Archer 1997), while other studies indicate a significant SOC decline with increasing precipitation (Scott *et al.* 1999, Jackson *et al.* 2002). After woody plant invasion on herbaceous vegetation a negative relationship between precipitation and SOC changes has been observed by Jackson *et al.* (2002) and Guo and 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 stages, SOC levels were stable and increased only in the last stage, while in the subsoil the changes in SOC levels occurred already in the first stage.

The main cause of the SOC increases in the topsoil of the last stage is possibly the increase in litter inputs, leading to a progressive C accumulation in the 0–5-cm layer of the different stages. In forests, litter production is a significant fraction of net primary productivity, higher than stemwood biomass production, hence representing an important C input to soils (Brown & Lugo 1990).

However, despite an increase in litter C, being expected to cause an increase in topsoil C (Guo & Gifford 2002), the increasing litter inputs along the different stages do not consistently affect the amount of topsoil C, aside from the last stage where the SOC concentrations and stocks increased by about 1 percent and 8.5 Mg/ha compared to savannas.

This fact suggests that in the long term there is a positive impact of litter inputs on SOC sequestration and may explain the increase in SOC levels in the last stage of the woody encroachment. The effect of the litter in increasing the SOC concentration is the result of a higher recalcitrance of litter 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 a protection mechanism 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 savanna, the SOC levels in the subsoil increased significantly in the first stage (+16.4 Mg/ha) and again in the last stage (+29.9 Mg/ha) suggesting that roots play a significant role in translocating SOC into deeper soil layers. In fact, while herbaceous vegetation has the root system concentrated in the topsoil, roots from woody vegetation extend much deeper into the soil. 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 stage of the woody encroachment increased by 43 percent compared to stocks in the savanna, and increased 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 savanna, with significant SOC increases only when the forest became established, while in the intermediate stages the SOC was rather stable. On the other hand, other studies report a decline in SOC following woody 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 behavior between the stages, with increasing litter inputs influencing the SOC accumulation in the topsoil and a different root distribution being responsible for the SOC accumulation in the subsoil. Finally, a crucial point is the long time needed for the natural transition to occur. White *et al.* (1995) hypothesized that the transition from savanna to colonizing forest takes 50–100 years, followed by the establishment of monodominant stands of *Aucoumea klaineana* and *Lophira alata,* which gradually evolve into Marantaceae forests that diversify over hundreds of years, eventually forming mature forests, highlighting the slowness of this natural land use change as also 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 woody encroachment on savannas.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Map of the Lopé National Park and 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 and subsoil of each plot considered in this study.*

TABLE S3. *Soil organic carbon concentration along the soil profile of all plots describing the woody encroachment process.*

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