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CONTRIBUTION AND STABILITY OF FOREST DERIVED SOIL ORGANIC CARBON DURING WOODY ENCROACHMENT IN A TROPICAL SAVANNA. A CASE STUDY IN GABON

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Abstract

In this study, we quantified the contribution of forest-derived carbon (FDC) to the soil organic C (SOC) pool along a natural succession from savanna (S) to mixed Marantaceae forest (MMF) in the Lopè National Park, Gabon. Four 1-hectare plots, corresponding to different stages along the natural succession, were used to determine the SOC stock and soil C isotope composition ($\delta^{13}C$) to derive the FDC contribution in different soil layers down to 1 m depth. Besides, to investigate changes in SOC stability, we determined the ^{14}C concentration of SOC to 30 cm depth and derived turnover time (TT). Results indicated that SOC increased only at the end of the succession in the MMF stage, which stored 46% more SOC (41 Mg C ha^{-1}) in the 0-30 cm depth than the S stage (28.8 Mg C ha^{-1}). The FDC contribution increased along forest succession affecting mainly the top layers of the initial successional stages to 15 cm depth, and reaching 70 cm depth in the MMF stage. The TT suggests a small increase in stability in the 0-5 cm layer from S (146 years) to MMF (157 years) stages. Below 5 cm the increase in stability was high, suggesting that FDC can remain in soils for a much longer time than savanna derived C. In conclusion, the natural succession towards Marantaceae forests can positively impact climate change resulting in large SOC stocks, which can be removed from the atmosphere and stored for a much longer time in forest soils compared to savanna soils.

Introduction

Over the past century, woody plant encroachment has been a widespread phenomenon in grassland and savanna ecosystems worldwide (Eldridge et al. 2011). Land use management practices such as reduction of grazing and fire frequency are often the cause. In addition, ongoing climate change, historic atmospheric carbon dioxide (CO_2) enrichment and the introduction of exotic plant species are also potentially important drivers contributing to forest expansion into savannas (Buitenwerf et al. 2012). Current trends in atmospheric CO_2 enrichment may exacerbate shifts from grass to woody plant dominated ecosystems, especially where the invasive woody vegetation is capable of symbiotic nitrogen fixation. Expansion of woody plants into savannas may also be favoured by increases in atmospheric nitrogen (N) deposition (Boutton and Liao 2010). In addition to influencing vegetation composition, woody encroachment may lead to changes in C storage and dynamics. Understanding the consequences of forest expansion on ecosystem and soil organic C (SOC) stocks is crucial for improving predictions of current and future effects of land use and land cover changes on the global C cycle.

Savannas have a discontinuous tree layer which lies within a continuous herbaceous layer (Veenendal et al. 2014). In tropical savannas, grasses and sedges are mainly C4 species, i.e. use the C4 photosynthetic pathway, and they are typically enriched in ^{13}C ($\delta^{13}C \approx -12‰$) compared to most trees, shrubs and herbaceous plants, which utilise the C3 photosynthetic pathway ($\delta^{13}C \approx -27‰$). In fact, the C3 metabolism is coupled with a high discrimination against ^{13}C during the atmospheric assimilation of CO_2 (Farquhar et al. 1989; Kohn 2010). The C isotope composition of soil organic matter (SOM) in the top mineral soil is determined by inputs of organic material from the standing vegetation (Boutton et al. 1998). The $\delta^{13}C$ of SOM is slightly enriched in ^{13}C compared with plant biomass ($\leq + 2‰$) and is stable over long-time periods (Wedin et al. 1995). Since SOM accumulates over time, the $\delta^{13}C$ of deep soil layers reflects inputs of organic matter from past vegetation. Thus, the $\delta^{13}C$ concentration along soil profiles can be used as an indicator of changes in the abundance of C3 and C4 plants over time (Boutton et al. 1998). Taking advantage of the fact that the C4-type organic matter of savanna grass is less depleted in ^{13}C than the C3-type organic matter of forest trees, it is possible to partition the SOC into forest-derived C (FDC) and savanna-derived C (SDC) by measuring the isotopic composition of SOC (Novara et al. 2013). This information is useful for understanding SOC dynamics along the woody encroachment process and the potential consequences for soil C stocks.

Due to the presence of a characteristic forest-savanna mosaic, Lopé National Park (LNP) in central Gabon represents an ideal situation for investigating the SOC dynamics as a result of the natural expansion of forests into savannas (Aubreville 1967). Anthropogenic fires have been used in the area for thousands of years, and Lopé's savannas are burned annually, either as part of the Park management burn plan or by fires caused by local people. Despite regular fire use, forest encroachment is occurring rapidly (Jeffery et al. 2014). As a result, different stages of forest colonization of soils formerly occupied by savannas can be found in the Park, with mixed Marantaceae forest formations representing an intermediate successional stage between colonising forests and mature forests (White 2001). Chiti et al. (2017) described the variation in SOC stocks along the natural succession from savanna to mixed Marantaceae forest within the LNP, showing how SOC increases as forests develop. To complement these results, we carried out another sampling campaign using pseudoreplicates (Hurlbert, 1984) on the same successional stages considered in the study by Chiti et al. (2017), with the aim of quantifying the contribution of FDC to the observed changes in SOC. Specifically, our aims were: (a) to assess the contribution of FDC versus SDC during SOC accumulation along a natural succession from savanna to mixed Marantaceae forest in the LNP by using ^{13}C/^{12}C stable isotope ratio measurements and, (b) to investigate possible changes in SOC stability along the natural succession using radiocarbon (^{14}C) measurements to derive SOC turnover time (TT).

Materials and Methods

Area description

The Lopé National Park, Gabon, (00° 10′ S; 11° 36′ E) covers an area of 4970 km^2. Mean annual temperature varies between 23 °C and 31 °C while mean annual rainfall is 1474±45 mm (measured from 1984 to 2004 at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) in the north-east of the Park). The park is part of the Congo-Ogouè Basin lowland forests and it is mainly covered by closed canopy rainforest, while the north of the park is characterised by a savanna-forest mosaic, with the savanna thought to be a remnant of savannas from the glacial periods (Maley et al. 2012). Over twenty vegetation types have been described in the Park, including young colonising forests, forests dominated by *Aucoumea klaineana* Pierre and *Sacoglottis gabonensis* (Baill.) Urb., Marantaceae forests and mature forests (White 1995). The geological substrate of the area is characterised by the presence of metamorphic rocks (Schlüter 2008) and typical soils are comprised within the order of Oxisols (Chiti et al. 2017).

Vegetation types and experimental design

According to the different vegetation types present within the LNP (White 2001), soil samples were collected in four distinct vegetation types which represent different successional stages of the natural succession from savanna to mixed Marantaceae forest: (1) savanna (S); (2) colonising forest (CF); (3) monodominant forest (MF) and; (4) mixed Marantaceae forest (MMF). Compared to the experimental design of the study by Chiti et al. (2017), an intermediate stage was not considered due to the non-significant differences observed with the other stages. The mixed Marantaceae forest is not the final stage of the succession, since it can eventually evolve into a mature forest without abundant Marantaceae (White 1995). However, this climax formation does not occur in the immediate vicinity, so this stage was not included in the experimental design. The S stage is dominated by herbaceous species such as: *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth., *Bridelia ferruginea* Benth., and *Psidium guineensis* Sw., with scarce presence of tree species (e.g.

no *Acacia* spp) (Cuni-Sanchez et al. 2016). The CF stage is characterised by an open canopy and the presence of heliophile species such as: Okoume (*Aucoumea klaineana* Pierre), *Lophira alata* Banks ex C.F. Gaertn., 1805 and *Sacoglottis gabonensis* (Baill.) Urb, which are typical of early stages of forest colonisation on savannas (Cuni-Sanchez et al. 2016). The MF stage is representative of areas where savanna colonisation occurred 50-100 years previously and colonising species have grown up in a dense stand (White 1995), being characterised by a closed canopy of Okoume trees of similar age and an open understory. The MMF stage is a mature Marantaceae forest that is several hundreds of years further along the successional gradient, where remaining colonising trees have matured into large trees and begun to die, allowing some recruitment of later successional species. The canopy is more heterogeneous, with very large trees and an understorey dominated by plant species of the *Marantaceae* and *Zingiberaceae* families (White 1995). This forest is characteristic of savanna-colonising forests in central Africa with abundant megafauna (e.g. forest elephants and gorillas) which greatly delay or arrest forest succession by feeding off the abundant and palatable Marantaceae tree seedlings (White 1995). In all successional stages the soil type is comprised within the order of Oxisols (Soil Survey Staff 2014), with a sandy clay loam texture and a pH of 4-5 in the topsoil (0-30 cm depth) and a sandy clay texture and a pH of 5-5.5 in the subsoil (30-100 cm depth) (Chiti et al. 2017). The soil homogeneity in the different stages excludes possible bias in SOC variations due to variations in soil parameters (Chiti et al. 2017).

Soil sampling and SOC stock determination

In 2012, we delimited a one-hectare plot for each of the four vegetation types. The plots were initially established for studies on vegetation dynamics (White 2001), and subsequently used for studies on SOC dynamics (Chiti et al. 2017) and for aboveground biomass and C mapping studies (Saatchi et al. 2011; Mitchard et al. 2012; Cuni-Sanchez et al. 2016). In each plot, a soil trench was digged for soil description down to 1 m depth. Samples from the organic horizon (litter layer) were randomly collected in ten sampling points by using a 20 cm by 20 cm frame. In the same points, samples from the mineral soil were collected in the topsoil at the depths of 0-5, 5-15 and 15-30 cm using a cylinder of known volume (diameter = 5 cm; height = 5 cm) to determine also bulk density (BD). In the case of subsoil, ten samples were collected at 30-50, 50-70 and 70-100 cm depth, using an auger, while the BD was determined collecting three samples per layer in the trench using a cylinder of known volume.

All samples were oven-dried (60 °C) to constant mass, except those for bulk density which were oven-dried at 105 °C till constant mass. The litter layer was ground in a ball mill, whereas the mineral soil was sieved at 2 mm and all the analyses were performed on the fine soil fraction (< 2 mm). In all soil samples (n=10 per layer), total C was measured on finely ground aliquots by dry combustion (Thermo-Finnigan Flash EA112 CHN, Okehampton, UK), which corresponded to organic C content given the absence of carbonates in these soils. The SOC stock was calculated for each soil layer according to Boone et al. (1999). Changes in SOC stocks for the mineral soil were discussed for two main soil compartments: 0–30 cm depth (topsoil), and 30–100 cm depth (subsoil) according to the IPCC guidelines (IPCC 2006).

Sources of SOC

Besides root turnover, the sources of SOC in forests are leaf litter and small or large woody debris and in savannas are litter of grasses and small trees. In the S stage, grass samples were collected within the plot on three out of the ten points used for soil sampling by using a 40 cm by 40 cm frame. In the forest stages CF, MF and MMF, woody debris from the main tree species contributing to litter deposition (n=3 per species) were also sampled by collecting small pieces of wood directly below trees. Samples were oven dried at 60 °C to constant mass, broken into small pieces using a grinder in the case of wood samples, and finally milled with a ball mill.

$\delta^{13}C$ determinations

The vegetation samples collected to identify C sources to soils, and three soil samples randomly selected from every layer of each stage were analysed with an isotope ratio mass spectrometer (CF-IRMS, IsoPrime, GV Instruments, Cheadle Hulme, UK) connected to an elemental analyser (NA-1500, Carlo Erba, Milan, Italy). Stable isotope compositions were calculated according to the equation: $\delta = 1 - R_s/R_{st}$, where R_s and R_{st} are the isotope ratios of the sample and of the standard, respectively. The δ-equation (in per mil; ‰) was expressed as suggested by the international standard (VPDB for $\delta^{13}C$) and calculated by considering the values of the following international reference materials: NBS-22 fuel oil (IAEA – International Atomic Energy Agency, Vienna, Austria) and IAEA-CH6 Sucrose, for $^{13}C/^{12}C$ isotope ratio measurements. The relative precision of the repeated analysis was ± 0.1‰.

The $\delta^{13}C$ values determined for each sample were used to calculate the fraction of SOC derived from the new woody vegetation (C3) and that derived from the SOC fraction of the previous savanna vegetation (C4). These proportions were calculated with the mixing equation reported by Gearing (1991):

$$\text{Forest derived C (FDC)} = \frac{\delta^{13}\mathrm{C}_{new} - \delta^{13}\mathrm{C}_{old}}{\delta^{13}\mathrm{C}_{new\,plant} - \delta^{13}\mathrm{C}_{old}} \qquad [1]$$

and

$$\text{Savanna derived C (SDC)} = 1 - \text{FDC} \qquad [2]$$

where FDC is the fraction (expressed as percentage) of C derived from new forest vegetation, $\delta^{13}C_{new}$ is the isotope ratio of the soil sample, $\delta^{13}C_{new\ plant}$ is the isotope ratio of the forest vegetation present in that specific stage and $\delta^{13}C_{old}$ is the isotopic ratio of the previous vegetation type, which correspond to the vegetation present in the former stage of the succession.

^{14}C measurements

An aliquot of the same samples collected at 0-5, 5-15 and 15-30 cm depth from each stage (n= 3 per layer) and used for ^{13}C determination was analysed for the ^{14}C relative concentration. The samples were combusted and the produced CO_2 reduced to produce Zn graphite over iron powder catalyst by means of TiH2 (at 560 °C for 8 hours), according to Marzaioli et al. (2008). Graphite was pressed in Al cathodes and measured by an Accelerator Mass Spectrometer (AMS) system based on a 3MV tandem accelerator at the Centre for Isotopic Research on Cultural and Environmental heritage (CIRCE) of the University of Campania, Italy. Unknown samples were measured in a wheel together with: i) machine (n=4) and preparation (n=3) blanks to correct for background; ii) Oxalic Acid II (OXII) samples (n=4) to normalise measured ^{14}C ratios to absolute values; iii) cellulose (IAEA C3) samples (n=2) and wood (IAEA C5) standards (n=1) to check for the accuracy of the entire procedure (Terrasi et al. 2008). Measured radiocarbon ratios were expressed in percent Modern Carbon (pMC) according to Stuiver and Polach (1977).

Soil organic carbon turnover time

The turnover time (TT) of SOC was calculated from the ^{14}C concentrations, using a time-dependent no steady-state (TDNSS) model for S, CF and MF stages (Gaudinski et al. 2000), while for the MMF stage we used a time-dependent steady-state (TDSS) model (Gaudinski et al. 2000).

The choice of different TT models was done because in the plots representing the first two forest stages of the succession (CF and MF), aboveground biomass increased over the past 20 years indicating unstable conditions, while in MMF plot no significant biomass changes were observed over the same period, suggesting stable conditions for the vegetation of this stage (Cuni-Sanchez et al. 2016). The S stage was also considered not stable given that it can evolve quite rapidly into CF (Jeffery et al. 2014). The TDSS model relies on important assumptions: a) being at the steady state, i.e. C inputs and C losses are equal; b) the ^{14}C signature of SOC at any time depends on the ^{14}C signature of the atmosphere in previous years; c) the time-lag between the ^{14}C value of the atmosphere and new inputs to a given pool is one year for both, savanna and forest stages (deciduous species); d) all C atoms in a given pool have the same probability of leaving that pool (i.e., normal distribution of TT within a pool), and e) any given pool is homogenous in terms of ^{14}C signature. An atmospheric radiocarbon dataset of the bomb-spike period (1950-2011) was developed from Hua et al. (2013) for the southern hemisphere (SH3 zone), annually averaging all available data to smooth the seasonal variability of atmospheric ^{14}C. Data gap filling and extrapolation from 2011 to the year of measurements (2012) for the SH3 zone was performed using the best fitting function. A pre-bomb dataset (^{14}C in the atmosphere before 1950) for the SH3 zone was obtained from Levin and Hesshaimer (2000).

Radiocarbon concentration on the bomb-spike curve results in two possible TT's on the opposite sides of the ^{14}C peak (Marín-Spiotta et al. 2008). In our case, this occurred only for ^{14}C concentration higher than 104 pMC. We identified the more likely of the two solutions based on the aboveground C inputs from litterfall and the SOC stock of that specific soil layer, according to McFarlane et al. (2013) and Marin-Spiotta et al. (2008). For example, a ^{14}C pM value of 105.9% for the 0–5 cm soil layer in the savanna corresponded to two possible TTs, 4 and 157 years. The consideration that a TT of 4 years for the 0–5 cm soil layer required the same C input as the above lying organic horizon, whereas a TT of 157 years required just one-third of the annual aboveground litterfall, led us to assume 157 years as the most likely solution.

Statistical analyses

The statistical analyses related to the differences in C concentration, SOC stocks, $\delta^{13}C$ and ^{14}C concentrations between the soil layers of the different successional stages consider the fact that this study is based on simple pseudoreplication (Hurlbert 1984; Millar and Anderson 2004). We used the statistical approach followed by Blanco-Canqui et al. (2006) and by Lai et al. (2014) when investigating the changes in SOC and other parameters in adjacent plots. Specifically, we applied a one-way ANOVA to test differences in the selected parameters (e.g. SOC stocks, $\delta^{13}C$ and ^{14}C

values) among the four successional stages of woody encroachment for each soil layer. The data were analysed assuming a randomized experiment using the ten sampling locations within each successional stage as pseudoreplicates. It is assumed that woody encroachment is mostly responsible for the differences in SOC stocks, δ^{13}C and ^{14}C values among the stages because all the considered plots are very close to each other. The fours stages are arranged in a natural field block confining the four stages on a very similar landscape position, slope, and soil features. Chiti et al. (2017) reported that differences in soil texture among these stages were not significant.

A post hoc mean comparison was performed using Fisher's protected least significant difference (LSD) method ($P<0.001$). Pearson's correlation coefficients and associated significances were calculated to assess interrelationships among the measured soil properties. The entire statistic was implemented using the R software with a $p<0.001$ (R Core Team 2016).

Results

SOC concentration and stocks along the succession

SOC concentration decreased with soil depth in all of the successional stages (Table 1). Along the natural succession, SOC increased from the S to the MMF stages in most layers (Table 1). This was particularly evident in the 0-5 cm layer when comparing the different stages: 12.8±0.3 g C kg^{-1} (S), 13.8±0.4 g C kg^{-1} (CF), 17.2±0.9 g C kg^{-1} (MF) and 30.7±1.9 g C kg^{-1} (MMF). For the 5-15 and 15-30 cm layers, no significant changes ($P > 0.001$ in all cases) were observed along the succession. Below 30 cm depth the SOC increased significantly already in the first stage of the succession and then remained stables along the different successional stages (Table 1).

In terms of C stocks, the amount of C in the litter layer (absent in the savanna plots) increased along the succession: 3.6±1.5 Mg C ha^{-1} in the CF, 4.8±1.9 Mg C ha^{-1} in the MF, and 6.8±3.4 Mg C ha^{-1} in the MMF (Table 1). Considering SOC stocks in the mineral soil, there were no significant differences in the top 0-30 cm compartment from the savanna (28.5±1.9 Mg C ha^{-1}) to the first stages, CF (31.6±2.4 Mg C ha^{-1}) and MF (32.3±3.4 Mg C ha^{-1}), while in the MMF stage the SOC stock increased significantly (41.0±3.2 Mg C ha^{-1}) compared to all previous stages (Table 1). On the other hand, a significant SOC increase was evident in the subsoil (30-100 cm depth) already in the first stage of the succession, CF (40.7±3.1 Mg C ha^{-1}), compared to savanna (23.4±2.1 Mg C ha^{-1}), and then remained quite stable in the following MF (41.0±4.3 Mg C ha^{-1}) and MMF (45.2±3.4 Mg C ha^{-1}) stages (Table 1).

Contribution from different C sources

Differences in δ^{13}C values for the SOC among the stages reflect the signature of the vegetation mostly contributing to C inputs (Figure 1). While in the S stage the δ^{13}C of the C source to soil was -20.2‰, when the woody species become dominant they impact greatly the δ^{13}C of SOC sources. This already happened in the CF stage with values reaching -28.7‰ (Figure 1). The source of SOC in the other stages clearly continue to reflect the signature of the main woody species contributing to C inputs to the soil, with δ^{13}C values of the SOC source clustering at -27.4‰ and -28.8‰ for MF and MMF forest stages, respectively (Figure 1). Looking at the soil, the δ^{13}C values varied in the S stage from -16.7‰ at the soil surface to -22.7‰ at 70-100 cm depth (Figure 2). In the other successional stages, the trend was inverted with the δ^{13}C values increasing with soil depth (Figure 2).

Within each stage, the contribution from FDC decreased normally with depth. The FDC pattern between stages indicates that in the CF and MF forest stages the standing vegetation contributed to the majority of the SOC in the top two layers while in the 15-30 and 30-50 cm layers less than 50% of SOC derive from the standing vegetation. Below 50 cm depth no SOC deriving from the forest vegetation was detected in the different layers (Figure 3). However, in the MMF forest stage all SOC in the top two layers derived from forest vegetation, while in the 15-30 and 30-50 cm layers the contribution was around 50%. The influence of FDC was detectable also in the 50-70 cm layer although with a small contribution, about 15% of total SOC (Figure 3).

^{14}C concentration and SOC turnover time

In the S and CF stages, the ^{14}C concentration increased from 0-5 cm to 5-15 cm and decreased in the 15-30 cm layer, while in the MF and MMF stages always decreased with depth (Figure 4). The comparison of the different stages and layers indicated a decrease in the ^{14}C concentration from the S stage to the MMF stage (Figure 4). Nevertheless, even small differences in ^{14}C concentration can produce appreciable differences in the SOC turnover time. In the 0-5 cm layer the TT become longer from the S stage (146±1 yr) to the CF (203±25 yr) and MF stages (204±16 yr). In the MMF stage the TT is shorter than previous stages, 157±2 yr, while remaining significantly higher than the S stage (Table 2). In the other two layers, the TT was significantly longer in the MMF than in the S stage, with values more than double (Table 2). In the two intermediate forest stages, CF and MF, the TT also increased with stand development with values significantly longer than savanna, particularly in the 15-30 cm layer.

Discussion

Effect of woody encroachment on SOC stocks

In central Africa a major vegetation change occurred three thousand years ago when savannas and secondary grasslands replaced mature evergreen forests (Ngomanda et al. 2009). This vegetation shift has been attributed to a regional climate change (Maley et al. 2012; Neumann et al. 2012). Today, the situation is reversed with savannas being encroached by forests (Delègue et al. 2001; White 2001) with an expected increase in C stocks at ecosystem level, which could potentially contribute to the stabilisation of the increasing atmospheric CO_2 concentration given the extent of the woody encroachment process in Africa (Mitchard et al. 2013).

In term of SOC variations, as soon as woody species increase, SOC increases too. The increase was immediately evident for the subsoil since the first stage. Differently, SOC changes in the topsoil appeared only in the last stage, the mixed Marantaceae forest, although savanna C can decompose faster than SOC deriving from woody vegetation (Wynn and Bird 2007). Thus, overall, SOC increased with woody encroachment in this area. Precipitation has been proposed as an important factor determining the trend in SOC changes upon encroachment (Jackson et al. 2002). Some studies have observed a negative relationship between precipitation and SOC changes after woody plant invasion on herbaceous vegetation, with SOC levels decreasing in areas of high precipitation (>1200 mm) and increasing in areas with low precipitation (Jackson et al. 2002; Guo and Gifford 2002). These studies suggest that high precipitation induces higher SOC losses as dissolved organic C diminishing the potential SOC accumulation. Besides, under optimal moisture conditions, C mineralisation is high and SOC losses via soil respiration are higher than in drier sites, where low precipitation limits microbial activity favouring SOC accumulation. However, even though precipitation in the Lope National Park is well above 1200 mm, we did not detect any SOC loss and, in the long term, we detected a considerable SOC increases on both 0-30 and 30-100 cm soil compartments. The increase in SOC stock observed in this study suggests that C inputs via litter and roots are higher than C losses even if precipitation is high. In particular, the change in the quality of the C inputs arriving to soil has been proved to have a significant impact on the microbial biomass, and as a consequence on the SOC decomposition (Shihan et al. 2017). The combined effect of increasing litter inputs along the successional stages, and the presence of herbs, which still dominate the understory layer of all the stages, could be responsible for the observed long-term SOC increase in the topsoil. In most of the encroached sites outside the tropical area, in mature forests the herbaceous layer is usually absent or greatly reduced (Gilliam 2007). The large increase in SOC observed in the subsoil at the beginning of the woody encroachment process is most likely the result of a different root distribution along the soil profile with deeper root systems of tree species compared to savanna herbaceous species, which are concentrated in the topsoil.

Forest contribution to soil carbon during natural succession

In terms of contribution from the different vegetation types to the SOC pool, the $\delta^{13}C$ values observed in top two layers of the colonising and monodominant forest stages, revealed an important contribution from FDC indicating that forest vegetation can rapidly contribute to the SOC of surface layers. The contribution of FDC below 30 cm depth, about 25% (colonising forest) and 20% (monodominant forest) of the total SOC in the 30-50 cm layer, is probably responsible for the SOC stock increase observed in the subsoil compartment of the first stages along the natural succession. The $\delta^{13}C$ values observed in the 50-70 cm and 70-100 cm layers of the first two stages, where the FDC contribution was absent, suggest that the intermediate forest stages developed over a soil formerly occupied by savanna vegetation. On the other hand, the $\delta^{13}C$ difference between the SOC source and the values observed in the lower layer of the savanna stage (+2.5‰) was lower than the enrichment reported in the literature, of up to +4‰ (Sanaiotti et al. 2002; Ehleringer et al. 2000), indicating that SOC inputs originate mostly from savanna vegetation. Similarly, in the forest stages a difference of +8.2‰ (CF), +9.1‰ (MF) and +6.6‰ (MMF) between the signatures of the SOC source and the lower soil layer revealed that SOC does not derive from forest vegetation only, suggesting that all forest stages developed over a soil formerly occupied by savanna. In forest ecosystems, the $\delta^{13}C$ of SOC commonly increases with soil depth by 1–3‰ relative to that of the litter layer, but the reasons for this increase are not yet fully understood (Nadelhoffer and Fry 1988; Wynn et al. 2005). According to Wynn et al. (2006), we quantified the uncertainty related to the occurrence of a possible fractionation, which could be due to mixing of SOC from different sources or ^{13}C distillation during SOC decomposing. Taking into consideration a fractionation factors of 0.999 (discrimination of 3‰) the measured $\delta^{13}C$ concentrations in the different layers of every stage can vary of about ± 2.5‰. This can results in an overestimation of the FDC contribution in the different stages, which is decreasing with depth and it is varying from 16% to 18% in the 0-5 cm layer, and from 5% to 14% in the 30-50 cm layer. Below 50 cm of depth the FDC overestimation could be possible only in the 50-70 cm layer of the last stage (about 10%), being absent in the other two forest stages. Nevertheless, even taking into account the possible SOC fractionation occurring along the soil depth the observed values suggest a C contribution from different sources. This fact is in agreement with the findings of Oslisly et al. (2006), which dated the savannas in the Lope Natural Park to more than 40,000 years ago. Given that at steady state the turnover time of SOM is equivalent to the radiocarbon age, and that the SOC turnover time in the mixed forest stage at 15-30 cm depth is about four centuries, the SOC from the layers below 30 cm depth most likely derived from the former savanna vegetation present when the natural succession took place. In the surface layers of all stages, the $\delta^{13}C$ difference between the signatures of C source and that of the SOC typically resembles the ^{13}C enrichment expected during the decomposition of the standing vegetation inputs (Boutton et al. 1998; Nadelhoffer and Fry 1988). These data demonstrate the rapid shift in $\delta^{13}C$ signature for topsoil layers, from values characteristic of savanna to values typical of forest-derived vegetation. In term of SOC stocks, the contribution from FDC in the topsoil almost doubled from the colonising forest stage (21.7 Mg C ha^{-1}) to the mixed Marantaceae forest stage (39.1 Mg C ha^{-1}) confirming the potential of woody vegetation to increase SOC stocks. Similarly, in the subsoil, the FDC was much higher in the final stage than in previous stages, despite a possible overestimation should be considered. Apart from the SOC increases during the natural succession, the overall pattern of C increases at ecosystem level, as a consequence of the transition from savanna to forest, is more clearly understood in the context of the C stored in above ground biomass. Cuni-Sanchez et al. (2016) measured the aboveground biomass in the same forest plots (savanna plot excluded), and observed an increase from colonising forest (51 Mg C ha^{-1}) to monodominant forest (194 Mg C ha^{-1}) and finally to mixed Marantaceae forest (247 Mg C ha^{-1}). In savannas, the aboveground C stocks can vary widely depending on tree cover, from 1.8 Mg C ha^{-1} where trees are absent, to over 30 Mg C ha^{-1} where there is substantial tree cover (Grace et al. 2006). Considering both, SOC and aboveground biomass increases during the transition to forest, it become evident the huge amount of C that can be sequestered during the woody encroachment process highlighting the importance of Marantaceae forest formations also for climate change mitigation purposes.

SOC stability along the natural succession

The comparison of the C turnover time in soils indicated longer recycle times for the SOC in the different layers within the topsoil of the forest stages than in the savanna, suggesting an effect of forest vegetation in stabilising SOC. The positive effect of woody vegetation in increasing the SOC stability can be explained by an increase in the recalcitrance of C inputs of woody tissues compared with herbaceous vegetation (Marín-Spiotta et al. 2008). Woody plants produce compounds such as waxes, suberin, cutin, and terpenoids, which are resistant to oxidation and consumption as protection against parasitism and herbivory (Gleixner et al. 2001). The production of these and other plant secondary compounds increase during tropical forest succession (Coley and Barone 1996). Compared to the 0-5 cm layer, the shorter turnover time observed in the 5-15 cm layer of the savanna and colonising forest stages is probably related to a SOC leaching operated by the abundant precipitations. The decrease in turnover time was particularly evident in the savanna stage, where rain impacts directly the soil surface and in the colonising forest stage that still showed a not uniform canopy cover. On the other hand, root depositions from herbaceous vegetation, which is still abundant in the CF stage, can contribute greatly to the observed turnover time reduction, by generating every year fresh C inputs, which are incorporated into the soil. Considering all the stages, the trace of the ^{14}C produced with the nuclear weapon tests in the 1950's (bomb C) was clearly detectable down to 30 cm depth, indicating that most of the SOC stored in the topsoil was derived from the standing vegetation existing at the sites, as previously showed by the ^{13}C measurements.

Finally, considering the two extremes of the succession, savanna and mixed Marantaceae forest, the increase in FDC in the three layers included in the topsoil coincided with an increase in the time of permanence of SOC in the same layers. In the final stage the time an atom of C stays in a layer within the topsoil was almost double the time determined in the savanna, except in the 0-5 cm layer where the increase was minimal.

Conclusions

The Marantaceae forest is an unusual successional forest for the tropics, being probably created by the synergy between Marantaceae, gorillas and elephants. Because of this, such a forest type is unique in respect to any other successional forests. Despite the observed results should be used with caution because of the limitations caused by the use of pseudoreplicates, it is suggested that Marantaceae forests have the capacity to greatly impact SOC cycling by replacing the organic matter from the former savanna vegetation and increasing SOC stocks in a relatively short time. Already few decades after the beginning of woody encroachment, most of the SOC in the topsoil was derived from the standing woody vegetation. Furthermore, an increased stability of SOC suggests that the input of carbon from Marantaceae vegetation can remain in soils for longer time periods than savannah derived carbon. In conclusion, the growth of Marantaceae forest vegetation into savannas had a positive impact on SOC stocks by inducing the sequestration of large amounts of CO_2 from the atmosphere and by storing carbon in more stable compartments, i.e. in soils and plant biomass. Therefore, woody encroachment processes, which are occurring throughout the African continent and other rainforest regions across the world, may contribute significantly to the terrestrial C sink by increasing stabilised forms of organic C into soil, the largest pool of the terrestrial C cycle.

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Figure legends

Figure 1. $\delta^{13}C$ concentration (n=3) of C sources in the different stages of the natural succession. S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

Figure 2. $\delta^{13}C$ concentration (n=3) of SOC in the different soil layers of each stage of the natural succession. S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

Figure 3. Contribution of forest derived C (FDC) and savanna derived C (SDC) to the total SOC stock in each layer of the colonising forest (CF), Marantaceae forest (MF) and mixed Marantaceae forest (MMF) stages.

Figure 4. ^{14}C concentration (pMC) of the SOC from the 0-5, 5-15 and 15-30 cm layers of the different stages of the natural succession. S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

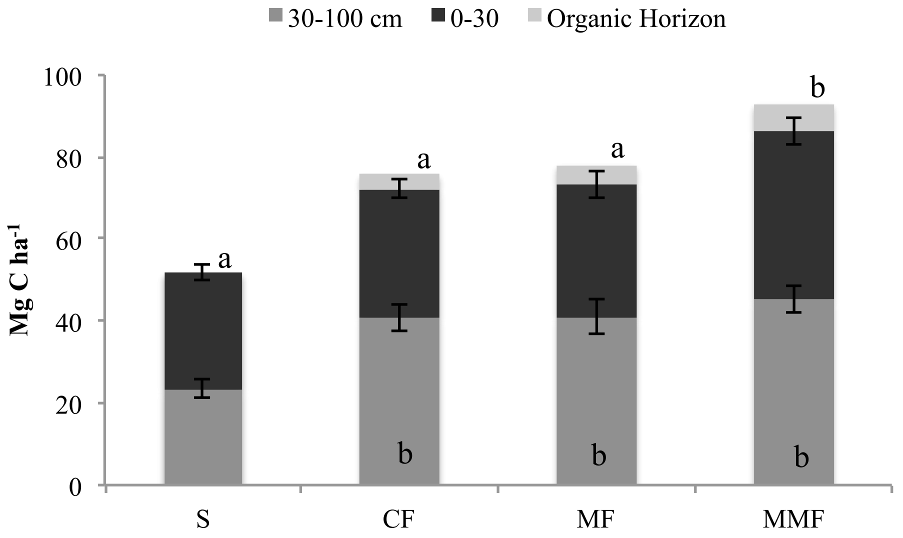
30-100 cm
0-30
Organic Horizon
Mg C ha^{-1}
100
80
60
40
20
0
S
CF
MF
MMF
a
a
a
b
b
b
b

Figure 1 -

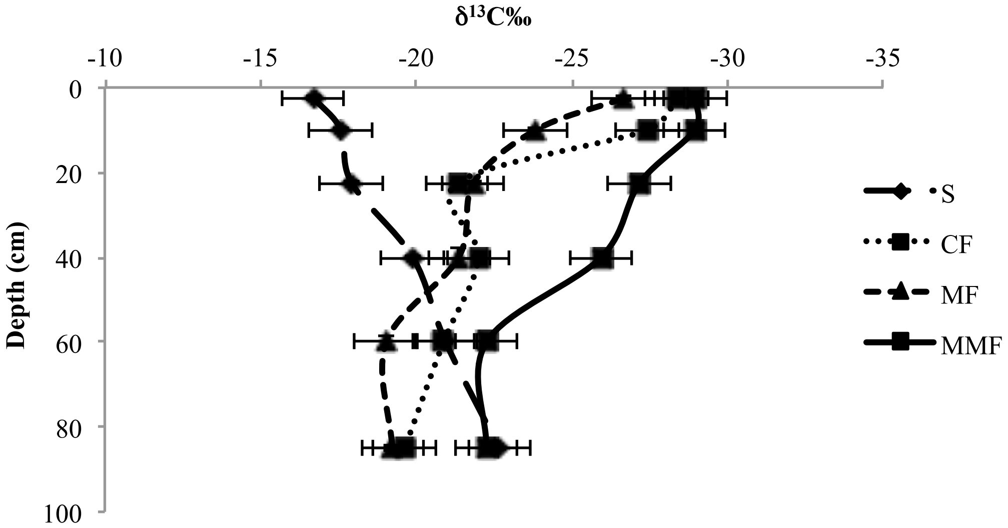

Figure 2 -

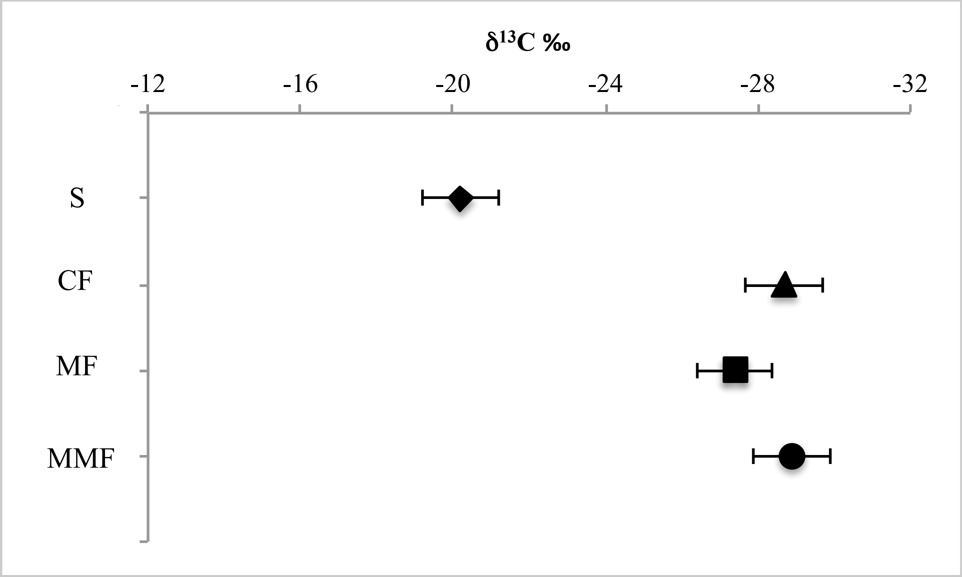

Figure 3 -

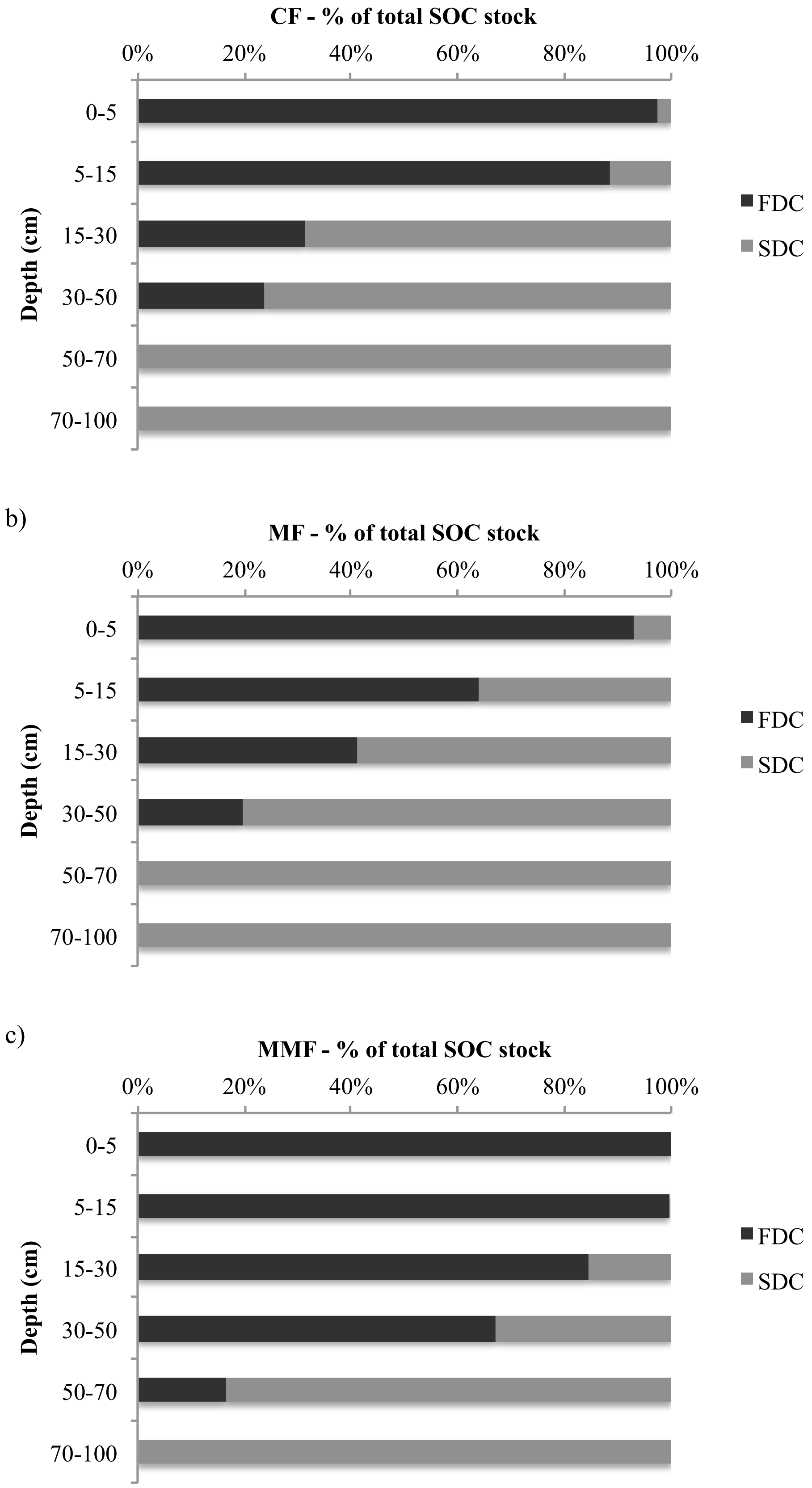
CF - % of total SOC stock
0%
20%
40%
60%
80%
100%
Depth (cm)
0-5
5-15
15-30
30-50
50-70
70-100
FDC
SDC
b)
MF - % of total SOC stock
0%
20%
40%
60%
80%
100%
Depth (cm)
0-5
5-15
15-30
30-50
50-70
70-100
FDC
SDC
c)
MMF - % of total SOC stock
0%
20%
40%
60%
80%
100%
Depth (cm)
0-5
5-15
15-30
30-50
50-70
70-100
FDC
SDC

Figure 4 -

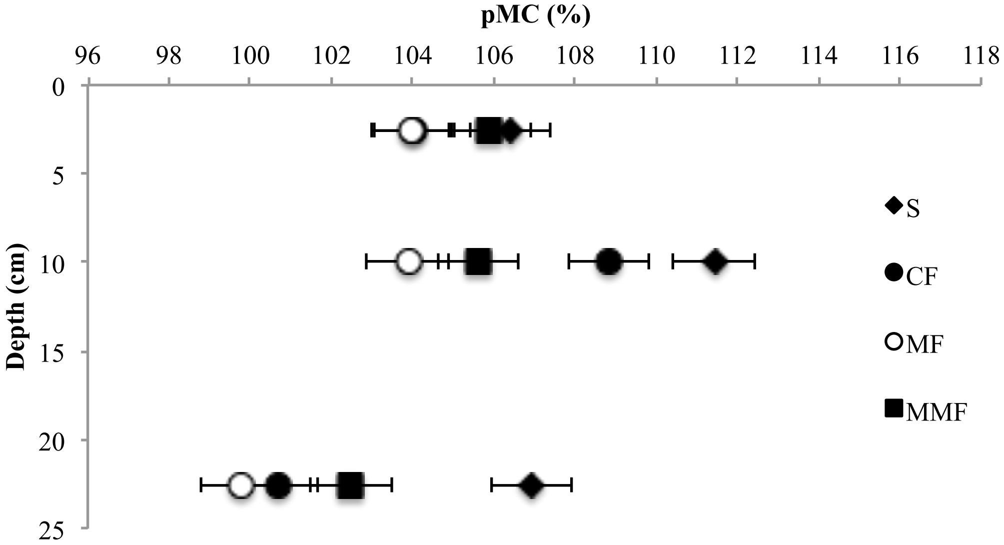
pMC (%)
96
98
100
102
104
106
108
110
112
114
116
118
Depth (cm)
0
5
10
15
20
25
◆S
●CF
○MF
■MMF

Figure 5 -

Table 1. Soil organic C (SOC) concentration (g C kg^{-1}) and stock (Mg C ha^{-1}) in the different soil layers of each stage of the natural succession. Values are the mean of 10 samples per layer ± 1 standard deviation. Different letters within each line indicate differences at $P<0.001$ for SOC concentration and stock separately (Fisher's protected LSD method).
S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

Depth	S		CF		MF		MMF	
cm	g C kg^{-1}	Mg C ha^{-1}	g C kg^{-1}	Mg C ha^{-1}	g C kg^{-1}	Mg C ha^{-1}	g C kg^{-1}	Mg C ha^{-1}
O. Horiz.				3.6±1.5		4.8±1.9		6.8±3.4
0-5	12.8±0.3a	7.8±0.8a	13.8±0.4a	8.4±1.0a	17.2±0.9a	10.4±1.3a	30.7±1.9b	18.5±2.5c
5-15	8.7±0.4a	11.1±1.1a	9.7±0.7a	11.0±1.5a	8.5±1.2a	10.1±2.0a	8.1±0.2a	10.4±1.3a
15-30	5.9 ±0.5a	9.5±1.2a	8.6±0.4b	12.3±1.6b	5.9±1.0a	11.8±2.4ab	6.1±0.2a	12.0±1.4b
30-50	3.6 ±0.2a	7.6±0.9a	4.7±0.5a	11.6±1.7b	5.7±0.6b	13.5±2.2b	5.5±0.3b	14.6±1.8b
50-70	2.8±0.3a	6.4±0.9a	4.5±0.3b	11.4±1.5b	4.7±0.5b	11.8±1.9b	4.9±0.3b	13.7±1.6b
70-100	2.3±0.3a	9.4±1.7a	4.5±0.3b	17.7±2.1b	4.6±0.6b	15.7±3.1b	3.7±0.3b	16.9±2.4b
0-30		28.5±1.9a		31.6±2.4a		32.3±3.4a		40.9±3.2b
30-100		23.4±2.1a		40.7±3.1b		41.0±4.3b		45.2±3.4b

Table 2. Bulk density (Mg m^{-3}) values for all the layers of mineral soil along the different stages of the natural succession toward forest. Within each column, no significant differences were observed for the same layer in the different stages (Fisher's protected LSD method). S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

Site	0-5 cm	5-15 cm	15-30 cm	30-50 cm	50-70 cm	70-100 cm
	Mg m^{-3}	Mg m^{-3}	Mg m^{-3}	Mg m^{-3}	Mg m^{-3}	Mg m^{-3}
S	1.1±0.1	1.2±0.2	1.3±0.2	1.4±0.2	1.4±0.2	1.5±0.2
CF	1.1±0.2	1.2±0.2	1.3±0.1	1.3±0.2	1.4±0.2	1.6±0.3
MF	1.2±0.2	1.3±0.2	1.3±0.2	1.4±0.3	1.4±0.2	1.6±0.2
MMF	1.2±0.2	1.3±0.2	1.3±0.2	1.3±0.2	1.4±0.2	1.4±0.2

Table 3. Soil organic C turnover time (TT) of the bulk soil samples (years) from the different stages of forest succession down to 30 cm depth. Values are the mean of 3 samples per layer ± 1 standard deviation. Numbers in brackets represent the TT that was discarded. Within each column different letters indicate significant differences between stages (Fisher's protected LSD method; *P*<0.001). S=savanna; CF=colonising forest; MF=Marantaceae forest; MMF=mixed Marantaceae forest.

	Turnover Time		
Site	0-5 cm	5-15 cm	15-30 cm
	Yr	Yr	Yr
S	146±1a (5)	75±1a (13)	137±1a (6)
CF	203±25b	106±1b (9)	329±2b
MF	204±16b	208±1c	370±1c
MMF	157±2c (4)	162±1d (7)	393±25c