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The origin of the forest-grassland mosaic of central Cameroon: What we learn from the isotopic geochemistry of soil organic matter

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Abstract

The end of the Holocene Humid Period was characterized by the massive collapse of forest ecosystems in central Africa. Was this large-scale environmental crisis dated between 3300 and 2500 years BP at the origin of the present-day wooded-grassland/forest mosaic of central Cameroon? Here we present carbon isotope data on soil organic matter collected from 29 sites from this area, including the Grassfield plateaus, with the aim of characterizing this environmental crisis and discussing the origin of the present-day landscape. ^{14}C data on total soil organic matter and charcoal fragments show that the organic matter in these soils originates from the Holocene. In our forest sites, the $\delta^{13}C$ profiles do not show any marked alteration of the forest cover throughout the Holocene. Discrete traces of forest expansion or retreat are observed only punctually at the forest margins. In the wooded-grassland/forest mosaic zone, the environmental crisis was of reduced amplitude. In the present grassland and wooded grassland areas, there was no true forest during the lower to middle Holocene, but a markedly more tree-covered landscape. The timing of this crisis revealed by our ^{14}C measurements, although only indicative at this stage, suggests that it occurred earlier at higher altitudes than in the lowlands due to marked topographic relief favoring drainage along the slopes. These results fit a climatic rather than anthropogenic origin of the vegetation opening in this region.

Keywords
Cameroon, Holocene, isotope, organic matter, soils, wooded grasslands

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Introduction

The presence of savannas (hereinafter referred to as grasslands and wooded grasslands according to White, 1983) in western Central Africa in areas where climatic conditions would allow the establishment of forests has long questioned naturalists (e.g. Aubréville, 1947; Letouzey, 1968) and paleoenvironmentalists (e.g. Schwartz, 1992; Schwartz et al., 1996a). These open landscapes do not occur only at the edge of the lowland forest block such as in central Cameroon or in Congo in the Batéké plateau, they also occupy less extensive areas within the rainforest as described by Cheek et al. (2004), in the Bakossi region in SW Cameroon. They are thought to have contributed to the recent isolation of forest populations such as the hunter-gatherers Bezan pigmies of Central Cameroon (Verdu et al., 2009). Whether these grasslands and wooded grasslands have a climate or anthropogenic origin is still an unanswered question. Numerous lines of evidence testify for the setting of intense dryness throughout the African tropics at the end of the Holocene Humid Period from 5.5 ka years ago (e.g. deMenocal et al., 2000; Gasse, 2000; Lézine et al., 2011, Vincens et al., 1999; Wirrmann et al., 2001). This climate crisis led to the regression of most of the tropical trees which widely expanded in northern tropical Africa during the Holocene (Hély et al., 2014; Watrin et al., 2009). In Central Africa, a dramatic decline of forests is also noted (e.g. Lézine et al., 2013b; Vincens et al., 1999) with a maximum between 3.3 and 2.4 ka BP. Central African forests were replaced either by secondary formations dominated by light-demanding trees or by grasslands or wooded grasslands, regardless of altitude. In this region, however, an additional factor has been

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evoked to explain the origin and/or magnitude of this event: the migration of Bantu farming people from the northern fringe of the forest, which gradually spread throughout Central Africa as evidenced by numerous linguistic and archaeological studies (Bostoen et al., 2015). In recording an abrupt event of intensified erosion dated 2.5 ka contemporaneous with a phase of herbaceous expansion, Bayon et al. (2012) then Garcin et al. (2018), among others, favored the hypothesis already evoked by Kadomura and Kiyonaga (1994) of an anthropogenic forest clearance. This hypothesis was questioned by most of the archeological community (Clist et al., 2018) because the population density was too low at that time to have such a widespread and dramatic impact on the forest environment. How deep was the environmental change in Central Africa? Do the present-day 'Grassfields' from the southern fringe of the Cameroon volcanic line (CVL) and the wooded grassland/forest mosaic of Central Cameroon originate from the environmental crisis dated from the end of the Holocene Humid Period? In focusing on this specific region our study complements earlier pollen (Lebamba et al., 2016; Lézine et al., 2013a; Maley and Brenac, 1998; Ngomanda et al., 2009; Reynaud-Farrera et al., 1996; Richards, 1986; Vincens et al., 2010) and soil studies (e.g. Bremond et al., 2017; Morin-Rivat et al., 2016; Thieblemont et al., 2013;) which documented different kind of present-day forests from both low- and high- elevation in Western Central Africa. Following an earlier, preliminary study based on six profiles (Desjardins et al., 2013), we present here isotope analyses on an extended dataset of 29 soil profiles collected in the wooded grassland/forest mosaic region, with the aim of discussing the origin of the present-day landscape of central Cameroon.

Materials and methods

Study area and sampling

The study area encompasses the large wooded grasslands (*Imperata cylindrica, Terminalia glaucescens, Annona* sp., *Bridelia ferruginea*) and wooded grassland/forest mosaic zone of central Cameroon and the Grassfield plateaus between 4°25′–6°10′N; 10°05′–12°25′E and 600–1800 masl (Table 1; Letouzey, 1968). The wooded grassland/forest mosaic zone includes isolated patches of semi-deciduous forests dominated by Sterculiaceae and Ulmaceae trees and forest regrowth or plantations (Coffea, Cacao) under forest. A sample (3°49′53″N; 13°19′54″) was also recovered in the semi-deciduous forest located to the South East, at the northern edge of the Congo Basin forest block (Figure 1). All the profiles lie under the Aw climate (Köppen classification) with annual rainfall from 1550 and 2100 mm with a dry season of 3–4 months and annual evaporation between 750 and 1500 mm (based on https://fr.climate-data.org).

The studied soils were located in the highest part of the relief on or near hilltops, and classified as ferralsols (IUSS Working Group WRB, 2014), with texture varying from clayey to sandy-loamy (Ségalen and Martin, 1965).

A total of 43 profiles were collected from pit or soil cores from which 29 were selected based on the quality of the isotope record (Table 1). We excluded from this study sites from hydromorphic or disturbed areas characterized by erratic isotope profiles. Our data set includes the six profiles already published (Desjardins et al., 2013). Each site yielded a single profile sampled at 10–20 cm interval from the surface to a maximum depth of 5 m. At two sites (CAM 12-1-02/17-4 and 12-1-06/17-3), the initial soil core recovered in 2012 was duplicated by a pit in 2017 where three profiles, <1 m apart, were sampled down to 2 m in order to measure the uncertainty of the data with respect to eventual lateral variations in the isotope record. The soil samples were air-dried, sieved with a 2-mm mesh, homogenized and crushed to <200 µm.

Organic carbon and stable isotopes

Aliquots of the samples ground at 70 meshes were submitted to an acid attack by HCl 3% to remove carbonates for both isotope measurements and radiocarbon dating. The organic carbon content and its isotopic composition from the soil profiles, expressed as mg g^{-1} and δ^{13}C ‰ values, respectively, were obtained using a continuous-flow gas-ratio mass spectrometer (Finnigan Delta PlusXL) coupled with an elemental analyzer (Costech; NSF Arizona), and an Isotopic Ratio Mass Spectrometer Delta V Thermofisher coupled with a Flash HT Elemental Analyzer (Alyses platform, Bondy). Standardization is based on acetanilide for elemental concentration, NBS-22 and USGS-24 for δ^{13}C. Precision is better than 0.10‰ for δ^{13}C, based on repeated internal standards.

The isotopic ratio ($R = {}^{13}C/{}^{12}C$) is reported in standard delta notation (δ^{13}C), defined as parts per thousand (‰) deviation from an international standard (Vienna Pee Dee Belemnite; Peterson and Fry, 1987): $\delta^{13}C = ((Rsample/Rstandard) - 1) \times 1000$. In comparing several soil profiles at the same site, we show that our isotope measurements are reliable with a mean distance between values at the same depth, <1.5‰. However, this value may increase up to 2.2‰ at levels from the center of the profile, between 50 and 150 cm depth. These fluctuations never affect the overall shape of the profile (Figure 2).

Radiocarbon dating

The radiocarbon measurements were performed on bulk soil organic matter and charcoal fragments which are sporadic in this region (only found in three of our sites). A total of 87 AMS radiocarbon dates were obtained from bulk organic matter of 17 profiles and 10 for charcoals. The AMS dating was performed with a 3 MV Pelletron (NEC, Middleton, Wisconsin, USA) at the Artemis radiocarbon laboratory facility (LMC14, Saclay, France). The radiocarbon measurements on the bulk OM represent a mixture of younger and older carbon pools whose residence time is increasing with depth and consequently do not correspond to the absolute age of soil organic matter (Bremond et al., 2017; Desjardins et al., 2013; Guillet et al., 2001; Schwartz et al., 1996b). As a consequence, the ^{14}C ages were not calibrated and the timing of past vegetation changes must be interpreted with caution (Boutton et al., 1998; Trumbore et al., 1995; Wiedemeier et al., 2012). For an easier comparison with earlier studies, ^{14}C values are expressed in ^{14}C years BP (apparent age according to Guillet et al., 2001).

Results

Distribution of organic carbon (data in Supplemental Table S1, available online)

All the soil profiles do not show significant differences in their total C distribution with depth (Figure 3). In the surface layer (0–10 cm), the organic carbon (C) content ranges from 16.3 to 49.8 mg g^{-1}. Then, the C content decreases abruptly until the 60–70-cm depth (4.5–16.3 mg g^{-1}). Below this level, the C content decreases slightly to reach 0.7–4.1 mg g^{-1} at 380–390-cm depth.

^{14}C dating of soil organic matter (data in Supplemental Table S2, available online) and charcoals

No dating of surface layers was realized, as high values of radiocarbon (>100% of the modern carbon) are generally found in the surface soil layers, due to the incorporation of carbon fixed from the atmosphere since atomic weapons testing in the early 1960s, which nearly doubled the amount of ^{14}C in the atmosphere (Balesdent and Guillet, 1982). The ^{14}C measurement are regularly

Table 1. List of soil profiles used in this study with their location within the main vegetation types defined by Letouzey (1985).

Site	Latitude	Longitude	Elevation (m)	Vegetation type (Letouzey, 1985)	Groups
CAM10-2-07	3.831278	13.331639	712	Semi-deciduous forest	1a
CAM10-2-17	5.650444	11.482778	773	Semi-deciduous forest	1a
CAM10-2-16	5.736139	11.561306	765	Semi-deciduous forest regrowth	1b
CAM12-1-05	5.762833	11.332639	710	Semi-deciduous forest regrowth	1b
CAM12-1-07	5.710500	11.137694	730	Semi-deciduous forest regrowth	1b
CAM12-1-08	5.745389	11.132889	724	Semi-deciduous forest regrowth	1b
CAM17-1-05	4.838500	11.073611	597	Semi-deciduous forest regrowth	1b
CAM10-2-20	5.018778	10.733389	796	Preforest wooded grassland	2
CAM10-2-21	5.026889	10.751083	743	Preforest wooded grassland	2
CAM15-1-03	5.641361	10.648417	1155	Montane wooded grassland	2
CAM10-2-09	4.852611	11.976639	607	Preforest wooded grassland	3a
CAM10-2-12	5.556333	12.220139	1007	Wooded grassland	3a
CAM10-2-13	5.606472	12.085944	884	Preforest wooded grassland	3a
CAM10-2-15	5.584167	11.703472	782	Preforest wooded grassland	3a
CAM10-2-18	5.451694	11.368556	640	Preforest wooded grassland	3a
CAM10-2-19	5.151722	11.326444	658	Preforest wooded grassland	3a
CAM12-1-04	5.478833	11.053972	785	Preforest wooded grassland	3a
CAM12-1-16	4.456500	11.926250	577	Preforest wooded grassland	3a
CAM12-1-17	4.568778	12.194778	601	Intraforest wooded grassland	3a
CAM15-1-16	5.278250	10.488028	1383	Preforest wooded grassland	3a
CAM10-2-10	5.987861	12.393056	963	Preforest wooded grassland	3b
CAM10-2-11	5.681778	12.370972	978	Wooded grassland	3b
CAM10-2-14	5.584667	11.840472	929	Preforest wooded grassland	3b
CAM12-1-02	5.410111	10.650306	1011	Preforest wooded grassland	3b
CAM12-1-03	5.436667	10.844139	945	Preforest wooded grassland	3b
CAM12-1-06	5.770728	11.153028	732	Preforest wooded grassland	3b
CAM12-1-11	5.537139	10.327167	1327	Preforest wooded grassland	3b
CAM12-1-14	6.007333	10.296694	1790	Montane wooded grassland	3b
CAM15-1-08	5.693167	10.460444	1248	Preforest wooded grassland	3b

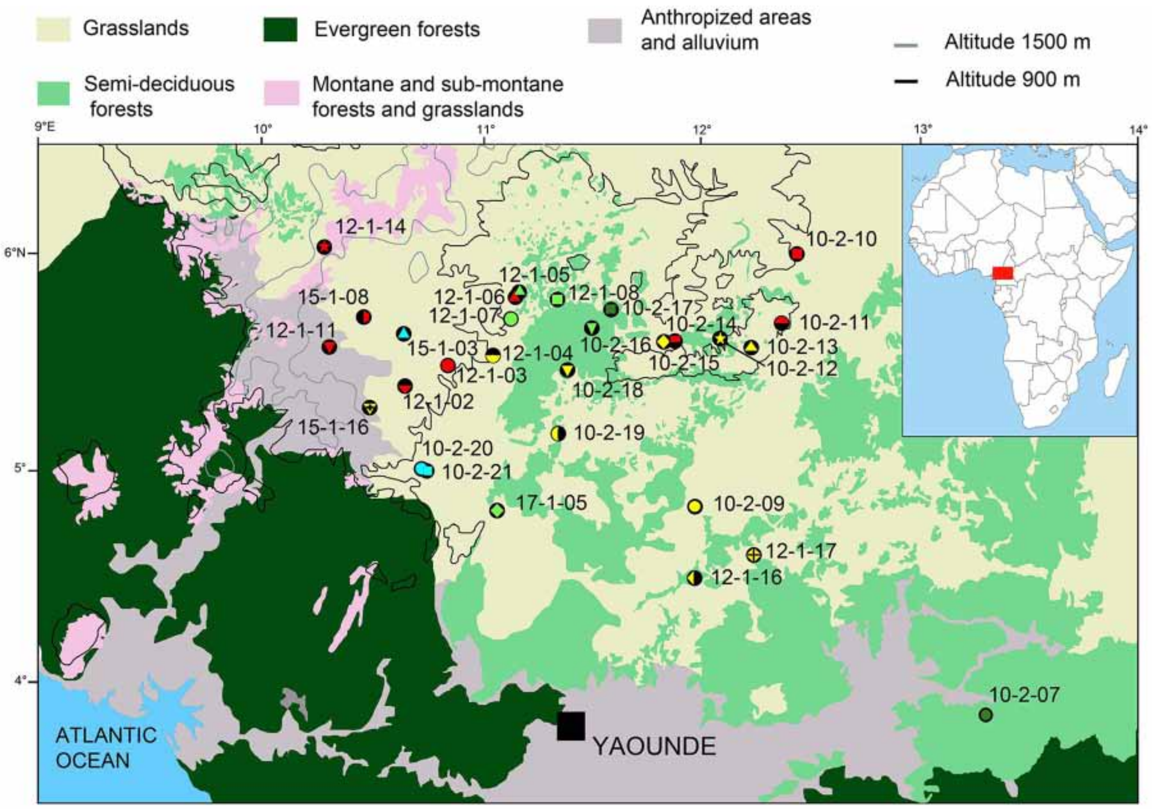

Figure 1. Location map of the soil profiles analyzed in this study. The simplified vegetation map is adapted from Letouzey (1985). The symbols are those used in Figures 5 to 8.

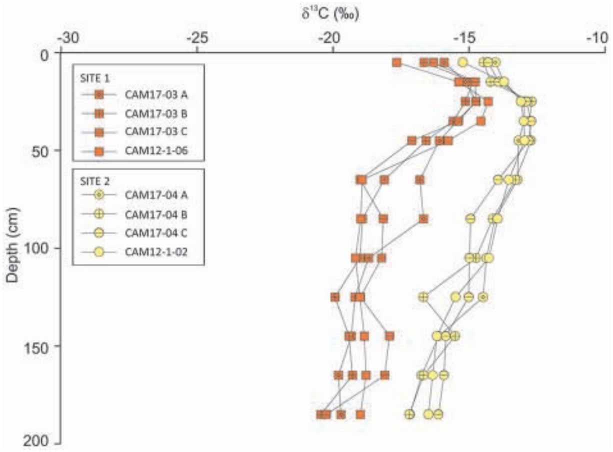

Figure 2. Variations of δ^{13}C values from four adjacent soil profiles at two sites from the Cameroon wooded grasslands.

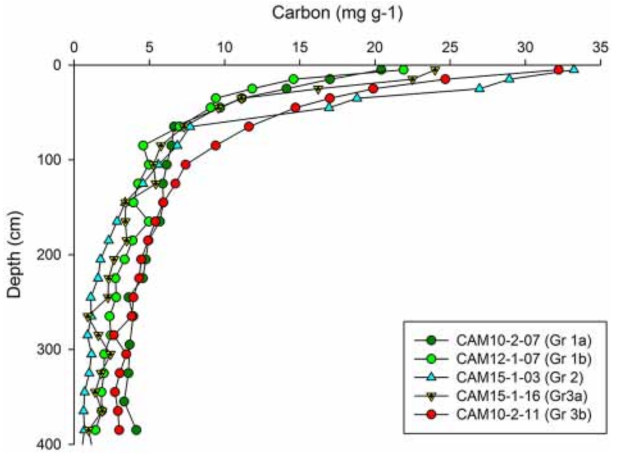

Figure 3. Organic carbon content of selected soil profiles representative of the five vegetation types defined in Table 1.

distributed from 9505 ^{14}C BP to the present except at three sites where inversions of 1350–2250 years were noted (CAM15-1-16, 15-1-8, and 15-1-3). These inversions could reflect local downward penetration of organic matter by roots, bioturbation and/or local anomalies of the lixiviation processes. Overall, the distribution of our ^{14}C measurements in depth is consistent with data from Guillet et al. (2001) and Bremond et al. (2017; Figure 4a). Of interest is the noticeable dispersion of the measurements, which increases significantly at the intermediate levels of the profiles to reach a maximum of 6850 years at 265 cm depth. This dispersion is significantly higher than that observed by Bremond et al. (2017) at close depths (6535 ^{14}C years at 165 cm vs ca. 3000 ^{14}C years at 125 cm in Bremond et al.'s study). The median calculated for our samples increases regularly with depth from 20 cm (modern) to 385 cm deep (6520 ^{14}C BP) giving an apparent age of 180 ^{14}C years at 25 cm, 1930 ^{14}C years at 85 cm, 3515 ^{14}C years at 165 cm and 5790 ^{14}C years at 265 cm.

Some charcoal fragments were sampled from soil cores and pit in both wooded grassland and forest soils. Fragments were scarcer in grassland than in forest soils. They were radiocarbon dated (Figure 4b) leading to their classification in some age groups; the first group with age ranging from 0 to 200 years BP, the second from 290 to 390 years BP, the third from 835 to 950 years BP and the last from 1575 to 2140 years BP.

Distribution of SOM δ^{13}C with depth (data in Supplemental Table S3, available online)

The isotope composition of SOM reflects that of the vegetation growing on the soil, except for a slight general increase of several ‰ with depth. This observed ^{13}C enrichment with depth can be explained as follows: (1) an alteration with time of the isotope composition of the vegetation as a consequence of recent content variations in atmospheric CO_2; (2) a differential preservation of ^{13}C-enriched SOM components could potentially account for the pattern of ^{13}C enrichment with depth: isotope differences up to 5‰ are reported between various biochemical components of plants; and (3) an isotope fractionation during SOM mineralization (for more details see Balesdent et al., 1987; Deines, 1980; Nadelhoffer and Fry, 1988).

Three Groups of profiles were distinguished on the basis of the top soil value of the δ^{13}C with forest profiles ranging from −28.4‰ to −23.5‰ and wooded grassland profiles ranging from −18.2‰ and −12.3‰; all profiles displaying a typical aspect already described by Schwartz (1991) in Congo. Variations of values along the profiles were then used to subdivide these two main categories with a particular attention of the grassland profiles.

(1) The forest profiles, Group 1 (Figure 5). This group is divided into two distinct sub-groups:

Group 1a: CAM-10-2-07 (Abong Mbang) and CAM10-2-17 (Ngambe Tikar; Figure 2; Desjardins et al., 2013) display a typical forest-type signal from the topsoil (−28.4‰ to −26.9‰) to the deepest layers at ca. 4 m (−24.3‰ to −23.3‰) with an increase in δ^{13}C values of about 2‰ in the subsurface levels between the surface and 30 cm. Then the shape of the curve is roughly linear, slightly increasing by $<$2‰ from 30 cm to 400 m.

Group 1b: this group encompasses two types of forest around the Ngambe Tikar forest: the forest edge to the north (CAM10-2-16 and CAM12-1-5) and plantations (coffee, cacao) to the north-west and south-west (CAM12-1-7 and 12-1-8, CAM17-1-5): they are characterized by topsoil δ^{13}C values between −27.3‰ to −23.5‰, typical of C3 vegetation. These values increase up to −21.8‰ to −20.3‰ at the 50–60 cm layer and remain roughly constant around this latter value down to the base.

(2) The wooded grassland profiles, Group 2 (Figure 6): Topsoil values of CAM10-2-20, 10-2-21, and CAM15-1-03 range from −17‰ to −15‰, δ^{13}C values typical of wooded grasslands. Toward the base of the profiles, they display a steady and continuous decay between −23.2‰ and −23.8‰, suggesting a likely origin from a C3 dominated landscape.

(3) The wooded grassland profiles, Group 3 (Figures 7 and 8): this group includes 19 profiles and can be divided into two sub-groups:

Group 3a: CAM10-2-09, 10-2-12,10-2-13, 10-2-15, 10-2-18, 10-2-19, CAM12-1-04, 12-1-16, 12-1-17, CAM15-1-16 display a topsoil δ^{13}C value ranging between −13.7‰ and −18.2‰. Below ca. 40 cm these values regularly decrease to values lower than −20‰ (minimum = −22‰) at the base of the profiles.

Group 3b: CAM10-2-10, 10-2-11, 10-2-14, CAM12-1-02, 12-1-03, 12-1-06, 12-1-11, 12-1-14, CAM15-1-08 differ from the above mentioned profiles by the deepest layers which are characterized by values never reaching −20‰. The profiles show a shift of ca 4.5‰ at levels varying from 35 to 100 cm. Then, δ^{13}C values remain roughly constant along the profiles giving them a vertical aspect until the base of the profiles.

Discussion

Due to the processes of bioturbation and illuviation, soil organic matter (SOM) is a complex mixture of compounds from different

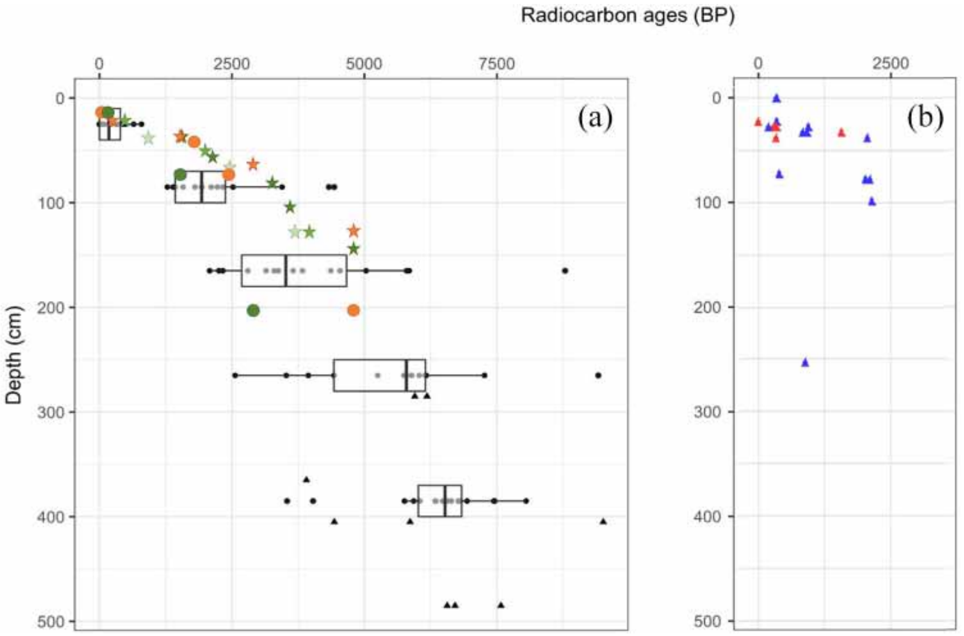

Figure 4. (a) Boxplots of the ^{14}C measurements of soil organic matter along 17 soil profiles. Data from Guillet et al. (2001; orange dot: grassland; green dot: forest) and from Bremond et al. (2017; orange star: grassland; green stars: forests) are also displayed and (b) ^{14}C measurements of soil charcoals (blue triangles: forest; red triangles: grasslands).

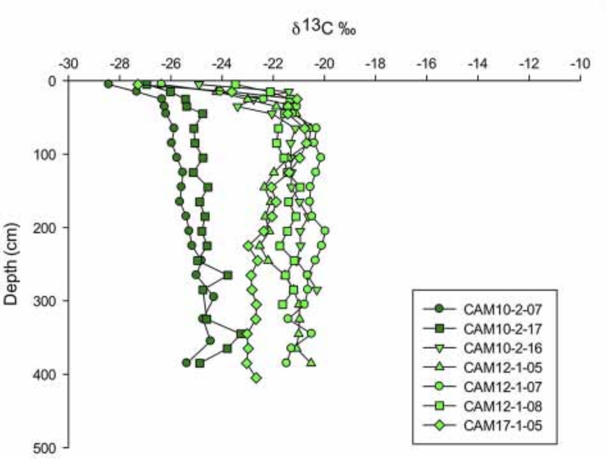

Figure 5. Variation of the values of $\delta^{13}C$ with depth of the soil profiles of Group 1, 1a (forest): dark green, 1b (forest edge, plantation): light green.

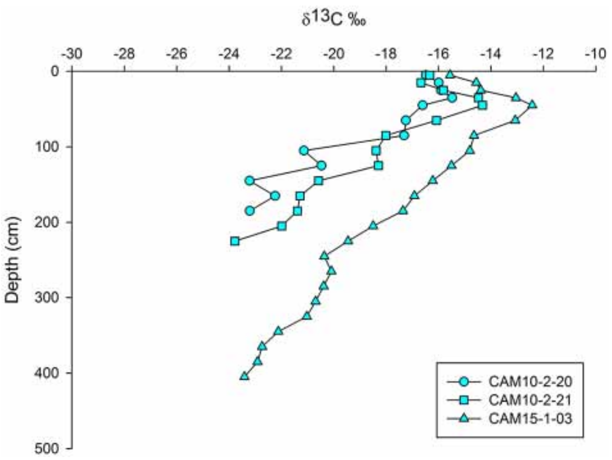

Figure 6. Variation of $\delta^{13}C$ values with depth of the soil profiles of Group 2 (grassland).

pools, ranging from very labile compounds with very fast cycling times to refractory components that accumulate over millennia (Martinelli et al., 1996; Trumbore et al., 1995). However, the proportion of young carbon decreases rapidly with depth, while the proportion of stable and old carbon increases. Recently, a meta-analysis conducted by Balesdent et al. (2018) on the age distribution of carbon in the first meter of 55 forest and grassland soils shows that the dynamics of subsoil carbon is around seven times slower than that of topsoil carbon. In deep layers, the age distribution reveals the large predominance of carbon older than 1000 years and a small but non-negligible direct incorporation of photosynthetically fixed carbon through deep roots or soluble carbon (for the youngest carbon). As a result, the organic matter located deep in the soil retains the signature of past plant cover. Based on this principle, since the 1980s, the SOM carbon isotope technique has been successfully applied to reconstruct paleoenvironmental changes in different parts of the world (e.g. Ambrose and Sikes, 1991; Bremond et al., 2017; Desjardins et al., 1996; Guillet et al., 1988; Krishnamurthy et al., 1982; Pessenda et al., 1998, 2005; Schwartz et al., 1986).

The $\delta^{13}C$ values of soil surface are in good agreement with present-day vegetation. As already discussed in Desjardins et al. (2013), Group 1a closely corresponds to mature forest profiles such as those from Kandara (Guillet et al., 2001) in south-eastern Cameroon and from the nearby central African massif (Bremond et al., 2017 and references therein). Isotopes values testify for the permanency of C3-dominated vegetation types over the last millennia at the sample sites. This challenges earlier assumptions that intense anthropogenic activity linked to slash-and-burn agricultural practices could have led to a large opening of the lowland forests of western equatorial Africa (e.g. Kadomura et al., 1986; Morin-Rivat et al., 2016; Vleminckx et al., 2014). Do soil profiles from dense forest massifs from central Africa not record short term environmental changes or were these change not dramatic enough to lead

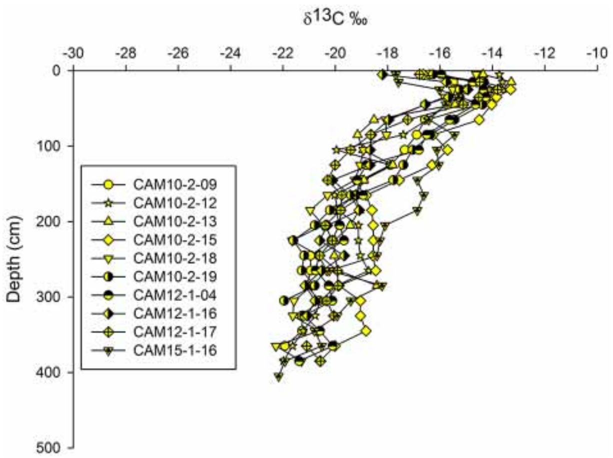

Figure 7. Variation of δ^{13}C values with depth of the soil profiles of Group 3a (grassland).

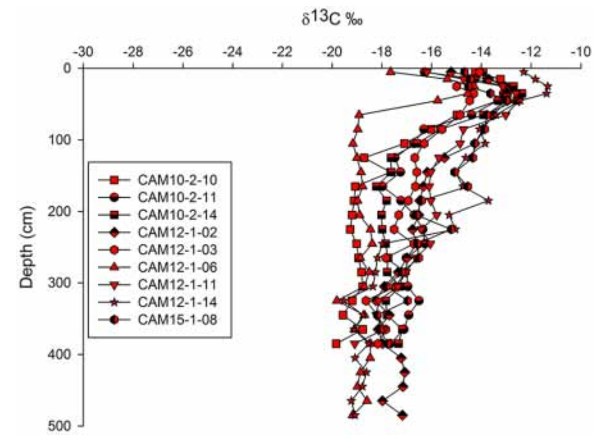

Figure 8. Variation of δ^{13}C values with depth of the soil profiles of Group 3b (grassland).

to the replacement of C3 by C4 dominated landscapes? The mixing of different pools of organic matter in soil prevents the records of limited and/or short duration disturbances. Contrary to a forest clearance or a disturbance signal, our soil profiles from the forest edges in Group 1b show the recent encroachment of the forest against more open formations characterized by the presence of C4 elements. Topsoils in this group record clearly forest values, similar to those of Group 1a, from −29‰ to −24‰, whereas levels lower than 30 cm record less depleted values ranging from −23‰ to −20‰ suggesting that a less densely forested environment was present in the past. Such a recent advance of lowland forests has already been detected in Congo and Gabon. It has been thought to originate from the last millennium (Delègue et al., 2001) and was still observable in the early 1990s in southern Cameroon at an annual rate from 0.5 to 1.6 m (Youta-Happi et al., 2000).

From our wooded grassland profiles, three only show an evolution from typical δ^{13}C forest values (around −24‰) at depth to a more open, wooded grassland landscape at the surface (Group 2). They come from sites located close to existing forests. Based on the present-day vegetation at these sites we can hypothesized the presence of larger gallery forests at CAM 15-1-3 and a slight advance of the semi-deciduous western forest massif near Tonga (CAM 10-2-20, 10-2-21) in the past.

The vegetation change from all the other wooded grassland profiles is of reduced amplitude since the basal values remain relatively high (−18‰ to −23‰). All the curves of these types (Figure 3a and b) have a profile where the −18/−23‰ values remain constant in depth and then gradually move upwards toward the present-day values. The stability of δ^{13}C signature at depth shows that the mixing with present-day vegetation is insignificant at these levels. As a consequence, our data suggest that a more densely forested grassland than today was present at these sites in the past. Values from the deep levels of Groups 3a and b lie within the range of the present-day '*Imperata* savannah' and the '*Chromolaena* fringe' at Nditam and Kandara in Cameroon (−18‰ to −22‰; Guillet et al., 2001) or of 'woodlands', that is mixed C3/C4 systems −20‰ to −24‰ (mean −21.9‰) in East Africa (Winowiecki et al., 2017). In some cases (group 3a), the depth variations reach the subsurface values of the forest colonization zone (from ca −20‰ to −23‰) but never those of the mature forest (−24‰ to −26‰). Since our samples cover most of the range of the wooded grassland area from Central Cameroon including the Grassfield plateaus, we suggest that this whole area has never been densely forested during the Middle Holocene. This could explain the absence of wood charcoals in most of our soil profiles. The landscape remained of wooded grassland-type with, at most, a denser woody cover.

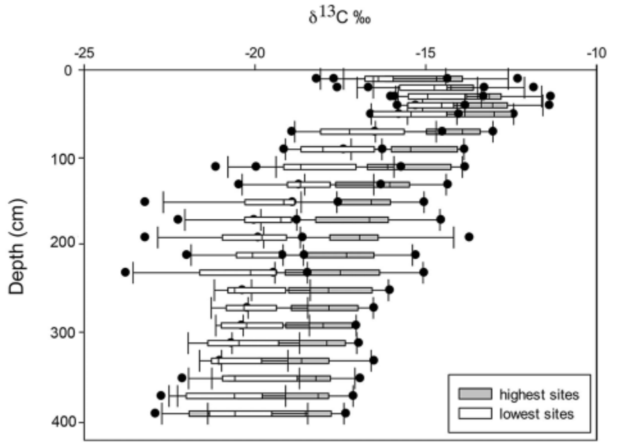

Figure 9. Boxplots of the δ ^{13}C values with depth of the soil profiles of Group 3, as a function of their elevation. Highest elevations (from 945 to 1790 m asl), the lowest ones (577–929 m asl).

All these profiles show a more or less progressive shift toward present-day values. The position of this shift in depth varies from 170 to 60 cm suggesting that, depending on the site, it took place from 3515 ^{14}C (from 2000 to 5795 ^{14}C BP) to ca 1955 ^{14}C BP (1430–2480 ^{14}C BP). However, these results have to be considered with caution, as the reported ^{14}C ages represent the average 'age' of the SOM, which is a mixture of old and young materials (Balesdent and Guillet, 1982; Trumbore, 2009).

Moreover, a relationship between the altitude of wooded grassland sites and δ^{13}C values is detected at certain depths. Figure 9 shows that the sites from the highest elevations (from 945 to 1790 m asl) show less negative values of δ^{13}C than those of the lowest ones (577–929 m asl). This is confirmed by the significant correlations, at each depth level within 30 and 300 cm depth, between altitude and δ^{13}C values (data in Supplemental Table S4, available online).

Significant correlations also exist between the altitude and ^{14}C ages for two layers: 80–90 cm and 160–170 cm (data in Supplemental Table S4, available online). The higher the site, the older the ages of OM are (data in Supplemental Table S5, available online). As the apparent ages of the organic matter come from the mixing of pools with different ages and eventually different δ^{13}C, an older apparent age combined with a more pronounced C4 grasses signature suggests that the vegetation change may have occurred earlier at higher altitude. This result is consistent with previous observations by Lézine et al. (2013b) on a delay (of about 1000 years) between the responses of upland vegetation compared to that of lowland vegetation during the environmental crisis at the end of the Holocene Humid Period. This delay could be explained (among other factors) by the availability of soil water along the slopes, with soils in the lower parts of the landscape being less well drained than the steeper slopes in the higher parts of the landscape. As a result, high elevations appear to have been more sensitive to climate drying than low and middle elevations, and vegetation change would have occurred earlier. These results support the hypothesis that the change in vegetation which characterized the end of the Holocene Humid Period was due to climatic rather than anthropogenic causes, although both factors may be involved.

Conclusion

From 29 soil samples from the present-day wooded grassland area of center Cameroon and its immediate surroundings (i) we do not show any marked alteration of the lowland forest massif. As already shown by Vincens et al. (1999) the impact of the environmental crisis which occurred at the end of the Holocene Humid Period in the Congo Basin was more a change in forest composition and density than the replacement of lowland forests by a C4 dominated landscape. When any, traces of forest expansion/retreat are observed only punctually at the present-day forest margins. These results suggest some resilience of low- and mid-altitude forest ecosystems which did not experienced such dramatic change compared to the high mountain ones (Lézine et al., 2013b). (ii) In the wooded grassland/forest mosaic zone, our results indicate the presence, a few millennia ago, of more wooded vegetation than today. However, the current wooded grasslands of central Cameroon have never been densely forested. The extent of grasslands and wooded grasslands over large areas in the Central Cameroon with a timing influenced by altitude (earlier in the highest areas), leads us to privilege a climatic cause rather than an anthropic one for their establishment.

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Supplemental material

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References

Ambrose SH and Sikes NE (1991) Soil carbon isotope evidence for Holocene habitat change in the Kenya Rift Valley. *Science* 253(5026): 1402–1405.

Aubréville A (1947) The disappearance of the tropical forests of Africa. *Unasylva* 1: 5–11.

Balesdent J, Basile-Doelsch I, Chadoeuf J et al. (2018) Atmosphere–soil carbon transfer as a function of soil depth. *Nature* 559(7715): 599–602.

Balesdent J and Guillet B (1982) Les datations par le ^{14}C des matières organiques des sols. Contribution à l'étude de l'humification et du renouvellement des substances humiques. *Science du sol* 20: 93–111.

Balesdent J, Mariotti A and Guillet B (1987) Natural ^{13}C abundance as a tracer for soil organic matter dynamics studies. *Soil Biology and Biochemistry* 19(1): 25–30.

Bayon G, Dennielou B, Etoubleau J et al. (2012) Intensifying weathering and land use in iron age Central Africa. *Science* 335(6073): 1219–1222.

Bostoen K, Clist B, Doumenge C et al. (2015) Middle to late-holocene paleoclimatic change and the early bantu expansion in the rain forests of Western Central Africa. *Current Anthropology* 56(3): 354–384.

Boutton TW, Archer SR, Midwood AJ et al. (1998) δ^{13}C values of soil organic carbon and their use in documenting change in a subtropical savanna ecosystem. *Geoderma* 82(1–3): 5–41.

Bremond L, Bodin SC, Bentaleb I et al. (2017) Past tree cover of the Congo Basin recovered by phytoliths and δ^{13}C along soil profiles. *Quaternary International* 434: 91–101.

Cheek M, Darbyshire I, Onana JM et al. (2004) *The Plants of Kupe, Mwanenguba and the Bakossi Moutains, Cameroon, a Conservation Checklist*. London: Royal Botanic Gardens, Kew.

Clist B, Bostoen K, de Maret P et al. (2018) Did human activity really trigger the Late-Holocene rainforest crisis in Central Africa? *Proceedings of the National Academy of Sciences of the United States of America* 115(21): E4733–E4734.

Deines P (1980) The isotopic composition of reduced organic carbon. In: Fritz P and Fontes JC (eds) *Handbook of Environmental Isotope Geochemistry, Volume. 1. The Terrestrial Environment*. Amsterdam: Elsevier, pp. 329–346.

Delègue MA, Fuhr M, Schwartz D et al. (2001) Recent origin of a large part of the forest cover in the Gabon coastal area based on stable carbon isotope data. *Oecologia* 129(1): 106–113.

deMenocal P, Ortiz J, Guilderson T et al. (2000) Abrupt onset and termination of the African Humid Period: Rapid climate responses to gradual insolation forcing. *Quaternary Science Reviews* 19(1–5): 347–361.

Desjardins T, Fiho AC, Mariotti A et al. (1996) Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene as revealed by soil organic carbon isotope ratios. *Oecologia* 108(4): 749–756.

Desjardins T, Turcq B, Nguetnkam JP et al. (2013) δ^{13}C variation of soil organic matter as an indicator of vegetation change during the Holocene in central Cameroon. *Comptes Rendus Geoscience* 345(7–8): 266–271.

Garcin Y, Deschamps P, Ménot G et al. (2018) Early anthropogenic impact on Western Central African rainforests 2,600 y ago. *Proceedings of the National Academy of Sciences of the United States of America* 115(13): 3261–3266.

Gasse F (2000) Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews* 19(1–5): 189–211.

Guillet B, Achoundong G, Happi JY et al. (2001) Agreement between floristic and soil organic carbon isotope (^{13}C/^{12}C/^{14}C) indicators of forest invasion of savannas during the last century in Cameroon. *Journal of Tropical Ecology* 17(6): 809–832.

Guillet B, Faivre P, Mariotti A et al. (1988) The C-14 dates and C-13/C-12 ratios of soil organic matter as a means of studying the past vegetation in the intertropical regions: Examples from Colombia (South America). *Palaeogeography Palaeoclimatology Palaeoecology* 65(1–2): 51–58.

Hély C and Lézine A-M and APD contributors (2014) Holocene changes in African vegetation: Tradeoff between climate and water availability. *Climate of the Past* 10(2): 681–686.

IUSS Working Group WRB (2014) *World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps*. World Soil Resources Reports No. 106. Rome: FAO.

Kadomura H, Hori N, Kuété M et al. (1986) Late Quaternary environmental changes in Southern Cameroon: A synthesis. In: Kadomura H (ed.) *Geomorphology and Environmental Changes in Tropical Africa. Cases Studies in Cameroon and Kenya. A Preliminary Report of the Tropical African Geomorphology and Late-Quaternary Palaeoenvironments Research Project 1984/85*. Sapporo, Japan: Hokkaido University, pp. 145–158.

Kadomura H and Kiyonaga J (1994) Origin of Grassfields landscape in the West Cameroon highlands. In: Kadomura H (ed.) *Savannization Processes in Tropical Africa*. Tokyo, Japan: Department Geography, Tokyo Metropolitan University, pp. 47–85.

Krishnamurthy RV, DeNiro MJ and Pant RK (1982) Isotope evidence for Pleistocene climatic changes I, Kashmir, India. *Nature* 298(5875): 640–641.

Lebamba J, Vincens A, Lézine A-M et al. (2016) Forest-savannah dynamics on the Adamawa plateau (Central Cameroon) during the “African Humid Period” termination: A new high-resolution pollen record from Lake Tizong. *Review of Palaeobotany and Palynology* 235: 129–139.

Letouzey R (1968) *Etude phytogéographique du Cameroun*. Paris: Lechevalier.

Letouzey R (1985) *Notice de la carte phytogéographique du Cameroun au 1: 500 000*. Toulouse: Institut de la Carte Internationale de la Végétation.

Lézine A-M, Assi-Kaudjhis C, Roche E et al. (2013a) Towards an understanding of West African montane forest response to climate change. *Journal of Biogeography* 40(1): 183–196.

Lézine A-M, Holl AFC, Lebamba J et al. (2013b) Temporal relationship between Holocene human occupation and vegetation change along the north western margin of the Central African rainforest. *Comptes Rendus Geoscience* 345(7–8): 327–335.

Lézine A-M, Zheng W, Braconnot P et al. (2011) Late-Holocene plant and climate evolution at Lake Yoa, northern Chad: Pollen data and climate simulations. *Climate of the Past* 7(4): 1351–1362.

Maley J and Brenac P (1998) Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years B.P. *Review of Palaeobotany and Palynology* 99(2): 157–187.

Martinelli LA, Pessenda LCR, Espinoza E et al. (1996) Carbon-13 variation with depth in soils of Brazil and climate change during the Quaternary. *Oecologia* 106(3): 376–381.

Morin-Rivat J, Biwolé A, Gorel AP et al. (2016) High spatial resolution of late-Holocene human activities in the moist forests of central Africa using soil charcoal and charred botanical remains. *The Holocene* 26(12): 1954–1967.

Nadelhoffer KJ and Fry B (1988) Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Science Society of American Journal* 52(6): 1633–1640.

Ngomanda A, Neumann K, Schweizer A et al. (2009) Seasonality change and the third millennium BP rainforest crisis in southern Cameroon (Central Africa). *Quaternary Research* 71(3): 307–318.

Pessenda LCR, Gomes BM, Aravena R et al. (1998) The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region. *The Holocene* 8(5): 599–603.

Pessenda LCR, Ledru MP, Gouveia SEM et al. (2005) Holocene palaeoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotope records. *The Holocene* 15(6): 812–820.

Peterson BJ and Fry B (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18(1): 293–320.

Reynaud-Farrera I, Maley J and Wirrmann D (1996) Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4770 ans BP: analyse pollinique des sédiments du lac Ossa. *Comptes Rendus de l’Académie des Sciences Paris* 322(Série II A): 749–755.

Richards K (1986) Preliminary results of pollen analysis of a 6,000 years’ core from Mboandong, a crater lake in Cameroun. In: Baker K, Richards K and Rimes CA (eds) *The Hull University Cameroon Expedition 1981–1982*.Hull: Department of Geography, University of Hull, pp. 14–28.

Schwartz D (1991) Intérêt de la mesure du δ^{13}C des sols en milieu naturel équatorial pour la connaissance des aspects pédologiques et écologiques des relations savane-forêt. *Cahiers ORSTOM, série Pédologie* 26(4): 327–341.

Schwartz D (1992) Climatic drying about 3,000 BP and Bantu expansion in Atlantic central Africa—Some reflections. *Bulletin de la Société Géologique de France* 163(3): 353–361.

Schwartz D, Dechamps R, Elenga H et al. (1996a) Les savanes d'Afrique centrale : des écosystèmes à l'origine complexe, spécifiques de l'Holocène supérieur. In: *Dynamique à long terme des écosystèmes forestiers intertropicaux*. Paris: ORSTOM, pp. 179–182.

Schwartz D, De Foresta H, Mariotti A et al. (1996b) Present dynamics of the savanna-forest boundary in the Congolese Mayombe: A pedological, botanical and isotopic (^{13}C and ^{14}C) study. *Oecologia* 106(4): 516–524.

Schwartz D, Mariotti A, Lanfranchi R et al. (1986) C-13/C-12 ratios of soil organic matter as indicators of vegetation changes in the Congo. *Geoderma* 39(2): 97–103.

Ségalen P and Martin D (1965) *Carte pédologique du Cameroun oriental à l’échelle du 1:1000 000*. Paris: ORSTOM, Office de la Recherche Scientifique et Technique Outre-Mer.

Thieblemont D, Flehoc C, Ebang-Obiang M et al. (2013) Geochronological arguments for a close relationship between surficial formation profiles and environmental crisis (c.3000–2000BP) in Gabon (CentralAfrica). *Comptes Rendus Geoscience* 345(7–8): 272–283.

Trumbore SE (2009) Radiocarbon and soil carbon dynamics. *Annual Review of Earth and Planetary Sciences* 37: 47–66.

Trumbore SE, Davidson EA, de Camargo PB et al. (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochemical Cycles* 9(4): 515–528.

Verdu P, Austerlitz F, Estoup A et al. (2009) Origins and genetic diversity of pygmy hunter-gatherers from Western Central Africa. *Current Biology* 19(4): 312–318.

Vincens A, Buchet G, Servant M et al. (2010) Vegetation response to the “African Humid Period” termination in Central Cameroon (7 N)—New pollen insight from Lake Mbalang. *Climate of the Past* 6(3): 281–294.

Vincens A, Schwartz D, Elenga H et al. (1999) Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *Journal of Biogeography* 26(4): 879–885.

Vleminckx J, Morin-Rivat J, Biwolé AB et al. (2014) Soil charcoal to assess the impacts of past human disturbances on tropical forests. *PLoS ONE* 9(11): e108121.

Watrin J, Lézine A-M and Hély C (2009) Plant migration and plant communities at the time of the “green Sahara”. *Comptes Rendus Geoscience* 341(8–9): 656–670.

White F (1983) *The Vegetation of Africa*. Paris: UNESCO.

Wiedemeier DB, Bloesch U and Hagedorn F (2012) Stable forest–savanna mosaic in northwestern Tanzania: Local-scale evidence from δ^{13}C signatures and ^{14}C ages of soil fractions. *Journal of Biogeography* 39(2): 247–257.

Winowiecki LA, Vågen TG, Boeckx P et al. (2017) Landscape-scale assessments of stable carbon isotopes in soil under diverse vegetation classes in East Africa: Application of near-infrared spectroscopy. *Plant and Soil* 421(1–2): 259–272.

Wirrmann D, Bertaux J and Kossoni A (2001) Late-Holocene paleoclimatic changes in Western Central Africa inferred from mineral abundance in dated sediments from lake Ossa (Southwest Cameroon). *Quaternary Research* 56(2): 275–287.

Youta-Happi J, Hotyat M and Bonvallot J (2000) La colonisation des savanes par la forêt à l’Est du Cameroun. In: Servant M and Servant-Vildary S (eds) *Dynamique à long terme des écosystèmes forestiers intertropicaux*. Paris: IRD, pp. 423–427.