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Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (^{13}C and ^{14}C) study

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Abstract Isolated savannas enclosed by forest are especially abundant in the eastern part of the Congolese Mayombe. They are about 3000 years old, and were more extensive some centuries ago. The boundary between forest and savanna is very abrupt, as a consequence of the numerous savanna fires lit by hunters. Floristic composition and vegetation structure data, organic carbon ratios, $\Delta^{14}C$ and $\delta^{13}C$ measurements presented here show that forest is spreading over savanna at the present time and suggest that the rate of forest encroachment is is currently between 14 and 75 m per century, and more probably about 20–50 m per century. As most savannas are less than 1 km across, such rates mean, assuming there are no changes in environmental conditions, that enclosed savannas could completely disappear in the Mayombe in about 1000–2000 years.

Key words Congo · Forest-savanna dynamics · ^{13}C natural abundance · Forest encroachment · Pioneer trees

Introduction

All over the African equatorial forest, but especially in the Congolese Mayombe, forest cover encloses some isolated savannas. It is widely held that the enclosed savannas of the Mayombe are recent anthropic savannas. This hypothesis has been supported only by the fact that these savannas were densely occupied by villages at the beginning of the twentieth century (Vennetier 1968; Cusset 1989; Gibert and Sénéchal 1989; Petit 1990). As demonstrated by Foresta (1990), savanna formation due to man's activities may be, in the Mayombe, unfounded. Despite the availability of efficient tools such as the chain saw, the development of commercial agriculture, and the fact that vegetation in the most inhabited areas testifies to an important forest degradation resulting from repeated agricultural clearing and that villages are located in the less humid areas of the Mayombe, savanna formation can never be observed. Data collected suggest that these savannas have a palaeoclimatic origin (Foresta 1990; Schwartz et al. 1990b), that they could be 3000 years old and were more extensive during past centuries. Moreover, archaeological data suggest that they were previously found as far as the Les Saras area, which is currently purely forested (Schwartz et al. 1990a). This evidence suggests that forest is at present encroaching onto savanna. Botanical observations, both floristic and structural, agree with this hypothesis (Massimba 1987; Foresta 1990), but this approach is only qualitative. To provide more conclusive evidence, other approaches have to be used, such as determination of the mean residence time (MRT) of soil organic matter (SOM) by ^{14}C dating combined with an isotopic (^{13}C) characterization of vegetation change recorded in SOM. This paper presents the results from a combined botanical and SOM approach along two forest-enclosed savanna sequences, as a means to understand the present dynamics of the vegetation in the Congolese Mayombe.

Materials and methods

Study sites

The location of the observations is shown in Figs. 1 and 2. The Mayombe is a mountain extending from Gabon to Zaïre parallel to the coastline. In the Congo, the highest crests culminate at about 900 m. The rainfall increases from the west (1200 mm/year) to the highest crests (1980 mm/year) and then decreases down to Loubomo (1160 mm/year). Rain falls from October until May. Mists and drizzles are abundant during the dry season, and contribute to the retention of some moisture in soils. The number of hours of sunshine is small, especially during the dry season: less than 1000 h/year at Dimonika (Clairac et al. 1989). This dry, fresh and cloudy weather explains the presence of rain-forest in the less humid areas. The soils of the Mayombe are ferralic cambisols (FAO

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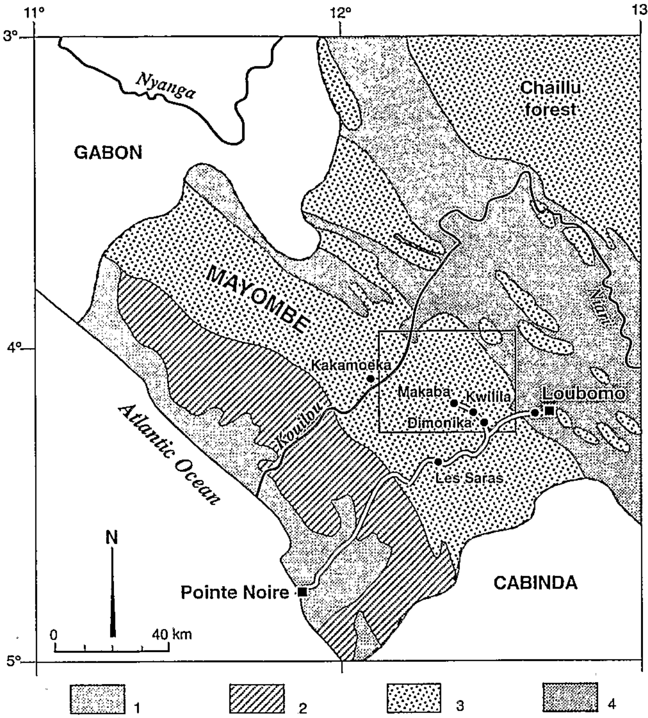

Fig. 1 The Congolese Mayombe (*1* coastal savannas, *2* forest-savanna mosaic of the western Congo, *3* forest areas, *4* savannas of the Niari-Nyanga synclinorium). The *inset* corresponds to Fig. 2

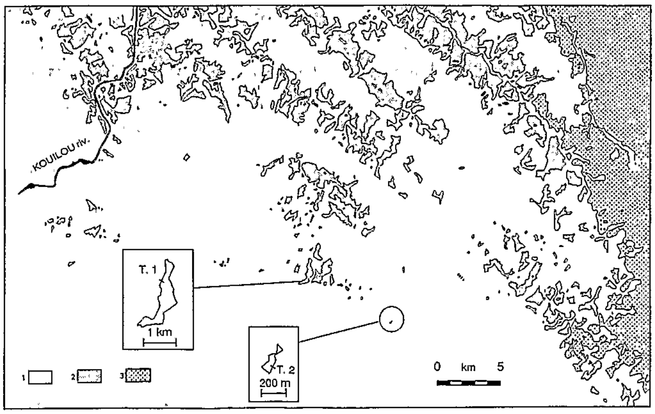

Fig. 2 Localization of the intramayombian savannas (after Schwartz et al. 1990b); (*1* Forest areas, *2* intramayombian savannas, *3* savannas of the Niari valley)

1976). A stone-line is present in about 80–90% of the soils. Its thickness ranges between 5 cm and 2 m. It is located just above the weathering horizons. The horizons above the stone-line form a cover the thickness of which ranges between 0 and 5–6 m, and more often between 0.5 and 2 m. These variations are linked to the erosion-colluviation processes (Gras 1970). The vegetation is composed essentially of rain-forest of an "evergreen transitional to a semi-deciduous" type (White 1983). The forest cover of the Mayombe includes isolated enclosed savannas. They are more numerous in the eastern Mayombe, where villages are rare and human influence is weak (Vennetier 1968; Schwartz et al. 1990b). A few are found right in the middle of the forest (Fig. 2).

The outline of savannas is geometric and angular. The boundary with the forest is as a general rule abrupt (cf. infra), which permits the definition without ambiguity of the limit between the two kinds of vegetation. In the savannas located north of Makaba, the main grass species is *Pobeguinea arrecta* (Gramineae). Occasional shrubs belong to familiar species: *Annona senegalensis*, *Bridelia ferruginea*, and *Nauclea latifolia*. It should be noticed that these savannas are burnt almost every year, even in the areas farthest from the villages. These bushfires are set by hunters to help their progression between forest zones.

Methods

Two forest-enclosed savanna transects are detailed. The first one is located to the WNW of Makaba, the second one to the west of Kwilila (Fig. 2). They are respectively 47 and 71 m long. The transects were carried out parallel to the contour lines in order to be as free as possible from erosion and colluviation processes. Makaba-transect was completed by a vegetation profile, carried out on 20×50=1000 m^2. As the vegetation profile was 20 m wide, and isotopic transects were linear, some differences appear in the vegetation limits as shown in Figs. 3–5. Only the forest part of the vegetation profile was studied, because the savanna vegetation is mainly composed of *P. arrecta* (Gramineae). It is possible to distinguish, in a simplified manner, four zones in the transects: in succession (1) a graminean zone (savanna *stricto sensu*), (2) an herbaceous zone dominated by ferns, (3) the edge of the forest which forms a thicket composed of pioneer trees and above all shrubs, and (4) the forest. The savanna-forest interface corresponds to the limit between ferns and shrubs from a botanical viewpoint, whereas the isotopic interface corresponds to the C3–C4 vegetation change, i.e. the limit between Gramineae and ferns. We defined the zero point of distances along the transects as the abrupt Gramineae-fern contact, as a consequence of the C3–C4 vegetation changes. Analytical data were derived from the determination of organic carbon content of soils, by measurement of the δ^{13}C and ^{14}C datings of SOM.

Soil samples were collected from 10 cm×10 cm plots between the surface of the soil and a depth of 5 cm. Carbon content and ^{13}C natural abundance were determined on each sample, whereas the ^{14}C datings were camed out on several bulked samples collected at different points (savanna, edge, forest) of the transects. Soil organic carbon content was determined by the Walkley and Black (1934) method, which is suitable for ferralitic soils.

The method of measurement of the ^{13}C natural abundance is given in detail by Girardin and Mariotti (1991). The ^{13}C content of a sample is expressed in delta units:

$$\delta^{13}\mathrm{C}\ ‰=[(^{13}\mathrm{R}\ \mathrm{sample}-{}^{13}\mathrm{R}\ \mathrm{standard})/{}^{13}\mathrm{R}\ \mathrm{standard}]\times1000$$

where ^{13}R stands for the isotopic ratio ^{13}C/^{12}C. Data are expressed versus the PDB standard.

The standard deviation, as determined by 40 measurements on a well-homogenized soil sample, is ±0.07 ‰ δ^{13}C. The ^{13}C content of plants varies according to their photosynthetic pathway (Bender 1971; Smith and Epstein 1971). Herbaceous plants of cold and temperate regions and all trees are C3 plants (Calvin cycle). They contain less ^{13}C than C4 plants (Hatch-Slack cycle), which are essentially tropical Gramineae and Cyperaceae. The δ^{13}C values of C3 plants are mostly between –23 and –34 ‰ (average of –26 ‰) whereas C4 plants range from –10 to –17 mg/ml (average of –12 ‰).

Mineralization of SOM and pedogenetic processes which occur during humus evolution lead to only slight variation in the ^{13}C ratio observed with depth in the soil profile (Troughton et al. 1974; Goh et al. 1976, 1977; O'Brien and Stout 1978; Dzurec et al. 1985; Nadelhoffer and Fry 1988; Martin et al. 1990; Mariotti 1991; Balesdent et al. 1993; Mariotti and Peterschmitt 1994). Consequently, the organic matter δ^{13}C in a soil in equilibrium with vegetation of a precise photosynthetic pathway is very similar to that in the dominant vegetation. Schwartz (1991) and Schwartz et al. (1986) show that it is possible in the Congo to differentiate without doubt forest humus (δ^{13}C≈–26.5 to –28 ‰) from savanna humus, where Gramineae are widely dominant (δ^{13}C≈–12 to

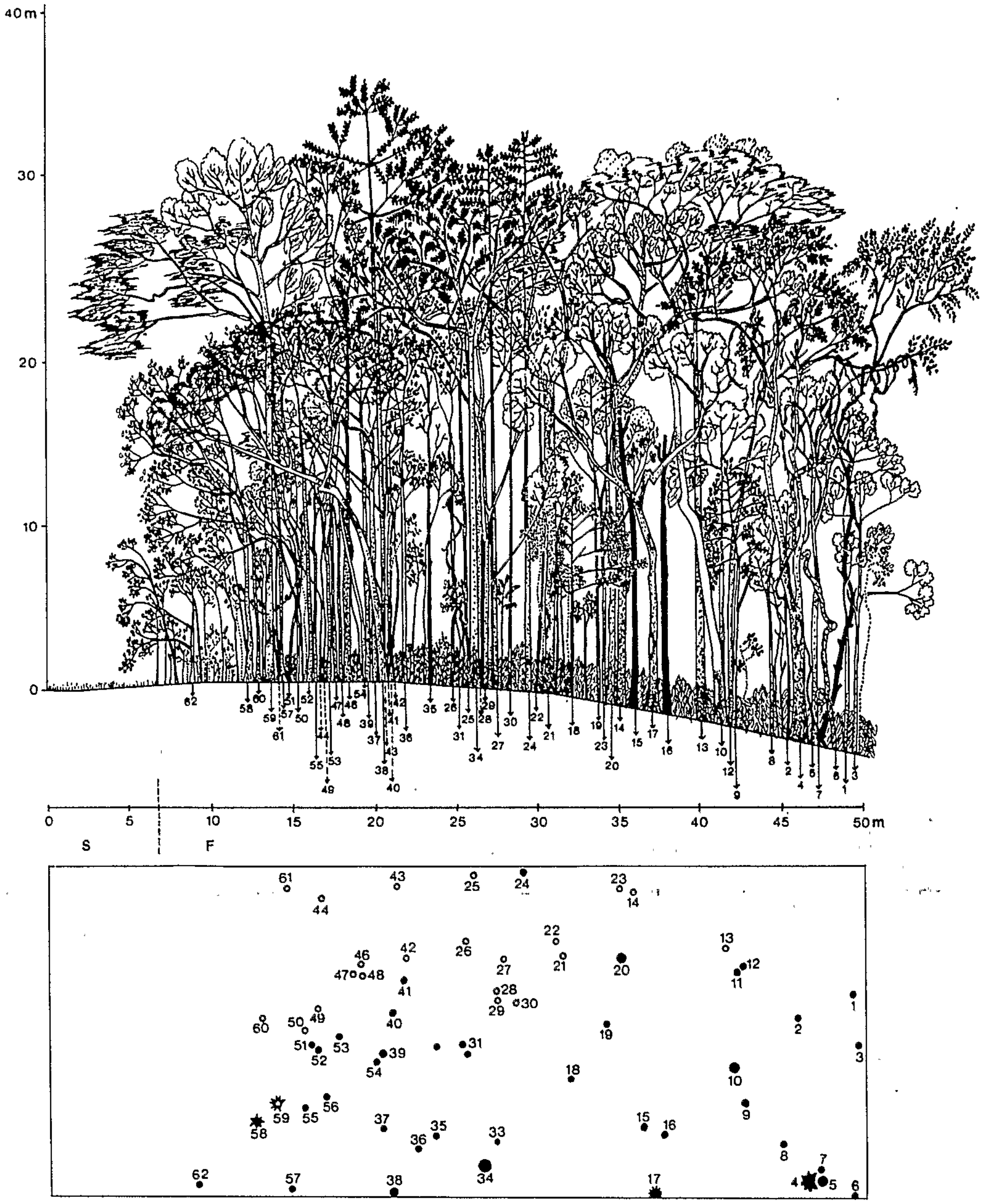

Fig. 3 Schematic profile of the vegetation for transect no 1, Makaba. Parcel of 20×50 m=1000 m^2, except for 1 cm <DBH <10 cm trees (=5×50 m). Tree serial numbers correspond to Table 2

–16 ‰). At the very most, it is possible to notice a slight increase of several ‰ with depth in the soil (Balesdent et al. 1987; Volkoff and Cerri 1987; Mariotti and Peterschmitt 1994). This enrichment can be explained by different factors: isotopic fractionation during the degradation of organic matter by micro-organisms, corresponding to the emission of ^{13}C depleted CO_2 with a correlative enrichment of the remaining organic matter (Kaplan and Rittenberg 1964; Blair et al. 1985); differential preservation of ^{13}C enriched SOM components (Nissenbaum and Schallinger 1974; Benner et al. 1987); a decrease of around 1.5 ‰ in the atmospheric CO_2 $\delta^{13}C$ during the last 150 years, as a consequence of the emission into the atmosphere of CO_2 resulting from the combustion of fossil fuels (Suess effect) and also from an increase in the SOM mineralization after cultivation (Marino and McElroy 1991). The $\delta^{13}C$ from these two CO_2 sources is close to –25 ‰, which is very different from the atmospheric CO_2 (–7 to –8 ‰). Although SOM becomes ^{13}C-enriched with depth in profiles, this enrichment (<4 ‰) is not large enough to mask the 14 ‰ difference between C3 and C4 plant litter. So, any vegetation change between C3 and C4 plants introduces a natural in situ labelling of organic matter incorporated into the soil (Flexor and Volkoff 1977, Schwartz et al. 1986; Balesdent et al. 1987; Mariotti and Balesdent 1990; Martin et al. 1990).

The ^{14}C datings were performed in the Radiocarbon Laboratory of the Ecole de Géologie de Nancy on humus samples by the classical liquid scintillation counting method. Radiocarbon activities were corrected for isotope fractionation and expressed as $\Delta^{14}C$ units, according to Craig's equation:

$$\Delta^{14}C=\delta^{14}C-(2\delta^{13}C+50)(1+\delta^{14}C/1000).$$

Positive $\delta^{14}C$ values reflect the incorporation of thermonuclear bomb radiocarbon in SOM, following the thermonuclear tests in the 1960s (O'Brien and Stout 1978). We used this natural tracer to calculate the mean residence time of SOM according to Balesdent and Guillet (1982). To compute the MRT-$\Delta^{14}C$ relationship, we integrated the radiocarbon activity of the atmospheric CO_2 incorporated in the soil until the date of sampling (e.g. 1990) with the assumption that SOM is a well-mixed compartment with an exponential decay. The datings were carried out in three zones of each

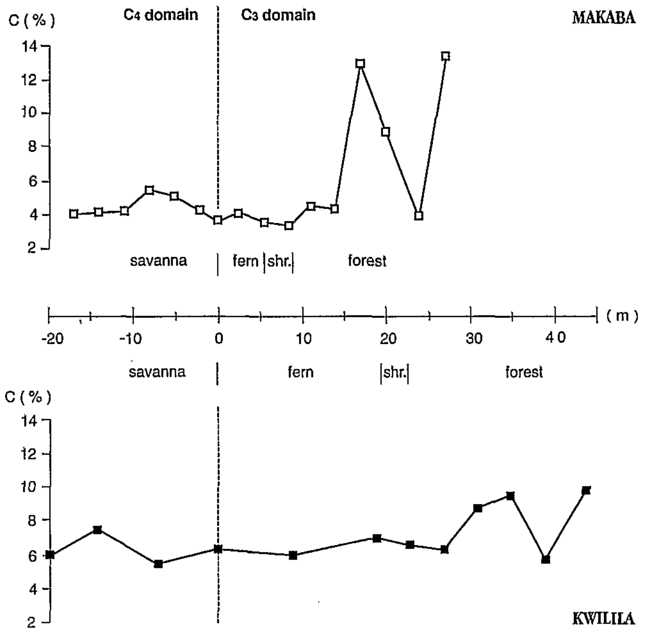

Fig. 4 Organic carbon contents in the 0–5 cm horizon for Makaba and Kwilila transects

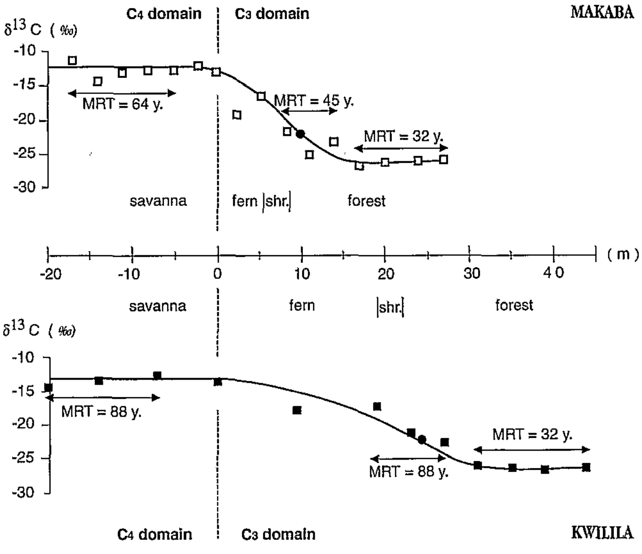

Fig. 5 $\delta^{13}C$ values of soil organic matter in the 0–5 cm horizon for Makaba and Kwilila) transects, and mean residence time values in each vegetation zone (mean sample obtained by gathering topsoil samples from several plots). (•) is the point where $y=\delta^{13}C$ value of the mixture of 63% forest organic matter and 37% savanna organic matter, and corresponding $x=D$ as defined in the text

transect (savanna, edge, forest), by gathering topsoil samples (0–5 cm) from several points (Fig. 5).

In the case of replacement of a savanna vegetation by forest vegetation, the $\delta^{13}C$ value of SOM is intermediate between $\delta^{13}C$ values of typical savanna and forest humus. Comparison of the intermediate value with the MRT as given by the ^{14}C datings provides information about the speed of replacement of the initial vegetation.

Results

Botanical study of the Makaba transect

All isolated enclosed savannas show evidence of forest expansion. In a few cases, the expansion is rapid and the forest-savanna interface is invaded by *Aucoumea klaineana*, as described by Foresta (1990). The studied transect, located near Makaba (Figs. 1, 2, transect number 1) corresponds to the general case of a slow forest expansion.

If burning influence is obvious in the savanna part of the vegetation profile, it is weak in the forest part. Flames reach the forest edge, but do not enter into the understorey. This fact is clear from the lack of traces of burning beyond the first shrubs of the boundary. The profile is presented in Fig. 3; Table 1 lists trees whose DBH (diameter at breast high=1.20 m) is greater than 10 cm, and Table 2 the list of 1 <DBH <10 cm trees.

Forest encroaching on savanna can be proved from two different viewpoints.

Floristic proof

Pioneer trees are abundant at the border (Fig. 3: *Aucoumea klaineana*, no. 59; *Pentaclethra eetveldeana*, nos. 22, 48, 50, 54, 56; *Parkia bicolor*, no. 52; *Hymenocardia ulmoïdes*, no. 62, *Uapaca guineensis*, nos. 46, 58, 61; *Croton* sp., no. 60). Tree species of primary forest only appear in the inner part (*Strombosiopsis tetrandra*, no. 23; *Coula edulis*, nos. 5, 8; *Dacryodes* cf. *igaganga*, nos. 4, 12, 21; *Garcinia* sp., no. 9; *Monodora* cf. *tenuifolia* no. 3; *Dialium* spp., nos. 17, 31). No savanna plants can be found under the forest cover. Outside the forest, some shrubs, too small to be represented in Fig. 3, are new anchor points for the forest expansion. These shrubs are almost always *H. ulmoïdes* and *Pentaclethra eetveldeana*.

Structural proof

Trees and shrubs which are growing at the border lean towards the savanna. This is due to uneven light conditions during growth, and shows that these trees developed on the edge of the forest and not in the understorey. Other trees (*Parkia bicolor*, nos. 38 and 52), which are now far inside the forest, also have this growth habit, which implies that they once grew at the edge. The morphology of these trees is a precious witness to the forest expansion.

The clearness of the transition between the savanna and forest, vegetation characterized by a "curtain" of almost-vertical leaf surfaces stretched out between the ground and the forest canopy, shows that the expansion of the forest onto the savanna is in this case very slow. If it was rapid, the forest-savanna interface would be less clear, with the presence of grasses and ferns under the trees, similar to some zones invaded by *Aucoumea* already described by Foresta (1990).

Table 1 Transect no. 1. List of diameter at breast height (DBH) >10 cm trees (20×50=1000 m^2; see Fig. 3)

	Species		Species
1	*Aidia micrantha* (K. Schum.) F. White	34	*Xylopia hypolampra* Mildbread
2	*Sapindaceae* sp. cf. *Pancovia*?	35	*Dyospyros* sp.
3	*Monodora* cf. *tenuifolia* Benth	36	*Dacryodes* cf. *igaganga* Aubr. & Pellegr.
4	*Dacryodes* cf. *igaganga* Aubr. & Pellegr.	37	*Aidia micrantha* (K. Schum.) F. White
5	*Coula edulis* Baill.	38	*Parkia bicolor* A. Cheval.
8	*Coula edulis.* Baill.	39	*Pausynistalia* sp. 1
9	*Garcinia* sp.	40	*Santiria trimera* (Oliv.) Aubr.
10	?	41	*Pausynistalia* sp. 1
11	*Plagiostyles africana* Prain. ex De Wild.	42	*Pausynistalia* sp. 1
12	*Dacryodes* cf. *igaganga* Aubr. & Pellegr.	43	*Coelocaryon preussii* Warb.
13	*Parkia bicolor* A. Cheval.	44	*Hymenocardia ulmoïdes* Oliver
14	?	46	*Uapaca guineensis* Muell. Arg.
15	*Parkia bicolor* A. Cheval.	47	cf. *Duboscia*?
16	Olacaceae sp.	48	*Pentaclethra eetveldeana* De Wild. et Th. L
17	*Dialium* sp.	49	*Parkia bicolor* A. Cheval.
18	Rubiaceae sp.?	50	*Pentaclethra eetveldeana* De Wild. et Th. L
19	?	51	*Santiria trimera* (Oliv.) Aubr.
20	*Psychotria* cf. *venosa* (Hiern) Petit	52	*Parkia bicolor* A. Cheval.
21	*Dacryodes* cf. *igaganga* Aubr. & Pellegr.	53	*Santiria trimera* (Oliv.) Aubr.
22	*Pentaclethra eetveldeana* De Wild. et Th. L	54	*Pentaclethra eetveldeana* De Wild. et Th. L
23	*Strombosiopsis tetrandra* Engl.	55	*Plagiostyles africana* Prain. ex De Wild.
24	*Symphonia globulifera* L. f.	56	*Pentaclethra eetveldeana* De Wild. et Th. L
25	*Pausynistalia* sp. 1	57	*Santiria trimera* (Oliv.) Aubr.
26	*Uapaca* sp.	58	*Croton* sp.
27	*Symphonia globulifera* L. f	59	*Aucoumea klaineana* Pierre
28	cf. Tiliaceae?	60	*Croton* sp.
29	*Parkia bicolor* A. Cheval.	61	*Uapaca guineensis* Muell. Arg.
30	?	62	*Hymenocardia ulmoïdes* Oliver
31	*Dialium* sp.	6	? climber
33	*Aidia micrantha* (K. Schum.) F. White	7	? climber

Pedological field observations

Soils under savanna-forest transects are of the same kind. Parent rocks, weathering horizons and stone-lines are absolutely similar. Differences only appear in the upper horizons.

The thickness of humus layers ranges from 3 to 7 cm under forest. In savannas, these horizons range from 15 to 25 cm corresponding to the depth of the root system, and extend into the transition horizon A/B. These differences are linked with the humification processes. In forest, the main part of SOM originates from leaves and branches which decay on the soil surface. In savanna, aerial organs of Graminaeae burn every year and SOM are only formed from root exudation and from the decomposition of a dense root system. Therefore, the differences in vegetation are not the result of soil variations. In other word, the few differences between forest and savanna soils result from variation in vegetation.

Erosion steps are very common in savanna. They generally stop at the savanna-forest boundary. Some continue a little under forest, suggesting a great stability of this interface or that forest is slowly encroaching onto savanna. Widely extended erosion steps into forest can only be observed in *Aucoumea* forests (Foresta 1990). This case provides formal proof of the rapid expansion of forest vegetation.

Organic carbon contents

The variations of the soil organic carbon content in the 0–5 cm horizon (Fig. 4) are similar in the two transects. Carbon contents are constant from the savanna up to about 12 m inside the forest. At this stage, the carbon content increases significantly, but very unequally. This irregular increase can be related to the great spatial heterogeneity of soil characteristics in all forests of the Mayombe area at the scale of some square metres (Tsakala 1988; D. Schwartz, unpublished data).

$\delta^{13}C$ values

The variations of $\delta^{13}C$ in the 0–5 cm horizon are similar in the two transects (Fig. 5). The $\delta^{13}C$ is constant under savanna and decreases under and beyond the fern zone. However, it becomes typical of forest only at 17 m (Makaba-transect), and 31 m (Kwilila transect) from the very abrupt Gramineae-fern limit, or at 12 m inside forest. These two points correspond exactly to the increase in organic carbon.

^{14}C ages of SOM

^{14}C ages of SOM (Table 3) are reported in Fig. 5. In the savanna part of the transect, the MRT of SOM in humus layer is 88 years for Kwilila and 64 years for Makaba.

Table 2 Transect no. 1. List of <1 cm <DBH <10 cm indivuals ($5 \times 50 = 250$ m^2)

	Species
1	*Dialium* sp. 1
2	Sapindaceae sp. cf. *Pancovia*
3	Sapindaceae sp. cf. *Pancovia*
4	*Dialium* sp. 2
5	Sapindaceae sp. cf. *Pancovia*
6	Sapindaceae sp. cf. *Pancovia*
7	*Diospyros* sp.
8	Sapindaceae sp. cf. *Pancovia*
9	*Aidia micrantha* (K. Schum.) F. White
10	cf. *Acioa* sp.
11	cf. *Enantia* sp.
12	*Dialium* sp. 3
13	*Dialium* sp. 4
14	Sapindaceae sp. cf. *Pancovia*
15	*Carapa procera* D.C.
16	*Oxyanthus schumannianus* De Wild. et Th. Dur.
17	Chrysobalanaceae sp.
18	Sapindaceae sp. cf. *Pancovia*
19	*Dacryodes* sp.
20	Annonaceae sp.
21	*Dialium* sp. 5
22	cf. *Acioa* sp.
24	Sapindaceae sp. cf. *Pancovia*
26	Sapindaceae sp. cf. *Pancovia*
28	cf. Chrysobalanaceae sp. 1
30	cf. *Enantia* sp.
32	cf. *Acioa* sp.
33	*Dialium* sp. 2
34	*Psychotria* cf. *venosa* (Hiern.) E. Petit
35	Sapindaceae sp. cf. *Pancovia*
37	*Dacryodes* sp.
38	cf. Chrysobalanaceae sp. 1
41	Sapindaceae sp. cf. *Pancovia*
46	cf. *Dialium* sp.
47	Sapindaceae sp. cf. *Pancovia*
48	*Aucoumea klaineana* Pierre
49	cf. *Duboscia* sp.
50	Chrysobalanaceae sp.
52	cf. Chrysobalanaceae sp. 1
53	*Aidia micrantha* (K. Schum.) F. White
54	cf. *Acioa* sp.
55	*Trichilia* sp.
57	cf. *Acioa* sp.
58	Sapindaceae sp. cf. *Pancovia*
59	Sapindaceae sp. cf. *Pancovia.*
60	*Uapaca guineensis* Muell. Arg.
61	*Symphonia globulifera* L.f.
62	*Santiria trimera* (Oliv.) Aubr.
63	*Pentaclethra macrophylla* Benth.
64	*Parkia bicolor* A. Cheval.
65	*Parkia bicolor* A. Cheval.
66	cf. Chrysobalaceae sp. 1
69	cf. Chrysobalanaceae sp. 1
73	cf. Chrysobalanaceae sp. 1
77	*Uapaca guineensis* Muell. Arg.
78	*Dialium* sp. 2
79	Rubiaceae sp.
80	Meliaceae sp. 1
83	*Dialium* sp. 2
84	cf. Chrysobalanaceae sp. 1
85	Meliaceae sp. 2
87	Rubiaceae sp.
88	cf. Euphorbiaceae
89	cf. Chrysobalanaceae sp. 1
90	Meliaceae sp. 2
91	*Pentaclethra eetveldeana* De Wild. et Th. Dur.
92	*Oxyanthus schumannianus* De Wild. et Th. Dur.
95	*Uapaca guineensis* Muell. Arg.
97	cf. *Acioa* sp.
98	*Aidia micrantha* (K. Schum.) F. White
99	cf. Chrysobalanaceae sp. 1
110	?
113	?
114	?
115	*Pentaclethra eetveldeana* De Wild. et Th. Dur.
116	*Pentaclethra macrophylla* Benth
117	?
118	cf. *Duboscia* sp.
119	*Dialium* sp. 2
121	*Pentaclethra eetveldeana* De Wild. et Th. Dur.
122	?
123	cf. Chrysobalanaceae sp. 1
125	cf. Tiliaceae
126	*Hymenocardia ulmoïdes* Oliver
127	*Aidia micrantha* (K. Schum.) F. White
128	?
129	*Hymenocardia ulmoïdes* Oliver
130	Meliaceae sp. 2
131	Meliaceae sp. 2
132	*Hymenocardia ulmoïdes* Oliver
133	*Hymenocardia ulmoïdes* Oliver
134	*Hymenocardia ulmoïdes* Oliver
135	*Hymenocardia ulmoïdes* Oliver
136	*Hymenocardia ulmoïdes* Oliver
23	Climber?
25	Connaraceae sp. 1 (climber)
27	Hippocrateaceae sp. 1 (climber)
29	*Salacia debilis* (G. Don.) Walp. (climber)
31	Hippocrateae sp. 2 (climber)
36	Climber
39	*Salacia debilis* (G. Don.) Walp. (climber)
40	*Salacia debilis* (G. Don.) Walp. (climber)
42	Climber
43	*Salacia debilis* (G. Don.) Walp. (climber)
44	*Salacia debilis* (G. Don.) Walp. (climber)
45	*Artabotrys* sp. (climber)
51	Connaraceae sp. 1 (climber)
56	Connaraceae sp. 1 (climber)
67	Connaraceae sp. 1 (climber)
68	Climber
70	Connaraceae sp. 1 (climber)
71	Apocynaceae sp. (climber)
72	*Salacia debilis* (G. Don.) Walp. (climber)
74	Connaraceae sp. 1 (climber)
75	*Salacia debilis* (G. Don.) Walp. (climber)
82	Apocynaceae sp. (climber)
86	Connaraceae sp. 1 (climber)
93	Connaraceae sp. 2 (climber)
94	Connaraceae sp. 1 (climber)
96	Connaraceae sp. 3 (climber)
100	Connaraceae sp. 1 (climber)
101	Connaraceae sp. 1 (climber)
102	Connaraceae sp. 1 (climber)
103	Connaraceae sp. 1 (climber)
104	Connaraceae sp. 1 (climber)
105	Connaraceae sp. 1 (climber)
106	Connaraceae sp. 1 (climber)
107	Climber
108	Connaraceae sp. 1 (climber)
109	Connaraceae sp. 1 (climber)
111	Connaraceae sp. 2 (climber)
112	Connaraceae sp. 1 (climber)
120	Climber
124	Connaraceae sp. 3 (climber)

Table 3 ^{14}C activity in year 1990 and mean residence time (*MRT*) of soil organic matter of average samples in different parts of the two transects

Sample	$\delta^{14}C$ (‰)	$\delta^{13}C$ (‰)	$\Delta^{14}C$ (‰)	MRT (years)
Makaba, savanna	171.7	−12.5	142.4	64
Makaba, shrub	180.9	−24.3	179.2	45
Makaba, forest	213.9	−27.0	218.8	32
Kwilila, savanna	138.8	−14.0	113.7	88
Kwilila, fern	122.0	−21.0	113.0	88
Kwilila, forest	210.6	−27.0	215.4	32

MRT of the sample from the shrub-zone and forest edge at Kwilila is close to that in the savanna. MRT of humus at the forest edge in Makaba is 45 years. In the forest, the MRT is 32 years in both cases. The lower MRT of SOM in the forest, when compared to the savanna, can be related to the higher carbon content. It can be explained by an increased carbon input to the soil surface and/or a higher turnover rate.

Discussion

Proof of forest encroachment

MRT and $\delta^{13}C$ indicate changes of biogeochemical characteristics of SOM. Are these facts proof of forest expansion or are they the observation of an edge effect occurring on a static boundary?

An answer is given according to recent data in Amazonia by Kapos et al. (1993), suggesting that the $\delta^{13}C$ composition of canopy leaves, understorey leaves and understorey air changes in relation with the distance to the edge in a 5-year-old static edge with frequent gaps. However, the response of two understorey species studied is different. The $\delta^{13}C$ composition of leaves of the first species does not present significant changes between edge and forest zones, whereas the $\delta^{13}C$ in leaves of the second species presents a decrease of 2 ‰ in absolute value from the edge up to 40 m in the forest. As a general rule, Kapos et al. (1993) never found decreases greater than 2 ‰ as edge effects.

On the other hand three different arguments lead us to consider that in the transects forest is encroaching on savanna:

Floristic and structural proof of forest expansion

The present position of trees showing ripicole behaviour and increasing diameters in relation with their distance to the edge, such as *Parkia bicolor* trees no. 57 (DBH=27 cm; distance from the edge: 6 m) and no. 38 (DBH=43 cm; distance; 10 m), provide a reference point as they germinated at the forest boundary.

$\delta^{13}C$ of SOM

Even if the 2 ‰ differences in the $\delta^{13}C$ values of leaves and atmospheric CO_2 observed by Kapos et al. (1993) could be transferred into litterfall, litter composition on the soil and into the following $\delta^{13}C$ values of SOM in humus layer, no edge effect can explain differences as high as 14 ‰. Moreover, the values of the $\delta^{13}C$ of SOM in forest humus layers at 12–17 m from the edge in both transects are becoming identical to the $\delta^{13}C$ values of other typical rain-forests from the south of the Congo, which range from −26.6 to −28.2 ‰ (Schwartz 1991). In other words, if the ecotone was static, differences between the $\delta^{13}C$ of SOM in savanna and forest topsoils should be more abrupt, in spite of the edge effects, as schematized in Fig. 6. Moreover the C4–C3 edge is not the savanna-forest ecotone, but the graminean-fern limit.

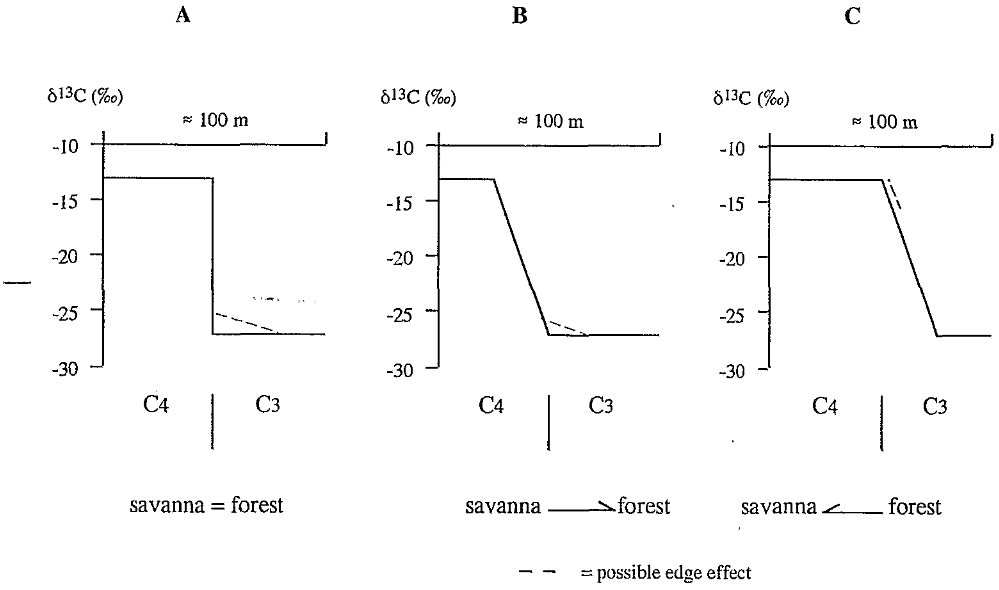

Fig. 6A–C Theoretical $\delta^{13}C$ variations in a savanna-forest transect in the three following hypotheses: **A** static ecotone, **B** savanna expansion, **C** forest encroachment. In a simplified manner: *C4*=graminean zone; *C3*=fern patch+forest. NB The inclination of the slope is an indicator of the speed of the encroachment

This fact could reduce the edge effect, which is a straight consequence of the difference of the $\delta^{13}C$ composition between atmospheric and understorey CO_2.

Organic carbon under forest

As additional proof, the increase in organic carbon content under forest also shows that this vegetation type is progressing compared to savanna in the two transects. If the savanna-forest boundary was stable, the carbon increase should only appear just beyond the boundary. If savanna is progressing, the carbon content under savanna near the edge should be comparable to the carbon content under forest. The irregular increase of organic carbon content is to be referred with the great lateral variability of topsoil horizons in the Mayombe forests on a metric scale (Tsakala 1988).

Estimation of the speed of forest progression

Combined $\Delta^{14}C$ and $\delta^{13}C$ data allowed us to estimate the speed of forest encroachment. According to the model of exponential decay we used to compute MRT of SOM after $\Delta^{14}C$ values in top soil samples (Balesdent and Guillet 1982), MRT is the time required for the replacement of 63% of the savanna SOM by forest SOM [i.e. 1–exp (−1)]. We measured the distance *D* between typical savanna $\delta^{13}C$ values and $\delta^{13}C$ values corresponding to the mixture of 63% forest organic matter and 37% savanna organic matter. Then we estimated that the distance *D* was covered within the time MRT:

$$\text{Speed}=D\cdot \text{MRT}^{-1} \text{ m/century.}$$

We estimated *D* from the data in Fig. 5. At Makaba (transect number 1) it is equal to 9 m. As MRT ranges between 64 and 32 years, the present speed of forest encroachment is between 14 and 28 m/century. At Kwilila (transect number 2), the same calculation, with D=24 m and MRT=32–88 years, leads to a speed between 27 and 75 m/century. As MRT progressively decreases from the savanna to the forest, medium values may be a better approximation of forest progression. We finally estimate that the mean speed of forest encroachment in enclosed savannas of the Mayombe probably ranges between 20 and 50 m century. This speed is slow in the absolute. Annual burnings of savannas explain this fact, but it is important to notice that burning cannot prevent forest progression.

History of vegetation

The history of the vegetation in the south of the Congo was reconstructed by palynological data, vegetable macroremains determination and $\delta^{13}C$ analyses (Dechamps et al. 1988; Elenga et al. 1992; Schwartz 1988, 1991, 1992; Schwarz et al. 1992; Vincens et al. 1994). These data show that forest covered all this area during early Holocene, that a climatic drying at about 3000 B.P. led to the expansion of the present savannas and that the climate became more humid again some centuries ago. The present forest encroachment in the enclosed savannas could correspond to this climatic episode. As a consequence, the savannas were certainly more extensive some centuries ago, and this confirms some archaeological data of Schwartz et al. (1990a), according to which savannas occurred within the Mayombean forest as far west as Les Saras.

Conclusions

The botanical study, organic carbon contents and $\delta^{13}C$ values on the two transects show undoubtedly that forest is encroaching onto savanna. The climatic conditions within the Mayombe are favourable to forest expansion. This expansion can be seen in the upper horizon. The transformation starts in the fern zone; ferns are C3 plants. Combination of $\Delta^{14}C$ and $\delta^{13}C$ data allows one to estimate that the speed of expansion in the two representative transects is between 14 and 75/m century, and more likely at about 20–50 m/century. It is clear that savanna bush fires slow down the forest encroachment, but it is also clear that they cannot prevent it. As most savannas are less than 1 km across, speeds of 20–50 m/century mean that, assuming environmental conditions remain the same, these savannas could disappear in about 1 or 2 millennia. The area of about 40% of the savannas is smaller than 0.1 km^2 (Rat Patron and Schwartz 1996): these little savannas could disappear in 100–200 years.

This expansion speed also leads to questions about the regeneration speed of upper horizons of soil. As opposed to savanna, the latter are never scoured down to the stone-line under forest. It seems very possible that these horizons can be regenerated under forest by means of different factors which remain to be precisely studied (biological factors, especially termite intervention and accumulation of colluviated particles). This regeneration could occur in a few centuries, which is very rapid in pedological terms.

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