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ORIGINAL ARTICLE

Forest progression modes in littoral Congo, Central Atlantic Africa

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ABSTRACT

Aim To understand the persistence of a forest–savanna mosaic in places where rainfall data suggest that forest take-over should take place. To study the various modes of forest encroachment, and the role of human activities to hamper it.

Location Data were collected on several forest–savanna ecotones in the coastal region of the Republic of Congo. The sites were chosen to illustrate the main different modes of forest expansion, corresponding to different levels of anthropic pressure.

Methods The sites were studied on five transects perpendicular to the ecotone (total sampled area: 1.7 ha) and 10 forest clumps in savanna (with diameters from 3 to 20 m). Along the transects botanical identification, diameter measurement and cartography were performed, while leaf area index was measured with a high resolution (every meter) along two of them. Collected data were analysed using a continuous quantification approach, much more useful than the classical quadrat analysis. Time calibration of progression rates was performed using a simple model of the growth of the characteristic pioneer species, *Aucoumea klaineana*.

Results The two main different modes are reflected in different successional patterns. The edge diffusion is slow (its rate is evaluated to *c.* 1 m year^{-1}) and is characterized by a progressive increase in high diameter trees density and shade tolerant trees density away from the ecotone. Conversely, savanna to forest phase transition by coalescence of clumps exhibits high tree density remnants distributed in established forest. The composition of these remnants is compatible with that of the forest clumps in savannas.

Main conclusions Three functional groups of pioneer trees are distinguished: some occupy the edge (edge pioneer), others establish clumps of forest in savanna (clump pioneers) and longer-living *A. klaineana* ensures the transition to 'mature' forest.The two different observed patterns (linear edge progression and clump coalescence) can be understood with a model of forest–savanna dynamics, 'FORSAT'. The two control parameters are the annual rainfall and the frequency of fires lighted in each savanna. In particular, an increase in the fire frequency can lead to a shift from the coalescence regime to the edge progression one.

Keywords

Congo, tropical forest, tropical savanna, forest expansion, *Aucoumea klaineana*, botanical inventories, leaf area index.

INTRODUCTION

The African equatorial rain forest is known to have expanded over peri-forest humid savannas during the last centuries, North as well as South of the equator, despite frequent savanna fires. This has been evidenced by botanical studies (e.g. Swaine *et al.*, 1976 in Ghana; Achoundong *et al.*, 2000 and Vincens *et al.*, 2002 in Cameroon), soil organic carbon isotopes analyses (Schwartz *et al.*, 1996 in Congo; Guillet *et al.*, 2001 in Cameroon; Delègue *et al.*, 2001 in Gabon), or by comparison of aerial photographs and/or satellite images (Gautier, 1990 in Ivory Coast; Runge & Neumer, 2000 in Democratic Republic of Congo, former Zaïre; Letouzey, 1968 or Youta Happi, 1998 in Cameroon). The distribution of forest and savannas mainly results of past strong climatic changes (succession of dry and humid periods) that led to the regression or the expansion of the forest domain in the tropics (Servant *et al.*, 1993). The last dry period which has affected the central African forest is dated around 3000 BP (Vincens *et al.*, 1999). After the recovering of more humid conditions, forest has started to transgress over savannas, despite increasing human disturbances.

During forest transgression episodes, typical light-demanding species play the role of pioneers (Hopkins, 1992). They establish in savanna, generally near the edge, grow, shade the grass layer and make it possible for successional shade-tolerant species to develop and then for forest to supplant savanna. A simple model of forest transgression in man-influenced environments (Favier *et al.*, 2004) evidences that environmental and anthropic factors determine the mode of progression. In the more favourable conditions, clumps of pioneer trees appear in savanna, grow and then coalesce, leading to a rapid encroachment of savanna. In less favourable conditions, the transgression is far slower and only takes place by a shifting of the forest edge, that is by a marginal extension of established forest plots. This means that a change in anthropic pressure (frequency of savanna fires) can lead the transgression to shift from the clump coalescence mode to the edge progression one and induce a dramatic slowdown of the transgression rate.

These two modes of progression were already described in field studies (e.g. Gautier, 1990; Guillet *et al.*, 2001; Puyravaud *et al.*, 2003) but rarely related to anthropic pressure, nor described in details. The goal of this study is to understand the mechanisms of the two modes of progression in the south-western extremity of the Congolese forest: the function of each pioneer species, the rates of forest progression, how the natural mechanisms may be used for forest management.

The observation of both the structure and the floristic composition of forest at different stages of development, especially along transects perpendicular to the forest–savanna boundary, provides important information about the process and timing of the forest invasion on savannas. Five transects crossing the forest–savanna boundaries are presented. Leaf area index (LAI) profiles and botanical inventories were performed, and the data analysed. In addition, clusters of forest trees inside savannas are described. The forest is studied from the most recent stages (establishment of pioneer tree species in open environment) to older successional ones (when pioneer species have disappeared).

STUDY SITES

Description of the region

The work was carried out in the littoral region of Congo, in the Kouilou district, near the Atlantic Ocean (Fig. 1). The Republic of Congo is located in central Africa, straddling the equator (5° N–5° S). The country is mostly occupied by humid tropical forests (*c.* 65%) and humid savannas (*c.* 35%) (CARPE, 2003). The Atlantic region (Kouilou district) is covered by savannas lying between the coastline and the Mayombe forest. In this area, Fabing (2000) has shown, by comparison of aerial photographs, that during the last decades forest has progressed over savannas with a rate of about 100 m per century. Similar results were obtained in nearby regions: edge progression with a rate between 20 and 50 m per century in savannas enclosed in the Congolese Mayombe forest (Schwartz *et al.*, 1996), and around 100 m per century on coastal Gabon (Delègue *et al.*, 2001).

Two main areas were studied. The Youbi area (4°00′–4°30′ S, 11°30′–12°00′ E) is located behind the littoral plain, between the Noumbi and Kouilou rivers, where occurs a zone of plateaux ('plateaux de Kayes') ranging from 60 to 130 m in altitude. This region is softly undulating, enclosing swamps or small lakes in the depressions (Hecketsweiler & Mokoko-Ikonga, 1991). The Kola area (4°00′–4°02′ S, 11°35′–37′ E) is located north of Youbi at the foot of the Mayombe mountains.

The climate of the Kouilou region is a two-season transition equatorial type (Aubréville, 1949), characterized by a long cool dry but cloudy season (4–5 months from May or June to September) followed by a rainy season (October to April or May) with about 1200 mm precipitation (Madingo-Kayes meteorological station 1982–2001). The annual temperature is about 25 °C, with small amplitude variation (Laclau *et al.*, 2002; Loumeto, 2002).

The vegetation in the study region is a mosaic of forest and grove-spread savannas. In the Youbi area, forest belongs to the Okoumé (*Aucoumea klaineana*) terra-firma forested landscape type depressions (Hecketsweiler & Mokoko-Ikonga, 1991) and for the Kola area to a forest with great floristic affinities with the Yombe forest type *stricto sensu* with many Leguminosae, belonging to the 'mixed moist semi-evergreen Guineo-Congolian rain forest' according to White terminology (White, 1986). The most common species are *Aucoumea klaineana* (okoumé), then *Coula edulis*, *Dichostemma glaucescens*, *Staudtia gabonensis* (niové), *Vitex pachyphylla*, associated with *Dialium* sp., *Polyalthia suaveolens*, *Santiria trimera*, *Synsepalum dulcificum*, *Trichoscypha acuminata* in the understory.

The herbaceous layer in savannas is low (Laclau *et al.*, 2002), dominated by short Gramineae and Cyperaceae (*Bulbostylis laniceps*, *Ctenium newtonii*, *Rhynchelytrum repens*…) with locally tall Gramineae such as *Hyparrhenia diplandra*, *Loudetia arundinacea*, *Imperata cylindrica* or

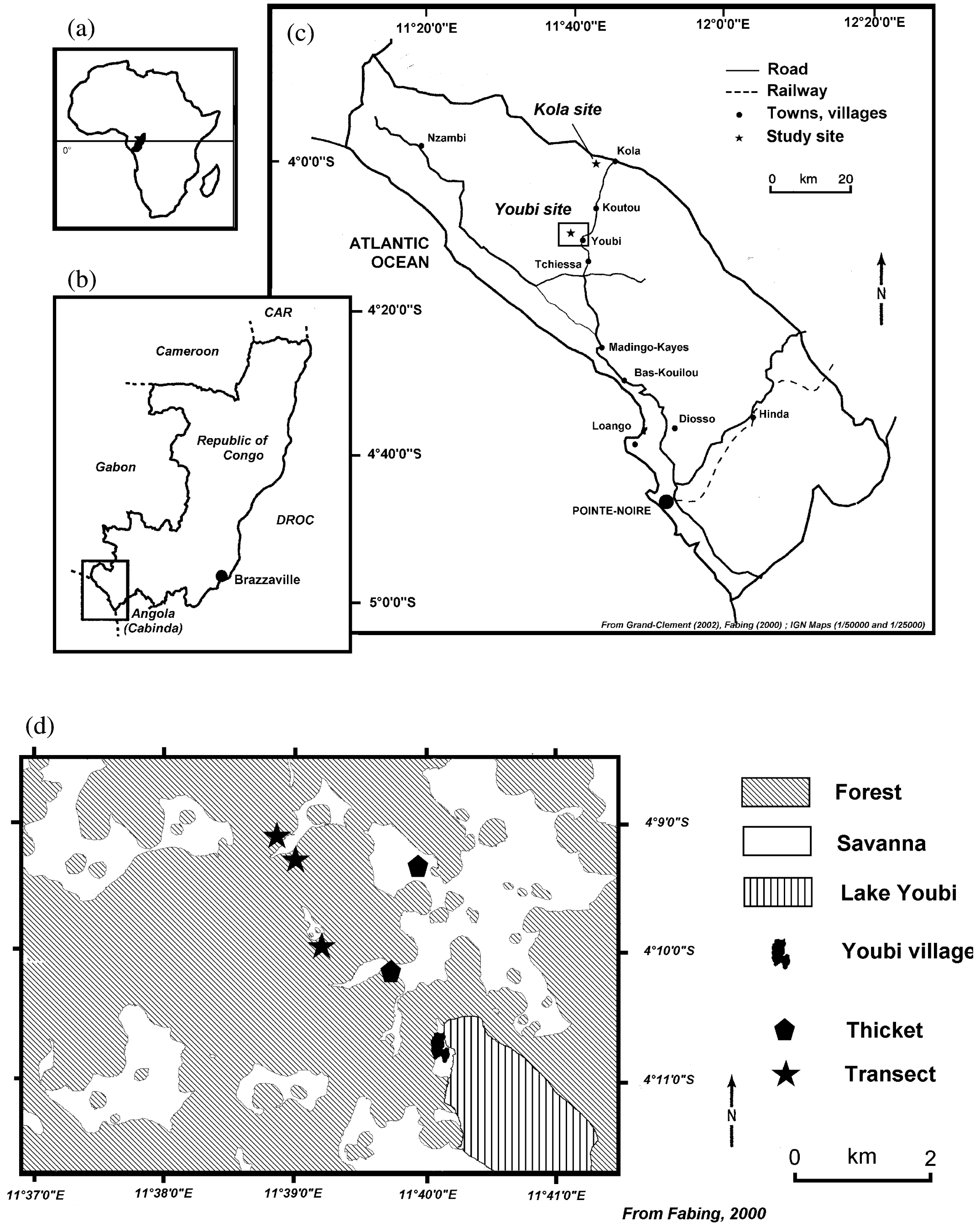

Figure 1 Location of (a) the Republic of Congo in Africa, (b) Kouilou region, (c) the two main study sites in the Kouilou region, and (d) transects and groves in the Youbi area. Modified from Fabing (2000) and Grand-Clément (2002).

Panicum maximum. Some shrubs of 1–2 m high are present: *Annona senegalensis*, *Bridelia ferruginea* and *Psorospermum febrifugum*.

Many of these savannas are today colonized by forest trees, mainly by okoumés. Locally, tree or shrub clusters of various sizes are present in these savannas, some of which are natural while some others have an anthropogenic origin and correspond to abandoned villages.

For these latter, human interference is easily deduced from the presence of plants such as oil-palms (*Elaeis guineensis*), avocados (*Persea americana*) and mango trees (*Mangifera indica*) (Vennetier, 1968; Hecketsweiler & Mokoko-Ikonga, 1991). On the other hand, natural tree clusters are characterized by the lack of the previously mentioned fruit-trees and are rich in pioneer forest species such as *Anthocleista schweinfurthii*, *Aucoumea klaineana*, *Barteria nigritiana*, *Macaranga* *spinosa*, *M. barteri*, *Xylopia aethiopica*. Other tree species are found in these clumps, such as *Klainedoxa gabonensis* and *Sacoglottis gabonensis*, typical of humid forests, and *Chrysobalanus icaco*, usually found in littoral groves.

A few words about okoumé ecology

Okoumé (*A. klaineana*) is a tree from the Burseraceae family, which is endemic in Gabon, Equatorial Guinea and in the South West of the Republic of Congo; this extension is limited by the short germinative lifespan of the seeds which do not survive extended dry seasons (Brunck *et al.*, 1990). It is a relatively fast growing tree of high economical value (plywood) which can survive up to 100–150 years and reach d.b.h. up to 120 cm. It is a light demanding pioneer tree which becomes quickly dominant in forest–savanna fronts, progressively eliminating almost all the other species. Adults left behind the forest front will not be replaced by young okoumés (due to the lack of available light for okoumés saplings), and some authors (White *et al.*, 2000) have suggested that the natural succession is a Marantaceae cover, which is not clearly evidenced by our observations – see discussion below.

FIELD METHODS AND DATA COLLECTION

Botanical inventories

Field work for botanical inventories was led in 1997, 2000 and 2002. In each study site, transects crossing perpendicularly the ecotone have been laid out, starting in savanna, not far from the forest edge, and ending 60–150 m inside the forest (Table 1). On each side of the transect, 10×10 m^2 plots were delimited using a lost threadmeter. In each plot, all woody plants of more than 5 cm diameter were identified to species and mapped, then their diameter at breast height (i.e. 1.3 m d.b.h.) was measured (full data are given in Appendix S1 to S5 in the Supplementary Material). Non-woody species were described qualitatively.

In addition, the trees in 11 clumps of forest in savanna of different size (from *c.* 3 to 20 m diameter), including that along the YOSI transect, were identified and discriminated according to their location in the clumps, either in the centre or in the edge.

Table 1 Characteristics of the transects and width of the pioneer zone (PZ) and of the secondary zone (SZ)

Transect	Site	Length (m)	Year of sampling	PZ width (m)	SZ width (m)
YOLI-1	Youbi	150	2002	30	65
YOLI-2	Youbi	70	2000	30	–
KOLA-1	Kola	130	1997	5	80
KOLA-2	Kola	110	1997	15	50
YOSI	Youbi	120 + 40 (clump)	2002	–	–

The list of taxa (after Hutchinson & Dalzied, 1972) is provided in Appendix 1.

LAI measurements

The LAI measurements were made in 2002 with a simple and inexpensive apparatus described by Cournac *et al.* (2002) that compares favourably to several other devices (Ferment *et al.*, 2001). The principle of this method is to measure the light transmitted I by the tree cover with a light-dependent resistor behind an off-the-shelf fish-eye lens (spy-hole optic).

The Beer-Lambert law relates the transmitted light to the incident light I_0:

$$I = I_0 \exp(-k \cdot \mathrm{LAI}).$$

The attenuation factor k depends on foliage characteristics and is equal to 0.88 for many tall evergreen forest (Wirth *et al.*, 2001). This value was considered here and a discussion on k variability can be found in Emmons & Dubois (2003). I_0 is evaluated and corrected for cloud cover conditions as explained in detail in Cournac *et al.* (2002).

Light readings were taken between 11:00 and 13:00 hours to ensure a nearly vertical insolation, at 1-m intervals on all the transects using a lost thread distance-measuring device. The light sensor was held at 2 m height and only foliage above this level has influenced the readings. Control readings were regularly taken in the open savanna, away from any trees, at the end of each transect.

DATA ANALYSIS

Ecological indicators for transect description

Identical representations and analyses were performed in the five transects. First, the position of the stems is represented as circles with area proportional to their girth. A proportionality between disc area and basal area (BA) would have been a more obvious solution but this method yielded to such discrepancies between small and large trees that the graphs were unreadable. On the graphs, the main characteristic species are highlighted by particular colours. Then, measures of density were computed:

1 The density of stems with diameter > 5 cm, measured in number of stems per hectare and the relative density (RD) of characteristic species, expressed as the ratio of the density of these species over the total density.

2 The BA of these stems, measured in m^2 ha^{-1}, and the relative basal area (RBA) of characteristic species, expressed as the ratio of the BA of these species over the total.

3 The normalized specific mean tree basal area (NMTBA$_{\mathrm{sp}}$), which is the ratio between the mean tree basal area (MTBA) of a particular species (sp) in a portion of the transect and the MTBA of this species over the whole transect. Last index values less (or greater) than 1 indicate that the local BA is supported by relatively small (or large) trees.

The transition between savanna and forest being short (about 100 m), a classical quadrat-based description considering adjacent square areas of 20×20 m^2 cannot correctly describe the fine succession. The local values of density were instead computed every metre using an optimized running mean (or moving average) method. The local density and BA were evaluated every metre in a surrounding 10-m wide portion of transect. It is important to note that this 10 m bandwidth was not arbitrarily chosen but is determined self-consistently with an original method which we developed to optimize data utilization (Favier *et al.*, 2004b). The NMTBA index is expressed as the ratio of the local BA over the local density of the considered species, normalized by the total number of stems in the transect d_{sp} over the total basal area $\mathrm{BA}_{\mathrm{sp}}$:

$$\mathrm{NMTBA}_{\mathrm{sp}}(x) = \frac{\mathrm{BA}_{\mathrm{sp}}(x)}{d_{\mathrm{sp}}(x)} \left(\frac{\mathrm{BA}_{\mathrm{sp}}}{d_{\mathrm{sp}}} \right)^{-1}.$$

Finally, richness, diversity and evenness along the transect over adjacent 400 m^2 square areas (quadrat method) were computed using both Shannon and Simpson indexes (Magurran, 1988): both give very similar curves, but we will show only the Shannon indexes as they are more commonly used in the published literature.

Map of local density

In the YOSI transects, the botanical inventories were performed on a larger area than in the others. The local density is evaluated here over this surface and defined as the ratio of the number of trees in a circle of radius $r = 5$ m over the surface of this circle. Zones of high local density are defined as those where the local density exceeds the median value.

Age estimation

Due to its commercial value, okoumé has been one of the best studied trees in the tropics. In particular, some studies have attempted to relate the diameter of the dominant okoumés to their age, either in natural stands (Nasi, 1997) or in plantations (Brunck *et al.*, 1990).

We propose a simple model of dominant okoumé growth (Fig. 2), which does not aim at a precise description of the mechanism of tree growth, but rather is an empirical model that rests on literature data. In this model, we consider that a dominant okoumé reaches a maximal diameter $\phi_{\max}$ with an exponentially decaying growth rate of parameter α:

$$\phi = \phi_{\max}[1 - \exp(-\alpha t)]$$

The maximal diameter is evaluated to $\phi_{\max} = 100$ cm (Nasi, 1997) and the parameter α is evaluated from two kinds of studies of annual growth rates: in natural stands and in plantations (Table 2). The resulting curves of evolution of diameter with age are compatible with the measures.

Then, the age of a dominant okoumé (the biggest in its neighbourhood) is considered to be included between the ages deduced from both models. Supposing that what is now a dominant okoumé established at the forest edge, it is possible to represent the evolution of the position of the edge through time and to deduce its progression rate. There are a lot of sources of uncertainties in this approach: in the formulation of the model, in the data used and in the choice of dominant okoumés, so it cannot lead to a precise evaluation of the progression rate. Nevertheless, it surely yields to a good estimate of the magnitude of this rate.

FIELD STUDY RESULTS

YOLI-1 and -2, KOLA-1 and -2

The botanical inventories and the data exploitation are summarized in Fig. 3 for YOLI-1, in Fig. 4 for YOLI-2, in Fig. 5 for KOLA-1 and in Fig. 6 for KOLA-2. In each of the four transects, the succession can be divided into three zones of various widths (Table 1).

The zone closest to the savanna (pioneer zone) is characterized by: (i) a progressive increase in the LAI signal; (ii) an increase in the stem density and an approximately constant high RD of okoumés; (iii) an increase in the BA and a high but irregular RBA of the okoumés; (iv) the evenness index is low.

The second zone (secondary zone) is characterized by: (i) a relatively constant LAI; (ii) a relatively constant stem density, with a relative okoumé density slowly decreasing to zero and an increasing RD of *D. glaucescens*; (iii) a relatively constant BA and RBA of okoumés to high levels; (iv) an increase of the okoumé NMTBA index, representing the progressive growth of

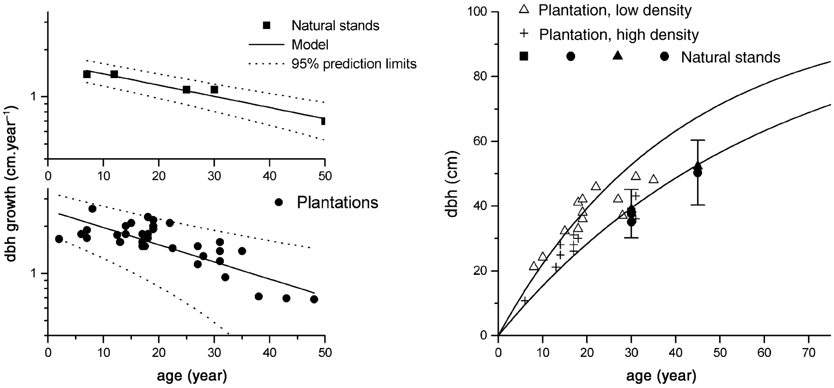

Figure 2 Model of diametrical growth of okoumés. (a) Data of diametrical growth of okoumés depending on their ages from Nasi (1997) (natural stands) and exponential fit (model A). (b) Similar data from Brunck *et al.* (1990) (plantations) and exponential fit (model B). (c) Data of tree diameter in function of their ages from (1) natural stands Nasi (1997) (2) and (3) plantations (Brunck *et al.*, 1990) and the extreme models A and B.

Table 2 Summary of the extreme models of okoumé diameter growth A and B

Model	Source of the data	Stand	ϕ_{max} (cm)	α (year^{-1})
A	Nasi (1997)	Natural	100	0.016
B	Brunck *et al.* (1990)	Plantation	100	0.026

okoumés together with their rarefaction (ii and iii); (v) an increasing evenness, denoting a progressive diversification of the lower layer (recruitment of other trees than okoumés) while the upper one is still dominated by okoumés.

The transition to the last zone (forest zone) is characterized above all by the disappearance of okoumés. The transition is particularly striking when considering the okoumé RBA profile, showing an abrupt decrease from very high values to zero, that surely results of commercial okoumé logging (old stumps were found as well as old log trailing paths). The other indexes do not show remarkable changes. In this forest zone, *D. glaucescens* RD and RBA profiles prove that a succession phenomena, analogous to that of okoumé, takes place.

Figure 7 displays evaluated rates of progression for the different transects. They are of the order of 1–2 m year^{-1} (100–200 m per century).

In the YOLI-1 study site, LAI was measured on a longer distance than the one where botanical inventories were performed: Fig. 8 shows the LAI signal from the forest edge to 350 m inside the forest. There is an obvious zone from *c.* 230–270 m where the LAI falls to values around 3. This corresponds to a zone where few trees are present, and where it exists a quasi mono-specific low and dense cover of Marantaceae *c.* 1–1.5 m high (LAI reaches values above 8 under this herbaceous cover). We will discuss this below.

YOSI

The YOSI pattern is quite different from that previously described for the other four transects (Fig. 9). The raise in LAI to a constant value is very steep after crossing the savanna–forest boundary. The stem density and BA profiles are characterized by four peaks. The okoumé RD and RBA also present peaks, but more or less shifted from the latter

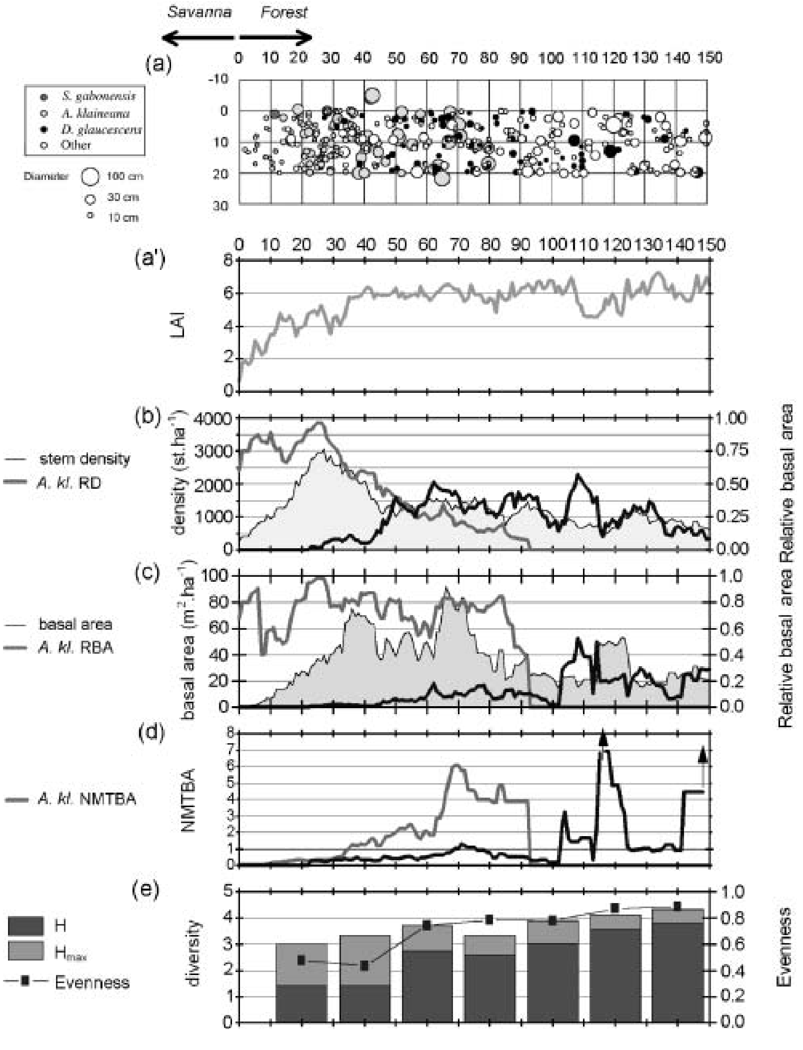

Figure 3 Description of the YOLI-1 transect. (a) Map of the trees (diameter > 5 cm). The size of each circle represents the diameter of the tree. The colours discriminate trees of characteristic species. (a′) Evolution of the LAI along the transect (resolution 1 m). (b) Yellow area, left scale: evolution of the local stem density along the transect (resolution 1 m). Magenta and blue lines, right scale: relative stem density of *Aucoumea klaineana* and *Dichostemma glaucescens*. (c) Blue area, left scale: evolution of the local basal area along the transect (resolution 1 m). Magenta and blue lines, right scale: relative basal area of *A. klaineana* and *D. glaucescens*. (d) Normalized specific basal area index for of *A. klaineana* and *D. glaucescens*. (e) Bars, left scale: Shannon diversity index H' (red) and maximum diversity H_{max} (green) of contiguous 20 × 20 m stands. Blue squares, right scale: evenness on the same quadrates.

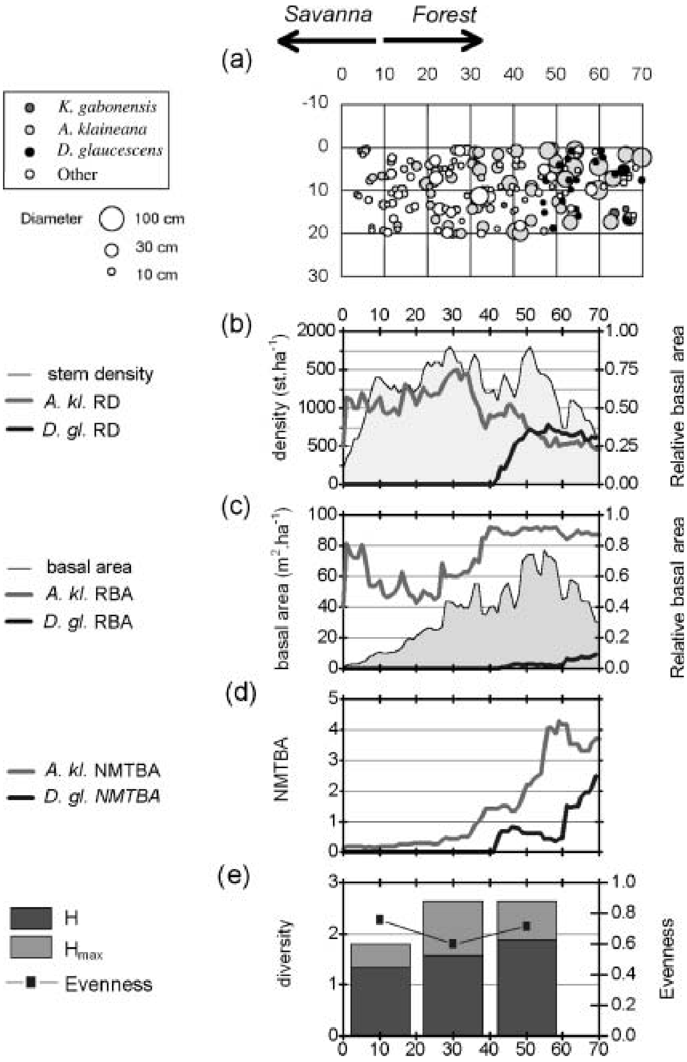

Figure 4 Description of the YOLI-2 transect. See legend of Fig. 3 for details.

ones, indicating that the centre of these high-density areas are occupied by big trees of other species (*Klainedoxa gabonensis*, *Sacoglottis gabonensis* and *Chrysobalanus icaco*). The okoumé NMTBA index oscillates around a value of 1, and except for the stand closest to the savanna, the evenness index stays at low levels. This indicates that the succession did not take place through the conventional edge progression scenario, but results of the aggregation of thickets that appeared in savanna.

Figure 10 displays the zones with local BAs greater than the median value of the whole map. In the transect, these zones correspond to the aggregated clusters of trees which appeared in savanna (clusters B, C, D and E). In the centre of most clusters, some trees of species *Chrysobalanus icaco*, *Sacoglottis gabonensis* or *Klainedoxa gabonensis* are found, surrounded by big okoumés (clusters A, A', B, C, D, D', D', E, G). Field observations show that these big trees generally have their first branching very low and are overgrown by the other trees and that most of them are dying from light deprivation, indicating that they have grown in an open landscape. This confirms the hypothesis that these clusters are issued from former clumps in savanna that aggregated to form a forest. The cluster F is rather different: it is larger and consists of a crown of okoumés bigger than in the other clusters, with a hole in the centre. The plausible hypothesis is that this cluster is a former clump, older than the other clusters and that the trees at the origin of the clump occupied its centre but have died (it is possible, as they are also dying in smaller clusters).

Forest clumps in savanna

The botanical inventories of the clumps and micro-clumps in savanna are summarized in Table 3. In the edges, light-demanding short-living forest species are found (especially *Hymenocardia ulmoides*, *Maprounea membranacea*, *Macaranga spinosa* and *Xylopia aethiopica*). As a rule, the micro-clumps organize around a savanna shrub and *Chrysobalanus icaco* or *Sacoglottis gabonensis* can also occupy the edges. In bigger clumps, these species with *Klainedoxa gabonensis* are the dominant trees and occupy their centre.

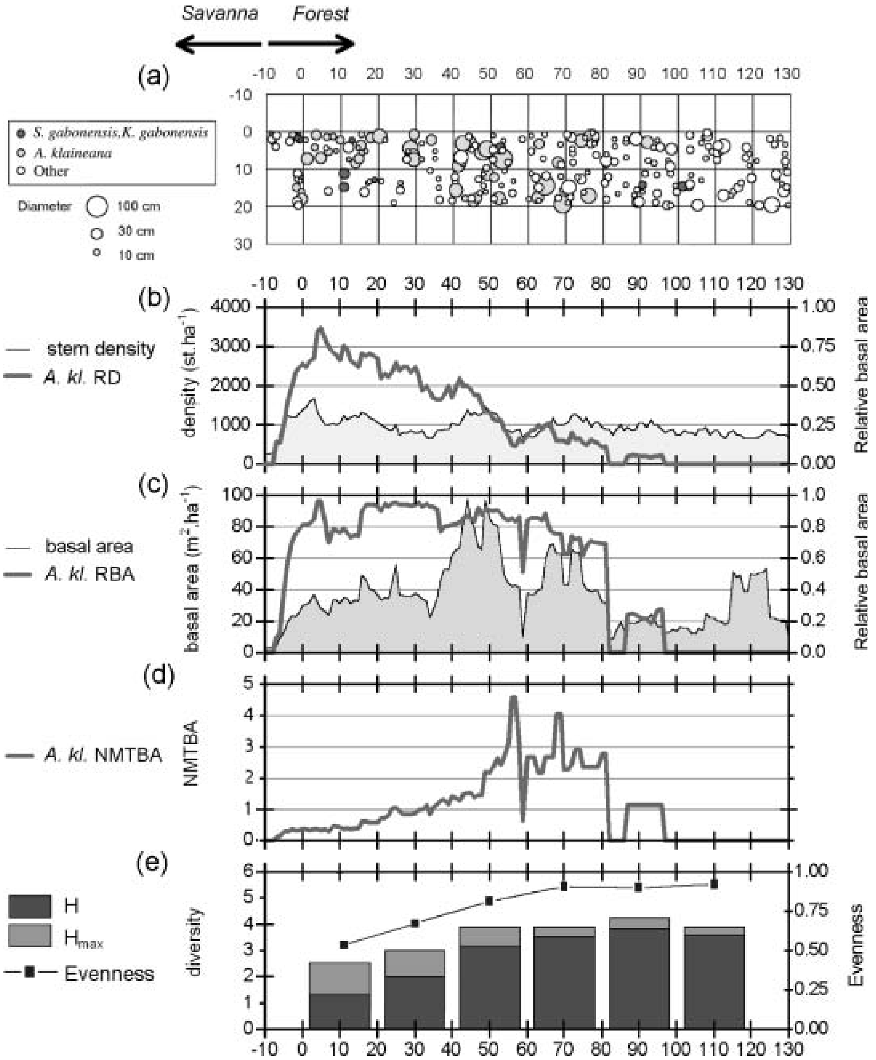

Figure 5 Description of the KOLA-1 transect. See legend of Fig. 3 for details.

DISCUSSION

Modes of forest transgression

The present study evidences the coexistence of two modes for the transgression of forest over savanna: edge progression (or diffusion) or clump coalescence.

In the case of edge diffusion, the rate of forest progression over savanna of 1–2 m year^{-1}, deduced from a model of diametrical growth of okoumés, is comparable with those estimated by other methods in other sites of Central Atlantic Africa. In the Congolese Mayombe, Schwartz *et al.* (1996) deduced from stable carbon isotope analysis a progression rate of 0.2–0.5 m year^{-1}. Using the same method, progression rate was estimated to be about 1 m year^{-1} in coastal Gabon (Delègue *et al.*, 2001). As ours, this method provides an estimation of the forest progression rate in a particular location. A comparison of aerial photographs and/or remote sensing images can provide a mean transgression rate over a region, thus giving an estimation of the regional balance between local regression or progression of forest. With such an approach, around the Youbi site, Fabing (2000) estimated the mean progression rate to 1 m year^{-1} and in different places in Cameroon, Youta Happi (1998) find a progression rate between 0.6 and 2 m year^{-1}.

We have shown that two dynamics of forest transgression coexist in coastal Congo. Outputs of a model of the evolution of forest–savanna mosaic in man-influenced environment (Favier *et al.*, 2004) can help us to interpret this result.

From this model, it appears that the stable phase (forest or savanna) and, in the case of forest transgression, its pattern and the rate at which it takes place, result of the balance between the favourable climate and the unfavourable recurrent savanna fires. Indeed, under conditions relatively unfavourable to forest (relatively dry climate or a severe fire regime in savanna) the progression of forest over savanna only takes place by an edge encroachment. In savanna,

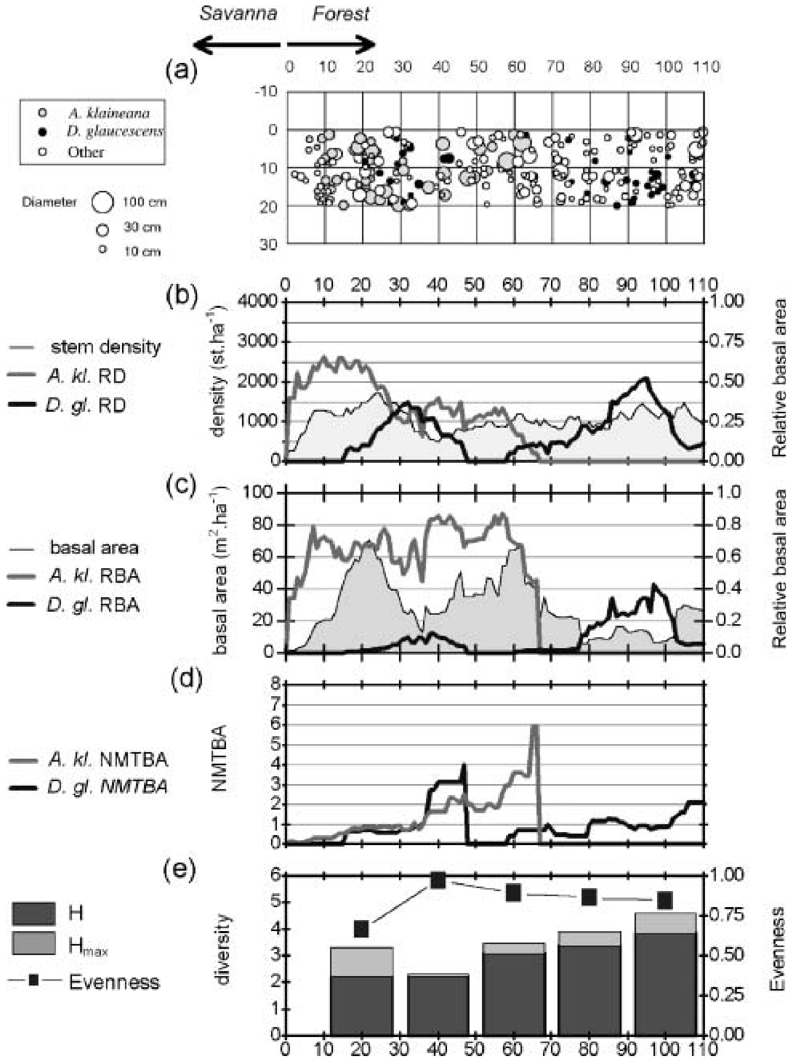

Figure 6 Description of the KOLA-2 transect. See legend of Fig. 3 for details.

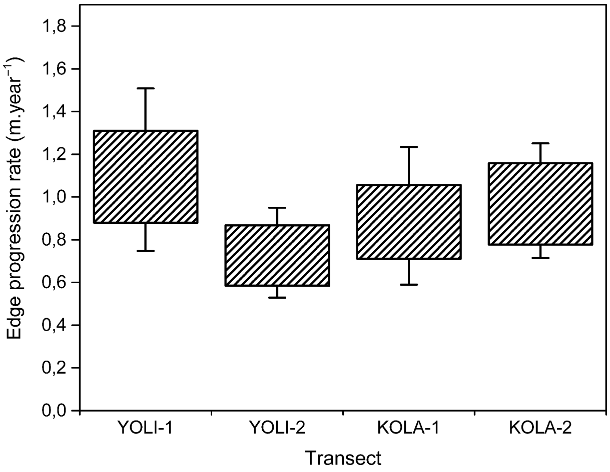

Figure 7 Estimated rate progression for the transects YOLI-1 and -2, and KOLA-1 and -2. The bars indicate the range of value comprised between the estimated progression rate of models A and B.

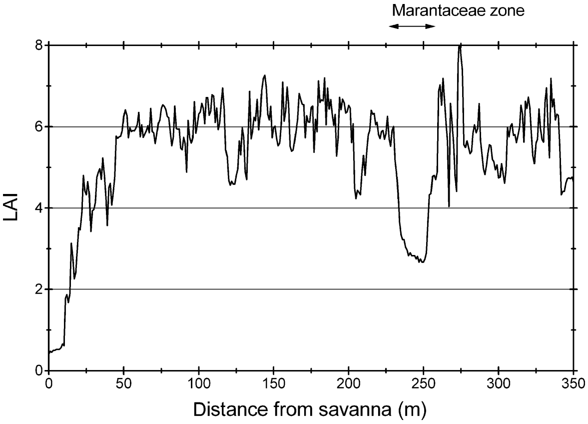

Figure 8 LAI along the complete YOSI transect.

thickets of forest trees can appear but never reach to develop and finally die. Conversely, under conditions more favourable to forest (wetter climate or irregular fires) these thickets can

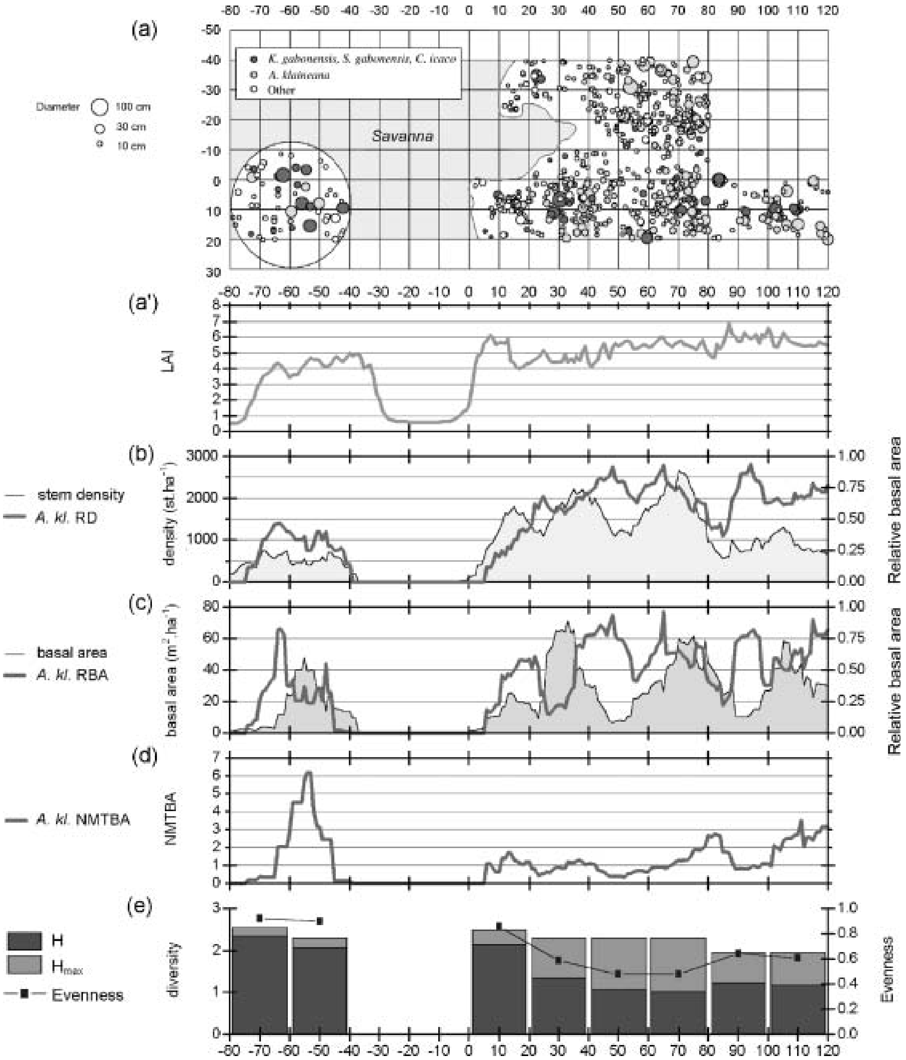

Figure 9 Description of the YOSI transect. See legend of Fig. 3 for details.

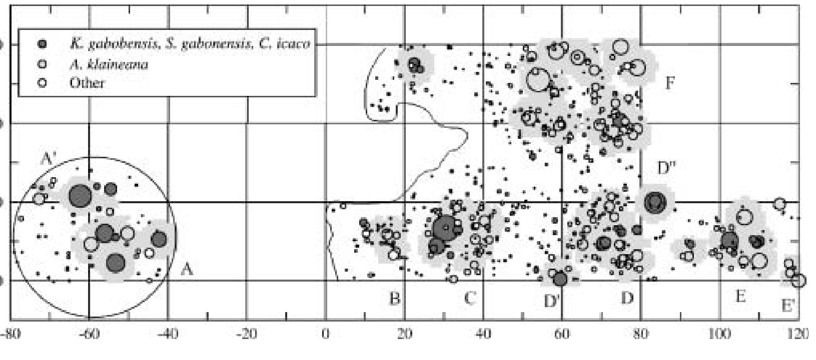

Figure 10 Map of the YOSI transect with in grey indicating the location of the maximum basal area (greater than the median values). The principal clusters are denoted by letters from A to G, secondary ones by primed letters.

establish, expand then finally coalesce. The transition between the two modes of transgression (edge progression only or clump coalescence) is very sharp and only a small change in climate or fire frequency can result in the shift from one mode to the other. Particularly the consequence of a change towards unfavourable conditions can then be dramatic for the transgression, the edge progression mode being considerably slower than the clump one.

Obviously, the dynamics of vegetation in the YOSI forest area indicates that conditions were favourable to the forest: a lot of clumps appeared, close one to another, transforming a whole surface of savanna into forest. However, in the

Table 3 Botanical inventories of the centres and edges of clumps of forest in savanna (YOSI, SI1-4 and Y1) and of microclumps (Y2-6)

Clump name	Diameter (m)	Centre of the cluster	Edge of the cluster
SI1	15	*Chrysobalanus icaco* (F; *c.* 10 m high) *Sacoglottis gabonensis* (F; *c.* 10 m high) *Bridelia ferruginea* (S), dying	*Aframomum* sp. (H) *Pteridium aquilinum* (H) *Chaetocarpus africanus* (F) *Hymenocardia ulmoides* (F) *Maprounea membranacea* (F) Several *Xylopia aethiopica* (sF) *Smilax kraussiana* (L.) *Manotes longiflora* (L.)
SI2	15	*Chrysobalanus icaco* (F; *c.* 10m high) *Chrysobalanus icaco* (F; *c.* 10 m high)	Same description as the first, with in addition *Cephaelis peduncularis* (F) *Macaranga spinosa* (sF) *Sacoglottis gabonensis* (F)
SI3	8	*Anthocleista schweinfurthii* (F; *c.* 4 m high) *Chrysobalanus icaco* (F) *Hymenocardia ulmoides* (F) *Xylopia aethiopica* (F) *Annona senegalensis* (S) *Bridelia ferruginea* (S)	Same description as the first, with in addition two *Psorospermum febrifugum* (S)
SI4	40	*Klainedoxa gabonensis* (F; 40 cm diameter) *Klainedoxa gabonensis* (F; 50 cm diameter)	Same description as the first, but (degraded)
Y1	15–20	*Chrysobalanus icaco* (F; *c.* 20–25 cm diameter) *Sacoglottis gabonensis* (F)	Same description as the first
Y2	3	*Psorospermum febrifugum* (S)	Seedlings of *Alchornea cordifolia* (sF), *Hymenocardia ulmoides* (sF), *Macaranga spinosa* (sF), *Xylopia aethiopica* (sF)
Y3	3	*Psorospermum febrifugum* (S)	Seedlings of: *Sacoglottis gabonensis* (sF, certainly disseminated from Y1: seeds on the soil, probably disseminated by small rodents *Chaetocarpus africanus* (sF), *Macaranga spinosa* (sF), *Xylopia aethiopica* (sF)
Y4	3	*Psorospermum febrifugum* (S)	Seedlings of *Chaetocarpus africanus* (sF), *Hymenocardia ulmoïdes* (sF), *Xylopia aethiopica* (sF)
Y5	4	*Psorospermum febrifugum* (S)	Seedlings of *Cephaelis peduncularis* (sF), *Chaetocarpus africanus* (sF), *Chrysobalanus icaco* (sF), *Hymenocardia ulmoïdes* (sF), *Macaranga barteri* (sF), *M. spinosa* (sF), *Xylopia aethiopica* (sF) *Annona senegalensis* (S), *Bridelia ferruginea* (S)
Y6	3	*Psorospermum febrifugum* (S)	Seedlings of Canthium sp. (sF), *Hymenocardia ulmoides* (sF), *Sacoglottis gabonensis* (sF), *Xylopia aethiopica* (sF)
YOSI	20	Three *Sacoglottis gabonensis* (F) Three *Aucoumea klaineana* (F) Three *Klainedoxa gabonensis* (F) One *Chrysobalanus icaco* (F) One *Trichoscypha acuminata* (F)	Trees (F) of *Aucoumea klainenana, Barteria fistulosa, Chaetocarpus africanus, Chrysobalanus icaco, Hymenocardia ulmoides, Klainedoxa gabonensis, Macaranga spinosa, Maprounea membranacea, Sacoglottis gabonensis, Sorindeia juglandifolia, Symphonia globulifera, Thomandersia butayei, Trichoscyphaacuminata, Xylopia aethiopica.* Seedlings of same species of SI1 at the very edge

The letter after the name indicates the kind of species. (S) savanna shrub; (F) forest pioneer tree; (sF) forest pioneer small tree or seedling; (H) herb.

surrounding savanna, there are two large clumps, few thickets or micro-clumps. Some years ago, a road was created which reaches this included savanna. This has led to an increase in human disturbance, and especially in fire frequency, and has induced a shift from a clump scenario to an edge progression one or, at least, has considerably decreased the rate of creation of forest clumps in savanna.

Pioneer subfunctions

Pioneer species, in the context of forest transgression, are defined as tree species able to establish in savanna, either at the edge or inside the savanna. This is a functional definition. These pioneer species can be themselves classified in three categories, depending on their functions in the transgression

Table 4 Groups of species involved in the forest transgression of forest over savanna

Group	Species
Savanna shrubs	*Psorospermum febrifugum* *Annona senegalensis* *Bridelia ferruginea*
Edge pioneers	*Maprounea membranacea* *Chaetocarpus africanus* *Hymenocardia ulmoides* *Xylopia aethiopica* *Anthocleista schweinfurthii* *Macaranga spinosa* *Cephaelis peduncularis*
Clump pioneers	*Chrysobalanus icaco* *Sacoglottis gabonensis* *Klainedoxa gabonensis*
Long-living pioneers	*Aucoumea klaineana*

(Table 4). First, there are a group of edge trees, found in recent forest plots (in small clumps or in the very edge of forest). This group gathers the largest variety of species, explaining the relative importance of the evenness in the forest edges. The second group (clump pioneers) is constituted by the pioneers found in the centre of the clumps of forest in savanna. They are semi-long-living trees that can survive well in open landscapes and then make it possible for other species to grow under their cover. The last group is reduced to the long-living pioneer okoumé, characteristic of the first decades of forest establishment over savannas. The presence of okoumés denotes the conversion of an open landscape to a forested one, the okoumés preparing the natural succession by typical forest species.

In the case of the linear progression scenario, the progression of a forest is governed by the establishment near the edge of the edge pioneers progressively replaced by a vegetation poorly diversified mainly dominated by okoumés. Because of their shade, okoumés prevent recruitment of their own seedling under them, but allows the establishment of late successional shade-tolerant forest species.

The study of forest clumps at different stages of development leads to define a general pattern for clump formation. First, a micro-clump organise around savanna with seedlings of pioneers of the edge pioneers group. Two explanations can be proposed for this: (i) fruits and seeds of these savanna shrubs and those of edge pioneers (*Maprounea membranacea*, *Cephaelis peduncularis*, *Chaetocarpus africanus*, *Macaranga spinosa*, *Xylopia aethiopica*) are small and may be eaten by the same birds; (ii) it is possible that savanna shrubs protect the seedlings from fire. In a second step, some trees (generally two) of the clump pioneers group establish. Their fruits and seeds are bigger than those of the first group and probably dispersed by rodents taking refuge in the micro-clumps (a lot of fruit stones were found under the savanna shrubs). Two of them are also eaten by elephants: *Chrysobalanus icaco* (Aubréville, 1949) and *Klainedoxa gabonensis*. Clump pioneer trees grow and rapidly become dominant. Their very low first branching indicates that they have developed in an open environment. Then, the edge pioneer trees get organized around these trees. Finally, okoumés settle, in the soft shade of the clump and can find light rapidly enough to survive and finally overgrow the central savanna pioneers and occupy the centre of the clumps, while a belt of edge pioneers occupies the edge of the clump. Once established, clumps grow by a process of edge progression similar to that described above. The clump pioneers in their centre, having their first branching very low, are rapidly overshadowed by surrounding okoumés and disappear.

A similar scenario of forest clump formation with savanna trees as nuclei was evidenced in Texan savanna (Archer, 1990) and, recently, in the Western Ghats of India (Puyravaud *et al.*, 2003). According to their authors, ‘species turnover’ was deterministic based on thicket size. That corresponds well to the observation that in the Kouilou pioneer trees can be grouped according to their role in clump formation and edge progression: initiator (savanna shrub), colonizers (edge pioneers), clump centre trees (clump pioneers) and secondary trees representing the transition to mature forest (long-living pioneer).

After the okoumés

This study is mainly devoted to the conversion of savanna into forest, that is to the set up of the okoumé forest. The physiognomy of the forest which supplants this okoumé pioneer stage is also of interest. White *et al.* (2000) suggest that the next normal successional stage is an open forest with a dense understory dominated by high forest herbs (mainly Marantaceae and Zingiberaceae), known as Marantaceae forest (de Foresta, 1990). Only after this stage, a mature forest would establish. Although in the YOLI-1 site such a Marantaceae zone is present, a different interpretation is proposed here. Indeed, the observed succession to the okoumé dominated forest is a dense forest (characterized by *D. glaucescens* in its early stage), as shown in all the transects. Moreover, stumps of old cut okoumés, indicate that a few decades ago, logging of these trees took place for commercial value, leaving in place the subadults trees. Therefore, we think that opportunistic Marantaceae development in the most disturbed zones, have prevented or, at least, considerably slowed forest regeneration. It would be interesting in the future to check forestry exploitation archives in Central Atlantic Africa to verify whether the same explanation can be given for the observations of White *et al.* (2000) and de Foresta (1990).

Hints for management

As is the case in the Western Ghats with the support of the Indian government (Puyravaud *et al.*, 2003), a conversion of savanna to forest is encouraged in Congo by the Société Nationale de Reboisement. One of the present options is to plant okoumés in savanna, but their sensitivity to fire and their shade tolerance in their earliest stages have led to the failure of this tentative. An alternative would then be to promote the formation of clumps in savannas, with respect to their formation process, with a plantation of clump pioneers surrounded by edge pioneers in the shade and under the fire protection of the widespread savanna trees.

CONCLUSION

Two modes of forest transgression are evidenced in the Congolese littoral region by the analysis of the vegetation near the ecotone. The linear edge progression comes easily in mind. The clump formation and coalescence one is however less often described (Guillet *et al.*, 2001). In fact, this second process is so dramatically effective that one is tempted to use the word 'strategies' rather than 'modes', as these processes exhibit to a large extent self-organization properties, the diffusion process being similar to a 'phalanx-like' strategy, opposed to the 'guerilla-like' strategy of clump installation and coalescence.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.backwellpublishing.com/products/journals/suppmat/JBI/JBI1094/JBI1094sm.htm

Appendix S1 Botanical inventory of the YOLI-1 transect.
Appendix S2 Botanical inventory of the YOLI-2 transect.
Appendix S3 Botanical inventory of the KOLA-1 transect.
Appendix S4 Botanical inventory of the KOLA-2 transect.
Appendix S5 Botanical inventory of the YOSI transect.

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BIOSKETCHES

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Appendix 1 List of taxa sorted by their preferential biotope, then in alphabetical order of species names after Hutchinson & Dalziel, 1972. Biotope: preferential location (S, savanna; E, edge; E/F, preferentially edge but also forest; F, forest; F/E, preferentially forest but also edge). Life form (H, herb; S, shrub; T, tree; L, liana; P, palm). The last columns indicate the sites in which trees of each species were inventoried. The column COM displays inventoried plants that were not mapped (herbs, tree species < 5 cm d.b.h. in all transects)

Biotope	Species	Family	Life form	YOLI-1	YOLI-2	YOSI	KOLA-1	KOLA-2	COM
S	*Annona senegalensis* Pers.	Annonaceae	S						●
S	*Bridelia ferruginea* Benth.	Euphorbiaceae	S						●
S	*Bulbostylis laniceps* C. B. Cl.	Cyperaceae	H						●
S	*Ctenium newtonii* Hack.	Poaceae	H						●
S	*Hyparrhenia diplandra* (Hack.) Stapf	Poaceae	H						●
S	*Imperata cylindrica* (L.) P. Beauv.	Poaceae	H						●
S	*Loudetia arundinacea* (Hochst. Ex A. Rich.) Steud.	Poaceae	H						●
S	*Panicum maximum* Jacq.	Poaceae	H						●
S	*Psorospermum febrifugum* Spach.	Hypericaceae	S						●
S	*Rynchelytrum repens* (Willd.) D.E. Hubb	Poaceae	H						●
S	*Thomandersia butayei* De Wild.	Acanthaceae	S						●
S	*Tristemma* cf. *hirtum* P. Beauv.	Melastomataceae	H						●
S	*Vernonia* sp.	Asteraceae	H						●
E	*Aframomum* sp.	Zingiberaceae	H						●
E	*Aframomun giganteum* (Oliv. Et Hanb.) K. Schum	Zingiberaceae	H						●
E/F	*Agelaea* sp.	Connaraceae	L						●
E	*Alchornea cordifolia* (Schum. et Thon.) Müll. Arg.	Euphorbiaceae	SL						●
E	*Anthocleista schweinfurthii* Gilg	Loganiaceae	S	●	●	●			
E/F	*Aucoumea klaineana* Pierre	Burseraceae	T	●	●	●	●	●	
E/F	*Barteria fistulosa* (Mast.) Steuner	Passifloraceae	S				●	●	
E/F	*Barteria nigritiana* Hook. f.	Passifloraceae	S		●	●			
E	*Bertiera racemosa* (G. Don.) K. Schum.	Rubiaceae	S						●
E	*Caloncoba welwitschii* (Oliv.) Gilg	Flacourtiaceae	S						●
E	*Canthium arnoldianum* Hepper	Rubiaceae	S	●	●				
E	*Cephaelis peduncularis* Salisb.	Rubiaceae	S						●
E/F	*Chaetocarpus africanus* Pax	Euphorbiaceae	S	●	●	●	●	●	
E	*Chromolaena odorata* (L.) R. King et H. Robinson	Asteraceae	SL						●
E/F	*Chrysobalanus icaco* L.	Chrysobalanaceae	ST			●			
E	*Cnestis ferruginea* DC.	Connaraceae	L						●
E	*Cnestis* sp.	Connaraceae	L						●
E	*Elaeis guineensis* Jacq.	Arecaceae	P						●
E	*Harungana madagascariensis* Lam. ex Poit	Hypericaceae	S						●
E/F	*Hymenocardia ulmoides* Oliv.	Euphorbiaceae	ST	●	●	●			
E	*Landolphia owariensis* P. Beauv.	Apocynaceae	L			●			
E	*Leptactina mannii* Hook. f.	Rubiaceae	S						●
E	*Loranthaceae* sp.	Loranthaceae	P						●
E	*Macaranga barteri* Müll. Arg.	Euphorbiaceae	S		●			●	
E	*Macaranga spinosa* Müll. Arg.	Euphorbiaceae	S		●				
E	*Manotes longiflora* Bak.	Connaraceae	L						●
E	*Maprounea membranacea* Pax et Hoffm.	Euphorbiaceae	S	●	●	●	●		
E	*Pavetta corymbosa* (DC.) F. N. Williams	Rubiaceae	S			●	●		
E	*Pteridium aquilinum* (L.) Kühn	Pteridophyte	H						●
E	*Rauvolfia vomitora* Afzel.	Apocynaceae	S						●
E	*Smilax kraussiana* Meisn.	Smilacaceae	L						●
E/F	*Tetracera alnifolia* Willd.	Dilleniaceae	L						●
E/F	*Tetracera potatoria* Afzel. et Don	Dilleniaceae	L						●
E	*Thomandersia butayei* De Wild.	Acanthaceae	S	●	●			●	
E/F	*Uvaria* sp.	Annonaceae	L						
E	*Xylopia aethiopica* (Dunal) A. Rich.	Annonaceae	T	●	●	●	●	●	
F	*Allanblackia floribunda* Oliv.	Clusiaceae	T	●					
F/E	*Allophyllus africanus* P. Beauv.	Sapindaceae	S	●					

Appendix 1 *continued*

Biotope	Species	Family	Life form	YOLI-1	YOLI-2	YOSI	KOLA-1	KOLA-2	COM
F/E	*Ancistrophyllum secundiflorum* Wendl.	Arecaceae	P						●
F	*Anonidium mannii* (Oliv.) Engl. et Diels	Annonaceae	T		●				
F	*Berlinia bracteosa* Benth.	Caesalpiniaceae	T	●				●	
F	*Bertiera subsessilis* Hiern	Rubiaceae	S						●
F	*Brenania brieyi* (De Wild.) Petit	Rubiaceae	T	●					
F	*Caloncoba glauca* (P. Beauv.) Gilg	Flacourtiaceae	S				●	●	
F	*Carapa procera* DC.	Meliaceae	T	●	●		●		
F	*Celtis adolfi-friderici* Engl.	Ulmaceae	T				●	●	
F	*Chytranthus* sp.	Sapindaceae	S					●	
F	*Cleistopholis patens* (Benth.) Engl. Et Diels	Annonaceae	T		●				
F	*Coelocaryon preussii* Warb.	Myristicaceae	T	●	●				
F/E	*Combretum* sp.	Combretaceae	L						●
F	*Coula edulis* Baill.	Olacaceae	T	●	●		●		
F/E	*Croton haumanianus* J. Léonard	Euphorbiaceae	T						●
F	*Dacryodes edulis* (G. Don) Lam.	Burseraceae	T				●	●	
F	*Dacryodes pubescens* (Verm.) Lam.	Burseraceae	T				●		
F	*Dialium corbisieri* Staner	Caesalpiniaceae	T				●		
F	*Dialium dinklagei* Harms	Caesalpiniaceae	T	●	●		●	●	
F	*Dialium pachyphyllum* Harms	Caesalpiniaceae	T	●	●		●	●	
F	*Dialium tessmannii* Harms	Caesalpiniaceae	T					●	
F	*Dichostemma glaucescens* Pierre	Euphorbiaceae	T	●	●			●	
F	*Diospyros hoyleana* F. White	Ebenaceae	S	●			●		
F	*Distemonanthus benthamianus* Baill.	Caesalpiniaceae	T		●				
F	*Enantia chlorantha* Oliv.	Annonaceae	T	●					
F/E	*Eremospatha cabrae* De Wild.	Arecaceae	P						●
F	*Eriocoelum macrocarpum* Gilg.	Sapindaceae	T		●				
F	*Gambeya africana* (Bak.) Pierre	Sapotaceae	T	●	●				
F	*Garcinia kola* Heckel	Clusiaceae	S				●		
F	*Guibourtia arnoldiana* (De Wild. et Dur.) Léonard	Caesalpiniaceae	T	●		●	●	●	
F	*Haumania liebrechtsiana* (De Wild. et TH. Dur.) J. Léon.	Marantaceae	HL						●
F	*Heinsia crinita* (Afzel) G. Tayl.	Rubiaceae	S	●					
F	*Klainedoxa gabonensis* Pierre	Irvingiaceae	T	●	●	●	●		
F	*Maesobotrya staudtii* (Pax) Hutch.	Euphorbiaceae	S						●
F	*Manniophyton fulvum* Müll. Arg.	Euphorbiaceae	L						●
F	*Maranthes glabra* (Oliv.) Prance	Chrysobalanaceae	T	●					
F	*Massularia acuminata* (G. Don) Bull. ex Doyle	Rubiaceae	S				●	●	
F	*Monodora myristica* (Gaernt.) Dunal	Annonaceae	T					●	
F	*Menispermaceae* sp.	Menispermaceae	L	●					
F	*Ongokea gore* Pierre	Olacaceae	T					●	
F/E	*Ouratea* sp.	Ochnaceae	S				●		
F	*Pachypodanthium staudtii* Engl. Et Diels	Annonaceae	T				●	●	
F	*Panda oleosa* Pierre	Pandaceae	T	●					
F	*Pausinystalia johimbe* (K. Schum.) Pierre ex Dup. et B.	Rubiaceae	T	●	●		●	●	
F/E	*Pentaclethra eetveldeana* De Wild. et Th. Dur.	Mimosaceae	T					●	
F/E	*Petersianthus macrocarpus* (P. Beauv.) Liben	Lecythidaceae	T	●					
F	*Piptadeniastrum africanum* (Hook. F.) Bren.	Mimosaceae	T					●	
F	*Plagiostyles africana* (Müll. Arg.) Prain	Euphorbiaceae	T	●					
F	*Polyalthia suaveolens* Engl. et Diels	Annonaceae	T				●	●	
F	*Psychotria* sp.	Rubiaceae	S						●
F	*Sacoglottis gabonensis* (Baill.) Urb.	Humiriaceae	T	●		●	●		
F	*Santiria trimera* (Oliv.) Aubr.	Burseraceae	T	●			●	●	
F	*Sorindeia juglandifolia* Engl.	Anacardiaceae	S	●	●				
F	*Staudtia gabonensis* Warb.	Myristicaceae	T	●			●		

Appendix 1 *continued*

Biotope	Species	Family	Life form	YOLI-1	YOLI-2	YOSI	KOLA-1	KOLA-2	COM
F	*Strombosia grandifolia* Hook. F.	Olacaceae	T		●				
F	*Strombosia pustulata* Oliv.	Olacaceae	T				●		
F	*Symphonia globulifera* L.	Clusiaceae	T			●	●		
F	*Synsepalum dulcificum* (Schumm.) Baill.	Sapotaceae	S	●			●	●	
F	*Tiliaceae* sp.	Tiliaceae	S	●					
F	*Treculia acuminata* Baill.	Moraceae	S				●	●	
F	*Treculia africana* Decne	Moraceae	S					●	
F	*Trichilia* sp.	Meliaceae	T	●	●	●	●	●	
F	*Trichoscypha acuminata* Engl.	Anacardiaceae	T	●	●		●	●	
F	*Uapaca guineensis* Müll. Arg.	Euphorbiaceae	T					●	
F	*Vitex pachyphylla* Bak.	Verbenaceae	T	●		●	●		
F	*Voacanga* cf. *bracteata* Stapf.	Apocynaceae	S	●					
F	*Xylopia hypolampra* Milbr.	Annonaceae	T	●	●		●	●	
F	*Xylopia pynaertii* De Wild.	Annonaceae	T				●	●	
F	*Xylopia* sp.	Annonaceae	T				●		