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RESEARCH PAPER

Abrupt shifts in African savanna tree cover along a climatic gradient

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ABSTRACT

Aim To describe patterns of tree cover in savannas over a climatic gradient and a range of spatial scales and test if there are identifiable climate-related mean structures, if tree cover always increases with water availability and if there is a continuous trend or a stepwise trend in tree cover.

Location Central Tropical Africa.

Methods We compared a new analysis of satellite tree cover data with botanical, phytogeographical and environmental data.

Results Along the climatic transect, six vegetation structures were distinguished according to their average tree cover, which can co-occur as mosaics. The resulting abrupt shifts in tree cover were not correlated to any shifts in either environmental variables or in tree species distributions.

Main conclusions A strong contrast appears between fine-scale variability in tree cover and coarse-scale structural states that are stable over several degrees of latitude. While climate parameters and species pools display a continuous evolution along the climatic gradient, these stable structural states have discontinuous transitions, resulting in regions containing mosaics of alternative stable states. Soils appear to have little effect inside the climatic stable state domains but a strong action on the location of the transitions. This indicates that savannas are patch dynamics systems, prone to feedbacks stabilizing their coarse-scale structure over wide ranges of environmental conditions.

Keywords
Alternative stable states, Central Tropical Africa, patch dynamics systems, phytogeographical classification, remote sensing data, savanna, spatial scales, tree cover.

INTRODUCTION

Savannas, defined as ecosystem associating trees and grasses without full tree canopy cover, are common throughout the world and have been studied extensively (Sankaran *et al.*, 2004). Yet no comprehensive framework exists to explain how trees and grass coexist and how their respective cover is determined by natural or anthropogenic influences (House *et al.*, 2003; Fraser *et al.*, 2008).

Most theoretical and field studies have focused on local scales (Scholes & Archer, 1997; Jeltsch *et al.*, 2000). These studies have given rise to a wide range of empirical evidence for and against the different theories of coexistence of trees and grass. In the context of tree–grass dynamics, broad-scale studies are needed to provide a general framework of patterns at regional or continental scales that involve climate variation and changes in species composition. In particular, to determine how tree cover responds to climate and anthropogenic influences, it is necessary to quantify the biogeochemical cycles at the global scale (Lloyd *et al.*, 2008) and to determine the resilience of savanna ecosystems to climate change. Climate, and especially rainfall, has long been considered as the primary driver of savanna structure at broad scale, with human-induced disturbances and soil characteristics, namely water availability and porosity, phosphorus and nitrogen content, as important secondary drivers. However, studies dealing with the broad-scale evolution of African vegetation appear to contradict one another.

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One set of studies have suggested that climate only imposes a maximal limit to the tree cover and that secondary factors, mainly anthropic disturbances, determine actual values. The reviews of field tree cover by Sankaran *et al.* (2005, 2008) support this view. Maximum tree cover is correlated with mean annual precipitation (MAP) and it steadily increases from 0 to 80% as MAP increases from *c.* 100 mm to *c.* 650 mm, though levelling off at higher rainfall values. Depending on site-specific characteristics (fire return interval, soil characteristics, browsing and grazing pressure), all values of tree cover, from zero to the climatic maximum, are achievable. This is supported by long-term fire experiments (Gignoux *et al.*, 2006; Furley *et al.*, 2008) and models of local vegetation dynamics (e.g. Favier *et al.*, 2004; D'Odorico *et al.*, 2006). These studies have reported trends for a wide range of potential states under different fire frequencies at particular sites. However, other studies have supported the hypothesis that there is a climatic trend in mean tree cover. For example, continental-scale remote-sensing studies have indicated that tree cover covaries continuously with MAP (Bucini & Hanan, 2007) or with MAP and a seasonality index (Good & Caylor, 2011), with residual tree cover variability explained by local secondary factors. Alternatively, Menaut *et al.* (1995) have reported a continuous, peaked pattern of evolution of tree cover along a precipitation gradient in West Africa, increasing initially but showing a strong reduction in tree cover in the most humid climates.

Despite the difficulty of establishing a definition of the different structures of vegetation at the continental scale (shrublands, wooded savannas, woodlands, etc.), such differences are locally generally obvious. Different vegetation types with clearly different average tree covers can be identified in the field and from aerial photographs or high resolution satellite images (Nangendo *et al.*, 2007). This has permitted the establishment of vegetation maps, partly based on vegetation structure, supporting the idea of discontinuous changes of tree cover (White, 1983). At the continental or regional scale, these vegetation types are related mainly to climate and associated with phytochorological classes (White, 1983). At this scale, soil shapes tree species distribution and communities (Lawesson, 1990; Fraser *et al.*, 2008) but its influence on savanna structure is not straightforward. For instance, Letouzey (1968) in Cameroon and Boulvert (1986) in the Central African Republic noted that the limits of different savanna types followed soil transitions while inside these limits soil had merely an influence on species composition but not on physiognomy.

The aim of this paper is to answer the three key questions ultimately arising when comparing different sources of information on savanna structures.

1. Under a particular climate, are all configurations of tree cover up to some maximal climatic value equally probable, or are there identifiable mean structures?

2. Does tree cover always increase with water availability, controlled by rainfall and soil properties, or is there a reduction in tree cover in the most humid sites?

3. Is there a continuous trend or a stepwise trend, and to what extent is it related to soil, fires and tree species distribution?

Disagreement in the answers provided to these questions up to now might reflect differences in the scale and resolution considered. First, field studies reviewed by Sankaran *et al.* (2005) were not a homogeneous sampling of savanna vegetation and their scale (*c.* 0.5 ha on average) made the values more sensitive to local peculiarities that may have overemphasized variations. On the other hand, MODIS data used by Bucini & Hanan (2007) and Good & Caylor (2011) covered the whole continent, independently of site accessibility, but their resolution (500 m) is comparable with the characteristic scales of mosaics of vegetation, so that pixels that overlap different vegetation types produce artefact data. Furthermore, MAP at the continental scale may not be a perfect proxy for water availability. Indeed, potential evapotranspiration during the dry and even humid seasons varies considerably, according to climatic region.

To address the discrepancies associated with comparing data from different literature sources, we have tried to avoid sources of inaccuracy in the data as much as possible. To that end, we first selected a location with a homogeneous climate system (dry season with the duration correlated with MAP) in a region as free as possible from intensive agriculture and land conversion. We then used systematic sampling of tree cover with medium-resolution satellite data, having beforehand defined a method of interpretation that avoids using inaccurate pixels. This allowed us to compute the evolution of tree cover along a climatic gradient from a humid to a dry tropical climate, to confront it with common phytogeographical classifications and to identify the impacts of likely key factors, specifically climate, soil, fire frequency and tree species distribution.

MATERIALS AND METHODS

Environmental setting

One climatic north–south transect was selected (Fig. 1), located at 18.8° E, from the equator to 15° N. The population density here is low and the region is only locally influenced by intensive land conversion and agriculture (Nachtergaele & Petri, 2011). From north to south, MAP increases continuously (Fig. 1), correlated with a decrease in mean annual evapotranspiration (MAE) and in a seasonality index (SI, equal to the difference between June–July–August and December–January–February rainfall relative to MAP). The mean annual temperature (MAT) pattern is different, with variations along the north–south transect between 23.4 °C and 29.6 °C. As a proxy of fire activity along the transect, we used Global VGT burnt area product 2000–07 (L3JRC) data (Tansey *et al.*, 2008), keeping in mind that global medium resolution burnt area data often underestimate fire occurrences and that the proportion of detected fires depends on the type of vegetation and varies widely among savannas (Silva *et al.*, 2005; Tansey *et al.*, 2008).

The transect crosses several phytogeographical domains (Figs 1 & 3f–h, Table 1) according to White's vegetation map of Africa (1983), national vegetation maps (Grondard, 1964; Peeters, 1965; Boulvert, 1986) and Rattray's map of grass asso-

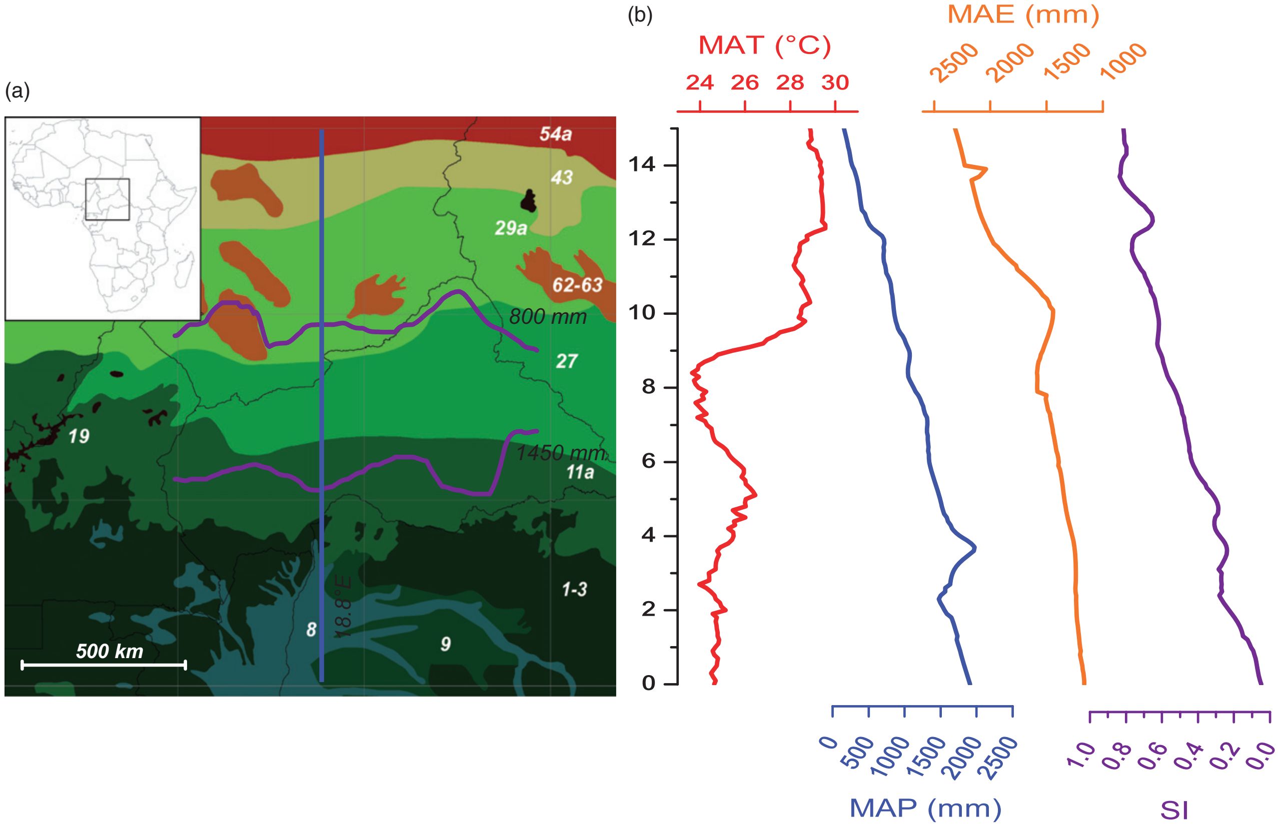

Figure 1 (a) Location map of the north–south transect (blue) and 1450-mm and 800-mm precipitation isopleths (purple) with White's phytogeographical domains: 1–3, lowland rainforest; 8, swamp forest; 9, mosaic of swamp and lowland rainforest; 11a, mosaic of lowland rainforest and secondary grasslands; 19, montane vegetation; 27, Sudanian woodland with abundant *Isoberlinia*; 29a, Sudanian undifferentiated woodland; 43, Sahel *Acacia* wooded grasslands and deciduous bushlands; 54a, northern Sahel semi-desert grassland and shrubland; 62–63, mosaic of edaphic grasslands and wooded grasslands. (b) Evolution along the transect at 18.8° E of mean annual temperature (MAT), mean annual precipitation (MAP), mean annual potential evapotranspiration (MAE) and seasonality index (SI, the difference between June–July–August and December–January–February precipitation over MAP).

ciations (Rattray, 1960). A botanical gradient of the tree layer was represented by the change in the presence and abundance of 29 characteristic woody species (Aubréville, 1950; Grondard, 1964; Boulvert, 1995, see list in fig. 5i).

The ISRIC-WISE soil properties estimates (Batjes, 2002) were used to characterize soils along the three transects and especially four characteristics recognized as potential determinants of savanna structure (Bucini & Hanan, 2007; Sankaran *et al.*, 2008): plant available water storage capacity (AWC), topsoil drainage, topsoil nitrogen content and pH as a crude surrogate of phosphorus availability. Every soil map unit comprises one to ten component soils, characterized by their relative proportion, their soil type according to the FAO-UNESCO classification and a set of physical and chemical variables. A total of 51 soil map units succeed along the north–south transect, the 1450 mm transect and the 800 mm one, respectively. To estimate the differential effect of soil on savanna structure, two additional transects from 16° E to 23° E along precipitation isopleths of 800 mm (28 soil map units) and 1450 mm (8 soil map units) were considered. For each soil map unit, we computed the main soil type, the percentage of surface within classes of AWC (40 mm step), of drainage, of N content (0.4% step) and with pH between 5.5 and 7.5, which is the optimal range for phosphorus uptake by plants (Devau *et al.*, 2009).

Tree cover estimation using MODIS

The MODIS Percent Tree Cover (Hansen *et al.*, 2003) is a publicly available composited database giving the percentage of skylight obstructed by canopies over 5 m high averaged on 500-m pixels, computed for the year 2001–02 (Vegetation Continuous Fields MOD44B product). Three factors indicate that these data should not be used directly as a proxy for tree cover of the different savanna formations. First, in addition to the error induced by the algorithm (Hansen *et al.*, 2003), the nature of the data induces a spatial imprecision (Wolfe *et al.*, 2002). Second, in the selected area, vegetation often occurs in mosaics (forest/savanna or different kinds of savanna), with characteristic spatial dimensions of the same order of magnitude as the data resolution. Because of this, the tree cover estimation in a particular cell might be the average between the

Table 1 Summary of vegetation units according to the different classifications considered.

Source	Unit name	Unit description
Vegetation map of Africa (White, 1983)	8 and 9	Guinea–Congolian region: lowland rain forest/swamp forest
	11a	Guinea–Congolian/Sudanian transition zone: mosaic of lowland rain forest and secondary grassland and wooded grassland (< 40% canopy cover)
	27	Sudanian region: Sudanian woodland (40% canopy cover, at least 8 m tall) with abundant *Isoberlinia*
	29a	Sudanian region: Sudanian undifferentiated woodland (40% canopy cover, at least 8 m tall)
	43	Sahel regional transition zone: Sahel *Acacia* wooded grassland and deciduous bushland (<40% canopy cover between 3 and 7 m tall)
	54a	Sahel regional transition zone: Sahel semi-desert grassland and shrubland (canopy less than 2 m tall)
National vegetation maps (Grondard, 1964; Peeters, 1965; Boulvert, 1986)	(I)	Tropical forest
	(II)	Savannas in DRC, periforest savannas in CAR
	(III)	Sudanian sector
	(IV)	Sahelo-Sudanian sector in CAR, clear forest and wooded savannas with Leguminosae in Chad
	(V)	Clear forest and wooded savannas with Combretaceae
	(VI)	Bush and steppes with Mimosaceae
Grass cover of Africa (Rattray, 1960)	UF1	Undifferentiated forest, without significant grass cover with enclosed savannas with *Pennisetum purpureum* or *Hyparrhenia diplandra*
	UF2	Forest and *Imperata cylindrica* savanna
	H22	*Hyparrhenia* spp.–*Andropogon* spp.–*Loudetia arundineacea* association under ungrazed wooded savannas succession
	AN3	*Andropogon gayanis–Hyparreania bagirmica* association under grazed savannas
	CE5	*Cenchrus biflorus–Eragrostis tremula–Andropogon pseudapricus–Panicum subulbidum* association under grazed and cultivated open savannas and steppes
	A13	*Aristida mutabilis–Panicum turgidum–Cymbopogon giganteus–Eragrostis tremula–Cenchrus biflorus* association on sandy soils and *Aristida funiculata–Aristida adscensionis–Schoenfeldia gracilis–Scizachyrium exile* association on clayey soils under thorn bushland

DRC, Democratic Republic of Congo; CAR, Central African republic.

tree covers of two kinds of vegetation. Third, the calibration of MODIS Percent Tree Cover (hereafter TC) for vegetation taller than 5 m leads to an underestimation of tree cover where shrubs are common.

In Appendix S1 in the Supporting Information we show that considering the frequency distribution of TC in a 0.1° × 0.1° area allows us to overcome the presence of artefact values in mosaic regions. When the frequency distribution is unimodal, the landscape is composed of one principal vegetation type with mean TC equal to the mode of the distribution; when the frequency distribution is multimodal, this corresponds to a mosaic of patches of vegetation whose average TCs are the first and last modes of the distribution (Fig. S1). Unsurprisingly, the ranges of TCs at coarse scale are smaller than the ranges at fine scale, due to upscaling averaging.

To delimit the region where the MODIS product can be used as a reliable proxy for tree cover, that is the region where shrub cover is not significant, we compared the field estimates of tree cover reviewed by Sankaran *et al.* (2005) and the TC frequency distribution in 0.1° × 0.1° areas around each location. We showed (Appendix 1, Fig. S2) that irrespective of differences in spatial sampling scale and dates, there was accordance when MAP > 575 mm, where woody cover appears to be dominated by trees. Within the studied transect, conditions for accordance are fulfilled for White's (1983) vegetation zones 1–3, 8, 9, 11a, 27 and 29a, that is approximately up to latitude 12–12.5° N.

Along the transects, we considered a 0.1° wide strip and computed the frequency distribution of TC in 0.1° × 0.1° square regions. For comparison along the north–south transect, estimation of tree cover was computed from MAP using the following.

1. The Sankaran *et al.* (2005) model, which states that the maximum achievable tree cover is $0.14 \times \mathrm{MAP} - 14.2$ if $102\ \mathrm{mm} < \mathrm{MAP} < 677\ \mathrm{mm}$, 0 if $\mathrm{MAP} < 102$ mm and 80% otherwise.
2. The Bucini & Hanan (2007) model, based on a regression of TC against MAP at the continental scale, which states that the average tree cover is:

$$110.9\%\frac{\mathrm{MAP}^{1.96}}{1435^{1.96} - \mathrm{MAP}^{1.96}} - 0.9\%.$$

RESULTS

Patterns of tree cover

The evolution of the TC values and frequency distributions along the north–south transect, with frequency distributions of some 0.1° × 0.1° plots as examples, are shown in Figure 2.

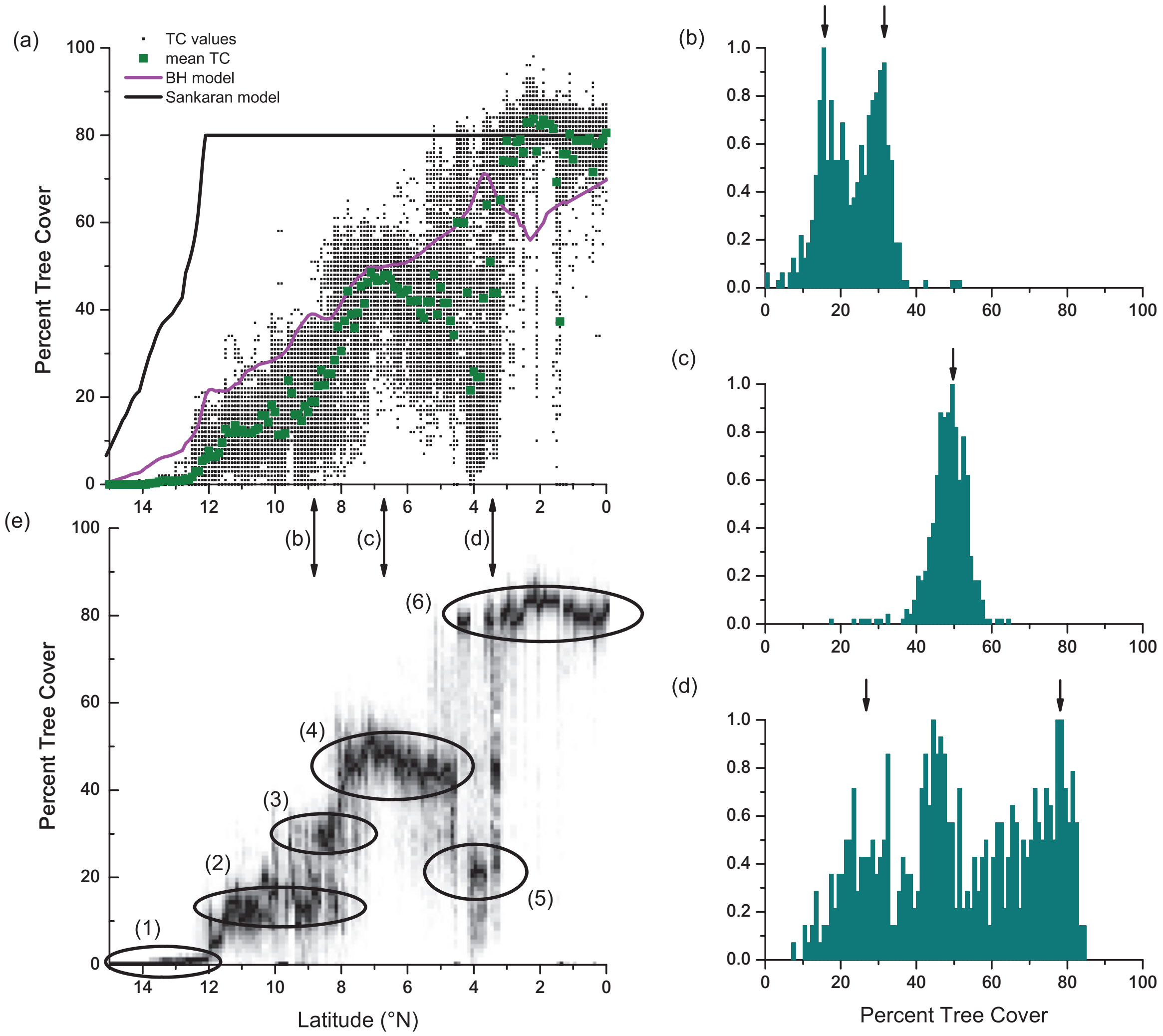

Figure 2 (a) Evolution along the transect of the values of per cent tree cover in each 500 m MODIS pixel (black points) and of average tree cover (TC) on each 0.1° × 0.1° plot (green/larger squares). The two lines represent the Sankaran *et al.* (Rattray, 1960) and Bucini and Hanan (2007) models relating maximal and mean tree cover to MAP. (b)–(d) Frequency distributions of per cent tree cover computed with 1% intervals and normalized to the its maximal value at: (b) 8.8° N interpreted as a mosaic of two savanna types with 15% and 30% tree cover on average (indicated by arrows), (c) 6.7° N, interpreted as a savanna type with 50% tree cover on average, and (d) 3.4° N, interpreted as a mosaic of forest (80% tree cover) and savanna with about 25% tree cover on average. (e) Evolution of normalized frequency distributions of tree cover along the transect, computed in each 0.1° × 0.1° plot, plotted as a greyscale (black represents the more frequent tree cover, white represents no tree cover). The six different vegetation structures individualized (see Table 2) are circled and numbered from (1) to (6).

Although individual plot frequency distributions were not all easily interpretable, a pattern emerges, with six vegetation structures rather stable over several degrees of latitude (Table 2). It was apparent that there was no progressive evolution of tree cover along the gradient, but rather abrupt shifts in stability of the different kinds of vegetation structure with areas where they coexist as mosaics. This gives rise to eight vegetation zones (Table 2, Fig. 3e).

The Sankaran *et al.* (2005) model of maximal savanna tree cover gave estimations well above those from TC. This has already been noted and explained by Bucini & Hanan (2007) as being the result of the cutoff in height in remote-sensing data and thus the exclusion of bushes from the MODIS estimates. Not surprisingly, the model of Bucini & Hanan (2007) more closely follows the changes in TC, though it does not reproduce the pattern of multiple stable states.

Along the precipitation isopleth transects (Figs S4 & S5), the identified savanna types were consistent with those of the north–south transect. The woodland type spans the whole 1450 mm transect, locally coexisting with open savannas, in a region of livestock farming. Sparsely wooded savanna is the major savanna type along the 800 mm transect, in mosaic with grassland/shrubland type reflecting the fields in regions of intensive land conversion to agriculture, or with wooded savannas. Very locally, a mosaic of wooded savannas and woodlands supplant the sparsely wooded savanna type.

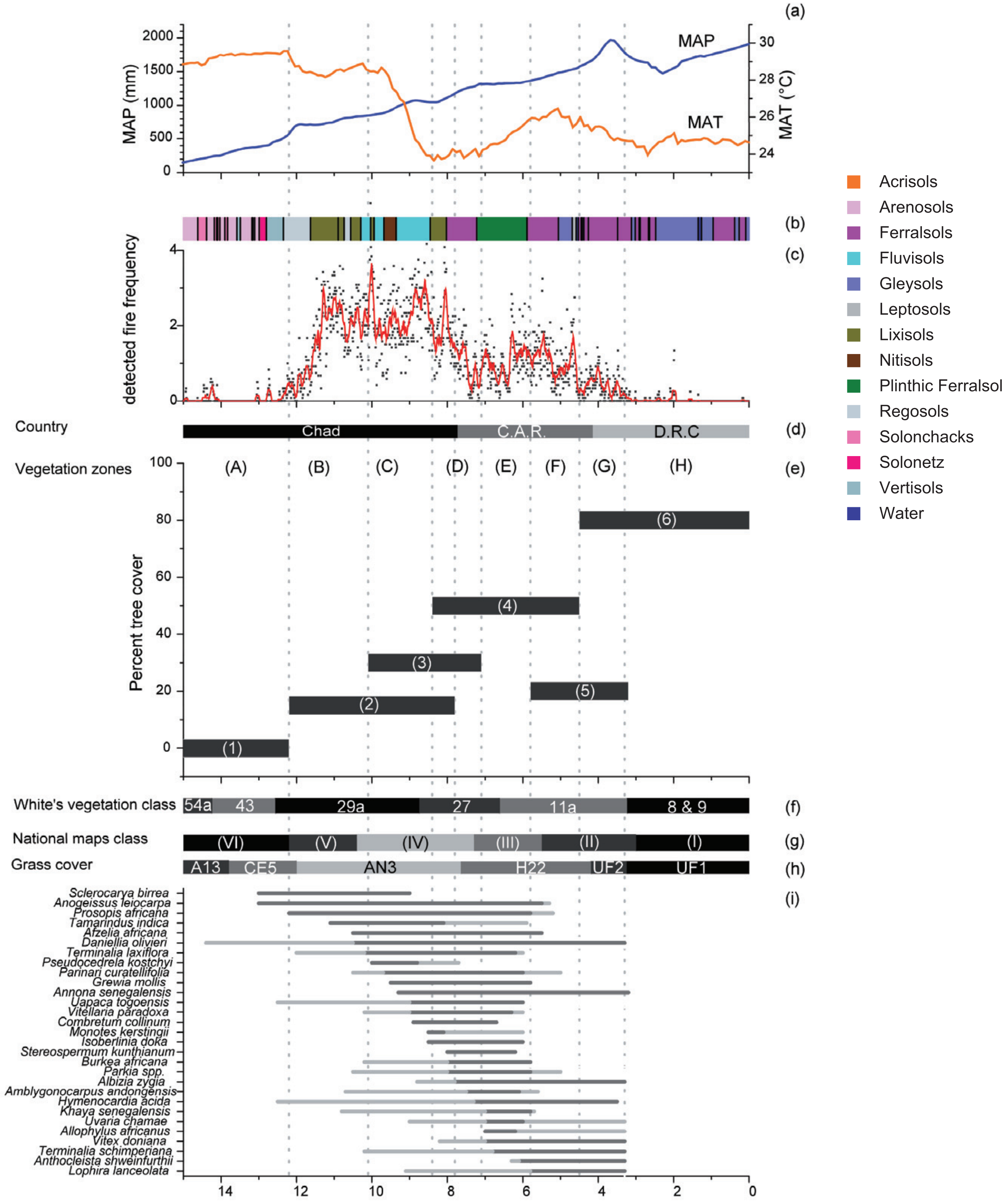

Figure 3 Changes along the transect of: (a) mean annual precipitation (MAP) and mean annual temperature (MAT); (b) soil map units, colour scale relating to the dominant soil type (Fig. S6); (c) mean detected number of fires per year in each 1-km pixel (black squares) and running average (red line); (d) countries (DRC, Democratic Republic of Congo; CAR, Central African Republic); (e) savanna types identified from Figure 2, with their average tree cover, and vegetation zones from (A) to (H), see Table 2; (f) vegetation classes *sensu* White (1983); (g) vegetation classes compiled from national vegetation maps (Grondard, 1964; Peeters, 1965; Boulvert, 1986); (h) grass association zones *sensu* Rattray (1960); (i) distribution of 29 common tree species: dark and light gray bars, respectively, represent latitude ranges where they are frequent and present but infrequent.

Table 2 Vegetation structures and vegetation zones identified along the climatic transect.

Vegetation structures		
(1)	Grasslands/bushlands (no trees detected)	North of 12.2° N
(2)	Sparsely wooded savannas (*c.* 15% TC)	12.2 to 11° N
(3)	Wooded savannas (*c.* 30% TC)	12.2 to 7.8° N
(4)	Woodland (*c.* 50% TC)	8.4 to 4.5° N
(5)	Humid wooded savannas(*c.* 20% TC)	5.8 to 3.2° N
(6)	Forest (*c.* 80% TC)	South of 4.5° N
Vegetation zones		
(A)	Grassland/bushland	North of 12.2° N
(B)	Sparsely wooded savannas	12.5 to 10.1° N
(C)	Mosaics of sparsely wooded and wooded savannas	10.1 to 8.4° N
(D)	Mosaics of wooded savannas and woodland, with some sparsely wooded savannas	8.4 to 7.1° N
(E)	Woodland	7.1 to 5.8° N
(F)	Mosaics of woodland and humid wooded savannas	5.8 to 4.5° N
(G)	Mosaics of forest and humid wooded savannas	4.5 to 3.2° N
(H)	Forest	South of 3.2° N

Correspondence with environmental and phytogeographical data

Vegetation shifts along the north–south transect (Fig. 3e) were compared with change in climate (Fig. 3a), soil (Fig. 3b) and fire activity records (Fig. 3c). The gradients in MAP, MAE and SI were continuous (Fig. 1), and thus the shifts in tree cover do not correspond with shifts in one any of these climatic indices. Moreover, these shifts in tree cover appear to be uncorrelated with the variations of MAT along the transect. Detected fire activity data indicated plateaus, each approximately corresponding with different savanna types. Although differences in fire frequency may depend on the proportions of fires detected due to the tree cover, the plateaus nevertheless indicated a fairly constant fire frequency for each savanna structure.

Unlike the discontinuous evolution of tree cover along the transect, the botanical gradient was smooth and displayed a progressive appearance and disappearance of tree species, without relationships with the shifts in tree cover (Fig. 3i). In contrast, a close correspondence was observed between the changes in tree cover and phytogeographical zones at both ends of the savanna regions. The transition with forest closely matched those from White's (1983) zones 8 and 9 to 11a (Fig. 3f) and Rattray's (1960) UF1–UF2 zones (Fig. 3h); the transition with grassland and bushland matched those from White's zones 29a to 43 and Rattray's AN3 to CE5 zones. In both classifications, the zonation inside the savanna regions did not match the shifts in tree cover. Moreover, the structural characteristics of White's zones were only partially represented, with woodlands in zone 11a (wooded grassland) and with more open savannas in the woodland zones 27 and 29a. The shifts in tree cover more closely matched the transition of broad vegetation zones taken from national vegetation maps (Fig. 3g). Finer classification (not shown), delimited on a botanical, rather than on a physiographic basis, had no correspondence with the recorded structures.

Whereas each savanna type spans different soil map units with contrasted physical and chemical properties, it appeared that shifts in tree cover consistently match a shift in soil map unit (Fig. 3, Fig. S3). This was verified along the precipitation isopleth transects (Figs S4 & S5), where changes in vegetation structure correspond to changes in soil conditions, though vegetation structure is generally stable over a wide range of soil properties. Where such changes do occur along on the precipitation transects, the savanna types observed are unfailingly the same ones as those identified on the north–south transect. In 1450-mm transect (Fig. S4), changes in soil map units are never able to destabilize the woodland state but often induce slight changes in average TC. Such changes in average woodland TC were also identifiable along the north–south transect (Figs 3 & S5).

DISCUSSION

Savannas as multi-scale vegetation mosaics

The first hypotheses to be tested were whether, under given climatic conditions: (1) all structural configurations up to a climatically determined maximum were realized, or (2) if stable states were reached. The results from our transect evidenced that these apparently alternative hypotheses can be reconciled. Indeed, in each 0.1° × 0.1° plot, a wide range of tree covers was recorded and the maximal value changed more or less continuously with rainfall, especially as the tree cover variance was smaller at the MODIS data scale than at smaller spatial scales. Nevertheless, the frequency distributions of tree cover indicated that some structural configurations were more frequent than others and that, despite local variability, stable states could be defined. This is consistent with a view of savannas consisting of asynchronously evolving small-scale patches (10^{-3} to 10^{-1} km^2), each of which is able to deviate greatly from the larger-scale average configuration (10 to 10^2 km^2) by expressing a wide range of tree cover, from pure grassland to the climatically determined maximum tree cover.

Such a contrast between high small-scale variability in tree cover and broad-scale predictability has been suggested as a general rule in ecological systems and demonstrated in savannas, for instance by Gillson (2004) in a palaeoenvironmental study in Kenya. The evolution through time of a pollen proxy of tree cover in a lake with a small pollen source area [10^{-1} km^2, a spatial scale in between field studies compiled by Sankaran *et al.*, (2005) and a MODIS pixel], showed intermittent variations from grassland to woodland. Conversely, this proxy in a lake with a large source area (10^2 km^2, an area comparable to our 0.1° × 0.1° plot) was much more stable over time. A field study in Namibian arid savannas by Wiegand *et al.* (2005) similarly reported small-scale (*c.* 10^{-1} km^2) variability characterized by mostly unimodal tree height frequency distributions with different modes. At the landscape scale, however, a steady state was reached, demonstrated by exponentially decreasing tree height frequency distributions. Asynchronous dynamics of small-scale patches have also been shown in vegetation studies in South African arid savannas (Moustakas *et al.*, 2008). Moreover, in some parts of the transects, the frequency distribution of tree cover was multimodal, which indicated there was a mosaic of two large-scale ecotypes. Such spatial coexistence of different vegetation states is a common signature of multistable ecological systems (Scheffer & Carpenter, 2003).

At any particular location along the transect, climate is more or less fixed, but other processes influencing tree cover might vary within a 0.1 × 0.1° plot. For instance, soil properties might vary over short spatial scales and fire occurrence and intensity vary from point to point and year to year, creating different fire histories in different locations. The high variability of tree cover at local scales then arises both from stochasticity in population dynamics and from spatial and temporal variability in forcings.

Considering the hypothesis that a wide range of structural states may be reached for different intensities of forcing (e.g. fire frequencies), the stability of vegetation states at the landscape scale and the possible coexistence of alternative stable states implies that there is strong feedback control of structure via the intensity of these factors (Cinquin & Demongeot, 2002). This is close to Jeltsch *et al.*'s ecological buffering concept (Jeltsch *et al.*, 2000), which states that savannas persist because mechanisms pull the system back towards the savanna state when it is driven far from the average state. Indeed, many positive and negative feedback mechanisms in savannas have been identified. For example, with increasing tree cover, one can expect an increase in tree–tree competition, a decrease in fire frequency or intensity (D'Odorico *et al.*, 2006), a decrease in grazer density and an increase in browser density.

When alternative stable states coexist, they can be defined by different stabilizing feedback mechanisms. From Walker *et al.* (1981), the possibility of coexistence of forest and savanna as alternate stable states has been a common result of modelling studies, based on interactions between grass biomass and fire frequency and intensity. Generally speaking, in these models, forest is stable because the dense tree layer has competitively excluded grasses by preferential access to light or soil resources. Then, the fire effect is too weak to significantly affect tree biomass. Savanna is then stable as long as grass biomass is large enough to ensure tree mortality, overriding the competitive advantage of trees. However, two alternative stable savanna states, differing in their woody cover or biomass, have never been demonstrated in models. This would require a combination of three types of processes: a positive feedback between trees and grasses able to produce alternative stable states (e.g. competitive advantage to trees with grass biomass feedback on fire inducing tree mortality) and two processes preventing competitive exclusion of trees and grasses, which could arise from stochasticity in the mechanisms and asynchronous dynamics across space. A feedback of tree cover on soil physical properties, for instance soil crusting (Mills & Fey, 2004), would be another or an additional possibility to explain this coexistence.

Abrupt transitions in tree cover

The pattern of tree cover along the north–south transect invalidated the hypothesis of a continuous trend in savanna tree cover. Rather, tree cover consisted of different stable structural states spanning several degrees of latitude, with areas of more or less constant tree cover succeeding each other through regions of mosaics. Each structural type is stable over wide gradients of climatic conditions and soil map units belonging to different soil types and covering a wide range of possible soil properties. This supports the hypothesis of strong stabilizing feedback mechanisms between structure and processes, leading to different regimes of the tree–grass dynamical system. Despite difficulty in interpretation, the rather constant fire frequencies for each savanna type also fitted this hypothesis. These savanna types would have a climatic range of stability, corresponding with the climatic range where stabilizing feedback mechanisms are sufficient to balance destabilizing forces. The stepwise pattern in tree cover contrasted with progressive climate-induced evolution in tree species distributions. This indicates that the stabilizing mechanisms are not dependent on the particular pool of tree species and are on a more general ecological level. The overlap of domains of stability of different savanna types gives rise to their coexistence as mosaics near the limits of their respective climatic range. This climatic hysteresis is characteristic of discontinuous transitions. Locally, bistability induce mutual exclusion of the two stable states. At a larger scale, spatial variability or biotic stochasticity, caused by disturbances, local changes of soil properties possibly amplified through feedback mechanisms, gives rise to regions of mosaics of bistable states (van Nes & Scheffer, 2005).

Under this theory, changes in environmental conditions well inside the domain of stability should have a limited impact, while similar changes near the boundaries of the domain of stability would induce changes in savanna types. This is verified when considering soil changes along the transects, especially AWC, which measures the soil storage capacity of plant-available water, and drainage, which influences the percolation of water to deep layers accessible to tree roots but not to grass roots, or nitrogen and phosphorus contents which affect competitive ability of trees and grasses (Sankaran *et al.*, 2008). While changes in soil properties only induce changes of the average TC of the savanna types in the core of their climatic domains, they induce or prevent their destabilization at the wet or dry climatic boundaries. This explains why shifts tend to occur at transitions between soil map units and predicts that association between soil and savanna type should be strong near the transitions between savanna types and poor in their core climatic domains (Letouzey, 1968; Boulvert, 1986).

The inconsistency between mechanisms promoting tree–grass coexistence in different field sites has dampened the hope that a single minimal model could describe all savannas adequately. Indeed, the pattern here suggests that there is not a single savanna ecosystem, but different savannas which differ from each other as much as from forest or grassland. When scanning the north–south transect, the change in environmental parameters and tree species induces changes in the ecological and biological mechanisms (resource competition, mortality, reproduction, fires, etc.) and also the strength of feedbacks of the savanna state on these mechanisms. Each savanna type within this transect could be sustained by a different group of processes and feedback mechanisms. Abrupt transitions would then denote changes in sustaining mechanisms, for instance when feedback intensity is suddenly insufficient to maintain stability. The opposition between the proposed models would only then be apparent, as they do not aim to model the same savanna type. For instance, current knowledge about savanna dynamics indicates that root niche separation and inter-annual rainfall variability are the drivers of tree–grass coexistence in semi-arid savannas (Higgins *et al*., 2000; D'Odorico *et al*., 2005), while inter-annual fire variability, escape of adult trees from the flame zone and negative effects on grasses influence the structure of humid savannas (Gignoux *et al*., 1997; Favier *et al*., 2004).

Open humid savannas

The third series of hypotheses to be tested were: (1) that tree cover always increases with water availability and (2) that most humid savannas display a decline in tree cover. In the north–south transect, there is a region of tree-poor savannas around the humid forest domain. Such open savannas in contact with humid dense tropical forest is a consistent pattern throughout Africa (Backéus, 1992). For a long time they were considered as artificial 'derived savannas' of recent anthropic origin. Though historical studies (Fairhead & Leach, 1996) and palaeoecological studies (Vincens *et al*., 1999; Ngomanda *et al*., 2009) have rather suggested that they appeared two to three millennia ago, subsequent to a dry climate phase. They are thus not simply areas of degraded forests and the question of the ecological processes allowing their persistence and their difference in tree cover from drier savannas is then raised. A reduction in tree cover in humid savannas has been shown in some models (Higgins *et al*., 2000; Favier & Dubois, 2004) and can be explained by a simple mechanism: for savannas to persist under such humid conditions and to prevent afforestation, fire occurrence must be very frequent. Due to heavy rainfall, high grass yield leads to intense fires, as savanna grasses dry out during the dry season. This in turn imposes a strong demographic bottleneck at the seedling stage and prevents most tree establishment. This model-based explanation is supported by numerous observations, reviewed, for example, by Backéus (1992), that fire exclusion for a period of some years leads to afforestation in this kind of savanna. Under drier climates, lower grass biomass and less rapid tree growth allow a stable state with higher tree cover. However, this explanation apparently contradicts satellite-derived data on fire occurrence, which is low in the humid savanna regions. This may result from inaccuracies in the fire index in such regions; as pointed out by Silva *et al*. (2005), the proportion of fire scars detected by middle resolution satellites strongly depends on vegetation type and is significantly lower for humid savannas as compared with mesic woodlands. Two local analyses in climatically similar regions indeed indicated that fire occurrence was underestimated by MODIS fire scar data. First, Kana & Etouna (2006) estimated from LANDSAT imagery that 33% of savannas were burned annually in a periforest region in Cameroon (although they omitted fires in the early and very late dry season). Bucini & Lambin (2002), using coarse-scale imagery, estimated that in the Central African Republic about 75% of periforest savannas were burnt during one dry season. This is consistent with expert-based knowledge that reported most humid savannas were burn annually (Menaut *et al*., 1991).

CONCLUSION

This study presents savanna ecosystems as complex dynamic tree–grass systems. Satellite imaging of savanna tree cover has revealed stable macroscale (10^2–10^5 km^2) organization constructed on the basis of microscale (10^{-2}–1 km^2) stochasticity and high variability. The patterns reported here are of climatically determined discontinuous succession of vegetation structures that are stable over several degrees of latitude. Each structure is in dynamic equilibrium, consisting of patches that can take up a wide range of configurations around the average. The occurrence of alternative stable states, demonstrated for the first time over such a wide spatial extent, is a consequence of the discontinuous transitions between these structural types. The macroscale decoupling between floral composition and structure indicates that, as for forests, ecological processes and feedbacks that shape savanna tree covers were largely independent of the climatically available species pool. Mechanisms that sustain each savanna type now need to be precisely elucidated. Including these mechanisms in global vegetation models would facilitate the simulation of realistic tree–grass ratios and of energy, carbon and water fluxes across the savanna biome, as well as likely impacts of humans and climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Comparison of frequency distribution of tree cover with fine and coarse spatial resolution.
Figure S2 Comparison between field and remote sensing estimated of savanna tree cover.
Figure S3 Comparison of soil properties and frequency distribution of MODIS Percent Tree Cover along the north–south transect.
Figure S4 Comparison of soil properties and frequency distribution of MODIS Percent Tree Cover along the 1450-mm transect.
Figure S5 Comparison of soil properties and frequency distribution of MODIS Percent Tree Cover along the 800-mm transect.
Figure S6 Colour scale for the main soil type in soil map units of Figs 3 & S3–S5.
Appendix S1 Interpretation of MODIS Percent Tree Cover data.

BIOSKETCHES

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