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ORIGINAL ARTICLE

Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change

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ABSTRACT

Aim Widespread reports of disappearing tree species and senescing savanna parklands in the Sahel have generated a vigorous debate over whether climate change or severe human and livestock pressure is principally responsible. Many of the tree taxa in decline are closely associated with human settlement and farming, suggesting that the parkland ecosystem may not be a natural vegetation assemblage. The aim of this study is to assess the possibility that human activities promoted the spread of taxa with edible fruit into dry Sudano-Sahelian areas during high-rainfall periods in the climate cycle.

Location West African savannas (Mali, Burkina Faso, Ghana, Togo, Benin).

Methods Cultivated savanna parklands and adjacent forests and transitional landscapes were inventoried at 27 sites in five countries. All trees with basal diameters > 10 cm were counted within 500-m^2 belt transects. Species composition and abundance were contrasted between three landscape classes to assess the degree of influence exerted by traditional human management. Twentieth century rainfall data were averaged for two sets of weather stations encompassing the north–south range of typical parkland tree species. Rainfall trends were used to evaluate the putative impact of climate change on edible and/or succulent fruit species at the northern limit of the parkland savanna zone.

Results Species composition and spatial distribution data indicate that the parkland ecosystem is significantly shaped by human activities. Indigenous land management favours edible-fruit-yielding taxa from the wetter Sudanian and Guinean vegetation zones over Sahelian species. Rainfall isohyets at the northern range limits of parkland species shifted southwards in the late 20th century, crossing the critical 600-mm mean annual rainfall threshold for Sudanian flora. Relict vegetation and historical records indicate that the Sudanian parkland system extended in the past to near 15° N latitude in middle West Africa, compared with 13.5° N today.

Main conclusions The current loss of mesic trees in the Sudano-Sahel zone appears to be driven by the sharp drop in rainfall since the 1960s, which has effectively stranded anthropogenically distributed species beyond their rainfall tolerance limits.

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Keywords

Agroforestry, archaeobotany, desertification, drought, Guinean zone, landscape ecology, parklands, savanna, senescence, Sudanian zone.

INTRODUCTION

The Sahel region of Africa underwent a 20–40% drop in precipitation from the mid to the late 20th century (1930–1965 vs. 1966–2000), representing the largest and most sustained rainfall shift of any contemporary region on Earth (Nicholson, 2001). Currently there are widespread reports of the disappearance of tree species in the Sahel (Gonzalez, 2001; Wezel & Lykke, 2006). This phenomenon has generated a debate over whether species losses are driven directly by climate change or

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by environmentally destructive human activities (Mahamane & Mahamane, 2005; Salzmann & Hoelzmann, 2005), or by a negative synergy of natural and anthropogenic effects (Nicholson, 2000; Hulme *et al.*, 2001). What has generally been overlooked is the degree to which long-term indigenous anthropic activities have determined the spatial structure and taxa found in many of the landscapes of the Sahel and the adjacent Sudan and Guinea zones (Pelissier, 1980; Seignobos, 1982; Fairhead & Leach, 1995; Turner, 2000). If centuries or millennia of human land use have enhanced the range and abundance of tree species with edible and/or succulent fruit, then the local disappearance of some taxa in drought-impacted areas may represent a shift from anthropogenically constrained landscapes to a vegetation that is better adapted to drought. In this case, the pattern of vegetation change would represent a form of post-agricultural ecological succession.

The savanna zones

The savanna landscapes of Africa north of the equator form a series of parallel latitudinal belts, with characteristic woody vegetation (Fig. 1a) reflecting the approximately longitudinal aridity gradient (White, 1983). The amount and seasonal duration of the rainfall characterizing these vegetation zones vary owing to strong interannual variability and longer-term climate oscillation. Mean annual rainfall can be generalized to be 100–300 mm for the Sahel vegetation region, 300–600 mm for the Sudano-Sahelian transition zone, 600–1200 mm for the Sudan savanna and 1200–1500 mm for the Guinean woodlands, with overlapping boundaries of *c.* 200 mm (Le Houérou, 1989; Malo & Nicholson, 1990). Sahel thornscrub, with typical bipinnately compound leaves and small leaflets, transitions to the deciduous trees of the Sudan zone, with larger, pinnately compound leaves, which then merge into the broadleaved evergreen woodlands of the Guinea zone (Gonzalez, 2001). Sahel woody species mostly have dry fruits or seed pods (von Maydell, 1990), whereas Guinean species often have fleshy fruits with higher moisture and sugar contents (Maranz *et al.*, 2004a).

Parkland savannas

The differences in fruit type translate in ethnobotanical terms to higher economic value for Sudanian and Guinean trees than

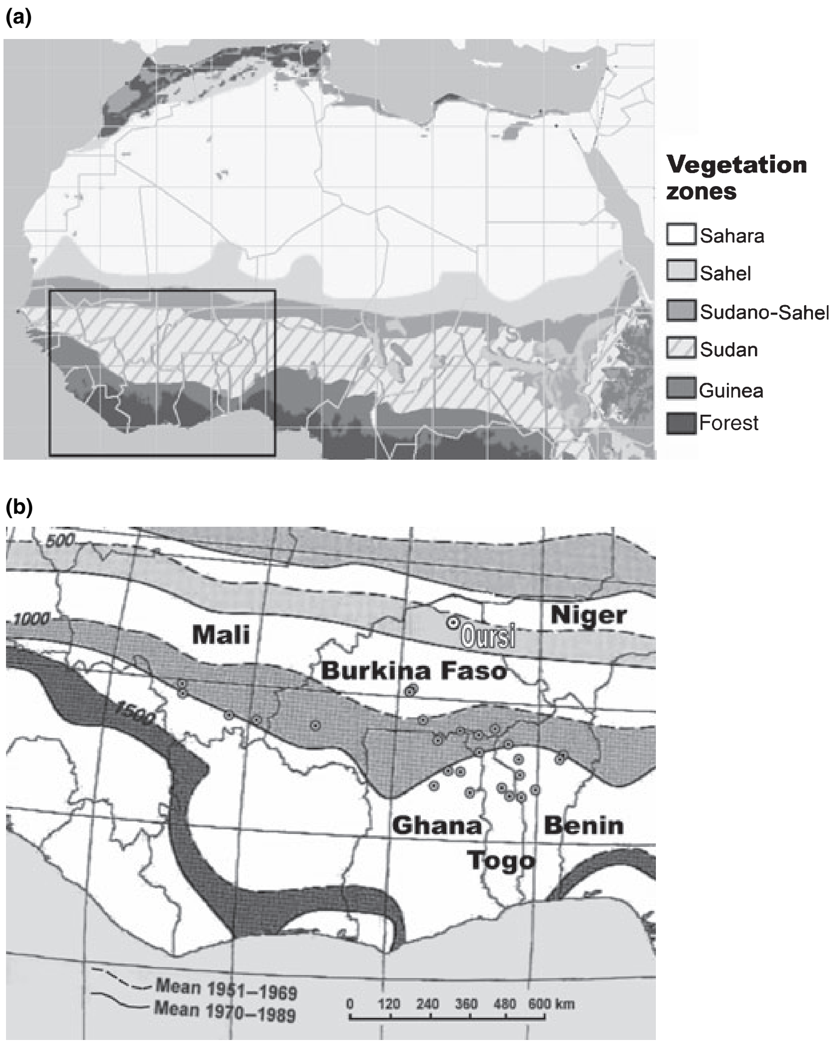

Figure 1 (a) Vegetation map of Africa north of the equator showing vegetation bands running roughly parallel to the equator, reflecting the north–south aridity gradient (adapted from White, 1983); (b) study area showing transect locations juxtaposed against shaded belts indicating late 20th century shifts in the 500-, 1000- and 1500-mm mean annual rainfall isohyets (adapted from L'Hôte & Mahé, 1996).

for Sahelian shrubs. The occurrence of economically important tree species, especially comestible fruit trees, outside their typical vegetation zones is common in Africa and is linked to human migration and settlement patterns (O'Brien & Peters, 1998; Duvall, 2007). A striking feature of the West African savanna parklands is that, among large trees (> 30 cm d.b.h.), comestible fruit taxa appear far more abundant than non-comestible species. A single comestible species frequently accounts for 50% or more of the trees in a given parkland landscape (Boffa, 1999; Maranz & Wiesman, 2003). The overall pattern that emerges is the prevalence of non-comestible woody species both in the dry Sahel zone to the north and in the forests to the south. Sandwiched in between is a broad belt of parkland savanna in which comestible fruit species predominate (for parkland species composition profiles, see Appendix S1).

This region was permanently settled by humans around 3000 years ago (Ballouche & Neumann, 1995) and was the centre of the great savanna civilizations of Africa, including the Ghana, Mali and Songhai empires and numerous other West African kingdoms. The ethnic groups occupying the region today consist of sedentary farmers descended from these civilizations, as well as semi-nomadic Peul and Tuareg pastoralists who lead seasonal migrations of large numbers of livestock across the landscape.

Traditional sedentary farming practices are based on clearing woodland and shrubland for annual crop cultivation while leaving valued tree species *in situ*. Exhausted fields are fallowed and may lapse back into dry forest before being cleared again a generation or more later (Maranz & Wiesman, 2003). Where human population densities are higher, or where drier climatic conditions limit the rejuvenation of parklands, cultivation can be permanent. Low annual crop yields are offset by fruit yields from large trees maintained in parklands, which form an important nutritional and trade component of local livelihoods (Maranz *et al.*, 2004a). The prevalence of comestible fruit species in both cultivated savanna and forest landscapes in the Sudan zone thus coincides with human settlement and traditional agricultural activities.

Despite the dominance of comestible fruit tree species in the Sudanian parklands, most biologists and ecologists working in the region continue to view the parkland ecosystem primarily as a natural vegetation assemblage (Blench, 2001; Wickens & Lowe, 2008). This is in contrast to the views of many social science observers, who typically perceive a much greater indigenous, traditional African role in forest/savanna dynamics (Pelissier, 1980; Turner, 2000; Duvall, 2003). Public policy promoted by international agencies and set by national governments generally treats the savanna landscape as a natural ecosystem imperiled by autochthonous deforestation (Fairhead & Leach, 1995).

The effects of climate change

The thesis of this paper is that the impact of climate change across the Sahel geo-political region must be understood within the context of centuries or millennia of human settlement and ecosystem alteration. If human activities have indeed altered species composition and abundance, then the widely observed senescence of the parklands and the localized disappearance of certain species during recent droughts may represent the collapse of an anthropogenic system no longer adapted to current conditions. This is substantially different from the prevailing view of anthropogenic desertification, in which indigenous people are held accountable for the destruction of the natural ecosystem (Aubréville, 1947; Mahamane & Mahamane, 2005). The alternative perspective explored in this study is that shrubland vegetation is simply replacing anthropogenic parkland trees as a consequence of the declining rainfall trend in the region. The effect of vegetation change therefore represents a loss of livelihood to Sahel peoples, but not necessarily an ecological catastrophe.

To test the thesis that late 20th century climate change is driving the replacement of an anthropogenic ecosystem featuring mesic tree species that are incompatible with the prevailing drier conditions, the following hypotheses were evaluated: (1) Sudanian parkland landscapes are fundamentally anthropogenic in origin, as evidenced by the high proportion and abundance of comestible fruit species and the low diversity indices in cultivated landscapes in comparison with fallows and forests; (2) the dominant tree species in the Sudanian parklands are disproportionately Guinean taxa, as defined by Aubréville (1950) and White (1983); (3) archaeobotanical records and indigenous landscape histories at the northern edge of the parklands (Sudano-Sahel zone) indicate a decline in Guinean and Sudanian taxa, with a corresponding increase in Sahelian species; and (4) 20th century meteorological data show ecologically critical rainfall shifts at the northern edge of the parkland savanna system, thus potentially accounting for comestible fruit tree senescence and mortality.

MATERIALS AND METHODS

Field data were obtained in conjunction with an extensive germplasm collection of the shea tree, *Vitellaria paradoxa* C.F. Gaert. (Sapotaceae). Shea fruits have a sweet, nutritious pulp (Maranz *et al.*, 2004a), surrounding a large single or double seed (shea nuts) with a very high lipid content (Maranz *et al.*, 2004b). Shea nuts are also an export commodity and a source of international interest and funding for savanna research. The seed fat (shea butter) is traditionally extracted and used for cooking oil, skin ointment and numerous other household and medicinal purposes. These qualities make shea the principal economic species of the Sudanian savanna zone across the African continent, from eastern Senegal to western Ethiopia (Ruyssen, 1957). Shea trees typify the West African savanna parkland ecosystem, in which extensive human management and exploitation of trees and tree products imply an agricultural system, whereas irregular tree spacing and natural regeneration indicate a wild-harvested natural savanna

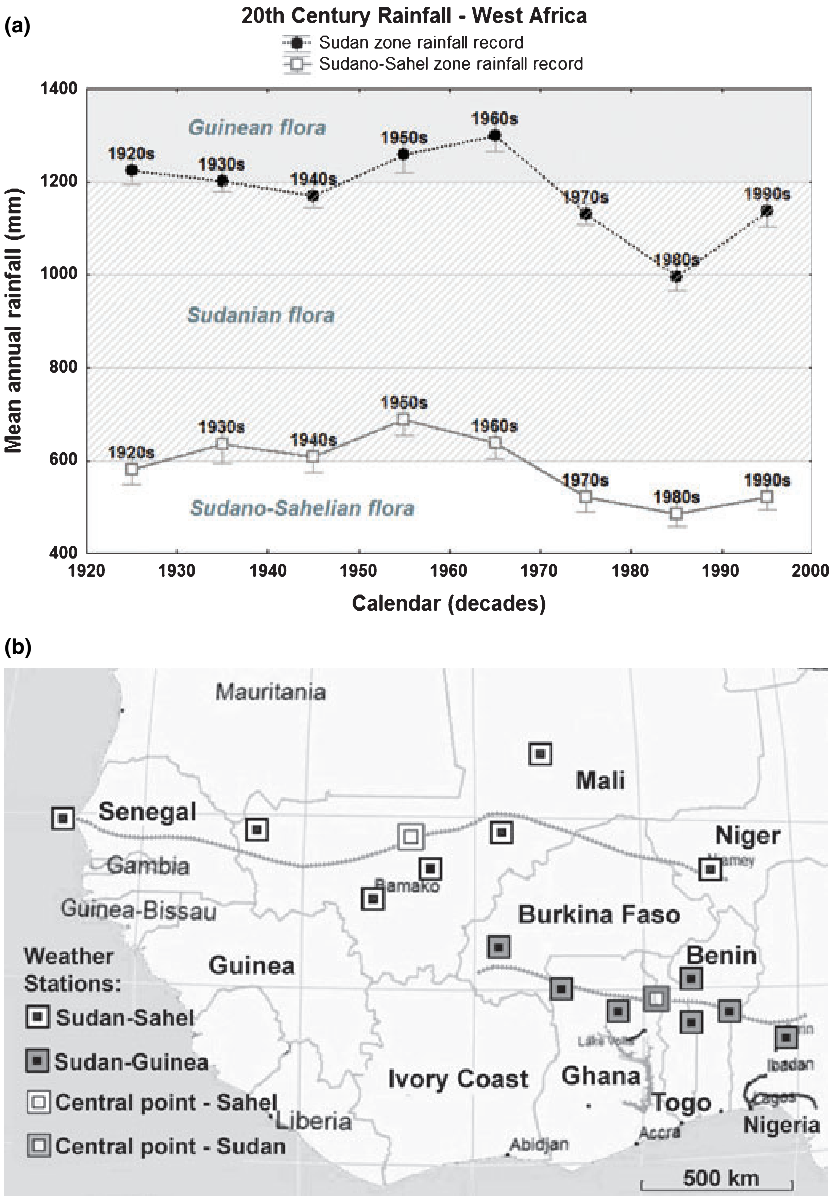

Figure 2 Twentieth century mean annual rainfall averaged for (a) seven West African weather stations representing the Sudano-Sahelian zone and seven stations representing the southern Sudanian zone. (b) Station locations are shown on the map, together with the two points representing the geographic centres of the northern and southern stations (the mean latitude and longitude of the grouped precipitation records). In the north, mean precipitation from the mid-1920s to the mid-1960s was sufficient for a Sudanian flora. Since the 1960s, the rainfall has shifted to a regime characteristic of Sudano-Sahelian flora, crossing the ecologically significant 600-mm threshold. In the south, rainfall was at Guinean levels during the middle of the century, but has decreased to Sudanian levels since the mid-1960s.

(Maranz & Wiesman, 2003). The shea tree is thus key to understanding a complex ecosystem that has confused both outside observers and national officials who are unfamiliar with the history of the landscape.

In this context, a rapid survey method was used to quantify the degree of human management detectable in common West African savanna and woodland landscapes by assessing species composition under various traditional land uses. Savanna parklands in West Africa were inventoried within a geographic area of *c.* 3° of latitude by 10° of longitude (Fig. 1b). The inventory route began south of Bamako, Mali, and continued through Burkina Faso, Ghana, Togo and Benin (12.3° N, 7.9° W to 9.3° N, 2.0° E). Landscapes representing typical cultivated Sudanian parklands, forests and fallows (referred to here as transitional areas) were chosen at intervals of 50–100 km, depending on road access, security conditions and the avoidance of urban and disturbed areas. In each representative landscape, three 100 m × 5 m belt transects were taken within a 0.5-km^2 area, and the species identities and counts of all woody plants with basal diameter > 10 cm were recorded (Aide *et al.*, 1996; Forester *et al.*, 2007). Transects were oriented to capture high, low and intermediate tree densities in each landscape and were averaged to produce site means. A total of 90 transects were taken at 27 sites. Fields with annual crops between mature trees or showing signs (tillage marks and crop residues) of having been cultivated the previous year were classified as cultivated parkland. Bush fallows consisting of shrubs, tree seedlings and coppicing stumps from earlier land clearance were designated as transitional areas. This category also includes the margins of cultivated fields containing a mix of woody species and grasses. Landscapes designated as forest refer both to woodland with no physical signs of cultivation and to woody vegetation on rocky outcrops and mesas.

Species patterns were investigated within functioning anthropic cultivation/fallow cycles in the Sudanian zone, where the parkland ecosystem is thriving. We also wished to assess landscape history in an area where the parkland system is breaking apart or has already become extinct. The Oursi watershed and dune system in the Sudano-Sahelian zone of northern Burkina Faso was chosen for a case study because of the existence of previous research conducted by French, German and Scandinavian groups documenting drought impact and ethnographic history. These investigations included aerial photographs (Lindqvist & Tengberg, 1993; Reenberg *et al.*, 1998; Rasmussen *et al.*, 2001), indigenous oral landscape histories (Rasmussen *et al.*, 2001), archaeobotanical data (Neumann *et al.*, 1998) and a palynological record from the Mare d'Oursi playa lake (Ballouche & Neumann, 1995).

Literature reports of species disappearances were verified in discussions with pastoral nomads and sedentary farmers at Oursi, Burkina Faso. A Peul elder with a keen interest in woody vegetation led a mobile group interview across the Oursi watershed, with *in situ* discussions of species along the landscape catena. Participants from the Peul, Bella and Sonrai ethnic groups were asked to name in vernacular language the woody species that had disappeared, decreased, increased or migrated to different landscape positions during their lifetimes. Tree identities were confirmed by identification of live trees indicated by members of the group, and by vernacular language species lists and tree photographs (von Maydell, 1990).

Rainfall data were taken from the Nicholson Africa rainfall database (NOAA, 2008), and supplemented with more recent data from West African weather stations. Rainfall data from before 1920 were excluded from regional means owing to missing data and uneven site representation. Rainfall records from seven Sudanian and Sahelian weather stations were averaged to generate a 20th century rainfall profile characteristic of the drought-affected Sudano-Sahel zone (Fig. 2a, lower graph line), with an average latitude and longitude of 14.3° N and 6.9° W, corresponding to the current northern limit of *Vitellaria* occurrence in Mali (Fig. 2b). In addition, rainfall records from seven Sudanian and Guinean stations were also averaged to generate a 20th century rainfall profile for the southern portion of the Sudan zone (Fig. 2a, upper graph line), with an average latitude and longitude of 9.7° N and 1.1° E (Fig. 2b).

Statistical analysis of the transect data was performed using Statistica 8 (StatSoft, Inc., 2008) and XLStat 2008 (Addinsoft, Inc., 2008) software. Transect count data were analysed using a generalized linear model (GLM) for a Poisson distribution with a log-link function and correction for over-dispersion. Wald (χ^2) statistics and corresponding *P*-values were calculated with landscape classes as the categorical variables and species abundance and diversity parameters as the dependent variables. Principal components analysis (PCA) was used to separate landscape classes and to identify the relative contributions of different variables to factor axes. The objective of both PCA and GLM analyses was to distinguish statistically the three landscape classes and to highlight differences attributable to anthropogenic selection, especially with regard to contrasts in the spatial distribution of trees and in the abundance of comestible fruit species. Spearman correlations were calculated between comestible fruit species and flora characteristic of the Sahelian, Sudanian and Guinean savanna zones within each of the three landscape classes. The goal of the pairwise correlations was to assess statistically the possibility that human landscape alteration favours comestible fruit species in general and mesic flora in particular (such as Guinean species, which often have more succulent fruit). If the three classes of landscape (forest, transitional and cultivated

Table 1 Comparison of woody vegetation parameters in three landscape classes: forest, transitional (fallow) and cultivated parkland.

	Mean value per 500-m^2 transect Landscape class					GLM-ANOVA	
Variables	Forest	Transition	Parkland	All	d.f.	Wald (χ^2)	*P*-value
Abundance – no. trees	24.3	17.6	6.2	14.6	2	117.5	< 0.001
No. species	7.3	5.7	2.5	4.7	2	162.9	< 0.001
No. comestible fruit species	2.1	2.8	2.1	2.4	2	8.4	0.015
No. comestible fruit trees	6.0	7.8	5.6	6.5	2	8.2	0.016
No. livestock/human comestible trees	7.5	8.2	5.7	7.0	2	10.6	0.005
Combretaceae – no. trees	3.2	2.6	0.1	1.8	2	23.7	< 0.001
Daniella-Isoberlinia – no. trees	11.0	4.0	0.3	4.2	2	17.1	< 0.001
Sahelian vegetation – no. trees	0.5	0.5	0.1	0.3	2	8.7	0.013
Sudanian vegetation – no. trees	9.7	9.2	4.4	7.4	2	41.7	< 0.001
Guinean vegetation – no. trees	14.1	7.9	1.6	6.8	2	39.3	< 0.001
n	21	33	36	90			

Means are shown for trees with basal diameter > 10 cm within 100 m × 5 m belt transects in each landscape class. Wald (χ^2) statistics and corresponding *P*-values were calculated using a generalized linear model (GLM) for a Poisson distribution with a log-link function. All transects were located in the Sudanian and Guinean zones of West Africa (Mali, Burkina Faso, Ghana, Togo, Benin).

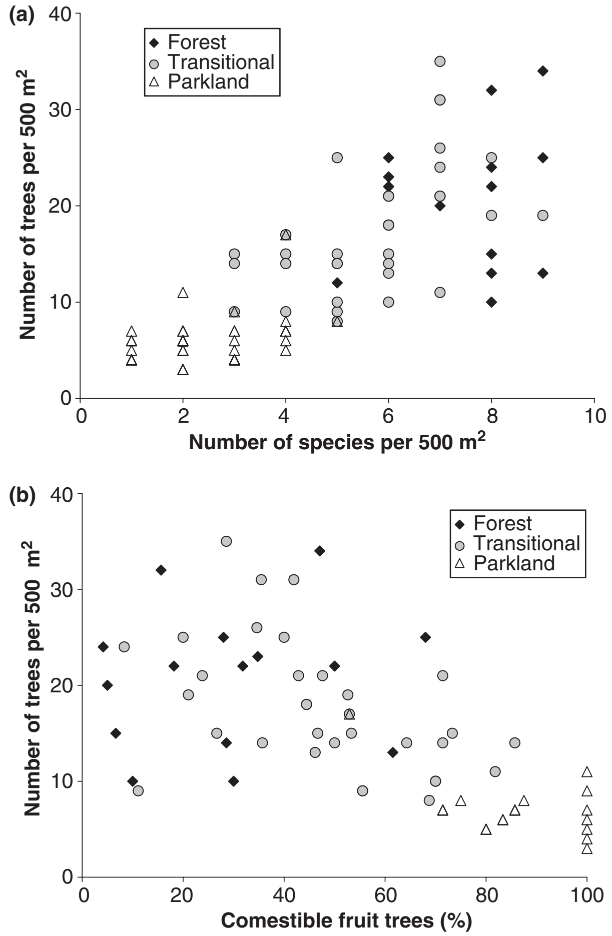

Figure 3 Scatter plots of woody plant counts (> 10 cm basal diameter in 100 m × 5 m transects) in three landscape classes showing: (a) a positive correlation between the number of species and the number of trees in the landscape ($r = 0.77$, $r^2 = 0.60$, $P < 0.001$); and (b) a negative correlation between the percentage of comestible fruit trees and the total number of trees ($r = -0.72$, $r^2 = 0.52$, $P < 0.001$).

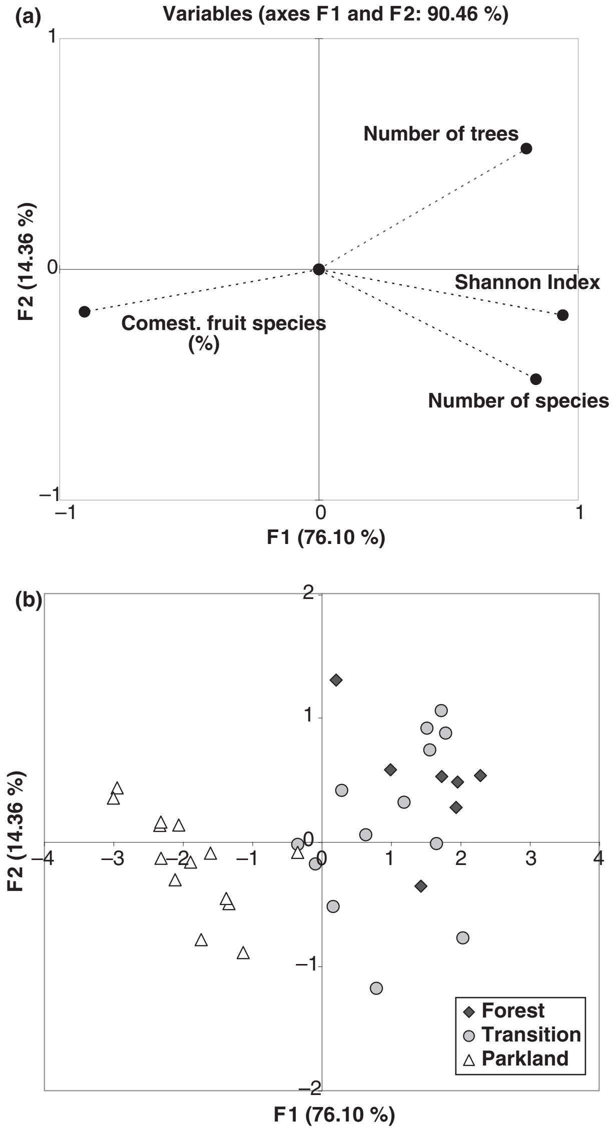

Figure 4 Principal components analysis of landscape transect data averaged by site showing: (a) the separation of the percentage of comestible fruit species from tree abundance and species diversity along the principal factor axis; and (b) the same separation showing a strong association between parkland landscapes and comestible fruit trees.

parkland, with progressively greater degrees of human impact) were to exhibit increasing correlation with mesic species, then the anthropogenically altered ecosystem should consequently be more vulnerable to a shift to a drier climate.

RESULTS

Sudanian savanna transects

The mean number of trees (> 10 cm basal diameter) recorded in the belt transects (100 m × 5 m) was far lower in cultivated parklands (6.2 trees per 500 m^2) than in transitional areas (17.6) and forests (24.3), with differences significant at $P < 0.001$ (Table 1). Mean species richness was also substantially lower in cultivated parklands (2.5 species per 500 m^2) than in transitional areas (5.7) and forests (7.3). Shannon index diversity was 0.80 for parklands, 1.71 for transitional areas and 1.80 for forests (see Fig. S1a in Appendix S1). For the Sudanian sites sampled in this study, the conversion of forest to parkland savanna resulted in a mean reduction of 18.1 trees (> 10 cm basal diameter) and 4.8 species per 500 m^2.

In contrast, the mean percentage of comestible fruit trees (see Fig. S1b in Appendix S1) was much higher in Sudanian parklands (93.2% of all trees > 10 cm basal diameter), where seasonal crops are cultivated between trees, than in woody fallow transitional areas (47.8%) and adjacent forests (29.2%). The mean number of comestible fruit trees (individuals) was 5.6 per 500 m^2 for cultivated parklands and 6.0 for Sudanian forest (Table 1). The mean number of

Table 2 Spearman correlations (r_s) between comestible fruit species and taxa characteristic of the Sahel, Sudan and Guinea zones within different landscape classes.

	All landscapes (n = 87)		Forest (n = 18)		Transitional (n = 33)		Parkland (n = 36)	
Variable A × variable B	r_s	P-value	r_s	P-value	r_s	P-value	r_s	P-value
Comestible species × Sahelian species	0.09	0.387	−0.14	0.590	−0.05	0.769	0.37	0.028
Comestible species × Sudanian species	0.21	0.056	−0.29	0.238	0.14	0.432	0.41	0.013
Comestible species × Guinean species	0.60	< 0.001	0.55	0.019	0.67	< 0.001	0.76	< 0.001

All data were derived from counts of trees with > 10 cm basal diameter within 500-m^2 transects in West African Sudanian zone savanna landscapes.

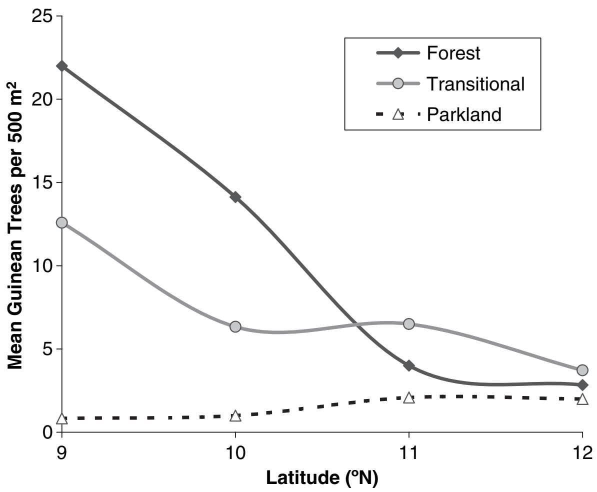

Figure 5 Change in Guinean tree abundance with increasing latitude and aridity. Values represent the mean number of trees (> 10 cm basal diameter) per 500-m^2 transect at four latitudes. Trends are shown for three landscape classes (Wald χ^2 = 19.9, P = 0.003).

comestible fruit species was also similar between cultivated and forest areas (2.1 species per 500 m^2 in both landscapes). This indicates that comestible fruit trees (both species and individuals) occur at approximately the same spatial distribution in Sudanian cultivated and forest landscapes; however, the latter contain other species as well, which are absent in the cultivated landscapes.

Scatter plots clearly separate Sudanian parkland landscapes from the others on the basis of tree density plotted against either comestible fruit tree percentage or mean number of species per 500 m^2 (Fig. 3). There is a positive correlation (r = 0.77) between tree numbers and number of tree species (Fig. 3a) and a negative relationship (r = −0.72) between the percentage of comestible fruit trees and the total number of trees across the three landscape classes (Fig. 3b). This indicates that a process of elimination occurs in the forest/cultivation/fallow cycle. The reduction in overall tree numbers and species in cultivated savanna therefore appears principally to involve the elimination of most non-comestible woody species.

While Sudanian cultivated savanna statistically represents forest with deletions of individual trees and tree species, transitional areas (consisting of formerly cultivated parkland, currently in bush fallow, and field margins) are richer in both comestible fruit individuals (7.8 per 500 m^2, P < 0.016) and comestible fruit species (2.8 species per 500 m^2, P < 0.015), compared with both forest and cultivated landscapes (Table 1). Compared with actively cultivated parklands, transitional areas average an additional 11 trees (> 10 cm basal diameter), three more species (including one additional comestible fruit species) and two more comestible individuals per 500 m^2. Principal components analysis (Fig. 4) clearly separates cultivated parklands from the other landscapes on the basis of: (1) comestible fruit tree percentage (positive correlation); and (2) the Shannon index of diversity (negative correlation), with transitional landscapes generally intermediate but overlapping with forest sites on the projected factor plane.

To understand better the nature of the differences between the three landscapes, affinities with the three characteristic floras of the region were evaluated. Spearman correlations (r_s) between the number of comestible fruit species and the number of Guinean taxa were 0.55 (P = 0.019) for forest, 0.67 (P < 0.001) for transitional areas and 0.76 (P < 0.001) for cultivated parklands, showing a significantly stronger association between Guinean flora and human-managed landscapes compared to forest (Table 2). Comestible Sudanian fruit tree species were negatively or weakly correlated with forest (−0.29) and transitional areas (0.14), and more strongly associated with cultivated parklands (0.41, P = 0.013). Comestible Sahelian fruit species were negatively correlated with both forest and transitional landscapes, and positively correlated with parklands (0.37, P = 0.028). This indicates that the relatively small number of Sahelian species recorded in Sudanian parklands (1.4% of trees > 10 cm basal diameter) are principally comestible fruit trees (Table 1). Thus, for all three floras (Sahelian, Sudanian, Guinean), selection by humans is occurring for comestible fruit trees within the parkland landscapes of the Sudan zone.

When species variation across the West African climate gradient is examined, anthropic preference for comestible fruit species from the Guinean flora is even more striking (Fig. 5).

At higher, drier latitudes, the number of Guinean trees decreases sharply in forest and transitional landscapes, reflecting the natural transition to Sahelian flora. In contrast, Guinean tree numbers increase in parklands at higher latitudes (Wald $\chi^2 = 19.9$, $P = 0.003$), indicating that mesic species with succulent fruits are especially esteemed in dry zones. This finding is supported by earlier indigenous fruit preference surveys along the climate gradient (Maranz *et al.*, 2004a). Nevertheless, Guinean tree numbers in all three landscape classes approach the same density at 12° N (Fig. 5), suggesting that there is a carrying capacity limit for large Guinean trees at this latitude and level of rainfall.

Post-drought vegetation changes

At Oursi in the Sudano-Sahelian zone north of the transect area, the group interview with Peul pastoralists and sedentary Bella and Sonrai farmers supported earlier reports (Rasmussen *et al.*, 2001) that locally extinct or rare trees include many taxa characteristic of the Guinean and Sudanian vegetation zones (see Table S1 in Appendix S1). Some north Sudanian species were considered by locals to be in severe decline as a result of heavy livestock browsing (*Combretum aculeatum* Vent. and *Pterocarpus lucens* Lepr. ex Guill. et Perr.) or human overexploitation (*Acacia senegal* (L.) Willd., used for making the reaping baskets commonly employed for harvesting grass seeds). Other species were reported to have maintained their historical abundance while shifting location from valley slopes down to the exposed upper lake-bed of the Mare d'Oursi (*Acacia nilotica* Guill. et Perrott.). It is noteworthy that *Balanites aegyptiaca* (L.) Del., a thorny shrub characteristic of Africa's drylands, was cited as having vastly increased in number, from having a very low abundance a generation ago to clearly being the dominant species at Oursi today. Other species with increased abundance include *Acacia raddiana* Savi and *A. laeta* R. Br. ex Benth., both Sahelian or Sahelo-Saharan species.

Twentieth century rainfall records

Rainfall records averaged from seven Sudan/Sahel meteorological stations (Fig. 2a, lower graph line) show that mean annual rainfall averaged by decade was always above 600 mm (643 mm ave.) from 1930 to 1965, but was always below 600 mm (524 mm ave.) from 1966 to 2000. Rainfall before 1930 appears to have been significantly below mid-century levels, but higher than that of the late-century droughts. Rainfall records for the seven southern weather stations (Fig. 2a, upper graph line) show a similar pattern of increased rainfall during the mid-20th century, with a sharp decrease after 1965. Rainfall levels at mid-century in the south correspond to Guinean ecozone conditions (> 1200 mm per annum), whereas Sudanian ecozone conditions prevailed in the 1930s to early 1940s and from the mid 1960s to 2000. The variable 20th century rainfall conditions in the southern savannas support the mix of Sudanian and Guinean floristic elements seen today.

DISCUSSION

The central argument of this paper is that tree mortality in the Sahel (specifically the southern part, or the Sudano-Sahel zone) is climate-related and predominantly affects trees that are components of an anthropogenic parkland savanna system developed during the wetter climatic conditions prevalent in earlier decades. The transect studies presented here were carried out in the Sudan zone to the south of the area of high tree mortality. There is historical evidence that the cultivated parkland system that is currently dominant in middle West Africa between 9° N and 12° N extended in the past to at least 15° N (Ballouche & Neumann, 1995; Neumann *et al.*, 1998). Thus, the structure of Sudanian parklands is important both for determining how anthropogenic selection occurs and for understanding the potential impact of climate change on the system.

Sudanian parkland savanna structure

In the Sudanian zone, the contrasts in tree density and species composition between cultivated parklands and adjacent woodlands reveal a distinctive pattern of tree selection and retention during land clearing and annual crop production. The transect data from sites in five West African nations indicate that comestible fruit tree numbers are similar for forests and cultivated savanna (Table 1). At the same time, there is a much lower tree density in the cultivated savanna, with nearly 75% of the trees removed in order to open up the landscape for cultivation (Table 1). Traditional decision making for tree retention heavily favours comestible fruit species from all three floristic zones, shown by the correlation values that increase with management level among all three floras (Table 2).

Intensive anthropogenic selection is clearly involved in the cultivated Sudanian parkland landscapes and in the adjacent field margins and bush fallows. Fallows have both higher tree density (including non-comestibles) and higher absolute numbers of comestible fruit species and individuals than the cultivated parklands (Table 1). Available space for trees in cultivated parklands is typically reserved for major economic species, but fallows and field margins can serve as anthropogenically encouraged refuges for minor edible fruits and medicinal species that do not find space in cultivated land (Etkin, 2002). These areas receive an influx of seeds from nearby forests as well as being reseeded *in situ* by the comestible fruit trees left in place during the cultivation phase of the cycle.

Historical importance and range of parklands

The antiquity of the parkland system is attested to by the Arab explorer Ibn Batuta, who travelled south of the Sahara in the 14th century and described shea fruits and shea butter as the dietary and market mainstay of the Mali empire (Ibn Batouta, 1843). He also mentions groves of exceptionally large trees,

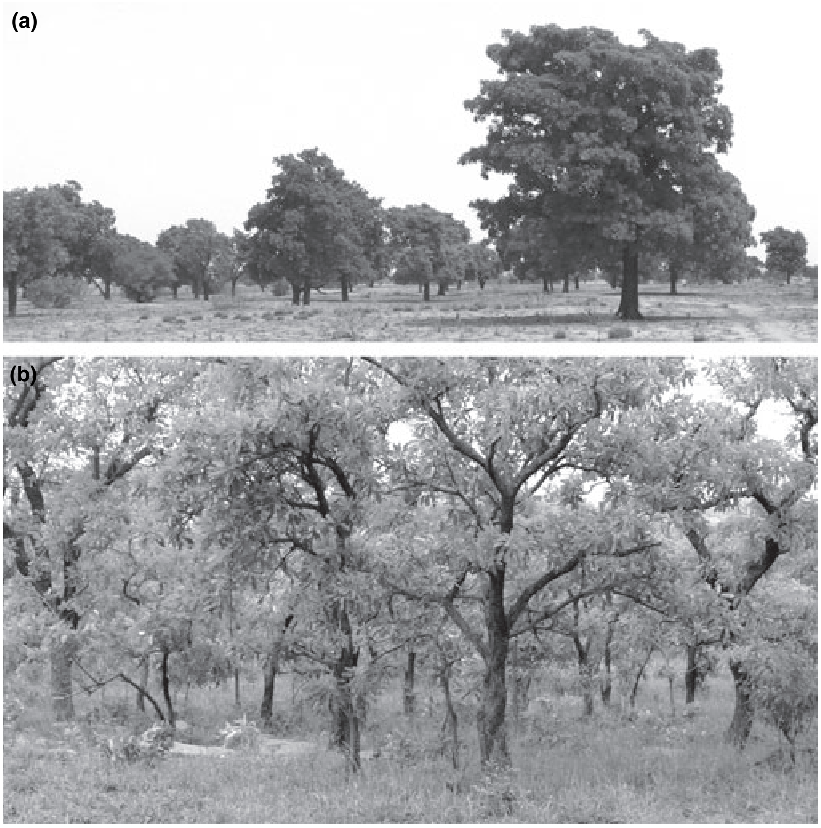

Figure 6 Climate limits of the West African parkland ecosystem: (a) mature *Vitellaria paradoxa* trees in a parkland landscape in Niger (northern Sudanian zone), with no natural regeneration or adjacent fallow or forest (latitude 12° N); and (b) *Vitellaria* fallow in Ghana (southern Sudanian zone) showing abundant regeneration (latitude 10° N).

which appear from his description to be baobab parklands. Palynological and archaeobotanical evidence indicate that this anthropogenic system has been in existence for at least 1000 years and perhaps as long as 3000 years (Ballouche & Neumann, 1995; Neumann *et al*., 1998). Archaeological excavations at Oursi (14.6° N) found *Vitellaria* charcoal and testae (shea nut shells) in households dating to 1000 years ago, together with abundant remains of pearl millet, the main cultivated crop of the northern parklands. At the present time, the northern *Vitellaria* range limit in Burkina Faso is 13.4° N, which is 130 km south of documented occurrence 1000 years ago. Other comestible fruit trees appear in the Oursi palynological record after the settlement of humans 3000 years ago, including the baobab (*Adansonia digitata* L.), *Sclerocarya birrea* (A. Rich) Hochst. and *Diospyros mespiliformis* Hochst. ex A. D.C. (Ballouche & Neumann, 1995).

The ageing of the parklands

In West Africa, there is a widely observed phenomenon of the absence of seedlings and young trees around mature parkland trees, referred to in the Sahel as 'le vieillissement des parcs' – the ageing of the parklands (Sina, 2006; Ministère de l'Agriculture, Mali, 2008). Although recruitment measurements were not part of this study, it is noteworthy that *Vitellaria* seedlings and young trees were not seen during travels in the Sudano-Sahelian transition zone (Fig. 6a), whereas abundant tree stand regeneration was observed in parkland fallows in the wetter zones to the south (Fig. 6b). The differences in stand regeneration that are apparent over 2° of latitude suggest that many current mature trees in the Sudano-Sahelian transition zone may have been established during the wetter conditions prevailing in the mid 20th century (Fig 2a). Although Sahel rainfall records prior to 1920 are less complete and reliable, conditions in the late 1800s to 1930 appear to have been generally dry (Nicholson, 2000), perhaps too dry for stand establishment. Tree age estimates from tree ring studies are not available for the region – such studies would be very helpful in understanding the potential link between climate fluctuation and the age of mature parkland tree landscapes.

Twentieth century vegetation change at Oursi

Local accounts indicate that the woody species that have disappeared or are in decline at Oursi, in the Sudano-Sahelian transition zone, are predominantly taxa characteristic of the wetter Sudan and Guinea zones (see Table S1 in Appendix S1). At the same time, there has been a rapid expansion of Sahelian species such as *Balanites aegyptiaca* in the valley and *Leptadenia pyrotechnica* (Forssk.) Decne. on the dunes. *Balanites* pollen first appears in a lake-bed core from the Mare d'Oursi at just 40 cm depth (Ballouche & Neumann, 1995). A radiocarbon date of 600 yr BP was determined for sediments at 58 cm depth (Ballouche & Neumann, 1995). Considering that the Mare d'Oursi lake-bed is composed of cracking clays with 40-cm-deep fissures during dry season lake recession, and given that

Balanites flowering occurs in the dry season, it is quite possible that recently deposited *Balanites* pollen has infiltrated lower strata. Local oral history suggests that most of the *Balanites* increase has occurred within the lifetimes of living elders.

Currently, there is a striking visual juxtaposition of dense stands of *Balanites* and acacia thornscrub in the Oursi valley and very large, fallen, dead trees (especially *Ficus sycamorus* L. and baobab). Indigenous oral histories from northern Burkina Faso report the occurrence of numerous large trees on stable dunes prior to the droughts of the 1970s (Rasmussen *et al.*, 2001). Cultivated parklands with baobabs and large *Faidherbia albida* (Delile) A. Chev. trees were present on the dunes at mid-century, although most of the trees have since died. A few large specimens can still be seen on the dune flanks and near the edge of the mare. Aerial photographs from 1955 and 1981 show that the dunes became active during the droughts, accelerated by intensive livestock activity that can be seen in a dense network of trails radiating from the lake (Lindqvist & Tengberg, 1993). More recent aerial photographs (1995) show that the dunes have now been heavily colonized by grasses and Sahelian shrubs, especially *Leptadenia pyrotechnica* (Rasmussen *et al.*, 2001). Currently, *Balanites* and *Prosopis juliflora* (Sw.) DC. thorn scrub near the base of the Oursi dunes form impenetrable thickets in some places.

The disappearance of Sudanian and Guinean species and their replacement by Sahelian species has been reported in studies comparing current species distributions with indigenous oral histories in Senegal (Gonzalez, 2001) and across the Sahel zone (Gonzalez *et al.*, 2004). Some researchers have argued that human over-exploitation of plant resources is more important than drought in accounting for tree mortality and species disappearances (Mahamane & Mahamane, 2005; Wezel & Lykke, 2006). This may be locally true, especially in proximity to villages, near urban centres or along transhumance corridors (annual livestock migration routes). However, an examination of species ranges in relation to rainfall shifts shows fundamental climate-related changes.

Significance of rainfall shifts for parkland savanna viability

Mean annual rainfall at the northern limit of *Vitellaria paradoxa* occurrence in Mali (representing the Sudanian parkland system) decreased by more than 100 mm between the periods 1930–1965 and 1966–2000. The drop in precipitation straddles the 600-mm mean annual rainfall line (Fig. 2a). Sankaran *et al.* (2005), in a review of 854 savanna sites in Africa, noted that woody cover increases linearly up to 600-mm mean annual rainfall, with a potential for maximum cover attainable at 650 ± 134 mm, barring disturbance. As 600–650 mm mean annual rainfall is considered the lower threshold of the Sudanian vegetation zone (Le Houérou, 1989), the late 20th century climate shift therefore has tipping-point ecological significance along the Sudano-Sahelian transition zone.

Palynological records show alternating periods of expansion and contraction of the Sahara and the equatorial rain forest, with savanna at times covering most of the current Saharan region (Adams, 2008). The presence of succulent euphorbias on rocky outcrops in the Sudanian zone and the sporadic occurrence of other xerophytic species indicates a mix of species left behind during a dynamic climatic past. 'Poleward' geographic range shifts have been noted in subtropical and temperate areas of both the Northern and Southern hemispheres, as heat-sensitive species respond negatively to warming at lower latitudes, for example *Aloe dichotoma* Masson in the Namib Desert of south-western Africa (Foden *et al.*, 2007). In tropical Africa, vegetation should contract towards the equator in response to reduced rainfall and higher temperatures in the arid belts that flank the humid equatorial zone.

Given a southward shift in West African rainfall isohyets, one would expect that the northernmost tree populations in a given species' range would be exposed to stresses that exceed the taxon's environmental tolerance, giving rise to mortality along the so-called 'trailing edge' of the migrating population (Davis & Shaw, 2001) – which could also be seen as the inadequately adapted leading edge of an earlier migration moving in the opposite direction. The area affected by climate change should include at a minimum the populations occurring in the zone between the rainfall isohyet of the previous northern range limit and the new latitudinally displaced isohyet. Because Sahel droughts involve greater temporal and spatial variability in rainfall as well as lower mean annual precipitation (Nicholson, 2000), acute moisture and heat stresses may be experienced by tree populations still receiving the putative rainfall minimum for the species. These stresses may not necessarily have an immediate effect on mature, established trees, but recruitment and stand rejuvenation could be greatly affected.

Vitellaria parkland in the Sudanian zone is typically contiguous with forest and transitional areas containing *Vitellaria* trees among other ligneous species. In contrast, mature *Vitellaria* trees in the drier Sudano-Sahel zone parklands stand virtually alone, with *Vitellaria* infrequent or absent in the surrounding landscape (Fig. 6a). This pattern fits with the well-documented 650-mm mean annual rainfall requirement for closed canopy woodland in Africa (Sankaran *et al.*, 2005). Below this threshold, forest is no longer present. Without forest, natural regeneration of indigenously managed parklands does not occur, because the system relies on the incorporation of young trees from the fallow–forest cycle.

Persistent false impressions

The current senescence and regeneration failure of parkland trees along the northern edge of species distribution ranges reflects the extension of an economically successful anthropogenic ecosystem into higher risk areas. From a map standpoint, the southward movement of rainfall isohyets is overtaking the northern range of economic tree species that have historically been extended as far into the dry regions as possible.

This pattern is in some sense the reverse of the prevailing view since colonial times, that the human population of the

Sahel is degrading the natural flora (Ribot, 2001; Duvall, 2003). Critical aspects of African savanna assemblages were noted by colonial scientists, but unfamiliarity with indigenous practices and landscape history resulted in some erroneous conclusions (Fairhead & Leach, 1995; Ribot, 1999). The influential French forester and ecologist André Aubréville, who is widely credited with coining the concept of desertification, stated:

> 'The typical African landscape of wooded savannahs is artificial, except in the desert borderland areas. It has come into existence from the effects of fire and clearings on the old, dense, close-canopied high forest…All the forests which in the past covered the arid regions of Africa with a huge unbroken mantle have today ceased to exist…Deforestation of Africa is going on now as it has been for ages past. At present we are witnessing the finishing touches to a process which probably started before the dawn of history and which reached a climax during the unknown era when the first great invasions of man into Africa took place. Man has set fire to the forest for the same reason that he has hunted, in order to be able to survive in the midst of a hostile nature. By destroying indiscriminately, however, he has only added to the difficulties a tropical climate imposes…'.
>
> (Aubréville, 1947)

The anthropogenic element that Aubréville feared was indeed present, but in a different form, as humans settled the landscape and developed an agricultural system based upon altering tree spacing and species composition to promote a synergy of cereal and perennial tree crop production. Aubréville recognized that the savanna was anthropogenically altered on a vast scale, but failed to perceive that the alteration was both highly discriminate and economically advantageous.

The climate-driven disappearance of mesic species in the Sahel has certainly been exacerbated by human over-exploitation of plant resources in many areas, including the effects of livestock as well as direct human use. Some Sahelian or Sudano-Sahelian species, which would otherwise be well adapted to reduced rainfall conditions, are also in decline in localized areas as a result of anthropic overuse, for example *Acacia senegal* at Oursi. Tree felling for fuel-wood, construction and household purposes, especially in and near expanding urban centres, can result in the local elimination of heavily targeted species. The declining importance of the parkland agroforestry system in the modern economy may also contribute to the willingness of villagers to fell trees that in an earlier era were more valuable to them alive. Despite the substantial impact of human and livestock pressure, the overall trend strongly indicates a climate-driven vegetation shift. In contrast to the perception that man is destroying the woody vegetation of the Sahel, the data suggest that an anthropogenic ecosystem is being replaced by flora more suited to the current dry conditions.

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SUPPORTING INFORMATION

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

Appendix S1 Savanna parklands and relict tree systems in the Sahel.

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