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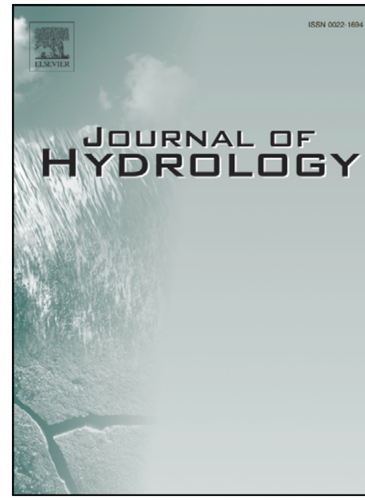

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Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali)

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Abstract

The patterns of the changes in woody plant population densities, size and species composition is documented and discussed for 24 rangeland sites monitored from 1984 to 2006 in Gourma (Mali). The sites are sampled along the North-South bioclimatic gradient on each of the main soils and levels of grazing intensity. Site woody plant populations range from extremely sparse on shallow soils, to scattered on sandy soils, to open forest in temporarily flooded clayed soils, and to narrow thickets on hard pans. Three different methods contributed to assess and monitor woody plant density and canopy cover.

In the short term woody populations were struck by the 1983-84 droughts irrespective of their edaphic situation and location along the bioclimatic gradient. Drought induced mortality was not more severe under drier climate within the Sahel gradient but occurred sooner after drought in shallow soils, and with a lag of a year or two on flooded clay soils. No evidences were found of higher mortality rates in stands with history of intense grazing. Although rainfall remained below average for a decade after the drought, active recruitment of woody plants occurred in all sites starting as soon as 1985. Recruitment proceeded by successive cohorts, often with short-living perennial undershrubs and pioneer shrubs settling first. *Acacia* species were among the first to settle or re-establish, especially on the sites most intensively grazed. The release of competition due to drought induced mortality and to the reduction of herbaceous cover contributed to the success of the recruitment. The species composition change that resulted could first be interpreted as a shift toward a more arid tolerant flora, then some diversification occurred since the mid 90's that could indicate a possible return to previous composition in the long term, confirming the resilience Sahel vegetation.

Keywords: Sahel, Mali, climate change, drought, woody plant population, vegetation dynamics, tree recruitment, resilience.

Introduction

In the Sahel that extends over 6000 km East-West at the southern edge of the Sahara, two catastrophic droughts occurred in 1972-73 and in 1983-84 within a dry period of 25 years, from 1968 to 1993, which followed a relatively wet period of 20 years from 1948 to 1968 (Nicholson, 2001). Since 1994, rains fluctuate up and down the century average (Frappart et al. this issue) at least in eastern and central Sahel (Nicholson, 2005). Both droughts had severe impact on the vegetation, crops, livestock and rural populations. Alarming reports of massive mortality of woody plant populations are made through out Sahel (Boudet, 1972; Poupon, 1980; Sinclair and Fryxell, 1985; Miehe, 1998; Andersen, 2007) associated to warnings of severe risks of diversity losses (Larwanou and Saadou, 2005). The woody plant decimation is attributed to the climatic droughts or to their impact on water tables. It is also imputed to natural resource management by rural populations with increased tree pollarding to feed hungry livestock (Breman and Cissé, 1977), cutting trees for fuel, construction and clearing for expending crop lands, especially in low lands (Lykke, 2000). Deforestation and soil erosion being major components of Sahel desertification, large efforts are locally invested in tree planting and contours building (Sumberg and Burke, 1991). However, since the 80's, some observations report contradictory evidence of strong regeneration of the woody populations (Boudet 1979; Couteron, 1997). Yet the amplitude, spatial extension and species composition of the post drought regenerations remain questioned. Unlike with herbaceous annuals (Hiernaux et al. this issue), the study of woody plant dynamics requires monitoring over large areas because of the low density and patchy pattern of populations, and because of the large size of some individual plants. The monitoring should also be conducted over several years or decades to cope with the long life cycle of most woody plants and the suspected sensitivity of their demography to rare events (Breman and Kessler, 1995).

The monitoring of 24 rangeland sites in Gourma (Mali) from 1984 to 2006 documents the pattern of the changes in woody plant population density, size, mass and species composition. Sites are sampled along the North-South bioclimatic gradient (Fig. 1) on main soils and levels of grazing intensity in order to represent the rangelands encountered across the region. The sites were initially described in 1984, and regularly monitored till 1993 (Table 1) to assess the impact of the 1983-84 droughts on forage resources available in this region of Sahel (Hiernaux et al., 1984; 1993). The monitoring was resumed from 1998 onwards to study the ecosystem response to climate changes in the framework of the AMMA project (Redelsperger et al., 2006; Mougin et al. this issue).

This papers aims at describing the woody populations of 32 rangeland sites in Gourma (Table 2) and analysing population dynamics in response to droughts on a subsample of 24 sites. Trends in woody plant populations are discussed and related to rainfall variations, taking forestry, pastoral and crop management into account. The interpretation of population dynamics also relies on the woody plant phenology monthly monitored for the main species on 13 of the rangeland sites (Hiernaux et al., 1994). A first hypothesis guiding the analysis is that the impact of droughts is more severe under drier climate, thus toward the north of the transect; and also in drier edaphic situations, thus more severe in shallow than in deep soils, and in coarse textured than in fine textured soils (Grouzis, 1988; Dembélé et al., 2006) or the reverse: more severe on fine textured than on sandy soils (Scholes, 1985). A complementary hypothesis is that woody plant populations suffer more from drought when subjected to heavy browsing by livestock or pollarding, which intensity has increased due to the desperate search of additional fodder by the herders facing drought (Bille, 1977; Hillerislambers et al., 2001). Another hypothesis highlighting the competition for water predicts that woody plants suffer more from drought if herbaceous plants do grow and use a large fraction of the soil moisture

(Knoop and Walker, 1985; Belsky, 1994; Akpo and Grouzis, 1996; Scholes and Archer, 1997; Picard et al., 2005).

Material and methods

The Gourma region and the Sahel bioclimate

Rainfall, soil and woody population data from 1984 to 1995 are provided by the ILCA (International Livestock Centre for Africa) and IER (Institut d'Economie Rurale) research project data base (Hiernaux and Diarra, 1993), while data from 1998 to 2006 are recorded under the long term observation program of the AMMA (African Monsoon Multidisciplinary Analyses) research project (Redelsperger et al., 2006; Mougin et al., 2008). Historical rainfall data are provided by the Mali meteorological service. Sites are sampled in four bioclimatic groups set along the South-North climate gradient in Gourma (Fig. 1 and Table 2). The gradient spans over most of the Sahel bioclimatic zone (Le Houérou and Popov, 1981) with a gradual decrease of mean total rainfall with latitude from 500 mm rainfall to the South, at the Burkina Faso border, to 150 mm to the North, by the Niger River close to Gourma Rharous (Frappart et al., this issue). The climate gradient is chiefly explained by a reduction in the number of rain events occurring over a shorter season, mostly because of the later start of the monsoonal rains (Le Barbé and Lebel, 1997) and secondarily by a reduction of mean size of rain events at the drier end of the gradient (Frappart et al. this issue).

Within each bioclimatic group three main edaphic situations are sampled: deep sandy soils, deep loamy-clay soils, shallow soils on rock or hard pans (Table 2). On the sandy soils that extend over about half the landscape (Kammerud, 1996), three level of grazing intensity are systematically sampled: low, medium and high (Table 3). Grazing intensity is determined by the proximity, size and seasonal duration of neighbour water points and associated villages and encampments. Grazing intensity is systematically high in sites with deep loamy-clay soil because they are close to water points, at least temporary pools, while grazing is generally low in shallow soil sites because of the poor forage resources offered.

Woody plant population record methods

Three different methods are used to monitor the woody plant populations depending on years and sites (Table 1). The aims of the three methods differ but they all contribute to assess some parameters of the woody plant population: plant density, crown cover, projected crown cover, foliage and wood masses, species composition. Plant species are named according to the Flora of West Tropical Africa second edition (Hutchinson and Dalziel, 1954-1972).

Crown Linear Intercept method (CLI). The linear intercept method initially aimed at studying the influence of woody plants on the herbaceous layer. As the herbaceous layer is stratified and sampled along the 1000 m long and 1m large linear transect (Hiernaux et al., this issue), woody plants which crown overcast the transect line are recorded with the exact position and length of the crown intercept with the transect line. The sum of these intercepts provides an estimate of the site canopy cover and projected canopy cover depending if crown overlaps are accounted for or not. The species name, height, longest and perpendicular crown diameters, and the base (avoiding bottom when it is swollen) circumference of the trunks of each of woody plant intercepted are recorded. Fast to record and needed to analyse impact on herbaceous distribution anyway, crown linear intercept records were carried out almost every year from 1984 to 1990 (*n=24* sites), in 1993 (*n=19*) and again in 2005-06 (*n=22*), (Table 1).

Circular Plots Census method (CPC)

This method was initiated in 1988 to better assess woody plant density contributing together with allometric functions established by species (Cissé, 1980) to the assessment of wood and foliage masses. It is a straightforward method that consists in recording the species name and size parameters (height, crown diameters, number and base circumference of the trunks) of each individual found within a set of 4 circular plots centred 200 meters apart along the 1000m linear transect that define the site (Hiernaux and Gérard, 1999). Because woody populations largely differ in densities, the radius of the circular plots is adapted to the expected (by visual estimate) density. The target is to ensure a minimum sampling of 10 individuals per plot, so a total of 40 per transect for each category of woody plants recorded separately. As a result, plot sizes used to record woody plants in Gourma sites range from 312 to 10 000 m². When the plant types or species that compose a population at a site contrast strongly by their sizes, densities or distribution patterns, they are recorded in two categories separately, i.e. on two series of plots of different sizes centred on the same points. Such circular plot census were performed on most of the Gourma sites (Table 1) at least once between 1988 and 1990 (*n=24*), once between 1993 and 1995 (*n=22*, sites 37 and 38 are missing) and once recently between 2002 and 2006 (*n=23*, site 22 is missing). Plot means and standard deviations are calculated for density, height, canopy cover (both total and projected thanks to the systematic record of the fraction of crown overcast by any other crown), basal areas by species, plant types, and for all woody plants.

<u>*Distance from Point Centred Quadrant method (PCQ)*</u>

The PCQ method was initiated in 1988 in parallel with the CPC. It aims assessing woody plant density especially when plant distribution is patchy, which question representativeness of the samples described with the CPC method (Engeman et al. 1994; Picard and Bar-Hen, 2007; White et al., 2008). In the PCQ method, the plant density of individual species or plant type is estimated by the mean distance of the closest individual to sampling points (20 or 10) taken systematically every 50 or 100 meters along the transect depending on plant density . At each sampling point, mean distance is calculated between the shorter distances measured for each four quadrants defined by the linear transect and the line perpendicular to transect line at the sampling point (Cottam and Curtis, 1956). The four individuals for which the distance is measured are described as in CPC: species name, height, crown perpendicular diameters, base circumference of trunks. As in CPC woody plants are recorded in two categories, i.e. two series of distances measured in same quadrants for the same series of points, when plant types or species contrast strongly by their sizes, densities or distribution patterns. For each category, the woody plant density (D) i.e. the number of individuals per unit area (ha) is estimated following two alternative algorithms:

(3) $D_1 = \frac{10000}{\bar{d}^2}$ with $\bar{d}$ the mean distance in the 4 sectors (Cottam and Curtis, 1956).

(4) $D_2 = 10000 \frac{4(k\,n - 1)}{\pi \sum_1^n \sum_1^k d_{ij}^2}$ with d_{ij} the distance (m) in the k (j =1 to 4) sectors, n (I =1 to n) the number of sampling points (Pollard 1971).

The PCQ method has been applied to most of the Gourma sites once in 1988 (*n=17*) and once recently in 2005-2006 (*n=20*), (Table 1). Site canopy cover by species, plant types, and for all woody plants are derived from respective density and mean crown area.

Results

Contrasted woody plant populations of Sahelian rangelands

The woody plant populations of 25 sites differ strongly in density, size of individual plants (Table 3) and species composition. They range from extremely sparse low shrub stands on shallow soils, to scattered stands of shrubs and low trees on sandy soils, to open *Acacia* or *Anogeissus* forest in temporarily flooded clay soils, and to the narrow and dense thickets of the 'tiger bush' on hard pans (Nasi and Sabatier, 1988). Indeed, site canopy cover of woody populations on shallow soils at most reaches 1% with plant density inferior to 50 ha^{-1}, except on the tiger bush type of vegetation in which the distribution extremely patchy. In tiger bush woody plants are organised in facieses that alternate along the gentle slope: extremely open stands on impluvium (0.4 ± 0.2% canopy cover with 21±12 plants ha^{-1}) covering 90% of site area at Ortondé site (# 22) and dense thickets (124.3 ± 61.1% canopy cover with 1568 ± 583 plants ha^{-1}) covering 10%, resulting in weighed averages of 12.8% canopy cover and plant density of 176 ha^{-1} (Hiernaux and Gérard, 1999). The woody plant populations in valleys and depressions with loamy-clay soils are taller and denser than on shallow soils as they benefit from run-off water and deep fertile soils (# 9). The distribution of woody plants in valleys is also very patchy with large extents almost deprived of woody plants either at the edges of the valley or else in the deepest part of the depressions with temporarily flooded cracking clay soils. On the other hand, dense and narrow thickets are found along streams and around pools, and open forests occur in temporarily flooded plains with clay soils such as the *Acacia seyal* (# 20, 21) or *Acacia nilotica* (# 7, 15) dominated forests. Woody populations on sandy soils present intermediary traits both in distribution pattern, plant density and canopy cover. Indeed, the canopy cover of monitored sandy soil sites averages 4.3 %, and plant densities 127 ha^{-1} with the low and aphyllous shrub *Leptadenia pyrotechnica* accounting for 1.8% cover and 63 plant ha^{-1} in average but highly variable proportions from site to site (Table 3). Moreover, the distribution pattern of woody plants range from apparent random (# 1, 4, 6, 10, 12, 18, 30, 31, 38) with coefficient of variation of between mean canopy cover and plant density equal to 20.7 and 20.3 respectively, to patchy distribution in relation with the repetitive pattern of dune and inter-dune (# 5, 14, 17, 25, 37) with corresponding coefficient of variations equal to 42.0 and 26.9%.

The dynamics of the canopy cover from CLI records

When canopy cover assessed in CLI records are analysed for all sites together there is an overall trend over years. Canopy cover first decreased from 1985 to 1988, then increased slightly from 1988 to 1993, and increased markedly from 1993 to 2006 as indicated by the regressions established for each pairs of canopy cover data (Table 4). When the trends are analysed per site and per species within site (Fig. 2) three main behaviours are observed:

- In a majority of sites (12 out of 22) canopy cover decreased in the years following the 1983-84 drought till 1993-95 due to extensive tree mortality. The canopy cover kept decreasing between 1993 and 2006 in four of these sites. These four sites include three of the four shallow soil sites (# 8, 22, 28) and one of the heavy grazed dune (# 31, Fig 2f). In that later site the woody plant population was initially dominated by a stand of *L. pyrotechnica* shrubs that developed following the 1973-74 drought and progressively thinned out from 1984 onwards. In the eight other sites canopy cover increased during the last decade, including sites on ungrazed but regularly burned sandy soil (# 30,Fig. 2e), heavily grazed dune (# 14), shallow soil (# 16, Fig. 2a) and clay soil (# 21, Fig. 2d).
- In a minority of sites (7 out of 22), canopy cover maintained itself following the drought in spite of selective mortality affecting the more sensitive species such as *Acacia senegal* or senescent individuals. The cover then decreased in the last decade in two of these seven sites (# 5 on sand dunes and neighbour # 2 in a clayed plain) and maintained itself on the others three with sandy soils and very sparse woody populations (# 6, 10, 12), and on two with dense mature stands of *A. seyal* (# 20) or *A. nilotica* (# 15) on temporarily flooded clay soils.
- In the three last sites (17, 18, 19), all on sandy soils, canopy cover increased rapidly following the drought, due to the strong encroachment of *L. pyrotechnica* that more than compensated the mortality of pre-established woody plant species, especially *A.*

senegal, *Combretum glutinosum* and *Guiera senegalensis* (Fig. 2b, 2c). Canopy cover further increased during the last decade in the almost pure stand of *L. pyrotechnica* (# 19), while it decreased slightly in the more diverse stands (# 17, 18) as the initial population of *L. pyrotechnica* thinned in part due to wild fires.

Woody plant densities from CPC and PCQ records

Although the first observations by CPC and PCQ were performed four to five years after the 1983-84 drought, the distinction of alive from dead plants in the records done in 1988-89 document the wave of woody plant mortality that resulted from the drought (Table 5). The proportions of dead woody plants vary largely between sites, and between species at each site. Actually, the wave of mortality affected all sites including sites in which no dead trees were recorded in 1989 (# 12, 18, 31), but with different timings and intensities. Among the faster and more intensively struck woody populations were the tiger bush and very sparse shrubby vegetation on shallow soils (# 8, 16, 22), but also the sparse *C. glutinosum* and *Acacia ssp.* dominated stands on sandy soils all over the bioclimatic gradient (# 1, 4, 5, 6, 10, 12, 14, 17, 18, 25, 30, 37, 38). Tree mortality was locally high in some of the open forest on clay soils in low lands (# 2, 9, 15, 20, 21), but occurred with one or two year lag after the drought as observed in the *A. seyal* mature stand (# 20, 21).

Because of the four year gap between the drought and the first record, the drought induced mortality does not always translate in a decrease of the overall woody plant density between 1988 and 1995. Indeed, after a wave of mortality, the drought was followed by active recruitment of woody plants in most sites. The recruitment started as soon as 1985 or 1988, explaining for the increase in plant density, followed by a slower increase in canopy cover (# 6, 14, 17, 19, 21; Fig. 3c, 3d). The trends observed on total plant density and canopy cover between 1988 and 1993 result from the combination of the wave of mortality and the recruitment. However, the exact timing and the magnitude of tree mortality and recruitment vary between sites (Fig. 3 and 4). It explains, for example, the sharp increase of plant density and slower increase of canopy cover observed from 1988 onwards on some clay soil (# 21, Fig. 3c, 3d) and sandy soils (# 6, 14, 19, 17; Fig. 4c, 4d).

Woody plant recruited mostly from new seedlings often for a few species only. The seedling species are either already established in the stand or relatively short life cycle species that may have been present in the stand but in very small numbers and suddenly recruit massively and are thus considered pioneers. Among the most prominent pioneers, *L. pyrotechnica* recruits actively on sandy soils, especially in the district of Hombori (# 17, 18, 19) and more recently further north (# 3, 6, 14). *Calotropis procera* recruits on more loamy or clayed soils (# 9, 16, 22, 28, 40) and in the interdune (# 5, 25). While *A. ehrenbergiana* and *Commiphora africana* recruits on shallow sandy-loam soils (# 2, 8, 16, 22, 28). For example, in addition to the 48 ha^{-1} established woody plants on heavy grazed sand soil (# 14), 28 ha^{-1} young *L. pyrotechnica* and 87 ha^{-1} seedlings were recorded in 1989. In some of the sites, the pioneer shrubs succeeded to a population of short-living under-shrubs such as *Chrozophora senegalensis* (# 10, 17, 19, 31), *Aerva lanata* (# 1, 2, 4), and *Sphaeranthus senegalensis* (# 9) that settled just following the drought starting in 1985 and disappeared after a couple of years. The temporary colonisation by *Chrozophora senegalensis* was particularly spectacular on the dune of Hombori Hondo (# 19), starting in 1985 with a peak in 1989 at a density of 4347 ha^{-1} with 4.4% cover and standing dry mass of 217 kg ha^{-1}.

Among the species that were established prior to the drought, thinned out and then recruited actively there are several acacia species: *A. raddiana* in sandy soils (# 1, 5, 6, 10, 14, 17, 18, 31; Fig 4e, 4f), *A. senegal* in loamy sands (# 17, 18, 25), *A laeta* in sandy loams (# 12, 28) and *A. seyal* in clay soil (# 20, 21). The recruitment of *A. seyal* in the stand gaps that resulted from the mortality of adult *Acacia* trees in 1984, developed in three main cohorts which germinated in 1985, 1988 and 1995 as noticed on the records of *A. seyal* densities (Fig. 3d) and distribution in classes of size for canopy area and basal area (Fig. 5) in 1989, 1993 and 2002. *Euphorbia balsamifera* also recruited progressively on sandy-loam soils or shallow sandy soils to the dryer end of the bioclimatic transect (# 4, 5). Some progressive recruitment were also observed for evergreen *Maerua crassifolia* (# 2, 10, 16; Fig. 3a, 3b), *Boscia senegalensis* (# 1, 4, 22, 28), *Maytenus senegalensis* and *C. aculeatum* (# 25, 28, 30; Fig. 4a, 4b), and *C. glutinosum* (# 38). The life duration of the new recruited woody plants depends on species, and could be relatively short with the pioneer shrubs which density already drop between 1995 and 2005 for *L. pyrotechnica* (# 6, 19, 17; Fig. 4c, 4d), *Calotropis procera* (# 40, 16; Fig. 3a, 3b), *Commiphora africana* (# 8, 22) and *Euphorbia balsamifera* (# 5). Thinning also affected some of the other species that recruited, especially *Balanites aegyptiaca* (# 5, 10, 12), *Boscia senegalensis* (# 5, 10) and *A. raddiana* (# 12), but this does not impede the canopy cover to progress.

Discussion

The short term impact of droughts on woody plant populations

In all three edaphic situations, populations were struck by the droughts irrespective of their location along the bioclimatic gradient (Table 5, Fig. 2). The hypothesis that drought induced mortality would be more severe under drier climate within the Sahel gradient, is not verified by the observations. However, the first observations followed the drought with a gap of one to four years and the record of dead individuals may have been incomplete because of some logs were harvested for fire wood or charcoal in the mean time (Benjaminsen, 1996; Andersen et al., 2007), this would lead to an underestimate of wood mortality. Moreover, the survey was only initiated after the second major drought of 1983-84, yet sites had suffered from a major drought a decade earlier that had already decimated woody populations (Boudet, 1972). Although there are evidence that woody populations were struck by the 1972-73 drought all along the Gourma bioclimatic transect (Boudet, 1977; Benoît, 1984), the impact may have been unequal, more severe at the drier end, and this could explain that the second drought is relatively less severe on woody population more severely stuck the first time because of the reduced competition between adult trees that escape the first drought (Mueller et al., 2005), and lower sensitivity of young individuals that established after the first drought (Boudet 1979, Slik 2004).

The results do not support either the associated hypothesis along which drought induced mortality would be relatively more severe in shallow than in deep soils and in coarse texture than in fine texture soils (Togola et al. 1975; Grouzis, 1988; Couteron 1997). However, as already observed by Boudet (1979) after the 1972-73 drought, mortality seems to occur faster in shallow soils followed by deep sandy soils, than in the fine texture soils of low lands. Indeed, the peak of tree mortality in the *A. seyal* stands (# 20, 21) only occurred in the dry season 1984-1985, while it had already occurred the previous year in sandy and shallow soils. However, as for previous hypothesis, a more severe impact of the first drought in edaphically dry situations could have masked the gradient of impact observed during the second drought.

Contrary to observations in Senegal (Bille, 1977; de Wispelaere 1980; Poupon, 1980; Miehe 1998) the woody plant mortality observed in the sandy soil sites subjected to high grazing pressure by livestock (# 6, 14, 31, 37) are not superior to that observed in the other sandy soil sites (Table 5). No evidence was found to support the hypothesis that woody plant populations would suffer more of droughts when subjected to heavy browsing by livestock or pollarding by herders as suggested by Boudet (1979). Yet, not all species are subjected to browsing and pollarding (Piot et al., 1980), and the density of woody plant stands may have been affected by the history of grazing long before the droughts, masking droughts effect by the selection of poor quality browse species. However, the species composition of the woody population of the sites exposed to high stocking rates include high proportions of good quality browse such as *A. raddiana*, *A. senegal*, *A. laeta*, *Balanites aegyptiaca*, which seed dispersion is facilitated by livestock (Le Houerou, 1980). On the other hand, in some of these sites (# 19, 31, 37) the density of woody plants (except *L. pyrotechnica*) is very low, perhaps reflecting the effect of a long history of high pastoral use or ancient clearing for crops (Fig. 2f, 4e, 4f).

The mid term impact of droughts on woody plant populations: stand recruitment

Although rainfall remained below average several years after the drought, active recruitment of woody plants occurred in most sites (Fig. 3 and 4). This recruitment often started as soon as 1985 or 1988, by new seedlings in successive cohorts. This recruitment first increased woody plant densities, while canopy cover was still decreasing at many sites, and only contributed to enhance canopy cover from the 90's onwards. In most sites, only a few species contributed to recruitment, at least to the first cohorts (Miehe, 1998). Among the first settlers, a number of short-living perennial undershrubs and tussock grasses and sedges, colonized temporarily some of the sites (Hiernaux and Le Houérou, 2006). *Chrozophora senegalensis* and *Aristida sieberiana* established at the edges of deflation patches on sandy soils recently eroded by wind as a consequence of two consecutive years of soil denudation because of the drought, while *Colocynthis vulgaris*, occasionally biannual, and *Cyperus jeminicus* helped trapping sands of the micro-dunes as already observed by Boudet following the first drought

(1977). Temporary colonization by short-living perennial also extended to other soil types in some sites, with *Aerva lanata* on sandy loam soils and *Sphaeranthus senegalensis* on clay soils. Simultaneously, the first cohorts of pioneer shrubs settled, among which *L. pyrotechnica* on sandy soils, *Euphorbia balsamifera* on loamy sands and *Calotropis procera* on all type of soils, are dispersed by wind (Breman and Kessler, 1995). *Acacia* species were among the first to settle or re-establish, especially on the sites the most heavily grazed by livestock. Even if particular changes in soil surface may have facilitated the development of the seedlings of species which seeds are dispersed by wind or by livestock, their simultaneous and wide spread appears as a response to the opening of the woody layer due the drought induced wave of tree mortality. For example, the recruitment of *A. seyal* in the low land clay soil sites only occurred in the gaps made in the previous mature stand by patchy mortality of trees or at the edges of the previous stand. This is in contradiction with the higher seedling density observed at the shade of trees by Akpo and Grouzis (1996) in Senegal.

An additional hypothesis is that the release of competition by the herbaceous could have contributed, as well, to the success of the recruitment (Belsky, 1994; Couteron, 1997; Picard et al., 2005). As indicated previously, the denudation of the soil during the drought, resultant activation of wind erosion and changes in soils surface features, certainly facilitated the installation of pioneer shrubs. The reduction in herbaceous cover due to grazing during the wet season and the trampling by livestock may have contributed also to dense recruitment by *Acacia* species observed in some of the sites submitted to high stocking rates (# 6, 14, 20). This observation is in contradiction with reduction in woody plant, and seedling densities, observed by Dembélé et al. (2006) as distance to water point decreased in a sandy area right to the North of Gourma but agrees with the increase woody plant densities observed by the authors as the distance to the Niger valley is reducing. It also contradicts higher seedling recruitment observed in fenced plots partially of totally protected from grazing in Senegal (Miehe, 1998).

Although, some thinning were observed during seedling development, especially among the pioneer shrub populations, the recruitment overall resulted in an increase in population density and canopy cover despite overall below average rainfall conditions. At the same time, species composition evolved in favour of a limited number of species dominated by the pioneer shrubs, *Acacia sp.*, and species adapted to drier climate such as *Balanites aegyptiaca*, *Maerua crassifolia* and *Commiphora africana*. This trend in species composition could initiate a latitudinal shift in species distribution in response to the reduction in rainfall observed since the late 60's (Breman and Cissé, 1977; Boudet, 1979). However, this shift could also only reflect the relatively dry period during which the recruitment took place. Indeed, the improvement in rainfall observed since the mid 90's triggered the recruitment of species that had not recovered yet from the drought such as *C. aculeatum*, *C. glutinosum* and *Guiera senegalensis* in the southern sandy sites. In shallow soil sites however, the changes in soil surface features and hydric functionning following the drought are so severe (Leprun, 1992; Ichaou, 2000; Leblanc et al., 2007) that the reestablishment of the previous woody plant flora is unlikely.

Conclusion and perspectives

In response to the 1983-84 drought woody plant mortality reduced population density and canopy cover in all Gourma sites irrespective of the soils, topography, grazing pressure and location along the bioclimatic gradient. However, active recruitment of woody plants occurred in most sites starting as soon as 1985 and in spite of below average rainfalls. The recruitment proceeded by successive cohorts, often with short-living perennial undershrubs and pioneer shrubs settling first. *Acacia* species were among the first to settle or re-establish, especially on the sites most heavily grazed. It seems that the release of competition due to drought induced mortality and also to the temporal reduction of herbaceous cover contributed to the success of the recruitment particularly vigorous in the stand gaps and sandy sites subjected to heavy grazing. After twenty years, post drought woody plant recruitment resulted for a large majority of sites in an increase of population density and canopy cover in spite of the overall below average rainfall conditions. The change in species composition that resulted from mortality and recruitment could first be interpreted as a botanic shift toward more arid tolerant species flora, however some recruitment diversification observed since mid 90's could prelude a long term return to previous composition, at least in sites that were not too severely affected by soil erosion. The mid term response to drought of the woody plant population sampled along the bioclimatic gradient in Gourma, on main soils types under an array of grazing pressure conditions, come in support of the resilience of the Sahel vegetation.

In a context of progressive trends and extreme events of climate and land use, the study of woody plant dynamics in Sahel requires that field data be recorded over long series of years. To better understand population dynamics there is need to improve on the data quality and the representativeness of the woody plant population monitored. A critical study of the sampling and observations methods used in woody population monitoring in the Gourma should be conducted. Because of the long time scale on which woody plant population evolves there is also a need to better document local climate and land use histories (fire, clearing for cropping, camp settlement) using interviews and remote sensing tools. Aerial photographs such as the IGN coverage over Gourma in 1954, Corona photos in 1965 should also be used to document past woody population canopy cover and densities. It would, for example, help verifying how far the woody plant decimation following the first drought (1972-73) has conditioned the woody population response to the second drought analysed in this paper.

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Table 1. Calendar of woody plant population records in 24 rangeland sites monitored from 1984 to 2006 in Gourma under three methods: L = crown linear intercept (CLI), C= circular plots census (CPC), Q = Point centered quadrant (PCQ). Grey underlines separate the group of years considered in data analysis.

year	site (code number, description table 2 and 3)																						
	1	2	4	5	6	8	9	10	12	14	15	16	17	18	19	20	21	22	25	28	30	31	37	38
1984	L	L		L				L	L		L		L	L	L	L		L		L	L			
1985	L	L	L	L	L	L		L	L		L	L	L	L	L	L	L	L		L	L	L		
1986	L	L	L	L	L	L		L	L		L	L	L	L	L	L	L	L		L	L	L		
1987	L	L	L	L			L	L	L	L	L	L	L	L	L	L	L	L		L	L		L	L
1988	L C Q	L C Q	L Q	L C Q	L C Q	L	L Q	L C Q	L C Q	L C Q	L	L C Q	L	L	L	L C Q	L C Q		L C Q	L C Q		L C Q	C Q	C Q
1989	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	C	L C	L C	L C	L C		C
1990	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	C	C
1991																								
1992																								
1993	C	C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	L C	C	L C		
1994																								
1995						C						C												
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2000																								
2001																								
2002								C	C	C	C	C	C	C	C	C	C		C	C	C	C		
2003																								
2004																								
2005	C Q	C Q	C Q	C Q	C Q	C Q	C	Q	Q	Q			L C Q	Q	Q	L Q	L Q	L	Q	Q	Q	Q	C	C
2006	L	L	L	L	L	L	L	L	L	L	 Q			L	L				L	L	L	L	L Q	L

Table 2. Sampling grid of 32 rangeland sites monitored in Gourma (Mougin, et al., this issue). The sites are figured by their code number (as in Fig. 1, except site 37 and 38 located at the South West of the area mapped). The woody plant populations of sites # 3, 23, 27, 32, 36, 40, 41, 42 have not been described until 2005 and are thus not included in the analysis of population dynamics that only consider the sites with historical data (codes in bold).

Hydrology ➔		Endoreic systems				Structured watershed	
Top soil texture ➔		Sandy and loamy-sands				Clay, loam	Rock, gravels
Grazing pressure ➔		Low	Moderate	High	Crop	High	Low
Range of annual rainfall (mm)	250-150	**5**	**1**, 3, **4**	**6**		**9**	**2, 8**
	350-250	**10**	**12**, 32	**14**		**15**	**16**, 40
	450-350	**18**	**17, 19**	**31**	41	**20, 21**	**22**, 42
	450-550	**30, 38**	**25**, 27	**37**	23	**28**	36

Table 3. Characterisation of woody plant population in 25 Gourma sites arranged by class of soil texture (Soil), climate aridity (Arid: increasing from 1=south Sahel to 4= north Sahel) and grazing intensity (increasing from 1= light to 4 = intense, 5 = crops, intensively grazed in dry season only). Mean (m.) and standard deviation (s.d.) of the mean canopy cover (%) with or without *Leptadenia pyrotechnica* (L.p.), woody plant density with or without L.p., and basal area without L.p. as calculated from circular plots census done on the indicated year.

Soil	Arid	Graze	Site #	year	canopy cover %				plant density ha^{-1}				basal area m^{-2}	
					all species		without L.p.		all species		without L.p.		without L.p.	
					m.	s.d.	m.	s.d.	m.	s.d.	m.	s.d.	m.	s.d.
Sandy	1	1	30	2002	1.9	0.6	1.9	0.6	36	14	34	12	0.32	0.11
	1	1	38	2005	3.7	0.3	3.7	0.3	17	2	17	2	0.50	0.02
	1	2	25	2002	1.8	0.6	1.8	0.6	118	36	118	36	0.79	0.29
	1	4	37	2005	0.6	0.3	0.6	0.3	8	4	8	4	0,14	0,07
	2	1	18	2002	6.9	1.1	1.5	0.5	182	32	32	5	0.23	0.07
	2	3	17	2005	3.1	0.9	1.5	0.3	106	27	30	9	0.39	0.11
	2	3	19	2002	10.2	1.9	0.0	0.0	173	105	1	0	0.00	0.00
	2	4	31	2002	7.1	1.2	0.8	0.3	237	46	17	8	0.16	0.07
	3	2	10	2002	2.0	0.6	1.8	0.6	85	11	59	10	0.42	0.12
	3	3	12	2002	3.1	0.9	3.0	0.9	30	5	24	5	0.55	0.16
	3	4	14	2002	13.0	6.6	10.5	5.2	672	69	428	139	2.44	1.14
	4	1	5	2005	2.9	1.3	2.8	1.3	36	8	34	8	0.11	0.02
	4	2	1	2005	0.6	0.2	0.5	0.2	25	2	12	2	0.11	0.07
	4	3	4	2005	2.1	0.4	2.0	0.4	45	10	40	8	0.33	0.19
	4	4	6	2005	5.5	0.8	5.3	0.7	132	43	108	38	0.89	0.15
Shallow	2	2	22	1993	12.8	-	12.8	-	176	-	176	-	1.70	-
	2	2	40	2005	0.7	0.3	0.7	0.3	15	5	15	5	0.20	0.14
	3	2	16	2002	0.6	0.2	0.6	0.2	25	4	24	4	0.11	0.04
	4	2	8	2005	0.3	0.2	0.3	0.2	49	19	46	17	0.16	0.07
	4	2	2	2005	1.0	0.1	1.0	0.1	31	2	31	2	0.27	0.04
Clay	1	3	28	2002	10.7	1.4	10.7	1.4	384	66	384	66	2.59	0.47
	2	4	20	2002	32.1	3.0	32.1	3.0	88	16	88	16	5.29	0.64
	2	4	21	2002	89.6	29.1	89.6	29.1	533	269	533	269	7.39	2.31
	3	4	15	2002	22.8	1.8	22.8	1.8	65	8	65	8	6.74	1.07
	4	3	9	2005	3.3	1.0	3.3	1.0	37	13	37	13	0.64	0.13

Table 4. Linear regressions established between the canopy cover of woody plants (Crown Linear Intercept method) in 85 (C85), 1988 (C88), 93 (C93) and 2005-06 (C06), rangeland sites in Gourma (Mali).

Number of sites	Linear regression	r^2
19	C88 = 0.6900 C85 + 1.0318	0.45
22	C93 = 1.0765 C88 + 0.4251	0.88
21	C06 = 1.4692 C93 – 0.7530	0.89

Table 5. Woody plant mortality following 1983-84 drought assessed by the density of living and dead plants (ha^{-1}) observed in 1989 in 24 rangeland sites in Gourma using CPC.

Site N°	Soil texture	Climat aridity	Grazing pressure	Density of living woody plants ha^{-1}		Density of dead woody plants ha^{-1}		Dead plants
				mean	s.d.	mean	s.d.	%
30	Sandy	1	1	35	12.7	9	4.4	20.5
38		1	1	25.5	4.9	5	2.1	16.4
25		1	2	19.5	9.6	0.3	0.3	1.3
37		1	4	7.9	4.3	39.7	5.7	80
18		2	1	70	20.8	0	0	0
17		2	3	17	4	2.5	1.2	12.8
19		2	3	17.8	3.6	0.5	0.5	2.7
31		2	4	116.7	26.6	0	0	0
10		3	2	33	19.5	5	3	13.2
12		3	3	23	4.4	0	0	0
14		3	4	94	40.7	4	4	4.1
5		4	1	62	23.4	1	1	1.6
1		4	2	15	7.2	2	1.4	11.8
4		4	3	36.5	6.2	3	2.4	7.6
6		4	4	46	11.5	21	6	31.3
16	Shallow	3	2	37	31.9	9	7.7	19.6
8		4	2	52	16.6	18.5	8.6	26.2
2		4	2	29.5	8.2	5	0.6	14.5
28	Clay	1	3	125	43.9	3	3	2.3
20		2	4	48	4.6	10	6	17.2
21		2	4	34	9	6	3.5	15
15		3	4	45	5	3	1	6.3
9		4	3	28	6.3	1	0.6	3.4
7		4	4	66	13.2	41	10.1	38.3

Figure captions

Figure 1. Location of the monitored rangeland sites along the bioclimatic gradient and on the main soil types in Gourma, Mali, and on the main soil types. The sites to the North of Niger River and the sites # 3, 23, 27, 32, 40, 41, 42 which woody populations were not described until 2005 are not included in the analysis of the population dynamics.

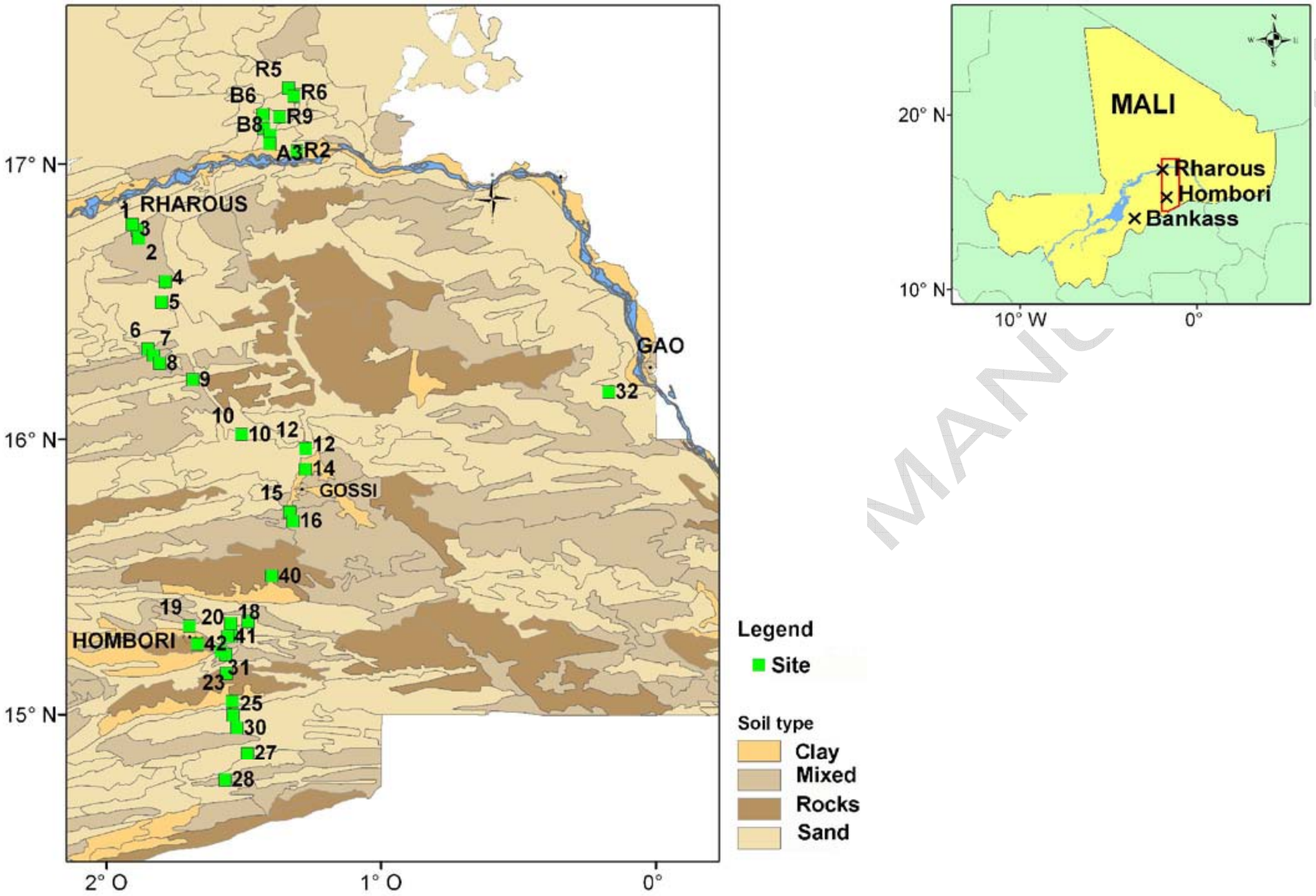
Figure 2. Trends in canopy cover (Cover %) of alive (diamond, solid line) or dead woody plants (square, dashed line) in Gourma sites between 1985 and 2006 as observed with the crown linear intercept method. Example of overall constant (# 16, 17), increasing (# 19, 21) or decreasing trends (# 30, 31).

Figure 3. Trends in canopy cover (Cover %) and in plant density (density ha^{-1}) per woody plant species in Gourma sites from 1988 to 2006, from circular plot census, sites 16, 21.

Figure 4. Trends in canopy cover (Cover %) and in plant density (density ha^{-1}) per woody plant species in Gourma sites from 1988 to 2006, from circular plot census records: sandy soils sites lightly grazed (# 30), moderately grazed (# 17) and intensely grazed (# 31).

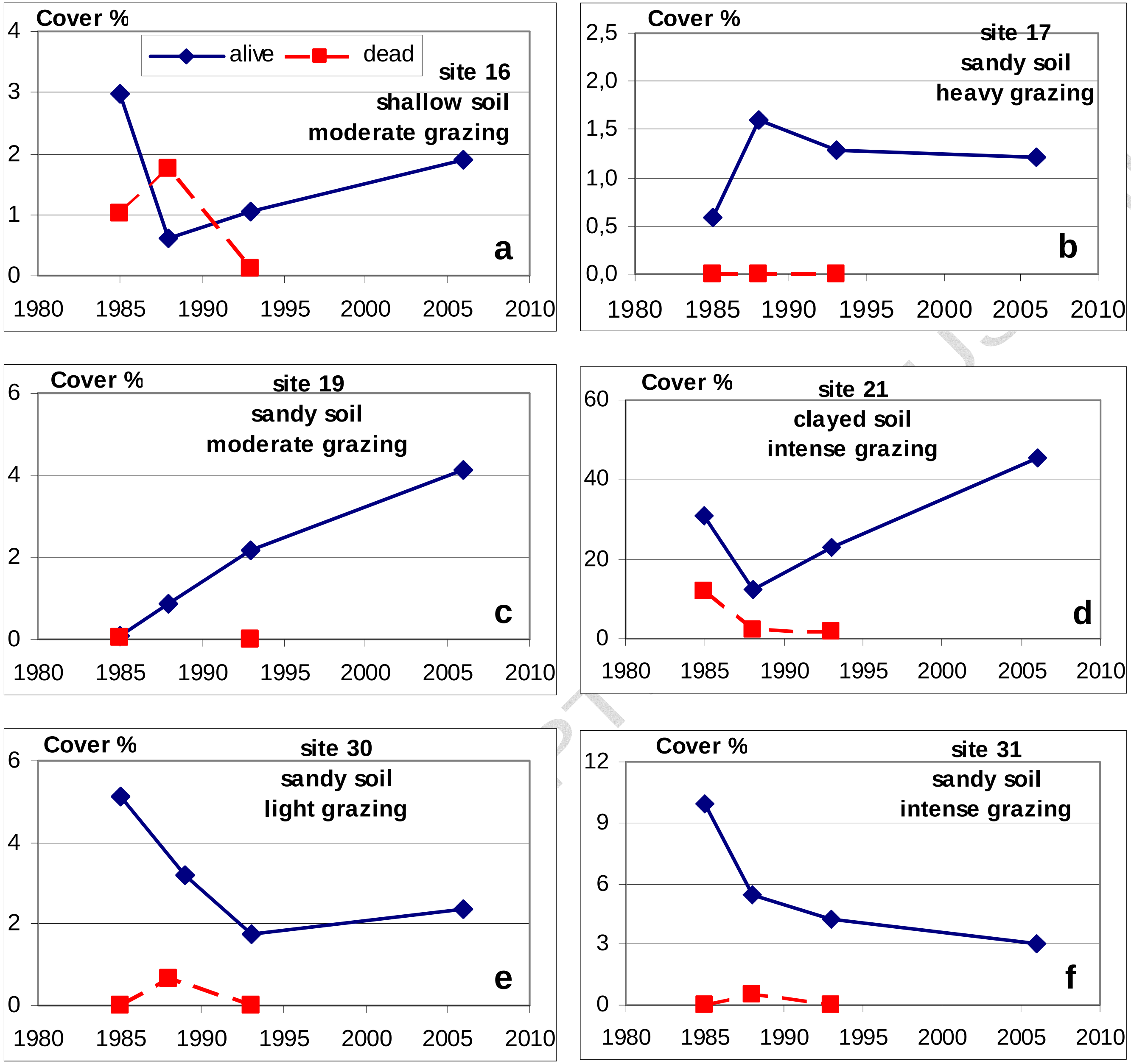
Figure 5. Dynamics over the years 1989, 1993 and 2002 of the distribution of the crown areas in m² (a,b,c) and basal areas in cm² (d,e,f) of the *Acacia seyal* individuals recorded over 1 ha at Kelma (# 21). Histograms figure the frequency distribution (ha^{-1}) while dashed lines figure cumulated distributions (%).

Figure 1.



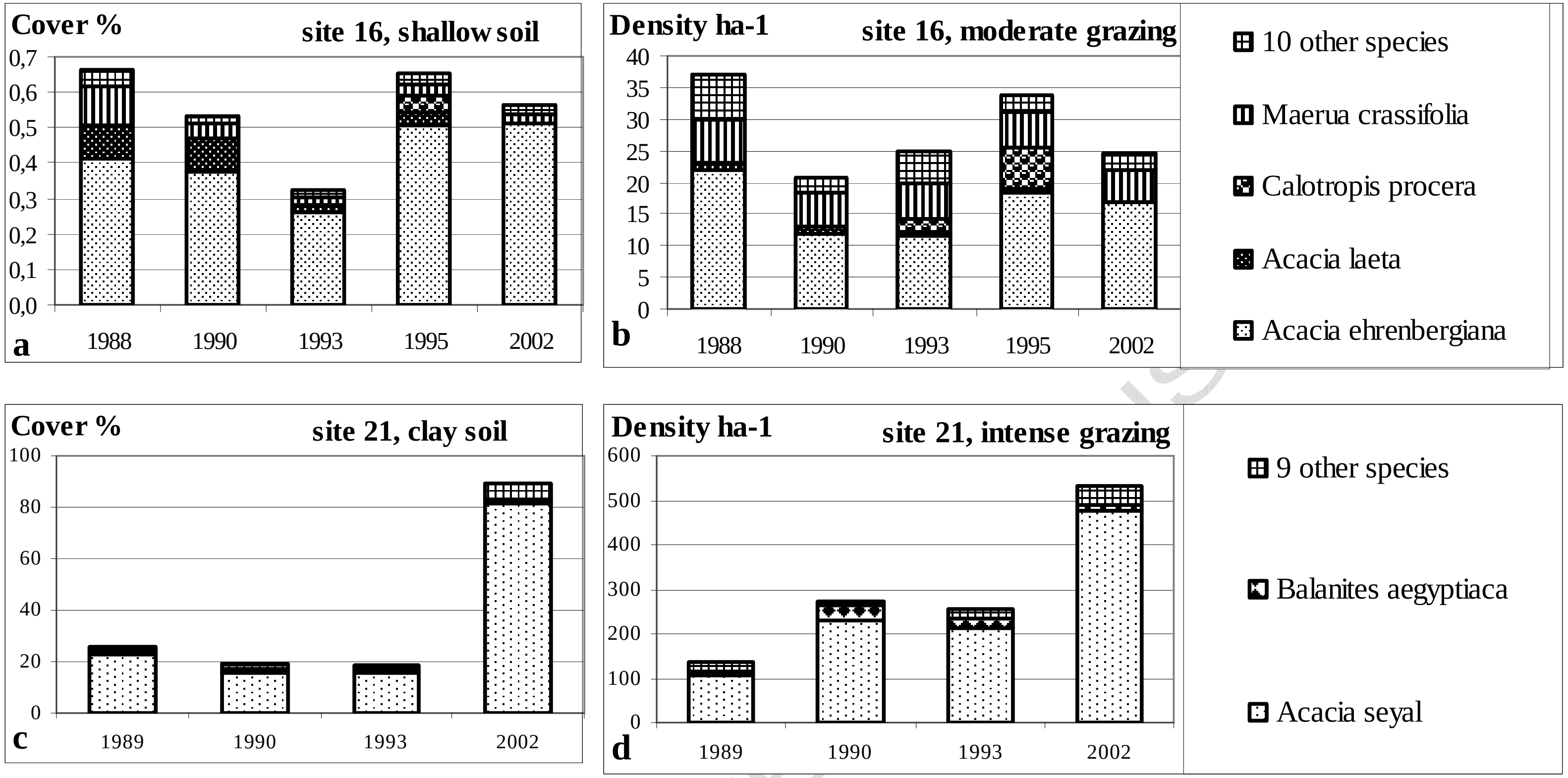
R5
R6
B6
R9
B8
A3
R2
RHAROUS
GOSSI
GAO
HOMBORI
1
2
3
4
5
6
7
8
9
10
12
14
15
16
18
19
20
23
25
27
28
30
31
32
40
41
42
17° N
16° N
15° N
2° O
1° O
0°
Legend
Site
Soil type
Clay
Mixed
Rocks
Sand
MALI
Rharous
Hombori
Bankass
20° N
10° N
10° W
0°

Figure 2



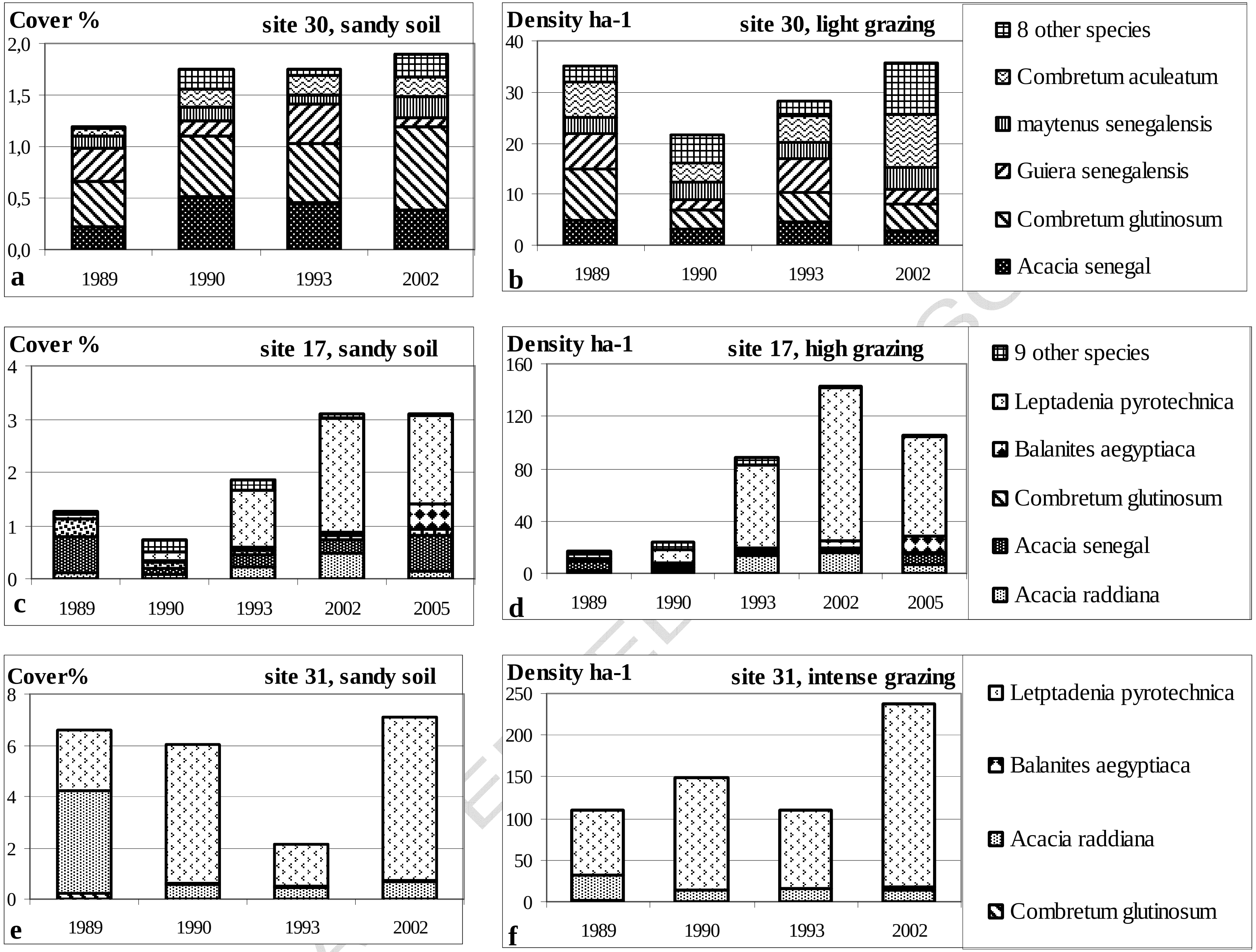
Cover %
alive
dead
site 16
shallow soil
moderate grazing
a
Cover %
site 17
sandy soil
heavy grazing
b
Cover %
site 19
sandy soil
moderate grazing
c
Cover %
site 21
clayed soil
intense grazing
d
Cover %
site 30
sandy soil
light grazing
e
Cover %
site 31
sandy soil
intense grazing
f
1980 1985 1990 1995 2000 2005 2010

Figure 3



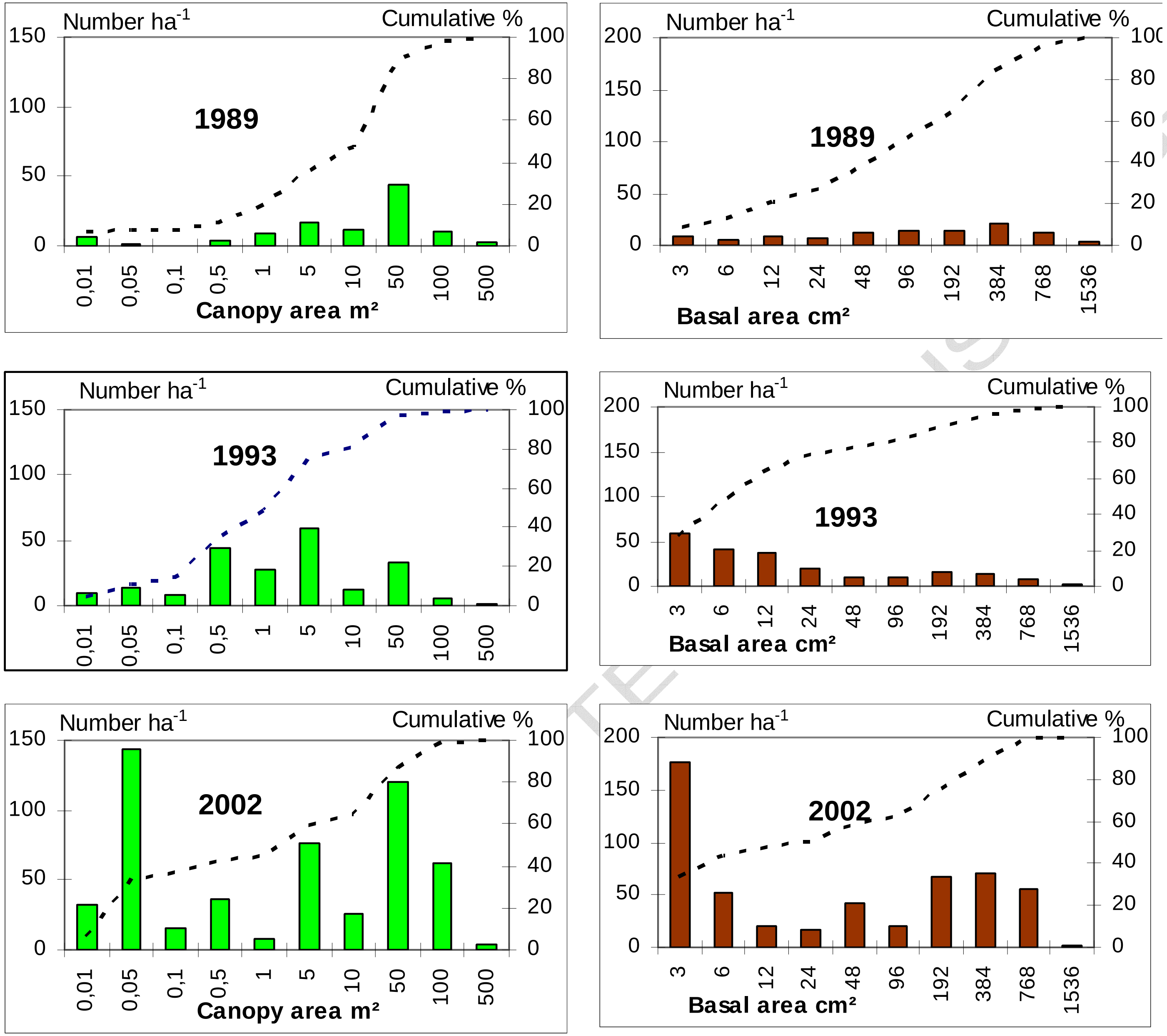
Cover %
site 16, shallow soil
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0,0
a
1988
1990
1993
1995
2002
Density ha-1
site 16, moderate grazing
40
35
30
25
20
15
10
5
0
b
1988
1990
1993
1995
2002
10 other species
Maerua crassifolia
Calotropis procera
Acacia laeta
Acacia ehrenbergiana
Cover %
site 21, clay soil
100
80
60
40
20
0
c
1989
1990
1993
2002
Density ha-1
site 21, intense grazing
600
500
400
300
200
100
0
d
1989
1990
1993
2002
9 other species
Balanites aegyptiaca
Acacia seyal

Figure 4



Cover %
site 30, sandy soil
2,0
1,5
1,0
0,5
0,0
a
1989
1990
1993
2002
Density ha-1
site 30, light grazing
40
30
20
10
0
b
1989
1990
1993
2002
8 other species
Combretum aculeatum
maytenus senegalensis
Guiera senegalensis
Combretum glutinosum
Acacia senegal
Cover %
site 17, sandy soil
4
3
2
1
0
c
1989
1990
1993
2002
2005
Density ha-1
site 17, high grazing
160
120
80
40
0
d
1989
1990
1993
2002
2005
9 other species
Leptadenia pyrotechnica
Balanites aegyptiaca
Combretum glutinosum
Acacia senegal
Acacia raddiana
Cover%
site 31, sandy soil
8
6
4
2
0
e
1989
1990
1993
2002
Density ha-1
site 31, intense grazing
250
200
150
100
50
0
f
1989
1990
1993
2002
Letptadenia pyrotechnica
Balanites aegyptiaca
Acacia raddiana
Combretum glutinosum

Figure 5



Number ha-1
Cumulative %
1989
Canopy area m²
Basal area cm²
1993
2002
0,01
0,05
0,1
0,5
1
5
10
50
100
500
3
6
12
24
48
96
192
384
768
1536