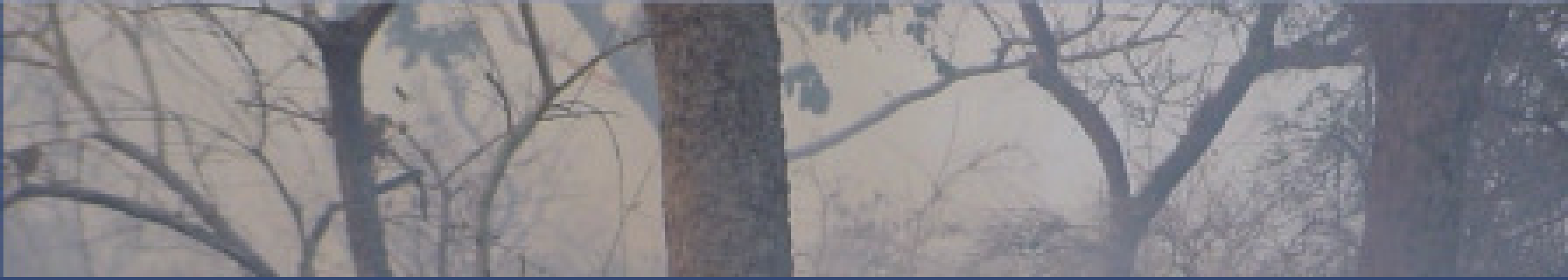

TREE RECRUITMENT IN WEST AFRICAN DRY WOODLANDS

The interactive effects of climate, soil, fire and grazing

Samadori S. Honoré Biaou

TREE RECRUITMENT IN WEST AFRICAN DRY WOODLANDS

The interactive effects of climate, soil, fire and grazing

VESTIGING VAN BOMEN IN WEST-AFRIKAANSE DROGE BOSSEN

De interactieve effecten van klimaat, bodem, brand en begrazing

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Samadori Sorotori Honoré Biaou

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To Fêtani Marc-Antoine

A lifetime passes, whether it is hard or not.

Patience is the remedy.

ABSTRACT

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Woodlands are among the most widespread seasonally dry forests, particularly in Africa. In dry regions, woodland is one of the few vegetation types having significant tree cover, thus supplying most forest products. Unfortunately, woodlands are disappearing rapidly due to the combined effects of unrestrained forest exploitation, increasing and frequent droughts, decreasing soil productivity, and disturbances by fire and herbivores. The scope of this study was to analyze how climate, soil, fire and grazing, and their interactions determine woodland dynamics: i.e. the competitive versus facilitative interactions between plants, the regeneration success of seedlings, and the species composition, richness and structure of woodlands. A broad-scale study was conducted in Benin where extensive examples of woodlands are still found. The results from this study confirmed that woodland dynamics is determined not only by the macro-climate (i.e. water stress), but also by soil-driven abiotic stress (i.e. salinity), disturbances by fire and grazing, facilitative plant-plant interactions, as well as interactions between these drivers. Facilitative plant-plant interactions contributed to successful recruitment in woodlands, and thus to high species richness and diversity at intermediate water stress levels. Disturbances by grazing and fire reduced competitive exclusion at intermediate water stress levels and improved the facilitative interactions among woodland tree species. Climate and soil conditions appeared to switch the direction of fire and grazing effects on tree recruitment and diversity, from positive at low abiotic stress levels to negative at high abiotic stress levels. Based on these results, it is suggested that forest managers should tune woodland harvesting in such a way that trees are left to create favourable conditions for new regeneration and plant nurse trees in degraded and open areas to create better conditions for seedling establishment.

Key-words: Fire, Grazing, Water stress, Woodland, Savanna, Species richness, Tree density, Facilitation, Tree clustering, Soil fertility, Soil salinity, Regeneration, West-Africa, Benin.

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Chapter 1

General introduction

Dry woodland in north Benin

SEASONALLY DRY WOODLANDS

Woodlands are part of the tropical dry forest vegetations that are characterized by precipitation levels below 1600 mm and a dry season of more than 3 months per year (Menaut *et al.*, 1995; Frost, 1996). Woodlands usually co-occur with patches of dense deciduous forest, savanna and steppe, with often sharp boundaries (Bellefontaine *et al.*, 1997). These different vegetation patches differ in structure, with an increasing grass and decreasing tree cover from dense deciduous forest, woodland, savanna to steppe. They are often referred to, altogether, as "seasonally dry forests" (Bullock *et al.*, 1995) or "woodland-savanna mosaics" because of their patchy distribution (White, 1983; Nangendo *et al.*, 2006). The reason for such different vegetation patches in the same region has been attributed to soil productivity and disturbances by fire and herbivores (Menaut *et al.*, 1995; Murphy & Lugo, 1995; Bellefontaine *et al.*, 1997), and by interactions between those factors and the macroclimate (Sankaran *et al.*, 2005). While dry forests as a whole are estimated to cover more than 40 % of the world vegetation (Murphy & Lugo, 1995), of which more than 50 % is on the African continent (Bellefontaine *et al.*, 1997), tropical woodlands cover 4 % globally (Adams & Faure, 1997) of which 60 % is encountered in Africa (Mayaux *et al.*, 2004). African woodlands consist essentially of two core types found in two distinct regions: the *Isoberlinia* woodland found in the northern hemisphere where they form almost continuous blocks from Mali to Uganda between 6-13^{0}N latitude; and the *Brachystegia* woodland also called miombo which covers extensive areas in the southern hemisphere between 5-20^{0}S latitude (Menaut *et al.*, 1995; Bellefontaine *et al.*, 1997; Sokpon *et al.*, 2006). So far, the potential mechanisms responsible for the patchy mosaic structure of woodlands and the associated patterns in species diversity and density are little understood because of the large array of factors affecting them and the complex interactions among those factors (Frost, 1996). In this dissertation, comparative and experimental studies were combined to disentangle such mechanisms to better understand the variation in structure, species composition, and diversity of woodlands, focusing on different vegetation patches across woodland-savanna mosaics and on woodlands along a climatic gradient in Benin, West Africa. The Beninese woodlands studied here belong to the *Isoberlinia* woodland type which is typical of Africa northern hemisphere. This broad-scale study of *Isoberlinia* woodlands is presented, in order to address the following general question: How do climate, soil, fire and grazing, and their interactions influence the competitive versus facilitative interactions between plants, the regeneration success of seedlings, and the species composition, richness and structure of woodlands?

THE DYNAMIC EQUILIBRIUM MODEL

Huston (1979; 1994) proposed a general model explaining species-environment relationships which integrates gradients in resources such as water and nutrients, and in disturbances such as fire and grazing. The interactive effects of disturbances and resources were described using a three-dimensional graphical model called the “dynamic equilibrium model”. The model predicts optimal growth conditions for species at both intermediate levels of stress and disturbances, with stress determined by resource availability and disturbance by events that take away biomass from the system. Huston’s model can be viewed as a synthesis of two existing models, the intermediate disturbance hypothesis (Connell, 1979) and the intermediate stress hypothesis (Grime, 1973; Kammer & Mohl, 2002). The unifying prediction of these hypotheses is that species richness and species diversity display a unimodal relationship with disturbances frequency or intensity and with ecosystem productivity. At low stress level and low disturbance frequency or intensity, competitive dominant species likely exclude others species, what results in lower community diversity. At high stress level and high disturbance frequency or intensity, the community diversity is potentially low because few species can survive under harsh conditions. At intermediate stress levels, higher community diversity is expected because of the overlap between the stress tolerant and stress intolerant species and/or the prevention of competitive exclusion due to the reduction of the species populations by disturbances. Huston's model is appealing in the sense that it integrates both resource factors and disturbances that are considered important determinants of the vegetation dynamics of woodlands (Frost, 1996), and this model can be tested empirically for tropical woodlands, such as those encountered in Benin or other African countries. Most studies on how species respond to resources and disturbances, and how such responses drive species richness and diversity for African woodlands remain descriptive (Menaut *et al.*, 1995; Fairbanks Dean, 2000; Chidumayo, 2001; Mosugelo *et al.*, 2002; Nangendo *et al.*, 2005; Nangendo *et al.*, 2006), or focus on single factors (Frost, 1996; Couteron & Kokou, 1997; Luoga *et al.*, 2004; Sawadogo *et al.*, 2005; Gambiza *et al.*, 2008).

In this thesis, Huston's model was used as a working hypothesis for predicting patterns in plant performance, vegetation structure, species richness of Beninese woodlands in response to soil and climate driven water stress gradients, to disturbances by grazers and fire, and to interactions between those factors (Figure 1). As the importance of the macro-climate in determining species distribution in dry regions has been frequently questioned (Gentry, 1995; Gillespie *et al.*, 2000), the effect of water availability on plant community diversity and species distribution was investigated in chapter 2, and the effect on the regeneration success and coexistence of different tree species in chapter 3. The interactive effects between climate and soil driven water stress and fire and grazing on woodland dynamics are presented in chapter 4, and the interactions between the vegetation structure, fire and tree diversity are shown in chapter 5. While chapter 2 used data from several vegetation types (i.e. dense deciduous forest, woodland, savanna, gallery forest) across woodland-savanna mosaics, all the remaining chapters focused on woodlands. Figure 1 shows how these studies presented in chapters 2 through 5 jointly contribute to understanding the structure, composition and dynamics of the woodlands. In the next section, the predictions for those four chapters and the general approach applied are shortly introduced.

WATER STRESS

The role of water stress as a driving factor in woodlands is not fully understood (Gentry, 1995; Gillespie *et al.*, 2000), probably because it is difficult to disentangle the effect of water stress from other environmental factors such as fire, herbivores and soil (Frost, 1996). In chapter 2, we tested the hypothesis that species richness shows a unimodal relationship with water stress whereas tree density decreases linearly with increasing water stress. The basic idea is that at high stress levels only stress tolerant species are successful, at low stress level few species dominate and exclude others, while at intermediate stress levels species of both extremes co-occur. Here and in the remaining of the thesis, water stress is indicated by the water deficit which is the difference between the mean annual precipitation and mean annual evapotranspiration (Paltineanu *et al.*, 2007).

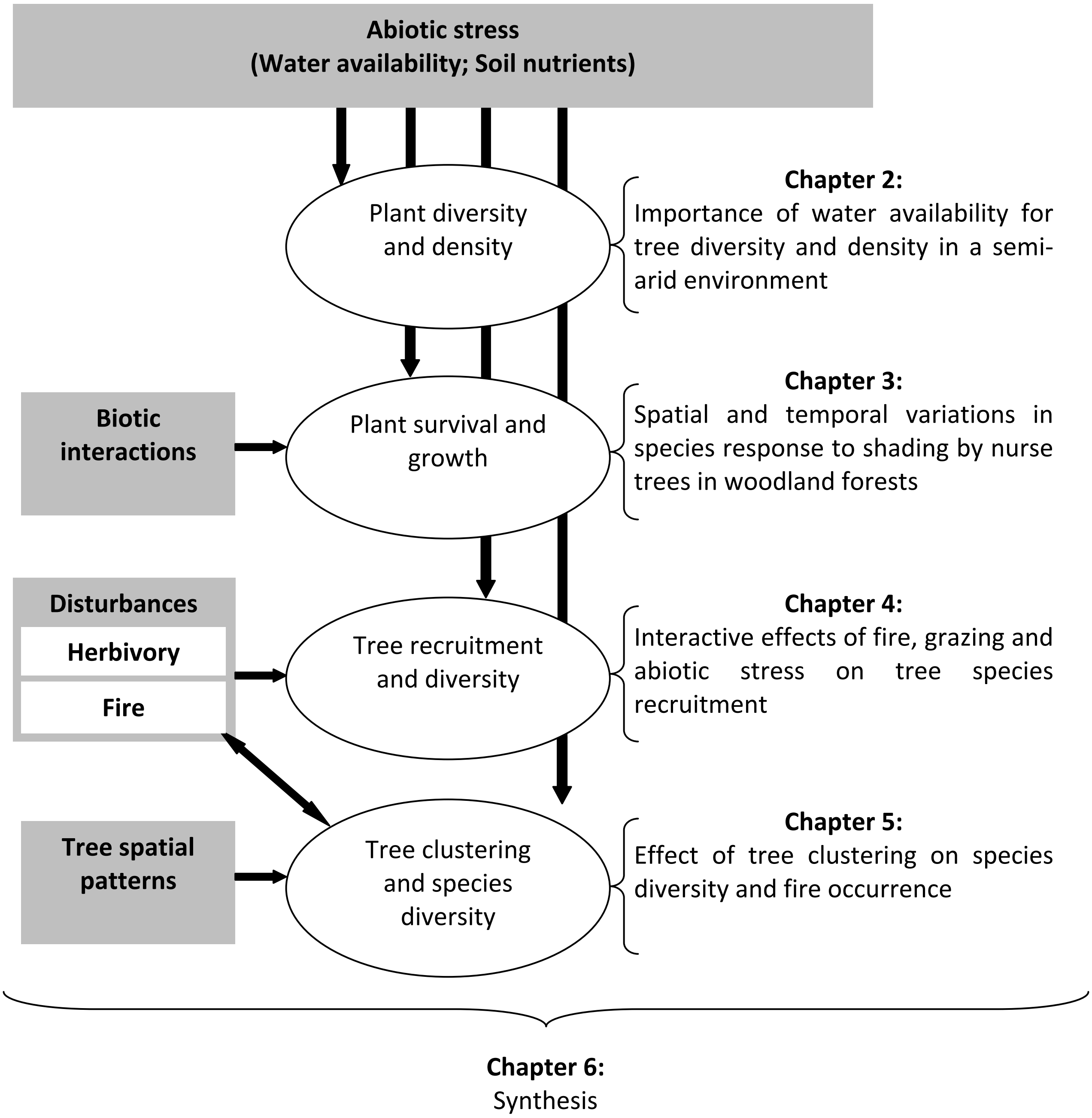


Figure 1: Flowchart showing linkages between chapters of the thesis and factors / mechanisms investigated. Grey rectangular boxes represent factors / mechanisms investigated and white oval boxes refer to the components of vegetation studied. Although not explicitly drawn, interactions between abiotic stress and other factors were considered.

FACILITATION

Under water-limited conditions, seedlings and saplings might benefit from close large neighbour trees, which reduce the evaporative demand and sometimes increase water availability in the soil by hydraulic lift (Horton & Hart, 1998). Dominant trees might thus facilitate the establishment and survival of seedlings, as has been shown for less productive arid and alpine ecosystems than the woodlands studied here (e.g. Choler *et al.*, 2001; Armas & Pugnaire, 2005). We conducted an experiment in Benin where we experimentally assessed the role of facilitation by woodland dominant trees on seedling establishment along a water stress gradient. We predicted that seedling establishment, growth and survival would be more successful under dominant trees in closed tree patches than in gaps (i.e. between trees in woodland), and in open fields. Moreover, we predicted that such facilitative effects would be stronger for drought-sensitive species than for drought-tolerant species.

FIRE AND GRAZING

Tree regeneration capacity in woodland, as in other seasonally dry forests, is strongly related to fire and grazing regimes (Freson *et al.*, 1974; Frost, 1996). Fire and herbivores can affect plant communities by reducing species populations, thus opening space whereby succession can be initiated or redirected (Welander, 2000) as well as preventing competitive exclusion by dominant species (Huston, 1979; 1994). Fire contributes also to maintain globally a higher ratio of grass to woody vegetation (Menaut *et al.*, 1995). Interestingly, herbivores can potentially reduce grass biomass to an extent that they reduce fire occurrence (Van Langevelde *et al.*, 2003), thus indirectly facilitating seedling establishment. Water availability not only conditions the species regrowth potential following disturbances (Proulx & Mazumder, 1998) but it can indirectly influence the extent of disturbances such as grazing and fire through its influence on grass biomass production (Coe *et al.*, 1976; Govender *et al.*, 2006). The actual consequences of such complex interactions are not yet clear (see Proulx & Mazumder, 1998; Osem *et al.*, 2002). We evaluated the independent and interactive effects of grazing, fire and abiotic stress (i.e. water stress and soil conditions) on tree regeneration in woodlands of Benin. We tested the hypotheses that frequent fires and frequent grazing reduce sapling species richness and sapling density, particularly in combination, and that the negative effects of the two disturbances is higher under high abiotic stress.

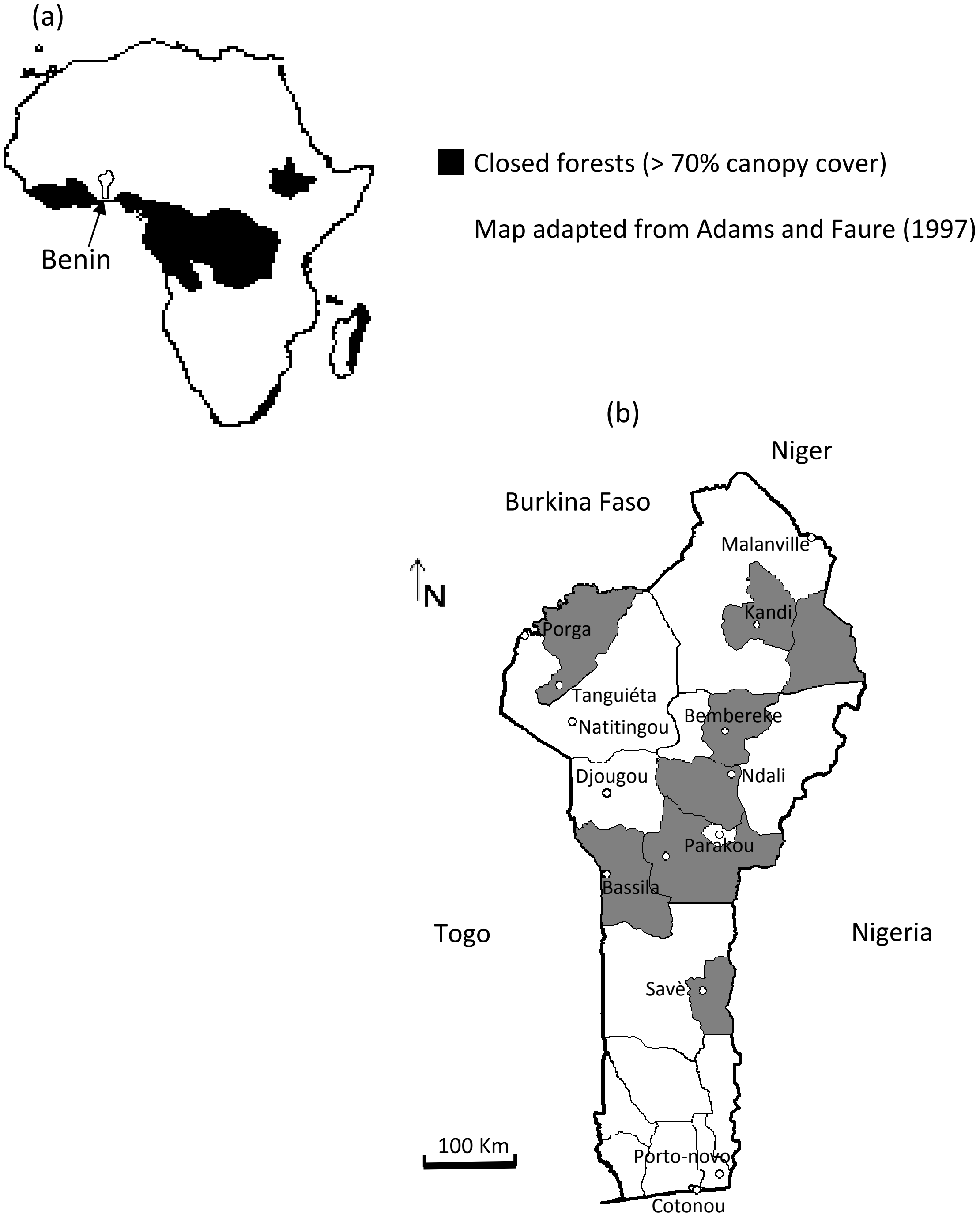
TREE CLUSTERING

A patchy structure with local tree clusters and more open herbaceous patches is a striking feature of the studied woodlands. Tree clustering can originate from biotic interactions between plants, for example due to facilitative effects of nurse plants on seedling establishment (Tirado & Pugnaire, 2003), dispersal limitation of the species (Condit *et al.*, 2002), soil heterogeneity (Getzin *et al.*, 2008), as well as disturbances such as fire (Groen *et al.*, 2008) and grazing (de Knegt *et al.*, 2008). Vice versa, tree clusters influence the spread of fire since they may act as natural fire-breaks (Miller & Urban, 2000). Whatever mechanism promotes or alters tree clustering, such clustering has important consequences for plant community diversity because it affects the microhabitat conditions and resource partitioning among species, and thus species coexistence (Adler *et al.*, 2001). We assessed the effect of tree spatial distribution on woody species diversity and explored the existence of potential feedbacks between tree spatial distribution and the probability of fire occurrence in woodlands of Benin. We tested the hypotheses that high fire frequency increases tree clustering, tree clustering reduces the probability of fire occurrence in woodlands and tree clustering increases species diversity.

STUDY AREA

The fieldwork for this study was conducted in Benin where extensive African woodland-savanna mosaics are found. Benin is located between $6^0$30’ - $12^0$30’N latitude and $1^0$00’ - $3^0$40’E longitude. It occupies the central position of the Dahomey Gap, a dry fringe separating the rain forest blocks from West and Central Africa (Ern, 1988; Jenik, 1994) (Fig 2a), and is characterized by a low annual precipitation ranging from 800 in the drier north to 1300 mm near the coast (Sokpon *et al.*, 2001; Sokpon *et al.*, 2006; Kokou *et al.*, 2008). Major contrasts between climate zones of Benin are for the most part due to variations in the length of dry season and rainfall distribution (two rainy seasons in the south and one in the north and the central zone). In West African countries located in the Dahomey gap (i.e. Benin and Togo) savanna mostly reaches the coast while tropical rain forests and semi-deciduous forests are rare.

This study focused on the vegetation north of $7^0$30’N (Fig. 2b), thus excluding the southernmost vegetation composed of islets of lowland rainforests and secondary grasslands. The study area is known as the domain of woodland-savanna mosaics in Benin and entails more than 75% of the country forest resources (Hountondji, 2008). Actually, the majority of forest reserves and the two National parks of Benin fall within this region. It also concentrates 85% of the total cattle population of the country (MEHU, 2002). Livestock production relies mainly on the natural vegetation for pastures and on the lopping of trees for fodder (Gaoue & Ticktin, 2007). Fire is a regular feature in this landscape dominated by open vegetation types. It is usually set deliberately, to clean bushes surrounding villages or to favour the regrowth of new grass for cattle and wild herbivores.



Map adapted from Adams and Faure (1997)

Figure 2: Map showing: (a) Location of Benin in West Africa, with black areas indicating rainforest blocks surrounding the country; (b) Location of the study sites, with shaded areas indicating administrative subdivisions within which fieldwork was conducted.

THESIS OUTLINE

The thesis consists of six chapters including this general introduction (chapter 1), one descriptive study (chapter 2), three experimental studies (chapters 3, 4 and 5) and the synthesis (chapter 6). For chapter 2, the vegetation types surveyed comprised gallery forests, dense deciduous forests, woodlands and savannas. The three experiments (chapters 3, 4 and 5) were conducted in woodlands only.

Chapter 2 describes biodiversity patterns across savanna-woodland landscapes in Benin and evaluates the limiting effect of water availability on tree species distribution and diversity. In this chapter, static vegetation data were used from 401 plots positioned along a gradient of water stress.

Chapter 3 evaluates the regeneration success of two tree species under different shading conditions and along a water stress gradient. We planted seedlings of the drought-sensitive *Afzelia africana* and the drought-tolerant *Khaya senegalensis* species under three shade conditions, at mesic and dry sites in Benin. Seedlings growth and survival were monitored during 13 months.

Chapter 4 examines how fire and herbivory affect tree regeneration in woodlands along water stress and soil gradients. In this chapter we used data from a field experiment with 68 plots exposed to four experimental treatments (no disturbance, fire alone, grazing alone, grazing and fire) across climate and soil gradients. We monitored these plots yearly between 2003-2006 for changes in sapling species richness and density.

Chapter 5 investigates how tree spatial distribution in woodlands affects tree species diversity and the probability of fire occurrence. It evaluates how these patterns change along abiotic stress and disturbance gradients. The data used here come from the same experiment as chapter 4.

Chapter 6 summarizes the main results of the thesis and discusses their theoretical and practical relevance.

Because each chapter was written in a paper format, overlap could not be avoided in the introduction and methods sections of the chapters. Also, given the number of factors and interactions among factors in each experiment, the hypotheses were often recalled to facilitate the reading of the results.

Study plot delineation and measurements

Chapter 2

Effects of water stress on tree diversity in dry woodland-savannas

(To be submitted)

Samadori S.H. Biaou, Milena Holmgren, Frank J. Sterck and Nestor Sokpon

ABSTRACT

Although the macro-climate is known as the primary determinant of species distribution around the world, some studies indicated that water availability might be a poor predictor of plant diversity and density in dry regions (< 1600 mm rainfall). We tested this assumption in woodland-savanna mosaics of Benin where the gradient of water availability is determined by an increasing dry season length from south (ca. 5 mo) to north (ca. 7 mo). We assessed the effect of water stress on species richness and density for all woody plants (trees and shrubs) and for adult trees (dbh ≥ 10 cm) and juvenile trees (dbh < 10 cm capable of reaching 10 cm dbh) separately. We used vegetation data from 401 plots surveyed between 2001 – 2006 and positioned along a gradient of increasing water stress, from 418 mm to 1020 mm water deficit (annual rainfall – evapotranspiration).

The total and juvenile species richness where highest at intermediate levels of water stress and lowest at the two extremes of the gradient. In contrast, adult species richness decreased monotonically with water stress. Total and juvenile tree density were not significantly related to water stress whereas adult density increased linearly with water stress. We observed large variations in the species richness and density across the gradient of water stress, possibly due to interactions with factors such as fire and grazing disturbances which might have reduced the maximum species richness achieved at different positions on the water stress gradient. Despite this, the water stress gradient resulted in a humped shaped pattern for the total and juvenile species richness, in line with the intermediate stress hypothesis.

The patterns observed in our study resulted probably from changes in the balance between facilitative and competitive interactions among species along the water stress gradient as well as interferences of disturbances such as fire and grazing which might affect the species populations differently along the gradient. These results confirm previous findings that disturbances influence strongly the dynamics of dry vegetations but they also show that water stress is a key driving force in dry woodlands and savannas of Benin. Water stress potentially interacts with or modifies the importance of other local factors such as fire and grazing along the climatic gradient.

Keywords: Benin, Dahomey gap, Dry ecosystems, Intermediate stress hypothesis, Savanna, Tree density, Tree diversity, Water stress, West-Africa, Woodland.

INTRODUCTION

Most of the world dry vegetation is in Africa, Asia, and Latin America, with the largest part (> 50 %) on the African continent (Bellefontaine *et al.*, 1997). Dry ecosystems share many similarities across continents; they occur in tropical regions receiving less than 1600 mm precipitation per year, with a highly seasonal rainfall and a prolonged dry season which generally exceeds three months per year (Menaut *et al.*, 1995); the vegetation in dry ecosystems is mostly composed of a mosaic of savannas and woodlands. The structure and species composition of these woodland-savanna mosaics are strongly influenced by disturbances such as fire and herbivores (Menaut *et al.*, 1995; Murphy & Lugo, 1995; Bellefontaine *et al.*, 1997). Although dry forests are generally less species-rich than moister forests, plant diversity and life-forms (i.e. structural and physiological characteristics) can vary greatly in dry ecosystems, due to high environmental fluctuations and variable frequency and intensity of disturbances (Medina, 1995). Numerous studies show how resource availability and disturbances can affect species co-occurrence (Huston, 1994; Rosenzweig, 1995), however, much uncertainty remains regarding the form of their relationship to species diversity (e.g. Wright, 1983; Currie, 1991; Kondoh, 2001; Mittelbach *et al.*, 2001; Pausas & Austin, 2001) as well as their relative importance (e.g. Gentry, 1995; Gillespie *et al.*, 2000; Kondoh, 2001; Cox *et al.*, 2006), particularly in these dry regions.

The macro-climate is known to influence species distribution around the world and tree diversity patterns. The intermediate stress hypothesis (Grime, 1973; Kammer & Mohl, 2002) proposed that species coexistence, thus diversity, is likely enhanced at intermediate levels of stress (i.e. resource availability) because a limited number of species can survive under unproductive conditions while few strong competitors tend to dominate the system under more productive conditions. The shape of the diversity-productivity relationship should depend on the spatial scale considered (Huston, 1994; Rosenzweig, 1995) but remains a subject of considerable controversy (Kondoh, 2001; Mittelbach *et al.*, 2001; Pausas & Austin, 2001). Mittelbach *et al.* (2001) showed that a hump-shaped relationship between plant diversity and productivity (measured as plant biomass, net primary productivity, rainfall or evapotranspiration) is most likely at scales smaller than continents while both hump-shaped and positive relationships co-dominate at larger geographical scales. In contrast to species diversity, tree density is expected to increase linearly with productivity, partly because individuals can partition more resources (Rosenzweig, 1992) and also because it cannot reach saturation due to constraints exerted by several other limiting factors such as disturbances (Huston, 1979; 1994).

In tropical regions, water variables represent the primary predictors for species distribution (Hawkins *et al.*, 2003). In wet forests (i.e. rainfall > 1600 mm), a strong linear increase in species diversity and density has been mostly found with increasing rainfall (Gentry, 1988; Wright, 1992; Clinebell *et al.*, 1995; Ter Steege *et al.*, 2003; Butt *et al.*, 2008). In dry forests however, some studies indicated a poorer prediction power of water variables and suggested a stronger control of other mechanisms such as fire and herbivores (Gentry, 1995; Gillespie *et al.*, 2000). The empirical support for this assumption is however poor as other studies found significant relationships between tree diversity and water availability in dry regions (e.g. Sagar & Singh, 2006). The role of water stress as a driving factor in dry forests is still not fully understood, probably because of the great array of factors such as disturbances and interactions among these factors interfering with climate gradient (Frost, 1996).

In this paper we assess whether water availability can explain the variability in species diversity in Benin's woodland-savanna mosaics and how it affects plant diversity and density. Benin is located in a woodland-savanna strip known as Dahomey gap (Ern, 1988; Jenik, 1994), Dahomey being the former name of Benin.

The Dahomey gap is a dry corridor in West Africa encompassing Togo and Benin and characterized by a low annual precipitation ranging from ca 800 in the drier north to ca 1300 mm near the coast (Sokpon *et al.*, 2006; Kokou *et al.*, 2008), thus contrasting with the Upper Guinea region where annual precipitation reaches 4000 mm (Bongers *et al.*, 2004). In the Dahomey gap, the gradient of water availability is determined by an increasing dry season length from south (ca 5 months) to north (ca 7 months). The understanding of plant distribution patterns in the Dahomey gap is rather poor and, like in the rest of West Africa, has a strong taxonomic emphasis (e.g. Keay, 1954-1968, Akoegninou et al. 2006, Hawthorne and Jongkind 2007). Only recently has plant species occurrence been studied along environmental gradients at the regional level (Poorter *et al.*, 2004; Holmgren & Poorter, 2007). However, all such studies have concentrated on the wet forests of Upper Guinea.

We studied woody species distribution in woodland-savanna mosaics of Benin and predicted that species richness will peak at intermediate levels of water availability whereas tree density should decrease linearly with decreasing water availability. Since shallow rooted juveniles are expected to be more vulnerable to water stress than more deeply rooted adult trees, we anticipated a stronger relationship between species diversity and water availability among juveniles than trees. To test these predictions, we used vegetation data from 401 plots located in four nature conservation reserves along a gradient of water stress in Benin. We defined water stress in our study as the difference between the mean annual precipitation and the mean annual evapotranspiration, also known as water deficit (Paltineanu *et al.*, 2007). Values ranged from 418 mm in our southernmost plots to 1020 mm in the northernmost plots, indicating an increasing water stress in the study region.

METHODS

Study region and water stress gradient

The study region is confined between latitudes 7.78°N – 11.47°N and longitudes 0.97°E – 2.70°E in Benin where we collected data from four nature conservation reserves: the Pendjari National Park, Ouénou-Bénou, Ouémé-Boukou and Monts-Kouffé forest reserves (Fig. 1, Table 1). Savannas and woodlands represent the most important vegetation types in Benin with 44.9% and 38.4 % land cover respectively (Mayaux *et al.*, 2004). Other vegetation types consist of gallery forests located alongside water strips and dry semi-deciduous forests, all represented in a lower proportion (< 5%). In our study region, the vegetation types consisted essentially of tree and shrub savannas, woodlands, gallery forests and dry semi-deciduous forests.

We expressed the water stress gradient in our study region by the water deficit calculated as the difference between the mean annual precipitation and mean annual reference evapotranspiration, after Paltineanu *et al.* (2007). This was preferred over simple measures of rainfall and evapotranspiration as it integrates both parameters and provides a good indication of the water stress potentially experienced by plants. Because evapotranspiration is typically higher than precipitation in dry ecosystems (Murphy & Lugo, 1995), water deficit values in all our study plots were negative (Table 1); thus we took the absolute value to facilitate interpretation of our results. Water deficit in the study region ranged from 418 to 1020 mm and was highly correlated with the latitudinal position of the study plots ($r = 0.96$, $p < 0.001$), precipitation ($r = -0.91$, $p < 0.001$) and evapotranspiration ($r = 0.97$, $p < 0.001$). The mean annual precipitation and mean annual reference evapotranspiration were between 1097 – 865 mm and 1514 – 1903 mm respectively. We obtained these climate data from the Aquastat database (FAO, 2008a) which contains mean monthly climate data at a 10 minute spatial resolution for the period

1961-1990. In the remaining of the paper we refer to water deficit as water stress which is a more intuitive way of expressing an increasing stress along the water gradient.

Table 1: Summary characteristics of the four study zones. Water stress is indicated by the annual water deficit calculated as: annual precipitation – annual evapotranspiration.

		Study zones			
Parameters	Units	Pendjari	Ouénou-Bénou	Monts-Kouffé	Ouémé-Boukou
General					
Area (ha)	ha	458041	35398	216568	20500
Number of study plots	count	157	109	60	75
Latitude	°N	10.8 - 11.5	10.2 - 10.4	8.6 - 9.2	7.8 - 8
Longitude	°E	1 - 1.9	2.5 - 2.7	1.8 - 2.3	2.4 - 2.5
Climate (averages)					
Rainfall	mm/year	933	1074	1073	1092
Evapotranspiration	mm/year	1836	1753	1576	1515
Water stress	mm/year	902.6	696	502.4	423.4
Species richness (range)					
Total	count	2 - 24	8 - 31	4 - 31	5 - 30
Adults	count	1 - 13	1 - 17	2 - 17	2 - 17
Juveniles	count	1 - 19	5 - 29	1 - 20	2 - 24
Tree density (range)					
Total	Count/ha	320 - 18290	450 - 16620	85 - 64403	510 - 12060
Adults	Count/ha	20 - 2170	10 - 580	85 - 651	80 - 560
Juveniles	Count/ha	150 - 17270	290 - 16170	0 - 27270	230 - 11690

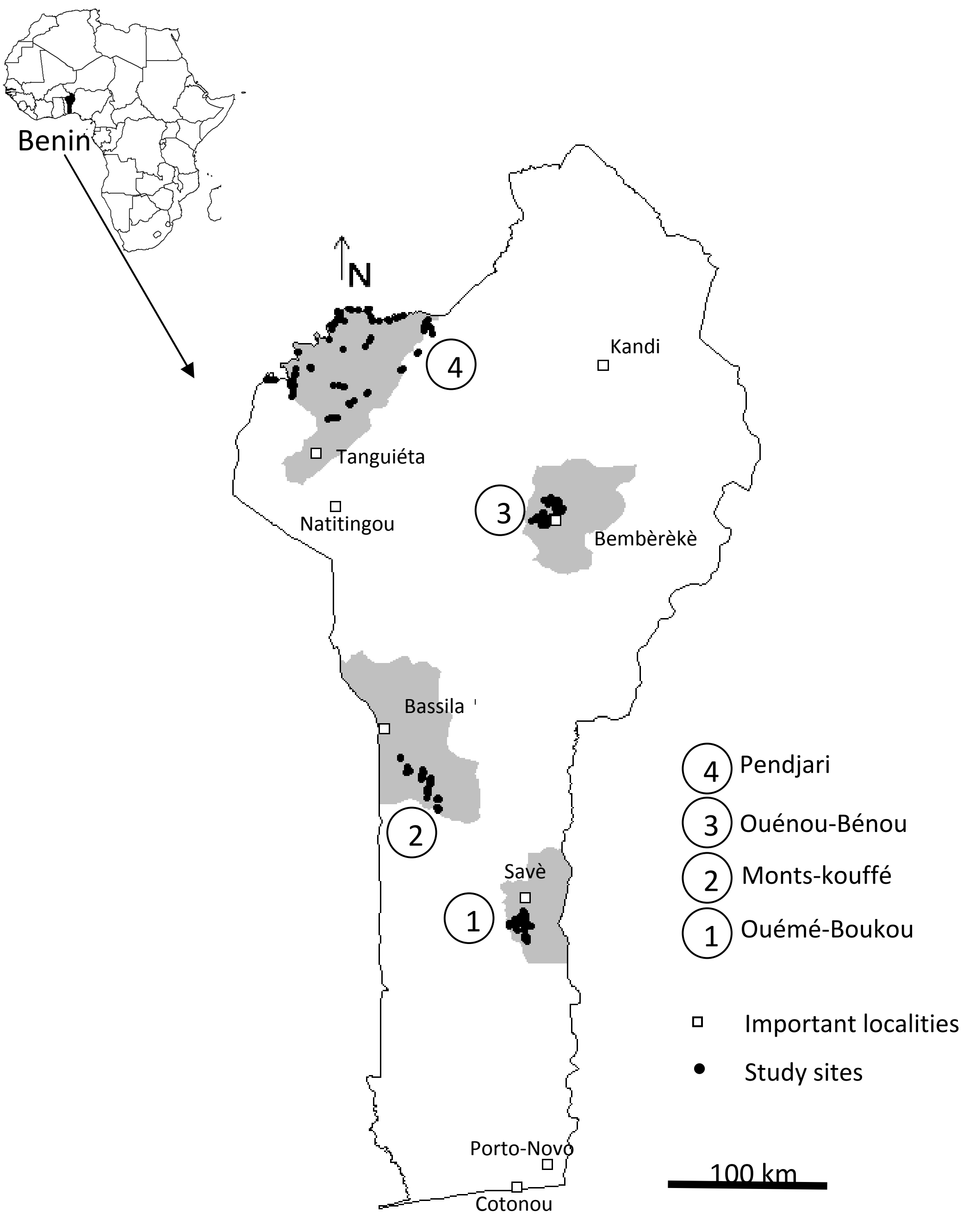


Figure 1: Location of the study sites in Benin. The study sites were sampled in four nature conservation reserves (numbers 1 to 4). Shaded areas on the map correspond to administrative subdivisions where the nature conservation reserves are located.

Vegetation sampling

We used vegetation data from 401 plots distributed across the four nature conservation reserves and which we collected in 2001 for Pendjari, in 2003 for Ouémé-Boukou and Ouénou-Bénou, and 2006 for Monts-Kouffé. In all four study zones, forest inventories were carried out during the dry season between December and March. We sampled adult trees (dbh ≥ 10 cm) in 0.1 ha (50 x 20 m) plots, measured them for dbh and identified them to species. For smaller trees and shrubs (dbh < 10 cm), we used subplots of 500 m^2 (50 x 10 m) at both Pendjari and Ouémé-Boukou, 100 m^2 (50 x 10 m) at Ouénou-Bénou and 50 m^2 (four circular subplots of 2 m radius) at Monts-Kouffé.

We calculated for each study plot the species richness (number of woody species), the rarefied species richness and density. We used the rarefied species richness and standardized species densities to the number of stems per ha to account for differences in samples size between adults and juveniles. The rarefied species richness is the expected number of species in random subsamples of 50 individuals in each plot (Hurlbert, 1971). In each case, the calculations were done separately for the entire plant community as well as subsets of adults (dbh ≥ 10 cm) and juveniles which we defined as smaller individuals (dbh < 10 cm) capable of reaching 10 cm dbh within our study area (Lieberman & Li, 1992). Thus, juveniles did not include shrub species that could not grow to larger diameter classes (i.e. ≥ 10 cm dbh). In other word, adults and juveniles were representative of the same species pool.

Statistical analysis

We assessed the effect of water stress on species richness and density for the total tree and shrub community (i.e. all woody individuals) and for subsets of adult trees (dbh ≥ 10 cm) and juvenile trees (species with dbh < 10 cm that have the capacity to grow up to dbh > 10 cm). Because species richness and density are likely constrained by several non-measured factors (e.g. burning, herbivory, soil properties) resulting in large dispersions in the data, we used quantiles regression (Koenker & Bassett, 1978; Koenker & Hallock, 2001) to assess the limiting effect of water stress on species richness and density. Quantile regression is increasingly used in ecology to estimate how any particular factor is limiting species distribution (e.g. Cade *et al.*, 1999; Ter Steege *et al.*, 2003; Sankaran *et al.*, 2005). It consists in modelling the maximum response in the dependent variable imposed by the environmental factor considered instead of modelling the central tendency of the response. The variation below the upper boundary reflects limiting effects of other non measured factors (Cade *et al.*, 1999).

Prior to quantile regressions fitting, we tested for spatial autocorrelation in our data using Moran's I statistic. We found a significant autocorrelation for distances up to 3.25 km for species richness ($p < 0.001$) and 0.81 km for tree density ($p < 0.001$; Table 2). Thus, to correct for spatial dependence in our data, we incorporated to the regression models an autocovariate (i.e. spatial weight) that describes the response at a given site as a function of the responses at the 4 nearest neighbouring sites (Augustin *et al.*, 1996).

In the quantile regressions, we chose the upper quantile (q) based on the number of plots (n) available so that: $n > 10 / (1-q)$ (see Scharf *et al.*, 1998). Thus, we explored the effect of water stress on species richness and density for the 10th (lower), 50th (median) and 95th (upper) quantiles. We included the quadratic term for water stress in each model to account for potential unimodal relationships and tested that the linear and quadratic coefficients were significantly different from zero using bootstrapped standard errors of the regression coefficients (Cade *et al.*, 1999). The quadratic term was eventually removed in case it was not significant.

We performed all analyses within the R 2.7.1 computing environment (R Development Core Team, 2008), with the packages “spdep” to test for spatial correlation and “quantreg” for quantile regressions. Significance tests for quantile regressions coefficients were performed using the Anova function available in the “quantreg” package.

Table 2: Test of spatial correlation in species richness and density. Moran’s I was computed for eight distance lags (upper bound in bracket) and values close to 1 indicate a strong spatial correlation in the data. Significant values are indicated by * (p < 5 %), ** (p < 1 %) and *** (p < 0.1 %)

Distance lags (upper bound in km)	Species richness	Tree density
1 (0.81)	0.31^{***}	0.21^{***}
2 (1.63)	0.18^{***}	0.02
3 (2.44)	0.13^{***}	0.01
4 (3.25)	0.17^{**}	-0.01
5 (4.6)	0.10	-0.01
6 (4.88)	0.08	-0.04
7 (5.69)	0.05	-0.04
8 (6.5)	0.07	0.02

RESULTS

Both the species richness and tree density showed great variations across the study region. The total number of tree and shrub species recorded per plot ranged from 2 to 31 while it was between 1 – 17 for adults (dbh ≥ 10 cm) and 1 – 29 for juveniles. Tree density was between 85 - 64403 stems per ha for the total, 10 - 370 stems per ha for adults and 0 – 27269 stems per ha for juveniles.

Relationship between species richness and water stress

We anticipated that the species richness will peak at intermediate levels of water stress. This hypothesis was found true for the total (trees and shrubs) and juvenile species richness but not for adults alone (Fig. 2). The total species richness displayed a unimodal pattern and reached its maximum at intermediate water stress, ca 650 mm. This relationship was significant across all quantiles explored (i.e. 10^{th} - 95^{th}), with typically positive coefficients for water stress and negative coefficients for its quadratic term ($P < 0.001$ in all cases; Table 3). The relationship between juvenile species richness and water stress was also unimodal and did not differ much from that of the total species richness. Clearly, the pattern for the total species richness was strongly determined by juvenile species richness. On the contrary, the relationship between adult trees species richness and water stress was monotonically decreasing. Regression coefficients for adult trees species richness were significant only for the lower (10^{th}, $P < 0.1$ %) and median quantile (50^{th}, $P < 0.1$ %) but not for the upper quantile (95^{th}). This suggests that water availability did not have a strong influence on adult trees species richness. For the total species richness as well as juvenile and adult species richness, the data showed large dispersion at all points of the water gradient (Fig. 2), thus indicating a strong effect of other non-measured factors contributing to set the species richness below the climate potential.

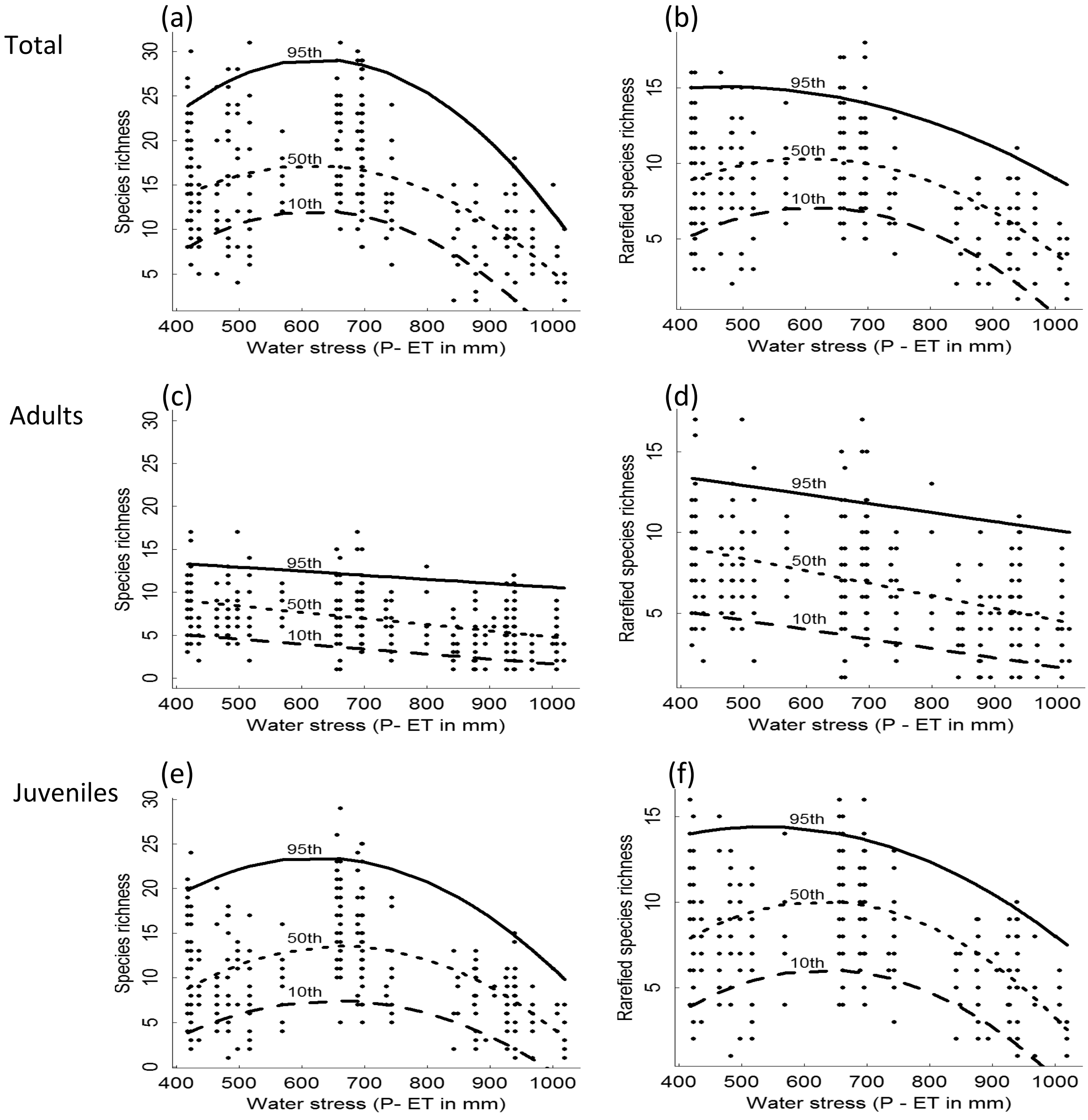


Figure 2: Effects of water stress on species richness in woodland-savanna mosaics of Benin. Graphs are presented for the actual species richness (a, c, e) and the rarefied species richness (b, d, f); and from top downward: for (a, b) total adults and shrubs, (c, d) adult and (e, f) juvenile species richness. Dots on the scatterplots represent the observed values while curves represent fitted values for the 95th, 50th and 10th regression quantiles.

Table 3: Quantile regression estimates for the effect of water stress on species richness, rarefied species richness and density in the woodland-savanna mosaics of Benin. We initially included the quadratic term (wd^2) in all models to account for potential unimodal relationships but it was removed in cases it did not significantly improve the model fit. Regression coefficients that are significantly different from zero are indicated by * (p < 5 %), ** (p < 1 %) and *** (p < 0.1 %) for the 10th, 50th and 95th quantiles (tau).

tau	Total (tree & shrubs)		Adult trees (dbh ≥ 10 cm)		Juveniles (dbh < 10 cm)	
	wd	wd^2	wd	wd^2	wd	wd^2
Species richness						
10th	0.122***	-0.0001***	-0.006***		0.085***	-0.0001***
50th	0.100***	-0.0001***	-0.007***		0.106***	-0.0001***
95th	0.153***	-0.0001***	- 0.005		0.108***	-0.0001***
Rarefied species richness						
10th	0.059***	-0.0001***	-0.006***		0.059***	-0.00005***
50th	0.049***	-0.00004***	-0.008***		0.061***	-0.00005***
95th	0.021	-0.00002	-0.006*		0.032*	-0.00003**
Tree density (number / ha)						
10th	-0.135		-0.155**		0.183	
50th	0.353		-0.119*		0.701	
95th	-22.430		1.081***		-5.181	

We did not find strong differences between the actual and the rarefied species richness regarding the form of their relationship with water stress. Although the hump-shaped curves tended to level off at lower water stress, the relationship was significantly unimodal for both the total and juvenile species richness (Fig. 2, Table 3). For adults the relationship between the rarefied species richness and water stress was linearly decreasing and quite similar to the pattern observed with the actual species richness.

Because there could have been some differences between gallery forests (i.e. vegetation alongside water strips) and upland vegetation types (i.e. savannas, woodlands, dense deciduous forests), we also analyzed the relationship between water stress and species richness separately for gallery forests and upland vegetation (graphs not shown). The patterns remained similar to those presented above for both gallery forests and upland vegetation types. In each case, the total and juvenile species richness were maximum at intermediate levels of water stress while for adults the species richness decreased linearly with increasing water stress. Thus, the species in gallery forests and upland vegetation seem to be constrained in a similar way by the climate-driven water stress gradient in the study region.

We further examined the distribution of unique (i.e. found in only one zone) and shared species (i.e. common to ≥ 2 zones) across the gradient of water stress and found little differences between the four study zones, particularly between the low stress (19 %) and high stress (16 %) extremes of the gradient (Fig. 3). The proportion of unique species peaked at intermediate levels of water stress between 500 – 600 mm (32.4 %).

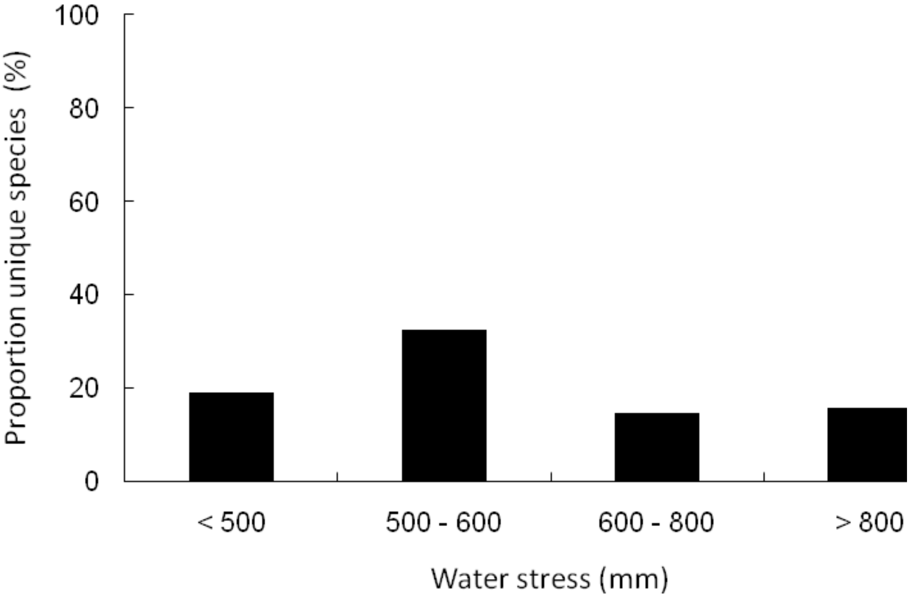
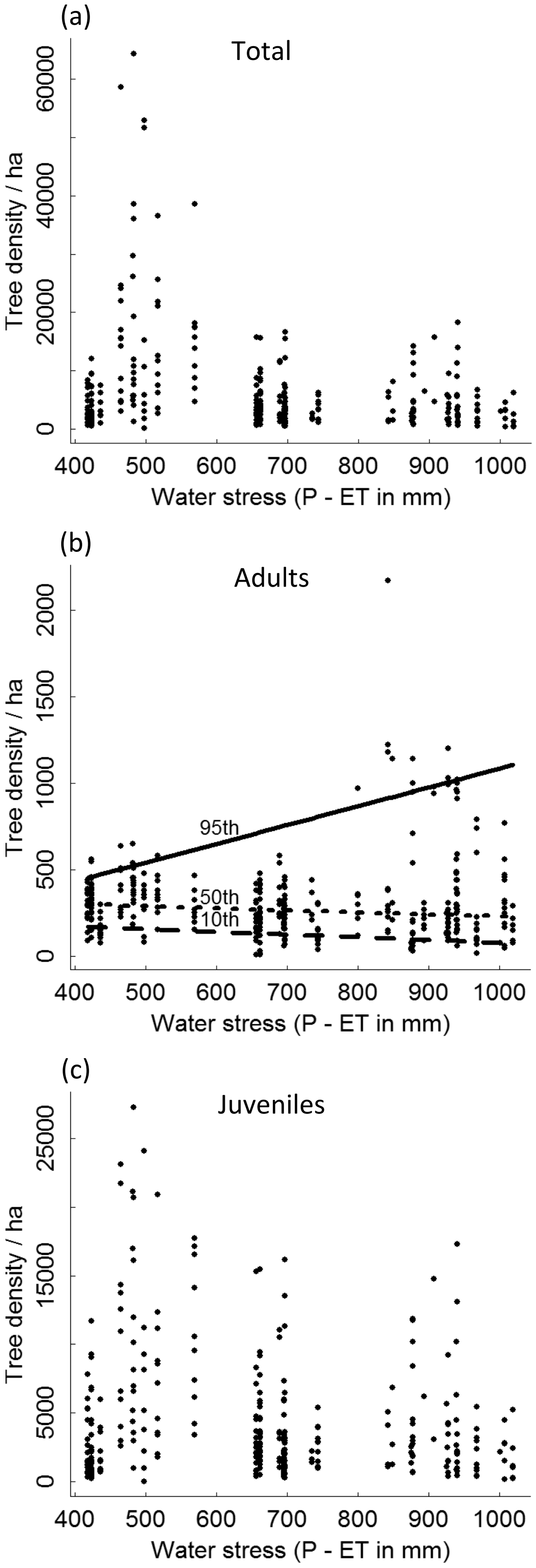


Figure 3: Proportions of unique species along the water stress gradient. Unique species are those found in only a particular portion of the water stress gradient. Positions on the water stress gradient (x-axis) correspond to the four study zones in order of increasing water stress: Ouémé-Boukou, Monts-Kouffé, Ouénou-Bénou and Pendjari (see Table 1).

Relationship between tree density and water stress

We expected a decrease in tree density with increasing water stress. In contrast, the relationship between water stress and tree density was not significant for the total (trees and shrubs) density and juvenile density whereas adult density increased with water stress contrary to our hypothesis (Fig. 4, Table 3). For adult density, the regression coefficients were significant across all the quantiles explored (10th – 95th). For the total and juvenile species, despite a perceptible decrease in density towards higher water stress, none of the regression coefficients was significant. As for the species richness, there was a large dispersion in tree density data suggesting that other non-measured factors were strongly influential along the water stress gradient.

Figure 4: Effect of water stress on the (a) total trees and shrubs density, (b) adult density and (c) juvenile density. Dots on the scatterplots represent the observed values while curves represent fitted values for the upper (95th, solid line), median (50th, dotted line) and lower quantile regression lines (10th, dashed line). Fitted curves are not plotted for total and juveniles because water stress has no significant effect on the total and juveniles density (see Table 3).



DISCUSSION

Effect of water availability on species diversity

We predicted that species richness will peak at intermediate levels of water stress and found it true for the total (tree and shrub) and juvenile species richness while adult species richness showed a monotonous decrease with increasing water stress (Fig 2). Not surprising, the total species richness was strongly determined by juvenile species. The results for total and juvenile species richness thus support the predictions by the intermediate stress hypothesis (Grime, 1973; Kammer & Mohl, 2002). This hypothesis has been tested in various environments and has yielded contrasting results as some found it true (Townsend *et al.*, 1997; Kammer & Mohl, 2002; Bruun *et al.*, 2006) while others did not (see Currie, 1991; Kondoh, 2001; Mittelbach *et al.*, 2001; Pausas & Austin, 2001). To our best knowledge, this hypothesis has not been tested previously for dry African woodlands.

At larger spatial scales plant diversity can increase almost linearly with productivity because habitat heterogeneity and dissimilarity in species composition within regions likely increase with productivity (Rosenzweig, 1992; Chase & Leibold, 2002). In contrast, within a region, peaked patterns can be expected in cases where species show clear differences in their tolerance to the environmental conditions along a gradient, with a clear advantage to strongest competitors at the most productive end of the gradient and to the species adapted to stressful conditions at the less productive end of the gradient (e.g. Bruun *et al.*, 2006). Under intermediate conditions the overlaps between the two types of species should result in higher species diversity than the extremes. In our study however, we did not find the predicted high proportion of shared species at intermediate position of the water stress gradient (Fig 4). Instead, the intermediate position of the water stress gradient showed a peak in the proportion of unique species, apparently adapted to intermediate conditions alone.

Other factors not measured here should then be determinant for patterns observed in woodlands and savannas of Benin, which was also indicated by the large dispersion of the data below the upper quantile regressions (Cade *et al.*, 1999). Environmental factors not included in this study and which could be influential comprise for example fire and herbivores. Disturbances regimes are far from uniform along a productivity gradient, particularly along a water stress gradient (Thonicke *et al.*, 2001). Actually, a strong correlation is often found between ecosystem productivity or water availability and factors such as fire and herbivory, which are thought to exert a stronger control on the vegetation in dry ecosystems (Chidumayo, 1988; Eva & Lambin, 2003; Sankaran *et al.*, 2008). Fire intensity and frequency are strongly conditioned by the available fuel (i.e. grass biomass) and ambient moisture. Thonicke et al. (2001) showed that the fire return interval on the African continent varies with latitude in a bimodal manner with peaks in the dry sahelian zone and the wet tropical rain forest. This suggests that fire frequency peaks at intermediate water stress levels. From this, we hypothesize that the hump-shaped pattern, as driven by a high proportion of unique species, resulted from the improved species coexistence promoted by the absence of competition as periodic burning and perhaps herbivory reduced the species populations (Huston, 1979; Huston, 1994). The decrease in adult species richness with increasing water stress that we observed in our study tend to confirm this view as adults are less susceptible to fire disturbances under surface fire regimes and to herbivores. Such complex interactions between climatic factors and disturbances might explain the lack of correlation between water variables and species diversity reported by some authors in other dry regions (e.g. Gentry, 1995; Gillespie *et al.*, 2000).

Effect of water availability on tree density

Our hypothesis that tree density will decrease linearly with increasing water stress was not supported by the results presented here. We did not find any significant correlation between water stress and both total (tree and shrub) and juvenile density while adult density increased with water stress (Fig. 3, Table 3). We noted also a large dispersion in the density data, as for species richness, indicating a strong influence of other non-measured factors along the entire water stress gradient (Cade *et al.*, 1999). Despite the lack of correlation with water stress, we observed that highest juvenile densities tended to occur at lower water stress, quite the opposite direction to adult that highest densities occurred at higher water stress. At lower water stress a great proportion of individuals apparently remain small while only a few grows up to the canopy. Since we eliminated the possibility that they belong to inherently small taxa, by selecting those capable of reaching larger diameter classes (i.e. dbh ≥ 10 cm), this could also be the result of interferences with disturbances along the water gradient.

Overall this study show that water availability is an important limiting factor for woody species distribution in woodland-savanna mosaics of Benin, and that the high species richness at intermediate water stress resulted from a high proportion of unique species apparently adapted to those conditions. We observed however that local influences such as disturbances by fire and herbivores may play a significant role in fine-tuning the species distribution. Inclusion of a larger set of environmental factors in future studies should help elucidating underlying interactions between climatic factors and disturbances.

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Seedling of *Khaya senegalensis* planted under a nurse tree

Chapter 3

Stress-driven changes in the strength of facilitative interactions in West African woodlands

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(Submitted)

Samadori S. H. Biaou, Milena Holmgren, Frank J. Sterck and Godefridus M.J. Mohren

ABSTRACT

The strength of competitive and facilitative interactions in plant communities is expected to change along gradients of resource availability. Contrasting theoretical models predict that with increasing abiotic stress, facilitative effects will be higher, lower or similar than those found under more productive conditions. While these predictions have been tested in very stressful environments such as arid and alpine ecosystems, they have hardly been tested for more productive tropical woodlands, which cover extensive areas in Africa. Woodlands are characterized by tree patches surrounded by open herbaceous vegetation where trees can have positive or negative effects on the growth and survival of plants growing underneath.

We experimentally assessed the role of facilitation for successful tree regeneration in woodlands along a climatic gradient in Benin, West Africa. We planted seedlings of the drought-sensitive *Afzelia africana* and the drought-tolerant *Khaya senegalensis* species under three shade conditions (tree shade in woodland, woodland gaps, and adjacent open fields), at mesic and dry sites. We found that tree seedling survival improved within woodlands compared to open fields along the whole climatic gradient. The relative benefits in seedling survival were larger at the dry site, especially for the drought-sensitive species. Nevertheless, plant interactions became neutral or negative during the dry season in the drier woodland, confirming that the net positive effects may be lost under very stressful abiotic conditions.

We conclude that facilitation also occurs in the relatively more productive conditions of African woodlands. We found empirical support for the idea that facilitative interactions become stronger with increasing drought stress, particularly for drought sensitive species, but these net positive effects may be lost under extremely stressful conditions. Our results underscore the role of environmental gradients in space and time and the stress tolerance of species to explain competitive and facilitative interactions within plant communities.

Key-words: *Afzelia africana*; Benin; Drought; Facilitation; *Khaya senegalensis*; Nurse tree; Positive interaction; Tree regeneration; Savanna; Seedling establishment.

INTRODUCTION

Woodlands in Africa constitute a large and almost uninterrupted strip from Mali to Uganda, along an annual rainfall gradient from 700 to 1200 mm (Bellefontaine *et al.*, 1997). They cover up to 14 % of the total continent surface and represent about 25 % of the natural vegetation (Mayaux *et al.*, 2004). Woodlands have the appearance of small open forests (Boughey, 1957) with larger woody cover and taller trees than savannas (Bellefontaine *et al.*, 1997). In general, medium-sized trees (8-20 m height) cover more than 20 % of the stand (Pratt *et al.*, 1966; Bellefontaine *et al.*, 1997).

Woodlands typically occur in areas with 6-7 months dry season with little or no rainfall (Bellefontaine *et al.*, 1997). Vegetation in such water limited environments is often characterized by a mosaic pattern, with woody patches of different density and size dispersed in a matrix of grassy plants (Lejeune *et al.*, 2002). This mosaic structure is characterized by an uneven distribution of resources (i.e. light, water and nutrients) across microsites (Vetaas, 1992; Belsky, 1994; Schenk & Mahall, 2002). Many experimental studies have demonstrated that seedlings in such patchy environments can benefit from neighbouring plants because of reduced abiotic stress (e.g. Vetaas, 1992; Holmgren *et al.*, 1997; Armas & Pugnaire, 2005; Aerts *et al.*, 2007), increased nutrient availability (e.g. Belsky, 1994; Armas & Pugnaire, 2005; Gómez-Aparicio *et al.*, 2005) or reduced herbivore pressure (e.g. Smit *et al.*, 2006; Aerts *et al.*, 2007; Callaway, 2007). However, these studies on facilitative effects on seedlings typically focused on less productive ecosystems than the African woodlands (see Castro *et al.* 2004, Armas and Pugnaire 2005, Aerts *et al.* 2007).

Bertness and Callaway (1994) proposed that the strength of facilitative interactions among plants should increase in more stressful environments. Later on, Holmgren *et al.* (1997) hypothesized that although positive and negative interactions probably occur simultaneously, a net facilitative effect should be expected when the improvement of growth conditions (for instance by improved water relations) under a nurse plant exceeds the costs of growing under shade. The harshness of the stress factor and the species sensitivity to that factor should determine the net outcome of the interaction. An alternative null hypothesis would predict that the impacts of factors changing in relative abundance under shade (e.g. light and water) are completely independent, implying that for instance drought reduces plant growth by the same proportion at any irradiance (Sack & Grubb, 2002). Because the availability of resources is also temporally variable (e.g. Frankie *et al.*, 1974; Gómez-Plaza *et al.*, 2001), one would expect that net facilitative effects of canopy trees become stronger during stressful periods such as dry seasons or dry years (Lortie & Callaway, 2006).

Moreover, tree species differ in their fundamental niche optima and stressful conditions for one species may be ideal for others (Liancourt *et al.*, 2005; Callaway, 2007). Consequently, plant-plant interactions can be expected to be positive, neutral, or even negative, depending on the species (Pennings *et al.*, 2003; Maestre *et al.*, 2006) at relatively small spatial scales. In general, one would expect the less tolerant species to the stressful conditions to be more likely facilitated, particularly towards the ends of their distribution ranges (Choler *et al.*, 2001; Liancourt *et al.*, 2005), because facilitation occurs only when the benefits exceed the costs to be paid (Holmgren *et al.*, 1997; Holmgren, 2000).

In this paper, we evaluate how tree seedling establishment is affected by a mosaic of shade conditions along a rainfall gradient across woodlands in Benin. We conducted a field experiment in order to test the following hypotheses: (1) seedling survival rate and height growth are highest under tree shade, intermediate in woodland gaps and lowest in open fields; (2) tree shade has a stronger facilitative effect in the dry season compared to the wet season; (3) tree shade has a stronger facilitative effect on the drought-sensitive species than on the drought-tolerant species, particularly in dry woodlands. This might be one of the first studies that tests for facilitation effects for successful regeneration in African woodland ecosystems, which are considered more productive than the more intensively studied alpine and arid systems in the context of positive interactions in plant communities. The Beninese woodlands are part of a large and almost continuous strip of *Isoberlinia* woodlands extending from Mali to Uganda in Africa north of the Equator.

METHODS

Study sites

The experiment was conducted at two sites in Benin: Kandi (11.17 °N, 3.04 °E) and Bassila (9.16 °N, 1.58 °E) differing in water stress condition (Fig. 1A). Woodlands represent the most abundant vegetation type in both experimental sites. Soils are of ferruginous type, usually limited in depth by gravel and lateritic formations, and characterized by low fertility (INRAB, 1995; Junge, 2004).

For each site, we used the water deficit (annual rainfall – annual evapotranspiration) as indicator of the water stress level (Paltineanu *et al.*, 2007). Climate data for the two sites were obtained from the ASECNA (Agency for the Safety of Aerial Navigation in Africa) and the closest meteorological stations located in Kandi and Parakou (9.35 °N, 2.61 °E). Kandi is a drier site with a rainy season (months with rainfall > 50 mm) lasting 5 months (May to September) (Fig. 1B). During the experimental year (August 2005 - August 2006), water deficit reached - 694 mm at Kandi. The total rainfall was 1087 mm which is slightly higher than the average 1012 mm recorded between 1971 - 2006. Temperatures ranged from 16.9 to 40.7 ^{o}C, with the highest recorded in March (39.7 ^{o}C) and April (40.7 ^{o}C). Bassila has moister conditions with a longer rainy season lasting 7 months (April to October) (Fig. 1C). During the experimental year, water deficit and total rainfall reached -105 mm and 1368 mm respectively. Temperatures varied from 21 to 38.8 ^{o}C with the highest ones recorded in March (38.7 ^{o}C) and April (38.8 ^{o}C). Longer climate data estimate average annual precipitation around 1168 mm (1960 - 2006) (Fig. 1C).

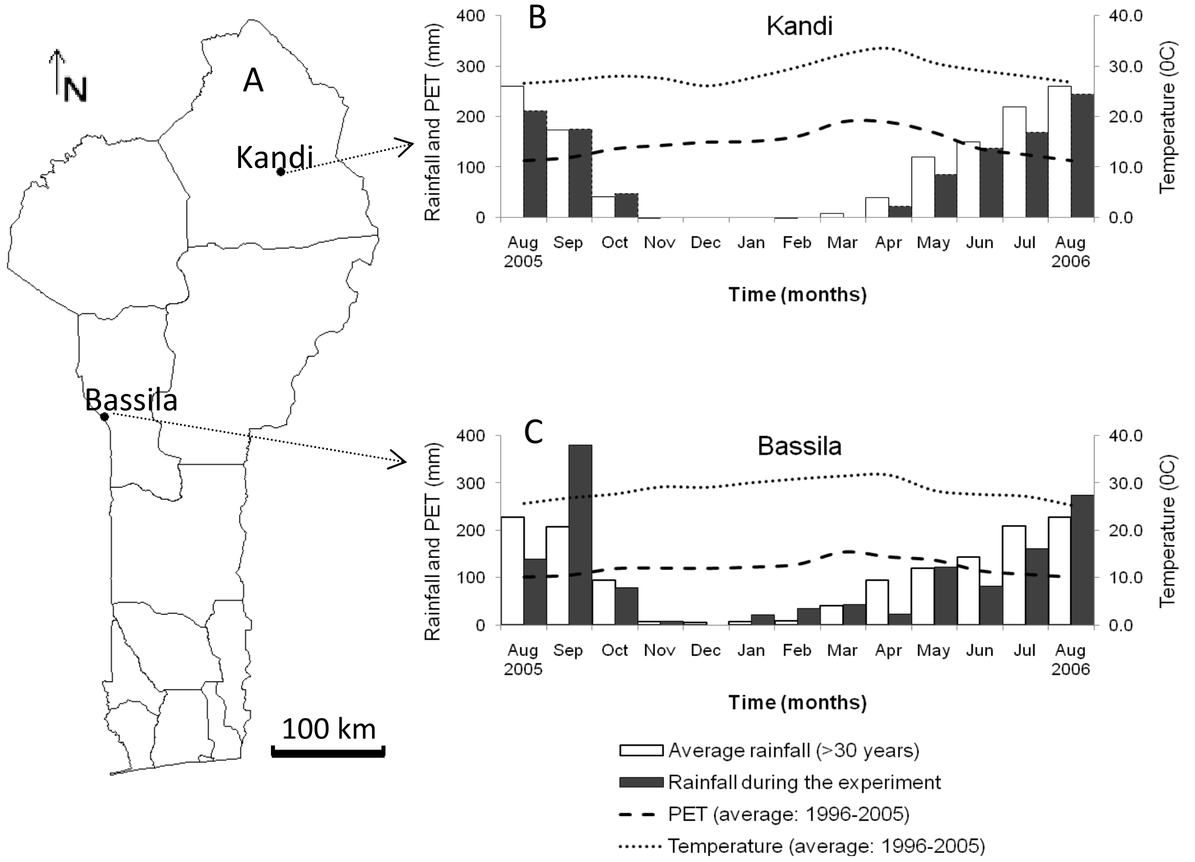


Figure 1: Location of the study sites (A) and climate diagrams for the dry Kandi (B) and mesic Bassila sites (C). Rainfall distribution during the experiments (shaded bars) is presented together with the long-term average (white bars), average potential evapo-transpiration (PET, broken line) and average temperature (dotted line).

Study species

We used seedlings of two tree species with contrasting drought tolerance: *Afzelia africana* Sm. (Fabaceae- Caesalpinioideae), a drought-sensitive species (Bationo *et al.*, 2001) and *Khaya senegalensis* A. Juss. (Meliaceae), a drought-tolerant species (Okali & Dodoo, 1973; Dickinson *et al.*, 2004; CAB International, 2008).

In Africa, *Afzelia* occurs naturally between latitude 5^{o}N and 13^{o}N and *Khaya* between 8°N and 15°N (CAB International, 2008). This latitudinal gradient is associated with a gradual increase in drought from the equator northward expressed by a lower annual precipitation and a longer dry season. Accordingly, natural populations of *Afzelia* are more abundant in the wetter Sudano-Guinean ecological region of Benin (Sinsin *et al.*, 2004; Adomou, 2005) while *Khaya* extends farther into the northern dry Sudanian region (Natta, 2003; Adomou, 2005; Gaoue & Ticktin, 2007).

Afzelia is a deciduous tree that may reach heights of 25 - 30 m and 1 m diameter (Arbonnier, 2000). It is common in dense evergreen and semi-deciduous forests as well as moist savannas (Hawthorne, 1995; Arbonnier, 2000). *Khaya* is a large semi-deciduous tree that grows up to 35 m tall and 2 m wide (Arbonnier, 2000). It is often found in uplands but in very dry regions grows mostly in riparian habitats or stream bottoms (Natta, 2003).

Afzelia and *Khaya* are frequent in West African woodlands although not as abundant as other species like *Isoberlinia doka* and *I. tomentosa* (Bellefontaine *et al.*, 1997; Sokpon *et al.*, 2006). We selected *Afzelia* and *Khaya* because they are important multipurpose trees in sub-Saharan Africa that produce high value timber and fodder (Arbonnier, 2000) and are extensively used for reforestation programs in West African countries (Bellefontaine *et al.*, 1997). Both species are classified as vulnerable species by the IUCN (2007) because of habitat loss and unrestrained exploitation of their natural populations.

Experimental design

We planted seedlings of *Afzelia* and *Khaya* species in 15 experimental plots at Bassila and 9 plots at Kandi. At each site, plots were randomly selected and equally distributed among three treatments (Fig. 2): (1) under tree shade, (2) in woodland gap and (3) in open field. These treatments represented a decreasing level of shading. Seedlings under trees were shaded during the entire day. Because of the size of the gaps (approximately 20 m x 20 m) and the height of the surrounding trees (5 - 15 m), seedlings in woodland gaps were exposed to direct sunlight only at mid day (i.e. between 11:00 - 14:00). Seedlings in open fields were exposed to direct sunlight during the entire day. These open fields were old agricultural fields adjacent to woodlands, with no trees and few small shrubs.

Plantation and monitoring

We collected 576 seedlings (149 of *Afzelia* and 427 of *Khaya*) from two local nurseries in Bassila. Seedlings were one to two years old with heights ranging between 6 to 44 cm for *Afzelia* and 9 to 69 cm for *Khaya*. For each species, we randomly allocated the seedlings to the treatments and sites, as well as the position within plot so that the whole range of seedling sizes was represented in all experimental treatments. At the beginning of August 2005, we cleared all experimental plots from present shrubs and planted 24 seedlings (6 *Afzelia* and 18 *Khaya*, based on the total seedlings available for each species) within each experimental plot. Seedlings were planted 1 m from each other to avoid competition between them.

For the under shade treatment, we distributed the 24 seedlings in 8 transects planting them at 1, 2 and 3 meters from the nurse tree trunk (see Fig. 2A). Most nurse trees were *Isoberlinia doka* between 10 - 16 m tall, with crown diameters larger than 6 m and stem diameters between 29 - 46 cm.

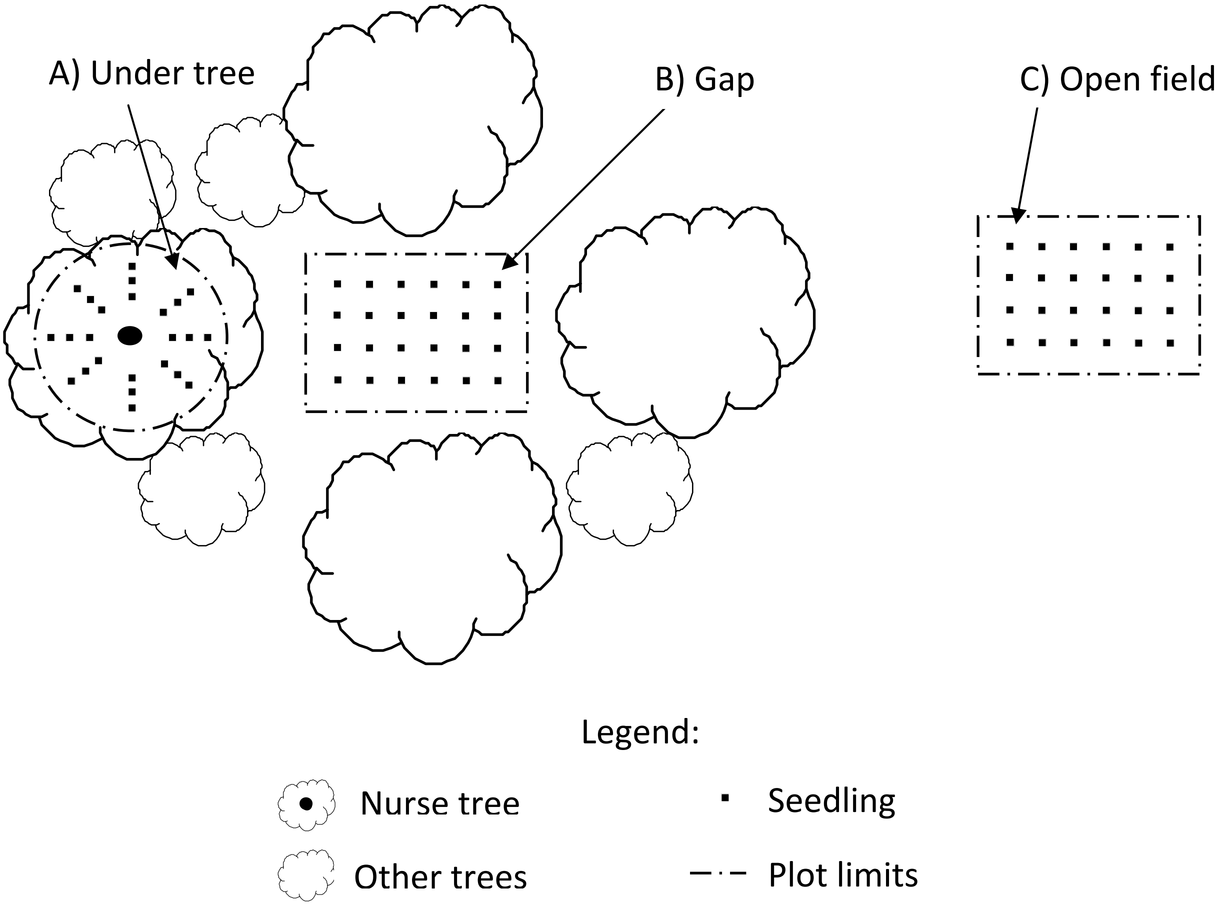


Figure 2: Experimental shading treatments: (A) under tree shade in woodland, (B) in woodland gap and (C) in open field.

Fire breaks and enclosures were installed around all plots but despite these precautions, four plots were burnt and we excluded them from the analysis. We also excluded from the analysis all accidentally broken seedlings. The remaining analyses are based on 477 seedlings (354 *Khaya* and 123 *Afzelia*), distributed among sites and shade conditions as presented in Table 1. We monitored seedling survival and height growth monthly between August 2005 and August 2006.

Table 1: Seedlings distribution across sites and microsites.

	Number of seedlings			
	Afzelia africana		*Khaya senegalensis*	
Microsites	Mesic	Dry	Mesic	Dry
Open field	36	14	84	34
Gap	19	16	53	56
Under tree	24	14	69	58
1 m from tree stem base	10	8	19	16
2 m from tree stem base	10	2	22	22
3 m from tree stem base	4	4	28	20
Total	79	44	206	148

Statistical analyses

We conducted a survival analysis to test for the effects of shading (under tree shade, gap and open field) and overall site conditions (dry and mesic sites) on seedling survival using Cox proportional hazard regression models. We calculated the hazard ratio (HR) corresponding to the relative risk of death with vs. without a particular treatment. We included initial seedling height as a co-variable and tested for the effects of single factors (shading and site) as well as the interactions "shading x site" and "shading x initial height". Seedling distance to nurse tree was excluded from this analysis as it had a linear relationship with shading (Chan, 2004a, b). For both species, the proportional hazard condition of the Cox model was satisfied (Chan, 2004b). We considered a seedling as dead only when no resprouting occurred during the whole study period. During the experiment, 57 seedlings successfully recovered after apparently dying, of which 14.6% of all *Afzelia* and 11% of all *Khaya* seedlings.

Differences in seedling height growth were tested using a nested ANOVA, with shading, site, and season as well as their two-way interactions as explanatory variables. We included plot as a nested term within shading and within site to account for spatial correlations between plots. Season corresponded to three periods: early establishment (October 2005), end of the dry season (April 2006) and the next rainy season (August 2006). Because the original size of the seedlings could have conditioned their subsequent growth, we used the standardized height growth (SHG) obtained by dividing seedling height at a given time by the initial one (after Aerts *et al.* 2007). Prior to the analysis, we excluded all dead individuals, averaged SHG per plot to avoid pseudo-replication and log transformed it to meet the normality assumption.

To assess the facilitative effect of tree shade on seedling survival and growth, we calculated the relative interaction index (Armas *et al.*, 2004) for each species and per site: $RII_{a/b} = (P_a - P_b)/(P_a + P_b)$, with P_a the performance (survival rate or growth) achieved in one shade level (e.g. under tree shade) and P_b the performance achieved in another shade level (e.g. in the open field or in the gap). For instance, to compare seedling survival rate under tree shade (UT) and in the open field (OF), we calculated the index as: $RII_{UT/OF} = (P_{UT} - P_{OF}) / (P_{UT} + P_{OF})$. This relative interaction index has several advantages compared to other indices such as the relative competition index (RCI) or the relative neighbour effect (RNE). It is symmetrical around zero (-1 to +1) with positive values indicating facilitation while negative ones indicate competition. It is also adapted to cases where plant performance is zero (e.g. survival) and is applicable to non-paired field experiments (see Armas *et al.*, 2004). We calculated RII at the end of the experiment to compare the final outcome and for every month to assess the temporal variations. All statistical analyses were done using SPSS 16.0 (SPSS Inc. 2007, Chicago).

RESULTS

Woodland versus open fields

We predicted higher seedling survival rate and higher height growth in woodlands compared to adjacent open fields. Seedling survival was indeed larger in woodlands compared to open fields, particularly for *Afzelia* (Fig. 3A and B). The higher survival in the woodland is reflected by rather low hazard ratios ($HR < 1$, $p < 0.001$) under tree shade and woodland gap (Table 2). We did not find a significant effect of shading on seedling growth but there was a significant interaction between shading and season (for *Afzelia* only) (Table 3). At both mesic and dry sites, seedling growth was higher in woodland compared to open field for *Afzelia* but not for *Khaya* (Fig. 3C and D). For *Afzelia*, standardized height growth ($SHG = H_{final}/H_{initial}$) dropped from 1.17 under tree shade and 1.23 in woodland gaps to 0.76 in open fields at the mesic site (Fig. 3C). At the dry site, the height growth was negative for the surviving seedlings in the woodland (SHG = 0.41 in gap and 0.49 under tree shade), whereas all seedlings died in the open field. *Khaya* showed little growth differences across shade levels at the mesic site (Fig. 3D; SHG = 1.04, 1.06 and 0.98 in the open field, gap and under tree shade respectively). At the dry site, *Khaya* seedling growth was higher in open fields (SHG = 0.99) compared to woodland gaps (SHG = 0.80) and under tree shade (SHG = 0.76) which is in contradiction with our hypothesis. Our results thus confirmed that seedling survival rate is higher in woodlands compared to adjacent open fields for both species, but in terms of seedling growth we only found it to be higher in woodlands for the drought-sensitive *Afzelia*.

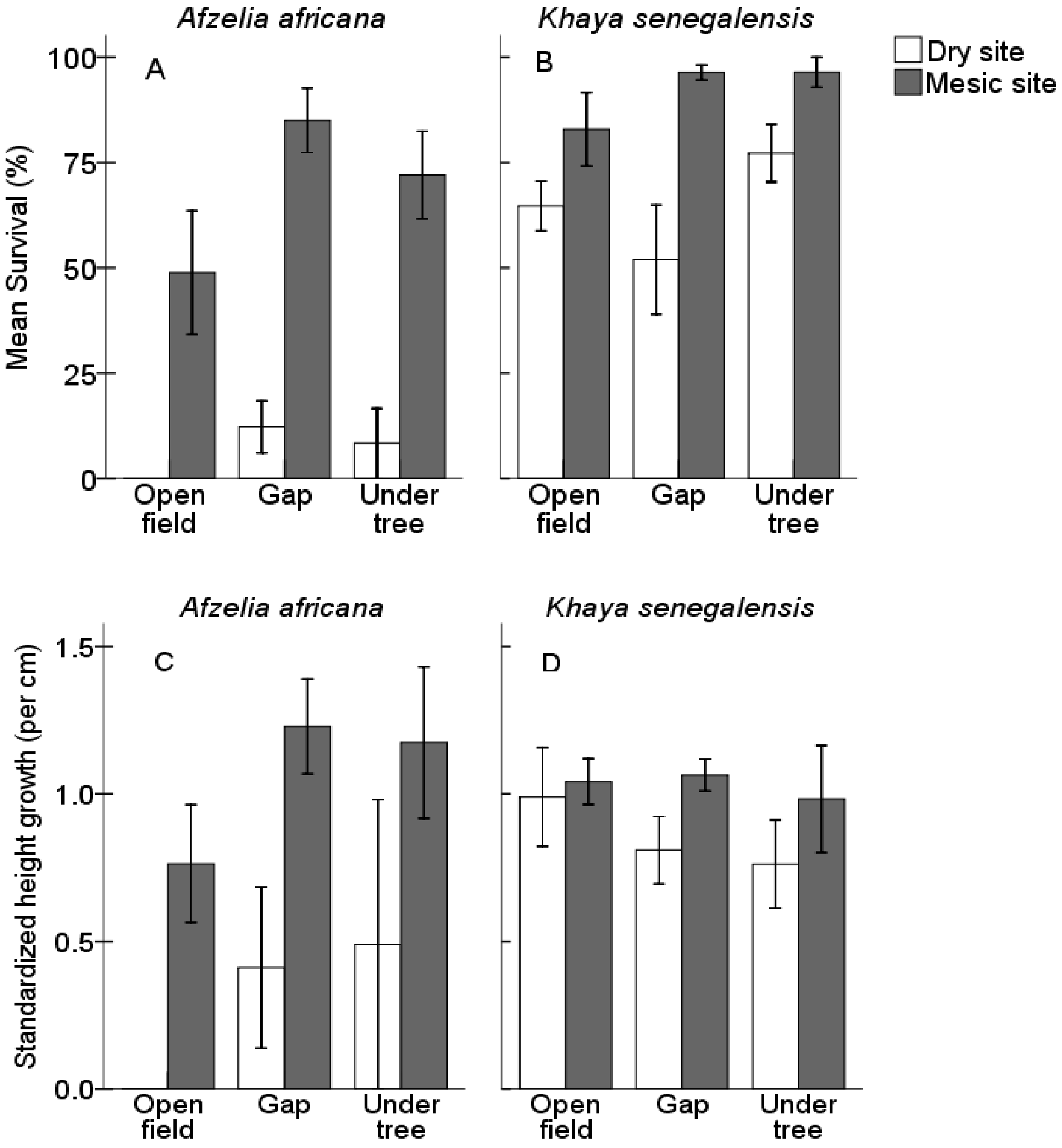


Figure 3: Seedling survival (% +/- 1 SE, A and B) and standardized height growth (mean +/- 1 SE, C and D) for *Afzelia africana* and *Khaya senegalensis* at the dry (white bars) and mesic sites (shaded bars) during a one-year period (August 2005 – August 2006). Lacking bars in the open field reflect 100% mortality.

Table 2: Effects of site (mesic vs. dry), shading (open field, woodland gap and under tree shade) and initial seedling height on the survival of *Afzelia africana* (n = 123) and *Khaya senegalensis* seedlings (n = 354) based on Cox proportional hazards regression.

	Afzelia africana		*Khaya senegalensis*	
	P	Hazard Ratio (HR)	*P*	Hazard Ratio (HR)
Main factors and interactions terms				
Site	<0.001		<0.001	
Shading	<0.001		<0.001	
Initial height	0.734		<0.001	
Shading*Site	<0.001		<0.001	
Site effect				
Dry site	<0.001	1.714	<0.001	2.742
Shading effect				
Gap	<0.001	0.166	<0.001	0.213
Under tree	<0.001	0.434	<0.001	0.200
Seedling size effect				
Initial height	0.734	-	<0.001	0.981

Note: P is the significance level of the factors; HR corresponds to the relative risk of death. For categorical variables, HR > 1 means that the category of interest likely have a shorter time to death compared to the reference category; the reference categories are mesic site and open field respectively for site and shading. For the continuous variable (i.e. initial height), HR < 1 means the relative risk of death decreases with one-unit increase in that variable.

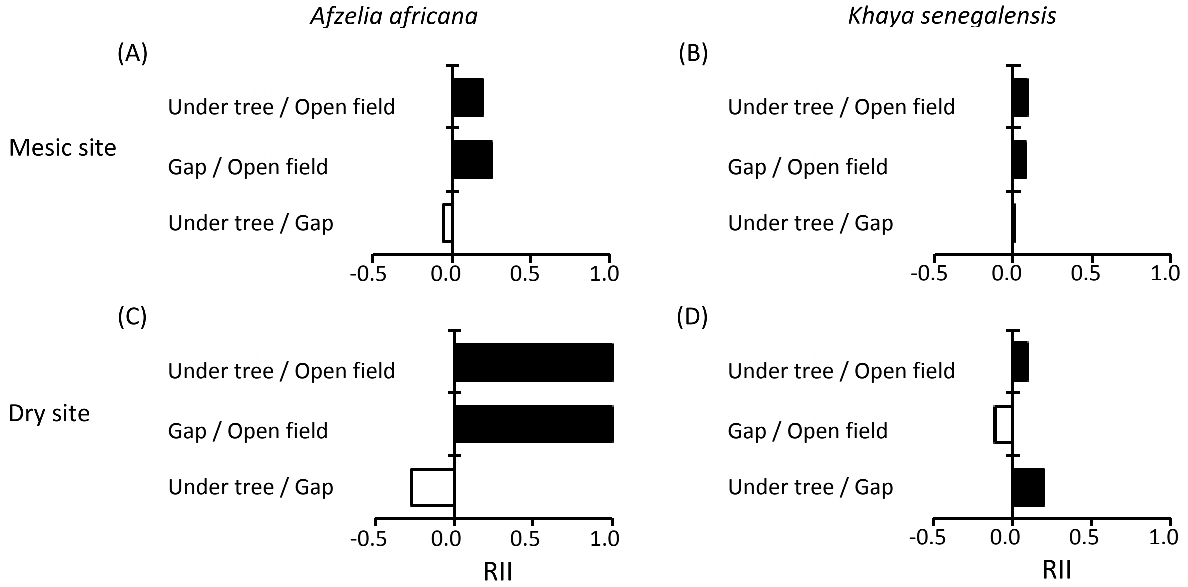
Table 3: Results of the nested ANOVA for the effects of site (mesic vs. dry), shading (open field, woodland gap and under tree shade) and initial seedling height on the standardized height growth of *Afzelia africana* and *Khaya senegalensis* seedlings. P indicates the significance level of the factors.

	Afzelia africana			*Khaya senegalensis*		
	df	F	P	df	F	P
Shading	2	0.39	0.687	2	0.12	0.889
Site	1	6.65	0.022	1	1.08	0.317
Season	2	9.20	0.001	2	4.61	0.017
Shading x Site	2	0.24	0.787	2	0.08	0.928
Shading x Season	4	2.86	0.039	4	0.99	0.428
Season x Site	2	9.52	0.001	2	3.25	0.052
Plot (nested within shading and site)	14	3.71	0.001	14	2.21	0.031

Woodland: tree shade versus gap

We predicted that within woodlands, seedling survival and growth would be higher under tree shade compared to gaps. In contrast, *Afzelia* seedling survival was higher in woodland gaps than under tree shade at both the mesic and the dry sites (Fig. 3 and 4). At the mesic site, almost all *Khaya* seedlings survived under tree shade and in gaps whereas at the dry site, this species survived better under tree shade (Fig. 4B). Both species showed similar SHG under tree shade and in gaps (Fig. 3 and 4) both at the mesic and the dry sites. Our prediction was thus only partially supported by the data.

I) Facilitative effect on seedling survival



II) Facilitative effect on seedling growth

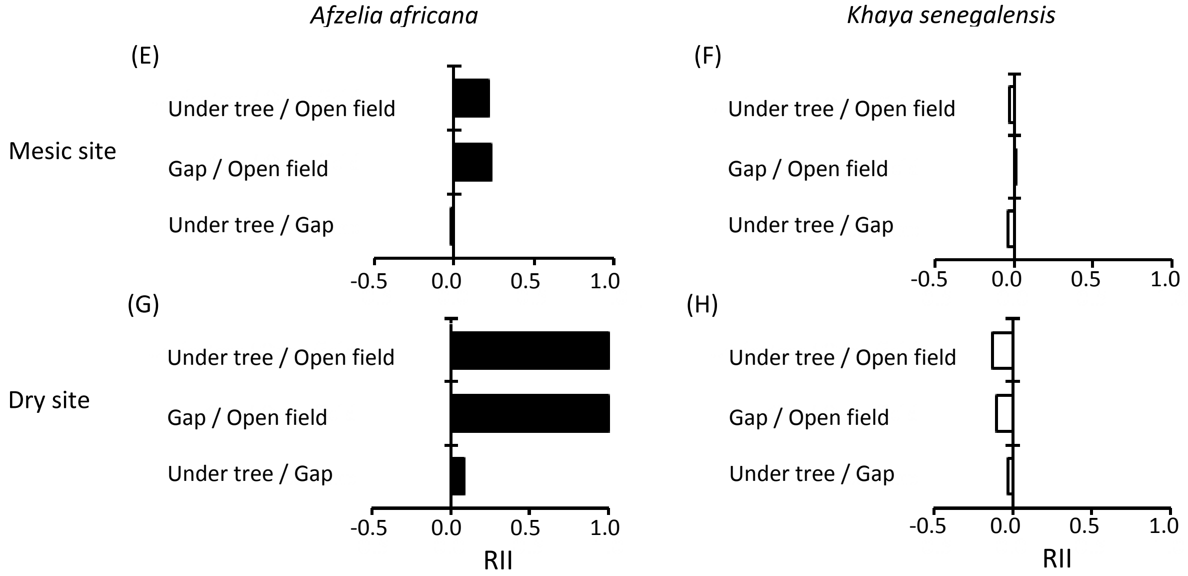


Figure 4: Facilitative effects on seedling survival and growth. The facilitative effect is indicated by the Relative interaction index (RII) which is calculated as RII a/b= (Pa – Pb) / (Pa + Pb), with P being the performance (i.e. survival or growth) achieved in contrasting shade conditions “a” and “b”.

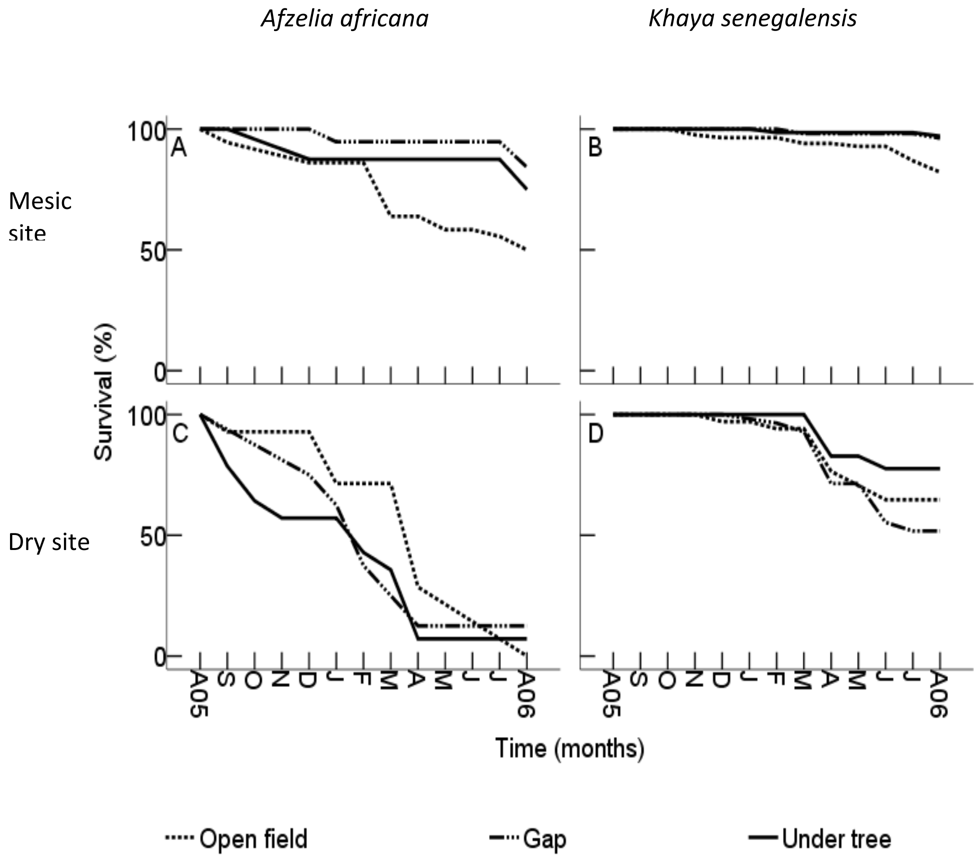


Figure 5: Seedling survival across time for *Afzelia africana* and *Khaya senegalensis* under the three shading treatments (open fields, woodland gap and under woodland tree) in the mesic and dry sites.

Temporal variations in facilitation strength

We predicted that the drop in seedling survival and growth during the dry season would be less pronounced under tree shade than in more open conditions (gaps and open fields). Survival decreased during the dry season (November - April) for both species, particularly at the dry site (Fig. 5). At the mesic site, mortality was strongest in the open field for both species, which is in line with the prediction. This is also reflected by the positive RII values for the comparison of under tree and gap conditions to open fields (Fig. 6). At the dry site, survival decreased dramatically during the dry season and the early subsequent rainy season in each of the three shading conditions. For *Khaya*, this decrease was stronger in open fields and gap conditions than under trees (Fig. 5D). For *Afzelia*, the decrease was initially slower in open fields; however, since survival in open fields continued to decrease in the subsequent rainy season, the ultimate survival was lowest for the open field (Fig. 5C). Overall, growth showed a similar temporal response as survival (data not shown). Except for *Afzelia* in the dry site, our results support the idea that the drop in seedling survival and growth during the dry season tends to be lower under tree shade than in more open conditions.

Species tolerance to drought stress and facilitation

We predicted that tree shade would have a stronger facilitative effect on the drought-sensitive species *Afzelia* than on the more drought-tolerant species *Khaya*, particularly in dry woodlands. *Afzelia* indeed showed a more positive and stronger response than *Khaya* when comparing woodland conditions to open fields (Fig. 4 and 6). Moreover, the responses in *Afzelia* were much stronger at the dry site. However, we did not find such obvious patterns when comparing microsites conditions within woodlands (under tree and gaps).

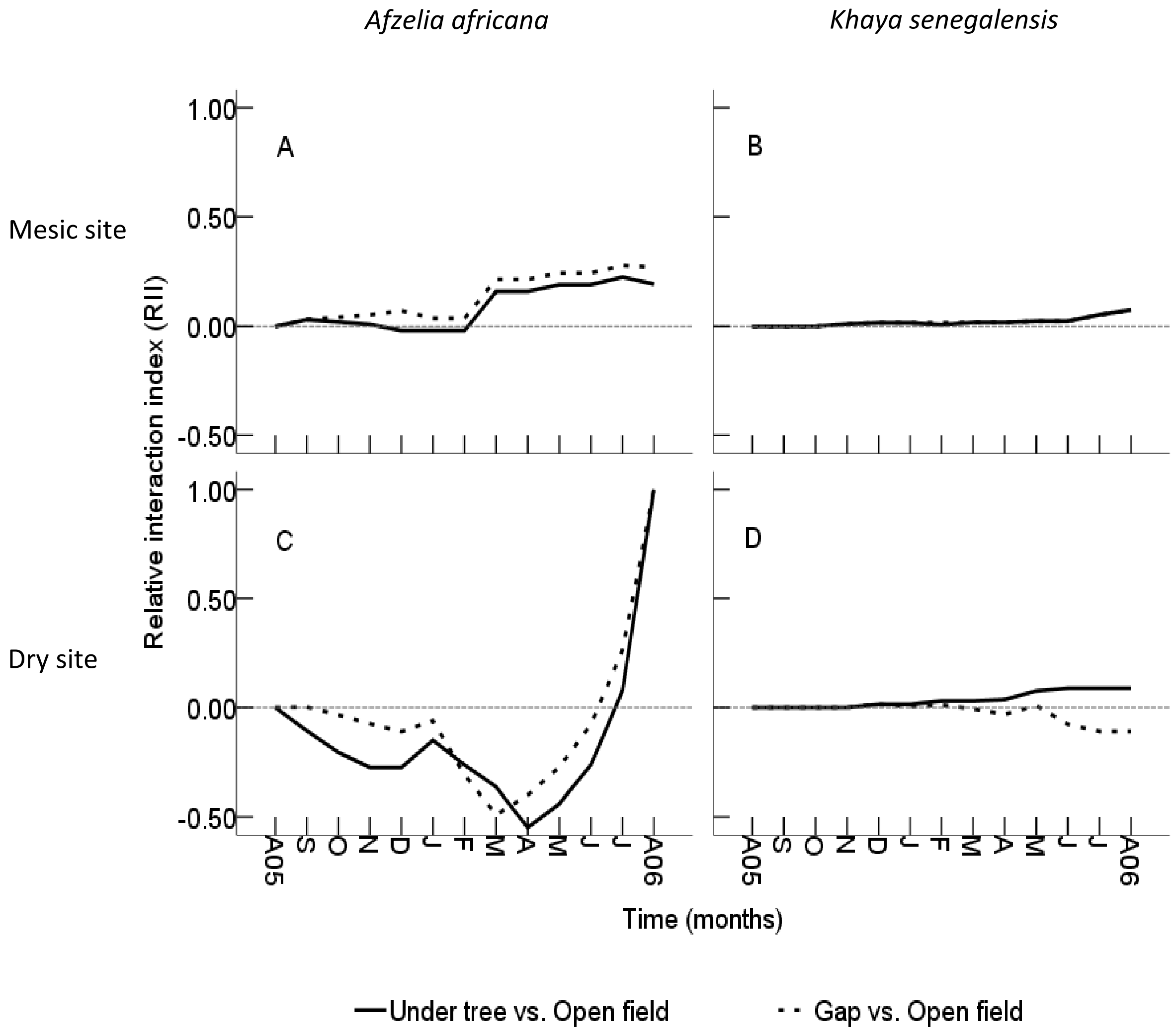


Figure 6: Seasonal change in the Relative Interaction Index for seedling survival under tree shade and gap conditions compared to open fields in the mesic and dry sites. Positive values of RII indicate positive effect of shading on seedling survival under tree (solid line) or in gap (broken line). The dotted horizontal line on the graphs correspond to the reference line (RII = 0).

DISCUSSION

Seedling facilitation in woodlands compared to open fields

We found evidence that seedling survival was improved in woodlands compared to open fields for both *Afzelia* and *Khaya* species (Fig. 3 and 4). However, the patterns for seedling growth were less strong and species dependent. *Afzelia*, a drought-sensitive species, grew more rapidly within woodlands, under nurse trees and in gaps, than in the open fields. In contrast, seedling height growth for the drought-tolerant *Khaya* species differed little between shade levels and practically did not change across time. Several facilitation experiments have shown increased growth and survival of the facilitated species (Castro *et al.*, 2002; Castro *et al.*, 2004) while others have found either increased survival (Aerts *et al.*, 2007; Callaway, 2007) or increased growth (Egerton *et al.*, 2000; Bertness & Ewanchuk, 2002). Our results are consistent with the findings indicating the predominance of facilitative interactions among plants in stressful environments (Bertness & Callaway, 1994; Holmgren *et al.*, 1997; Callaway *et al.*, 2002; Brooker *et al.*, 2008). Since in dry regions, water limitation is an important bottleneck for the successful regeneration of tree species, we suspect that the improved seedling survival for both species and growth for the drought sensitive species (*Afzelia*) within the woodlands compared to the open fields resulted from reduced water stress conditions.

Facilitation within woodlands: tree shade versus gaps

We predicted that within woodlands, seedling survival and growth would be higher under tree shade compared to gaps. Surprisingly, *Afzelia*, the drought-sensitive species, survived better in gaps than under trees at both the mesic and dry sites (Fig. 3 and 4). For *Khaya*, seedling survival was higher under nurse trees than in gaps at the dry site, while at the mesic site survival was similarly high in gaps and under trees. Curiously, despite its presumed tolerance to drought (Okali & Dodoo, 1973; CAB International, 2008), water stress seems to be the dominant factor limiting *Khaya* seedling performance within woodlands. These rather simple explanations exclude more complex interactions that might occur within woodlands. A fuller explanation of tree facilitation in woodlands would have to take into account the improvement of soil conditions and microorganisms under nurse trees (Belsky, 1994; Armas & Pugnaire, 2005; Gómez-Aparicio *et al.*, 2005) as well as changes in herbivory or disease levels (Callaway, 2007).

Seasonal variation in seedling response to shade

We predicted that the drop in seedling survival and growth during the dry season would be less pronounced under tree shade than in more open conditions. Seedling response to shading varied across time, with largest shifts at the dry site, particularly for the drought-sensitive species (Fig. 5 and 6). At the mesic site, seedlings growing in the open field showed a stronger decline in survival during the dry season than seedlings in the woodland. At the dry site, both *Afzelia* and *Khaya* showed a very rapid decline in survival under all shading conditions. For *Khaya*, this decline was strongest in open fields and gap conditions. These results support our hypothesis. In contrast, survival of *Afzelia* seedlings declined more rapidly during the dry season in woodlands than open fields. Nevertheless, although the rate of mortality was faster in woodlands, some seedlings survived until the end of the experiment while in the open fields seedling survival continued declining until no survivors were left.

Facilitation strength and species tolerance to stress

The hypothesis that in dry conditions the facilitative effect of tree shade would be stronger on the drought-sensitive species was confirmed in this study (Fig. 4 and 6). At the dry site, all *Afzelia* seedlings in open fields died while some seedlings survived under tree shade (7.1 %) and in the gaps (12.5 %) whereas at the mesic site they were able to survive also in the open fields. Such strong contrasting responses were not found for *Khaya*, the drought-tolerant species. Our results support the idea that the species with the lowest tolerance to abiotic stress is more likely facilitated (Choler *et al.*, 2001; Liancourt *et al.*, 2005). A net facilitative effect should be expected when the improvements of growth conditions (e.g. water availability) under a nurse exceed the costs of growing under shade (Holmgren *et al.*, 1997; Holmgren, 2000). Given the drought intolerant nature of *Afzelia*, this species might be at the extreme end of water stress, where plant interactions might turn from positive to neutral or even negative, emphasizing the species specific nature of plant responses along environmental gradient (Maestre *et al.*, 2005; Maestre *et al.*, 2006).

CONCLUSION

Our results show that tree seedling survival improved within woodlands compared to open fields along the whole climatic gradient. But the relative benefits in seedling survival were larger at the dry site especially for the drought-sensitive species. Nevertheless, plant interactions became neutral or even negative during the dry season at the drier woodland, confirming that the net positive effects may be lost under extreme stressful conditions. These results underscore the role of tree shade for facilitating regeneration in woodland systems with implications for the development of restoration programs. We thus show that facilitation might play a key role in the success of seedling regeneration in tropical woodlands, which are considered more productive than the more intensively studied alpine and arid systems in this context. Our results also emphasize that the individual species stress responses, rather than the overall environmental stress conditions, determine the outcome of plant interactions.

ACKNOWLEDGMENTS

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Enclosure construction for cattle exclusion in a woodland plot

Chapter 4

Shifts in the effects of fire and herbivory on tree regeneration along climate and soil gradients

(To be submitted)

Samadori S.H. Biaou, Milena Holmgren and Frank J. Sterck

ABSTRACT

Fire and herbivory are the most frequent disturbances shaping tropical savannas and woodlands. Although these disturbances usually co-occur, their interactive effects on tree regeneration have rarely been experimentally assessed. We examined how fire and grazing affect tree regeneration in woodlands along gradients of soil conditions and water availability. We predicted that frequent fire and grazing combined would have a stronger negative effect on tree recruitment than each of these disturbances separately and that effects on tree recruitment would be more negative under high abiotic stress such as high salinity, low water availability or low soil fertility. We conducted a field experiment in Benin and applied four experimental treatments (no disturbance, fire alone, grazing alone, grazing and fire) to 68 plots distributed across climate and soil gradients. Each plot was monitored annually between 2003-2006 for changes in sapling species richness and density.

Overall, an increase in fire frequency increased sapling species richness but did not have any significant effect on sapling density while grazing alone had no significant effect on either species richness or density. The two disturbances combined had a positive effect on sapling species richness but not density. However, under conditions of high soil salinity both species richness and density were reduced by grazing, whereas positive effects were observed under low salinity. Thus, the studied woodlands were resilient to fire and grazing disturbances but this resilience was lost under conditions of high abiotic stress. Our results emphasize that interactions between disturbances and abiotic stress are more important than the independent effects of these factors on tree regeneration. These results show that effects of the disturbances are reversed when critical thresholds are crossed in the abiotic environment. As grazing and fire are increasingly used as management tools in nature conservation, it is important to account for such shifts in the ecosystem response under changing environmental conditions.

Keywords: Burning, Disturbance, Grazing, Sapling recruitment, Savanna, Soil salinity, Soil fertility, Species richness, Water stress, Woodland.

INTRODUCTION

Woodlands cover almost 14 % of the total surface in Africa and represent 25 % of its natural vegetation (Mayaux *et al.*, 2004). They have larger woody cover than savannas (Bellefontaine *et al.*, 1997) and are often characterized by a mosaic pattern, with woody patches of varying density and size dispersed in a matrix of herbaceous plants (Frost, 1996; Lejeune *et al.*, 2002). While climate and soil set the limits to vegetation growth in tropical regions (Bond *et al.*, 2005), fire and herbivory are the most frequent disturbance factors driving vegetation dynamics (Frost, 1996; Bond, 2005; Sankaran *et al.*, 2005; Mourik *et al.*, 2007) and affecting species composition (Keeley *et al.*, 2003; Zida *et al.*, 2007), vegetation structure (Higgins *et al.*, 2000; Sankaran *et al.*, 2005; Zida *et al.*, 2007), as well as nutrients cycling (van de Vijver, 1999; Wan *et al.*, 2001). As a result, woodlands can exhibit shifts between an open grassy state and a dense woody state. A decrease in woody biomass is generally accompanied by an increase in grass biomass and any factor such as disturbances that prevents one of these life forms will likely favour the other (Huston, 1994; Van Langevelde *et al.*, 2003).

Fire and herbivory usually co-occur in woodlands and savannas but most of our knowledge is based on studies focusing on each disturbance factor alone. Persistent and intensive browsing as well as frequent and intense fires can strongly limit tree recruitment (Bond & Keeley, 2005). On the other hand, there are several interesting indirect effects of herbivory and fire (Zimmerman & Neuenschwander, 1984; Van Langevelde *et al.*, 2003). By reducing grass biomass, grazers can potentially reduce fuel loads and reduce fire occurrence which indirectly facilitates tree seedling recruitment. Lower grass biomass can also reduce grass-tree seedling competition (Jeltsch *et al.*, 1996; Ball *et al.*, 2002). Several studies of vegetation dynamics in tropical regions noted that the increase in woody biomass is often associated with increased herbivores populations (e.g. Jeltsch *et al.*, 1997; Eckhardt *et al.*, 2000; Roques *et al.*, 2001; Sankaran *et al.*, 2008). However, there is scarce empirical evidence of such positive effects of herbivory on tree recruitment (e.g. Silva *et al.*, 2001; Zida *et al.*, 2007) and negative effects are also reported (Proulx & Mazumder, 1998; Stern *et al.*, 2002). The suggested indirect positive effects should depend on herbivores foraging behaviour since increased trampling and potential tree seedling consumption are often found as well (Pettit *et al.*, 1995; Alemayehu Wassie, 2007). In regions with a prolonged dry season cattle browsing seems frequent because of increased food stress (e.g. Ouédraogo-Koné *et al.*, 2006).

The effects of herbivory and fire are expected to depend on abiotic stress determined by the availability of resources (Huston, 1994; Sankaran *et al.*, 2005; Bucini & Hanan, 2007). Stress can be due to either a toxic level (e.g. salinity) or a low level of resources (e.g. water and fertility) and it affects mostly species growth while disturbances involve removal or destruction of plant biomass (Huston, 1994). The dynamic equilibrium model (Huston, 1979; Huston, 1994) predicts optimal conditions for species growth at both intermediate level of disturbances and intermediate level of stress. Dry conditions (Holmgren & Scheffer, 2001) and low soil fertility (Proulx & Mazumder, 1998) reduce plant resilience to disturbance, and clearly affect also the frequency and intensity of the disturbances themselves (Govender *et al.*, 2006; Bucini & Hanan, 2007). Under productive conditions (e.g. high fertility and high water availability), competition between species is increased and few species tend to dominate the ecosystem, unless the species populations are reduced by an externally-imposed mortality by for example fire and grazing (Huston, 1994; Bond & Keeley, 2005). Although disturbances could limit sapling recruitment into adult size-classes, particularly at high frequency and intensity of disturbances (Bond & Keeley, 2005), plants can recover faster under productive conditions. Thus, the interplay of fire and herbivory can probably have more pronounced negative effects under low productivity conditions.

In this study, we evaluate how herbivory and fire affect tree regeneration in West African woodlands. We focus on how their independent and joint effects change with increasing abiotic stress of soil salinity, soil fertility and water availability. We hypothesized that (1) frequent fire reduces sapling species richness and sapling density, (2) frequent grazing reduces sapling species richness and sapling density (3) frequent fire and grazing combined have a stronger negative impact on sapling species richness and sapling density than each of the disturbances separately, (4) the negative effects of the two disturbances is higher under high abiotic stress. We also examined how woodland individual species were affected by the disturbances and stress factors and we checked whether species responses were consistent with those from the entire sapling community. In order to test the hypotheses, we applied four experimental treatments (no disturbance, fire alone, grazing alone, grazing and fire) to 68 plots distributed across climate and soil gradients in Benin and monitored each plot annually between 2003 and 2006 for changes in sapling species richness and density.

METHODS

Study area

We conducted the experiment at 17 woodland sites along a latitudinal gradient in Benin. The sites were primarily selected so as to encompass the climatic range associated with woodlands distribution (Fig.1) (see Sokpon *et al.*, 2006). Woodlands represent, after savannas, the second most important vegetation type in Benin, with 38.4 % of total land cover (Mayaux *et al.*, 2004). The annual precipitation (989 - 1198 mm) and the reference evapotranspiration (1587 - 1898 mm) in the study area (FAO, 2008a) are significantly correlated with the latitudinal position of the sites, expressing an increasing drought from south to north (Appendix 1). Accordingly, the dry season (i.e. months with precipitation less than half of evapotranspiration) is only 5 months (November-March) in the southern range of our study area while it extends to 7 months (October-April) towards the north. Altitude of the study sites ranges between 250 and 400 m. a. s. l. Soils derive from metamorphic and crystalline rocks and are mostly of ferruginous type (Faure & Volkoff, 1998). Soil texture on experimental sites varied from loamy sand (i.e. 6-12 % of clay, 11-34 % of silt and 70-82% of sand) to sandy loam (i.e. 10-18 % of clay, 18-23 % of silt and 55-67 % of sand).

Experimental design and vegetation monitoring

Across the climate gradient, we selected 17 sites in woodland forests and installed four treatment plots (20 x 20 m) at each of these sites in September-October 2003. We randomly assigned four treatments (control; fire only; grazing only; fire + grazing) to the four experimental plots of each site. This corresponded to a total of 68 plots initially equally distributed among the four treatments across the study area. We constructed enclosures for the grazing-free plots and cleared a fire break around all plots each year.

At the initial sampling, we divided each experimental plot in four 100 m^2 (10 x 10 m) subplots and selected one randomly four sapling monitoring. We counted the number of sapling stems and species in this permanent subplot (100 m^2) during the second half of the rainy season (August to October) each year from 2004 to 2006. Sapling refers here to woody species between 30 and 150 cm height and for multi-stemmed individuals we counted each stem as a separate individual. Species identification and nomenclature followed Akoègninou *et al.* (2006).

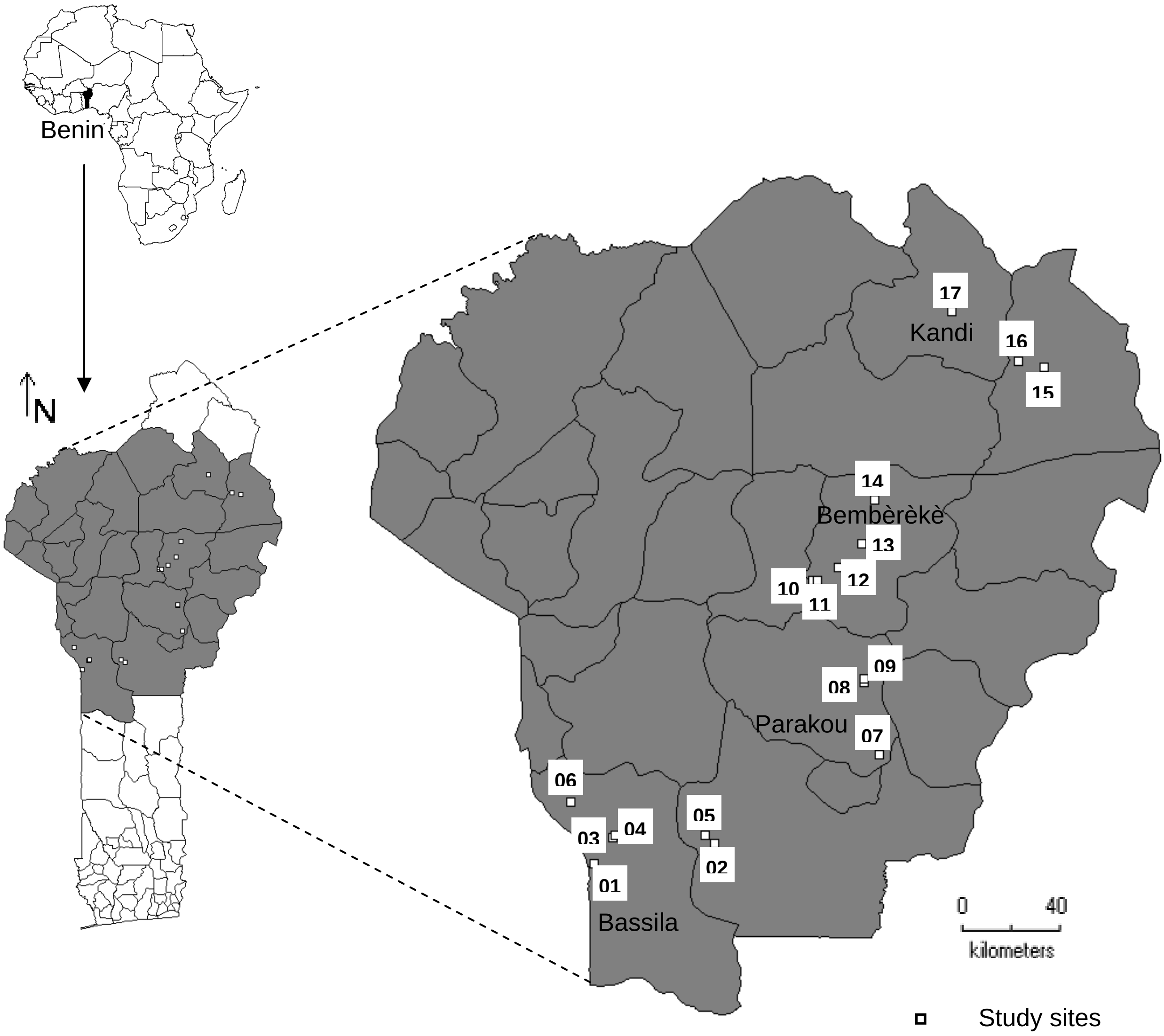

Figure 1: Study sites locations in Benin. The shaded area on the graph corresponds to regions where woodlands occur in Benin and numbers (1 to 17) represent study sites.

Water stress

We expressed water stress differences between experimental sites by the water deficit (in mm), calculated as the difference between the precipitation (P) and the reference evapotranspiration (ET) following Paltineanu *et al.* (2007). The annual water deficit was correlated with the latitudinal position of the sites and ranged from -414 mm to -919 mm from South towards North of the study area. Because all values for water deficit were negative, we took the absolute value in the following analysis to facilitate the interpretation of results. We obtained the average precipitation and reference evapotranspiration for each experimental site from the Aquastat climate database (FAO, 2008a). The FAO Aquastat is an interactive tool to query a spatial data-set containing mean monthly climate data at a 10 minute spatial resolution for the period 1961-1990.

Soil conditions

In August 2004, we collected soil samples in the first 30 cm soil surface within each of the 68 experimental plots in order to characterize soil variability. We collected the samples at the four corners and the centre of each experimental plot, and mixed them to form one composite sample per plot. The analyses comprised soil texture (i.e. sand, silt and clay proportions) and chemical properties (i.e. pH, total carbon, total nitrogen, organic matter, available phosphorus, cation-exchange capacity and exchangeable bases). Soil analysis was performed in Benin at the soil laboratory of the National Institute for Agricultural Research (Laboratoire des sciences du sol d’Agonkanmey, INRAB).

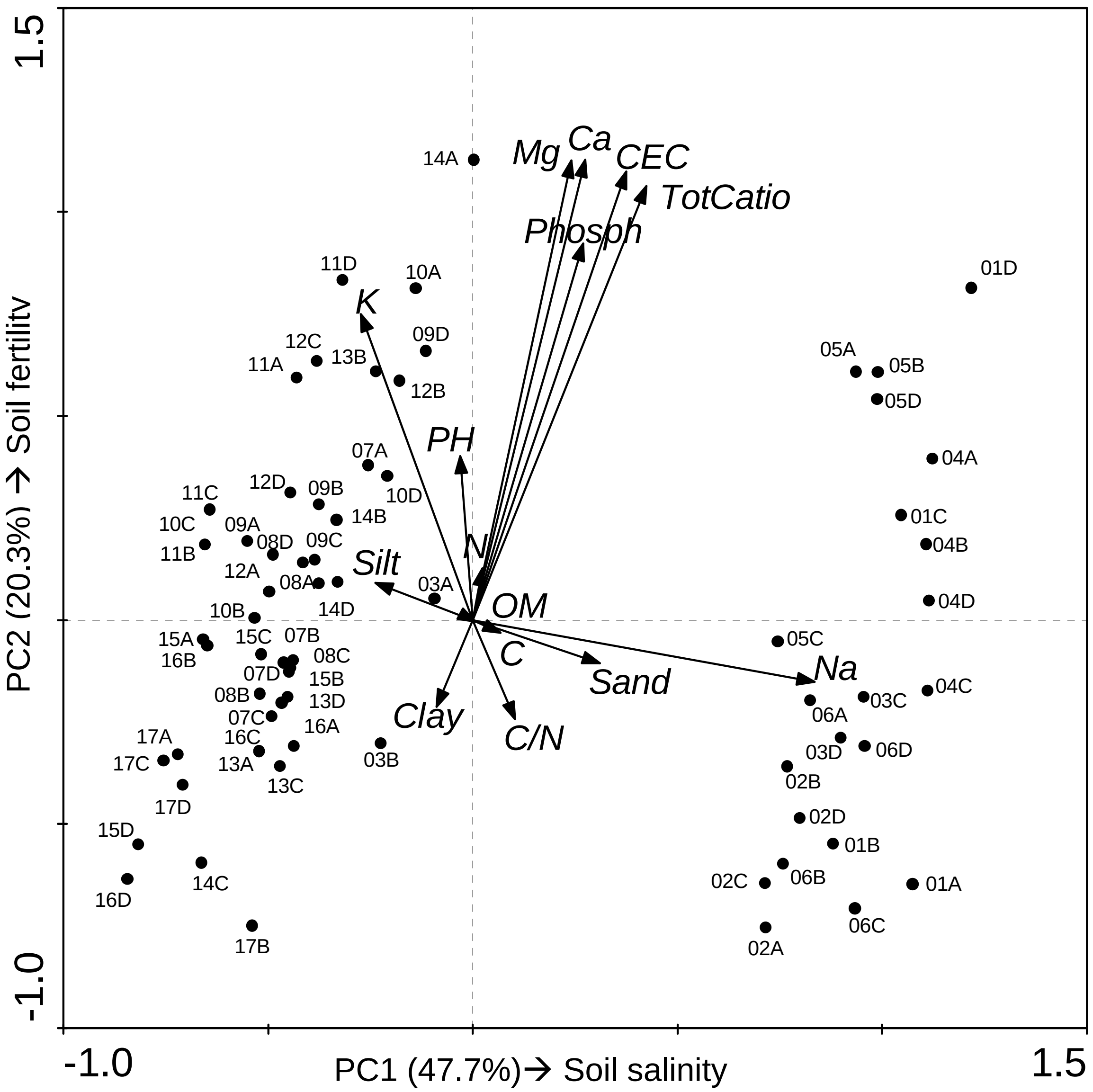

Figure 2: PCA ordination graph of woodlands soil samples. Numbers on the graph represent study sites (1 to 17) and letters (A –D) differentiate the four treatments plots from each site. The first axis is significantly correlated with Na content and explains 47.7 % of the variance in woodland soil conditions. The second axis is significantly correlated with soil fertility elements (Mg, Ca, CEC, total cations, phosphorus) and explains 20.3 % of the variance.

We reduced the dimensionality of soil data using Principal Component Analysis (PCA) with canoco software (ter Braak, 1987) after log transforming the data to account for differences in measurement scales. The PCA produced two main soil gradients: soil salinity and soil fertility which accounted together for 68 % of the total soil variance. Soil salinity (sodium content, Na) emerged as the predominant gradient, with 47.7 % of the total soil variance explained and it was highly correlated ($r = 0.98$) with the first PCA axis (PC1) (Fig. 2). This axis clearly separated sites characterized by a higher Na content (0.16-1.5 cmol kg^{-1}) from those with a lower Na content (<0.16 cmol kg^{-1}). The second axis (PC2) was characterized by strong positive loadings of major soil fertility elements: total cations (TotCatio, $r = 0.82$), cation-exchange capacity (CEC, $r = 0.85$), exchangeable bases ($r = 0.87$, 0.87 and 0.58 respectively for Ca, Mg and K) and available phosphorus (P, $r = 0.71$). Soil total cations (3.3 - 13.3 cmol kg^{-1}), CEC (3.8 - 13.8 cmol kg^{-1}) and available phosphorus (1- 14 mg kg^{-1}) varied greatly across experimental sites. We used plot scores on the first two principal components as proxies for soil salinity (PC1) and soil fertility (PC2) in the subsequent analysis.

Fire and grazing disturbances

Detailed fire and grazing history was not available for any of the experimental plots. Our observations during this four-year study indicate that woodlands in the study area usually burn at 1 to 2 years intervals, and mostly in the dry season between December and February. The study sites are located in woodlands that are grazed by cattle all the year except during the rainy season (April – October) when cows are tied to avoid their incursion in crop fields. Average cattle population density in the study area in 2004 was 13-22 animals / km^2 (FAO, 2008b). At all sites, our grazing plots were visited mainly by domestic livestock composed essentially of cows (see photograph Appendix 2A). There was no grazing by large wild herbivores as all plots were located outside forest reserves. Due to logistical constraints (i.e. duration of the experiment, number and geographical range of the study sites), we could not monitor precisely the grazing intensity and frequency in our experimental plots. Thus, we relied only upon our cattle exclusion treatment.

Every experimental year, we burned the fire-only and fire+grazing plots in December-January when grasses are dry. This resulted in an almost homogeneous burning of the plot surface (see photograph Appendix 2B). Because most woodland species drop their leaves during the dry season, leaves frequently form a continuous and highly flammable layer that makes wild fires extremely difficult to control (see photograph Appendix 2C). Unintended fires occurred in several plots and complicated the initial two-factor design of the experiment. Thus, instead of using the initial treatment variable in our statistical analysis, we recorded every year the grazing occurrence (yes/no), the number of fires since the beginning of the experiment (nf) and the time since the last fire (tlf, in year).

Statistical analysis

To test for changes in sapling species richness and density across disturbances and abiotic stress gradients we used linear mixed effects models (Pinheiro & Bates, 1998). This approach allowed accounting for the unbalanced structure of our data (i.e. different number of observations per disturbance type per site after unintended fires) and the pseudo-replication (i.e. measurements of the same plots over time and plots nested within sites). We expressed the relative change in sapling species richness and sapling density as the ratio between the value at a given year (N_t) and the initial value (N_0): N_t/N_0 to estimate the extent of change from the original condition (i.e. values greater than one indicate an increase in sapling species richness or density). For each of the two dependent variables (density and species richness), we conducted the analysis in three steps: (i) baseline model comprising the random effect and errors covariance structure, (ii) full model including all fixed effects added to the baseline model and (iii) determination of the best fitting model through the simplification of the full model.

We compared alternate baseline models, with different random effect types and different error covariance structures, using likelihood ratio tests to check whether adding more complexity improved the model fit (see Pinheiro & Bates, 1998; Crawley, 2007). For both sapling species richness and density the model was significantly improved with plots nested within sites and the inclusion of a random intercept. We did not find a significant departure from homoscedasticity regarding errors variance for the two dependent variables. However, the model for sapling density was significantly improved with autocorrelation of responses, contrary to sapling species richness.

We constructed the full model for each dependent variable by adding to the baseline model all available predictors and their two-way interactions. We excluded interactions with year because the available predictors were not time-dependent except the number of fires and time since last fire. Predictors used to model changes in sapling species richness and density were: year, grazing, number of fires, time since last fire, water deficit, soil salinity (PC1 scores), soil fertility (PC2 scores) and initial woody biomass (Table 1). Initial woody biomass was estimated by the total woody species basal area (dbh > 5 cm) in each plot at the first inventory. To provide an insight in the order of the subsequent removal of predictors, we segregated the variance explained by each variable for changes in sapling species richness and density using hierarchical partitioning of variance (Table 1). This consisted in computing the increase in the fit (measured here as R^2) of all models with a specific variable compared with the equivalent model without that variable (Chevan & Sutherland, 1991; Mac Nally, 2002).

Table 1: Variables used for modelling changes in sapling species richness and density in woodlands. The explanatory power of each predictor is indicated by the percentage of variance it explained in the full model for sapling richness and density.

Variable	Encoding	Description	Range	Effect included	% Variance explained	
					Richness	Density
year	Integer	Year after the initial sampling	1 to 3	Fixed	2.3	5.8
graz	Categorical	Grazing: Plot opened to grazing (Yes) or protected (No)	-	Fixed	6.0	2.3
nf	Integer	Number of fires since the initial sampling	0 to 4	Fixed	8.6	0.9
tlf	Integer	Time since last fire (in years)	0 to 4	Fixed	1.7	2.1
wd	Real	Water deficit (mm)	414 to 909	Fixed	10.9	21.4
sal	Real	Soil salinity = sites scores of PCA axis 1	-0.84 to 1.22	Fixed	49.2	61.2
fert	Real	Soil fertility = sites scores of PCA axis 2	-0.75 to 1.13	Fixed	21.2	5.3
biom	Real	Initial biomass = Basal area of trees (m2/ha, dbh > 5cm)	6.2 to 29	Fixed	0.2	1.1
Plot	Categorical	Plot identity (nested within sites); 68 plots	-	Random	-	-

We reduced the full model step by step, starting with the removal of the interactions involving variables with the lowest explanatory power as indicated by the hierarchical variance partitioning. At each step of the model simplification, we compared alternate models using the likelihood ratio test and selected the model that significantly improved the model fit with the lowest Akaike information criterion (AIC). We ultimately used the restricted maximum likelihood (REML) method to estimate parameters in the best fitting model following Pinheiro and Bates (1998). Final checking of the best fitting models indicated that residual errors were reasonably close to a normal distribution and that the linear model adequately explained the variation in changes of sapling species richness and density.

To assess how species were individually influenced by disturbances and abiotic conditions, we analyzed the relative change in the density of each species separately, using the best fitting model obtained for the entire sapling community density. The relative change in the species density was calculated as previously described but we added 1 to the denominator to avoid dividing by zero for species that were not present at the initial sampling. In total 91 sapling species were observed during the whole study period but many were infrequent and valid statistical tests could not be performed on them. We conducted the analysis only for the 43 most common species (those observed at least in 15% of all samples). We then counted the proportion of negative and positive responses among the species for each predictor variable and used a chi-square test to assess whether the two outcomes are equally likely to occur (i.e. half of the responses are negative and half are positive).

All analyses were performed within the R 2.7.1 computing environment (R Development Core Team, 2008) with the packages nlme for mixed models fitting and hier.part for variance partitioning. Likelihood ratio test was implemented with the Anova function available in R.

RESULTS

Overall, grazing and fire explained less variation in sapling species richness and density than stress variables such as soil salinity and water deficit. In the full model for sapling species richness, the number of fires and grazing explained respectively 9 % and 6 % of the variance while soil salinity and water deficit accounted respectively for 50 % and 11 % (Table 1). For sapling density, the number of fires and grazing explained respectively 1 % and 2 % of the variation compared to 61 % for soil salinity and 21 % for water deficit. Variance partitioning in the reduced models for sapling species richness and density confirmed this predominant role of stress variables (data not shown) as for the full models.

Effects of fire

We predicted a decline in sapling species richness and density with increasing fire frequency. In contrast, species richness increased significantly with the number of fires (P = 0.02) but not density (Table 2). The relative increase in sapling species richness was 38% at the highest fire frequency (burning four times) while it was 32 % in unburned woodlands and ranged from 22 % to 39 % at intermediate fire frequency (one to three fires). Clearly sapling species richness was promoted by fire and showed a monotonous increase under increasing fire frequency.

Effects of grazing

Contrary to our expectation grazing alone had no significant effect on sapling species richness and density (Table 2). The most probable reason is the significant interaction between grazing and other variables in the model such as fire and stress factors. Otherwise species richness tended to increase more in grazed (38 %) than ungrazed (24%) woodlands while the increase in density was similar in grazed (57 %) and ungrazed (57 %) woodlands, regardless of the influence of other factors.

Combined effects of grazing and fire

Our third hypothesis stated that fire and grazing combined would have a more negative impact on sapling species richness and density than either fire or grazing alone. In contrast, grazing combined with high frequency of fires increased sapling species richness but had no significant effect on density (Table 2, Fig. 3A and 3B). Indeed, the increase in species richness was higher in grazed (27 - 48 %) than ungrazed woodlands (18 - 31 %) at any fire frequency, and it was highest (48 %) in grazed and most frequently burned woodlands (i.e. burned four times). Conversely, sapling species richness also increased under grazing combined with increasing time between fires by 37-44 %. These results suggest that grazing had a positive effect on species richness both with and without fire but the increase in species richness was larger at the highest fire frequency than without fire. In contrast, sapling density differed little between grazed and ungrazed plots at any fire frequency. We conclude that grazing and fire combined had a positive effect on sapling species richness but not density.

Effects of grazing and fire along stress gradients

We expected a more negative impact of both grazing and fire disturbances under high abiotic stress. High soil salinity had a negative effect on both sapling species richness and density (Table 2). High water deficit had also a negative effect on sapling species richness but not on sapling density while soil fertility had no significant effect on any of the dependant variables. We found a significant interaction effect of grazing and soil salinity on both sapling species richness and density. Under higher soil salinity, sapling species richness and density were further reduced by grazing (Fig. 3C and 3D) while under lower soil salinity grazing increased sapling species richness and density. These results confirmed our hypothesis and suggest that grazing had a negative effect on both sapling species richness and density under high abiotic stress but a positive effect under low abiotic stress.

Table 2: Parameters estimate for change in sapling species richness and sapling density in woodland forests. The symbol "-" indicates variables removed during models fitting while for other variables the significance is indicated by the *P*-value. All independent effects are listed on the table whereas only significant interactions are presented.

Variable	Sapling species richness		Sapling density	
	Estimate	*P*-value	Estimate	*P*-value
<u>Independent effects:</u>				
Year			0.120	< 0.001
Grazing				
Number of fires	0.055	0.022		
Time since last fire				
Water deficit	- 0.001	0.036		
Soil salinity	- 0.294	0.005	- 0.327	0.013
Soil fertility	0.212	0.016		
Woody biomass				
<u>Disturbances interactions:</u>				
Grazing x Time since last fire	0.131	0.010		
Grazing x Number of fires	0.050	0.045		
<u>Disturbances interactions with abiotic stress:</u>				
Grazing x Soil salinity	- 0.225	0.045	- 0.588	< 0.001

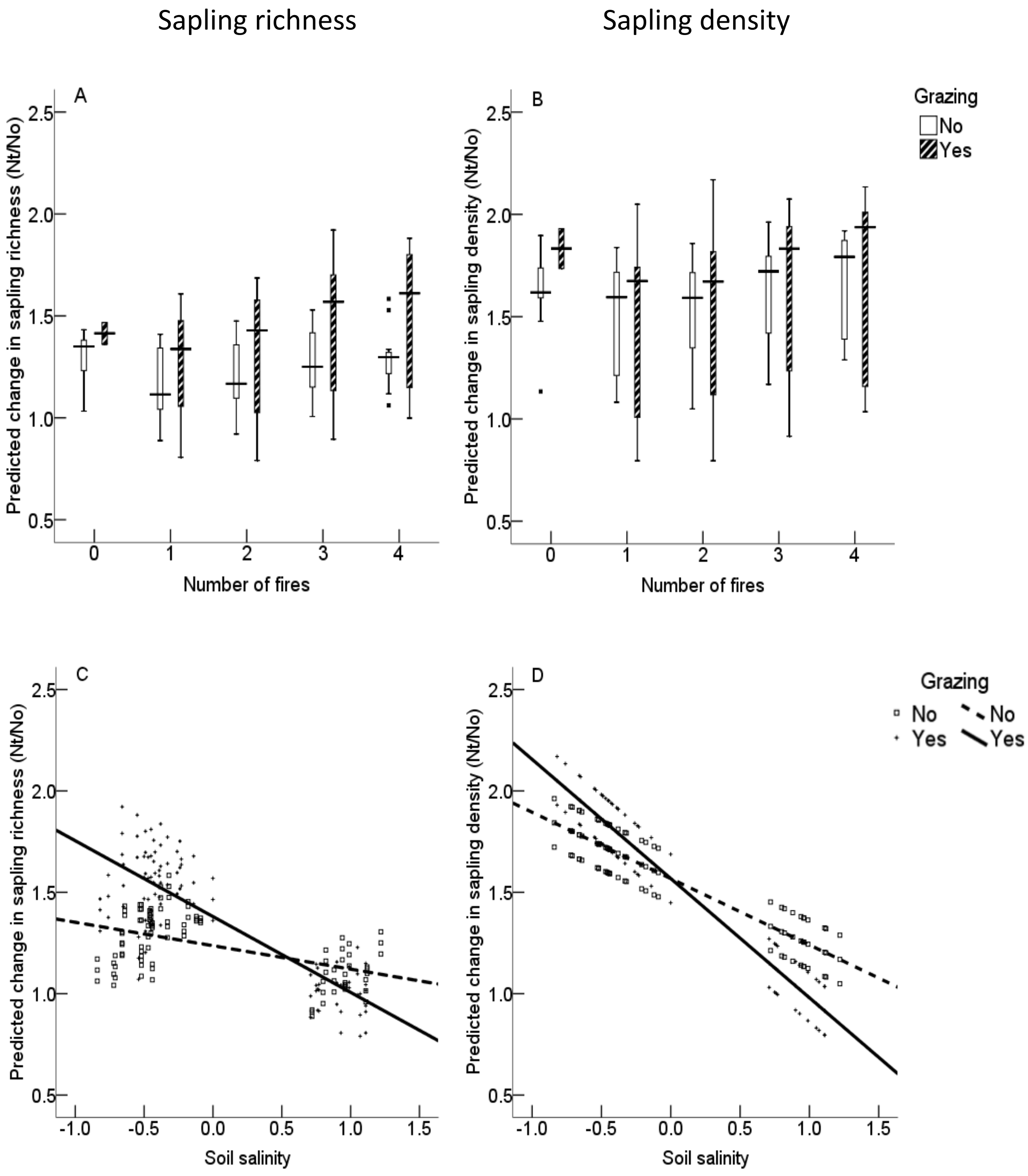

Figure 3: Interactive effects of grazing with fire disturbances (box plots) and grazing with soil salinity (scatter diagrams) on sapling species richness (left panel) and density (right panel). The predicted changes in sapling species richness and density are based on parameters of the best fitting models (Table 2) which account for the pseudo-replication in the design.

Individual species responses

The selected 43 sapling species represented 90.3 % of the total sapling stems counted at all sites during the experiment. We analyzed the relative change in density of these species using the best fitting model for the entire sapling community density which included soil salinity and the interaction of grazing with soil salinity. In line with the results at the entire sapling community, 63 % of the species responded negatively to high salinity (χ^2 = 2.81, df = 1, p = 0.094) and 70 % responded negatively to grazing combined with high salinity (χ^2 = 6.72, df = 1, p = 0.010) (Table 3). The patterns observed in the species populations thus confirmed our hypothesis that disturbances have a negative impact on sapling recruitment at higher abiotic stress.

Table 3: Effects of grazing and soil salinity on the density of individual woodland species. We assumed the same model as for the entire sapling community which included soil salinity and grazing as predictors.

	Individual species responses (n = 43)		Test statistics		
	Negative	Positive	df	χ^2	*p-value*
salinity	62.8 %	37.2 %	1	2.81	0.094
salinity x grazing	69.8 %	30.2 %	1	6.72	0.010

DISCUSSION

We noted that grazing and fire explained less variation in sapling species richness and density than stress conditions such as soil salinity and water deficit (Table 1). This is not particularly surprising given the broad array of climatic and soil conditions covered in our experiment. Climate and soil conditions are generally good predictors of species distribution and vegetation growth potential in tropical regions (Bond *et al.*, 2005). The actual species growth is however expected to be locally constrained by the frequency and intensity of disturbances (Huston, 1994; Sankaran *et al.*, 2005). In the following sections, although our results give emphasis to the significant role of interactions between disturbances and abiotic stress for sapling recruitment, we first consider the individual effects of the disturbances and evaluate how our results fit into the current knowledge. Finally we discuss the effects of the disturbances in the context of stress gradients and their implications for vegetation dynamics.

Effects of fire and grazing on species diversity

Contrary to our predicted negative effects of frequent fire and grazing on sapling, species richness increased significantly under high fire frequency but not under grazing (Table 2; Fig 3). In addition, the two disturbances combined resulted in a higher increase in sapling richness (48 % at the highest fire frequency) than for fire alone (22 - 39 %). Previous studies on the effect of fire and grazing disturbances on species diversity have yielded contrasting results and indicated that species richness can increase along a gradient of increasing disturbances (Schwilk *et al.*, 1997; Hill & French, 2004; Kennard, 2004), decrease (Laris & Wardell, 2006; Zida *et al.*, 2007) or peak in the middle of the gradient (Huston, 1979; Mackey & Currie, 2001). The generally accepted explanation for the disturbance-diversity relationship is that species diversity should reach its maximum at intermediate levels of disturbance (Intermediate Disturbance Hypothesis: Connell, 1979; Huston, 1994) because few species can survive under frequent and intense disturbances while under conditions of infrequent disturbances the species richness decreases due to competitive exclusion by dominant species.

In our experiment, saplings showed a monotonic increase in species richness under increasing fire frequency in contrast to the typical hump-shaped curve suggested by the Intermediate Disturbance Hypothesis. Apparently our burning plan did not cover the entire fire disturbance gradient and the observed pattern suggests a relatively low to moderate fire disturbance. The effect of fire could become negative under late burning in the dry season and probably under longer exposure (i.e. several more burning years). Other experiments indicated significant changes in species richness under grazing (Pettit *et al.*, 1995; Proulx & Mazumder, 1998; Alemayehu Wassie, 2007) but in our experiment grazing alone had no significant effect on species richness. However, fire and grazing combined had more positive effect on sapling richness than fire alone in our experiment. There are several possible explanations underlying the interactive effects of fire and grazing on sapling diversity. Fire and grazing can increase plant diversity by opening space for colonization by new species (Collins, 1987; Chaneton & Facelli, 1991) and by reducing the competitive superiority of dominant species (Huston, 1994; Osem *et al.*, 2002). Other probable influences on the ecosystem include seed dispersal by herbivores (Huston, 1994) and the creation of spatial heterogeneity by both fire and grazing (Groen, 2007) favourable to a higher diversity of species.

Effects of fire and grazing on regeneration density

We predicted a decline in sapling density with increasing fire and grazing frequencies. In contrast, sapling density was not significantly affected by fire and grazing disturbances alone or in combination (Table 2; Fig 3). Depending on their intensity and frequency, fire and herbivores can lower tree regeneration (Brookman-Amissah *et al.*, 1980; Cave & Patten, 1984; Laris & Wardell, 2006) or increase it (Ben-Shahar, 1996; Hoffmann, 1998; Jacobs & Biggs, 2001). Besides, grazing is often cited as probable causal factor for the increased woody biomass observed around the tropics (e.g. Jeltsch *et al.*, 1997; Eckhardt *et al.*, 2000; Roques *et al.*, 2001; Sankaran *et al.*, 2008). The increased woody biomass following disturbances usually results from increased resprouting. The removal of the aerial biomass following fire can activate dormant buds to produce more root suckers or sprouts (Zida *et al.*, 2007). Similarly, herbivores can stimulate resprouting through damages caused by browsing and trampling (Roques *et al.*, 2001; Zida *et al.*, 2007). Although we also observed increased resprouting in our experimental plots (e.g. Appendix 2D), our results suggest that there was no significant effect of fire and grazing on regeneration density.

Influence of abiotic stress

We predicted a stronger negative impact of grazing and fire disturbances under high abiotic stress. The patterns observed in both the entire sapling community (Table 2; Fig 3) and in individual species responses (Table 3) supported this prediction. Soil salinity (potentially causing soil water stress) was the predominant abiotic stress factor influencing tree regeneration in the woodlands. High soil salinity combined with grazing had a negative impact on sapling species richness and sapling density, while the effects were positive under low soil salinity. Soil fertility had no significant effect in our experiment but results from other experiments suggest that stress factors can change from one region to the other. For example, Proulx and Mazumder (1998) found a reversal of grazing impact on species richness in nutrient-rich vs. nutrient-poor ecosystems including forests, grasslands and aquatic systems. Similar shifts were found in annual plant communities along a productivity gradient (Osem *et al.*, 2002). Other studies reported a positive effect of grazing in wet ecosystems (Peltier & Eyog Matig, 1989) and a negative effect in dry ecosystems (Stern *et al.*, 2002). It could be that under unproductive environment, cattle compensate for food shortage by increased seedling consumption (e.g. Ouédraogo-Koné *et al.*, 2006; Alemayehu Wassie, 2007). An alternate explanation for shifts in the effects of disturbances along resource gradients is that high stress can hamper woody plants regrowth following a disturbance (Proulx & Mazumder, 1998) while at lower stress, the disturbances reduce competitive dominance among species and promote high species richness (Huston, 1979).

Factors regulating the balance between trees and grasses are of primary importance for the vegetation dynamics and can induce dramatic changes in the ecosystem. Our experimental results demonstrate that shifts can occur in the effects of disturbances as a result of changes in abiotic stress conditions. Woodlands studied here were apparently resilient to fire and grazing disturbances but this resilience was lost under high abiotic stress. This has great implications for ecosystem dynamics as change in feedbacks involves reduced tree regeneration. As trees and grasses respond in an opposite way to disturbances and stress (Huston, 1994), an increase in grass biomass could create positive feedbacks whereby the probability of fire increases and lock the ecosystem into a grassland state. Such changes in the trajectory of the system could lead ultimately to a highly resilient alternate state (i.e. more grassy state) (Holling, 1973; Ludwig *et al.*, 1997; Kinzig *et al.*, 2006).

CONCLUSION

Overall, our results indicate that interactions between disturbances and abiotic stress are more important than the independent effects of these factors on tree regeneration in woodlands and can lead to significant changes in the ecosystem dynamics. Frequent fires increased sapling species richness but not density while grazing alone had not significantly influenced saplings species richness or density. Fire and grazing combined had a positive effect on sapling species richness but not on density. However, under conditions of high abiotic stress (i.e. soil salinity) sapling species richness and density were reduced by grazing. Thus, the ecosystem resilience to disturbances was lost under conditions of high abiotic stress. The results of the present study illustrate that the effects of grazing and fire can be better understood by taking into account abiotic stress gradients as well as potential interactions between the disturbances.

ACKNOWLEDGMENTS

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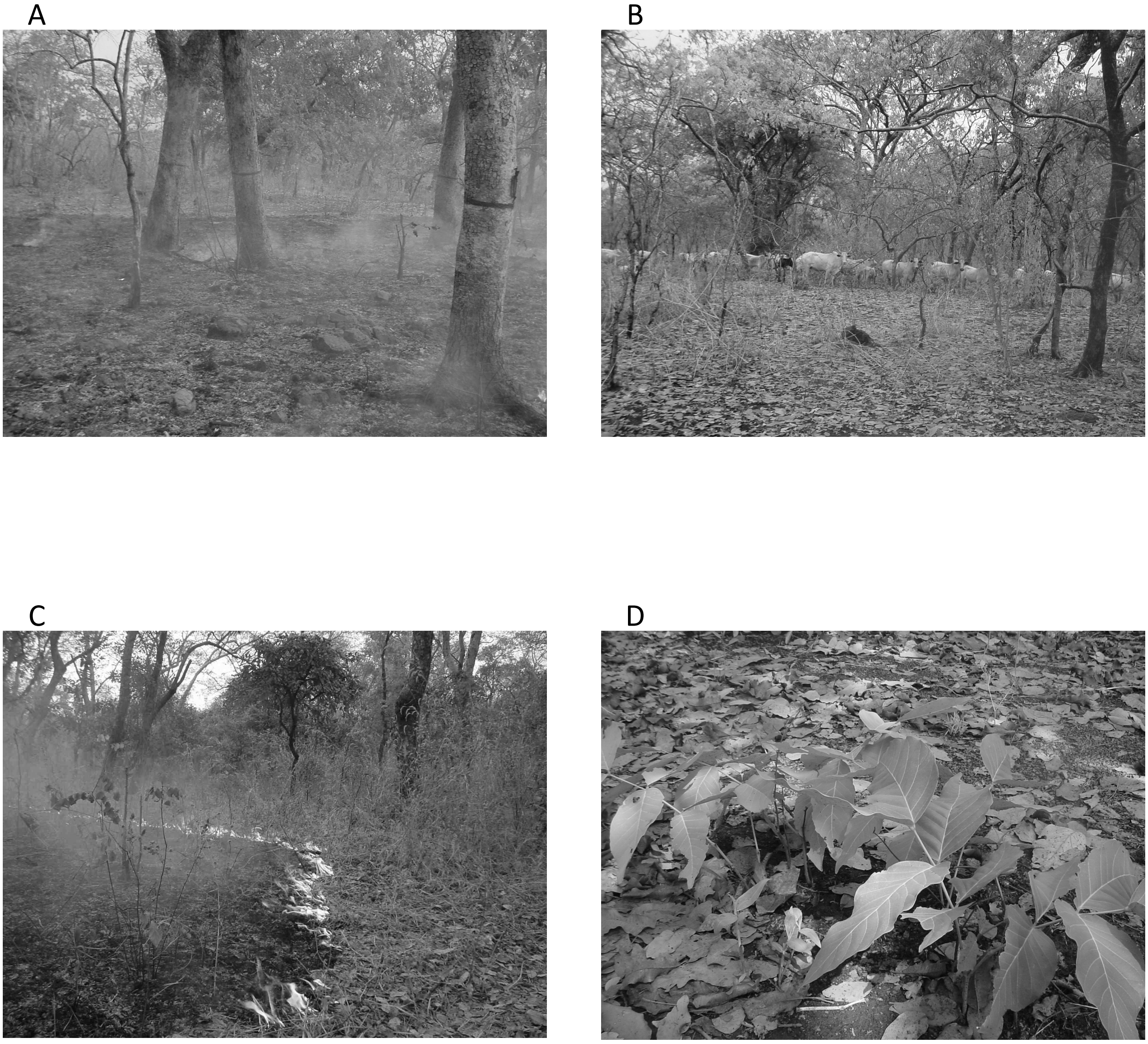
Appendix 1: Main characteristics of the study sites. Sites are ordered by increasing latitude. Only average values per site are presented here since each site is composed of four experimental plots. Water deficit is calculated as Rainfall – PET, which yields negative values. Thus, in the analyses we took the absolute values for water deficit. We used tree basal area (m^2/ha, dbh≥5 cm) as proxy for initial woody biomass.

Sites	Latitude (^{0}N)	Longitude (^{0}E)	Rainfall (mm)	PET (mm)	Water deficit (mm)	Soil salinity (PC1 scores)	Soil fertility (PC2 scores)	Initial woody biomass (m^2/ha, dbh≥5 cm)
1	9.047	1.652	1112	1587	- 475	0.33	0.01	17.82
2	9.133	2.119	1059	1628	- 569	0.23	0.17	12.31
3	9.150	1.719	1124	1606	- 482	0.12	0.06	13.33
4	9.159	1.731	1124	1606	- 482	0.34	- 0.04	16.58
5	9.163	2.082	1077	1622	- 545	0.28	- 0.13	14.90
6	9.288	1.565	1198	1612	- 414	0.27	0.14	17.88
7	9.468	2.759	1094	1672	- 578	- 0.12	0.00	14.83
8	9.755	2.697	1094	1707	- 613	- 0.13	0.00	17.65
9	9.765	2.698	1094	1707	- 613	- 0.11	- 0.10	20.80
10	10.136	2.500	1082	1739	- 657	- 0.12	- 0.11	11.39
11	10.142	2.524	1082	1738	- 656	- 0.15	- 0.14	19.32
12	10.185	2.596	1079	1741	- 662	- 0.12	- 0.12	13.62
13	10.276	2.692	1068	1765	- 697	- 0.13	0.02	19.29
14	10.453	2.736	1053	1788	- 735	- 0.11	- 0.07	17.17
15	10.964	3.397	1001	1859	- 858	- 0.19	0.06	18.43
16	10.980	3.298	1001	1859	- 858	- 0.19	0.10	16.90
17	11.170	3.041	989	1898	- 909	- 0.21	0.14	20.30

Appendix 2: Photographs showing: (A) a freshly burned experimental plots with red paint mark-ups indicating the level of measurement for tree diameter; (B) cattle grazing in recently burned woodland; (C) a ground fire fuelled by a mixture of dry grasses and fallen tree leaves which is typical of the woodlands studied; (D) resprouting from *Isoberlinia doka* species following fire. Photos credit: S.S.H. Biaou.



Tree clusters in woodland

Chapter 5

Tree clustering, sapling species diversity and fire occurrence in woodlands

(To be submitted)

Samadori S.H. Biaou, Milena Holmgren, Frank J. Sterck and Godefridus M.J. Mohren

ABSTRACT

Plants in arid and water-limited environments are expected to cluster due to facilitative interactions among plants. Little is known however about the consequences of facilitative interactions and tree clustering for plant community diversity. In this study, we evaluated the relationship between tree spatial clustering and species diversity using data from woodlands of Benin. Because fire has been proposed as one of the main drivers in vegetation patterning in woodlands and savannas, and because tree clustering can affect in return the probability of fire, we also explored the existence of feedback loops between tree spatial distribution and fire occurrence in woodlands. We tested the hypotheses that tree clustering improves plant diversity; fire promotes tree clustering; and tree clustering reduces the probability of fire.

Tree clustering was predominant at most woodland sites and occurred at two spatial scales. At a fine scale (plant to plant association), tree clustering increased the species diversity through facilitation of rare species. At a coarse scale (patch to patch association), clustering had no significant effect on the species diversity. Tree clustering was not promoted by fires. Fire reduced inter-patch distances at the coarse scale, probably due to intense resprouting. Fine scale clustering of trees reduced the probability of fire while clustering at the coarse scale and total woody cover increased the probability of fire. Our results provide evidence that tree clustering increased plant diversity at a fine scale, which is compatible with Hacker and Gains (1997) theoretical model predicting a positive relationship between facilitation and species diversity. These results however did not provide enough support to potential feedback loops between tree spatial clustering and fire in the woodlands studied.

Key-words: Benin, Facilitation, Feedbacks, Fire probability, Spatial patterns, Species diversity, Tree clustering, West-Africa, Woodland

INTRODUCTION

Woodland represents approximately 25 % of the natural vegetation in Africa and is the second most important vegetation type on the continent after savanna (Mayaux *et al.*, 2004). Woodland occur predominantly in areas with prolonged (6 - 7 months) dry season and generally have larger woody cover (> 20 %) and taller trees (8-20 m height) than savannas (Bellefontaine *et al.*, 1997). In water limited environments like woodlands, plants often exhibit a strong clustering pattern with woody patches of varying density and size dispersed in a matrix of herbaceous plants (Couteron & Kokou, 1997; Aguiar & Sala, 1999; Lejeune *et al.*, 2002). Because tree spatial distribution determines how the species use available resources such as water, light and soil nutrients it has direct consequences for species coexistence and plant community diversity (Callaway, 1997; Condit *et al.*, 2000).

Tree clusters might result from positive interdependence or facilitation between plants (Tirado & Pugnaire, 2003). Plant spatial association in harsh environments often results in improved growth and survival because of reduced abiotic stress (e.g. Aerts *et al.*, 2007), increased nutrient availability (e.g. Gómez-Aparicio *et al.*, 2005), reduced herbivore pressure (e.g. Brooker *et al.*, 2006; Smit *et al.*, 2007) as well as increased protection from fire (Groen, 2007). By facilitating the species that would not normally survive under harsh conditions, tree clustering can enable species to increase their realized niche and thereby enhance the overall community diversity (Callaway, 1997; Hacker & Gaines, 1997; Liancourt *et al.*, 2005; Michalet *et al.*, 2006). Conceptual models (Holmgren *et al.*, 1997; Brooker & Callaghan, 1998) and experimental studies (Holmgren, 2000; Maestre & Cortina, 2004; Maestre *et al.*, 2006; Smit *et al.*, 2007) suggest however that plant-plant interaction can be positive, neutral, or even negative, depending on the level of abiotic stress (e.g. water and nutrients availability) or disturbance (e.g. fire and grazing). Therefore, facilitation is expected to promote species diversity at intermediate stress and disturbance levels (Hacker & Gaines, 1997; Michalet *et al.*, 2006).

Tree clustering is not necessarily associated with facilitation among plants and several other factors can modify or generate patterns in tree spatial distribution, including fire and herbivores. At high frequency, fire can promote tree clustering by preferentially killing isolated trees (Hochberg *et al.*, 1994; Groen *et al.*, 2008). Interestingly, the expansion of tree clusters might in turn alter the spread and the probability of future fires as they may serve as natural fire-breaks in surface fires regime (Turner *et al.*, 1989; Miller & Urban, 2000), or by indirectly reducing grass biomass due to competition between tree and grasses (Minnich & Chou, 1997). Such a negative feedback between tree clustering and fire could give rise to potential feedback loops in the ecosystem, with direct consequences for plant community dynamics and species coexistence. Herbivores can also promote tree clustering through selective or repetitive grazing of some patches due to the positive feedback between grazing and forage quality (Adler *et al.*, 2001; de Knegt *et al.*, 2008), or by accentuating small scale heterogeneity through trampling and deposition of dungs and urines in discrete patches (Afzal & Adams, 1992; Steinauer & Collins, 1995). However, at high grazing and fire frequencies, tree clusters can be disrupted as well.

In this study we assess the effect of tree spatial distribution on woody species diversity and explore the existence of potential feedbacks between tree spatial distribution and the probability of fire occurrence in woodlands of Benin. We tested the hypotheses that (1) tree clustering increases species diversity; (2) high fire frequency increases tree clustering; and (3) tree clustering reduces the probability of fire occurrence in woodlands. An implicit assumption made here is that there may be feedback loops between tree spatial distribution and fire. Our analysis is based on a four years experiment in woodlands of Benin with fire and grazing disturbances along gradients of water stress, soil salinity and fertility. We monitored changes in sapling species richness from 2003 to 2006 and assessed the limiting effect of tree clustering on the species diversity using quantiles regression. During the experiment, unplanned fires occurred from zero to three times in 32 fire-protected plots and we used those data to quantify the effect of tree spatial distribution on the probability of fire occurrence. We used tree spatial distribution at a given year as predictor of fire incidence the following year, after accounting for potential effects of other environmental factors (grazing, water stress, soil salinity and fertility).

METHODS

Study area and abiotic conditions

The experiment was conducted at 17 sites located between 9.05^{o} - 11.17^{o} N latitude and 1.65^{o} - 3.4^{o} N longitude in Benin (Fig. 1). The mean annual precipitation and mean annual reference evapotranspiration are comprised respectively between 989 – 1198 mm and 1587 – 1898 mm across the study sites (averages 1961 - 1990: FAO, 2008a) and they were mostly correlated with the latidunal positions of the sites. Accordingly, the dry season (i.e. months with precipitation less than half of evapotranspiration) is only 5 months (November-March) in the southern range of our study area while it extends to 7 months (October-April) towards the north. Instead of using simple measures of rainfall and evapotranspiration in the analyses, we used water deficit (Paltineanu *et al.*, 2007) as it integrates both parameters and provides a good indication of the water stress potentially experienced by plants. We calculated the water deficit (in mm) in each study site as the difference between the precipitation (P) and the reference evapotranspiration (ET) (Paltineanu *et al.*, 2007). Because evapotranspiration is usually higher than precipitation in dry ecosystems (Murphy & Lugo, 1995), the annual water deficit was negative for all study sites and ranged from - 414 mm to - 919 mm from South towards North of the study area. To avoid manipulating negative numbers and to facilitate the interpretation of results, we took the absolute value for water deficit in the subsequent analyses, and we refer to it as water stress from here onwards.

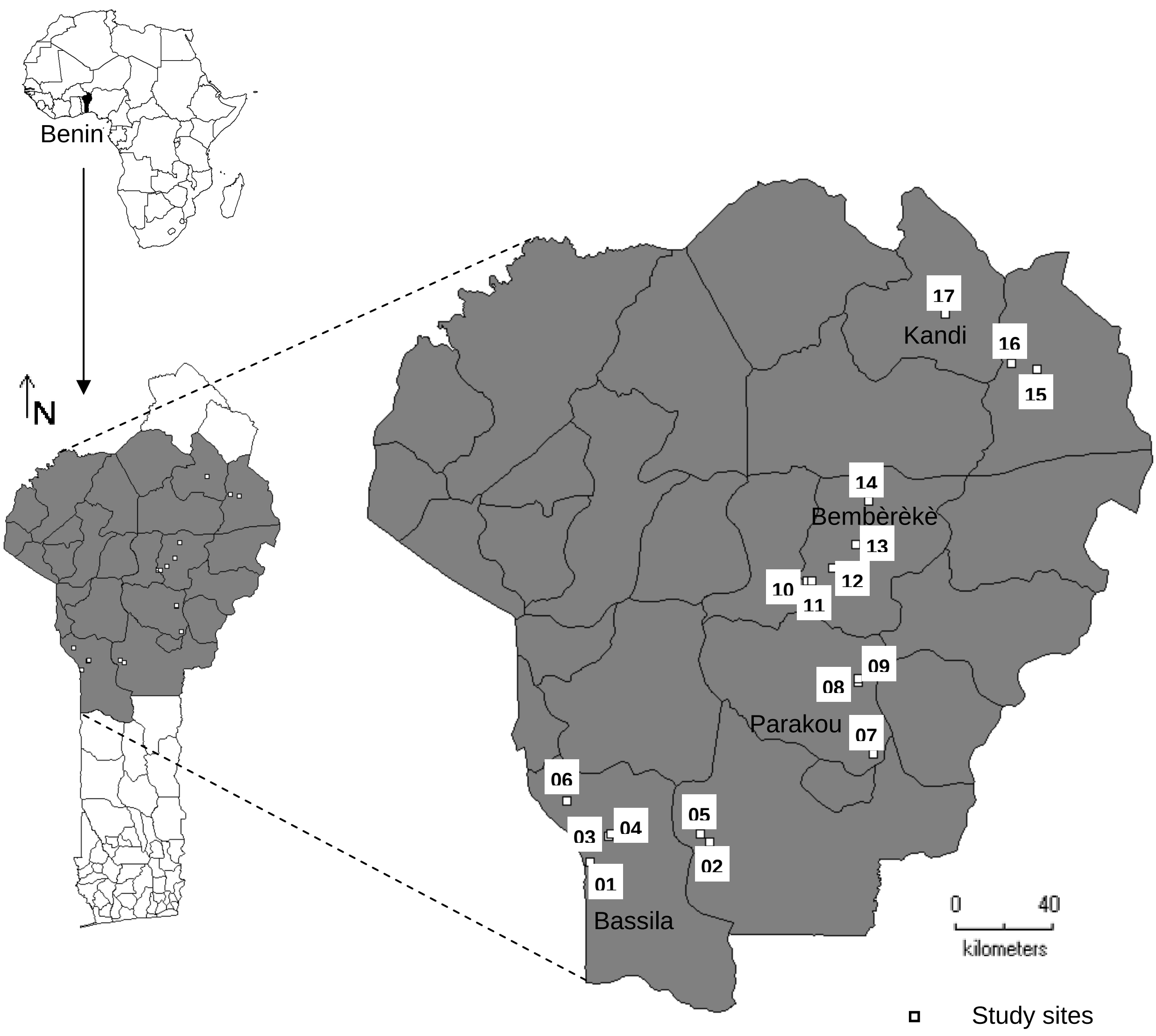


Figure 1: Study sites locations in Benin. The shaded area on the map corresponds to regions where woodlands occur in Benin and numbers (1 to 17) represent study sites.

Soils in the study area are mostly of ferruginous type (Faure & Volkoff, 1998). In order to characterize soil variability in our experimental plots, we collected soil samples in the first 30 cm soil surface from all experimental plots in August 2004 and analyzed them for soil texture (i.e. sand, silt and clay proportions) and chemical properties (i.e. pH, total carbon, total nitrogen, organic matter, available phosphorus, CEC and exchangeable bases). We used one composite sample per plot consisting of a mixture of five sub-samples collected at the four corners and the centre of each plot. Soil analysis was performed in Benin at the soil laboratory of the National Institute for Agricultural Research (Laboratoire des sciences du sol d'Agonkanmey, INRAB).

Soil texture on experimental sites varied from loamy sand (i.e. 6 - 12 % of clay, 11 - 34 % of silt and 70 - 82% of sand) to sandy loam (i.e. 10 - 18 % of clay, 18 - 23 % of silt and 55 - 67 % of sand). Sodium (Na) content was between 0.08 - 1.5 cmol kg^{-1} while soil total cations, cation-exchange capacity (CEC) and available phosphorus were respectively between 3.3 - 13.3 cmol kg^{-1}, 3.8 - 13.8 cmol kg^{-1} and 1 - 14 mg kg^{-1}. To reduce the number of soil variables and identify major soil gradients in our study area, we used a principal component analysis (PCA) with canoco software (ter Braak, 1987) after log transforming the data to account for differences in measurement scales. Soil salinity (sodium content, Na) emerged as the predominant gradient, with 43.3 % of the total soil variance explained and it was highly correlated (r = 0.98) with the first PCA axis (PC1). The second axis (PC2) was characterized by strong positive loadings of major soil fertility elements: total cations (TotCatio, r = 0.82), cation-exchange capacity (CEC, r = 0.85), exchangeable bases (r = 0.87, 0.87 and 0.58 respectively for Ca, Mg and K) and available phosphorus (P, r = 0.71). We eventually used plot scores on these two principal components as proxies for soil salinity (PC1) and soil fertility (PC2) in the subsequent analysis.

Experimental design

In September-October 2003, we selected 17 sites in woodland forests across the climatic gradient and installed four treatment plots (20 x 20 m) at each of these sites. We randomly assigned four treatments (control; fire only; grazing only; fire + grazing) to the four experimental plots of each site and constructed enclosures for the grazing-free plots and cleared a fire break around all plots each year. The whole experiment involved 68 plots which were initially equally distributed amongst our four treatments. From 2003 to 2006 we measured and recorded the x-y coordinates of all individual woody species ≥ 30 cm height in each 10 x 10 m sub-plot.

Using data from our consecutive samplings, we calculated the species richness and evenness for each plot by year. Data presented here were restricted to sapling species which we define as woody species between 30 and 150 cm height. To account for differences in sapling species density, we calculated the rarefied species richness (i.e. expected species richness) from a random subsamples of 25 individuals drawn in each plot (Hurlbert, 1971). For the species evenness we used Smith and Wilson’s index (Evar) which is independent from species richness and has equal sensitivity to minor and abundant species (Smith & Wilson, 1996). Evar is comprised between 0 - 1, with 1 indicating equal abundance of all species and values close to 0 indicating dominance.

Fire and grazing disturbances

Because detailed fire and grazing history was not available for any of the experimental plots, we used only information collected during our experiment from 2003 to 2006. The study sites are located in woodlands that are grazed by cattle all the year except during the rainy season (April – October) when cows are tied to avoid their incursion in crop fields. There was no grazing by large wild herbivores as all plots were located outside forest reserves. Average cattle population density in the study area in 2004 was 13-22 animals / km2 (FAO, 2008b).

Every experimental year, we burned the fire-only and fire+grazing plots in December-January when grasses are dry. Unplanned fires occurred in several plots and instead of using the initial treatment variable in our statistical analyses, we monitored fire occurrence every year and recorded for each plot the number of fires since the beginning of the experiment and the time since the last fire (in year).

Measures of tree spatial clustering

We assessed the importance of tree spatial clustering in the studied woodlands and characterized changes in tree distribution pattern within plots using point pattern analysis based on the L-function (Fortin *et al.*, 2002). The L-function is the linearized form of Ripley's K-function (Ripley, 1977). Ripley’s K describes how spatial interactions change through space and is calculated as the mean number of points lying within a circular window of varying radius t: $K(t) = \lambda^{-1} \Sigma \Sigma I_t (e_i, e_j) / n$, for $i \neq j$ and $t > 0$; λ is estimated as the density n/A where A is the area of the plot; I_t is an indicator function that takes value 1 when e_j is within distance t of event e_i and 0 otherwise; n is the total number of points. The corresponding L-function is $L(t) = \mathrm{sqrt}(K(t) / \pi)$, with sqrt standing for “square root”. We applied Ripley's isotropic correction in the determination of the L-function and restricted t values to a maximum of 1/4 of the side length of the study plot to reduce bias arising from edge effects (Ripley, 1988). Tree spatial pattern is evaluated by plotting L(t) against t. The theoretical value of the L-function for a completely random (uniform Poisson) point pattern is $L(t) = t$. To test whether there is evidence to allow rejection of the complete spatial randomness hypothesis, a 95 % confidence interval for the theoretical L-function was obtained through Monte Carlo simulations. At distances where significant clustering occurs among plants the observed L-function lies above the upper envelope of the theoretical distribution while it is below the lower envelope in case of a regular plant distribution (see Fig. 2).

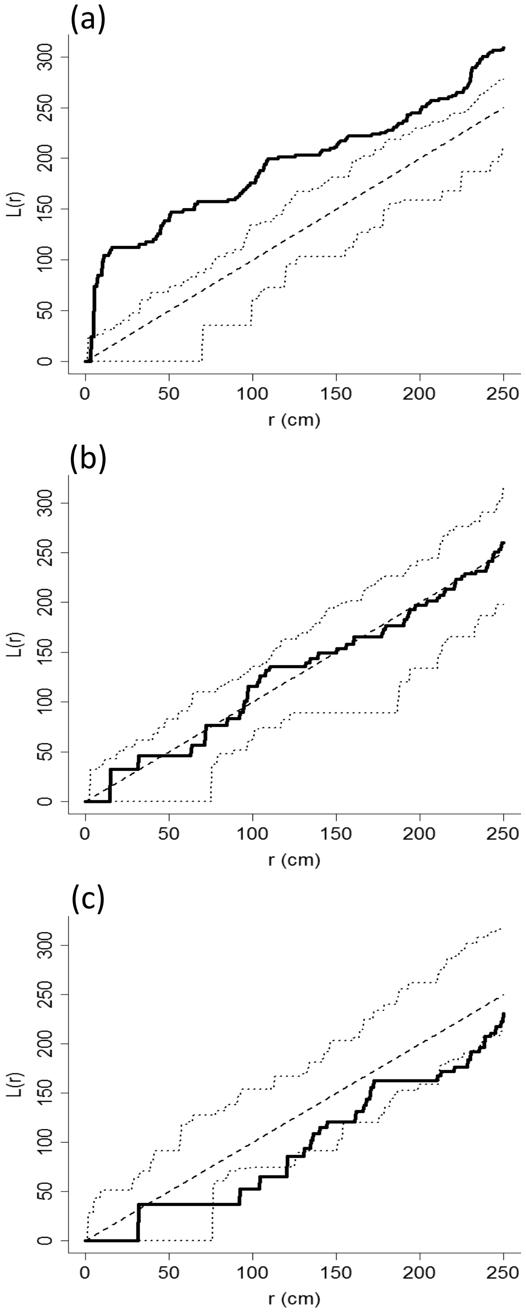
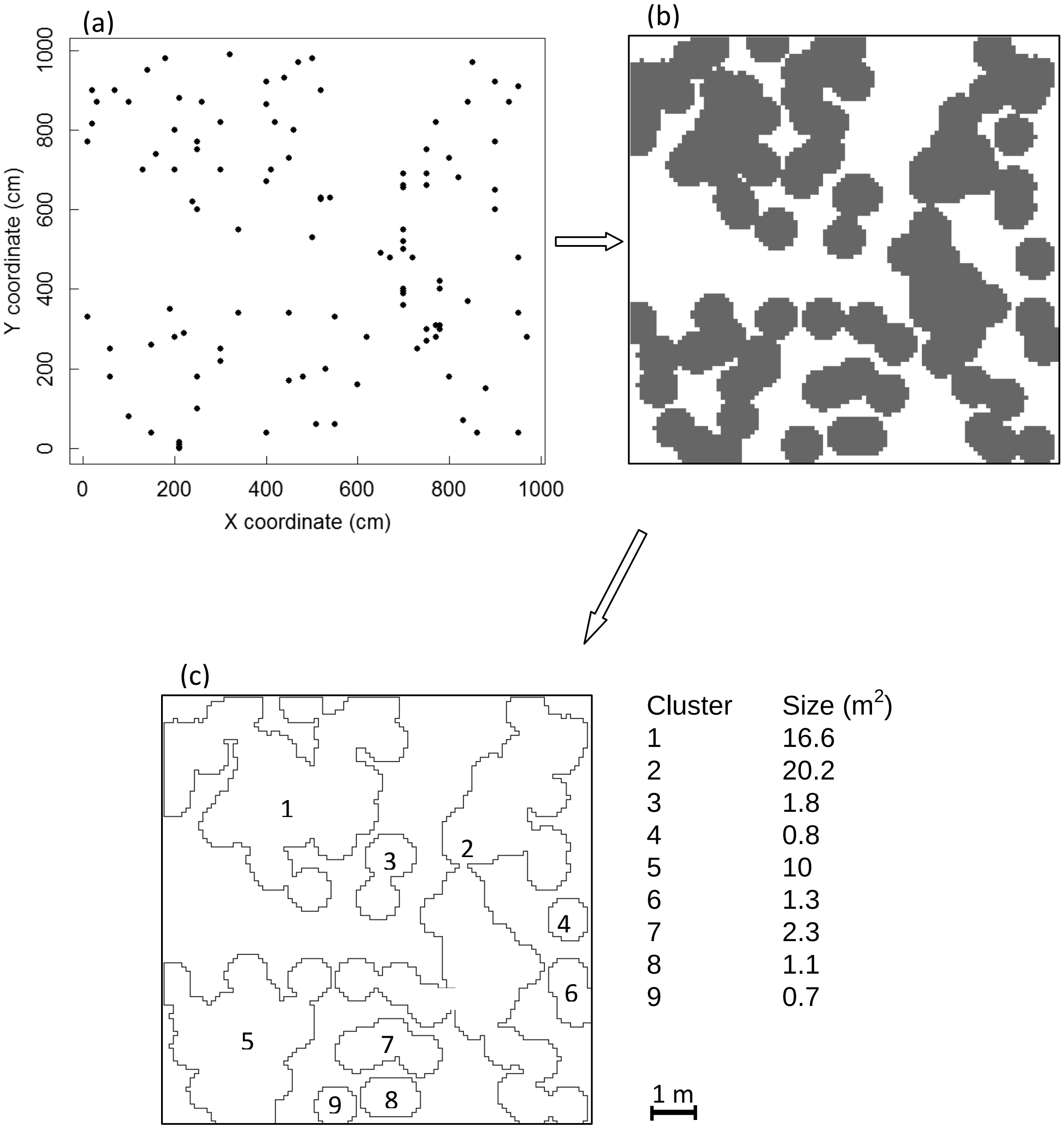


Figure 2: Examples of characterization of tree spatial distribution in woodland plots based on L-functions. The solid black line on each graph represents the observed L function; the oblique dashed line represents the theoretical distribution under complete spatial randomness; the dotted lines represent the lower and upper envelopes of the theoretical distribution (p = 5 %). At distances (r in cm) where spatial clustering is significant, the observed L-function lies above the upper envelope of the theoretical distribution (a; r > 10 cm) while it is between the upper and lower envelopes for a random distribution (b; r > 20 cm) and below the lower envelop for a regular distribution (c; r = 75 - 125 and r > 200 cm).

To quantify the degree of spatial clustering and facilitate comparison among plots in the subsequent analyses, we used the average nearest neighbour distance (NND). When plants are clustered NND should be smaller than situations where plants show random and regular patterns (Condit *et al.*, 2000; Perry *et al.*, 2008). We calculated NND based on the x-y coordinates of individual trees (≥ 30 cm height, including adult trees) in each plot. NND has the advantage of capturing information on how individual plants are associated on a fine scale but do not give indication on the overall importance of woody cover in a plot or clustering at larger spatial scale (i.e. beyond neighbour scale). Thus, we also estimated the number of tree clusters (NCL) and the total cluster size (area covered , ACL) in each plot using the image processing software NIH ImageJ 1.40g (Abramoff *et al.*, 2004). For this purpose, we mapped all individual trees and identified tree clusters by connecting neighbouring trees that are separated by distance ≤ 0.5 m (Fig. 3). Clusters statistics (i.e. number and total size) were then estimated using ImageJ. We eventually used the nearest neighbour distance as indicator of fine scale tree clustering (plant to plant association) while we use the total cluster size to estimate woody cover in a plot respectively. The number of tree clusters in a plot was regarded as the degree of fragmentation of woody patches or spatial clustering at a coarse scale (patch to patch association). The average distance to nearest neighbour was correlated negatively with cluster size (Spearman correlation: $r = -0.83$, $p < 0.001$) but not with the number of clusters ($r = 0.07$, $p = 0.237$). The number of clusters had a unimodal relationship with nearest neighbour distance (graph not presented), indicating that fine scale tree clustering could occur at both low and high degree of clusters fragmentation in a plot.



Cluster	Size (m^2)
1	16.6
2	20.2
3	1.8
4	0.8
5	10
6	1.3
7	2.3
8	1.1
9	0.7

Figure 3: Procedure for clusters identification in woodland plots: (a) all individual trees within a plot were mapped and (b) surrounded by shaded circles of 0.5 m radius; (c) individuals separated by distance ≤ 0.5 m were then assembled into clusters (numbers 1 – 9) which sizes (m^2) were estimated using the image processing software ImageJ.

Statistical analyses

To assess the relationship between tree spatial clustering and sapling species diversity we used quantiles regression (Koenker & Hallock, 2001) with species richness and species evenness as dependent variables and nearest neighbour distance, number of clusters and cluster size as predictors. We explored the effect of tree clustering on sapling species richness and evenness for the 10th (lower), 50th, 75th and 95th (upper) quantiles. However, since we were interested in assessing the limiting effect of tree clustering on the potential / maximal sapling diversity, we considered the relationship significant only if regression coefficients were significant for quantiles > 50th. We included a quadratic terms of each predictor variable in the models to account for potential unimodal relationships and they were eventually removed in case they were not significant.

To assess which factors determined changes in tree spatial patterns we used linear mixed effects models (Pinheiro & Bates, 1998) with fire, grazing, water deficit, soil salinity and fertility as fixed effects and plot as random factor. We calculated the relative change in tree spatial pattern as changes in nearest neighbour distance (NND), number (NCL) and size of tree clusters (ACL). For each of the three response variables we calculated the relative change as the ratio between the value of at a given year (t) and the initial value (t=0); for example: NND_t/NND_0. We added all two-way interactions to the full model for each dependent variable and reduced it step by step, starting with the removal of the interactions. At each step of the model simplification, we compared alternate models using a likelihood ratio test and selected the model that significantly improved the model fit with the lowest Akaike information criterion (Crawley, 2007). We ultimately used the restricted maximum likelihood (REML) method to estimate parameters in the best fitting model (Pinheiro & Bates, 1998).

We checked for potential feedback relationships between fire and tree spatial pattern using data from unplanned fire events that occurred during our experiment. Unplanned fires occurred from zero to three times in 32 fire-protected plots. Because fire was assessed consecutively on the same plots, we tested for potential pseudo-replication in the data using a generalized mixed model but found no support for spatial pseudo-replication (plots nested within sites) nor for temporal pseudo-replication (same plot censored consecutively). Therefore, we used logistic regression with binomial errors (i.e. fire: yes or no) to assess how the probability of fire occurrence at a given year (t) was affected by tree spatial distribution the preceding year (t-1). Since fire could also be determined by climatic conditions, grazing and soil properties, we included water stress, grazing, soil salinity and soil fertility in our model. To assess the quality of the fire model, we used McFadden's "pseudo-R^2" (McFadden, 1974) which is the proportional deviance explained by the best fitting model compared to the null model (intercept only). It was calculated as: (deviance of the model) - (deviance of the null model) / (deviance of the null model).

We performed all analyses within the R 2.7.1 computing environment (R Development Core Team, 2008), with the packages “spdep” for spatial patterns analyses, “quantreg” for quantile regressions and “MASS” for logistic regressions.

RESULTS

Overall, point pattern analyses based on L-functions suggested that tree clustering represented the predominant type of tree spatial distribution in the woodlands studied and this observation was consistent during the four study years (Fig. 4a-d). Trees were significantly clustered at distances < 150 cm for 54 - 84 % of the study plots and at distances between 150 – 250 cm for 45 – 59 % of the plots. For 16 - 43 % of the plots tree distribution did not deviate significantly from a random distribution at distances < 150 cm but the proportion of plots exhibiting random patterns increased at larger distances, reaching 49 - 54 % at distances between 200 – 250 cm. Trees showed some regularity at distances greater than 50 cm, though in only 1 - 3 % of the plots. The mean nearest neighbour distance for the great majority of study plots was < 100 cm (Fig. 4e), thus confirming the high tendency towards tree spatial clustering in the woodlands studied.

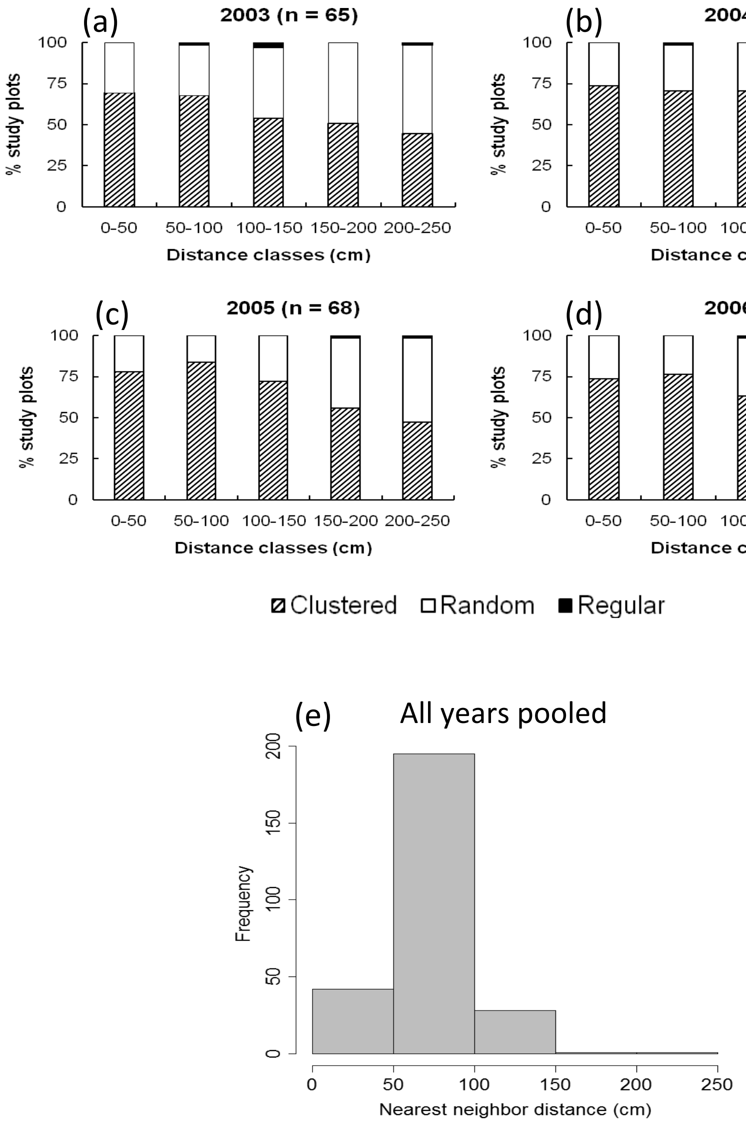


Figure 4: Relative frequency of tree spatial patterns identified in woodlands of Benin from 2003 and 2006. For each study year (a – d), stacked bars show proportions of study plots having clustered (hatched), random (white) and regular (black) spatial patterns per distance classes as suggested by point pattern analyses based on the L-function. The number of plots studied is 65 in 2003 and 68 from 2004 to 2006 because 3 plots were inventoried only after 2003. For all the four years pooled (e), each bar represents the proportion of plot having a mean distance to nearest neighbour in the range indicated on the x-axis.

Effects of tree clustering on sapling diversity

Our hypothesis that sapling species richness increases with tree spatial clustering was found true at the fine scale clustering (i.e. smaller distance to nearest neighbour) but not at the coarse scale (number of tree clusters). Sapling species richness was strongly correlated with nearest neighbour distance (10th to 75th quantiles) and tree cluster size (10th - 95th quantiles), but not with the number of clusters (50th quantile only) (Table 1, Fig. 5). The species richness decreased with neighbour distance (i.e. tree spacing) while it showed a unimodal pattern with increasing tree cluster size and was highest at intermediate cluster size. In order to check for potential influences of rare species, we assessed the effect of tree clustering on the species evenness (Fig. 5b & d, Table 1). The species evenness increased with distance to neighbour while it decreased with the size of tree clusters.

Thus, the highest species richness was found in woodlands with small distances to neighbours and large tree clusters but there were no strong differences regarding the number of clusters. Clearly, high species richness in the woodlands was associated with fine scale tree clustering and was accompanied with reduced species evenness.

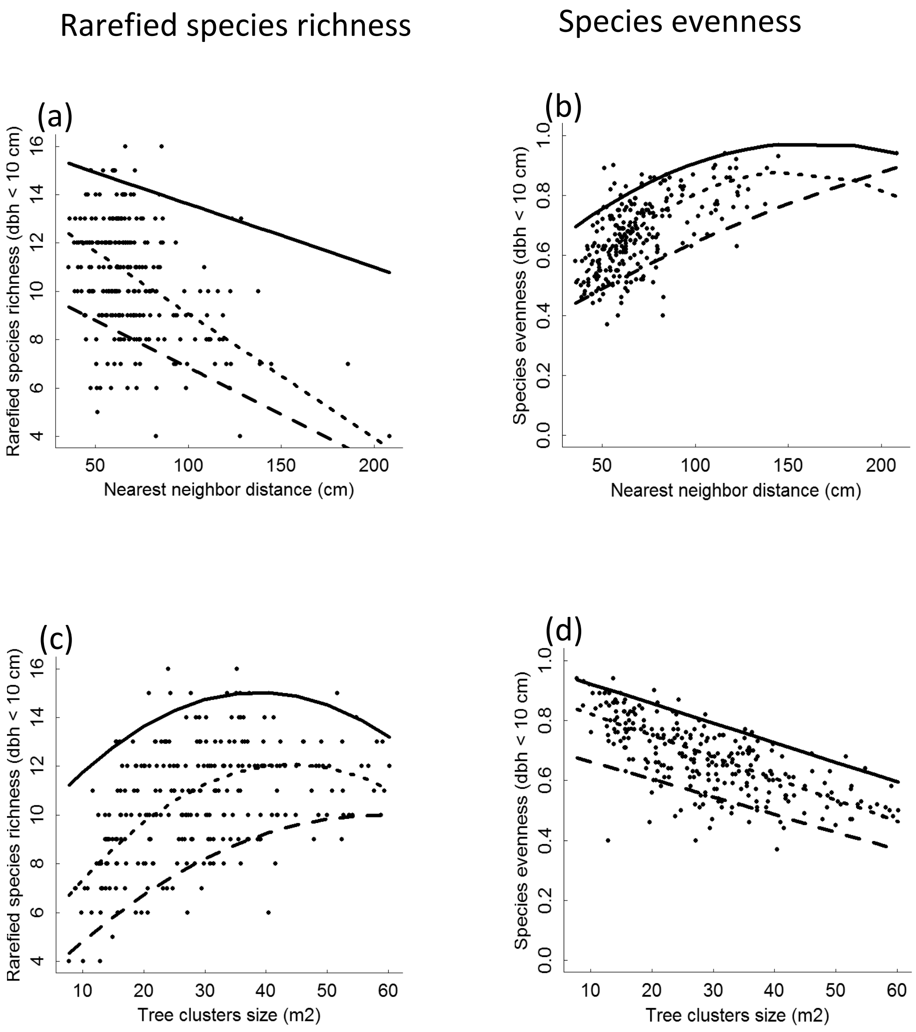


Figure 5: Effect of tree clustering on (a, c) sapling species richness and (b, d) evenness. We used the mean distance to nearest neighbour in each plot as proxy for fine scale tree clustering while cluster size indicate the total woody cover in a plot. Because the number of tree clusters had no significant effect on species richness (see Table 1), graphs with the number of clusters are not presented. Each dot on the scatterplots represents a study plot at a given year (2003 – 2004). The lines represent the 95th (solid, upper line), 50th (dotted, intermediate line) and 10th (dashed, lower line) quantiles.

Table 1: Effect of tree clustering on sapling species richness and evenness. Quadratic terms for the nearest neighbour distance (NND^2), the number of tree clusters (NCL^2) and cluster size (ACL^2) were included in the quantile regressions only if they significantly improved the model fit. Regression coefficients that are significantly different from zero are indicated by * (p < 5 %), ** (p < 1 %) and *** (p < 0.1 %).

	Rarefied species richness (dbh < 10 cm)						Species evenness (dbh < 10 cm)					
tau	NND	NND^2	NCL	NCL^2	ACL	ACL^2	NND	NND^2	NCL	NCL^2	ACL	ACL^2
10th	-0.039***		0.72	-0.015	0.26***	-0.002*	0.004*	0.00001	0.005*		-0.006***	
50th	-0.051***		-0.80*	0.035**	0.36***	-0.004***	0.008***	-0.00003*	0.002		-0.007***	
75th	-0.037**		-0.59	0.023	0.32***	-0.004***	0.007***	-0.00002*	-0.01*		-0.008***	
95th	-0.026		-0.75	0.028	0.31**	-0.004**	0.006**	-0.00002	-0.01***		-0.007***	

Change in the strength of tree clustering along gradients of resources and disturbances

We predicted an increase in tree clustering at high fire frequency but our data did not support this hypothesis. We found that fire had a negative effect on clustering at the coarse scale (i.e. reduction in the number of clusters) while it had no significant effect at fine scale (i.e. neighbour distance). The number of tree clusters significantly decreased at high fire frequency ($P = 0.020$) while it increased with time since last fire ($p = 0.026$) (Table 2). Both the nearest neighbour distance and cluster size were not significantly affected by fire.

Changes in tree spatial patterns were also significantly influenced by abiotic conditions (i.e. soil salinity and water deficit) but not by grazing (Table 2). High soil salinity significantly reduced tree cluster size ($p < 0.001$) but had no significant effects on the nearest neighbour distance and the number of clusters. At high water deficit, both the distance to the nearest neighbour ($p = 0.022$) and the number of tree clusters ($p = 0.040$) increased significantly while cluster size was not affected by water deficit. We found also a significant interaction between water deficit and time since last fire which reduced the number of tree clusters but did not affect the distance to nearest neighbour, nor cluster size.

Clearly, fire did not have any significant effect on fine scale clustering of trees, nor on total cluster size. Long time interval between fires increased the number of tree clusters (coarse scale clustering) but not at high water deficit where the number of clusters was reduced.

Table 2: Parameters estimate for the effect of fire, grazing and abiotic conditions on the change in woodlands tree spatial patterns. The relative change in each dependent variable was calculated as the ratio of the value at a given sampling occasion (2004 - 2006) over the initial value recorded in 2003.

	Dependent variables					
	Relative change in the number of clusters		Relative change in the clusters size		Relative change in the nearest neighbour distance	
Factors	Coef.	P-value	Coef.	P-value	Coef.	P-value
Year			0.067	< 0.001		
Number of fires	- 0.041	0.020				
Time last fire	0.286	0.026				
Grazing						
Soil salinity			- 0.266	< 0.001		
Soil fertility						
Water deficit	0.0001	0.040			0.0001	0.022
Water deficit x time last fire	- 0.001	0.013				

Unplanned fire events and their relation to tree spatial distribution

Using data from unplanned fire events in our experiments, we tested the hypothesis that tree clustering lowers the probability of fire in woodlands. Our fire model explained 37 % of the variation (Pseudo R^2) in fire incidence with nearest neighbour distance, number and size of tree clusters, water deficit, soil salinity and grazing as predictors variables. The effect of tree clustering on fire was scale-dependent. Tree clustering at a fine scale (small neighbour distance) reduced the probability of fire occurrence while high fragmentation of woody clusters (i.e. large number of tree clusters) increased the probability of fire (Table 3). These results suggest that highly dispersed trees and highly scattered woody clusters favoured the spread of fire in woodlands. Surprisingly, larger woody cover (i.e. cluster size) also increased the probability of fire. However, the interaction between cluster size and the number of clusters reduced the probability of fire, suggesting that under large woody cover (i.e. high tree cluster size) fire was less probable in highly fragmented woodlands (i.e. large number of clusters).

Abiotic conditions such as water deficit and soil salinity also influenced the probability of fire occurrence. Fire was less likely at high water deficit and more likely at high soil salinity. However, at high soil salinity combined with high water deficit the probability of fire was reduced. Grazing affected the probability of fire occurrence in a more complex way. Grazing alone increased the probability of fire occurrence while it reduced the probability of fire at high nearest neighbour distance and at high number of tree clusters. Apparently, grazing had a negative effect on fire only in woodlands with highly dispersed trees (i.e. high neighbour distance) and highly dispersed woody patches (i.e. large number of clusters).

Table 3: Parameters estimate for the effects of tree clustering and abiotic conditions on the probability of fire occurrence in woodlands of Benin. We modelled fire occurrence at a given year as a function tree clusters characteristics (i.e. nearest neighbour distance, size and number of clusters) the preceding year, while accounting for other factors such as grazing and abiotic stress.

	Fire occurrence (yes / no) (Pseudo R^2 = 37.04 %)	
	Coefficient	P-value
Nearest neighbour distance (cm)	0.05	0.050
Cluster size (m^2)	0.46	0.012
Number of clusters	1.31	0.013
Water deficit (mm)	- 0.01	0.062
Soil salinity (index)	15.56	0.001
Grazing	22.83	0.006
Water deficit x Soil salinity	- 0.03	0.002
Grazing x Nearest neighbour distance	- 0.11	0.005
Grazing x Number of clusters	- 0.79	0.036
Cluster size x Number of clusters	- 0.03	0.014

DISCUSSION

Effect of tree spatial aggregation on sapling diversity in woodlands

We predicted that species diversity should increase with tree spatial clustering and we used the mean nearest neighbour distance (plant to plant association) and the number of clusters (degree of fragmentation of tree clusters) as indicators of tree spatial clustering at fine and coarse scale respectively. Our results indicated that the species diversity increased with tree clustering at fine scale (Fig. 5, Table 1), which is in line with our hypothesis. In contrast, at the coarse scale, species diversity was not significantly correlated with the number of tree clusters. We also looked at the relationship between species richness and tree cluster size (total woody cover) and found that species richness increased with cluster size. This was not surprising since tree cluster was strongly correlated, negatively, with the mean nearest neighbour distance. We conclude that species richness was probably promoted by plant to plant associations in the studied woodlands.

These results conform to the previous findings indicating positive interdependence between plants in stressful environments (e.g. Callaway, 1997; Barnes & Archer, 1999; Tielborger & Kadmon, 2000; Choler *et al.*, 2001; Tewksbury & Lloyd, 2001; Tirado & Pugnaire, 2003; Gómez-Aparicio *et al.*, 2005; Aerts *et al.*, 2007). For similar environmental conditions in Burkina Faso, Couteron and Kokou (1997) found tree clusters composed of multiple tree species but did not explicitly relate such patterns to facilitation among plants. Interestingly, we found that species evenness decreased at the same time the species richness increased, thus indicating that the proportion of rare species increased with fine scale clustering. It has been proposed that less tolerant (rare) species to the stressful conditions should be more likely facilitated (Choler *et al.*, 2001; Davis *et al.*, 2005; Liancourt *et al.*, 2005). Our results thus confirm this idea.

Determinants of tree spatial distribution and effect of fire

We hypothesized that tree clustering would increase with fire frequency but this was not found true in the conditions of the woodlands studied here. At a fine scale, fire had no significant effect on the nearest neighbour distance (Table 2). In contrast the number of tree clusters in a plot (coarse scale clustering) was significantly reduced by frequent fires while it increased with long time intervals between fires. These results suggest that other processes than fire determined the fine scale clustering of trees and that for some reasons, frequent fires promoted the interconnection of woody patches, thus reducing the number of tree clusters.

In South African savannas, Groen *et al.* (2008) found that high fire frequency increased tree spatial clustering for rare species but not for dominant species. In this study we did not separate between rare and dominant species but the patterns we observed suggest a similar trend. An explanation for the negative effect of fire on the number of woody clusters here would be the increase in resprouting following fire. It has been demonstrated that the removal of aerial biomass following fire can activate dormant buds to produce more root suckers or sprouts. Most woodland species in West Africa have such a capacity to resprout vigorously (Bellefontaine, 1997; Zida *et al.*, 2007). Conversely, our data suggest that this did not induce an increase of the total woody cover as cluster size did not change significantly. This could be due to sensible differences in fire intensity, with moderate fire intensity between patches enabling tree regeneration through resprouting while at the same time higher fire intensity at the peripheries of woody patches likely result in losses of woody cover. Without any measurements of fire intensity in our study plots we could however not prove the existence of such mechanisms.

While grazing and soil fertility had no significant effects on tree spatial distribution, we noted a significant increase in both the nearest neighbour distance and the number of tree clusters at high water deficit. This suggest an increase in competition between plants at the drier extreme of our water gradient which likely induced spacing of both individual plants (i.e. increase in neighbour distance) and woody patches (i.e. increase in number of clusters). This is in accordance with previous researches indicating that plant relationships can shift from facilitation to competition towards extremely stressful conditions (Holmgren *et al.*, 1997; Brooker & Callaghan, 1998; Maestre & Cortina, 2004; Maestre *et al.*, 2006).

Tree spatial clustering could have resulted from other processes such as soil heterogeneity or limited dispersal. Under high soil heterogeneity we would expect the species richness to increase with the number of clusters within a plot, due to an increase in the number of potential niches (Chase & Leibold, 2002). The absence of relation between the species richness and the number of clusters that we noted previously provides little support for soil spatial heterogeneity in the studied woodlands. If dispersal limitation would apply to the woodlands studied here, we would expect the prevalence of mono-specific tree patches, thus a decreasing species richness with increasing clustering (e.g. Plotkin *et al.*, 2000; Perry *et al.*, 2008). Although it was suggested that tree resprouting could generate the same pattern (Groen *et al.*, 2008), our data did not provide such evidence.

Effect of tree spatial patterns on fire occurrence

We predicted a decrease in the probability of fire with increasing tree clustering. We found that the effect of tree clustering on fire was also scale-dependent. Whereas fine scale clumping of trees reduced the probability of fire, coarse scale clustering (i.e. number of tree clusters) and larger woody cover (i.e. cluster size) increased the probability of fire (Table 3). These results highlight three important determinants of fire in the woodlands. First, the fine scale clustering of trees may be associated with low grass cover and thereby a lower probability of fire. Second, the coarse scale clustering implies high fragmentation of woody patches and apparently a higher probability of fire possibly due to more space left for grasses between patches. These two observations are in accordance with previous findings related to fire behaviour in savanna-woodland ecosystems as determined by grass and woody biomasses (e.g. Jeltsch *et al.*, 1996; Van Langevelde *et al.*, 2003). Third, the total woody cover might indicate a higher availability of dead tree leaves, possibly fuelling fire. It was noted that dead leaves of the litter layer often constitute a larger proportion of fuel load in dry forests compared to grassland (Kauffman *et al.*, 1994). In semi-arid conditions such as woodlands in Benin, where most tree species are deciduous, it is likely that dead leaves play an important role in the spread of fire.

Surprisingly, we found that grazing alone increased fire probability whereas it reduced it in woodlands with highly dispersed trees (i.e. high neighbour distance) and highly dispersed woody patches (i.e. large number of clusters). Several possible reasons could explain such results. Fire could have been initiated on purpose by cattle herders to stimulate grass regrowth for their livestock. Another possible explanation might be that, because of the positive feedback between grazing and forage quality (Adler *et al.*, 2001; de Knegt *et al.*, 2008), cattle grazing could have been most intense in woodlands with lighter tree cover, thus suppressing enough grasses to prevent fire in those woodlands.

Overall, fire occurrence in the studied woodlands appeared to be the result of several opposing factors with complex interactions at different scales. We did not find enough evidence for a strong feedback loop between tree clustering and fire occurrence as tree clustering at fine scale and coarse scale produced opposite effects on fire probability. These results tend to confirm the observation by Thonicke *et al.* (2001) that in semi-arid Africa, it is not sufficient to consider fuel load (particularly grasses) and soil moister as key driver to simulate fire regimes. Several other mechanisms need to be considered such as interactions between the woody component and grazing, among others.

Taken together, our results suggest that tree clustering had a positive effect on species diversity through facilitation between plants at fine spatial scale. This conforms to models predicting a positive effect of facilitation on plant community diversity (Hacker & Gaines, 1997; Michalet *et al.*, 2006). We also found support to the idea that this increase in species diversity was due to the facilitation of rare and probably stress-intolerant species (Hacker & Gaines, 1997; Liancourt *et al.*, 2005; Michalet *et al.*, 2006). Our data did not provide however evidence for the existence of feedback loops between fire and tree clustering in the woodlands studied. The fine scale tree clustering appeared to have a negative effect on fire but fire did not improve such tree clustering. On the contrary, fire seemed to reduce the coarse scale clustering of trees and to promote conditions favourable to future fires. Our results indicate also complex interactions between fire and other processes, such as grazing and tree clustering at different spatial scales, which need to be clarified by future researches.

ACKNOWLEDGMENTS

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Recently cleared woodland for charcoal production

Chapter 6

General discussion

Dry woodlands cover large areas in the tropics and particularly in Africa. The African woodlands are currently being used extensively and locally degenerated to poorer and more open vegetation. To come up with sustainable management strategies for woodlands, the interactive effects of multiple factors such as fire, herbivore grazing, and climate and soil conditions need to be understood. These drivers of woodland dynamics may buffer or reinforce each other while simultaneously influencing tree recruitment and species diversity in woodlands. The research reported here attempted to disentangle the effects of these multiple drivers on plant-plant interactions, tree recruitment, diversity and structure of dry woodlands in Benin. The Beninese woodlands are part of a large and almost continuous strip of *Isoberlinia* woodlands extending from Mali to Uganda in Africa north of the Equator. The following general question guided this research: How do climate, soil, fire and grazing and their interactions influence the competitive versus facilitative interactions between plants, the regeneration success of seedlings, and the species composition, richness and structure of woodlands? In the following sections the main results of this research are presented and discussed for their theoretical and practical relevance.

WOODLAND ECOLOGY

Huston's dynamic equilibrium model (Huston, 1979; 1994) was used as main working hypothesis to make predictions regarding patterns in plant performance, species richness, structure of Beninese woodlands in response to soil and climate driven stress gradients, to disturbances by grazers and fire, and to interactions between those factors. This model predicts facilitative rather than competitive plant interactions, improved seedling establishment, improved species coexistence, and higher species richness and diversity at intermediate levels of stress and disturbance.

Patterns in diversity driven by water shortage

The limiting effect of water stress on woody species richness and tree density was tested for trees in the semi-arid woodland-savanna mosaics of Benin. The predicted unimodal response in species richness to water stress was found to be true for the total tree and shrub community as well as for only the juvenile trees in the system, but not for adult trees that decreased in species richness with increasing water stress. The predicted linear decrease in tree density with increasing water stress was not found for the total community, nor for juveniles, while surprisingly adult tree density increased with water stress.

It has been suggested that the highest tree species diversity occurs at intermediate stress levels because stress tolerant species dominate high stress conditions, stress sensitive species dominate the low stress conditions, and species of both groups co-exist at intermediate stress levels (e.g. Bruun *et al.*, 2006). However, this was not observed in the Benin woodland-savanna landscapes studied here, as a high proportion of unique species explained the high diversity at intermediate stress level. It is probable that disturbances by fire and herbivores improved species coexistence at intermediate stress levels by reducing species populations, and thus preventing competitive exclusion among the species (Huston, 1979; Huston, 1994). This result suggests that disturbances did not affect the species the same way across the water stress gradient. While these results corroborate previous findings that disturbances strongly determine the dynamics of dry vegetation (e.g. Gentry, 1995; Gillespie *et al.*, 2000), they also show the important role of water stress, potentially interacting with or modifying the importance of other local factors such as fire and grazing. We thus suggest that the hump-shaped pattern in species richness along the water stress gradient, as predicted from Huston's model (1979; 1994), resulted from positive plant-plant interactions and low competition between plants imposed by fire and grazing at intermediate stress levels.

Facilitation by nurse trees

While interactions between a water stress gradient and disturbances by fire and grazing potentially determine species distribution and species richness in woodland-savanna mosaics of Benin, such interactions are likely to be modified by the structure of woodlands. The *Isoberlinia* woodland typically consists of mixtures of small isolated tree patches, small gaps and more open conditions. More specifically, it was expected that adult trees would improve the establishment of seedlings by reducing effects of drought (e.g. by modifying microclimate and evaporative demand). In chapter 3 the hypothesis was tested that seedling growth and survival is most successful under dominant trees, intermediate in woodland gaps, and lowest in open fields. It was also predicted that seedling performance would be improved by neighbouring trees during the dry season. Finally, it was tested whether these facilitative effects were stronger for stress intolerant species than for stress tolerant species.

These hypotheses were mostly true as tree seedling survival improved within woodlands, both under trees and in gaps, compared to open fields along the whole climatic gradient, and seedling survival was the best in woodlands during the dry season, particularly for the drought-intolerant species. However, plant interactions changed with the level of stress, becoming neutral or even negative during the dry season in more water stressed woodlands. Tree regeneration in tropical woodlands is thus facilitated by the presence of so-called nurse trees that are expected to reduce the drought experienced by the seedlings. However, facilitation of the seedlings by nurse trees was observed when the water stress was not too extreme. As expected, this trend was stronger for the drought-intolerant than for drought-tolerant species.

These results indicate that species differ in their response to adult tree shade, and such differential responses determine the species coexistence.

Disturbances by fire and grazing

The results of chapter 2 suggested complex interactive effects of water stress and disturbances on tree species distribution, species richness, and tree density. Fire and herbivory are the most frequent disturbances shaping tropical savannas and woodlands. In chapter 4 the independent and interactive effects of fire, grazing, soil salinity, soil fertility and climate driven water stress on the density and species richness of tree regeneration were experimentally evaluated. Specific predictions were that frequent fire and frequent grazing reduce sapling species richness and sapling density, particularly in interaction. Moreover, negative effects of the two disturbances were expected to be stronger at a high abiotic stress level determined by climatic and soil conditions.

Soil salinity was the predominant abiotic stress factor influencing tree regeneration in the woodlands. Soil salinity and disturbances had a stronger influence on the sapling species composition and richness than on sapling density. Frequent fires and fires combined with grazing increased sapling species richness contrary to our first prediction. In line with our second prediction, sapling species richness and density were reduced by grazing at high soil salinity, while the effects were positive at low soil salinity. These results demonstrate how important interactions between disturbances and abiotic stresses are in the woodlands under study. They also show that the effects of a disturbance may shift from positive to negative depending on the level of accompanying abiotic stresses. Our results thus suggest that woodland management by fire and grazing should take into account these potential reversals in the disturbances effects across abiotic stress gradient such as illustrated here by soil salinity.

Tree clusters, species diversity and fire

A patchy structure with local tree clusters and more open herbaceous patches is a striking feature of *Isoberlinia* woodlands in Benin and elsewhere. It was shown in Chapter 4 that fire, grazing and abiotic stress had little impact on tree density in woodlands. Thus, other mechanisms to explain local tree clusters in the woodlands of Benin needed to be explored, including the potential consequences of these tree clusters for tree diversity. Because tree clustering may affect the probability of fire occurrence, the existence of potential feedback loops between tree spatial distribution and fire occurrence was also addressed. It was hypothesized that fire promotes tree clustering, tree clustering reduces the probability of fire and tree clustering improves plant diversity. For this purpose, tree clusters were defined at a fine spatial scale by plant to plant associations, i.e. nearest neighbour distances, and at a coarser spatial scale by patch-to-patch associations, i.e. number of tree clusters in a plot.

High levels of climate-driven water stress negatively affected tree clustering at the fine scale. This is in line with the results from chapter 2, indicating that facilitative effects of neighbouring trees could shift to negative effects at high water stress. Fire operated at a coarse scale: frequent fires reduced the number of patches because it probably promoted resprouting of trees, and thus isolated tree clusters became connected to each other. Vice versa, the tree clustering also influenced the probability of fire. The probability of fires decreased with shorter distances between trees in a cluster, but increased with the presence of more tree clusters because more open, inflammable, open patches were left in-between.

Sapling diversity increased with fine scale clustering (plant-to-plant association) but not with coarse scale clustering (patch-to-patch association), suggesting that trees within clusters facilitate each other. Since rare species were better able to survive in those tree clusters, tree clusters contribute to a higher species richness of the woodlands. These results confirmed the observation from chapter 2 that rare species (i.e. those less tolerant to stress) were apparently the most facilitated. Overall, these results provide evidence that tree clustering enhances tree species richness within tree clusters, thus confirming theoretical models predicting high species richness and diversity by facilitation between neighbouring plants in water stressed conditions (Hacker & Gaines, 1997; Michalet *et al.*, 2006).

Huston's model revisited

Huston's general model for species-environmental relationships provided a conceptual basis for understanding the relationships between plant community dynamics and environmental factors in Beninese woodlands. Huston's model prediction is based essentially on two mechanisms: plant-plant interactions and the externally imposed mortality by disturbances across resource gradient (Huston, 1979). In our study, it was observed that the underlying mechanisms were more complex and diverse, and included a multitude of resource gradients (e.g. soil salinity and climate driven water stress) and disturbances (e.g. fire and grazing). Our study suggested that facilitative interactions dominated over competitive ones and contributed to successful recruitment, and thus to high species richness and diversity at intermediate stress levels. Moreover, the disturbance by grazing and fire reduced competitive exclusion at intermediate stress levels and improved these facilitative effects. Overall, these trends resulted in a high species richness and diversity particularly because rare species were facilitated at intermediate stress levels. This complex of interactions seems to drive the hump-shaped pattern in tree recruitment success and species richness at intermediate levels of stress and disturbances, as predicted by Huston's model.

WOODLAND MANAGEMENT

Woodland is the most abundant vegetation type having significant woody cover in savanna dominated ecosystems where rainforests are absent while closed forests such as gallery and dense deciduous forests are rare. As such, woodlands are ecosystems on which a great number of people in tropical countries depend for their livelihoods. Woodland tree species are typically exploited for fuel wood, charcoal, construction and furniture woods. Now that the traditional timber “hard wood” species are being depleted, threats are becoming more acute on woodland “soft wood” tree species such as *Isoberlinia* species in West Africa which are being cleared (e.g. Orthmann *et al.*, 2006; Sokpon *et al.*, 2006). The dangers that would result from the destruction of these woodlands are: the extension of savannas, an increase in fire damages, the denudation and drying up of soils, the reduced wood production and loss of tree species diversity. What is more, the wide extent of woodlands means that these changes, even locally, are likely to have globally significant impacts such as changes in climate (Malhi & Grace, 2000; Hoffmann *et al.*, 2002; Bonan, 2008). It is therefore urgent to take appropriate measures for the conservation of woodlands. Based on the insights gained from this study, we put forward the following recommendations for a sustained use and management of woodlands.

Fire and grazing disturbances

Lessons from many different ecosystems showed that fire suppression is often not a viable option as it allows fuel to accumulate and increases the risk of more damaging fires (Rackham, 2008). On the other hand, expansion of cattle populations in dry regions is expected to follow the trend of human population growth while the traditional long-range movements of pastoralists and their livestock are being reduced. This suggests that an increasing grazing pressure should be expected in the future. While fire and grazing seem unavoidable, they could be used as tools for conservation management because of their influence on habitat structure and biodiversity (Collins *et al.*, 1998; Fuhlendorf & Engle, 2004). However, to use fire and grazing as a management tool, we must be able to predict when they will impact negatively or positively on tree recruitment and diversity. In this dissertation, it is shown that climate and soil conditions can induce significant shifts in the effects of disturbances by fire and grazing on tree recruitment and diversity (chapters 4 & 5). Positive influences of fire and grazing on woodlands tree diversity can be expected under productive conditions such as high water and soil nutrients availability. On the contrary, stressful conditions such as high salinity or low water and soil nutrients availability can hamper tree regrowth following disturbance and increase competition among the species.

Woodland harvesting – planting – and facilitation of tree regeneration

Plant community dynamics is largely dependent on the recruitment of new individuals to sustain the vegetation cover. In the dry regions where natural regeneration faces severe constraints such as water stress, and disturbances by fires and grazing, forest managers often seek methods that can ensure or accelerate tree regeneration. Our study demonstrated that seedlings regeneration success could be enhanced by building upon natural mechanisms such as facilitation. This implies that forest managers should tune woodland harvesting in such a way that trees are left to create favourable conditions for new regeneration, accounting for natural disturbances occurring at a particular site. For woodland restoration, the results presented here emphasize the need to plant nurse trees in degraded, open areas to create better conditions for seedling establishment and gradual re-establishment and recovery of degraded woodlands. Particularly at intermediate water stress levels, we expect positive effects of such measures for woodland restoration and for sustainable woodlands use.

Isoberlinia doka; a dominant woodland species increasingly exploited for timber

Woodland in the wetter Bassila region in Benin

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Summary

Woodlands are among the most widespread seasonally dry forests, particularly in Africa. The so-called *Isoberlinia* woodlands extend from Mali to Uganda, north of the Equator. In these regions, woodland is one of the few vegetation types having significant tree cover, thus supplying most forest products. Unfortunately, woodlands are disappearing rapidly due to the combined effects of unrestrained forest exploitation, increasing and frequent droughts, decreasing soil productivity, and disturbances by fire and herbivores. For a sustainable use and management of these woodlands, we need to understand how these drivers influence, both individually and combined, woodland structure, dynamics and composition. This study aims at disentangling the effects of these multiple drivers on woodlands. The central question is how climate, soil, fire and grazing, and their interactions determine the competitive versus facilitative interactions between plants, the regeneration success of seedlings, and the species composition, richness and structure of woodlands. To answer this question, a broad-scale study was conducted in Benin where extensive examples of *Isoberlinia* woodlands are still found. Huston's model for species-environment relationships was used as a working hypothesis. In line with this model, it was predicted that facilitative plant interactions would dominate over competitive plant interactions at intermediate levels of stress and disturbance and that, consequently, seedling establishment, species coexistence, and species richness and diversity would improve at such intermediate levels of stress and disturbance.

Because the role of the macro-climate as a driving factor in dry woodlands is not fully understood, in chapter 2 the hypothesis was tested that species richness shows a unimodal relationship with water stress, whereas tree density decreases

linearly with increasing water stress. The results show that woodland species distribution is indeed strongly determined by climate-driven water stress and that species richness is highest at intermediate levels of water stress. Moreover, water stress appeared to interact with other local factors such as fire and grazing. It is proposed that the hump-shaped pattern in species richness along the water stress gradient results from positive plant-plant interactions and low competition between plants imposed by fire and grazing at intermediate stress levels.

To further explore this facilitation hypothesis between tree species, the effect of large dominant trees on seedling establishment was investigated along the water stress gradient in chapter 3. Because seedlings in water stressed conditions can benefit from large neighbour trees that potentially reduce the evaporative demand and may increase soil water availability by hydraulic lift, it was hypothesized that seedling growth and survival would be more successful under dominant trees in closed tree patches than in gaps (i.e. between trees in woodland), and open fields. It was also expected that facilitative effects would be stronger for drought-sensitive species than for drought-tolerant species. In line with these predictions, tree regeneration in woodlands was found to be facilitated by the presence of large neighbour trees and this facilitative effect was stronger for the drought-intolerant than for drought-tolerant species. However, facilitation of seedlings by nurse trees was observed when the water stress was not too extreme. Thus, both the drought-intolerant and the drought-tolerant species were facilitated by nurse trees at intermediate stress levels.

In chapter 4, the potential interactive effects of water stress and disturbances by fire and grazing were studied in a large field experiment. Four treatments (no disturbance, fire alone, grazing alone, grazing and fire) were applied to woodlands distributed across climate and soil-driven water stress gradients. Changes in sapling species richness and density were monitored annually between 2003-2006. Soil salinity (causing soil water stress) was the predominant abiotic stress factor influencing tree regeneration in the woodlands. Sapling species richness and density were reduced by grazing at high soil salinity, while they increased with grazing at low soil salinity. These results thus confirm that the effects of the disturbances were reversed: from positive at low abiotic stress to negative at high stress. The effect of the disturbances and abiotic stress were particularly strong for sapling species composition and richness, and much less for sapling density.

Since a strong impact of fire and grazing was not observed for sapling density, the mechanisms that could be responsible for the patchy structure typical of the woodland studied were further investigated. Thus, in chapter 5, several mechanisms that could be determining the patchy structure of the woodland vegetation and its consequences for tree species diversity were explored. It was predicted that fires promote tree clustering while, vice versa, tree clusters reduce the probability of fire and improve tree species diversity. Tree clustering was studied at two scales: at a fine spatial scale by plant to plant associations, i.e. nearest neighbour distances, and at a coarser spatial scale by patch to patch associations, i.e. number of tree clusters in a plot. Tree clustering at the fine scale appeared to be reduced by high water stress while fire reduced the number of tree patches at the coarse scale. The probability of fires decreased with shorter distances between trees in clusters, but increased with the presence of more tree clusters because more open and inflammable patches were left in-between. Sapling diversity increased with fine scale clustering (plant-to-plant association) but not with coarse scale clustering (patch-to-patch association), thus confirming that trees within clusters facilitate each other.

Overall, the results from this study confirmed the complex nature of woodlands and indicated that woodland dynamics were determined not only by the macro-climate (i.e. water stress), but also by soil-driven abiotic stress (i.e. salinity), disturbances by fire and grazing, facilitative plant-plant interactions, as well as

interactions between these drivers. Three important conclusions could be drawn: (1) facilitative interactions contribute to successful recruitment in woodlands, and thus to high species richness and diversity at intermediate stress levels; (2) disturbances by grazing and fire reduce competitive exclusion at intermediate stress levels and improve the facilitative interactions among woodland species; (3) climate and soil conditions can induce significant shifts in the effects of disturbances by fire and grazing on tree recruitment and diversity. Based on these results, it is suggested that forest managers should tune woodland harvesting in such a way that trees are left to create favourable conditions for new regeneration. As for woodland restoration, the planting of nurse trees in degraded and open areas could create better conditions for seedling establishment and thus help to restore degraded areas.

Samenvatting

Droge open bossen zijn wijdverspreid in de tropen, en in het bijzonder in Afrika. De zogenaamde *Isoberlinia* bossen strekken zich uit van Mali tot Oeganda, ten noorden van de Equator. In deze regio zijn deze bossen een belangrijke bron van bosproducten. Helaas verdwijnen deze bossen snel als gevolg van de gecombineerde effecten van onbeteugelde bosexploitatie, toename van frequentie en intensiteit van droogte, afnemende bodemproductiviteit, en verstoring door vuur en begrazing. Deze studie richt zich op de effecten van deze verschillende factoren op de structuur, dynamiek en soortenrijkdom van deze droge bossen. De centrale vraag is hoe het klimaat, de bodem, vuur en begrazing van invloed zijn op de concurrentie versus facilitatie tussen planten, het vestigingssucces van zaailingen, en de soortenrijkdom en bosstructuur. Om deze vraag te beantwoorden werd een grootschalig onderzoek uitgevoerd in Benin, waar uitgestrekte *Isoberlinia* bossen nog steeds voorkomen. Het model van Huston voor soort-omgeving relaties werd gebruikt als werkhypothese. Uitgaande van dit model, werd voorspeld dat faciliterende plant interacties domineren en dat daarom zaailing vestiging, co-existentie van soorten en soortenrijkdom en –diversiteit bevorderd wordt bij een intermediair niveau van klimaatsstress (droogte) en verstoring.

Omdat de rol van het klimaat als sturende factor niet goed bekend is, werd in Hoofdstuk 2 de hypothese getest dat de soortenrijkdom het hoogste is bij een intermediair niveau van water stress, zoals bepaald door het klimaat. De resultaten laten zien dat soortenrijkdom inderdaad het hoogste is bij een intermediair niveau van water stress. Bovendien werd een interactie van water stress met vuur en begrazing geobserveerd, hetgeen suggereert dat de soortenrijkdom langs de water stress gradiënt het resultaat is van positieve plant-plant interacties in combinatie met geringe onderlinge concurrentie. Het lijkt erop dat de concurrentie afgezwakt wordt door het optreden van vuur en begrazing, bij intermediaire water stress niveaus.

Om deze hypothesis over facilitatie tussen boomsoorten verder te onderzoeken, werd een experiment uitgevoerd waarbij het effect van grote, dominante bomen op de vestiging van zaailingen langs de water stress gradiënt bestudeerd werd in Hoofdstuk 3. Bij water stress kunnen zaailingen voordeel halen uit grote buurbomen, omdat zij door beschaduwing de transpiratie kunnen verminderen en mogelijk, middels “hydraulic lift”, de waterbeschikbaarheid in bodem verhogen. Op basis hiervan werd voorspeld dat groei en overleving van zaailingen hoger zouden zijn onder dominante bomen in vergelijking met zaailingen op open plekken in het bos, of in het open veld. Tevens werd verwacht dat dat dit faciliterende effect groter zou zijn voor soorten die minder tolerant zijn voor effecten van droogte. De resultaten suggereren dat zaailingregeneratie gefaciliteerd wordt door de aanwezigheid van grote buurbomen. Overeenkomend met de verwachting is dit positief effect sterker voor een droogte-intolerante soort dan voor een droogte-tolerante soort. Het faciliterend effect van moederbomen werd waargenomen wanneer de droogte niet al te extreem was, en beide soorten hadden voordeel van moederbomen bij intermediaire stress niveaus.

In hoofdstuk 4 werden de effecten van water stress en verstoringen door vuur en begrazing onderzocht in een veldexperiment. Vier behandelingen (geen verstoring, alleen vuur, alleen begrazing, en begrazing gecombineerd met vuur) werden toegepast op bossen verspreid langs een klimaat- en bodem-gerelateerde waterstress gradiënten. De veranderingen in soortenrijkdom en dichtheid van jonge bomen werden jaarlijks geregistreerd tussen 2003-2006. Een hoog bodemzoutgehalte (als veroorzaker van droogtestress) bleek de belangrijkste factor die soortenrijkdom en dichtheid van bomen beïnvloedt. Soortenrijkdom en dichtheid van jonge bomen, vooral in combinatie met begrazing, zijn lager bij hoge zoutgehaltes, terwijl lage zoutegehaltes in combinatie met begrazing resulteerden in positieve effecten op soortenrijkdom. Deze resultaten laten zien hoe de effecten van de verstoringen kunnen omkeren, van positief bij lage abiotische stress naar negatief bij hoge abiotische stress. Deze effecten van verstoring en abiotische stress zijn vooral duidelijk voor de zaailingsamenstelling en soortenrijkdom, veel minder voor zaailingdichtheid.

Daar er geen sterke invloed op zaailingdichtheid werd waargenomen, werden de mechanismen die verantwoordelijk zouden kunnen zijn voor het geclusterd voorkomen van bomen nader onderzocht in hoofdstuk 5. Omdat boomclustering de verspreiding van vuur kan veranderen, en vuur tegelijkertijd boomclustering kan bevorderen, en indirect de soortenrijkdom (door facilitatie), werden potentiële feedbacks tussen ruimtelijke verdeling van bomen en het voorkomen van vuur onderzocht. Boomclustering werd onderzocht door te kijken naar zogenaamde ‘nearest neighbour distances’, en ook werd gekeken naar het aantal boomclusters in een plot. Afstanden tussen planten werden groter bij toenemende waterstress, terwijl het aantal boomclusters af nam bij optreden van vuur. Vuur kwam minder voor bij kortere afstanden tussen de bomen in de clusters, maar nam toe bij grotere aantallen cluster in een plot, waarschijnlijk omdat er meer open en brandbare plekken tussen clusters overbleven. Zaailingdiversiteit nam toe met clustering op kleine schaal (met kleinere afstanden tussen de planten binnen het cluster), maar niet bij toename van het aantal clusters. Dit bevestigt dat in deze bossen bomen in een cluster elkaar faciliteren.

De resultaten van deze studie bevestigen dat de dynamiek van droge open bossen niet alleen bepaald wordt door het macroklimaat (m.n. waterstress), maar ook door bodemgerelateerde abiotische stress (m.n. zoutgehalte), verstoringen door vuur en begrazing, facilitatie door moederbomen, en combinaties van deze sturende factoren. Drie belangrijke conclusies konden worden getrokken: (1) positieve interacties dragen bij aan de succesvolle vestiging van zaailingen en aan een hoge diversiteit en soortenrijkdom bij intermediaire stressniveaus; (2) verstoringen door begrazing en vuur beperken de concurrentie en onderlinge uitsluiting bij intermediaire stressniveaus en ondersteunen daardoor onderlinge facilitatie tussen de bomensoorten in deze droge bossen; (3) klimaat en bodemcondities kunnen significante veranderingen veroorzaken in de effecten van verstoring door vuur en begrazing op vestiging en diversiteit van zaailingen. Deze resultaten suggereren dat ook in deze droge bossen bosbeheerders bomen kunnen gebruiken om gunstige condities te creëren voor de vestiging van nieuwe generaties zaailingen. Voor herstel van gedegradeerde droge open bossen kan het planten van moederbomen leiden tot betere omstandigheden voor zaailingvestiging, en aldus voorwaarden scheppen voor het herstel van gedegradeerde gebieden.

Résumé

Les forêts claires font partie des forêts tropicales sèches les plus répandues, particulièrement en Afrique. Les forêts claires à *Isoberlinia* s'étendent du Mali à l'Ouganda, au nord de l'équateur. Dans ces régions, la forêt claire constitue l'une des rares formations végétales possédant un taux de recouvrement important de ligneux, fournissant ainsi la plupart des produits forestiers. Malheureusement, les forêts claires disparaissent rapidement en raison des effets conjugués de l'exploitation forestière effrénée, l'augmentation de l'intensité et de la fréquence des sécheresses, la baisse de fertilité des sols, et des perturbations par le feu et les herbivores. Pour une utilisation et une gestion durable des forêts claires, il est important de comprendre comment ces facteurs influencent, aussi bien individuellement qu'en interactions, la structure, la dynamique et la composition spécifique des forêts claires. L'objectif de la présente étude est d'évaluer les effets de ces multiples facteurs sur les forêts claires. La question centrale est de comprendre comment le climat, le sol, le feu, les herbivores, et les interactions entre ces facteurs déterminent les interactions compétitives ou facilitatrices entre les plantes, le succès de la régénération, ainsi que la composition, la richesse spécifique et la structure des forêts claires. Pour répondre à cette question, une étude à grande échelle a été conduite au Bénin où de nombreux îlots de forêts claires à *Isoberlinia doka* sont encore retrouvés. Le modèle de Huston qui prédit la relation entre la distribution des espèces et les facteurs environnementaux a été utilisé comme hypothèse de travail. En conformité avec ce modèle, il a été prédit une prédominance des interactions facilitatrices sur la compétition entre les plantes aux niveaux intermédiaires de stress et de perturbations, et par conséquence une amélioration de la régénération des

arbres, de la coexistence des espèces, de la richesse spécifique et de la diversité des espèces à de tels niveaux intermédiaires de stress et de perturbations.

Du fait que le rôle du macroclimat en tant que facteur déterminant la dynamique des forêts sèches n’est pas entièrement compris, au chapitre 2 il a été testé l'hypothèse selon laquelle la richesse spécifique présente une distribution unimodale le long du gradient de stress hydrique, alors que la densité des arbres diminue linéairement avec l'augmentation du stress hydrique. Les résultats obtenus montrent que la distribution des espèces ligneuses est effectivement largement influencée par le climat qui détermine essentiellement le niveau de stress hydrique et que la richesse spécifique est plus élevée aux niveaux intermédiaires de stress hydrique. En outre, le stress hydrique semble interagir avec d'autres facteurs locaux tels que les feux et le pâturage par les herbivores. Il a donc été proposé que la structure unimodale de la richesse spécifique le long du gradient de stress hydrique résulte de la prédominance des interactions facilitatrices entre les plantes et de la réduction de la compétition entre les plantes par le feu et les herbivores aux niveaux intermédiaires de stress hydrique.

Pour explorer davantage cette hypothèse de facilitation entre les plantes, l'effet des arbres dominants sur la régénération a été étudié le long du gradient de stress hydrique au chapitre 3. Puisque dans des conditions de stress hydrique élevé les jeunes plants peuvent bénéficier de meilleures conditions à proximité des arbres dominants du fait de la réduction de l'évapotranspiration et de l’augmentation de la disponibilité en eau par effet de captation hydrique, il a été émis l'hypothèse que la croissance des semis et leur survie seraient meilleures sous les arbres dominants en forêt claire que dans les trouées (entre les arbres), et dans les espaces dénudés. Il a été également prévu que l’effet de facilitation serait plus important pour les espèces intolérantes à la sécheresse que pour les espèces tolérantes à la sécheresse. En accord avec ces prédictions, la régénération des arbres dans les forêts claires est facilitée par la proximité des arbres dominants et cet effet de facilitation est plus important pour l'espèce intolérante à la sécheresse que pour l'espèce tolérante à la sécheresse. Toutefois, la facilitation de la régénération par les arbres dominants n'a été observée que lorsque le stress hydrique n'était pas extrême. Ainsi, aussi bien l'espèce intolérante à la sécheresse que l'espèce tolérante à la sécheresse ont été facilitées par la proximité des arbres dominants aux niveaux intermédiaires de stress hydrique.

Au chapitre 4, les effets interactifs potentiels entre le stress hydrique et les perturbations par le feu et les herbivores ont été étudiés dans le cadre d'une expérimentation à grande échelle dans les forêts claires. Quatre traitements (pas de perturbation, perturbation par le feu uniquement, perturbation par le pâturage uniquement, perturbation par le pâturage et feu combinés) ont été appliqués aux forêts claires distribuées le long d'un gradient de stress hydrique déterminé essentiellement par le climat et le sol. Les changements dans la richesse spécifique et la densité de la régénération ont été suivis annuellement entre 2003-2006. La salinité du sol (provoquant un stress hydrique) a été le principal facteur abiotique affectant la régénération des arbres en forêt claire. La richesse spécifique et la densité de la régénération ont été réduites sous pâturage dans les conditions de forte salinité du sol, alors qu'elles avaient augmenté sous pâturage dans les conditions de faible salinité du sol. Ces résultats confirment ainsi que l'effet de la perturbation a été inversé: de positif dans les conditions de faible stress abiotique à négatif dans les conditions de stress abiotique élevé. Les effets des perturbations et du stress abiotique ont été particulièrement plus important sur la composition et la richesse spécifique de la régénération, et moindre sur la densité de la régénération.

Partant du constat que le feu et le pâturage n'avaient pas un impact important sur la densité de la régénération, les mécanismes qui pourraient être responsables de la structure agrégative des arbres, typique des forêts claires étudiées, ont été davantage évalués. Ainsi, au chapitre 5, plusieurs mécanismes qui pourraient déterminer la structure spatiale des arbres en forêt claire et leurs conséquences pour la diversité spécifique des ligneux ont été analysés. Il a été émis l’hypothèse que les feux entretiennent la structure agrégative des arbres alors que, vice versa, la structure agrégative des arbres réduit la probabilité d’occurrence du feu et améliore la diversité des espèces. La structure spatiale des arbres a été étudiée à deux niveaux: à une échelle spatiale fine par l’analyse des associations entre les individus, c'est-à-dire la distance moyenne au plus proche voisin, et à une échelle spatiale plus grossière par l’analyse des associations entre les agrégats d’arbres, notamment le nombre des agrégats d'arbres dans une parcelle. Les résultats ont montré que l’agrégation des arbres à l'échelle fine tend à diminuer dans les conditions de stress hydrique élevé alors que le feu tend à réduire le nombre des agrégats d'arbres à l’échelle grossière. La probabilité d’occurrence du feu a diminué avec la plus courte distance entre les arbres dans les agrégats, mais a augmenté avec la présence d’un plus grand nombre d’agrégats d'arbres du fait de l’accroissement des espaces ouverts et de la biomasse inflammable entre les agrégats. La diversité spécifique de la régénération était plus élevée avec l’agrégation des arbres à l’échelle fine (association des individus d’arbres), mais pas avec l’agrégation à l’échelle grossière (nombre d’agrégats), confirmant ainsi l’hypothèse de facilitation entre les arbres au sein des forêts claires.

Globalement, les résultats de cette étude ont confirmé la nature complexe des forêts claires et ont indiqué que la dynamique de ces forêts claires est déterminée non seulement par le macroclimat (stress hydrique), mais aussi par le sol (salinité), les perturbations par le feu et les herbivores, les relations facilitatrices entre les arbres, ainsi que les interactions entre ces facteurs. Trois conclusions importantes sont à retenir: (1) la facilitation entre les arbres contribue au succès de la régénération dans les forêts claires, et par conséquent à une richesse spécifique et une diversité des espèces plus élevées aux niveaux intermédiaires de stress hydrique; (2) les perturbations par les herbivores et le feu réduisent la compétition entre les arbres aux niveaux intermédiaires de stress hydrique, améliorant ainsi les relations facilitatrices entre les espèces en forêt claire; (3) les conditions de stress abiotique déterminées par le climat et le sol induisent des changements significatifs dans les effets des perturbations par le feu et le pâturage sur la régénération et la diversité de cette régénération. Sur la base de ces résultats, il a été proposé que les gestionnaires des forêts programment les coupes de manière à épargner des arbres qui pourront créer des conditions favorables à la régénération. Quant à la restauration des forêts, la plantation d'arbres-abri dans les terrains dénudés et les zones dégradées pourrait créer de meilleures conditions pour l'établissement des semis et contribuer à restaurer ces zones dégradées.

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Samadori Honoré Biaou

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Curriculum Vitae

Samadori S. Honoré Biaou was born on the 17th of September 1974 in Cotonou, Benin. In 1993, he obtained his high school degree from the "Collège d'Enseignement Général Gbegamey" in Cotonou and went to the National University of Benin (renamed as University of Abomey-Calavi) for a five-year study at the Faculty of Agronomy, with major in agronomy, forestry and natural resources management.

He obtained a general agronomy degree in 1998 and passed his engineer degree in 1999 with distinction. During his study at the Faculty of Agronomy he carried research on the possibilities for a sustainable management of Bassila forest reserve in Benin. He investigated the structure and dynamics of plant communities that served as a basis for the formulation of a management plan for the Bassila forest reserve.

From 1999 to 2000, he was employed by the Beninese NGO "TENSEERI" as Agronomist and projects coordinator. His major tasks at TENSEERI were initiating new projects and evaluating ongoing agricultural development projects. He then worked for the international NGO EnterpriseWorks Worldwide (EWW), as Agronomist from 2000 to 2002, and as Consultant / Advisor for new projects development from 2003 to 2004. At these positions, he was committed to pilot researches and feasibility studies on the possibility of growing sunflowers, strawberries and grapes in Benin. During the same period he carried several consultancy jobs for EWW about fruits, vegetables and timber production in Benin, Chad, Cameroon and Nigeria between 2003 and 2006.

In November 2001 he was admitted to the Sandwich Fellowship program of Wageningen University and joined the Forest Ecology and Forest Management group for a PhD study that led to this dissertation. While doing his PhD research, he started working at the University of Parakou in Benin as junior assistant from 2004 to 2005 and as researcher from 2005 till now.

List of publications

Published in peer reviewed journals

Sokpon, N. ; **Biaou, S.H.** ; Ouinsavi, C. et Hunhyet, O. (2006) Bases techniques pour une gestion durable des forêts claires du Nord-Bénin : rotation, diamètre minimum d'exploitation et régénération. *Bois et Forêts des Tropiques,* 60, 45-57.

Afouda, C.L.A. ; **Biaou, S.H.** ; Sidi, S. et Ahodo-Ounsou, F.T. (2006) Essais de culture de la Passiflore (*Passiflora edulis* var flavicarpa) à Parakou au Nord-Bénin : résultats préliminaires et pistes d'amélioration. *Bulletin de la recherche Agronomique du Bénin*, 53, 1-8.

Sokpon, N. and **Biaou, S.H.** (2002) The use of diameter distributions in sustained-use management of remnant forests in Benin: Case of Bassila forest reserve in North Benin. *Forest Ecology and Management*, 161, 13-25.

Sokpon, N.; Sinadouwirou, Th.; Gbaguidi, F. et **Biaou, S.H.** (2001) Aperçu sur les forêts édaphiques hygrophiles du Bénin. *Belgian Journal of Botany,* 134, 79-93.

Submitted and in preparation

Biaou, S.H.; Holmgren, M.; Sterck, F.J. and Mohren, G.M.J. (submitted) Stress-driven changes in the strength of facilitative interactions in West African woodlands.

Biaou, S.H.; Holmgren, M. and Sterck, F.J. (in prep.) Shifts in the effects of fire and herbivory on tree regeneration along abiotic stress gradients in West African woodlands.

Biaou, S.H.; Holmgren, M.; Sterck, F.J. and Sokpon, N. (in prep.) Effects of water stress on tree diversity in dry woodland-savanna mosaics of Benin.

Biaou, S.H.; Holmgren, M.; Sterck, F.J. and Mohren, G.M.J. (in prep.) Tree clustering, sapling species diversity and fire occurrence in woodlands of Benin.

Communications at international conferences

Biaou, S.H. (2008) Tree regeneration across woodland mosaics of Benin and the importance of tree facilitation. PhD day on Tropical Ecology – Amsterdam, The Netherlands, 24 January 2008.

Biaou, S.H.; Sterck, F.J.; Holmgren, M.; Sokpon, N.; Mohren, G.M.J. (2007) Tree species distribution patterns in Benin and their predictive value as indicators of disturbance. XVIIIth congress of the Association for the Taxonomic Study of the Flora of Tropical Africa (AETFAT) – Yaoundé, Cameroun, 26 February - 3 March 2007.

Sokpon N.; **Biaou S. H.**; Ouinsavi C.; Hunhyet O. and Gaoué O. (2001) Species composition and structure of the woody vegetation of the Pendjari National Park and its buffer zones in North-Western Benin. Communication, International Workshop on dry forest integrated management in West Africa. Parakou, 25-29 June 2001.

Biaou S. H. et Sokpon N. (2001) Aménagement des forêts denses sèches du Nord Bénin: bases techniques pour une gestion durable. Communication présentée au séminaire international sur l'Aménagement des forêts naturelles des zones tropicales sèches en Afrique de l'Ouest; Parakou, Bénin, 25 - 29 Juin 2001.

Sokpon N.; **Biaou S. H.**; Hunhyet O. et Ouinsavi C. (2001) Gestion durable des forêts claires du Nord Bénin: Principaux résultats et défis. Communication présentée au séminaire international sur l'Aménagement des forêts naturelles des zones tropicales sèches en Afrique de l'Ouest; Parakou, Bénin, 25 - 29 Juin 2001.

Other publications

Sokpon, N.; **Biaou, S.H.**; Ouinsavi, C. Amahohoué, I. et Gbédji, E. (2006) Installation de placettes permanentes pour le suivi de la dynamique de la végétation dans les massifs forestiers des Monts-Kouffé et de Wari-Maro. PAMF, Parakou, Bénin.

Biaou, S.H. (2004) Etude de faisabilité sur la production du raisin et de la fraise au Bénin. EnterpriseWorks Worldwide, Cotonou, Bénin.

Sokpon, N.; **Biaou, S.H.** et Ouinsavi, C. (2004) Inventaire d'aménagement des forêts classées de Ouénou-Bénou et de l'Ouémé-Boukou au Bénin. Laboratoire d'Etude et de Recherche Forestières, Parakou, Bénin.

Biaou, S.H. (2004) Assessment of the export potential for fruits and vegetables in Federal Republic of Nigeria. EnterpriseWorks Worldwide, Cotonou, Bénin.

Biaou, S.H. (2003) Compléments d'analyses sur le projet de développement des filières fruits et légumes dans la zone pétrolière au sud du Tchad. EnterpriseWorks Worldwide, Cotonou, Bénin.

Biaou, S.H. (2003) A proposal for expanded tree crop and timber production in Southern Chad. EnterpriseWorks Worldwide, Cotonou, Bénin.

Sokpon, N.; **Biaou, S.H.**; Ouinsavi, C. et Adomou, A. (2002) Inventaire des populations et quantification de la production de feuilles de *Combretum micranthum* au Bénin. Rapport d'étude de cas FAO sur les techniques d'étude des produits forestiers non ligneux. Laboratoire d'Etude et de Recherche Forestières, Cotonou, Bénin.

Sokpon, N.; **Biaou, S.H.**; Gaoue, O.; Hunhyet, O.; Ouinsavi, C. et Barbier, N. (2001) Inventaire et caractérisation des formations végétales du complexe parc national de la Pendjari, zones cynégétiques de la Pendjari et de l'Atacora (Région de Konkombri). CENAGREF - Projet Pendjari, Cotonou, Bénin.

Biaou, S.H. (2001) Rapport d'essai sur le comportement de quatre variétés de Tournesol (*Helianthus annuus*) dans le Nord-Bénin. Appropriate Technology International (ATI), Cotonou, Bénin.

Biaou, S.H. (2001) Rapport d’enquête sur les huiles consommées dans la ville de Natitingou et des tests de qualité de l’huile de tournesol. Appropriate Technology International (ATI), Cotonou, Bénin.

Biaou, S.H. (1999) Inventaire de la Forêt Classée de Bassila. Rapport synthèse. Projet de Restauration des Ressources Forestières dans la Région de Bassila (PRRF), Cotonou, Bénin.

Biaou, S.H. (1999) Etude des possibilités d'aménagement de la forêt classée de Bassila (Nord Bénin): structure et dynamique des principaux groupements végétaux et périodicité d'exploitation. Mémoire d’Ingénieur Agronome, Faculté des Sciences Agronomiques, Université Nationale du Bénin, Abomey-Calavi, Bénin.

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of Literature (5.6 ECTS)

- Effects of fire, herbivores and environmental gradients on vegetation dynamics (presented in the PE&RC discussion group: statistics, maths and modelling in production ecology and resource conservation) (2002)

Writing of Project Proposal (7 ECTS)

- The effects of spatial gradients (climate and soil) and man induced disturbances on the structure and dynamics of woodland forests in Benin (2002)

Post-Graduate Courses (7.7 ECTS)

- Multivariate analysis: PE&RC (2008)
- Fire as a driver of system processes – past, present and future; PE&RC (2008)
- Modelling techniques and systems engineering; PE&RC (2002)
- Managing diversity in living systems; PE&RC (2002)

Deficiency, Refresh, Brush-up Courses (3.1 ECTS)

- GIS Basics; Lab. GIS and remote sensing (2002)
- English course; CENTA (2002)
- Introduction to EndNote; WUR Library (2002)

Competence Strengthening / Skills Courses (6.1 ECTS)

- Introduction to R for statistical analysis; WIAS (2008)
- Scientific publishing; PE&RC (2008)
- Methods in scientific research and grant proposal writing; NPT / Univ. of Parakou (2006)
- Techniques for writing and presenting scientific papers; SENSE (2002)
- System analysis, simulation and system management; PPS (2002)

Discussion Groups / Local Seminars and Other Scientific Meetings (8 ECTS)

- Mini symposium: patterns and mechanisms of facilitation in plant and animal communities; REG (2008)
- Mini symposium: functional traits and the ecological performance of tropical trees; Forest Ecology and Forest Management Group (2008)
- PhD DAY, presentation: tree regeneration across woodland mosaics of Benin and the importance of tree facilitation; Tropical Ecology, Amsterdam (2008)
- Ecological theories and applications; PE&RC (2008)
- Weekly chair group seminars and presentations (6 months participation in 2002 and 12 months in 2008), given 3 presentations in 2002 and 4 presentations in 2008 (2002 & 2008)
- Statistics, maths and modelling in production ecology and resource conservation; PE&RC discussion group (2002)
- Production Ecology and Resource Conservation; PE&RC discussion group (2002)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (0.9 ECTS)

- PE&RC Introduction weekend (2008)

International Symposia, Workshops and Conferences (4.5 ECTS)

- Annual meeting of the Netherlands Ecological Research Network (NERN) (2008)
- XVIIIth congress of the Association for the Taxonomic Study of the Flora of Tropical Africa (AETFAT); Yaoundé, Cameroun; presentation: tree species distribution patterns in Benin and their predictive value as indicators of disturbance (2007)
- Tropenbos conference on Restoration and Sustainable Management of Forests in Ghana (2005)

Courses in which the PhD Candidate Has Worked as a Teacher

- Forest inventory and forest measurements; 5 days; FA-Univ. Parakou (2006)
- Forest ecology; 3 days; FA-Univ. Parakou (2006)
- Introduction to Informatics; 20 days; FA-Univ. Parakou (2005 to 2008)
- Data analysis with SPSS; 20 days; FA-Univ. Parakou (2005 to 2008)