Tropical Ecology **50**(2): 339-353, 2009
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www.tropecol.com

ISSN 0564-3295

Regeneration and spatial distribution of seedling populations in Sudanian dry forests in relation to conservation status and human pressure

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Abstract: Effects of conservation status and human population pressure on species composition, density and spatial distribution of seedling populations in Sudanian dry forests of Burkina Faso were studied. Data were collected from protected and unprotected forests at two sites differing in human population densities. A total of 62 species were recorded, representing 23 families and 48 genera, and the dominant families were Combretaceae and Caesalpiniaceae. Population pressure influenced significantly the species richness, but not conservation status. There were moderately significant differences in seedling densities between protected and unprotected forests at each site. The mature-juvenile relationships were generally weak in all cases ($r^2 < 50\%$). The spatial distribution of the seedlings was mainly clumped, reflecting the dominance of clonal propagation. The protection provided by the present conservation status was inefficient in promoting regeneration. As most species have few seedlings, expediting the natural regeneration process inside and outside the forest reserve is recommended.

Resumen: Se estudiaron los efectos del estado de conservación y la presión de la población humana sobre la composición de especies, la densidad y la distribución espacial de poblaciones de plántulas en bosques secos sudaneses de Burkina Faso. Se obtuvieron datos en bosques protegidos y no protegidos en dos sitios que difieren en las densidades de la población humana. Se registró un total de 62 especies que representan 23 familias y 48 géneros, y las familias dominantes fueron Combretaceae y Caesalpiniaceae. La riqueza de especies estuvo influenciada significativamente por la presión poblacional pero no por el estatus de conservación. Hubo diferencias significativas modestas en las densidades de las semillas entre los bosques protegidos y no protegidos en cada sitio. Las relaciones maduro-juvenil fueron en general débiles en todos los casos ($r^2 < 50\%$). La distribución espacial de las plántulas fue principalmente agregada, lo que refleja la prevalencia de la propagación clonal. La protección que brinda el estatus actual de conservación no fue efectiva para promover la regeneración. Dado que la mayoría de las especies tienen pocas plántulas, se recomienda acelerar el proceso de regeneración natural dentro y fuera de la reserva forestal.

Resumo: Os efeitos do status da conservação e da pressão da população humana na composição das espécies, densidade e distribuição espacial das populações de plântulas na floresta seca sudanesa do Burkina Faso foram estudados. Os dados foram colectados em florestas protegidas e não protegidas em duas estações diferentes em relação à densidade

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populacional. Um total de 62 espécies foram registadas, representando 23 famílias e 48 géneros sendo as famílias dominantes as *Combretaceae* e as *Caesaliniaceae*. A pressão da população influenciou significativamente a riqueza específica, mas não o status conservacionista. Houve diferenças moderadamente significativas nas densidades das plântulas entre as florestas protegidas e não protegidas em cada estação. As relações adulto-juvenil eram geralmente fracas em todos os casos ($r^2 < 50\%$). A distribuição espacial das plântulas era principalmente agregada, reflectindo a dominância da propagação clonal. A protecção proporcionada pelo status conservacionista actual era ineficiente na promoção da regeneração. Como a maior parte das espécies têm poucas plântulas, a promoção do processo de regeneração dentro e fora da reserva florestal é recomendada.

Key words: Burkina Faso, clumped distribution, dry forest, protected areas, seedling recruitment.

Introduction

Dry forests comprise more than 40% of all tropical forests (Murphy & Lugo 1986). In Africa, dry forests account for 70% of the forested area and occur within the savanna biome (Abbadie *et al.* 2006). However, increasing growth in human population has caused rapid degradation of the dry forests, resulting in conversion to agricultural land and excessive exploitation of the forests for fuelwood and construction material (Huang *et al.* 2003; Lambin 1999; Paré *et al.* 2008; Stephenne & Lambin 2001). West Africa is one of the world's biodiversity hotspots (Poorter *et al.* 2004), and the forests, in both reserves and parklands, contain a large part of the diversity. Large rural households are strongly dependent on the forests for their livelihoods, and this, coupled with a high demand for fuelwood, is increasing the pressure on the remaining forests (Forester & Machlis 1996; McKee *et al.* 2004; Neke *et al.* 2006). Overall, such pressures are likely to cause large changes in the size class distribution and recruitment of harvested woody species (Kennard *et al.* 2002; Luoga *et al.* 2004).

The challenges involved in ensuring that forests are used sustainably can only be met if efforts are made to maintain the remaining forests, while restoring deforested and degraded areas. Therefore, an understanding of natural regeneration processes and the distribution of recruits is of paramount importance to examine the build-up of future forest structure and composition (Ceccon *et al.* 2006; Tesfaye *et al.* 2002). The processes involved in tree regeneration can be influenced by many factors, such as variations in seed dispersal intervals, seed quality, wind direction and speed, slope gradients and aspects, and soil moisture availability (Vieira & Scariot 2006). Patterns of forest regeneration following natural or anthropogenic disturbances are also influenced by interactions between disturbance regimes (intensity, frequency, scale) and biological features of species, such as their life cycles and behavior (Hoffmann & Solbrig 2003; Kennard *et al.* 2002; Menaut *et al.* 1995; Scholes & Walker 1993). In addition, intra- and inter-specific competition for water, nutrients, and space are also important factors in regeneration and growth of species (Bellefontaine *et al.* 2000; Dembele *et al.* 2006; Picard & Bar-Hen 2002).

Not only the quantity of recruited individuals but also their spatial distribution determines the structure of the future forest stand. The spatial distribution of seedlings mainly results from their establishment patterns, which in turn are affected by seed dispersal mechanisms, the distribution of regeneration niches, and density-dependent population dynamics, such as seedling and seedling-sapling mortality rates as well as environmental and anthropic influences (Condit *et al.* 2000; Khurana & Singh 2001; Linares-Palomino 2005; Teketay 1997; Uasuf *et al.* 2009). In general, individuals of a given species can exhibit three primary patterns of distribution throughout the community: random, uniform or clumped (Barbour *et al.* 1999). Clumped distributions have been found to be the most common pattern of species distribution in tropical dry forests (Hubbell 1979), since many plants in the savanna biome are highly clonal (Bellefontaine 2005).

In West Africa, most of the forest management activities that concern fuelwood supply and biodiversity conservation occur in the State Forest Reserves. However, documentation of the forests' natural regeneration processes (e.g. seed germination, seedling establishment, population change and spatial pattern) is still limited. Previous studies have tended to focus on regeneration mechanisms after selective tree cutting (Ky-Dembele *et al.* 2007), the spatial distribution and germination patterns of particular species (Bationo *et al.* 2005), or the effects of fire and grazing disturbances on vegetation structure and plantlet dynamics (Zida *et al.* 2007). Information on the effect of human pressure on seedling-sapling population composition and spatial distribution in the forest reserves is still lacking. Such knowledge is vital when developing guidelines for long-term management and/or restoration strategies (Bariteau 1992; Bationo *et al.* 2005; Bellefontaine 2005).

Hence, this study examined the species composition, density and spatial distribution of seedling populations in relation to conservation status and human population pressure. We gathered data from protected and unprotected forests in two villages in Sissili province, southern Burkina Faso that differ in human population pressure to test the following hypotheses: (i) Species richness and density of seedling populations are higher in protected area and in a village with low human population pressure than in unprotected areas and in a village with high human population pressure due to continuous severe disturbance in the latter and moderate disturbance in the former; (ii) The spatial distribution of seedling populations differs in relation to conservation status of forests and human population pressure. According to intermediate disturbance hypothesis, moderate disturbance enhances species diversity (e.g. Molino & Sabatier 2001).

Materials and methods

Site description

The study was conducted in the protected and unprotected forests of the villages of Boala (8 249 ha) and Yale (10 641 ha) located at 300 m above sea level in Sissili Province (11º02'- 12º00'N and 1°30'- 2º80'W) southern Burkina Faso, West Africa (Fig. 1). The protected forest was delimited by the colonial French administration in 1955. In principle, no livestock grazing, settlement, hunting, fishing or fuelwood extraction is permitted in the protected forest. However, this protection is loose and the protected forest is being utilized both legally and illegally by an increasing number of local people in the reserve fringe villages, such as Boala and Yale.

Phytogeographically, the study sites are situated in the Sudanian regional centre of endemism in the south Sudanian Zone (White 1983). The climate is tropical with a unimodal rainy season lasting from May to October. The mean (± SE) annual rainfall for the years 2000-2003 was 875.6 ± 26.0 mm, with 55 ± 2 rainy days per annum. The average annual temperature is 28ºC, with a maximum average monthly temperature of 37.9ºC in April and a minimum average monthly temperature of 17.6ºC in December. The vegetation comprises of clusters of dry forests that are mainly located in the protected areas, gallery forests along the water courses, dominant woodlands, and shrublands. The woody flora is dominated by *Burkea africana* Hook. f., *Pteleopsis suberosa* Engl. & Diels, *Terminalia avicennioides* Guill. & Perr., *Isoberlinia doka* Craib & Stapf, *Detarium microcarpum* Guilt. & Perr., and *Vitellaria paradoxa* C.F. Gaertn. The herbaceous layer is dominated by *Andropogon gayanus* Kunth and *Andropogon ascinodis* C.B.Clarke (Fontes & Guinko 1995).

Data collection and analysis

A stratified systematic design was applied where the study site was first stratified based on human population pressure as low (Boala) and high (Yalé) and then based on conservation status as protected and unprotected forests. A vegetation map, obtained by visually interpreting aerial photographs from 1997, was used to select and lay out the sample plots. The number of plots in each unit was proportional (1%) to the size of each forest. A total of 127 circular plots of 456.16 m^2 were used. All seedlings with a diameter at breast height (dbh) < 2.5 cm and a height < 1.5 m were counted in each plot. Mature trees with dbh > 2.5 cm and height > 1.5 m were also recorded. Species were identified *in situ* in and nomenclature of species followed Arbonnier (2002).

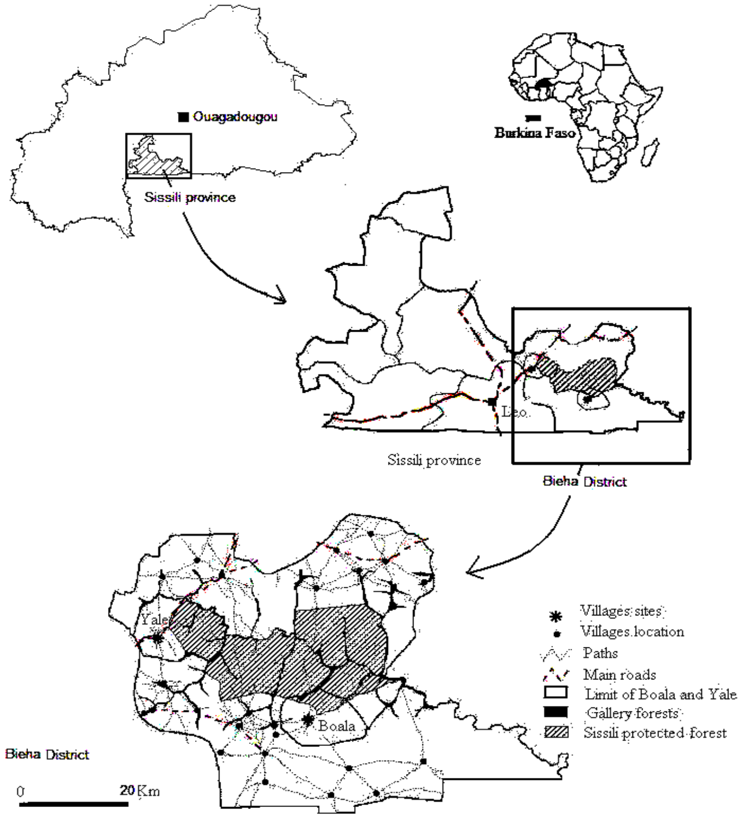

Fig. 1. Location of the study area.

Unbalanced two-way ANOVA based on Type II sums of squares (Langsrud 2003) was performed to examine whether dry forest conservation status and human population pressure affected the seedling richness and/or density. Soil characteristics and shortest distance of plots from forest edge were introduced as covariates during the analysis to reduce the effects of potential confounding factors on regeneration. The magnitude of any significant effect was determined by a statistic called partial eta squared, η_p^2. It is a measure of association between an effect (e.g. main effect, an interaction, a linear contrast) and the dependent variable, which can be calculated as the ratio of the effect variance (SS_{effect}) to the sum of the effect and error variances ($SS_{effect} + SS_{error}$). The effect is considered to be small, moderate or large if the value of this statistic is 0.01, 0.06 or 0.14, respectively (Cohen 1988). Both linear and non-linear curves were fitted to find the best function for describing the relationship between seedling and adult tree densities. The best function was selected based on the amount of variation explained (adjusted coefficient of determination) and statistical significance. The statistical analyses were performed using SPSS 15 software (Copyright SPSS for Windows, Release 2006. Chicago: SPSS Inc).

Principal Component Analyses (PCA) was performed to explore the pattern of seedling populations with regards to forest conservation status and human population pressure. The data matrix for PCA was the density of rows of species in protected and unprotected forest at each site (see Table 1). PCA was performed on mean centered and standardized density data using the software package CANOCO 4.5, and the ordination diagrams were drawn in CANODRAW (ter Braak & Smilauer 2002).

The similarity in species composition of seedlings in the protected and unprotected forests at each village was compared using Sorensen's similarity index (Krebs 1999) calculated by using the following formula:

$S_s = 2a / (2a + b + c)$

where, S_s= Sorensen's similarity coefficient, a = number of species with seedlings present in both protected and unprotected forests, b = number of species with seedlings exclusively present in the protected forests, and c = number of species with seedlings exclusively present in the unprotected forests. Sorensen's coefficient has a range between zero (no species in common) and 1 (complete similarity).

The spatial distributional patterns of the seedling populations within the different sites and forest conservation types were analyzed using the standardized Morisita's index (I_p), since it is relatively independent of population density (Krebs 1999). First the Morisita's index was computed as:

$I_d = n (\sum x^2 - \sum x) / [(\sum x)^2 - \sum x]$

where, n is the sample size, $\sum x$ and $\sum x^2$ are the sum of the quadrat counts, and the sum of the quadrat counts square, respectively. Then two critical values for the Morisita's index were calculated using the following formulae:

Uniform index; $M_u = (\chi^2_{0.975} - n + \sum x_i) / (\sum x_i - 1)$

Clumped index; $M_c = (\chi^2_{0.025} - n + \sum x_i) / (\sum x_i - 1)$

where, $\chi^2_{0.975}$ and $\chi^2_{0.025}$ are values of chi-squared with (n-1) degrees of freedom that has 97.5% and 2.5% of the area to the right, respectively; x_i = given a set of counts of organisms in a set of quadrats and n = number of quadrats.

Finally, the standardized Morisita's index was calculated using the relevant formula out of the following four:

(1) $I_p = 0.5 + 0.5 (I_d - M_c) / (n - M_c)$; when $I_d \geq M_c > 1.0$
(2) $I_p = 0.5 (I_d - 1) / (M_u - 1)$; when $M_c \geq I_d > 1.0$
(3) $I_p = -0.5 (I_d - 1) / (M_u - 1)$; when $1.0 > I_d > M_u$
(4) $I_p = -0.5 + 0.5 (I_d - M_u) / M_u$; when $1.0 > M_u > I_d$

The standardized Morisita index of dispersion (I_p) has a range between -1 and +1, with 95% confidence limit at ± 0.5, where values of 0.0 indicate random dispersion, above 0.0 clumped dispersion, and below 0.0 uniform dispersion.

Results

Species composition

A total of 63 species, representing 23 families and 48 genera, were recorded as seedlings; 43 species representing 35 genera were found in the protected forest, and 56 species representing 44 genera were recorded in the unprotected forest (Table 1). The families with the highest number of species were Combretaceae and Caesalpiniaceae, which jointly accounted for one third of the total species richness of the Sissili forest. These were followed by Rubiaceae and Mimosaceae, which together accounted for one third of the total seedling species recorded. *D. microcarpum* and *V. paradoxa* were the most frequently occurring species in both forest types, followed by *Piliostigma thonningii* (Schumach.) Milne-Redh. in the protected forest at Yale and *Gardenia erubescens* Stapf & Hutch. in the unprotected forest at Boala. Both forest types were generally characterized by a low proportion (18%) of abundant species (those with > 40 individuals ha^{-1}) and a low frequency of occurrence. In addition, the proportion of abundant species was higher in the unprotected forests (19%) than in the protected ones (5%).

At plot level, ANOVA revealed that there was no significant effect of conservation status on the species richness of seedlings ($p > 0.05$) while human pressure decreased ($F_{[1,\ 122]} = 8.94$; $p = 0.003$; $\eta_p^2 = 0.068$) richness after significant adjustment by the covariate, distance to forest edge ($p = 0.008$). The interaction between conservation status and site did have a significant effect on species richness of moderate magnitude ($F_{[1,\ 122]} = 6.01$; $p = 0.016$; $\eta_p^2 = 0.047$). Species richness was slightly higher in the unprotected forest at Boala than Yale (Table 2).

A comparison, using Sorensen's similarity index, of the seedling population richness between the forest types of the two sites showed that plots in the protected area of Yale and the unprotected area of Boala had the greatest similarity in species composition (Table 3). The unprotected areas of the two sites had the least similarity.

Density of seedling populations

The overall mean seedling population density was 731 ± 79 individuals ha^{-1}. There was significant decrease ($F_{[1,\ 122]} = 10.48$; $p = 0.002$; $\eta_p^2 = 0.079$) in seedling population density due to human pressure while conservation status had a marginally significant effect ($F_{[1,\ 122]} = 3.48$; $p = 0.064$). The average density of seedlings was slightly higher in the unprotected than in the protected forests at both sites (Table 2). The highest density was observed in the unprotected forests of Boala (1120 ± 199 individuals ha^{-1}), while the lowest was seen in the protected forests of Yale (468.50 ± 51.28 individual ha^{-1}). The species with the highest density were *P. suberosa* in Boala and *D. microcarpum* in Yale, irrespective of forest type

(Table 1). Seedling densities of *Grewia bicolor* Juss., *Prosopis africana* (Guilt. & Perr.) Taub., *Lannea velutina* A. Rich. and *Cassia sieberiana* DC. were all low at both sites. The pattern of juvenile - adult density relationship varied from quadratic to exponential depending on the forest type (Fig. 2), and the relationship was significant but the magnitudes were generally low ($r^2 < 0.50$) in all cases.

Table 1. Species composition, density (number ha^{-1}) and frequency (number of plot in which a species occurred) of seedling at high (Yale) and low (Boala) human pressure sites, southern Burkina Faso.

A. Protected Forest (n = 13 and 49 at Boala and Yalé, respectively)

Family	Species	Code	Density		Frequency	
			Boala	Yale	Boala	Yale
Annonaceae	*Annona senegalensis* Pers.	anse		29		16
	Hexalobus monopetalus Engl. & Diels	hemo	177		1	
Anacardiaceae	*Lannea acida* A. Rich.	laac		35		1
	Lannea velutina A. Rich.	lave	22	33	1	1
Caesalpiniaceae	*Burkea africana* Hook.	buaf	140		3	
	Cassia sieberiana DC.	casi		22		2
	Daniellia oliveri (Rolfe) Hutch.& Dalz.	daol	66	22	1	1
	Detarium microcarpum Guilt. & Perr.	demi	97	226	5	37
	Isoberlinia doka Craib & Stapf	iso	22	75	1	1
	Piliostigma thonningii (Schumach.) Milne-Redh.	pith	22	102	1	19
	Tamarindus indica L.	tain		59		1
Celastraceae	*Maytenus senegalensis* (Lam.) Exell	mase	22	22	1	2
Combretaceae	*Anogeissus leiocarpa* Guill. & Perr.	anle		85		3
	Combretum glutinosum Guill. & Perr.	cogl	122	64	2	10
	Combretum molle R. Br. ex G. Don	como	44	50	1	4
	Combretum nigricans Leprieur ex Guilt. & Perr.	coni		71		3
	Pteleopsis suberosa Engl. & Diels	ptsu	323	62	8	13
	Terminalia avicennioides Guilt. & Perr.	teav	210	71	4	9
	Terminalia glaucescens Planch. ex Benth.	tegl		62		4
	Terminalia macroptera Guilt. & Perr.	tema	519	80	2	10
Fabaceae	*Lonchocarpus latiflora* (Willd.) DC.	lola		22		1
	Pericopsis laxiflora (Benth. ex Baker) van Meeuwen	pela		39		1
	Xeroderris stuhlmannii (Taubert) Mendonca & E.P. Sousa	xest		44		2
Ebenaceae	*Diospyros mespiliformis* Hochst. ex A.DC.	dime		37		1
Euphoriaceae	*Bridelia ferruginea* Benth.	brfe		22		1
Loganiaceae	*Strychnos spinosa* Lam.	stsp	154	55	1	4
Meliaceae	*Pseudocedeala kotschyi* Harms	psko		59		3
	Trichilia emetica Vahl	trem	22		1	
Mimosaceae	*Acacia dudgeoni* Craib	acdu	55	88		4
	Acacia macrostachya Rchb. ex DC.	acma		177		3
	Dichrostachys cinerea (L.) Wight. & Arn.	dici		44		2
	Prosopis africana Taub.	praf	22	28	1	5
Moraceae	*Ficus sycomorus* subsp *gnaphalocarpa* (Miquel) CC. Berg	fisy	22		1	
Olacaceae	*Ximenia americana* L.	xiam	66	33	2	11
Rhamnaceae	*Ziziphus mucronata* Willd.	zimu		44		2
Rubiaceae	*Crossopteryx febrifuga* Benth.	crfe	66	98	3	9
	Feretia apodanthera Delile	feap	287		1	
	Gardenia aqualla Stapf & Hutch.	gaaq	154	22	1	1
	Gardenia erubescens Stapf & Hutch.	gaer	66	33	2	4
	Gardenia ternifolia Schumach. & Thonn.	gate		44		1
Sapotaceae	*Vitellaria paradoxa* C.F.Gaertn.	vipa	98	74	7	22
Sterculiaceae	*Sterculia setigera* Delile	stse		22		1
Tilaceae	*Grewia bicolor* Juss.	grbi		22		2

Table 1B. Unprotected forest (n = 43 and 22 at Boala and Yalé, respectively).

Family	Species	Code	Density		Frequency	
			Boala	Yale	Boala	Yale
Annonaceae	*Annona senegalensis* Pers.	anse	44	57	4	3
	Hexalobus monopetalus Engl. & Diels	hemo	83		4	
Anacardiaceae	*Lannea acida* A. Rich.	laac	37		3	
	Lannea microcarpa Engl. &K.Krause	lami	44		1	
	Lannea velutina A. Rich.	lave	22		1	
	Ozoro insignis Delile	ozin	22		1	
Bignoniaceae	*Stereospermum kunthianum* Cham.	stku	33		2	
Bombaceae	*Bombax costatum* Pellegr. & Vuillet	boco	44		1	
Caesalpiniaceae	*Afzelia africana* Sm.	afaf	22		1	
	Burkea africana Hook.	buaf	113		8	
	Cassia sieberiana DC.	casi	44		1	
	Daniellia oliveri (Rolfe) Hutch.& Dalziel	daol	94		11	
	Detarium microcarpum Guilt. & Perr.	demi	133	164	26	11
	Isoberlinia doka Craib & Stapf	isdo	55		3	
	Piliostigma thonningii (Schumach.) Milne-Redh.	pith	99	177	11	10
	Pterocarpus erinaceus Lam.	pter	265	22	1	1
Celastraceae	*Maytenus senegalensis* (Lam.) Exell	mase	58	27	5	3
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth	pacu	232		2	
Combretaceae	*Anogeissus leiocarpa* Guill. & Perr.	anle		162		1
	Combretum collinum Fresen.	coco	44		1	
	Combretum fragrans F. Hoffm.	cofr	96		3	
	Combretum glutinosum Guill. & Perr.	cogl	69	74	9	7
	Combretum molle R. Br. ex G. Don	como	472	100	3	1
	Combretum nigricans Leprieur ex Guill. & Perr.	coni	131	71	13	4
	Pteleopsis suberosa Engl. & Diels	ptsu	546	80	18	5
	Terminalia avicennioides Guilt. & Perr.	teav	236	102	13	5
	Terminalia laxiflora Engl.	tela		354		1
	Terminalia macroptera Guilt. & Perr.	tema	447	22	9	1
Fabaceae	*Xeroderris stuhlmannii* (Taubert) Mendonca & E.P. Sousa	xest	77		2	
Ebenaceae	*Diospyros mespiliformis* Hochst. ex A. DC.	dime	48	52	6	1
Euphoriaceae	*Bridelia ferruginea* Benth.	brfe	66		1	
Hymenocardiaceae	*Hymenocardia acida* Tul.	hyac	22		1	
Loganiaceae	*Strychnos spinosa* Lam.	stsp	150	44	14	1
	Strychnos innocua Delile	stin	44		2	
Meliaceae	*Azadirachta indica* A. Juss.	azin	66		2	
	Pseudocedeala kotschyi Harms	psko	656		3	
	Trichilia emetica Vahl	trem	66		1	
Mimosaceae	*Acacia dudgeoni* Craib	acdu	111		11	
	Acacia macrostachya Rchb. ex DC.	acma	88		1	
	Acacia sieberiana DC.	acsi	177		1	
	Dichrostachys cinerea (L.) Wight. & Arn.	dici	348	22	4	3
	Parkia biglobosa (Jacq.) R. Br. ex G.Don	pabi	22		1	
	Prosopis africana Taub.	praf	22	44	1	1
Moraceae	*Ficus thonnigii* Blume	fith	105		4	
Olacaceae	*Ximenia americana* L.	xiam	33		5	
Polygalaceae	*Securidaca longepedunculata* Fresen.	selo	575	22	1	1
Rhamnaceae	*Ziziphus mucronata* Willd	zimu		22		1
Rubiaceae	*Fadogia agrestis* Schweinf. ex Hiern	faag		22		1
	Feretia apodanthera Del.	feap		44		1
	Crossopteyx febrifuga Benth.	crfe	234	88	7	2
	Gardenia erubescens Stapf & Hutch.	gaer	157	74	23	2
	Sacrcocephalus latifolius (Sm.) E.A.Bruce	sala	22		1	
Sapotaceae	*Vitellaria paradoxa* C.F.Gaertn.	vipa	93	92	19	9
Sterculiaceae	*Sterculia setigera* Delile	stset	22		1	
Tilaceae	*Grewia bicolor* Juss.	gebi	265		1	
	Grewia lasocdiscus K. Schum.	gela	22	44	1	1

Table 2. Species richness (number plot^{-1}) and density (number ha^{-1}) of seedling population in relation to conservation status of the forests at two sites in southern Burkina Faso (mean ± SE).

Attributes	Sites	Conservation status	
		Protected	Unprotected
Richness	Boala	4 ± 1	6 ± 1
	Yale	5 ± 1	4 ± 1
Density	Boala	611 ± 203	1120 ± 199
	Yale	494 ± 51	627 ± 120

For the overall seedling populations, the two principal components were significant ($p < 0.05$). The eigenvalues for PCA axes 1 and 2 were 0.463 and 0.214, respectively thus capturing 67.7% of the total variation in the data. The first axis described the disproportionately large number of species with low seedling densities irrespective of the conservation status and human pressure (Fig. 3A). The first principal component also revealed that *D.*

Table 3. Sorensen's similarity index between protected and unprotected forests at two sites in a Sudanian dry forest of Burkina Faso.

Sites	Forest status	Boala		Yale	
		Protected	Unprotected	Protected	Unprotected
Boala	Protected	1	0.62	0.57	0.65
	Unprotected		1	0.76	0.53
Yale	Protected			1	0.62
	Unprotected				1

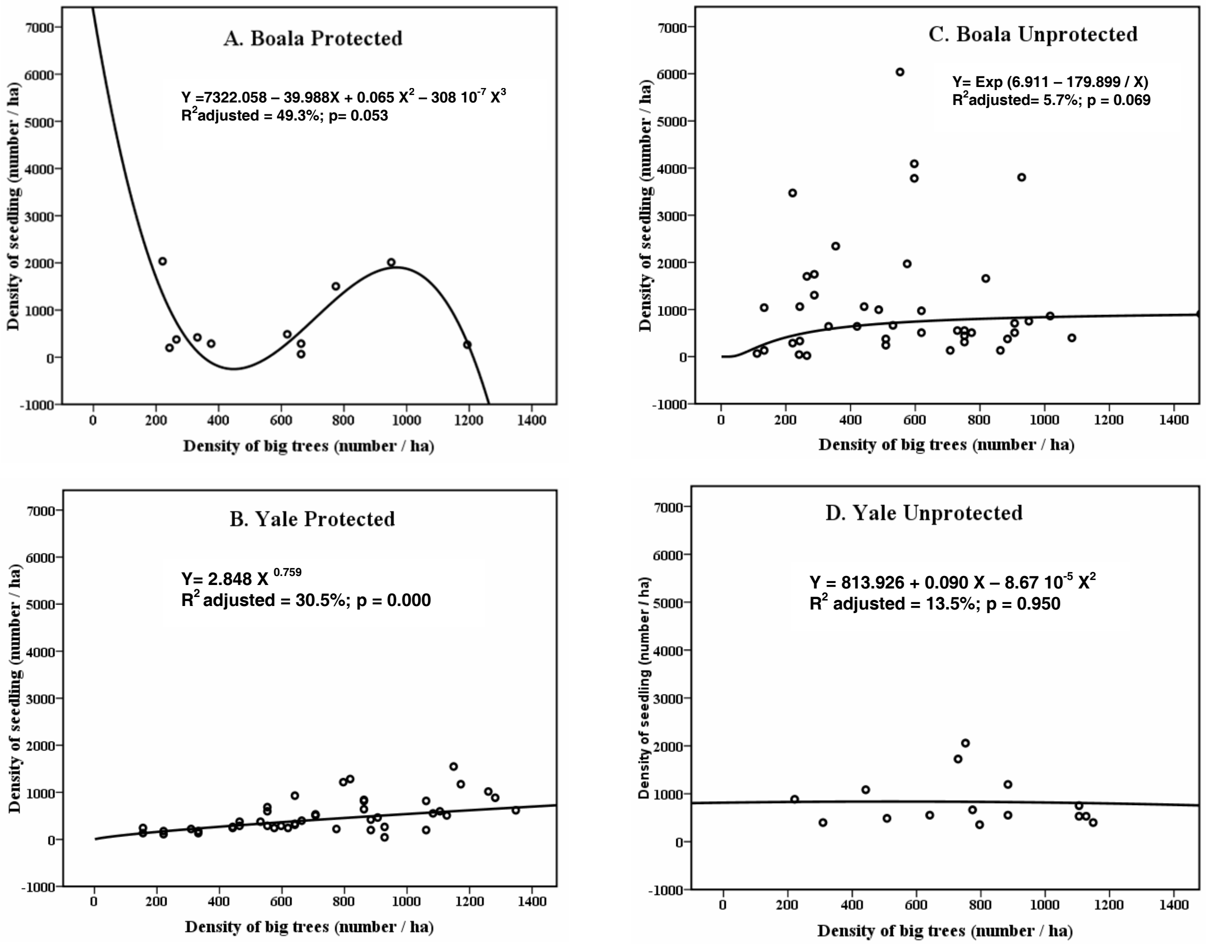

Fig. 2. Relationship between density of seedlings and mature trees in Sudanian dry forests of Burkina Faso. A = Boala protected, B = Yale protected, C = Boala unprotected, D = Yale unprotected.

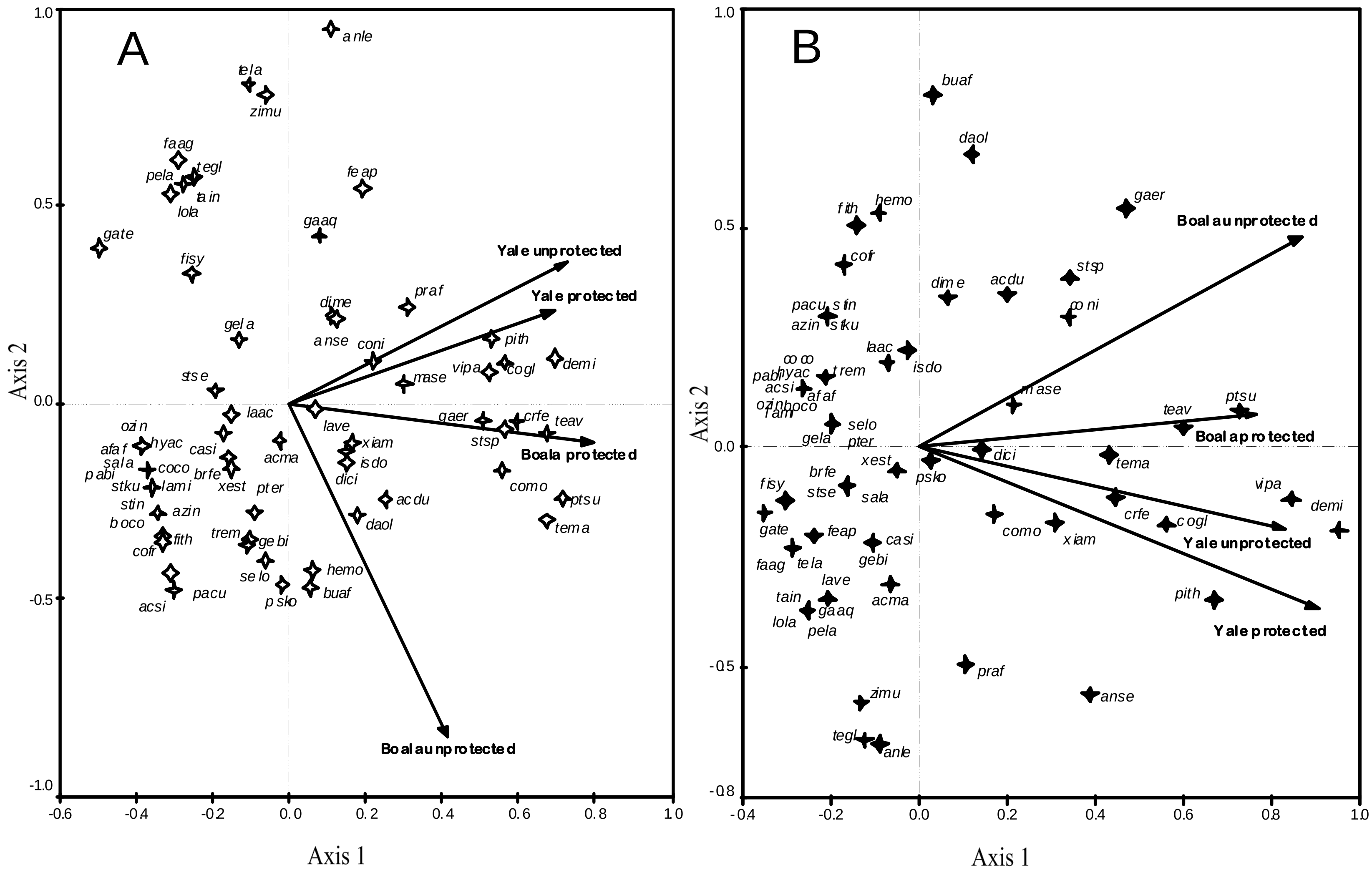

Fig. 3. Score and loading plots from PCA ordination of species by seedling density (number ha-1) [A] and frequency of occurrence (number of plots in which seedling occur) [B] for the first two principal components. For species code, see Table 1.

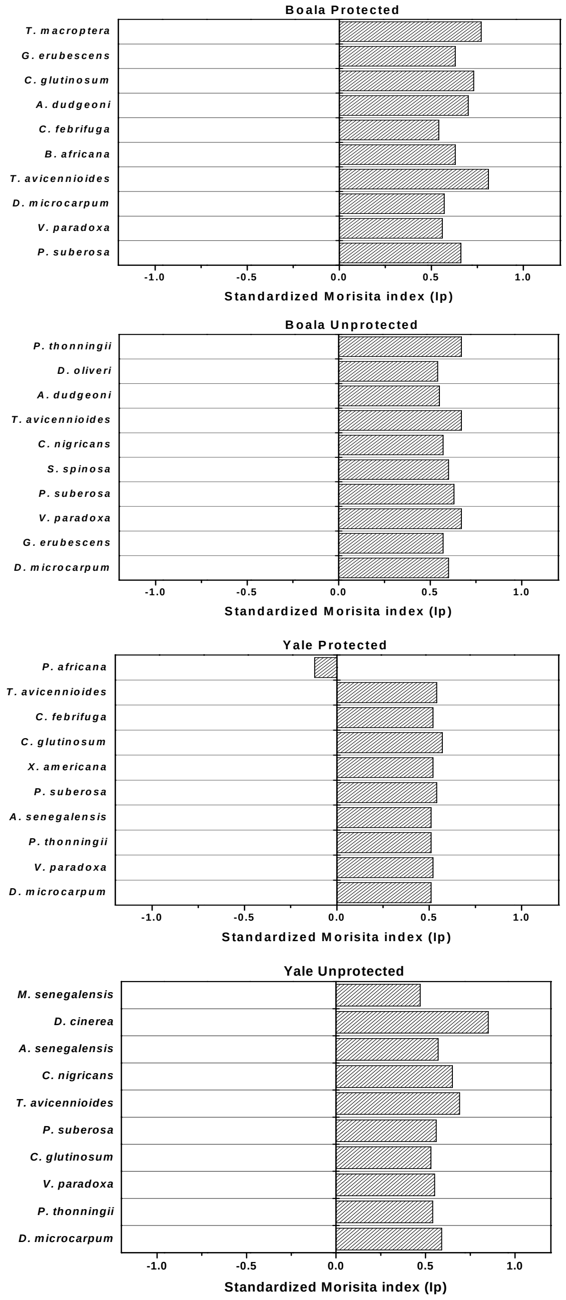

Fig. 4. Spatial distribution of seedling populations at two sites with high human pressure (Yale) and low human pressure (Boala) in the Sudanian dry forests of Burkina Faso. Only the ten most frequent species were presented for the sake of clarity; Ip > 0 for all unreported species.

microcarpum, *Combretum glutinosum* Guill. & Perr. and *V. paradoxa* were abundant in both protected and unprotected forest of the site with high human pressure (Yale) while *P. suberosa*, *Terminalia avicenoides* Guilt. & Perr., and *T. macroptera* were abundant at the site with low human pressure (Boala) compared to the majority of the species. The second component identified mainly *B. africana* and *Hexalobus monopetalus* Engl. & Diels. as an abundant species at the site with low human pressure while at the site with high human pressure *Anogeissus leiocarpa* (DC.) Guill. & Perr and *Piliostigma thonningii* were abundant. The majority of the species were distributed in all forest types irrespective of human pressure. For the seedling frequency in the inventoried plots, the fraction of the variance explained by the first two axes, which were significant, was 87.9%. The first axis explained 68.5% of the variance and the second axis 16.1%. PCA exhibited a pattern similar to the species density for each forest type and site (Fig. 3B).

Spatial distribution of seedling populations

The Standardized Morisita's index value varied depending on the species and was greater than 0.5 for 98% of the species in the protected forests and 97% of the species in the unprotected forests at both villages (Fig. 4). As a whole, the seedling populations displayed clumped distribution for all species examined at both sites except *P. africana* in the protected forest of Yale that showed a random pattern.

Discussion

Overall, seedlings representing 63 species were recorded across the surveyed area. The number of species with seedlings seen in the protected forests (43) was lower than the numbers observed in other regions, such as Laba (59) and Tiogo protected forests (64), which are located in the transition from the North to South Sudanian Zone of Burkina Faso (Zida *et al.* 2007). The number of species recorded in the Nazinon reserve (54), which is also located in the same region as the sites examined in the present study (Alexandre 1992; Ky-Dembele *et al.* 2007), was also higher than the number recorded here. However, 32 species reported by Ky-Dembele *et al.* (2007) were also seen in this study, most of which were common woody species recorded in the Sudanian Zone of Burkina Faso (Fontes & Guinko 1995). Apart from other site-specific factors, the observed differences in species richness among sites could be related to sampling efforts. In addition, 13 species out of all those recorded in this survey have previously been identified as root suckering species in an earlier study (Alexandre 1992), and more recently in the Nazinon reserve (Bationo *et al.* 2005; Bellefontaine 2005; Ky-Dembele *et al.* 2007), although they also regenerate by seeds. The protected and unprotected forests were highly similar in their seedling species composition as indicated by the even distribution of the majority of the species on the PCA plots. This is due to a similar prevalence of common species from the four dominant families, which form two thirds of the total seedling species recorded.

In this study, we also found that most of the species had low frequencies of seedlings and generally low densities, which is consistent with results obtained in a study made in the Nazinon forest (Ky-Dembele *et al.* 2007). The relatively high seedling density observed in the unprotected forests is similar to those recorded by Mwima & McNeilage (2003), who also found regeneration conditions to be more favorable in the areas surrounding a protected forest than inside it. Protected forests are generally assumed to be less affected by external disturbances, and hence favor natural regeneration processes. However, species such as *B. africana* and *Anogeissus leiocarpa* Guill. & Perr. had lower frequencies of occurrence and seedling densities in the protected forests (and were sometimes completely absent) than in the unprotected forests. Whereas other dominant tree species in the unprotected forests, such as *Pterocarpus erinaceus* Lam., *Afzelia africana* Sm. and *I. doka*, were characterized by low frequencies and seedling densities, and were totally absent in the protected forests. Most of the species had a marginally lower seedling densities in the protected forests than the unprotected forests contrary to our expectation (disturbance is mild in protected areas, thus yielding higher species richness and density). One possible explanation could be the loose protection of the protected forests (e.g. part of the protected forest was open for ranching in Yale) that led to heavy disturbance than expected. The other explanation would be better tenure security in the unprotected forest, as it includes secondary forests derived from privately owned fallows. It could also be explained by the dominance of species with few individuals, which is a characteristic of African savanna-woodlands (Luoga *et al.* 2004; Menaut *et al.* 1995; Paré *et al.* 2009). In addition to species composition, several abiotic factors (e.g. water, nutrients and space) also affect the regeneration of plant species in dry forest ecosystems (García & Zamora 2003; Menaut *et al.* 1995; Scholes & Walker 1993; Singh & Kushwaha 2006). For instance, water stress can cause high seedling morality or affect the growth of the young trees (Ceccon *et al.* 2006) irrespective of forest conservation status.

It is important to note that changes in the management regimes of the protected forests at both sites have occurred since 1996 (e.g. a patch of ranches and grazing management projects have been established throughout the protected forests at Yale). These changes have led to an increase in the grazing pressure on the area, which might influence the seedling regeneration dynamics, particularly in Yale forests. Furthermore, the institutional protection of many protected areas (including Sissili forest reserve) is weak (Ouedraogo 2001), and this increases in anthropogenic-induced bushfires and illegal extractions of wood (Ouedraogo 2006; Paré *et al.* 2008). The prevalence of individual species with a small size (ca. 57%, Table 1) illustrates the importance of potential threats (establishment constraints) facing seedlings or young trees, which could accelerate the decline of many species (Hoffmann & Solbrig 2003). The PCA ordination highlighted that species that were abundant in the unprotected forest subjected to high human pressure were *D. microcarpum* and *C. glutinosum*. This could be related to their ability to sprout profoundly following disturbances (Ky-Dembele *et al.* 2007). At the site with low human pressure, *P. suberosa* was found abundantly probably due to its ability to regenerate by root suckering (Bationo 1996) or sexual means (Ky-Dembele *et al.* 2007) in the study area.

Generally, seedling frequency and density, along with the proportion of abundant species, were lower in the protected forests than in the unprotected forests. The seedling flora in the sampled plots was dominated by two species: *V. paradoxa*, one of the most socio-economically valued species (Lamien *et al.* 2007), and *D. microcarpum*, the most highly valued fuelwood species in the country (Sawadogo *et al.* 2002). These are two of the common species that are subjected to over-exploitation for food and fuelwood by rural households. The natural regeneration of these species could be affected if the households collect fruits or cut small trees excessively. Overall, the ‘protected’ forest conservation status does not appear to favor seedling species richness or abundance, contrary to expectations. This disparity may be attributed to the canopy condition, the biology and ecology of the species present, complex interaction of biotic and abiotic factors as well as seedling resilience to disturbances that make unpredictable seedling population with forest conservation status. Indeed, the loose protection (illegal cutting, grazing and charcoal production) lead to human interference in the different inventory plots.

The high species richness in the unprotected forest of Boala could be explained by the relatively low human population density (15 inhabitants km^{-2}), and hence (presumably) moderate anthropogenic disturbance. Sampling effort, natural variability and/or wildlife pressures could contribute to explain the low richness in the protected forest. In contrast, the low richness in the unprotected forest at Yale can be explained by the increased pressure associated with a comparatively high human population density (30 inhabitants km^{-2}). Much of the vegetation in the unprotected forest at Yale consists of degraded savanna and shrubs.

The relationships between seedling and adult tree densities were marginally significant in the unprotected forest of Boala and significant in the protected forest of Yale most likely due to the fact that among the surveyed forests, these two areas experience the least disturbance. A significant interaction of moderate effect between site and conservation status on species richness was detected, indicating that the species richness between protected and unprotected forests differs at each site. The unprotected area of Boala was dominated by woodlands and savanna with relatively low pressure. Hence, the relatively high proportion of adult trees may explain the significant regression observed between seedling and adult tree densities in this area. Support for this explanation comes from the common density dependence between adult and juvenile trees found in tropical dry forests (Hubbell 1979).

Seedling establishment does not depend only on natural factors, but also on anthropogenic-induced factors, such as man-made fire and grazing, which commonly affect African dry forest ecosystems (Hoffmann & Solbrig 2003; Menaut *et al.* 1995; Scholes & Walker 1993; Zida *et al.* 2009). If fire stimulates the development of root suckers, it is a serious threat for the survival of seed-derived seedlings due to severe competition (Luoga *et al.* 2004; Sankaran *et al.* 2005). Hence, frequent bush fires in the region could lead to the decline of species such as *Lonchocarpus latifolius* (Willd.) DC. and *I. doka*, which are known to be fire-sensitive (Zida *et al.* 2007). Fire can also reduce the density of the woody plant species (Hoffmann 1999). Damage caused to juvenile plants by grazing can further influence the regeneration performance. Trampling, mainly caused by elephants, is occurring in the protected forest at Boala, and this can also decrease seedling regeneration (Djossa *et al.* 2008). Selective cutting operated by illegal extractions creates canopy openness, inducing a gap competition between species (Bebber *et al.* 2002; Khumbongmayum *et al.* 2005), which, therefore, influences the regeneration performance.

All the recorded species, with the exception of *P. africana*, were characterized by a clumped distribution irrespective of forest type. This distribution pattern most likely reflects the dominance of the clonal propagation mode in the area. Clonal or vegetative propagation is an important plant survival strategy, which is induced by the fires that frequently occur in most African savanna ecosystems (Bellefontaine *et al.* 1997; Bellefontaine 2005; Hoffmann 1998). Several species in the surveyed area have been identified as resprouters, although they also regenerate by seeds, namely, *Acacia macrostachya* Rchb. ex DC., *Azadirachta indica* A. Juss., *B. ferruginea*, *D. cinerea*, *D. mespiliformis, P. biglobosa*, *P. erinaceus*, *S. latifolius* and *V. paradoxa*, *I. doka*, *Lannea velutina* A.Rich., Xeroderris stuhlmannii (Taubert) Mendonça & E.P.Sousa, *P. suberosa*, *D. microcarpum* and *Pseudocedrela kotschyi* Harms (Alexandre 1992; Bationo *et al.* 2005; Bellefontaine 2005).

Conclusions

The results of this study revealed that forests with a protected status in the studied area did not have greater seedling richness than unprotected forests. The majority of the species were under-populated at the seedling level irrespective of the conservation status of the forest and human pressure. In addition, seedling density is generally low on our study sites compared to similar forests in the Sudanian Zone. Hence, the natural regeneration inside and outside the forest reserve should be assisted through direct seeding, seedling planting, and site manipulation to improve environmental conditions for seedling establishment and growth.

Acknowledgments

This study was funded by the Swedish International Development Cooperation Agency (Sida). Thanks are also due to Siaka Nebie, Lambert Zougrana, and the inventory crews in Boala and Yale for their help during the fieldwork.

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