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RESEARCH

Sahelian woody communities are endangered by regeneration impoverishment in three land management types

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Abstract
Monitoring regeneration in woody communities and understanding the drivers of its success is crucial for gaining insight into the long-term persistence of trees in African drylands, where they play key socio-ecological roles. While fire, grazing and water availability are key factors for regeneration in these ecosystems, seed arrival, germination and seedling recruitment are still poorly documented under natural conditions in the West African Sahel. Tree planting is commonly carried out in West Africa to promote regeneration. The cost is considerable, the success is variable and its influence on spontaneous regeneration is unknown. We conducted a field inventory to ascertain the regeneration ability of woody communities in a Sahelian savanna in three land management types (plantations, communal grazing, old enclosures) to determine (i) the proportion of the different regeneration mechanisms; (ii) the influence of adult trees; (iii) the influence of management type and topography and (iv) their temporal dynamics. We first showed that regeneration diversity was poor, with half of the adult species not recorded in the regeneration phase. Secondly, regeneration mostly came from true seedlings compared to resprouting. Thirdly, adult communities were found to greatly influence regeneration density and composition. Fourthly, topography proved to influence regeneration density, whereas we observed little effect of the land management type. Lastly, historical data highlighted a steep decline in regeneration density over recent decades. These results raise questions about the persistence of woody vegetation in Sahelian savannas and highlight the need to protect large trees in suitable microsites, such as topographic depressions, to promote regeneration.

Keywords Sahel · Woody vegetation · Regeneration · Pastoralism · Plantation · Dynamics

Extended author information available on the last page of the article

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Introduction

Trees play a key socio-ecological role in the drylands that cover 41% of Earth's land mass (FAO 2019). In Africa, a third of these woody communities are located in areas usually classed as non-forests, such as grasslands and savannas (Reiner et al. 2023). Savannas with an annual herbaceous stratum and scattered trees and shrubs are the typical plant formation of the African Sahel, a biogeographic zone with 200 to 600 mm of annual rainfall during a short rainy season of 3 to 4 months. (Le Houérou 1980; White 1983). Woody communities influence ecosystem functioning and the local population largely depends on woody resources for wood, food and fodder for livestock (Sinare and Gordon 2015). Indeed, pastoralism is the dominant livelihood activity in the Sahel (Le Houérou 1980), which subjects this vegetation to permanent grazing.

Sahelian woody vegetation became the center of attention after the severe droughts (i.e., the "great drought") that occurred in the 1970–1980s (Nicholson 2005). Since then, several studies have shown a decrease in woody vegetation density and species richness, and/or changes in species composition (e.g., Dendoncker 2020; Gonzalez et al. 2012; Hänke et al. 2016). Although some studies have observed a "greening" trend since the mid-1980s (Anyamba and Tucker 2005; Brandt et al. 2015; Olsson et al. 2005), such greening is not synonymous with a return to the pre-drought conditions as regards tree species composition (Herrmann and Tappan 2013). In view of repeated droughts, in combination with increasing human pressure on natural resources, there are concerns for woody vegetation dynamics and resilience in this region.

Analyzing natural regeneration is key to gaining insights into the long-term dynamics of woody communities, because regeneration is a critical feature for their long-term renewal. As rainfall is highly variable in drylands, regeneration is an inconsistent phenomenon: the success rate is not constant from year to year and germination only occurs in years with sufficient rainfall (Breman and Kessler 1995; Chesson et al. 2004; Whitford and Duval 2020). Plants have to pass three environmental filters to secure the establishment of new individuals: seed arrival, seed germination (or resprouting) and seedling recruitment (survival and growth). Firstly, seed arrival depends on dispersal mechanisms (e.g., anemochory, zoochory) or on the presence of a soil seed bank. On the one hand, the formation of such a seed pool depends on different factors, such as the species, along with the frequency and intensity of disturbances (dos Santos et al. 2018). Only a few studies have investigated soil seed banks in African drylands (Argaw et al. 1999; Kassahun et al. 2009; Sanou et al. 2022; Skoglund 1992; Witkowski and Garner 2000). On the other hand, reseeding is not the only way for savanna species to reproduce, as vegetative reproduction (via root suckering, coppicing or resprouting) is also a means for numerous species (Bellefontaine 1997; Luoga et al. 2004; Tredennick et al. 2015), such as *Balanites aegyptiaca* (L.) Delile. The ratio of true seedlings compared to vegetative possibilities is poorly documented in the Sahel (e.g., Catinot 1994; Ky-Dembele et al. 2007).

The second phase, germination, is influenced by several factors, such as dispersal mechanisms, predation, fire, soil and water availability (Tybirk 1991). The germination of Sahelian species is affected in different ways by livestock and depends on various factors, such as tree species (Danthu et al. 1996; Miller and Coe 1993), livestock species (Ouédraogo et al. 2021), the year and the location (Miller and Coe 1993). For instance, some species of *Vachellia* Wight & Arn. and *Senegalia* Raf. tend to be eaten and dispersed by large ungu-

lates, with dung providing suitable conditions for germination (Miller 1996). On the other hand Danthu et al. (1996) showed that bovines excrete a larger quantity of intact seeds than sheep and goats and Ouédraogo et al. (2021) found a higher seed bank potential in goat feces. As for water requirements, these have been studied for the germination of several African dry tropical species under controlled conditions (Coughenour and Detling 1986; Merine et al. 2014; Sarr et al. 2024; Wilson and Witkowski 1998). Lastly, the third phase, seedling survival and establishment, is also influenced by climate (water availability and temperature) (Whitford and Duval 2020), fire (Gignoux et al. 2009) and consumption by livestock and wild fauna (Archibald et al. 2021; Chidumayo and Gumbo 2010) in African drylands. As a result of these pressures, few seedlings will survive through their first dry season (Tybirk 1991).

Overall, few studies have focused on the regenerative features of Sahelian woody vegetation under natural conditions, nor on their relationship with adult communities. Studies have mostly focused on particular groups, such as legumes (Tybirk 1991), technical specifications/requirements for successful establishment under controlled conditions (e.g., Ky-Dembele et al. 2023; Merine et al. 2014) and on more humid Sudanian savannas (e.g. Zida et al. 2007).

Mature trees have a positive impact on regeneration by providing favorable microsites for germination and establishment. The positive effect of tree canopies on seedlings has already been demonstrated (Akpo and Grouzis 1996), via a positive effect on soil seed banks (Sanou et al. 2022), or the hosting ability of large trees (Dendoncker and Vincke 2020). The persistence of large trees is crucial for maintaining these functions. In the West African Sahel, pastoral management does not actively promote woody cover, while on farmlands shade trees are protected around villages and farmer-managed natural regeneration is a common practice (Brandt et al. 2018).

Tree planting is also commonly used in West Africa to promote regeneration. The initiative of the Great Green Wall (GGW, Sarr et al. 2021) is one example. In Senegal, several plantations have been launched since 2008 to counteract the decrease in density and species richness of woody vegetation observed in the Sahelian zone. These plantations consist of rows of one or two indigenous species that are ecologically adapted, as well as having some values for traditional uses (Wade et al. 2018). The costs of these plantations are huge and success is not always guaranteed (Turner et al. 2023). In addition, nothing is known about their influence on the spontaneous regeneration of woody stands already present before planting.

In this context, the main objective of our study was to gain a better understanding of the characteristics of woody regeneration in a Sahelian savanna in Senegal using a field inventory. We distinguished four specific objectives. Firstly, we sought to characterize regeneration mechanisms (true seedlings as opposed to resprouting). Secondly, we examined how adult trees influenced regeneration density and composition. We put forward the hypothesis that mature trees have a positive effect on regeneration density, with more young individuals located under crown cover than outside, due to the more suitable microclimate under the crown and/or the direct provision of propagules near adult trees. Thirdly, we determined the effect of the management type (free grazing, ex-controlled plots, plantation of the GGW) and topography on richness, densities and botanical composition. Our hypothesis was that (i) plantations have a positive impact on regeneration density due to an increase in tree cover, which has been shown to positively influence regeneration density in Sahelian savan-

nas (Dendoncker and Vincke 2020), (ii) plantations have no clear impact on regeneration richness and composition as only one or two species are planted, and (iii) ex-controlled plots display greater regeneration density and a more diverse species composition than in free grazing, through long-lasting effects of having partially protected regeneration for more than 20 years. Lastly, we evaluated the temporal evolution of regeneration in ex-controlled plots from 1981 to 2021 and in free grazing from 2015 to 2021.

Materials and methods

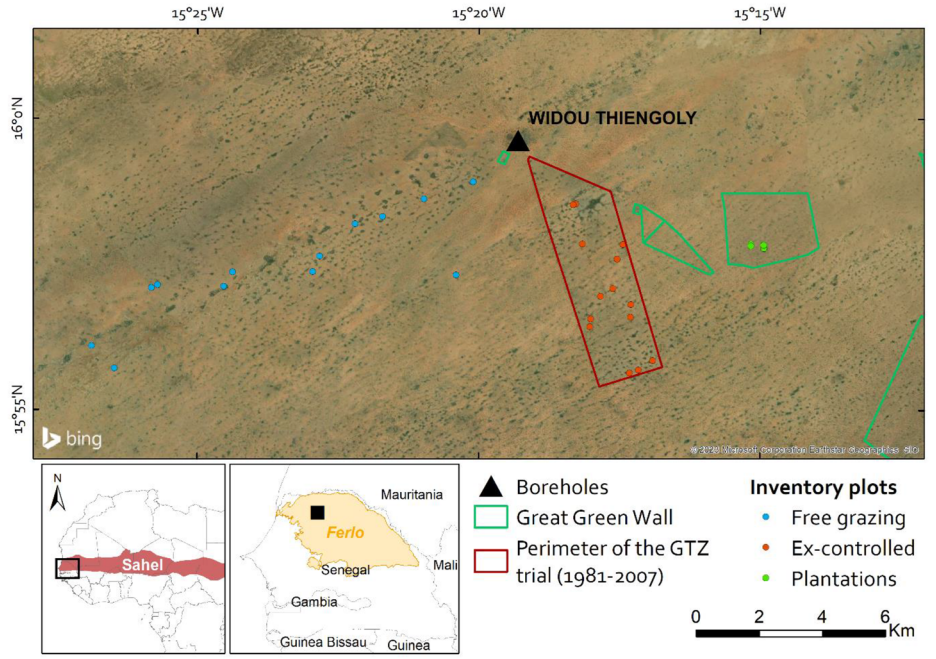
Study area

The study area was located in the sylvo-pastoral zone of Senegal, in the sandy Ferlo, near the Widou Thiengoly borehole (15,99 N, 15,32 W, Fig. 1). The climate in the area is typically Sahelian, with a short rainy season from July to September and an average rainfall of 300 mm/year. Land use is mainly pastoral, and livestock (cattle, sheep and goats) is usually allowed to roam freely and graze in a landscape of spontaneous open savanna. Soils are predominantly arenosols, though with a slight variation depending on the landform with Ferralic Arenosols (Jones et al. 2013) on the dunes and Brunic Arenosols in the plains, which contain slightly more organic matter (Le Houérou 1989). The study area was part of a former grazing trial project conducted by the German Agency for Technical Cooperation (GIZ) from 1981 to 2007 (Miehe et al. 2010). The project set out to study the impact of livestock intensity on vegetation. To achieve that goal some plots of land were enclosed, in which the stocking rate was controlled or zero up to 2007. Overall, woody vegetation regeneration was more successful inside the enclosures than in the common rangelands (André 2001; Miehe 2002). The study area was also part of the Great Green Wall (GGW) project and some plots were planted with indigenous species, such as *Senegalia senegal* (L.) Britton and *Balanites aegyptiaca* (Diallo et al. 2017) more than 10 years previously.

Field inventory

A field inventory of regeneration was carried out in the second half of July 2021. Forty-six plots measuring 50×50 m were inventoried according to the management type, with 20 plots in free range pastures, 14 plots in the GIZ experimental area (ex-controlled plots) and 12 in the plantation plots of the Great Green Wall (GGW) project, hereafter called "free grazing", "ex-controlled" and "GGW" (Fig. 1). As topography had already been shown to influence regeneration in the same area (Dendoncker and Vincke 2020), we also included local topography in the stratified sampling. For each management type, whenever possible, we located half the plots in topographic depressions and half on hilltops.

The GIZ plots were subjected to a theoretical constant stocking rate of 0.1 to 0.12 Tropical Livestock Units per hectare from 1987 to 2007 (Miehe et al. 2010). However, in practice, these stocking rates were not possible to maintain during the severe drought years when herd migration was necessary, and the concept of constant stocking rates was abandoned after the dry years of 1990-92. Thereafter, the plots were mostly used as a fodder reserve during the dry season. In 2014, Assouma et al. (2018) recorded an animal charge of between 0.31 and 0.43 TLU/ha (depending on the season) in the Widou Thiengoly service area of the



Management type	Topography	Number of plots	Historical data used
Free grazing	Depressions	10	2015
(n = 20)	Hilltops	10	2015
Ex-controlled grazing	Depressions	4	1987, 1990, 1994, 2002
(n = 14)	Hilltops	10	1987, 1990, 1994, 2002
GGW	Depressions	6	-
(n = 12)	Hilltops	6	-

Fig. 1 Location of the inventory plots near Widou Thiengoly for the three management types: free grazing (blue), ex-controlled grazing (red), plantations of the Great Green Wall (green) and sampling details according to the management type and topography. The collection year of the historical data used in this study is indicated in the right-hand column

community rangeland. The GGW initiative directly planted saplings of several indigenous species along strips. Prior to planting, the soil was prepared by local plowing before the digging of furrows (Fig. 2). The plots were enclosed, but not locked, so livestock were able to roam within them. The GGW parcels selected for this study were planted with *Senegalia senegal* individuals, which were old and tall enough at the time for spontaneous regeneration of this species not to be mistaken for small planted trees. To summarize, the three management types differed in tree density (higher in GGW), stocking rates (lower, prior to 2007, in the ex-controlled plot) and livestock mobility (local herds in the ex-controlled plots and GGW fences preventing free roaming and requiring herder intervention to open the fences). These differences are stated here qualitatively as it is very difficult to obtain accurate estimates in the Sahelian sylvo-pastoral zone, with no systematic and reliable monitoring of livestock or plantation success.

In each plot, all regeneration defined as woody individuals with a stem circumference of less than 10 cm was recorded. Two stages were distinguished within that regeneration: (i) seedlings, i.e., individuals shorter than 30 cm and (ii) saplings, i.e., individuals taller than

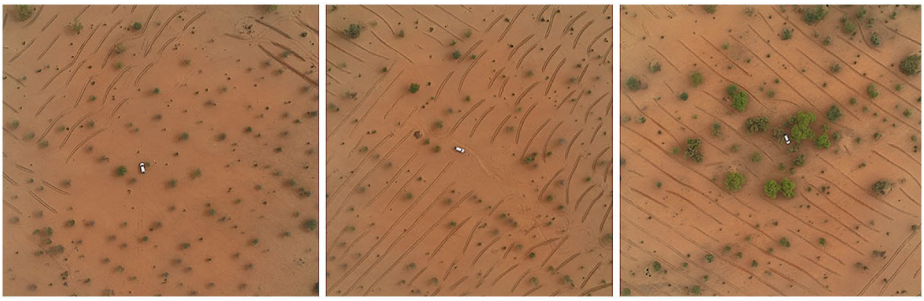


Fig. 2 UAV orthomosaic over a site of the Great Green Wall in Widou Thiengoly taken in June 2022 just after plowing. The furrows appear as dark stripes

30 cm. For each regeneration we recorded the origin of the regeneration (seed or resprouting/root sucker) with the help of a local herder who was used to working with researchers and was specialized in botanical identification and ecology. We also recorded locations in relation to adult crowns (under crown cover, or outside) and, if under cover, the adult species hosting the regeneration. Adult composition (species and density) was determined in the 46 plots, of which 32 plots were inventoried in the summer of 2022 and 14 in the summer of 2015.

Data analyses

The species richness of seedlings, saplings and adults, along with their density, were computed for each plot. Sapling and seedling species frequencies, i.e., the percentage of plots in which the species was encountered, were computed throughout the whole dataset. Unless otherwise stated, all analyses were carried out by separating seedlings and saplings. Taxon names correspond to the Plant of the World Online database (POWO 2023).

The origin of regenerations was investigated by computing the percentage of seedlings and saplings that came from seeds, as opposed to resprouts. Secondly, the relationships between regeneration and adult individuals were examined. The percentage of regeneration located under the crown of the nearest adult and outside the crown was calculated. The adult species most conducive to regeneration were then determined by summing up the number of regenerations (whatever the species) sheltered under the crown of each adult species for all plots. The regeneration of species under crowns belonging to the same species as the hosting adult was also examined.

The way in which adult abundance affected the botanical composition of regeneration was assessed by a Canonical Correspondence Analysis (CCA), a constrained ordination method that tests the influence of a matrix of fixed predictors (here the abundance of adults) over our community data (abundance of seedlings and saplings). The abundance matrices were corrected using a square root transformation to avoid an over-weighted effect of large counts. Variance Inflation Factors (VIF, Fox and Monette 1992) of the predictors were computed to check for collinearity. The threshold above which we considered that VIF indicated a collinearity problem varied between 3 and 20 (Borcard et al. 2011). Here, if factors showed a VIF above 5, we computed the CAA by removing factors one by one using the *drop1* function in R software (R Core Team, 2022) and looking at factors that had less influ-

ence on the AIC of the model. Those factors were then removed from the subsequent CCA to avoid collinearity (Legendre and Legendre 2012).

The way in which management type affected regeneration species richness and density was studied using Wilcoxon tests to compare the mean of these two indicators between the three types of management. A principal coordinates analysis (PCoA) was then applied on a Bray-Curtis dissimilarity matrix derived from the matrix of species abundances. The mean coordinates of the inventoried plots on the first two PCoA axes were compared according to the management type. As topography was considered as a stratifying factor for plot sampling, its influence on the same parameters as those considered for the management type, using mean comparisons of density and species richness, was also checked.

The temporal dynamics of saplings was assessed using historical inventory data available for the free grazing and ex-controlled plots. Saplings were inventoried in 2015 in the 20 free grazing plots by Dendoncker and Vincke (2020) and between 1987 and 2007 in the 14 ex-controlled plots by Miehe (GIZ data in evaluation by S. Miehe). However, due to missing data for certain plots and years, and as the regeneration of the *Calotropis procera* (Aiton) W.T. Aiton bush was not counted every year, only the years 1987, 1990, 1994 and 2002, for which complete data were available, were selected.

Mean paired comparisons on sapling density were applied separately on the free grazing plots and the ex-controlled plots. We did not apply this test to seedling density, as seedling counts largely depend on rainfall in the previous year and on the inventory date (counting at the end of the rainy season as opposed to counting at the end of the dry season), which was not the same in 2021 as in 1987–2002. Changes in botanical composition were perceived with a PCoA computed on the Bray-Curtis distance on the sapling abundances using all the data from the ex-controlled plots (1987 to 2021) and the free grazing plots (2015 and 2021).

Results

Species composition and regeneration mechanisms

We inventoried 19 species in the adult phase over the 46 plots, at a mean density of 129.0 (±170.4) individuals/ha (Table 1). The tree *Balanites aegyptiaca* and the shrub *Boscia senegalensis* Lam. dominated the adult stands with a mean density of 56.3 (±143.2) and 46.6 (±56.1) individuals/ha, respectively. The densities of the remaining 17 species were far lower, with the next four species being *Senegalia senegal* (7.3 individuals/ha), *Calotropis procera* (5.0 individuals/ha), *Sclerocarya birrea* (A.Rich.) Hochst. (4.8 individuals/ha) and *Vachellia tortilis* (Forssk.) Galasso & Banfi (2.9 individuals/ha). It is important to note that the mean densities given in Table 2 are the means of species density *per plot*, taking the 46 plots into account. The densities were not weighted by the percentage of area occupied by each management type within the study area and should therefore not be extrapolated to the whole study area. The mean densities of the free grazing plots (Table 1) were the most representative of the whole study area, as free grazing was dominant in the study area (see also Table 3 in Appendix for mean density in the three land management types).

Nine species were recorded at the seedling phase and eight at the sapling phase. The mean species richness per plot was 1.53 (±1.21) for seedlings and 1.63 (±0.83) for saplings. Seedlings were present at a mean density of 24.3 individuals/ha (±29.9, Table 1) and sap-

lings at 21.5 individuals/ha (±19.9). The large standard deviations highlight the tremendous variability of seedling and sapling densities between the plots. Indeed, no seedlings were inventoried in 11 out of 46 plots (5 in the ex-controlled plots, 2 in free grazing, 4 in GGW). For saplings the number was smaller, with three plots in which no saplings were encountered (2 in the ex-controlled, 1 in the free grazing).

Two species largely dominated regeneration (Fig. 3a): *Balanites aegyptiaca* and *Boscia senegalensis*, which were present in more than half of the plots at a mean density of 6.7 (±10.5) and 15 (±23.4) seedlings per ha, and 9.7 (±13.8) and 7.5 (±10.2) saplings per ha, taking into account all management types. *Vachellia tortilis* was encountered in the three management types at a mean density of 17 seedlings/ha, and with a higher frequency (40%) in free grazing plots. The other six seedling species were only encountered in one or two management types. Seedlings of *Senegalia senegal*, for instance, were present in 41.7% of the Great Green Wall plots at a mean density of 0.4 seedlings/ha. It should be noted that seedlings recorded within the GGW were spontaneous (i.e., not planted), as the old plots were specifically selected (see Materials and Methods). The other seedling species were relatively rare and only present in less than 5% of the inventoried plots. At the sapling phase, *Vachellia tortilis* was the third most frequent species, with a total frequency of 15.2%, but was absent from the GGW plots. Despite a low total frequency of 8.7%, *Calotropis procera* was largely represented inside the GGW plots (33.3%). True seedlings, compared to resprouts, accounted for the majority of the inventoried seedlings (87.5%) and saplings (83.9%, Fig. 3b). The only two species most often derived from resprouting were saplings of *Senegalia senegal* and *Calotropis procera*.

Influence of adult trees

Overall, 70% of seedlings and 59.5% of saplings were located under the crown of an adult tree (Table 2; Fig. 3c). In particular, *Boscia senegalensis* showed a clear pattern of location under the adult crowns with 81.5% of seedlings and 74.4% of saplings found under cover. *Vachellia tortilis* was the only species at the seedling phase to be found more often outside crown cover. *Balanites aegyptiaca* showed no preference of location regarding the crown, as about half of regeneration was found under and outside crown cover. The rarest species in the regeneration phase (seedlings of *Combretum aculeatum* Vent., *Grewia bicolor* Juss., *Guiera senegalensis* J.F.Gmel., *Sclerocarya birrea* and saplings of *Vachellia seyal* (Delile) P.J.H. Hurter, *Combretum aculeatum, Grewia bicolor*) were always found under crown cover, although the total numbers of individuals were small (Table 2).

Balanites aegyptiaca and *Sclerocarya birrea* were the species that hosted the largest number of regenerations under their crowns (Table 2). The first hosted 41.4% and 42.4% of the seedlings and saplings located under any crowns, respectively, whereas *Sclerocarya birrea* hosted 20.2% and 12.5% of the seedlings and saplings located under any crowns. Overall, of the species located under adult crowns, 30.3% of the seedlings and 45.1% of the saplings recorded belonged to the same species as the hosting adult (Fig. 3b; Table 2). Interestingly, none of the numerous regenerations sheltered under *Sclerocarya birrea* crowns belonged to that species.

Boscia senegalensis sheltered 15.6% of the total seedlings found under a crown, but nearly all those seedlings (83.9%) belonged to the same species. The number of saplings

Table 1 Species inventoried at seedling, sapling and adult phases, ordered by their number of recorded individuals (N) and their mean density per plot (Mean d±sd) over the 46 plots. "Mean d±sd in free grazing" is the mean density encountered in the 20 free grazing plots. "Frequency (%)" indicates the percentage of plots in which species were inventoried, in all the 46 plots and according to the management type (free grazing, ex-controlled, Great Green Wall). "n" indicates the number of plots. "Under crown" indicates the percentage of regeneration (in number of individuals) found under a crown. "True seedlings" gives the percentage of regeneration coming from a seed (true seedlings) as opposed to resprouting

Adults	Acronym	N	Mean d±sd (ind/ha)	Mean d±sd in free grazing (ind/ha)	Frequency (%)				Under crown (%)	True seedlings (%)
					All plots (n=46)	Free grazing (n=20)	Ex–controlled (n=14)	GGW (n=12)		
Balanites aegyptiaca (L.) Delile	BAA	648	56.3 (±143.2)	40.4 (±61.2)	73.9	65	71.4	91.7	–	–
Boscia senegalensis Lam.	BOS	536	46.6 (±56.1)	43.0 (±62.3)	76.1	70	64.3	100	–	–
Senegalia senegal (L.) Britton	SSN	84	7.3 (±17.2)	0.6 (±2.7)	30.4	5	14.3	91.7	–	–
Calotropis procera (Aiton) W.T. Aiton	CAP	58	5.0 (±27.7)	10.6 (±41.9)	15.2	20	0	25	–	–
Sclerocarya birrea (A.Rich.) Hochst.	SCB	55	4.8 (±8.8)	3.0 (±4.3)	39.1	40	42.8	33.3	–	–
Vachellia tortilis (Forssk.) Galasso & Banfi	VAT	34	2.9 (±7.0)	2.4 (±3.4)	30.4	35	14.3	41.2	–	–
Grewia bicolor Juss.	GRB	18	1.6 (±4.6)	2.6 (±6.0)	15.2	25	14.3	0	–	–
Vachellia seyal (Delile) P.J.H. Hurter	VSY	16	1.4 (±5.1)	3.2 (±7.5)	13.0	30	0	0	–	–
Combretum glutinosum Perr. Ex DC.	COG	10	0.9 (±4.8)	0.4 (±1.8)	4.3	5	0	8.3	–	–
Guiera senegalensis J.F.Gmel.	GUS	9	0.8 (±3.7)	0	6.5	0	0	25	–	–
Leptadenia pyrotechnica (Forssk.) Decne.	LEP	6	0.5 (±2.1)	0.6 (±2.7)	6.5	5	7.1	8.3	–	–
Terminalia leiocarpa (DC.) Baill.	TEL	2	0.2 (±0.8)	0.4 (±1.2)	4.3	10	0	0	–	–
Ziziphus mauritiana Lam.	ZIM	2	0.2 (±0.8)	0.4 (±1.2)	4.3	10	0	0	–	–
Adansonia digitata L.	ADD	1	0.1 (±0.6)	0.2 (±0.9)	2.2	5	0	0	–	–
Adenium obesum (Forssk.) Roem. & Schult.	ADO	1	0.1 (±0.6)	0.2 (±0.9)	2.2	5	0	0	–	–
Combretum aculeatum Vent.	COA	1	0.1 (±0.6	0.2 (±0.9)	2.2	5	0	0	–	–
Commiphora africana (A.Rich.) Engl.	COM	1	0.1 (±0.6)	0	2.2	0	0	8.3	–	–
Feretia apodanthera Delile	FEA	1	0.1 (±0.6)	0.2 (±0.9)	2.2	5	0	0	–	–
Sterculia setigera Delile	STS	1	0.1 (±0.6)	0	2.2	0	7.1	0	–	–
All adults		1484	129.0 (±170.4)	108.4 (±104.1)	–	–	–	–	–	–
Seedlings										
Boscia senegalensis		173	15.0 (±23.4)	16.2 (±24.9)	52.2	50	42.9	66.7	81.5	85.5

Table 1 (continued)

Adults	Acronym	N	Mean d±sd (ind/ha)	Mean d±sd in free grazing (ind/ha)	Frequency (%)				Under crown (%)	True seedlings (%)
					All plots (n=46)	Free grazing (n=20)	Ex–controlled (n=14)	GGW (n=12)		
Balanites aegyptiaca		77	6.7 (±10.5)	8.8 (±13.4)	50.0	55	64.3	25.0	51.9	89.6
Vachellia tortilis		17	1.5 (±3.1)	2.8 (±4.1)	23.9	40	14.3	8.3	35.3	100
Senegalia senegal		5	0.4 (±1.2)	0	10.9	0	0.0	41.7	80	80
Combretum aculeatum		2	0.2 (±0.8)	0.2 (±0.9)	4.3	5	7.1	0.0	100	100
Grewia bicolor		3	0.3 (±1.3)	0.6 (±1.9)	4.3	10	0.0	0.0	100	100
Guiera senegalensis		1	0.1 (±0.6)	0	2.2	0	0.0	8.3	100	0
Sclerocarya birrea		1	0.1 (±0.6)	0.2 (±0.9)	2.2	5	0.0	0.0	100	100
Vachellia seyal		1	0.1 (±0.6)	0	2.2	0	7.1	0.0	0	100
All seedlings		280	24.3 (±29.9)	28.8 (±32.9)	–	–	–	–	70.7	87.5
Saplings										
Balanites aegyptiaca		112	9.7 (±13.8)	13.2 (±16.5)	60.9	70	71.4	33.3	43.8	92
Boscia senegalensis		86	7.5 (±10.2)	6.2 (±10.2)	58.7	45	50.0	91.7	74.4	89.5
Vachellia tortilis		13	1.13 (±3.2)	1.0 (±2.2)	15.2	20	21.4	0.0	23.1	100
Calotropis procera		12	1.0 (±4.5)	0	8.7	0	0.0	33.3	83.3	8.3
Senegalia senegal		13	1.1 (±5.0)	0.2 (±0.9)	8.7	5	0.0	25.0	92.3	23.1
Grewia bicolor		4	0.3 (±1.4)	0.8 (±2.1)	6.5	15	0.0	0.0	100	100
Combretum aculeatum		1	0.1 (±0.6)	0.2 (±0.9)	2.2	5	0.0	0.0	100	100
Vachellia seyal		1	0.1 (±0.6)	0	2.2	0	7.1	0.0	100	100
All saplings		242	21.5 (±19.9)	21.6 (±17.7)	–	–	–	–	59.5	83.9

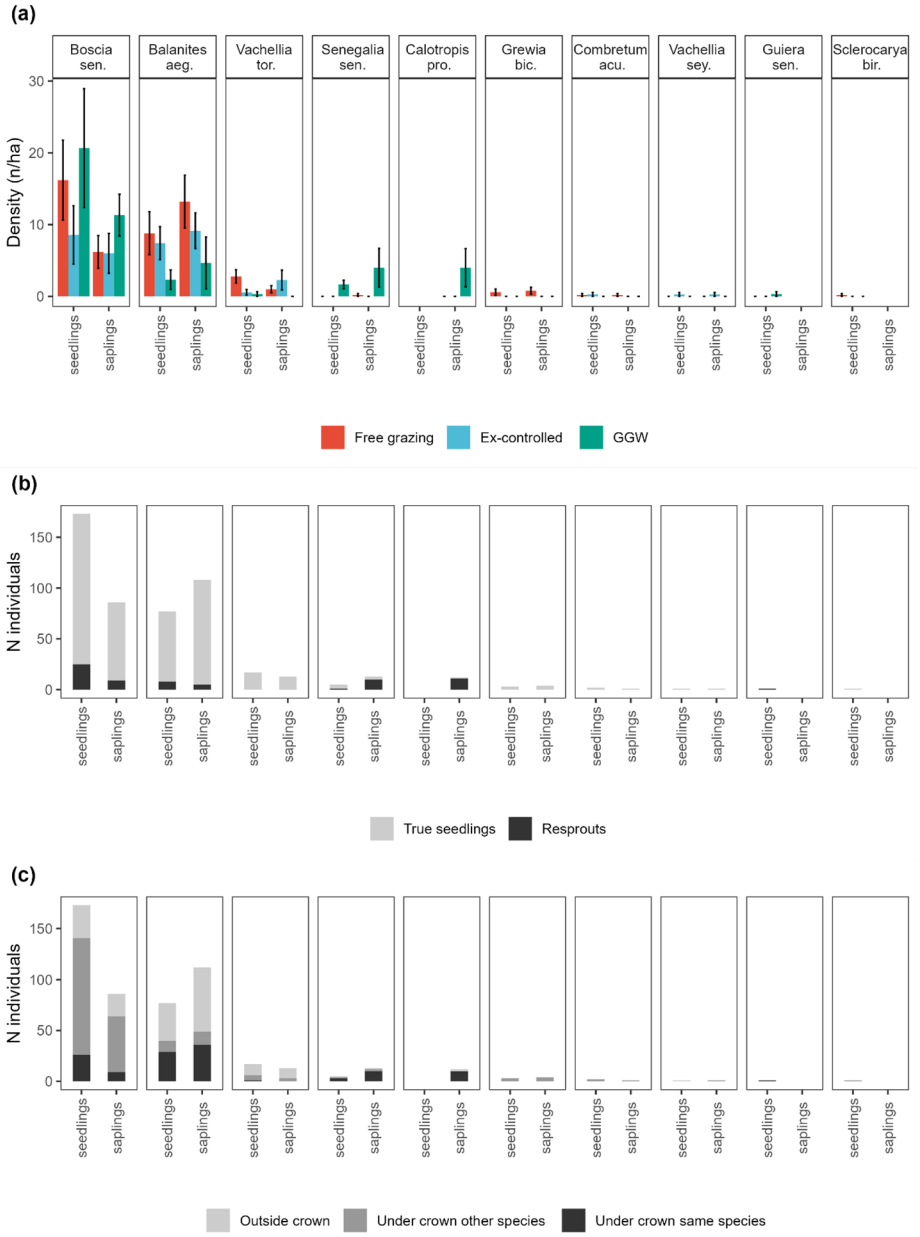


Fig. 3 Seedling and sapling distribution: (**a**) mean densities (all plots), (**b**) according to their origin (true seedlings or resprouts); (**c**) outside and under adult crown (same or other species)

found nearby *Boscia senegalensis* was much smaller and in 90% of cases they belonged to the same species. The same observation was made for *Calotropis procera.*

To ensure VIF below five in the CCA, we removed the species *Adenium obesum* (Forssk.) Roem. & Schult., *Terminalia leiocarpa* (DC.) Baill., *Feretia apodanthera* Delile and *Lep-*

Table 2 Total number of regenerations (seedlings and saplings) sheltered by species under their crown and proportion of regeneration of the same species as the hosting adult. Numbers between [] indicate special cases when regenerations were located under two adult trees with overlapping crowns. In that case, we recorded the species of the two adults

		Hosted seedlings		Hosted saplings	
Adult species	Total of rg*	Total	Of the same species	Total	Of the same species
Balanites aegyptiaca	143 [+13]	82 [+6] (41.4%)	29 (35.4%)	61 [+7] (42.4%)	36 (59.2%)
Sclerocarya birrea	58 [+7]	40 (20.2%)	0	18 [+7] (12.5%)	0
Boscia senegalensis	41	31 (15.6%)	26 (83.9%)	10 (6.9%)	9 (90%)
Senegalia senegal	26	9 (4.5%)	3 (33.3%)	17 (11.8%)	10 (58.8%)
Combretum glutinosum	9 [+6]	2 [+6] (1%)	0	7 (4.9%)	0
Combretum aculeatum	14	7 (3.5%)	0	7 (4.9%)	0
Calotropis procera	11	1 (0.5%)	0	10 (6.9%)	10 (100%)
Grewia bicolor	8	7 (3.5%)	0	1 (0.7%)	0
Sterculia setigera	8	5 (2.5%)	0	3 (2.1%)	0
Vachellia tortilis	5	4 (2%)	1 (25%)	1 (0.7%)	0
Vachellia seyal	5	0	0	2 (1.4%)	0
Ziziphus mauritiana	2	2 (1%)	0	0	0
Guiera senegalensis	1	1 (0.5%)	1 (100%)	0	0
Adenium obesum	1	1 (0.5%)	0	0	0
Total under crown cover	342	198	60 (30.3%)	144	65 (45.1%)
Total outside crown cover	180	82	-	98	-

tadenia pyrotechnica (Forssk.) Decne. The CCA on seedling abundances was significant (P-value < 0.001, Fig. 4) with 71.9% of the inertia of the seedling matrix explained by the predictors, leaving 28.1% unexplained. This means that adult abundances explained 71.9% of the variation observed between the seedling communities. The first two CCA axes represented a cumulative explained proportion (for all the components: constrained and not constrained) of 36.5% (48.4% for the three first axes) and 50.7% if only the constrained components were taken into account (and 67.3% for the three first axes). The significant predictors for the seedling communities were the adult abundances of the following species: *Vachellia seyal* (P-value = 0.003**), *Calotropis procera* (P-value = 0.001***), *Combretum glutinosum* Perr. Ex DC. (P-value = 0.008**), *Grewia bicolor* (P-value = 0.013*), Guiera senegalensis (P-value = 0.001***) and *Sterculia setigera* Delile (P-value = 0.042*).

The CCA on sapling abundances was also significant with 70.1% (P-value < 0.001) of the inertia of the sapling matrix explained by the predictors, leaving 29.9% unexplained (Fig. 4). The first two CCA axes represented a cumulative explained proportion (for all the components: constrained and not constrained) of 35.9% and the first three axes 48.8%. If only constraint components were taken into account, the cumulative proportion was 51.3% and 69.7% for the first two and three axes, respectively. The significant predictors were the adult abundances of the following species: *Vachellia tortilis* (P-value = 0.012*), *Senegalia senegal* (P-value = 0.029*), *Vachellia seyal* (P-value = 0.042*), *Boscia senegalensis* (P-value = 0.003**), *Calotropis procera* (P-value = 0.001***), *Combretum aculeatum* (P-value = 0.001***), *Combretum glutinosum* (P-value = 0.001***), *Grewia bicolor* (P-value = 0.002**) and *Guiera senegalensis* (P-value = 0.001***).

Influence of management types and topography

The influence of the local topography was confirmed for seedling and sapling density and species richness (Fig. 5). Seedling density averaged 45.5 (±30.7) individuals/ha in depressions and 6.7 (±10) individuals/ha on hilltops (P-value from Wilcoxon's paired test < 0.001). Saplings were present at a mean density of 35.4 (±22.1) individuals/ha in depressions and 11.0 (±9.6) individuals/ha on hilltops (P-value from Wilcoxon's paired test < 0.001). Regeneration species richness was higher in depressions with an average of 2.5 (±1) seedling species and 2.1 (±0.8) sapling species, compared to an average of 0.8 (±0.8) seedling species and 1.2 (±0.6) sapling species on hilltops (P-value < 0.001). However, topography did not influence the botanical composition of seedling and sapling communities, nor the ratio of true seedlings compared to resprouting.

Regenerations were found at a density of 28.8 (±32.9) seedlings/ha and 21.6 (±17.6) saplings/ha in the free grazing plots, 17.1 (±22.6) seedlings/ha and 17.7 (±22.8) saplings/ha in the ex-controlled plots and 25.3 (±32.6) seedlings/ha and 24 (±21) saplings/ha in the GGW plots. These differences in density were not significant. Mean species richness was also the same between management types (Fig. 5). The same observation was made when separating the data according to the topography.

The PCoA revealed that the management type influenced the botanical composition of seedling (Fig. 6a) and sapling (Fig. 6b) communities. The mean plot coordinates on the first axis of the PCoA differed for plantation seedling communities compared to ex-controlled (P-value = 0.0017**), but not to free grazing (P-value = 0.07), and for plantation sapling communities compared to free grazing (P-value = 0.032*) and to ex-controlled

Table 3 Mean density (±sd) per species in the three types of management

Seedlings	Free grazing	Ex-controlled	GGW
Boscia senegalensis	16.2 (±24.9)	8.6 (±15.2)	20.7 (±28.6)
Balanites aegyptiaca	8.8 (±13.4)	7.4 (±8.6)	2.3 (±4.6)
Vachellia tortilis	2.8 (±4.1)	0.6 (±1.4)	0.3 (±1.1)
Senegalia senegal	0	0	1.7 (±2.0)
Combretum aculeatum	0.2 (±0.9)	0.3 (±1.1)	0
Grewia bicolor	0.6 (±1.9)	0	0
Guiera senegalensis	0	0	0.3 (±1.1)
Sclerocarya birrea	0.2 (±0.9)	0	0
Vachellia seyal	0	0.3 (±1.1)	0
Saplings			
Balanites aegyptiaca	13.2 (±16.5)	9.1 (±9.3)	4.7 (±12.5)
Boscia senegalensis	6.2 (±10.2)	6 (±10.4)	11.3 (±10.1)
Vachellia tortilis	1 (±2.2)	2.3 (±5.1)	0
Calotropis procera	0	0	4 (±9.2)
Senegalia senegal	0.2 (±0.9)	0	4 (±9.3)
Grewia bicolor	0.8 (±2.1)	0	0
Combretum aculeatum	0.2 (±0.9)	0	0
Vachellia seyal	0	0.3 (±1.7)	0

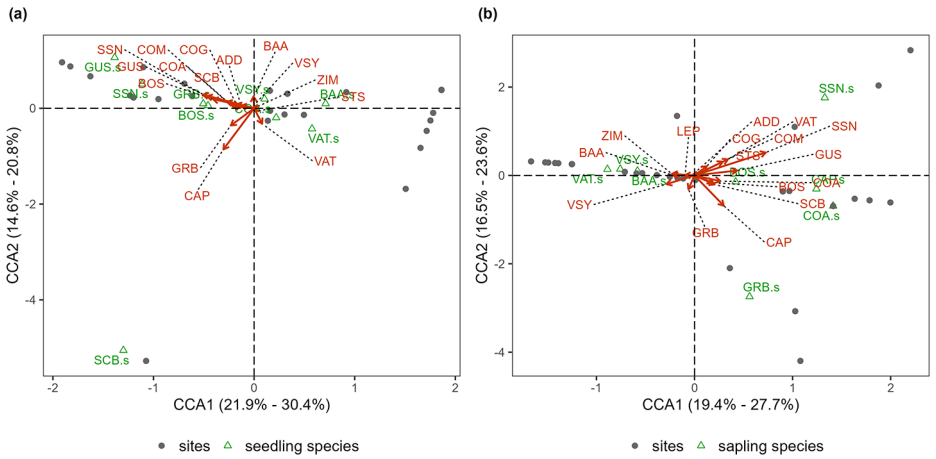


Fig. 4 CCA on seedlings (left panel) and saplings (right panel). Red arrows indicate the constrained predictors, i.e., the adult species. The first value (%) indicates the proportion of the total inertia (constrained and unconstrained) explained by the CCA axis and the second value (%) corresponds to the proportion with the constrained components only

(P-value = 0.039*). GGW plots were located on the right-hand side of the PCoA for seedlings (Fig. 6a) and on the left-hand side of the PCoA for saplings (Fig. 6b). Regeneration communities within the GGW plots therefore tended to have a smaller abundance of *Balanites aegyptiaca*. The botanical composition of seedling and sapling communities did not differ between the ex-controlled and free grazing plots.

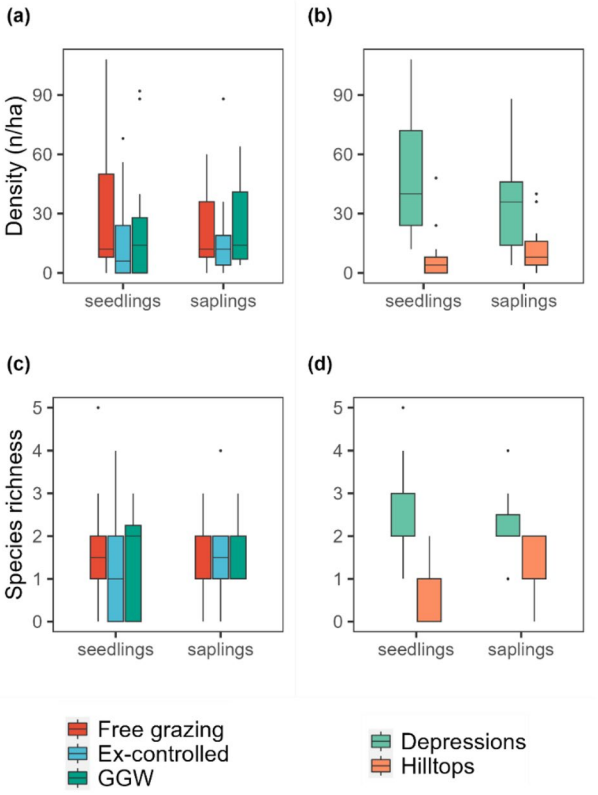


Fig. 5 Mean density (**a**-**b**) and species richness (**c**-**d**) for saplings and seedlings according to management type and topography

Temporal dynamics

In the 20 free grazing plots, sapling density decreased from 82.4 (±114.0) saplings/ha in 2015 to 21.6 (±17.7) in 2021 (p-value=0.029*; Fig. 7a). The same drastic decrease was observed in the 14 ex-controlled plots between 1987 and 2021: from a mean density of 92.6 (±66.2) to 17.7 (±22.8) in 2021 (p-value=0.021*, Fig. 7b). The variability (25th and 75th percentiles) followed the same trend over the same period and plots with high density values were no longer encountered in 2021. Interestingly, the decrease started after 2002, as the mean densities in 1987, 1990 (61.7±55.2), 1994 (87.7±77.8) and 2002 (70.3±49.0) were not significantly different (P-value >0.05). The botanical composition of the sapling communities in the ex-controlled plots and in free grazing plots also changed over time between 1987 and 2021. Indeed, the PCoA on sapling abundances (Fig. 7c) showed that the mean plot coordinates for 2021 on the first axis were significantly different (p-values<0.05) from the mean coordinates of the other years.

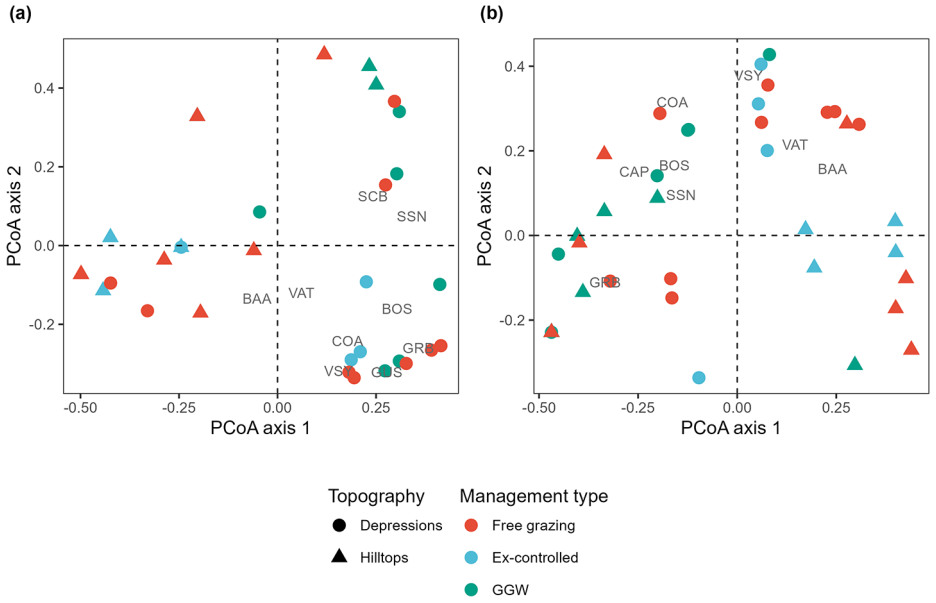


Fig. 6 Principal coordinates analyses for: (**a**) seedlings and (**b**) saplings. The significance of the species acronyms are in Table 1

Discussion

Regeneration strategy

Of the 19 species recorded in the adult phase, 11 failed to regenerate as they were not found in the sapling phase. Compared to adults (trees and bushes; mean density of 129.0 individuals/ha), regeneration density was very weak (mean density of 24.3 individuals/ha for seedlings and 21.5 individuals/ha for saplings). *Sclerocarya birrea*, which was frequently found in adult communities (present in 39.1% of the plots) was absent from sapling communities. *Grewia bicolor* and *Vachellia seyal* also showed a frequency over 13%, but with sparse saplings (isolated individuals).

Regeneration by true seedlings was generally the dominant mechanism in the study area. Five species were found to regenerate solely by true seedlings: *Vachellia tortilis*, *Vachellia seyal*, *Combretum aculeatum*, *Grewia bicolor* and *Sclerocarya birrea*. For four of them, Bellefontaine (1997) mentioned that resprouts had been observed, but no clear evidence of root suckers, or there were contradictions between authors (*Vachellia tortilis* was not mentioned in his study). To our knowledge, no studies have quantified the relative proportion of regeneration mechanisms in Sahelian savannas. Sudanian woodlands are more frequently studied (e.g., Ky-Dembele 2007).

Adult communities strongly influence regeneration

Tree cover was seen to have a strong influence on seedling and sapling density, as most of the regeneration was found under adult crown cover. This positive effect of tree cover

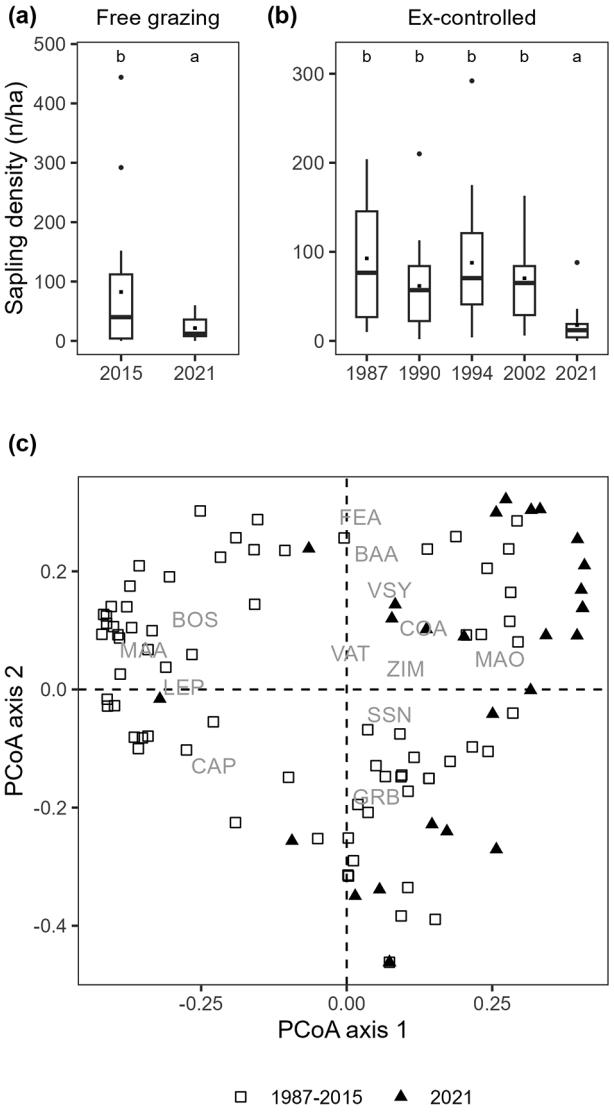


Fig. 7 Temporal dynamics of saplings in the free grazing plots and in the ex-controlled plots. (**a**-**b**) Evolution of sapling density in (**a**) the free grazing plots ($n=20$) from 2015 to 2021 and (**b**) in the ex-controlled plots ($n=14$) from 1987 to 2021. Means with no letter in common above the boxes are significantly different according to Wilcoxon's paired tests (P-value<0.05). (**c**) PCoA on the sapling density for all the plots. The significance of the species acronyms are in Table 1

on understory vegetation has already been reported by several previous studies in similar savanna environments (Akpo and Grouzis 1996; Tessema and Belay 2017). It can arise from two factors: (i) greater availability of seeds under cover (Sanou et al. 2022) and (ii) improvement of the conditions required for seedling establishment. The greater availability of seeds under mature trees can be explained by the attraction that those trees exert on animals, for instance, as resting places for livestock and birds (Aikins et al. 2023), which both disseminate seeds (Danthu et al. 1996; Zwarts et al. 2018). This can also be explained by seeds directly falling to the ground near the parental tree (Sanou et al. 2022), as well as by the impact of trees on the microclimate and water availability (Akpo et al. 2005; Kuyah et al., 2016). Indeed, tree cover decreases the temperature, thereby reducing evaporative

demand. Soil fertility is also improved under tree cover (Akpo et al. 2005; Grouzis and Akpo 2006; Sinare and Gordon 2015).

Furthermore, the CCA revealed a strong link between the botanical composition of regenerations and adult abundances. These results corrobrated the observation of Wade et al. (2018) regarding similarities between adults and regeneration composition in a surrounding area. This raises questions about the occurrence of seed dispersal over large distances. For the most common species, such as *Balanites aegyptiaca*, finding regeneration (arising from a true seedling) under a tree of the same species does not guarantee that the adult tree is a parent tree. Indeed, as these species were found everywhere within the area, regeneration could have come from animal or wind dispersal. We might question the ability of certain tree species to be better "nurse" species for regeneration than others, because of certain particular traits (e.g., leaf area, litter quality), or by being a faunal attractor (Aikins et al. 2023). The different "hosting ability" of several species had already been observed in the same area by Dendoncker and Vincke (2020), with a higher hosting potential for large trees than for shrubs. Future research involving a trait-based approach could help in understanding this nursing effect.

Influence of management type and topography

No evidence was found of a positive influence that plantations might have on regeneration density. Seedling and sapling densities within the GGW plots were not significantly different from the free grazing and ex-controlled plots. It is worth noting that the plantations were not enclosed and livestock were able to roam freely. The GGW plots tended to have a slightly different botanical composition of sapling communities from the other plots, with fewer *Balanites aegyptiaca*, though no significant difference was observed between free grazing and ex-controlled plots.

There may have been two reasons for the very limited effect of the GGW plantations. Firstly, it may have been an effect of the planted species. In the GGW plots inventoried the species planted more than 10 years earlier was *Senegalia senegal*. We found that this species hosted fewer seedlings and saplings under its crown in the other plots compared to species like *Balanites aegyptiaca* and *Sclerocarya birrea*. This observation can be related to a lower adult density of *Senegalia senegal* compared to *Balanites*, hence a lower probability of seeds being dropped under its crown (though *Sclerocarya birrea* was also present at a much lower density than *Balanites aegyptiaca*). It could also be a specific effect and a "poorer" quality of the microsite conditions under the crown of *Senegalia senegal*. Secondly, planting was carried out in strips, meaning that there may have been fewer microsites formed by the clusters of joined crowns, such as we found in topographic depressions. While this study showed that this GGW plantation (monospecific *Senegalia senegal* planted in rows) had a limited effect on regeneration, it is tricky to extrapolate that no GGW plantation has an effect on regeneration (either positive or negative). Indeed, it is likely that the potential plantation effect depends on several factors, such as the species planted, the age of the plantation, and the existence of fences at the early stages of the plantation.

In addition, the ex-controlled plots were found not to affect regeneration densities and species composition. It may be that, as animal stocking rates were not totally controlled after 1990 and as the plots had been totally open to livestock since around 2007, the positive effect observed during the GIZ experimental trial was counteracted by the effect of live-

stock since then. Lohbeck et al. (2020) found that grazing was the most important human factor that decreased the presence and abundance of regeneration in agroforestry parklands of Burkina Faso. They also found a higher regeneration density on degraded soil (by erosion and low topsoil nitrogen content). They suggested that this could have been due to an increase in species more adapted to the degradation conditions.

In our study, we did not find any influence of topography on the botanical composition of seedlings and saplings, whereas in 2015, in the same area, a significant effect of this factor was observed (Dendoncker and Vincke 2020). This new result might be due to a sampling effect, but it might also indicate a homogenization of woody stands, where rare species in depressions (Dendoncker et al. 2023) have lost the ability to regenerate even in these areas with higher water availability.

A drastic decrease in sapling density over time

A strong decrease in sapling density in the free grazing plots was highlighted from 2015 to 2021 and in the ex-controlled plots from 1987 to 2021. It is difficult to determine the causes of this decline without comparative studies and control plots. Poor recruitment could be the result of poor seed production (per plant or globally if die-back of parent trees occurred between 2015 and 2021), or a failure in establishment due to drought, livestock browsing and fires (Venter and Witkowski 2013). It may be that the adult mortality observed during the droughts of the 1970–1980 s still has some legacy effect on the current ecosystem.

In addition, seedling and sapling establishment can be hindered by drought and/or animal consumption (livestock, rodents, etc.). In South Africa, it was found that a two-year drought had a negative effect on the abundance of juveniles (Trotter et al. 2022). In our study area, a decrease in the number of rainy days was observed (Dendoncker 2020) and could have prevented seedling establishment since they often need several consecutive or regular rainy episodes to germinate and grow. Livestock has also been found to prevent seedling establishment in other savannas (Archibald et al. 2021). In our study area, Wade et al. (2018) found an increase in regeneration density over two years inside an enclosure within the GGW plots. In a West African savanna, Tredennick et al. (2015) found no influence of herbivores on tree regrowth (resprouting), but they did not study the effect on true seedlings. For *Adansonia digitata* L., it was proved that a lack of regeneration was due to a failure of establishment and not a lack of seed production; seedlings in a southern African savanna were impeded by a combination of a lack of rainfall and destruction by browsing and trampling (Venter and Witkowski 2013).

The decrease in regeneration density highlights the need for constant monitoring of saplings, bearing witness to seedling survival and establishment in these Sahelian savannas, in order to manage regenerated landscape and sustain productivity and biodiversity. Trials under natural conditions in the field could also shed some light on factors that most prevent seedling and sapling establishment. Lastly, competition for water availability between herbaceous and woody plants should be investigated to determine whether a seasonal management type (e.g., grazing only during the rainy season) could help the establishment of woody regeneration.

Limitations and caveats

This study involved certain limitations. Firstly, the identification of true seedlings as opposed to resprouts was not achieved by digging but by a local herder, which, although he was specialized in botany and ecology, could have been a source of error. Secondly, we carried out our first regeneration inventory at the end of July 2021, which is normally in the middle of the rainy season and seeds would have already germinated. However, the rains came late in 2021, meaning that the number of seedlings counted most likely did not represent the true potential of the ecosystem that year, as some seeds might have germinated in the weeks following our inventory. To take account of intra-and inter-annual variability in rainfall, we only examined the temporal dynamics of sapling counts instead of seedlings. Thirdly, only individuals below a threshold of 10 cm in circumference, often used in these arid zones to distinguish adults from regeneration, were recorded. However, this threshold does not have the same ecological meaning for every species encountered in the zone: for a species that often reaches a circumference of over 100 cm at the adult phase (e.g., *B. aegyptiaca* and *V. tortilis*) as opposed to a species growing to 50 cm at the adult phase (e.g., *Senegalia senegal*), versus a bush like *B. senegalensis*. The inventoried saplings of *S. senegal* may have been "young adults" rather than true saplings. Nevertheless, it shows the ability of the ecosystem to regenerate. Seedling counts do not present this ecological inconsistency. We also took the same threshold applied in the previous inventory of 2015 and 1987–1990 so that our results could be compared.

Conclusion

In this research, the regeneration features of woody vegetation was studied across the Sahelian savanna of the sylvo-pastoral zone of Senegal using a field inventory and historical data. Several characteristics were highlighted. Firstly, poor diversity was observed among regenerations: 10 species were recorded as regeneration against 19 species in the adult phase. Secondly, the proportion of true seedlings was dominant compared to resprouts. Thirdly, adult abundances was shown to be an important driver of regeneration composition, which raises questions about the occurrence of long dispersal events. Mature trees also showed a positive effect on regenerations by sheltering them under their crown. The regeneration of rare species was always found under adult crowns. Fourthly, the influence of management type on density and species richness was not significant. The plantations had a slight difference in their botanical composition, with less regeneration of *Balanites aegyptiaca*, though it was difficult to disentangle the effects of grazing intensity and land management, as grazing intensities in the three variants could not be quantified. We also confirmed the positive influence of topographic depressions on regeneration density. Lastly, we observed a steep decline in sapling density between 1987 and 2015 in the free grazing and ex-controlled plots. These results cast doubt on the persistence of woody vegetation in Sahelian savannas. In addition, they highlight the need for continuous monitoring of regeneration and the importance of protecting large trees in suitable microsites, such as topographic depressions, to foster regeneration.

Appendix

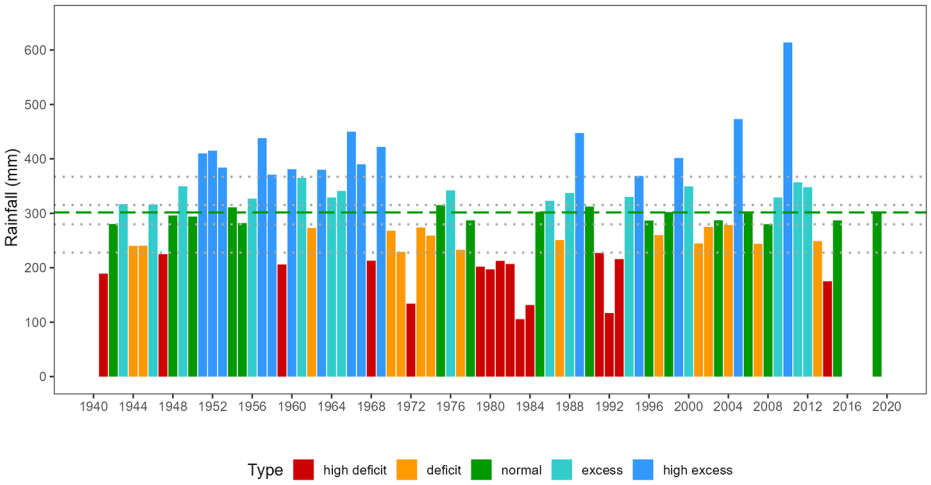


Fig. 8 Annual rainfall in Widou Thiengoly from 1940 to 2020 (missing data for 2016-2017-2018) with the classification of years according to Cornet (1978)

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11056-024-10041-1.

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Author contributions Conceptualization: Morgane Dendoncker, Simon Taugourdeau and Caroline Vincke; Methodology: Morgane Dendoncker and Simon Taugourdeau. Formal analysis and investigation: Morgane Dendoncker, Simon Taugourdeau, Ramata Ndianor, Sabine Miehe. Writing - original draft preparation: Morgane Dendoncker. Writing - review and editing: Morgane Dendoncker, Caroline Vincke, Ramata Ndianor, Abdoul Aziz Diouf, Sabine Miehe, Daouda Ngom and Simon Taugourdeau.

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Data availability Inventory data from 2015 and 2021 are available on request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Aikins TK, Thomson RL, Cramer MD (2023) All savanna islands of fertility are not equal: colonial birds influence soil nutrient stoichiometries with consequences for tree seedling growth. Plant Ecol 224(8):685–696. https://doi.org/10.1007/s11258-023-01333-1

Akpo LE, Grouzis M (1996) Influence Du couvert sur la régénération de quelques espèces ligneuses sahéliennes (Nord Sénégal, Afrique occidentale). Webbia 50(2):247–263

Akpo A, Goudiaby VA, Grouzis M, Le Houérou HN (2005) Tree shade effects on soils and environmental factors in a savanna of Senegal. West Afr J Appl Ecol 7:41–52

André D (2001) Dix sept ans de suivi de la végétation lgineuse et herbacée dans le périmètre expérimental de widou thiengoly (Ferlo, Nord-Sénégal). Verlag Ulrich E. Gauer, Beuren ⁄ Stuttgart

Anyamba A, Tucker CJ (2005) Analysis of Sahelian vegetation dynamics using NOAA-AVHRR NDVI data from 1981–2003. J Arid Environ 63(3):596–614. https://doi.org/10.1016/j.jaridenv.2005.03.007

Archibald S, Twine W, Mthabini C, Stevens N (2021) Browsing is a strong filter for savanna tree seedlings in their first growing season. J Ecol 109(10):3685–3698. https://doi.org/10.1111/1365-2745.13745

Argaw M, Teketay D, Olsson M (1999) Soil seed flora, germination and regeneration pattern of woody species in an Acacia woodland of the Rift Valley in Ethiopia. J Arid Environ 43(4):411–435. https://doi.org/10.1006/jare.1999.0532

Assouma MH, Lecomte P, Hiernaux P, Ickowicz A, Corniaux C, Decruyenaere V, Diarra AR and Vayssières J (2018) How to better account for livestock diversity and fodder seasonality in assessing the fodder intake of livestock grazing semi-arid sub-Saharan Africa rangelands. Vet Sci 216:16–23. https://doi.org/10.1016/j.livsci.2018.07.002

Bellefontaine R (1997) In: Ambouta J-MK, Régis R, Peltier (eds) Synthèse des espèces des domaines sahélien et soudanien qui se multiplient naturellement par voie végétative. In Fonctionnement et gestion des écosystèmes contractés sahéliens. J.M. d'Herbès. John Libbey Eurotext, Paris, pp 95–104

Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer, New York, NY, p 306. https://doi.org/10.1007/978-1-4419-7976-6

Brandt M, Mbow C, Diouf AA, Verger A, Samimi C, Fensholt R (2015) Ground- and satellite-based evidence of the biophysical mechanisms behind the greening Sahel. Glob Change Biol 21(4):1610–1620. https://doi.org/10.1111/gcb.12807

Brandt M, Rasmussen K, Hiernaux P et al (2018) Reduction of tree cover in west African woodlands and promotion in semi-arid farmlands. Nat Geosci 11(5):328–333. https://doi.org/10.1038/s41561-018-0092-x

Breman H, Kessler JJ (1995) Woody plants in agro-ecosystems of semi-arid regions. Springer-, Berlin, p 340

Catinot R (1994) Aménager les savanes boisées africaines: un tel objectif semble désormais à notre portée. Bois et forêts des tropiques 241:53–70

Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplanksy A, Weltzin JF (2004) Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236253. https://doi.org/10.1007/s00442-004-1551-1

Chidumayo EN, Gumbo DJ (2010) The dry forests and woodlands of Africa. Routledge, p 288

Coughenour MB, Detling JK (1986) Acacia tortilis seed germination responses to water potential and nutrients. Afr J Ecol 24(3):203–205. https://doi.org/10.1111/j.1365-2028.1986.tb00363.x

Danthu P, Ickowicz A, Friot D, Manga D, Sarr A (1996) Effet Du passage par le tractus digestif des ruminants domestiques sur la germination des graines de légumineuses ligneuses des zones tropicales sèches. Revue Elev Méd vét Pays trop 49(3):235–241

Dendoncker M (2020) 50 years of woody vegetation dynamics in the Senegalese Sahel (Ferlo): bases for a functional diversity approach. Phd in agronomical sciences and bioengineering Université catholique de Louvain. 328 p

Dendoncker M, Vincke C (2020) Low topographic positions enhance woody vegetation stability in the Ferlo (Senegalese Sahel). J Arid Environ 175:104087. https://doi.org/10.1016/j.jaridenv.2019.104087

Dendoncker M, Brandt M, Rasmussen K, Taugourdeau S, Fensholt R, Tucker CJ, Vincke C (2020) 50 years of woody vegetation changes in the Ferlo (Senegal) assessed by high-resolution imagery and field surveys. Reg Environ Change 20(4):137. https://doi.org/10.1007/s10113-020-01724-4

Dendoncker M, Vincke C, Bazan S, Madingou MPN, Taugourdeau S (2023) The size of topographic depressions in a Sahelian savanna is a driver of woody vegetation diversity. J Arid Environ 210:104923. https://doi.org/10.1016/j.jaridenv.2022.104923

Diallo MD, Goalbaye T, Mahamat-Saleh M et al (2017) Effects of major woody species of the Senegalese Great Green Wall on N mineralization and microbial biomass in soils. Bois et forêts des tropiques 333(3):43–54

dos Santos DM, da Silva KA, dos Santos JM, F F and Araújo E d L (2018) Soil seed bank and its importance in the natural regeneration of degraded areas. Ethnobiol Conserv. 7https://doi.org/10.15451/ec2018-03-07.05-1-7

FAO (2019) Trees, forests and land use in drylands: the first global assessment. Full report. (eds.), FAO forestry paper Rome, 193 p

Fox J, Monette G (1992) Generalized Collinearity Diagnostics. J Am Stat Assoc 87(417):178–183. https://doi.org/10.1080/01621459.1992.10475190

Gignoux J, Lahoreau G, Julliard R, Barot S (2009) Establishment and early persistence of tree seedlings in an annually burned savanna. J Ecol 97(3):484–495. https://doi.org/10.1111/j.1365-2745.2009.01493.x

Gonzalez P, Tucker CJ, Sy H (2012) Tree density and species decline in the African sahel attributable to climate. J Arid Environ 78:55–64. https://doi.org/10.1016/j.jaridenv.2011.11.001

Grouzis M, Akpo LE (2006) Interactions arbre-herbe Au Sahel. Sci et changements planétaires/Sécheresse 17(1–2):318–325

Hänke H, Börjeson L, Hylander K, Enfors-Kautsky E (2016) Drought tolerant species dominate as rainfall and tree cover returns in the West African Sahel. Land Use Policy 59:111–120. https://doi.org/10.1016/j.landusepol.2016.08.023

Herrmann SM, Tappan GG (2013) Vegetation impoverishment despite greening: a case study from central Senegal. J Arid Environnements 90:55–66. https://doi.org/10.1016/j.jaridenv.2012.10.020

Jones A, Breuning-Madsen H, Brossard M et al (2013) Soil atlas of Africa. European Commission, Publications Office of the European Union: Luxembourg, 173 p. https://doi.org/10.2788/52319

Kassahun A, Snyman HA, Smit GN (2009) Soil seed bank evaluation along a degradation gradient in arid rangelands of the Somali region, eastern Ethiopia. Agric Ecosyst Environ 129(4):428–436. https://doi.org/10.1016/j.agee.2008.10.016

Ky-Dembele C, Tigabu M, Bayala J, Ouédraogo SJ, Odén PC (2007) The relative importance of different regeneration mechanisms in a selectively cut savanna-woodland in Burkina Faso, West Africa. For Ecol Manag 243(1):28–38. https://doi.org/10.1016/j.foreco.2007.01.091

Ky-Dembele C, Keita MK, Traore FT, Savadogo P, Bayala J, Muchugi A, Carsan S (2023) Direct seeding of six agroforestry tree species indigenous to the Sahel: the effect of fungicide and planting-hole depth on seed germination and seedling emergence capacity. Agroforest Syst 97(7):1261–1274. https://doi.org/10.1007/s10457-022-00752-9

Le Houérou HN (1980) The rangelands of the Sahel. J Range Manag 33(1):41–46

Le Houérou HN (1989) The grazing land ecosystems of the African Sahel. Springer-, Berlin Heidelberg: Berlin, Germany, p 282

Legendre P, Legendre L (2012) Chap. 11 - canonical analysis. In: Legendre P, Legendre L (eds) Developments in Environmental Modelling. Elsevier, pp 625–710

Lohbeck M, Albers P, Boels LE et al (2020) Drivers of farmer-managed natural regeneration in the Sahel. Lessons for restoration. Sci Rep 10(1):15038. https://doi.org/10.1038/s41598-020-70746-z

Luoga EJ, Witkowski ETF, Balkwill K (2004) Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. For Ecol Manag 189(1):23–35. https://doi.org/10.1016/j.foreco.2003.02.001

Merine AK, Rodríguez-García E, Alía R, Pando V, Bravo F (2014) Effects of water stress and substrate fertility on the early growth of Acacia senegal and Acacia seyal from Ethiopian Savanna woodlands. Trees 29(2):593–604. https://doi.org/10.1007/s00468-014-1138-3

Miehe S (2002) Inventaire et suivi de la végétation dans le périmètre expérimental de widou thiengoly dans le cadre Du Projet Sénégalo-allemand d'autopromotion pastorale dans le ferlo (PAPF). Rapport final. (eds.) Saint-Louis, Sénégal, p 57

Miehe S, Kluge J, von Wehrden H, Retzer V (2010) Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal. J Appl Ecol 47(3):692–700. https://doi.org/10.1111/j.1365-2664.2010.01815.x

Miller MF (1996) Dispersal of Acacia seeds by ungulates and ostriches in an African Savanna. J Trop Ecol 12(3):345–356

Miller MF, Coe M (1993) Is it advantageous for Acacia seeds to be eaten by ungulates ? Oikos 66(2):364–368. https://doi.org/10.2307/3544827

Nicholson S (2005) On the question of the "recovery" of the rains in the West African Sahel. J Arid Environ 63:615–641. https://doi.org/10.1016/j.jaridenv.2005.03.004

Olsson L, Eklundh L, Ardö J (2005) A recent greening of the Sahel-trends, patterns and potential causes. J Arid Environ 63(3):556–566. https://doi.org/10.1016/j.jaridenv.2005.03.008

Ouédraogo P, Traoré S, Nacoulma BM, I, Daboue E, Bationo BA (2021) Dissémination et germination de semences issues des fèces de bétail Au Sahel Du Burkina Faso. Bois et forêts des tropiques 350:15–27. https://doi.org/10.19182/bft2021.350.a36826

POWO (2023) Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet: http://www.plantsoftheworldonline.org/. https://doi.org/10.1038/s41597-021-00997-6
Reiner F, Brandt M, Tong X et al (2023) More than one quarter of Africa's tree cover is found outside areas previously classified as forest. Nat Commun 14(1):2258. https://doi.org/10.1038/s41467-023-37880-4
R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Sanou L, Savadogo P, Zida D, Thiombiano A (2022) Variation in soil seed bank and relationship with aboveground vegetation across microhabitats in a savanna-woodland of West Africa. Nord J Bot 2022 5(e03304). https://doi.org/10.1111/njb.03304
Sarr MS, Diallo AM, King-Okumu C (2021) A review of public versus private reforestation programs in the Senegalese Sahel: taking stock of realities and challenges. Restoration Ecology, n/a (n/a. e13582. https://doi.org/10.1111/rec.13582
Sarr MS, Seiler JR, Sullivan J (2024) Effect of drought stress on the physiology and early growth of seven Senegalia (Acacia) Senegal (L.) Britton provenances. https://doi.org/10.1007/s11056-023-10027-5. New Forests
Sinare H, Gordon LJ (2015) Ecosystem services from woody vegetation on agricultural lands in Sudano-Sahelian West Africa. Agric Ecosyst Environ 200:186–199. https://doi.org/10.1016/j.agee.2014.11.009
Skoglund J (1992) The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. J Veg Sci 3(3):357–360. https://doi.org/10.2307/3235760
Tessema ZK, Belay EF (2017) Effect of tree species on understory vegetation, herbaceous biomass and soil nutrients in a semi-arid savanna of Ethiopia. J Arid Environ 139:76–84. https://doi.org/10.1016/j.jaridenv.2016.12.007
Tredennick AT, Karembé M, Dembélé F, Dohn J, Hanan NP (2015) No effects of fire, large herbivores and their interaction on regrowth of harvested trees in two west African savannahs. Afr J Ecol 53(4):487–495. https://doi.org/10.1111/aje.12238
Trotter FD, Lehmann CER, Donaldson JE, Mangena HE, Parr CL, Archibald S (2022) Drought and fire determine juvenile and adult woody diversity and dominance in a semi-arid African savanna. Biotropica 54(4):1015–1029. https://doi.org/10.1111/btp.13126
Turner MD, Davis DK, Yeh ET, Hiernaux P, Loizeaux ER, Fornof EM, Rice AM, Suiter AK (2023) Great Green Walls: Hype, Myth, and Science. Annual Review of Environment and Resources. https://doi.org/10.1146/annurev-environ-112321-111102
Tybirk K (1991) Regeneration of woody legumes in Sahel. Botanical Institute Aarhus University: Denmark, p 81
Venter SM, Witkowski E, T F (2013) Where are the young baobabs? Factors affecting regeneration of Adansonia digitata L. in a communally managed region of southern Africa. J Arid Environ 92:1–13. https://doi.org/10.1016/j.jaridenv.2012.12.010
Wade TI, Ndiaye O, Mauclaire M, Mbaye B, Sagna M, Guissé A, Goffner D (2018) Biodiversity field trials to inform reforestation and natural resource management strategies along the African Great Green Wall in Senegal. New Forest 49(3):341–362. https://doi.org/10.1007/s11056-017-9623-3
White F, Paris (1983) 356
Whitford WG, Duval BD (2020) Chap. 5 - Patch—Mosaic dynamics. In: Edition) WG, Whitford, Duval BD (eds) Ecology of Desert systems, Second edn. Academic, pp 109–133
Wilson TB, Witkowski ETF (1998) Water requirements for germination and early seedling establishment in four African savanna woody plant species. J Arid Environ 38(4):541–550. https://doi.org/10.1006/jare.1998.0362
Witkowski ETF, Garner RD (2000) Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites. Plant Ecol 149(1):91–106. https://doi.org/10.1023/A:1009850706843
Zida D, Sawadogo L, Tigabu M, Tiveau D, Odén PC (2007) Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. For Ecol Manag 243(1):102–115. https://doi.org/10.1016/j.foreco.2007.02.013
Zwarts L, Bijlsma RG, van der Kamp J (2018) Large decline of birds in Sahelian rangelands due to loss of woody cover and soil seed bank. J Arid Environ 155:1–15. https://doi.org/10.1016/j.jaridenv.2018.01.013

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