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SPECIES RICHNESS, DIVERSITY, DENSITY, AND SPATIAL DISTRIBUTION OF SOIL SEED BANKS IN THE MOREMI GAME RESERVE RIPARIAN WOODLANDS OF THE OKAVANGO DELTA, NORTHERN BOTSWANA

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This study aimed to investigate the soil seed banks in the Moremi Game Reserve Riparian Woodlands (MGRWs) of the Okavango Delta, northern Botswana, from March 2019 to June 2019. We examined species richness and diversity, determined densities, assessed the spatial distribution of seeds in the soil, and compared the similarity in species composition between the standing vegetation and soil seed bank flora. A total of 124 plant species were identified in the litter and top 9 cm soil layers with a mean density of 1933 seeds m^{-2}. Herbs, grasses, sedges, and woody plants were represented by 69, 25, 17, and 13 species, respectively, in 33 families and 92 genera. The overall H' diversity and evenness of the soil seed bank in the MGRWs were 3.7 and 0.77, respectively. The results revealed that Poaceae, Cyperaceae and Asteraceae are the most dominant families in all the germinated species. Four plant communities, namely *Kohautia virgata-Ammania baccifera, Bidens pilosa-Urochloa mosambisensis, Setaria verticillata-Brachiaria deflexa,* and *Cynodon dactylon-Cyperus longus* were identified from the soil seed bank. Bray-Curtis ordination showed that there was an overlap between these communities in terms of seed bank composition. However, MRPP analysis showed that there was significant ($P < 0.05$) separation between germinated soil seed bank communities. The overall spatial horizontal distribution of seeds varied among sampling quadrats while the vertical distribution of seeds exhibited the highest densities occurring in the upper 3 cm of the soil and gradually decreasing densities with increasing depth.

Keywords: Diversity, Evenness, Germination, Soil seed density, Spatial seed distribution, Species richness

INTRODUCTION

About 31% of the earth's land surface is covered by forests, which provide many critical ecosystem services, including moderating the hydrologic cycle, climate change mitigation, biodiversity preservation, and soil conservation (Sheram 1993, FAO 2018). Africa has approximately 17% of the world's forests, covering an estimated 650 million ha (Mansourian & Berrahmouni 2021). However, an increase in human population densities and increasing demand for energy, water, and land has aggravated land degradation (Imasiku & Ntagwirumugara 2020). The destruction of forests has been accelerated by the expansion of crop fields and harvest of resources to meet the rapidly growing demands for food, fresh water, timber, fiber, and fuel (MEA 2005, Gregory & Polsterer 2017). Forests in the tropics are being depleted at an alarming rate as a result of natural and human-induced disturbances (Kozlowski 2002).

Forests contribute significantly to the economies of many countries (Shackleton et al. 2007, Bhatt et al. 2021). Riparian woodlands offer ecosystem services, such as water filtration, nutrient cycling, bank protection, wildlife habitat, food and shade to aquatic and terrestrial ecosystems (Pusey & Arthington 2003, Capon et al. 2013, Riis et al. 2020). They also provide

corridors for the movement of biota (Naiman & Décamps 1997) and have many important roles for humans (Kemper 2001). Riparian habitats also provide services, which include both use values and non-use values (Holmes et al. 2004). The use value benefits arise from in-stream uses such as boating, fishing or swimming, irrigation and drinking, flood mitigation, consumptive activities such as hunting and non-consumptive activities such as bird watching. Riparian systems also provide benefits such as the knowing that a healthy ecosystem exists.

Riparian woodlands play a significant role in woodland biodiversity conservation and provide habitats that are important to the lifecycle of freshwater organisms (Little et al. 2008). However, high human population densities put pressure on the use of forest resources for various purposes, such as fuel, food, and timber, thus, over-utilizing and over-exploiting them (MEA 2005). Therefore, in some parts of the globe, restoration measures are urgently required to rehabilitate degraded woodlands and ensure a healthy ecosystem for sustainable provision of ecosystem services (Lamb & Gilmour 2003, Mansourian & Berrahmouni 2021, Indrajaya et al. 2022). Where woodlands are still relatively untransformed, measures to protect and conserve regenerative processes are needed.

Soil seed banks are all seeds or vegetative propagules that are viable and present on or in the soil or associated litter or humus. They can either be transient or persistent; transient seeds remain in the soil for a short period, while persistent seeds remain in the soil for more than one year (Bakker et al. 1996). Soil seed banks are useful tools in restoration and rehabilitation projects and initiating natural regeneration after disturbance (Chazdon & Guariguata 2016, Abreu et al. 2021, Luo et al. 2023). They play a critical role in plant genetics (Anderson et al. 2012), biodiversity maintenance (Hosogi et al. 2006, Bufalo et al. 2016, Kapás et al. 2020) and restoration of degraded lands (Chazdon & Guariguata 2016, Tiebel et al. 2018, Bekele et al. 2022, Luo et al. 2023). Soil seed bank processes begin with the dispersal of the seed and end with the germination or death of the seed (Mall & Singh 2013). A variety of factors, which include seed rain, dispersal, predation, longevity, and factors controlling germination and recruitment determine the composition of soil seed banks (Anderson et al. 2012, Long et al. 2015, Abreu et al. 2021). The composition of soil seed banks differs with soil depth. A high density of seeds is found in the soil surface and this generally gradually decreases as depth increases (Teketay & Granström 1995, Tesfaye et al. 2004, Zhang et al. 2016, Mmusi et al. 2021). The soil seed bank reveals and integrates past biotic and abiotic conditions, and its diversity and species composition tend to be different from that of the above-ground flora (Díaz-Villa et al. 2003).

The Okavango Delta is one of the World Heritage sites, and one of the few large inland delta systems without an outlet to the sea, known as an endorheic delta, its waters drain instead into the desert sands of the Kalahari Basin. The riparian vegetation in the Okavango Delta provides a variety of goods and services to local communities, residing in the Delta (Mmopelwa 2006). Even though they play an important role, climate change and anthropogenic activities threaten the riparian vegetation. Wild animals, such as elephants may also cause changes in the composition and population structure of riparian woodland communities (Skarpe et al. 2004, Rutina & Moe 2014). Despite these threats, information on the soil seed banks, tree composition, and regeneration status of riparian woody species in the Moremi Game Reserve is limited. Moremi Game Reserve is the core of the Okavango Delta and is a protected area in which biodiversity conservation is the primary objective of management.

In this study, riparian woodland soil seed banks in the Moremi Game Reserve were investigated to help generate information that could help us to conserve and manage them sustainably. The soil seed banks were studied to better understand the potential contribution of the soil seeds and seedling banks to the natural regeneration and generate information that would assist in selecting appropriate rehabilitation and restoration activities. The specific objectives of this study were to examine species richness and diversity of the seeds in the soil, to determine densities of seeds in the soil by species and to assess the spatial (vertical and horizontal) distribution of seeds in the soil and to compare the similarity in species composition between the standing vegetation and the soil seed bank flora of the riparian vegetation in the Moremi Game Reserve in northern Botswana.

MATERIALS AND METHODS

Study area

This study was carried out in the Moremi Game Reserve (MGR), which is located in the middle of the Okavango Delta in Botswana at coordinates (23°22′38″ E, 19°17′9″ S) (Figure 1). The Okavango Delta is a pristine wetland and a Ramsar site. The Delta emanates from Angola and receives almost all its water as a flood pulse from its headwaters in the Angolan Highlands. The Delta's climate is semi-arid with an average rainfall of 490 mm that falls in one distinct season between October and March. The Delta floods annually and the flooded area varies from 5000 to 12,000 km² (McCarthy & Ellery 1998), the Delta has variable channel morphology, flow regimes, and ecosystems. Channels within the delta have been classified into upper or primary channels, distributary channels and outlet channels (Gumbricht et al. 2004). The Okavango Delta can also be classified in terms of flow regime and habitat; permanent swamps, seasonal swamps, occasionally flooded areas, and drylands (McCarthy et al. 1988).

The annual floods peak at Mohembo, between February and April, but this peak only reaches the end of the Delta at Maun between June and August, five months later (McCarthy et al. 2000). The Okavango Delta comprises of riparian woodland, which has been estimated at around 7.5% (Ecosurv 1988).

The Moremi Game Reserve (MGR) is one of the protected areas in Botswana and was named after Chief Moremi of the Batawana tribe. The MGR is Botswana's second-largest game reserve and was proclaimed in 1963 through the Fauna and Flora Preservation Society of Ngamiland, by the Batawana people to protect the wildlife in the area (Tyler & Bishop 1998). The reserve is 4871 km² in land area, and was the first official reserve on tribal land, covering much of the eastern side of the Okavango Delta. Chief's Island was proclaimed in the late 1970s and added to the MGR (Campbell 2004), and the Department of Wildlife and National Parks took over the game

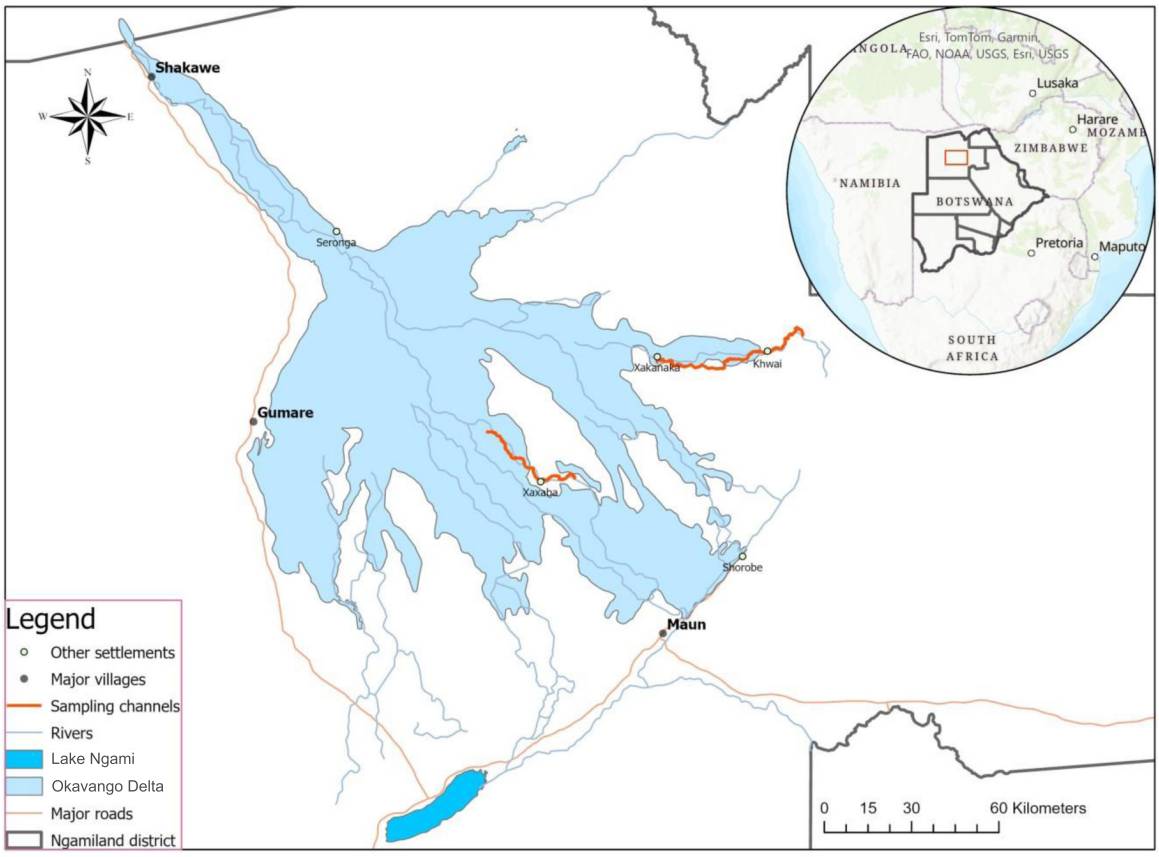


Figure 1 The study site in the Moremi Game Reserve

reserve in 1979 (Grossman et al. 2007). The reserve has buffer zones of wildlife management areas and hunting concessions that allow for the free movement of wild animals around the MGR. The Chobe National Park borders MGR to the northeast side. The MGR has diverse habitats that combine Mopane woodland and *Senegalia/ Vachellia* forests, floodplains, and lagoons.

The game reserve is primarily used for the conservation of fauna and flora and wildlife-based tourism. The Basarwa people, who inhabited the MGR area for over 10,000 years before its establishment, utilised the reserve's veld products, which include woodland and wildlife resources (Tlou 1985). Moremi Game Reserve has been free from human exploitation of its woodland resources since 1963 (Mbaiwa 2005). The reserve's woody species include dryland and riparian tree species. Common riparian tree species in MGR are *Croton megalobotrys* Müll.Arg., *Hyphaene petersiana* Klotzsch ex Mart., *Philenoptera violacea* (Klotzsch) Schrire, and *Diospyros mespiliformis* Hochst. ex A.DC. Flooding frequency, herbivory, and fire are major influences on the tree species composition of woodlands in MGR (Tsheboeng & Murray-Hudson 2013).

Common herbivores in MGR include elephant, buffalo, giraffe, zebra, kudu, lechwe, tsessebe, and impala, which may have transformed some of the woodland structure from trees to shrubs (Hamandawana 2012). MGR is home to over 400 of the Okavango's species of birds, including the African fish eagle, crested crane, and sacred ibis. These mammals, birds, insects, plants, fish, and reptile species have adapted to the Okavango Delta's swampy conditions.

Methods

In order to determine the species composition, density, and vertical distribution of riparian woodland vegetation and soil seed bank samples were collected from different channels in the MGR. A total of 42 plots, each measuring 20 × 50 m, were selected randomly in the vegetation physiognomy identified (Figure 2). The sampled plots were initially selected in Google Earth maps and were, then, given codes. The selected plots were, then, subjected to random number selection in Excel, and the coordinates

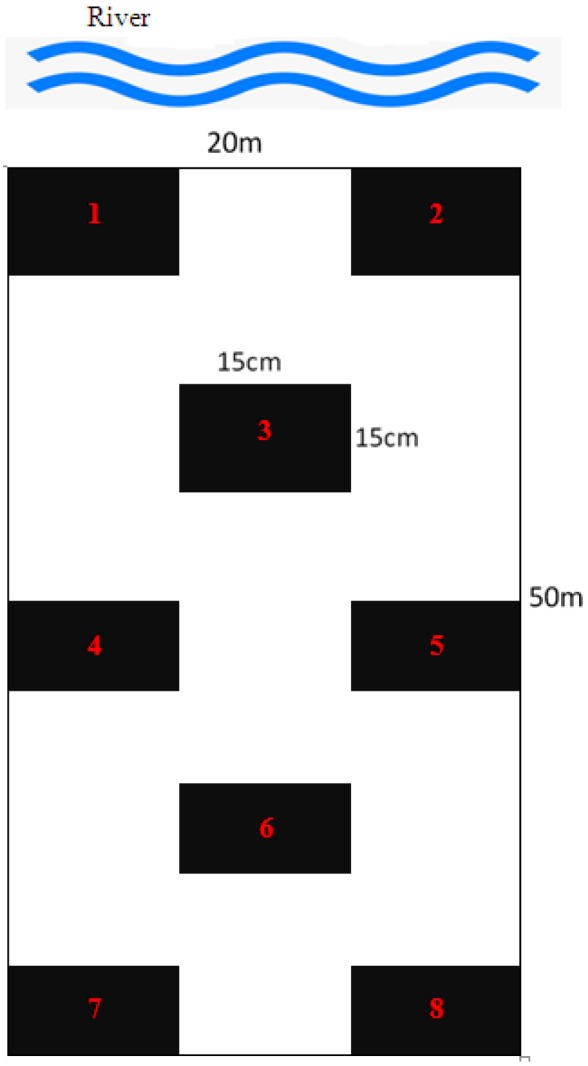


Figure 2 Schematic representation of sampled plots (20 × 50 m) and sub plots (15 × 15 cm) in the study area

of quadrats from Google Earth maps were used to locate them in the field. A Global Positioning System (GPS) Garmin GPSMAP 64S was used. Fieldwork for vegetation survey and soil sample collection were undertaken from March to June 2019. Seed germination, seedling identification and data analyses were conducted from November 2019 to November 2020.

The woody species composition and soil seed banks were surveyed within the same selected plots. Height and diameter at breast height (DBH) were measured for vascular species, and a Vernier caliper was used to measure DBH of individuals greater than 2 cm in DBH. For tree species that could not be measured with a Vernier caliper, a measuring tape was used. Tree height was measured using a calibrated stick.

The number of seedlings of each woody species was counted and recorded. All woody species encountered in each plot were identified to genus level in the field if possible, and specimens of unknown species were collected, pressed, dried, and identified in the Peter Smith University of Botswana Herbarium (PSUB) at the Okavango Research Institute (ORI).

Soil samples for the soil seed bank study were collected from eight sub plots of 15 × 15 cm within the 20 × 50 m plots (Mmusi et al. 2021). The eight sub plots were situated inside each plot at each corner and at the center to capture the variation in the distribution of seeds. Four different soil layers, from each sub plot, including the litter layer, the first soil layer (0–3 cm), the second soil layer (3–6 cm), and the third soil layer (6–9 cm) were collected using hand trowels, following the methods used by Teketay & Granström (1995). In each of the plots, the samples from all the eight litter, first, second, and third layers were pooled and mixed to form one composite soil sample, separately mixed thoroughly and, then, divided into eight from which one working sample was randomly selected from each layer for soil seed bank germination study. The random selection for plots was carried out in Microsoft Excel (using the RANDBETWEEN (1, 8) function).

Soil incubation

Seedling emergence and seed extraction through soil sieving were the methods used to characterize the soil seed banks (Baskin & Baskin 1998, Lemenih & Teketay 2006). Each soil layer was separately placed into plastic bags, which were properly labeled and transported to ORI where they were incubated. The selected soil samples were, then, incubated in open-topped plastic bags with perforations at the bottom to allow free drainage of excess water. The incubation of soil samples was carried out under a shade-net enclosure constructed at ORI to minimise the impact of direct sunlight on the emerging seedlings for 12 months. The soil samples were watered daily. The number of viable seeds and the composition of the soil seed bank were used to measure the number of seedlings of different species emerging from the soil samples (Roberts 1981). Seedling germination was monitored daily, and the emerging seedlings were identified, counted, recorded, and discarded. The seedlings were identified to the species level, and this was achieved when the seedlings were fully grown for some of the species. Every four weeks, the soil samples were stirred to stimulate further seed germination. After twelve months of incubation, the germination experiment was terminated, and the soil samples were sieved to recover seeds that had not germinated using a sieve stack of mesh sizes ranging from 0.5 to 5 mm. The recovered seeds were then identified, counted, and categorised as intact, eaten, or rotten. The cutting test method was used to determine the viability of seeds recovered after they were sieved. Seeds were considered viable when they had a firm white embryo and were considered dead when they were covered with fungi, collapsed when pinched, and/or had grey, yellow, or brownish embryos (Teketay & Granström 1995, Baskin & Baskin 1998). Plant nomenclature used in this study follows that of Setshogo & Venter (2003), Setshogo (2005), Heath & Heath (2009) and Kyalangalilwa et al. (2013). The seeds recovered by sieving were collected and identified using local reference material.

DATA ANALYSES

Species richness is a biologically appropriate measure expressed as the number of different species per sample unit (Whittaker 1972). Species richness (S) was determined as the total number of different plant species recorded from the soil seed bank and standing vegetation and did not consider the proportion and distribution of each species. Species composition, seed density, species richness of grasses, herbs, sedges, and woody species were recorded. The Shannon Diversity Index (H') (Krebs 1989, Magurran 2004) was calculated for all plant species that germinated from the seed banks and seeds recovered from the soil samples. The index considers species richness and relative abundance of each species in all sampled plots. The Shannon-Wiener diversity index is the most widely used measure of community diversity because it combines species richness with species evenness (relative abundance) (Kent & Coker 1992). The following formula was used to determine the Shannon Diversity Index:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where, H′ = Shannon's Diversity Index, S = species richness, P_i = proportion of S made up of the ith species (relative abundance).

Evenness or equitability, a measure of similarity of the abundances of the different plant species encountered in the soil samples, was analysed by using Shannon's Evenness or Equitability Index (E) (Krebs 1989, Magurran 2004). Equitability assumes a value between 0 and 1, with 1 being complete evenness. The following formula was used to calculate evenness.

$$E = H'/\ln S$$

where, E = evenness and S = species richness.

The similarity in woody species composition between the soil seed flora and the standing vegetation in Riparian Woodlands (MGRWs) was computed by using Jaccard's Similarity Coefficient (JSC) (Krebs 1989). The values of SJ range between 0 and 1, where 0 and 1 indicate complete dissimilarity and similarity in species composition, respectively. The following formula was used:

$$JSC = \frac{a}{(a + b + c)}$$

where a = number of woody species common to the standing vegetation and soil seed bank, b = number of woody species recorded only from the standing vegetation, and c = number of woody species recorded only from the soil seed bank in MGR.

Spatial distribution of seeds in the soil

Agglomerative Hierarchical Cluster Analysis (flexible β linkage, β = 0.25, Sorensen distance, data relativised by maximum) (McCune & Grace 2000) were conducted to determine different soil seed bank groups across different soil layers. For each community of germinated seeds, the indicator value for each species was calculated through indicator species analyses (Dufrêne & Legendre 1997). The statistical significance of the indicator value for each species was determined using Monte Carlo testing (Dufrêne & Legendre 1997). The Monte Carlo test was also used to statistically compare variation in indicator values of different species across different soil layers. Bray-Curtis Ordination (Sorensen distance, data relativised by maximum), using the variance-regression method (Beals 1984), was used to infer the different plant communities between the different soil layers in the soil seed bank. This was based on the communities that were *a priori* determined through Agglomerative Hierarchical Cluster Analysis of the seed bank. PC-ORD version 6 was used for all the analyses.

Soil seed bank composition from different layers

Multi-Response Permutation Procedures (MRPP) were used to compare the soil seed bank communities across different soil layers to determine whether they were significantly different from each other (McCune & Grace 2000).

RESULTS

Diversity of standing vegetation

The vegetation survey revealed a total of 41 woody species, representing 15 different families (Table 1). The family with the highest number of species was Fabaceae with 13 species, followed by Combretaceae with six species, and Ebenaceae, Capparaceae, and Euphorbiceae had three species each while Anacardiaceae, Moraceae, Arecaceae, and Rhamnaceae had two species each. The remaining families had one species each. A total of 27 genera were encountered. *Combretum* was the richest genus with four species followed by *Vachellia* with three species. The other genera had one or two species.

Diversity of seeds in the soil

The species richness of the soil seed banks in MGR was 124, representing 33 families, with herbs, grasses, sedges, and woody species represented by 69 (56%), 25 (20%), 17 (14%), and 13 (10%) species, respectively (Table 2). The family Poaceae exhibited the highest richness in all the germinated species (25 species = 21%), followed by the Cyperaceae (17 species = 15%) and Asteraceae (13 species = 11%) (Table 3). A

Table 1 List of woody plant species identified in the MGR Riparian Woodlands of the Okavango Delta, northern Botswana, and the species that were recovered/germinated from the soil seed banks

Species	Family	Above ground vegetation	Soil seed bank
Albizia anthelmintica Brongn.	Fabaceae	✓	×
Albizia harveyi E.Fourn.	Fabaceae	✓	×
Albizia versicolor Welw. ex Oliv.	Fabaceae	✓	×
Berchemia discolor (Klotzsch) Hemsl	Rhamnaceae	✓	✓
Boscia albitrinca (Burch.) Gilg & Gilg-Ben	Capparaceae	✓	×
Capparis tomentosa Lam.	Capparaceae	✓	×
Carissa edulis Vahl	Apocynaceae	✓	×
Colophospermum mopane (J.Kirk ex Benth.) J.Kirk ex J.Léonard	Fabaceae	✓	✓
Combretum apiculatum Sond.	Combretaceae	✓	×
Combretum hereroense Schinz	Combretaceae	✓	×
Combretum imberbe Wawra	Combretaceae	✓	✓
Combretum mossambicense (Klotzsch) Engl.	Combretaceae	✓	×
Croton megalobotrys Müll. Arg	Euphorbiaceae	✓	✓
Dichrostachys cinerea (L) Wight & Arn.	Fabaceae	✓	×
Diospyros lycioides Desf.	Ebenaceae	✓	✓
Diospyros mespiliformis Hochst. Ex A. DC.	Ebenaceae	✓	✓
Euclea divinorum Hiern	Ebenaceae	✓	×
Ficus sycomorus L	Moraceae	✓	×
Ficus thonningii Blume	Moraceae	✓	×
Flueggea virosa (Roxb. Ex Willd.) Voigt	Euphorbiaceae	✓	×
Garcinia livingstonei T. Anderson	Guttiferae	✓	×
Gymnosporia senegalensis (Lam.) Loes	Celastraceae	✓	×
Hyphaene petersiana Mart.	Arecaceae	✓	✓
Kigelia africana (Lam.) Benth.	Bignoceae	✓	×
Philenoptera nelsii (Schinz) Schrire	Fabaceae	✓	×
Philenoptera violacea (Klotzsch) Schrire	Fabaceae	✓	✓
Phoenix reclinata Jacq.	Arecaceae	✓	×
Phyllanthus reticulatus Poir.	Euphorbiaceae	✓	×
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	✓	✓
Searsia tenuinervis Engl.	Anacardiaceae	✓	×
Senegalia mellifera (Vahl) Seigler & Ebinger	Fabaceae	✓	×
Senegalia nigrescens (Oliv.) P.J.H.	Fabaceae	✓	×
Syzygium cordatum Hochst.ex C.Krauss.	Myrtaceae	✓	✓
Terminalia prunioides M. A. Lawson	Combretaceae	✓	✓
Terminalia sericea Burch. ex DC.	Combretaceae	✓	×
Vachellia erioloba (E. Mey)	Fabaceae	✓	×
Vachellia nilotica (L.) P.J.H.Hurter & Mabb	Fabaceae	✓	×
Vachellia sieberiana (DC.) Kyal. & Boatwr	Fabaceae	✓	×
Vachellia tortilis (Forssk) Galasso & Banfi	Fabaceae	✓	×
Ximenia americana Welw. ex Oliv.	Olacaceae	✓	×
Ziziphus mucronata Willd.	Rhamnaceae	✓	×

Grewia flavescens Juss. was found in the soil seed bank but was not identified in the standing vegetation.
✓ = present, × = absent.

Table 2 List of plant species recovered (through incubation and soil sieving) from soil samples collected in the riparian woodland in the MGR riparian woodlands, their families, densities and the different groups of depth distribution of seeds

No	Species	Family	Number of germinated seeds					
			L	1	2	3	Total	Group
	Grasses							
1	*Setaria verticillata*	Poaceae	32	98	65	60	255	A
2	*Cynodon dactylon*	Poaceae	94	30	10	3	137	B
3	*Brachiaria deflexa*	Poaceae	10	10	17	24	61	E
4	*Brachiaria negropedata*	Poaceae	1	34	13	6	54	A
5	*Setaria sagitifolia*	Poaceae	9	10	12	6	37	E
6	*Urochloa mosambicensis*	Poaceae	12	7	3	13	35	B
7	*Acrachne racemosa*	Poaceae	2	23	9	0	34	A
8	*Oplismenus burmanii*	Poaceae	1	6	4	13	24	A
9	*Eragrostis cilianensis*	Poaceae	1	9	6	1	17	A
10	*Panicum maximum*	Poaceae	3	7	4	0	14	A
11	*Digitaria velutina*	Poaceae	5	4	4	0	13	E
12	*Chloris virgata*	Poaceae	3	5	1	0	9	A
13	*Eragrostis viscosa*	Poaceae	0	1	6	0	7	D
14	*Dactylectonium aegyptium*	Poaceae	2	2	1	2	7	A
15	*Oryza longistaminata*	Poaceae	6	0	0	0	6	B
16	*Eragrostis rotifer*	Poaceae	0	6	0	0	6	A
17	*Digitaria eriantha*	Poaceae	4	0	0	0	4	B
18	*Eragrostis porosa*	Poaceae	0	0	2	1	3	A
19	*Pennisetum macrourum*	Poaceae	1	1	0	0	2	E
20	*Echinochloa stagnina*	Poaceae	1	1	0	0	2	E
21	*Digitaria eyelesii*	Poaceae	0	1	0	1	2	A
22	*Enteropogon macrostachyus*	Poaceae	1	0	0	0	1	A
23	*Eragrostis superba*	Poaceae	0	1	0	0	1	A
24	*Setaria pumila*	Poaceae	1	0	0	0	1	B
25	*Digitaria milanjiana*	Poaceae	0	0	1	0	1	A
		Total	189	256	158	130	733	
	Herbs							
26	*Kohautia virgata*	Rubiaceae	14	176	58	67	315	A
27	*Ludwigia stolonifera*	Onagraceae	12	26	18	1	57	A
28	*Ammania baccifera*	Lythraceae	2	26	7	10	45	A
29	*Acanthospermum hispidum*	Asteraceae	24	3	2	1	30	B
30	*Alternanthera sessilis*	Amaranthaceae	4	0	5	15	24	B
31	*Alternanthera pungens*	Amaranthaceae	17	4	0	0	21	B
32	*Bidens pilosa*	Asteraceae	13	4	1	0	18	B
33	*Acalypha fimbriata*	Euphorbiaceae	7	1	8	2	18	D
34	*Justicia heterocarpa*	Acanthaceae	13	0	0	4	17	B
35	*Chenopodium album*	Amaranthaceae	0	0	1	15	16	A
36	*Pentodon pentandrus*	Rubiaceae	2	8	4	1	15	A
37	*Heliotropium ovalifolium*	Boraginaceae	11	1	1	1	14	B
38	*Nidorella resedifolia*	Asteraceae	7	5	1	1	14	B
39	*Erlangea misera*	Asteraceae	1	9	1	0	11	A
40	*Sesbania bispinosa*	Fabaceae	0	6	4	1	11	A

continued

Table 2 Continued

41	*Eclipta prostrata*	Asteraceae	2	0	3	3	8	D
42	*Ipomoea plebeia*	Convolvulaceae	1	0	2	4	7	D
43	*Hibiscus sidiformis*	Malvaceae	3	0	3	1	7	D
44	*Phyllanthus purvulus*	Euphorbiaceae	1	1	2	1	5	E
45	*Corchorus tridens*	Tiliaceae	3	1	0	1	5	B
46	*Kalanchoe lanceolata*	Crassulaceae	0	0	5	0	5	D
47	*Pechuel-loeschea leubnitziae*	Asteraceae	0	0	0	4	4	A
48	*Indigofera trita*	Fabaceae	3	1	0	0	4	B
49	*Amaranthus thumbergii*	Amaranthaceae	1	1	2	0	4	E
50	*Portulaca oleraceae*	Portulacaceae	1	2	1	0	4	E
51	*Amaranthus hybridus*	Amaranthaceae	0	0	0	4	4	D
52	*Commelina forskaoli*	Commelinaceae	0	0	0	4	4	D
53	*Spermacoce sinensis*	Rubiaceae	1	1	1	0	3	E
54	*Sphaeranthus indicus*	Asteraceae	0	1	0	2	3	A
55	*Triumfetta pentandra*	Tiliaceae	2	0	1	0	3	D
56	*Ipomoea coptica*	Convolvulaceae	0	1	1	1	3	C
57	*Vernonia glabra*	Asteraceae	1	1	1	0	3	E
58	*Bidens schimperi*	Asteraceae	1	0	1	1	3	B
59	*Abutilon angulatum*	Malvaceae	0	0	3	0	3	D
60	*Centella asiatica*	Apiaceae	3	0	0	0	3	C
61	*Sida cordifolia*	Malvaceae	1	0	0	2	3	D
62	*Hibiscus spp.*	Malvaceae	0	0	2	1	3	D
63	*Gomphrena celosioides*	Amaranthaceae	3	0	0	0	3	B
64	*Rhyncosia minima*	Fabaceae	0	1	0	1	2	A
65	*Commelina benghalensis*	Commelinaceae	0	1	0	1	2	A
66	*Cyathula orthocantha*	Amaranthaceae	1	0	1	0	2	D
67	*Acrotome inflata*	Lamiaceae	0	1	1	0	2	C
68	*Jamesbrittenia elegantissima*	Scrophulariaceae	1	0	1	0	2	D
69	*Dicliptera paniculata*	Acanthaceae	2	0	0	0	2	B
70	*Ipomoea nil*	Convolvulaceae	2	0	0	0	2	B
71	*Flaveria bidentis*	Asteraceae	0	0	2	0	2	D
72	*Xanthium strumarium**	Asteraceae	2	0	0	0	2	B
73	*Diclis petiolaris*	Scrophulariaceae	0	0	2	0	2	D
74	*Calostephane divaricata*	Asteraceae	0	0	2	0	2	D
75	*Commelina subulata*	Commelinaceae	1	0	0	0	1	B
76	*Zornia glochidiata*	Fabaceae	1	0	0	0	1	D
77	*Ocimum gratissimus*	Lamiaceae	0	1	0	0	1	A
78	*Sopubia manii*	Scrophulariaceae	1	0	0	0	1	B
79	*Justicia betonica*	Acanthaceae	1	0	0	0	1	B
80	*Polygala erioptera*	Polygalaceae	0	1	0	0	1	A
81	*Achyranthes aspera*	Amaranthaceae	1	0	0	0	1	B
82	*Jusminum fluminense*	Oleaceae	1	0	0	0	1	B
83	*Asparagus africanus*	Asparagaceae	1	0	0	0	1	B
84	*Hibiscus ovalifolius*	Malvaceae	0	0	1	0	1	D
85	*Sonchus asper*	Asteraceae	1	0	0	0	1	B
86	*Pseudognaphalium luteo-album*	Asteraceae	0	1	0	0	1	A

continued

Table 2 Continued

87	*Ipomoea sinensis*	Convolvulaceae	0	0	1	0	1	D
88	*Commelina petersii*	Commelinaceae	0	0	1	0	1	D
89	*Sida alba*	Malvaceae	0	1	0	0	1	A
90	*Glinus bainesii*	Molluginaceae	0	0	0	1	1	D
91	*Chamaecrista spp.*	Fabaceae	1	0	0	0	1	B
92	*Gomphocarpus fruticosus*	Apocynaceae	0	1	0	0	1	D
93	*Aerva leucura*	Amaranthaceae	1	0	0	0	1	B
94	*Persicaria limbata*	Polygonaceae	0	0	1	0	1	D
		Total	172	287	152	151	762	
	Sedges							
95	*Kyllinga erecta*	Cyperaceae	11	17	6	23	57	A
96	*Cyperus longus*	Cyperaceae	5	8	8	7	28	C
97	*Cyperus compressus*	Cyperaceae	0	15	1	1	17	A
98	*Fimbristylis dichotoma*	Cyperaceae	2	7	4	4	17	A
99	*Cyperus tenuiculmis*	Cyperaceae	0	8	9	0	17	A
100	*Bulbostylis hispidula*	Cyperaceae	2	4	2	8	16	A
101	*Cyperus squarossus*	Cyperaceae	0	11	0	0	11	A
102	*Pycreus polystachyos*	Cyperaceae	0	9	0	0	9	A
103	*Cyperus difformis*	Cyperaceae	1	2	4	0	7	A
104	*Cyperus denudatus*	Cyperaceae	1	4	2	0	7	A
105	*Schoenoplectus corymbosus*	Cyperaceae	1	2	0	3	6	E
106	*Schoenoplectus erectus*	Cyperaceae	0	0	0	3	3	A
107	*Pycreus macrostachyos*	Cyperaceae	1	0	0	2	3	B
108	*Cyperus esculentus*	Cyperaceae	0	0	2	0	2	D
109	*Cyperus iria*	Cyperaceae	0	0	1	0	1	A
110	*Cyperus fulgens*	Cyperaceae	1	0	0	0	1	B
111	*Courtoisina cyperoides*	Cyperaceae	0	1	0	0	1	A
		Total	25	88	39	51	203	
	Woody species							
112	*Combretum imberbe***	Combretaceae	37	11	0	0	48	B
113	*Syzygium cordatum***	Myrtaceae	29	7	1	0	37	B
114	*Colophospermum mopane***	Fabaceae	28	3	0	0	31	B
115	*Diospyros lycioides**	Ebenaceae	27	0	0	1	28	B
116	*Diospyros mespiliformis***	Ebenaceae	16	7	3	0	26	B
117	*Sclerocarya birrea**	Anacardiaceae	12	5	0	0	17	B
118	*Grewia flavescens***	Malvaceae	7	4	2	0	13	B
119	*Croton megalobotrys**	Euphorbiaceae	12	0	0	0	12	B
120	*Philenoptera violacea***	Fabaceae	9	1	0	0	10	B
121	*Terminalia prunioides**	Combretaceae	4	0	0	0	4	B
122	*Hyphaene petersiana**	Arecaceae	4	0	0	0	4	B
123	*Ficus sycomorus***	Moraceae	3	0	0	0	3	B
124	*Berchemia discolor***	Rhamnaceae	2	0	0	0	2	B
		Total	190	38	6	1	235	
		Grand Total	576	669	355	333	1933	

* = seeds that only germinated from the litter layer, ** = seeds recovered only from soil sieving.
L = litter layer, 1 = 0-3 cm, 2 = 3-6 cm and 3 = 6-9 cm soil layers.

total of 92 genera were recorded from all the 124 species with herbs, grasses, sedges, and woody species represented by 57 (62%), 15 (16%), 7 (8%), and 12 (13%) genera, respectively.

The overall total Shannon Diversity Index (H') of the soil seed bank in MGR was 3.67 with herbs, grasses, sedges, and woody species having H' values of 2.73, 2.22, 2.33 and 2.24, respectively. The overall species evenness was 0.77 with herbs, grasses, sedges, and woody species having evenness values of 0.64, 0.68, 0.82 and 0.88, respectively.

Density of seeds in the soil

The overall density of seeds recovered from the soil samples collected in the MGRWs was 1,933 seeds m^{-2} (Table 1). The seed density patterns

Table 3 List of families represented by species recovered from the soil samples collected in the MGR riparian woodlands

No	Family	Total	Proportion (%)
1	Poaceae	25	21
2	Cyperaceae	17	15
3	Asteraceae	13	11
4	Amaranthaceae	9	8
5	Malvaceae	7	6
6	Fabaceae	7	6
7	Acanthaceae	4	3
8	Commelinaceae	4	3
9	Convolvulaceae	4	3
10	Euphorbiaceae	3	3
11	Rubiaceae	3	3
12	Scrophulariaceae	3	3
13	Tiliaceae	2	2
14	Lamiaceae	2	2
15	Ebenaceae	2	2
16	Combretaceae	2	2
17	Portulacaceae	1	1
18	Molluginaceae	1	1
19	Boraginaceae	1	1
20	Crassulaceae	1	1
21	Asparagaceae	1	1
22	Apiaceae	1	1
23	Polygonaceae	1	1
24	Polygalaceae	1	1
25	Oleaceae	1	1
26	Lythraceae	1	1
27	Moraceae	1	1
28	Arecaceae	1	1
29	Onagraceae	1	1
30	Apocynaceae	1	1
31	Anacardiaceae	1	1
32	Myrtaceae	1	1
33	Rhamnaceae	1	1
	Total	124	

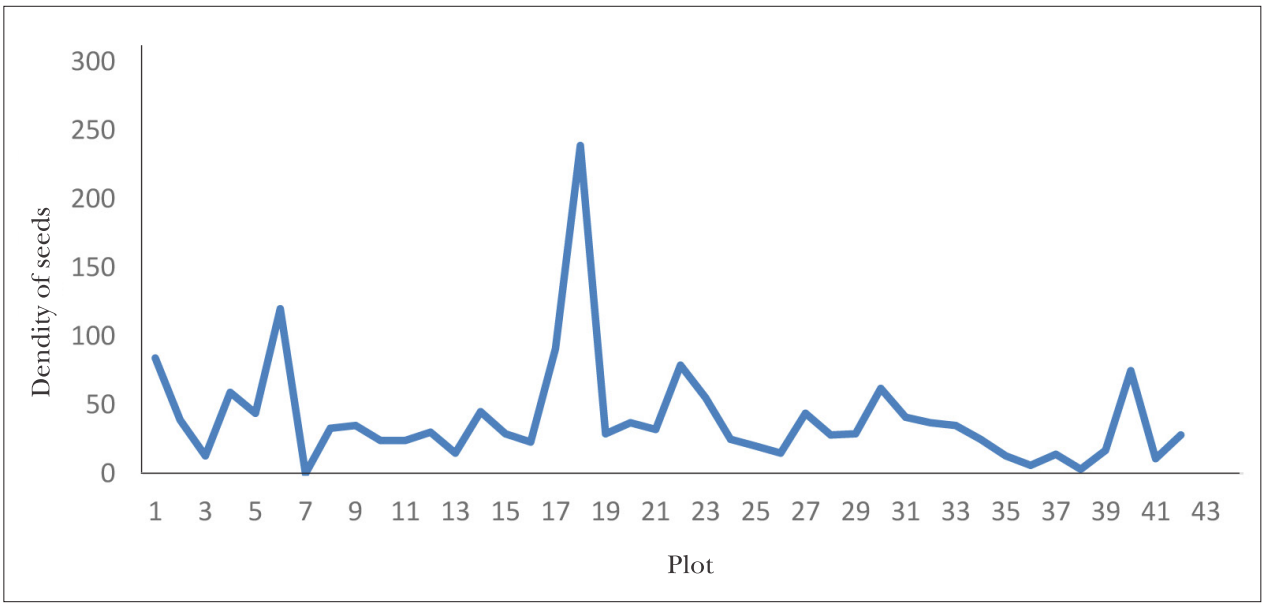


Figure 3 Horizontal distribution of the soil seed bank in the MGR riparian woodlands

from the litter layer to the bottom layer revealed various trends. The densities of seeds for grasses, herbs, sedges, and woody species were 733, 762, 203 and 235 seeds m^{-2}, respectively. Of these, 576, 669, 355 and 333 seed m^{-2} were recorded from the litter, first (0–3 cm), second (3–6 cm), and third (6–9 cm) layers, respectively (Table 2). The five species with the highest density of seeds were *Kohautia virgata* (315 seeds m^{-2}), *Setaria verticillata* (255 seeds m^{-2}), *Cynodon dactylon* (137 seeds m^{-2}), *Brachiaria deflexa* (61 seeds m^{-2}) and *Ludwigia stolonifera* (57 seeds m^{-2}), and the species with the lowest density were *Digitaria milanjiana, Setaria pumila, Cyperus fulgens, Courtoisina cyperoides,* and *Persicaria limbata*, each represented by only one seed m^{-2} (Table 2).

Similarity between soil seed banks and standing vegetation

The similarity in woody species composition between the soil seed flora and standing vegetation in the MGRWs was very low. Of the 41 woody species recorded in the standing vegetation, only 11 of them were represented in the soil seed flora [JCS = 0.2] (Table 1). Common species found in both the soil seed bank and standing vegetation in the MGRWs included *Berchemia discolor, Colophospermum mopane, Combretum imberbe, Diospyros lycioides, Hyphaene petersiana, Syzygium cordatum* and *Terminalia prunioides.*

Spatial distribution of seeds in the soil

Great variations were observed in the horizontal distribution of the soil seed bank across all the 42 plots sampled, which ranged between 1 and 239 seeds per m^{-2} (Figure 3).

The first layer had the highest seed density in all the sampled plots, which mostly consisted of the seed rain. The densities of seeds declined with soil depth. The overall vertical/depth distribution of seeds in the soil exhibited a lower density of seeds at the litter layer with increasing trends up to the first layer and decline trends thereafter (Figure 4 - All species). The total densities of seeds recovered from the litter, first, second and third soil layers were 576 (30%), 669 (35%), 355 (18%) and 333 (17%), respectively (Table 2). Of the total number of species recovered from the soil seed bank study, 22 (18%) species had 316 seeds m^{-2}, represented in all the layers (e.g. *Setaria verticillata* and *Kohautia virgata*) (Table 1). On the other hand, 25 species (20%, 60 seeds m^{-2}, e.g. *Terminalia prunioides* and *Oryza longistaminata*), ten species (8%, 33 seeds m^{-2}, e.g. *Eragrostis rotifer* and *Cyperus squarossus*), 12 species (10%, 22 seeds m^{-2}, e.g. *Kalanchoe lanceolata* and *Flaveria bidentis*) and five species (4%, 16 seeds m^{-2}, e.g. *Amaranthus hybridus* and *Commelina forskaoli*) were represented in the litter, first, second and third soil layers, respectively. The other 50 species (40%, 544 seeds m^{-2}, e.g. *Syzygium cordatum* and *Acrachne racemosa*) were

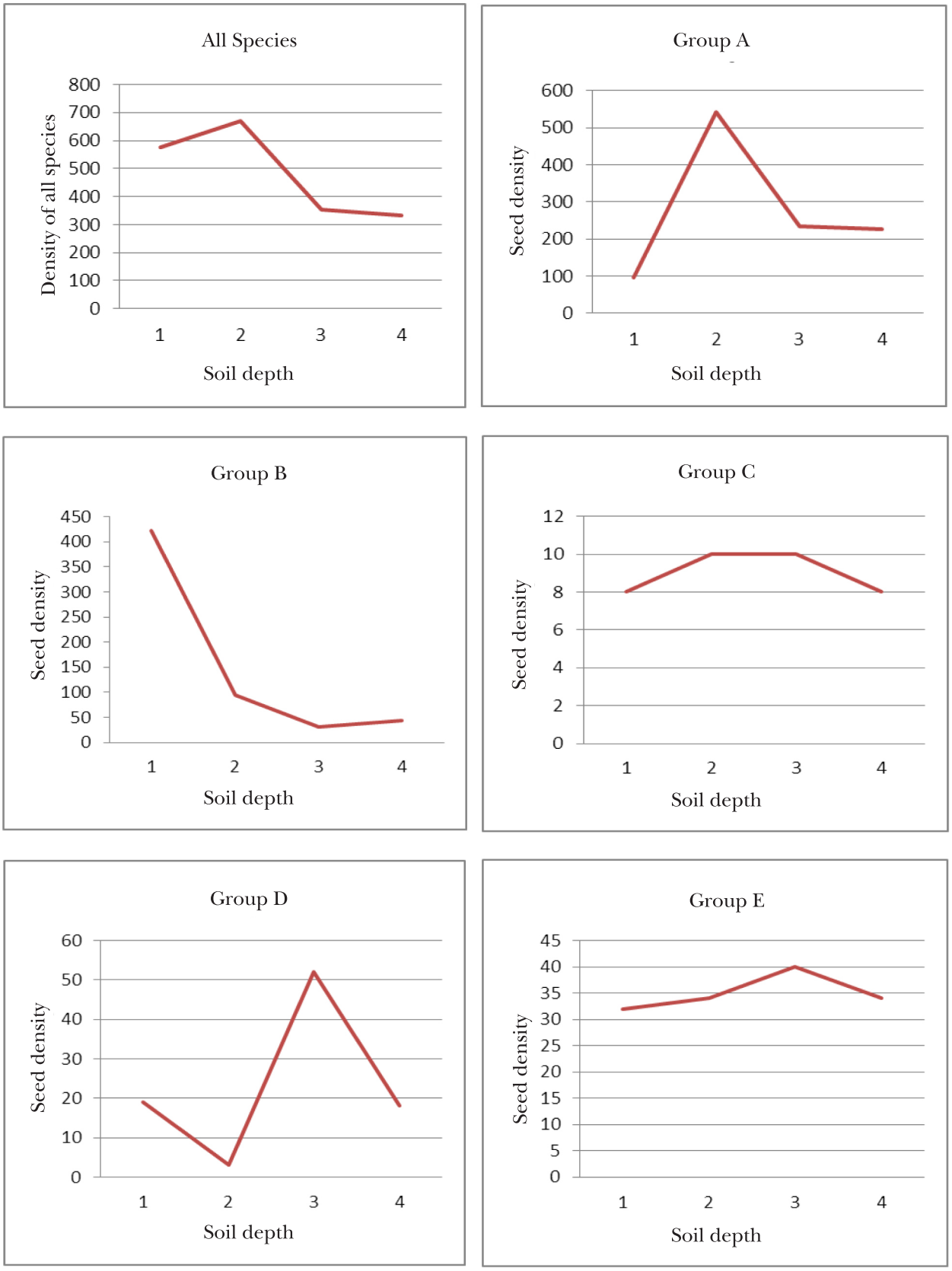


Figure 4 Vertical (depth) distribution of the soil seed bank in the MGR riparian woodlands

recovered from two to three different layers (Table 2, Figure 5A and Figure 5B).

Based on the trends of the depth distribution of their seeds, the species recorded during the study were categorised into five different groups. These were:

i) Group A: exhibited low seed densities in the litter layer, increasing densities in the first layer and, then, declining in the second and third layers (Table 2; Figure 4. - Group A); e.g. *Setaria verticillata*, and 41 species (33%) exhibited this trend;

ii) Group B: exhibited high densities of seeds in the litter layer and declining densities in the next layers (Table 2; Figure 4. - Group B); e.g. *Acanthospermum hispidum*, and 43 species (35%) exhibited this trend;

iii) Group C - exhibited low densities of seeds in the litter layer, increasing densities in the first layer and becoming constant in the second layer, then, declining in the third layer (Table 2; Fig. 4. - Group C); e.g. *Centella asiatica*, and four species (3%) exhibited this trend;

iv) Group D - exhibited high densities of seeds in the litter layer, declining in the first layer, increasing in the second layer and, then, declining in the third layer (Table 2; Figure 4. - Group D) e.g. *Eragrostis viscosa*, and 25 species (20%) exhibited this trend; and

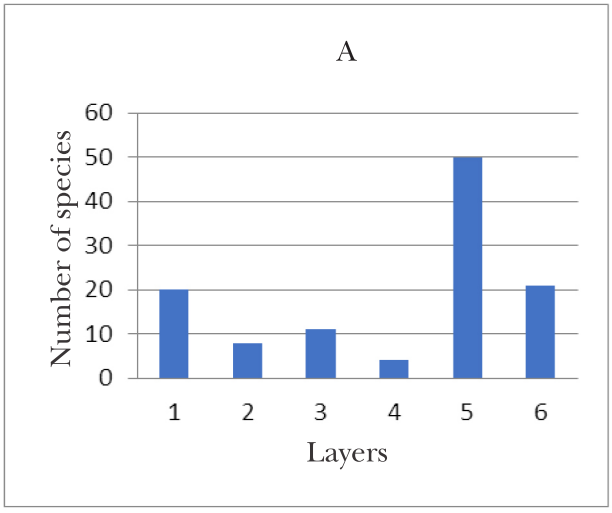
v) Group E - exhibited high densities of seeds in the litter layer, becoming constant in the first layer and, then, declining in the second and third layers (Table 2; Figure 4. - Group E) e.g. *Setaria sagitifolia*, and 11 species (9%) exhibited this trend.

Plant species recovered by sieving soil samples

The number of species recovered from sieving soil samples was 13, representing nine families and 235 seeds m^{-2} (Table 4). Of these, *Combretum imberbe* had 48 seeds m^{-2}, *Syzygium cordatum* had 37 seeds m^{-2}, *Grewia flavescens* had 13 seeds m^{-2} and *Berchemia discolor* had 2 seeds m^{-2}. Viable seeds of species were recovered from the soil samples, after their incubation was completed, and the densities ranged between two and 48 seeds m^{-2}. *Berchemia discolor* had the lowest seeds (two seeds) while *C. imberbe* had the highest number of seeds (48 seeds) recovered. All the recovered seeds were not viable, they were either rotten or eaten.

Different soil seed bank plant communities

The results from the soil seed bank identified four different plant communities, namely *Kohautia virgata-Ammania baccifera, Bidens pilosa-Urochloa mosambisensis, Setaria verticillata-Brachiaria deflexa,* and *Cynodon dactylon-Cyperus longus* (Table 5).



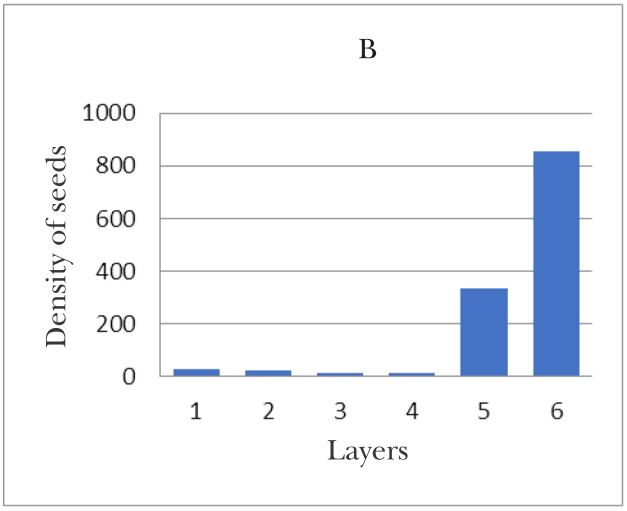


Figure 5A Depth distribution from different soil layers and number of species 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, 4 = 6–9 cm, 5 = found in 2–3 layers and 6 = All layers

Figure 5B Depth distribution from different soil layers and density of 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, 4 = 6–9 cm, 5 = found in 2–3 layers and 6 = All layers

Table 4 Density of seeds recovered from different layers after sieving the soil samples

No	Species	Family	Density of seeds				
			L	1	2	3	Total
1	*Combretum imberbe*	Combretaceae	37	11	0	0	48
2	*Syzygium cordatum*	Myrtaceae	29	7	1	0	37
3	*Colophospermum mopane*	Fabaceae	28	3	0	0	31
4	*Diospyros lycioides*	Ebenaceae	26	0	0	1	27
5	*Diospyros mespiliformis*	Ebenaceae	16	7	3	0	26
6	*Sclerocarya birrea*	Anacardiaceae	11	4	0	0	15
7	*Grewia flavescens*	Malvaceae	7	4	2	0	13
8	*Croton megalobotrys*	Asteraceae	11	0	0	0	11
9	*Philenoptera violacea*	Fabaceae	9	1	0	0	10
10	*Terminalia prunioides*	Combretaceae	3	0	0	0	3
11	*Berchemia discolor*	Rhamnaceae	0	2	0	0	2
12	*Hyphaene petersiana*	Arecaceae	2	0	0	0	2
13	*Xanthium strumarium*	Asteraceae	2	0	0	0	2
		Total	181	39	6	1	227

Table 5 Multi-response permutation procedures pairwise comparisons for different plant communities' composition from the soil seed bank in the Moremi Game Reserve

	Species	Indicator value	P-value
	Kohautia virgata-Ammania baccifera		
	Kohautia virgata	72.9	0.0002
	Ammania baccifera	20.5	0.0018
	Kyllinga erecta	18.4	0.0026
	Ludwigia stolonifera	13.4	0.0142
	Pentodon pentandrus	13.2	0.0032
	Achrachne racemosa	11	0.0206
	Cyperus compressus	10.5	0.0108
	Bidens pilosa-Urochloa mosambicensis		
	Bidens pilosa	18.5	0.0038
	Urochloa mosambicensis	13.5	0.0098
	Setaria sagitifolia	12.5	0.1106
	Acanthospermum hispidum	9.9	0.0476
	Phyllanthus purvulus	9.4	0.0352
	Justicia heterocarpa	6.7	0.1400
	Digitaria velutina	6.1	0.1482
	Setaria verticillata-Brachiaria deflexa		
	Setaria verticillata	74.1	0.0002
	Brachiaria deflexa	21.1	0.0064
	Acalypha fimbriata	8.4	0.1256
	Ipomoea sinensis	3.7	0.3679
	Cyperus esculentus	3.7	0.4591
	Portulaca oleraceae	3.2	0.4001
	Dactylectonium aegyptium	3	0.5961
	Cynodon dactylon-Cyperus longus		

continued

Table 5 Continued

Cynodon dactylon	54.5	0.0002
Cyperus longus	29.8	0.0002
Panicum maximum	23.2	0.0004
Brachiaria negropedata	8.4	0.0572
Alternanthera sessilis	8	0.0580
Eragrostis cilianensis	7.3	0.1328
Sopubia manii	6.2	0.1042
Spermacoce sinensis	2.5	0.5483

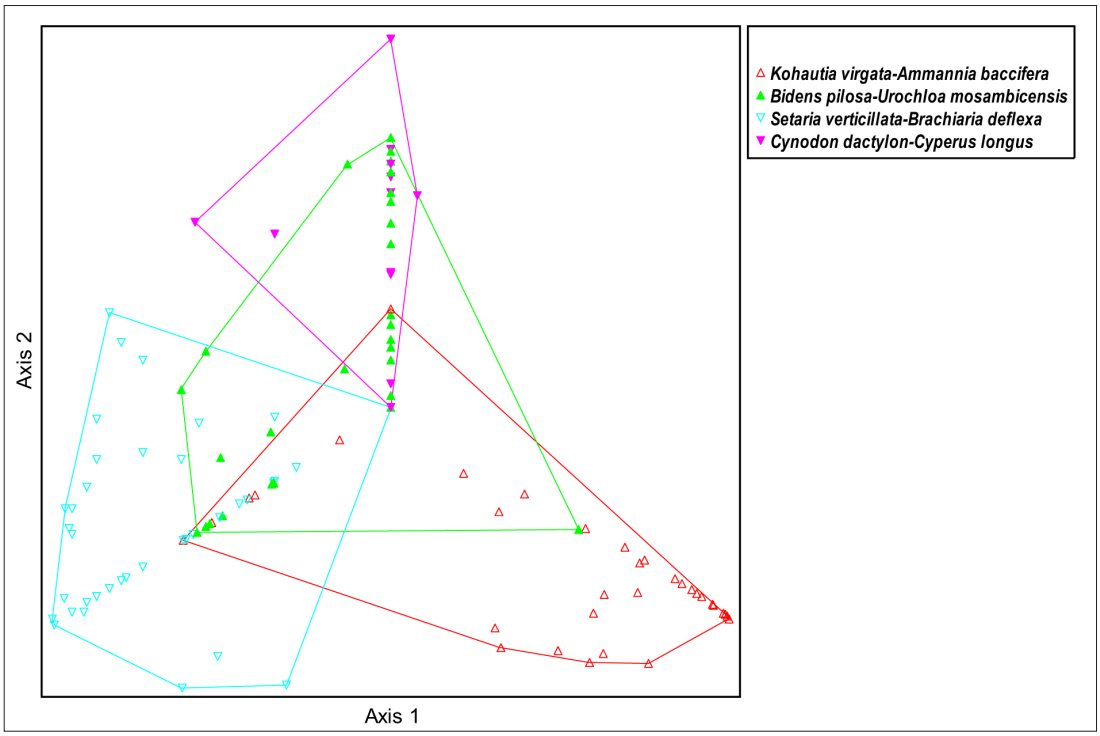


Figure 6 Bray-Curtis distinction of riparian plant communities in the MGR riparian woodlands in the Okavango Delta

Soil seed bank composition showed overlaps between different soil layers (Figure 6). Despite this, MRPP pairwise comparisons showed that the soil seed bank plant communities differed significantly (P < 0.05) from each other in terms of seed composition across the different soil layers (Table 6). The distribution of these communities across the different soil layers was as follows:

i. The first community was the seeds of *Kohautia virgata-Ammania baccifera* which were found in all the soil layers. Their distribution was as follows: 6 plots of litter layer, 11 plots of layer 1 (first layer), 11 plots of layer 2 (second layer), and 10 plots of layer 3 (third layer) out of 38 plots. This community was unlike that of *Setaria verticillata-Brachiaria deflexa* community (T = -45.57) than it was from *Bidens pilosa-Urochloa mosambisensis* (T = -32.56) and *Cynodon dactylon-Cyperus longus* (T = -20.66) communities (Table 6).

ii. Seeds of the *Bidens pilosa-Urochloa mosambisensis* community were mostly found in litter layer. Their distribution was as follows; 20 plots of litter layer, 12 plots of layer 1 (first layer), 11 plots of layer 2 (second layer), and 10 plots of layer 3 (third layer) out of 53 plots. The *Bidens pilosa-Urochloa mosambisensis* community was separated from *Setaria verticillata-Brachiaria deflexa* community (T = -46.35)

Table 6 Multi-response permutation procedures pairwise comparisons of seed bank clusters in the Moremi Game Reserve riparian woodlands

Plant communities	T	P-value
KV-AB[1] vs. BP-UM[2]	-32.6	0.00
KV-AB vs. SV-BD[3]	-45.6	0.00
KV-AB vs. CD-CL[4]	-20.7	0.00
BP-UM vs. SV-BD	-46.3	0.00
BP-UM vs. CD-CL	-16.0	0.00
SV-BD vs. CD-CL	-27.7	0.00

[1] = *Kohautia virgata-Ammania baccifera*
[2] = *Bidens pilosa-Urochloa mosambisensis*
[3] = *Setaria verticillata-Brachiaria deflexa*
[4] = *Cynodon dactylon-Cyperus longus*
T = test statistics

while it was comparatively closely related to *Cynodon dactylon-Cyperus longus* community in terms of species composition (Table 6).

iii. In the *Setaria verticillata-Brachiaria deflexa* community seeds were mostly found in the third layer. This community had a total of 54 plots. Layer 3 had 17 plots followed by layer 2 with 15 plots, then layer 1 with 14 plots and the litter layer with 8 plots.

iv. The seeds in *Cynodon dactylon-Cyperus longus* community were found across all the layers. Out of a total of 16 plots in this community, 6 were for the litter layer, layer 1 had 5 plots, layer 2 had 4 plots, and layer 3 had 1 plot.

In this study, some species like, *Cynodon dactylon, Ludwigia stolonifera, Brachiaria deflexa, Setaria sagittifolia, Nidorella resedifolia, Pentodon pentandrus, Eragrostis cilianensis, Acalypha fimbriata, Bulbostylis hispidula* and *Kyllinga erecta* were found across all the soil layers, while some species had seeds that were deeply distributed in the soil, e.g. *Setaria verticillata, Alternanthera sessilis*, *Justicia heterocarpa, Kohautia virgata,* and *Brachiaria negropedata*, suggesting that these seeds can be buried deep in the soil and become dormant (Table 7).

DISCUSSION

Soil seed banks play an important role in the establishment, maintenance, regeneration, and restoration of vegetation in many plant communities (Zhao et al. 2021, An et al. 2022). The results of this study showed that the soil seed bank presented viable seeds, which is an important indicator of the recovery potential of plant communities through natural regeneration. The results of the seed bank in the MGR showed a significant number of species dominated by herbaceous species over grasses, sedges, and woody species. This is in accordance with the results of other studies that have found that herbaceous growth forms were the most dominant in their respective study areas (Richter & Stromberg 2005, Kohagura et al. 2020, Mmusi et al. 2021, Ling et al. 2023, Zivec et al. 2023).

The results from our study suggest that the dominance of the herbaceous life form might be related to the short life cycle of these species and their high seed production. Seeds of herbaceous plants are more dominant than those of woody plants because they have high seed longevity (Middleton 2003, Zida et al. 2020). The ability of seeds of herbaceous plants to resist several unfavorable conditions could also be the other reason for the abundance of herbaceous seedlings in the litter/upper soil layer (Teketay 2005). Herbaceous plants are also essential for early colonisation during early successional stages. Pioneer species contribute to high seed density in soil seed banks, by producing a large number of seeds (Ekasari et al. 2021).

Herbs, grasses, and sedges produce smaller seeds than most woody species, and smaller-sized seeds stand a better chance of being buried in the deeper soil layers (Savadogo et al. 2017). The

other reason could be that herbs are abundant, can disperse in a variety of ecosystems, can adapt to harsh conditions, and can easily associate with other populations (Girmay et al. 2022).

The soil seed bank results revealed that viable seeds of woody species are generally few in the soil seed bank than the aboveground flora (Legesse et al. 2018, Mmusi et al. 2021, Birhanu et al. 2022, Sanou et al. 2022). The seeds of most woody species begin seed germination within a short period after dispersal (Teketay 1996). Some seeds of large trees are fleshy and have poor long-distance dispersal, thus, heavily predated and decompose rapidly before they emerge as seedlings (Tenkir 2006). Some woody species use seed rain and coppicing from stumps as alternative regeneration routes (Senbeta & Teketay 2002). Most of the species found in the seed bank produce large quantities of small and dormant seeds (Bekker et al. 1998). Degraded forests reveal higher species richness and diversity than the seed banks in intact forests (Garwood 1989, Dupuy & Chazdon 1998, De Medeiros-Sarmento et al. 2021).

Frequent wildfires have the potential to affect benefits derived from the forest by interrupting the flow of goods and services by affecting the biodiversity (Pivello et al. 2021). The soil seed banks present viable seeds and are composed mostly of pioneer seeds, which are important indicators of the recovery potential of plant communities through natural regeneration (Da Silva Fonseca et al. 2023).

Similarity between the seed bank and standing vegetation

There was low similarity between the composition of the seed bank and the standing vegetation in the study area, which means that seeds of many woody species are lacking in the seed bank. The composition of seeds recovered from the litter layer was richer than the other sampling depths as it is continuously enriched through the seed rain (Drake 1998, Lambers et al. 2005), awaiting burial, dormancy, germination, or eventual predation.

Vertical distribution of the soil seed bank

The soil seed density decreased with soil depth with the highest seed density observed in the upper soil layers. Tóth et al. (2022) observed a similar pattern in the Hortobágy National Park, East Hungary. The highest seed density in our study was recorded in the first layer (0–3 cm) and the lowest seed density was found in the lowest layer (6–9 cm). Different soil depths contain a variety of widely distributed seeds in the soil seed banks starting from the soil surface. Soil types, seed size, seed shape and seed dormancy are some of the factors that play a very critical role in the vertical distribution of soil seed banks (Tóth et al. 2022).

The continuous seed rain might be responsible for the accumulation of seeds at the soil surface, and some seeds are small and can remain dormant for some time and survive at great depths (Schwienbacher et al. 2010). Larger seeds are usually trapped in the litter and soil surface (Bekker et al. 1998). The number of seed species in the soil depends on the size of the seeds and is influenced by their lifespan (Long et al. 2015).

Seedlings of some herbs were mostly found in the first layer (0–3 cm) and the litter layer. However, seedlings of a few woody species were mostly found in the litter layer. This might be because seeds of these species possess a hard seed coat, which enables them to bury themselves for an extended period until conditions become favorable for them to germinate (Bekker et al. 1998, Ferrandis et al. 1999).

Soil seed bank and its implication in biodiversity conservation

The presence and absence of viable seeds in soil is an important feature that implies the restoration potential of the plants to conduct conservation measurements (Teketay 2005). The potential for regeneration of woodlands in semi-arid environments may depend on the number of viable seeds in the soil, namely soil seed banks (SSB) (Sileshi & Abraha 2014). In the study area, seedlings of herbs were found in abundance. Herbaceous vegetation produces many seeds that have great seed longevity and a better chance of recovering (Wassie et al. 2009). The soil seed banks had few seedlings that germinated from woody species from the study area. The poor regeneration of woody species might indicate that there are some existing perturbations in the study area. The

other reason for poor woody species in the SSB could be associated with dispersal mechanisms and predation of seeds by herbivores. This implies that the soil seed bank is not reliable for the restoration of the woody species. In order to overcome such challenges, active restoration approaches including plantations of indigenous plant species from the nursery-grown seedlings, as well as manipulation of disturbances are recommended.

CONCLUSIONS

The soil seed banks play a very important role in understanding vegetation restoration and dynamics. A total of 124 plant species belonging to 33 families were identified, with a total density of 1,933 seeds m^{-2}. Poaceae was the dominant family followed by Cyperaceae and Asteraceae. We conclude that soil seed banks in the Moremi Game Reserve Riparian Woodlands possess large populations of buried seeds of herbs, grasses and sedges. The results from our study also revealed a lower resemblance between the soil seed bank flora and standing vegetation, like other studies carried out elsewhere. Herbaceous species dominated seed density and species composition of the soil seed banks. Most of the riparian woody species had no viable seeds in the soil. The potential of the soil seed bank to contribute to the restoration of riparian woodlands is limited by the low similarity between the soil seed bank flora and standing vegetation. This, therefore, calls for the establishment of nurseries from which seedlings of threatened species would be transplanted to the natural habitat for their restoration. Future research should study the factors that influence the life-history strategies of riparian woodland species and those that affect the soil seed bank longevity. Raising and planting of seedlings of certain species in nurseries and riparian woodland, respectively, are, therefore, critical efforts to restore and conserve them.

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