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Species richness, diversity, density and spatial distribution of soil seed banks in the riparian woodland along the Thamalakane River of the Okavango Delta, northern Botswana

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ABSTRACT

Soil seed banks serve as reservoirs of seeds for subsequent regeneration of plants. Soil seed banks were investigated along the Thamalakane Riparian Woodlands (hereafter referred to as TRWs) of the Okavango Delta, northern Botswana, from January-July 2015 and January-July 2016. The study aimed at examining species richness and diversity, determining densities, assessing the spatial distribution of seeds in the soil and comparing the similarity in species composition between the standing vegetation and soil seed bank flora. The vegetation was sampled in 71 plots (20 × 50 m) and soil samples were collected from 568 subplots. Agglomerative hierarchical cluster analysis was used to determine soil seed bank communities. Indicator species analysis was used to calculate indicator values for species in each community of germinated seeds and across different soil layers. Multi-response permutation procedures (MRPP) were used to compare similarity in soil seed bank composition. Bray-Curtis ordination was used to infer spatial relationships of soil layers in terms of soil seed bank composition. A total of 109 plant species were identified in the litter and top 9 cm soil layers with a mean density of 2101 seeds m^{-2}. Herbs, grasses, sedges and woody plants were represented by 68, 19, 9 and 13 species, respectively, in 30 families and 87 genera. The overall total diversity and evenness of the soil seed bank in the TRWs was 3.25 and 0.69, respectively. Four plant communities were identified from the soil seed bank, namely *Setaria verticilata-Amaranthus hybridus, Acanthospermum hispidum-Setaria sagittifolia, Digitaria eriantha-Eclipta prostrata* and *Cyperus longus-Fimbristylis dichotoma*. Bray-Curtis ordination showed that there was 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 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. Relatively high densities also occurred in the litter layer. There were large differences in depth distribution between species, suggesting differences in seed longevity. The similarity in species composition between the soil seed flora and standing vegetation was low (27%). The results demonstrated that many species in TRWs store quantities of seeds in the soil. The fact that most of the woody species do not accumulate more seeds in the soil suggests that their regeneration from seeds would be unlikely if mature individuals disappeared (die or are harvested). Because of its diverse seed banks, the herbaceous flora would have a better chance of re-establishing in the event of anthropogenic or natural disturbances. Therefore, the future of the TRW woody flora seems to depend on the successful conservation of the standing vegetation.

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1. Introduction

Woodland regeneration extends beyond mere reproduction to include germination of propagules and successive growth and survival of young trees until they are mature (Woodland and Shaw, 1981). Plants produce seeds, which disperse from the mother plant by different mechanisms, including wind, water runoff and animal vectors (Bakker et al., 1996; Havel and Shurin, 2004), and become incorporated into the soil and form part of a store or bank of seeds (Silvertown, 1982; Leck et al., 1989 . Germination of these seeds may take place immediately or may be delayed for an indefinite period (Fenner, 2012). Most of the seeds in the seed bank come from nearby parent plants, while some seeds may be contributed by plant communities a long distance away from the parent plants (Solomon, 2011). The distribution of seeds, in terms of diversity, time and space, is a controller of population development and necessary for plant diversity maintenance in fragmented landscapes (Plue and Cousins, 2018).

Ecosystem services provided by healthy forests include preservation of biodiversity, clean water, climate regulation and productive soils (Sheram, 1993), benefitting people through their provisioning, regulating, cultural and supporting services (Masiero et al., 2019). Forests are home to more than 80% of all species living on land. They are also important sources of food, medicine and drinking water as well as providing recreational, aesthetic, and spiritual benefits for many people (Jenkins and Schaap, 2018). The degradation of forests worldwide and habitat loss threaten biodiversity and natural resources through increasing demand for food and energy, expanding urban areas and population growth, and climate change (Pickett and White, 1985; Kozlowski, 2002; Morris, 2010).

Population dynamics of woodlands are driven by reproduction, recruitment and survival. Herbivory and fires are known to be important drivers of vegetation dynamics in African savannas. Shifts in the amount of woody cover as a result of climate change, fire, herbivory and human agency have the potential to exert strong impacts on ecosystem function in savannas (Ringrose et al., 1998).

Healthy forests are characterized by three main life stages in plants, namely: (1) seedlings, which are newly emerged plants, (2) saplings, established plants, between seedlings and trees and (3) trees, which are the mature version and normally undisturbed by micro-environmental conditions (Rawat et al., 2014). Trees and shrubs influence the composition of vegetation beneath their canopies, and some habitats provide suitable sites for seeds to accumulate and persist, subsequently enabling germination and seedling establishment (Kinloch and Friedel, 2005). The life cycle of seeds starts with seed maturation, followed by dispersal, storage in the soil, dormancy, germination and seedling establishment (Fenner, 1985; Fenner and Thompson, 2005). However, many factors influence seed dispersal and their accumulation in the soil. The physical properties of seeds determine how far seeds are capable of being dispersed from their mother plant and how deep in the soil they are capable of surviving (Bekker et al., 1998).

Soil seed banks are the reservoir or collection of viable seeds in the soil and associated litter at any given time potentially capable of replacing adult plants (Simpson et al., 1989). They have both a spatial and temporal dimension and can be either transient (germinating within a year after dispersal) or persistent (seeds that remain in the soil for more than a year) (Thompson and Grime, 1979; Leck et al., 1989; Simpson et al., 1989). Soil seed banks play a critical role in the regeneration of plant species by replacing adult ones (Taiwo et al., 2018). They also play an important role in vegetation maintenance, succession, ecosystem restoration and conservation of genetic variability (Teketay, 2005a; Lemenih and Teketay, 2006). Major sources of natural regeneration are seed rain, seedling banks, coppices and soil seed banks (Garwood, 1989; Argaw et al., 1999; Teketay, 2005a; Kebede et al., 2012). Seed banks are critical repositories of woodland diversity that can contribute to local population persistence and biodiversity maintenance through temporal storage effects (Chesson and Huntly, 1997).

Although soil seed banks are understood to be crucial to the vegetation dynamics and restoration of many ecosystems, little is known about their role in riparian zones (Williams et al., 2008; De León Ibarra et al., 2019). Riparian plant communities are exposed to frequent natural (flooding, fire and browsing) and human (tree cutting and cultivation) disturbances in the riparian zones. As the human population grows, demand for natural resources and ecosystem services also increases (Tedder, 2012). In countries like Kenya, rapid population growth, deforestation, overgrazing, agricultural activities, fuelwood collection and construction material has resulted in the decline of riparian ecosystems (Ndalilo et al., 2020). Conservationists may benefit from the knowledge of the relation between soil seed bank and aboveground vegetation, as this might help to make informed decisions on management of exotic species, diversity restoration and better understand the resilience of an ecosystem (Hopfensperger, 2007). The relationship between soil seed banks and their standing vegetation is the key point in evaluating the revegetation potential (Lu et al., 2010).

The forests and woodlands of Botswana cover about sixty percent (60%) of the land area and the diversity of both the herbaceous and woody vegetation provides goods and services that satisfy many of the needs of the nation (Anthony et al., 2015). Major population centers and settlements in Botswana are the main causes of woodland depletion, as increase in human populationcontributes to high demand for wood products and has increased the demand for fuel wood, building and construction material, and driven an expansion of arable agriculture. To meet the increasing demands of the rapidly increasing human population, natural forest resources are being utilized far beyond their regenerative capacity. This has resulted in declining size of natural forests in most parts of the world (FAO and UNEP, 2020; Ritchie and Roser, 2021).

Despite the importance of soil seed banks in the regeneration of plant species, information on the soil seed banks of riparian woodland vegetation in the Okavango Delta, including the Thamalakane River, is lacking. Riparian vegetation along the Thamalakane River is exposed to communal land use, which might also be a threat. The vegetation is cleared to make way for human settlements, fields and kraals (Neelo et al., 2013; FAO and UNEP, 2020). This study is, therefore, relevant in a system such as the Okavango Delta which is characterized by changing weather seasons and changes in river flows, to explain patterns of diversity and dynamics of riparian woodlands in these habitats. The results will be helpful for vegetation restoration and riparian woodland conservation in the Okavango Delta, and in similar regions all over the world.

Riparian vegetation in the Okavango Delta has extensive economic, social and environmental benefits. However, despite its relevance, it is threatened by changes in variation in hydrology, anthropogenic activities and other environmental conditions. Thamalakane riparian woodland communities may change rapidly in response to both long- and short-term disturbances caused by human exploitation and domestic animals. For riparian woodland species to be managed sustainably, information on the current regeneration status and soil seed banks of the trees under different land uses is needed.

The overall objective of this study was to assess species richness, diversity, density and spatial distribution of the soil seed bank in the Thamalakane riparian woodland communities under different land uses. Therefore, the specific objectives of this study were to: (a) examine species richness and diversity of the seeds in the soil, (b) determine densities of seeds in the soil by species, (c) assess the spatial (vertical and horizontal) distribution of seeds in the soil and (d) compare the similarity in species composition between the standing vegetation and soils seed bank flora of the riparian vegetation along the Thamalakane River in northern Botswana.

2. Materials and methods

2.1. Study area

The study was conducted along the Thamalakane River in the distal southeast regions of the Okavango Delta in Botswana on a 50 km stretch from Dikgatlhong Junction to Matsaudi Village (Fig. 1). The Okavango Delta is flooded from the Angolan highlands and has a mean annual precipitation and potential evapotranspiration of 450 mm and 2000 mm, respectively (Scudder et al., 1993). It receives almost all its water as a flood pulse from its headwaters in the Angolan Highlands. 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 flood traverses the Delta, about 250 km, reaching the distal seasonal Thamalakane River, which is the main outlet from the Delta, in the months of July/August (Wilson and Dinçer, 1976; Porter and Muzila, 1989; Snowy Mountains Engineering Corporation, 1990).

The Thamalakane River runs along the Thamalakane Fault and drains into Lake Ngami and the Boteti River. The Boteti receives the floodwater through the Boro River, which is one of the outlets of the Okavango Delta. When the flood reaches the Boro and Thamalakane Junction, the floodwater initially flows towards the northeastern segment (Thangarajan et al., 1999). The Thamalakane River passes through Maun Village in northern Botswana. During low flooding periods, the Thamalakane River becomes dry from January to June (Smith, 1976). In terms of temperature in the area, the Thamalakane River is characterized by maximum temperatures ranging between 30 and 35 °C in the summer (November to January) and minimum temperatures ranging between 3 and 12 °C in winter (May to July) (Bhalotra, 1987; Snowy Mountains Engineering Corporation, 1987, 1990). The soils along the Thamalakane River are generally sandy.

The Thamalakane River supports a variety of different aquatic plants, e.g, the floating blue water lily (*Nymphaea nouchali* Burm. f. and floating heart [*Nymphoides indica* (L.) Kuntze], and riparian woody species e.g, real fan palm [*Hyphaene petersiana* Klotzsch ex Mart], sycamore fig [*Ficus sycomorus* L.], rain tree [*Philenoptera violacea* (Klotzsch) Schrire] and umbrella thorn [*Vachellia tortilis* (Forssk.) Hayne] (Teketay et al., 2016).

2.2. Methods

A total of 71 quadrats, each measuring 20 × 50 m, were used for woodland vegetation sampling and soil sample collection for the study. The quadrats were selected along the Thamalakane River from Dikgatlhong junction to Matsaudi and covered about 50 km (Tsheboeng et al., 2020). They were selected at 1 km intervals on either bank of the Thamalakane River with the distance measured using a Global

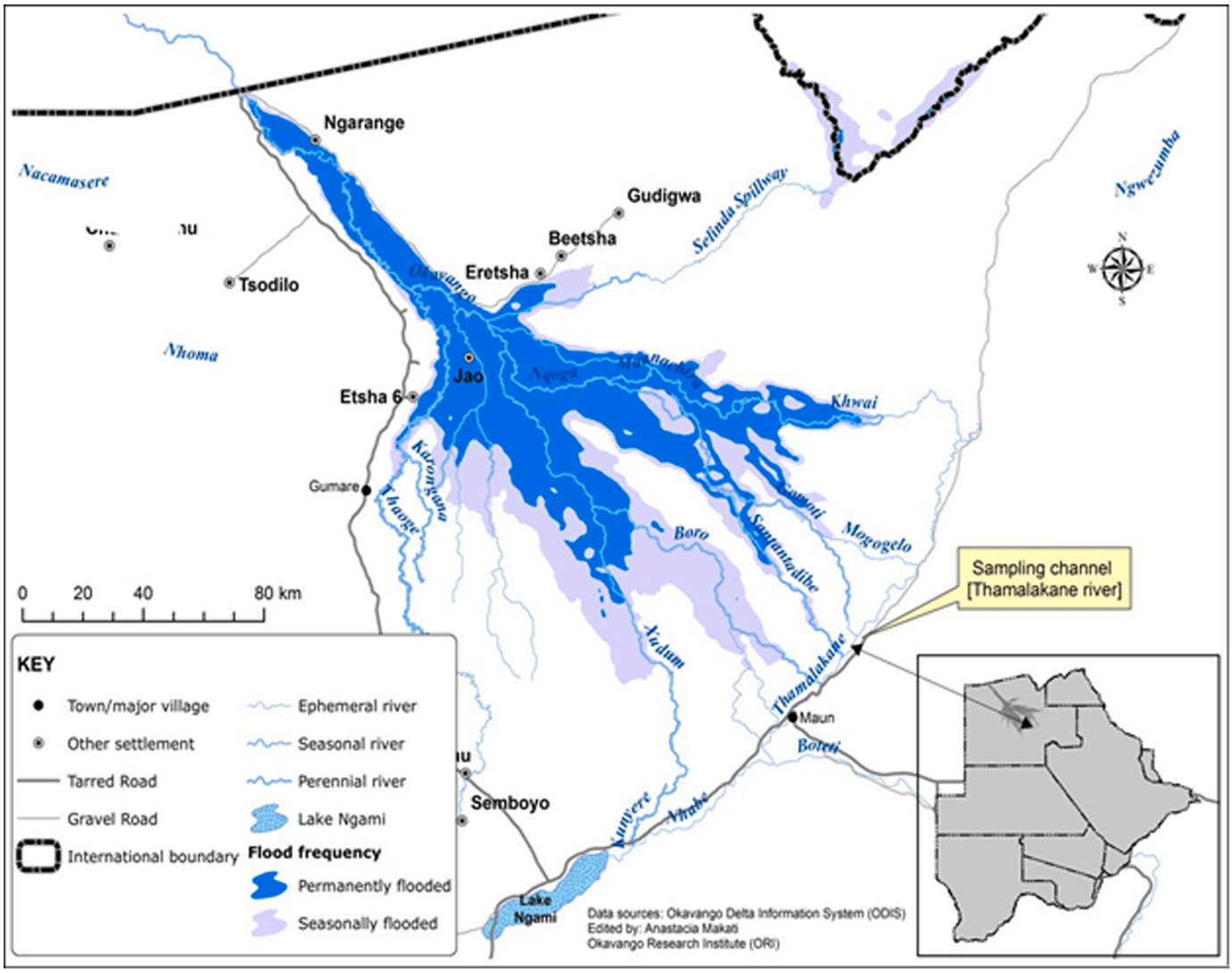

Fig. 1. Map showing the study site along the Thamalakane River.

Positioning System (GPS) Garmin GPSMAP 64S. The sampled quadrats were oriented perpendicular to the riverbank such that their short axes were parallel to the water edge, and the longer axes were perpendicular to the water edge as per Tsheboeng et al. (2016).

To compare the woody species composition of the soil seed bank and standing vegetation, the standing woody vegetation was surveyed within the same quadrats described for the soil seed bank study above. The identity of all woody species encountered in each of the quadrats was determined on site as far as 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), University of Botswana (UB).

Soil samples for the soil seed bank study were collected from eight plots of 15 × 15 cm within the 20 × 50 m quadrats. The eight plots were situated inside each quadrat to capture the variation in the distribution of the seeds (Fig. 2). From each plot, four separate soil layers, consisting of the litter layer, first soil layer (0–3 cm), second soil layer (3–6 cm) and third soil layer (6–9 cm) were collected using hand trowels following the methods used by Teketay and Granström (1995). In each of the quadrats, the samples from all the eight litter, first, second and third layers were separately mixed thoroughly and, then, divided into eight from which one working sample was randomly selected from each layer. The random selection was carried out in Microsoft Excel (using the RANDBETWEEN (1, 8) function).

2.2. Soil incubation

Two commonly used methods were used to characterize soil seed banks, namely seedling emergence and seed extraction through sieving (Baskin and Baskin, 1998; Lemenih and Teketay, 2006). First, the soil samples were put into plastic bags (each layer separately), labelled and transported to ORI where they were incubated. The soil samples were incubated in open-topped plastic bags with perforations at the bottom to allow free drainage of excess water.

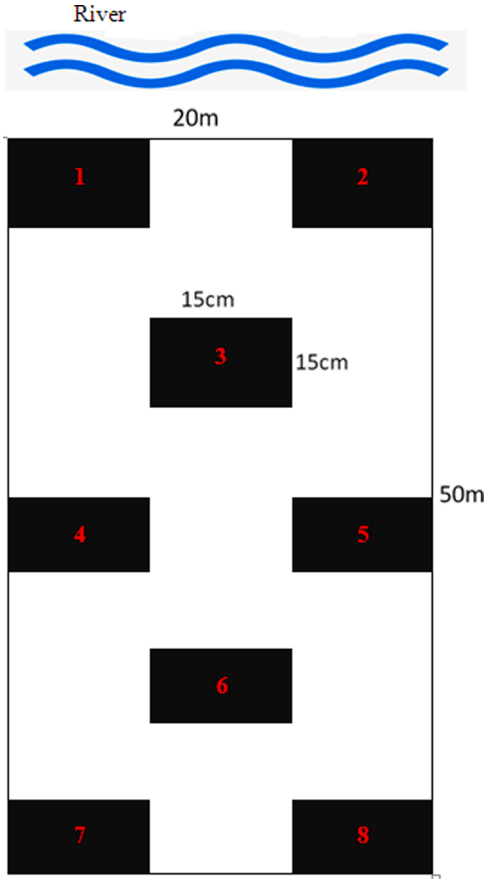

Fig 2. Schematic representation of sampled quadrats (20 × 50 m) and plots (15 × 15 cm) in the study.

The incubation of soil samples was carried out for 12 months under a shade-net enclosure constructed at ORI to minimize the impact of direct sunlight on the emerging seedlings, with daily watering of the soil samples. Seedling germination was monitored, 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. Daily temperatures in the enclosure ranged from 12 to 45 °C. 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 with decreasing mesh sizes ranging from 0.5 to 5 mm. The viability of seeds recovered by sieving was determined by cutting tests after they were identified. Seeds with a firm white embryo were considered viable while seeds that were covered with fungi, collapsed when pinched and had grey, yellow or brownish embryos were considered dead (Teketay and Granström, 1995; Baskin and Baskin, 1998).

Plant nomenclature used in this article follows that of Setshogo and Venter (2003); Setshogo (2005) and Kyalangalilwa et al. (2013). The seeds recovered by sieving were collected and identified using local reference material.

2.3. Data analyses

Species richness (S) was determined as the total number of different plants species recorded from the soil seed bank and standing vegetation and did not consider the proportion and distribution of each species. The Shannon Diversity Index (H') (Krebs, 1989; Magurran, 2004) was calculated for all plant species that germinated from the seed banks and recovered from the soil samples, by different growth forms. The index considers species richness and proportions of each species in all sampled quadrats. The following formula was used to determine the Shannon Diversity Index:

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

where, H′ = Shannon '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 analyzed 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.

$$E = \mathrm{H}'/\ln \mathrm{S}$$

where, E = evenness and S = species richness.

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

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

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, c = number of woody species recorded only from the soil seed bank in TRWs.

2.4. Spatial distribution of seeds in the soil

Agglomerative Hierarchical Cluster Analysis (flexible β linkage, $\beta = -0.25$, Sorensen distance, data relativised by maximum) (McCune and Grace, 2000) was conducted to determine different soil seed bank groups across different soil layers. For each community of germinated seeds, indicator value for each species was calculated through indicator species analysis (Dufrêne and Legendre, 1997). The statistical significance of indicator value for each species was determined using Monte Carlo Test (Dufrêne and Legendre 1997). 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 relativized by maximum), using the variance-regression method (Beals, 1984), was used to infer soil layers spatial relationships in terms of soil seed bank composition. This was based on the communities that were determined through Agglomerative Hierarchical Cluster Analysis. All the analyses were undertaken in PC-ORD version 6.

2.5. Soil seed bank composition from different layers

The soil seed bank communities across different soil layers were compared through Multi-Response Permutation Procedures (MRPP) to determine whether or not they were significantly separated from each other (McCune and Grace, 2000).

3. Results

3.1. Diversity of standing vegetation

A total of 48 species representing 17 families were recorded (Table 1). The Fabaceae family had the highest number of species (15 species) followed by Combretaceae with 5 species, Tiliaceae with four species, Ebenaceae, Capparaceae and Euphorbiceae had three species each while Bignoceae, Anacardiaceae and Rhamnaceae had two species each. The remaining families had one species each. A total of 32 genera were encountered. *Vachellia* was the richest genus with six species followed by *Combretum, Senegalia* and *Grewia* with four species each. The other genera had between one and two species.

3.2. Similarity in woody species composition

The similarity in woody species composition between the soil seed flora and standing vegetation along the TRWs was very low. Of the 48 woody species recorded in the standing vegetation (Tsheboeng et al., unpublished), only 12 of them were represented in the soil seed flora [JCS = 0.27 (27%)] (Table 1). The Shannon diversity index and Evenness of the woody species along the Thamalakane River were 1.23 ± 0.10 and 0.35 ± 0.05, respectively.

3.3. Diversity of seeds in the soil

The total species richness of the soil seed banks in the TRW was 109, representing 30 families, with herbs, grasses, sedges and woody species represented by 68 (62%), 19 (17%), 9 (8%) and 13 (12%) species, respectively (Table 2). The family Poaceae exhibited the highest richness in all the germinated species (19 species = 17%), followed by Fabaceae (15 species = 14%) and Asteraceae (10 species = 9%) (Table 3). A total of 87 genera were recorded from all the 109 species with herbs, grasses, sedges and woody species represented by 58 (67%), 12 (14%), 5 (6%) and 12 (14%) genera.

The overall total diversity of the soil seed bank in the TRWs was 3.25 with herbs, grasses, sedges and woody species having diversity values of 2.4, 2.2, 1.6 and 1.7, respectively. The overall species evenness was 0.69 with herbs, grasses, sedges and woody species having evenness values of 0.57, 0.75, 0.73 and 0.66, respectively.

Table 1
List of woody plant species identified along the Thamalakane River in Botswana, and the species that germinated from the soil seed banks.

Species	Family	Above ground vegetation	Soil seed bank
Philenoptera violacea (Klotzch) Schrire	Fabaceae	✓	✓
Garcinia livingstonei T. Anderson	Guttiferae	✓	×
Diospyros mespiliformis Hochst. Ex A. DC.	Ebenaceae	✓	×
Terminalia prunioides M. A. Lawson	Combretaceae	✓	✓
Vachellia luederitzii (Engl.) Kyal. & Boatwr.	Fabaceae	✓ ✓	×
Maerua angolensis DC	Capparaceae	✓	×
Vachellia tortilis (Forssk) Galasso & Banfi	Fabaceae	✓	✓
Gardenia volkensii K. Schum	Rubiaceae	✓	×
Senegalia erubescens (Welw. ex Oliv.) Kyal. & Boatwr.	Fabaceae	✓	×
Vachellia hebeclada (DC.) Kyal. & Boatwr.	Fabaceae	✓	×
Markhamia zanzibarica (Bojer ex DC) K. Schum.	Bignoceae	✓	×
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	✓	✓
Dichrostachys cinerea (L) Wight & Arn.	Fabaceae	✓	×
Flueggea virosa (Roxb. Ex Willd.) Voigt	Euphorbiaceae	✓	✓
Grewia bicolor A.Juss	Tiliaceae	✓	×
Searsia tenuinervis Engl.	Anacardiaceae	✓	×
Combretum mossambicense (Klotzsch) Engl.	Combretaceae	✓	×
Berchemia discolor (Klotzsch) Hemsl.	Rhamnaceae	✓	✓
Grewia retinervis Burret	Tiliaceae	✓	×
Combretum hereroense Schinz	Combretaceae	✓	×
Albizia harveyi E. Fourn.	Fabaceae	✓	✓
Capparis tomentosa Lam.	Capparaceae	✓	×
Diospyros lycioides Desf	Ebenaceae	✓	×
Ximenia americana Welw. ex Oliv.	Olacaceae	✓	×
Phyllanthus reticulatus Poir.	Euphorbiaceae	✓	×
Euclea divinorum Hiern	Ebenaceae	✓	×
Boscia albitrinca (Burch.) Gilg & Gilg-Ben	Capparaceae	✓	×
Kigelia africana (Lam.) Benth.	Bignoceae	✓	×
Albizia anthelmintica Brongn.	Fabaceae	✓	×
Croton megalobotrys Müll. Arg	Euphorbiaceae	✓	×
Colophospermum mopane (J.Kirk ex Benth.) J.Kirk ex J.Léonard	Fabaceae	✓	✓
Hyphaene petersiana Mart.	Arecaceae	✓	×
Senegalia galpinii (Burtt Davy) Seigler & Ebinger	Fabaceae	✓	×
Combretum imberbe Wawra	Combretaceae	✓	✓
Gymnosporia senegalensis (Lam.) Loes	Celastraceae	✓	×
Senegalia nigrescens (Oliv.) P.J.H. Hurter.	Fabaceae	✓	×
Ziziphus mucronata Willd.	Rhamnaceae	✓	×
Senegalia mellifera (Vahl) Seigler & Ebinger	Fabaceae	✓	×
Ficus sycomorus L	Moraceae	✓	✓
Cordia sinensis Lam	Boraginaceae	✓	×
Commiphora glandulosa Schinz	Burseraceae	✓	×
Combretum albopunctatum Suess	Combretaceae	✓	×
Grewia villosa Willd.	Tiliaceae	✓	×
Vachellia sieberiana (DC.) Kyal. & Boatwr.	Fabaceae	✓	×
Vachellia nilotica (L.) P.J.H.Hurter & Mabb	Fabaceae	✓	×
Vachellia erioloba (E. Mey)	Fabaceae	✓	✓
Ehretia rigida (Thunb.) Druce	Boraginaceae	✓	×
Grewia flavescens Juss	Tiliaceae	✓	✓

Leucaena leucocephala (Lam.) de Wit germinated from 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 along the Thamalakane River, their families as well as densities and depth distribution of seeds (*L* = litter, 1 = 0–3 cm, 2 = 3–6 cm and 3 = 6–9 cm soil layers).

No	Species	Family	Density of germinated seeds					
			L	1	2	3	Total	Group
Herbs								
1	*Kohautia virgata*	Rubiaceae	46	305	192	66	609	A
2	*Acanthospermum hispidum*	Asteraceae	78	20	9	0	107	B
3	*Xanthium strumarium**	Asteraceae	24	0	0	0	24	B
4	*Ammannia baccifera*	Lythraceae	18	6	3	0	27	B
5	*Gomphrena celosioides*	Amaranthaceae	13	3	0	0	16	B
6	*Spermacoce sinensis*	Rubiaceae	11	6	1	0	18	B
7	*Amaranthus hybridus*	Amaranthaceae	11	29	6	2	48	A
8	*Nesaea crassicaulis*	Lythraceae	10	21	13	3	47	A
9	*Eclipta prostrata*	Asteraceae	10	13	13	8	44	C
10	*Flaveria bidentis**	Asteraceae	10	6	23	10	49	D
11	*Alternanthera pungens**	Amaranthaceae	8	2	0	0	10	B
12	*Justicia heterocarpa*	Acanthaceae	7	13	0	0	20	A
13	*Achyranthes aspera var sicula*	Amaranthaceae	7	9	0	0	16	A
14	*Phyllanthus parvulus*	Euphorbiaceae	6	20	6	3	35	A
15	*Bidens pilosa**	Asteraceae	4	2	1	0	7	B
16	*Mollugo cerviana*	Molluginaceae	3	2	0	1	6	B
17	*Cyathula orthocantha*	Amaranthaceae	3	2	1	0	6	B
18	*Corchorus tridens*	Malvaceae	3	11	1	1	16	A
19	*Triumfetta pentandra*	Malvaceae	2	6	1	1	10	A
20	*Heliotropium ovalifolium*	Boraginaceae	2	10	11	10	33	C
21	*Commelina benghalensis*	Commelinaceae	2	0	1	0	3	D
22	*Abutilon angulatum*	Malvaceae	2	5	5	2	14	C
23	*Tribulus terrestris*	Zygophyllaceae	1	2	1	0	4	A
24	*Sida cordifolia*	Malvaceae	1	0	1	0	2	D
25	*Sesbania microphylla*	Fabaceae	1	4	0	1	6	A
26	*Ruellia prostrata*	Acanthaceae	1	0	0	0	1	B
27	*Hibiscus mastersianus*	Malvaceae	1	1	0	0	2	E
28	*Crotalaria barkae*	Fabaceae	1	0	0	0	1	B
29	*Commelina diffusa*	Commelinaceae	1	1	0	0	2	E
30	*Blainvillea acmella*	Asteraceae	1	1	0	0	2	E
31	*Vernonia glabra*	Asteraceae	1	0	0	1	2	B
32	*Thumbergia reticulata*	Acanthaceae	1	0	0	0	1	B
33	*Tephrosia purpurea*	Fabaceae	1	1	0	0	2	E
34	*Justicia exigua*	Acanthaceae	1	0	0	0	1	B
35	*Justicia bracteata*	Acanthaceae	1	1	1	0	3	E
36	*Ipomoea dichroa*	Convolvulaceae	1	0	0	0	1	B
37	*Ipomoea coptica*	Convolvulaceae	1	1	0	0	2	E
38	*Boerhavia coccinea*	Nyctaginaceae	1	1	0	0	2	E
39	*Asparagus africanus*	Asparagaceae	1	0	0	0	1	B
40	*Acalypha fimbriata*	Euphorbiaceae	1	3	3	0	7	C
41	*Zornia glochidiata*	Fabaceae	0	1	0	0	1	A
42	*Waltheria indica*	Sterculiaceae	0	1	0	1	2	A
43	*Solanum nigrum*	Solanaceae	0	1	0	1	2	A
44	*Sida chrysantha*	Malvaceae	0	0	1	1	2	A
45	*Sida alba*	Malvaceae	0	1	0	0	1	A
46	*Sesuvium hydaspicum*	Aizoaceae	0	1	0	0	1	A
47	*Sesbania rostrata*	Fabaceae	0	0	1	0	1	A
48	*Portulaca oleraceae*	Portulacaceae	0	2	0	0	2	A
49	*Portulaca hereroensis*	Portulacaceae	0	1	1	1	3	A
50	*Pechuel-loeschea leubnitzii*	Asteraceae	0	0	1	0	1	A
51	*Oxalis corniculata*	Oxalidaceae	0	0	1	0	1	A
52	*Ocimum americanum*	Lamiaceae	0	0	1	1	2	A
53	*Nidorella resedifolia*	Asteraceae	0	0	0	1	1	A
54	*Lobelia angolensis*	Campanulaceae	0	2	0	0	2	A
55	*Jamesbrittenia elegantissima*	Scrophulariaceae	0	0	0	1	1	A
56	*Ipomoea plebeia*	Convolvulaceae	0	6	0	0	6	A
57	*Indigofera tinctoria*	Fabaceae	0	1	0	0	1	A
58	*Indigofera astragalina*	Fabaceae	0	2	0	1	3	A
59	*Glinus oppositifolius*	Molluginaceae	0	0	1	0	1	A
60	*Dicliptera paniculata*	Acanthaceae	0	1	0	0	1	A
61	*Cucumis anguria*	Curcubitaceae	0	0	2	0	2	A
62	*Crotalaria steudneri*	Fabaceae	0	1	0	0	1	A
63	*Chamaesyce prostrata*	Euphorbiaceae	0	3	0	1	4	A
64	*Chamaecrista absus*	Fabaceae	0	1	0	0	1	A
65	*Acrotome inflata*	Lamiaceae	0	0	1	0	1	A
66	*Tradescantia pallida**	Commelinaceae	0	0	1	0	1	A
67	*Sonchus asper**	Asteraceae	0	1	1	0	2	C
68	*Datura stramonium**	Solanaceae	0	1	1	0	2	C
		Total	**298**	**534**	**306**	**118**	**1256**	
Grasses								
69	*Setaria verticillata*	Poaceae	74	56	17	11	158	B

(*continued on next page*)

Table 2 (*continued*)

No	Species	Family	Density of germinated seeds					
			L	1	2	3	Total	Group
70	*Urochloa mosambicensis*	Poaceae	50	30	6	1	87	B
71	*Cynodon dactylon*	Poaceae	11	3	9	1	24	D
72	*Digitaria eriantha*	Poaceae	10	24	32	3	69	C
73	*Digitaria debilis*	Poaceae	10	3	2	0	15	B
74	*Setaria sagittifolius*	Poaceae	8	18	4	3	33	A
75	*Eleusine coracana*	Poaceae	8	15	8	6	37	A
76	*Digitaria velutina*	Poaceae	6	3	1	0	10	B
77	*Eragrostis aspera*	Poaceae	4	2	3	2	11	D
78	*Eragrostis rotifer*	Poaceae	3	7	1	1	12	A
79	*Eragrostis sarmentosa*	Poaceae	2	17	5	0	24	A
80	*Panicum maximum*	Poaceae	1	4	0	0	5	A
81	*Dactyloctenium aegyptium*	Poaceae	2	2	1	0	5	E
82	*Chloris virgata*	Poaceae	1	3	1	0	5	A
83	*Eragrostis viscosa*	Poaceae	1	0	0	0	1	B
84	*Tragus racemosus*	Poaceae	1	1	0	0	2	E
85	*Brachiaria deflexa*	Poaceae	1	1	0	0	2	E
86	*Eragrostis cilianensis*	Poaceae	0	1	1	1	3	A
87	*Echinochloa jubata*	Poaceae	0	1	0	0	1	A
		Total	**193**	**191**	**91**	**29**	**504**	
Sedges								
88	*Bulbostylis hispidula*	Cyperaceae	11	24	2	3	40	A
89	*Cyperus longus*	Cyperaceae	5	15	10	4	34	C
90	*Cyperus squarrosus*	Cyperaceae	4	5	1	2	12	A
91	*Fimbristylis dichotoma*	Cyperaceae	2	51	24	15	92	A
92	*Pycreus pelophilus*	Cyperaceae	1	5	0	1	7	A
93	*Cyperus compressus*	Cyperaceae	0	3	4	1	8	C
94	*Cyperus pectinatus*	Cyperaceae	0	4	1	0	5	A
95	*Kyllinga erecta*	Cyperaceae	0	4	0	0	4	A
96	*Cyperus articulatus*	Cyperaceae	0	1	0	0	1	A
		Total	**23**	**112**	**42**	**26**	**203**	
Woody species								
97	*Combretum imberbe***	Combretaceae	35	2	0	0	37 [a]	B
98	*Vachellia tortilis***	Fabaceae	30	17	4	1	52 [b]	B
99	*Berchemia discolor***	Rhamnaceae	15	7	1	1	24	B
100	*Vachellia erioloba***	Fabaceae	8 [c]	0	0	1	9	B
101	*Philenoptera violacea***	Fabaceae	3	0	0	0	3	B
102	*Terminalia prunioides***	Combretaceae	3 [d]	0	0	0	3	B
103	*Grewia species***	Malvaceae	3	0	0	0	3	B
104	*Flueggea virosa*	Euphorbiaceae	1	0	0	0	1	B
105	*Albizia harveyi*	Fabaceae	1	1	0	0	2	E
106	*Colophospermum mopane***	Fabaceae	1	0	0	0	1	B
107	*Ficus sycomorus*	Moraceae	0	1	0	0	1	A
108	*Leucaena leucocephala**	Fabaceae	0	1	0	0	1	A
109	*Sclerocarya birrea***	Anacardiaceae	0	0	1	0	1	A
		Total	**100**	**29**	**6**	**3**	**138**	
		Grand Total	**614**	**866**	**445**	**176**	**2101**	

*Exotic species; **seeds recovered only through sieving soil samples;.

A, B, C, D and E - different trends of depth distribution of seeds in the soil.

[a] = all seeds sieved from the soil samples, except one which germinated from the litter layer.

[b] = all seeds from sieving the soil samples, except two which germinated from the litter layer.

[c] = one seed sieved from the soil sample and.

[d] = two seeds sieved from the soil samples.

3.4. Density of seeds in the soil

The overall density of seeds recovered from the soil samples collected in the TRWs was 2101 seeds m^{-2} (Table 1). The densities of seeds for herbs, grasses, sedges and woody species were 1256, 504, 203 and 138 seeds m^{-2}, respectively. Of these, 614, 866, 445 and 176 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 densities of seeds were *Kohautia virgata* (609 seeds m^{-2}), *Setaria verticillata* (158 seeds m^{-2}), *Acanthospermum hispidum* (107 seeds m^{-2}), *Urochloa mosambicensis* (87 seeds m^{-2}) and *Digitaria eriantha* (69 seeds m^{-2}), and the species with the lowest densities were *Echinochloa jubata, Cyperus articulatus, Flueggea virosa, Leucaena leucocephala* and *Eragrostis viscosa*, each represented by only one seed m^{-2} (Table 3).

3.5. Spatial distribution of seeds in the soil

There were great variations in the numbers of seeds distributed horizontally across all the 71 quadrats sampled, ranging between 14 and 118 seeds (Fig. 3).

Also, the overall vertical/depth distribution of seeds in the soil exhibited a lower density of seeds at the litter layer with increasing trend up to the first layer and declining trends thereafter (Fig. 4 - All Species). The total densities of seeds recovered from the litter, first, second and third soil layers were 614 (29%), 866 (42%), 445 (21%) and 176 (8%), respectively (Table 2). Of the total number of species recovered from the soil seed bank study, 24 (22%) species had 1590 seeds m^{-2}, represented in all the layers (e.g. *Amaranthus hybridus* and *Kohautia virgata*) (Table 1). On the other hand, 13 species (12%, 42 seeds m^{-2}, e.g. *Xanthium strumarium*), 15 species (14%, 25 seeds m^{-2}, e.g. *Zornia glochidiata*), eight species (7%, 9 seeds m^{-2}, e.g. *Sesbania rostrata*) and two

Table 3
List of families represented by species recovered from the soil samples collected along Thamalakane River.

No	Family	Species Recorded Total	Proportion (%)
1	Poaceae	19	17
2	Fabaceae	15	14
3	Asteraceae	10	9
4	Cyperaceae	9	8
5	Malvaceae	8	7
6	Acanthaceae	6	6
7	Amaranthaceae	5	5
8	Euphorbiaceae	4	4
9	Commelinaceae	3	3
10	Convolvulaceae	3	3
11	Rubiaceae	2	2
12	Lythraceae	2	2
13	Molluginaceae	2	2
14	Solanaceae	2	2
15	Portulacaceae	2	2
16	Lamiaceae	2	2
17	Combretaceae	2	2
18	Boraginaceae	1	1
19	Zygophyllaceae	1	1
20	Nyctaginaceae	1	1
21	Asparagaceae	1	1
22	Sterculiaceae	1	1
23	Aizoaceae	1	1
24	Oxaliaceae	1	1
25	Campanulaceae	1	1
26	Scrophulariaceae	1	1
27	Cucurbitaceae	1	1
28	Moraceae	1	1
29	Rhamnaceae	1	1
30	Anacardiaceae	1	1
	Total	**109**	**100**

species (2%, 2 seeds m^{-2}, e.g. *Nidorella resedifolia*) were represented in the litter, first, second and third soil layers, respectively. The other 47 species (43%, 433 seeds m^{-2}) were recovered from two to three different layers (Table 2; Fig. 5A and B).

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

i Group A: exhibited low densities of seeds in the litter layer, increasing densities in the first layer and, then, declining in the second and third layers (Table 2; Fig. 4. - Group A); e.g. *Amaranthus hybridus*, and 54 species (50%) exhibited this trend;
ii Group B: exhibited high densities of seeds in the litter layer and declining densities in the next layers (Table 2; Fig. 4. - Group B); e.g. *Setaria verticillata*, and 30 species (28%) 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. *Eclipta prostrata* and 9 species (8%) 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; Fig. 4. - Group D); e.g. *Eragrostis aspera*, and 5 species (5%) 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; Fig. 4. - Group E); e.g. *Dactyloctenium aegyptium* and 11 species (10%) exhibited this trend.

3.6. Plant species recovered by sieving soil samples

The number of species recovered from sieving soil samples was nine, representing five families and 119 seeds m^{-2} (Table 4). Of these, *B. discolor* had 24 seeds m^{-2}, *Grewia sp*. 3 seeds m^{-2}, *C. mopane* and *S. birrea* each with 1 seed m^{-2}. Viable seeds of species were recovered through sieving the soil samples, after their incubation was completed, and the densities ranged between one and 51 seeds m^{-2}. *Vachellia erioloba* had the lowest seeds (one seed) while *Vachellia tortilis* had the highest number of seeds (79 seeds) recovered. Recovered seeds of *S. birrea, C. mopane*, C. *imberbe, B. discolor, Grewia* sp., *P. violacea* and *T. prunioides* were not viable.

3.7. Description of the different soil seed bank plant communities

Four plant communities were identified from the soil seed bank, namely *Setaria verticilata-Amaranthus hybridus, Acanthospermum hispidum-Setaria sagittifolia, Digitaria eriantha-Eclipta prostrata* and *Cyperus longus-Fimbristylis dichotoma* (Table 5).

Soil seed bank composition showed overlaps between different soil layers (Fig. 6). Despite this, MRPP pairwise comparisons showed that the

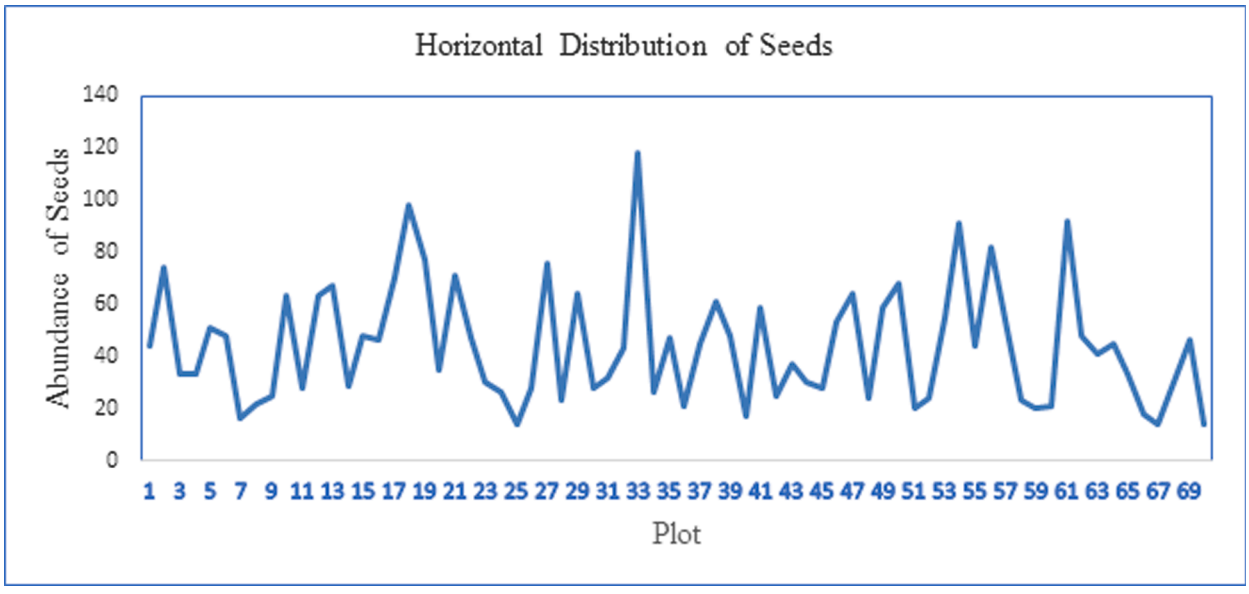

Fig. 3. Horizontal distribution of the soil seed bank seeds in the riparian woodland across all the four different soil layers from the 71 sampled quadrats.

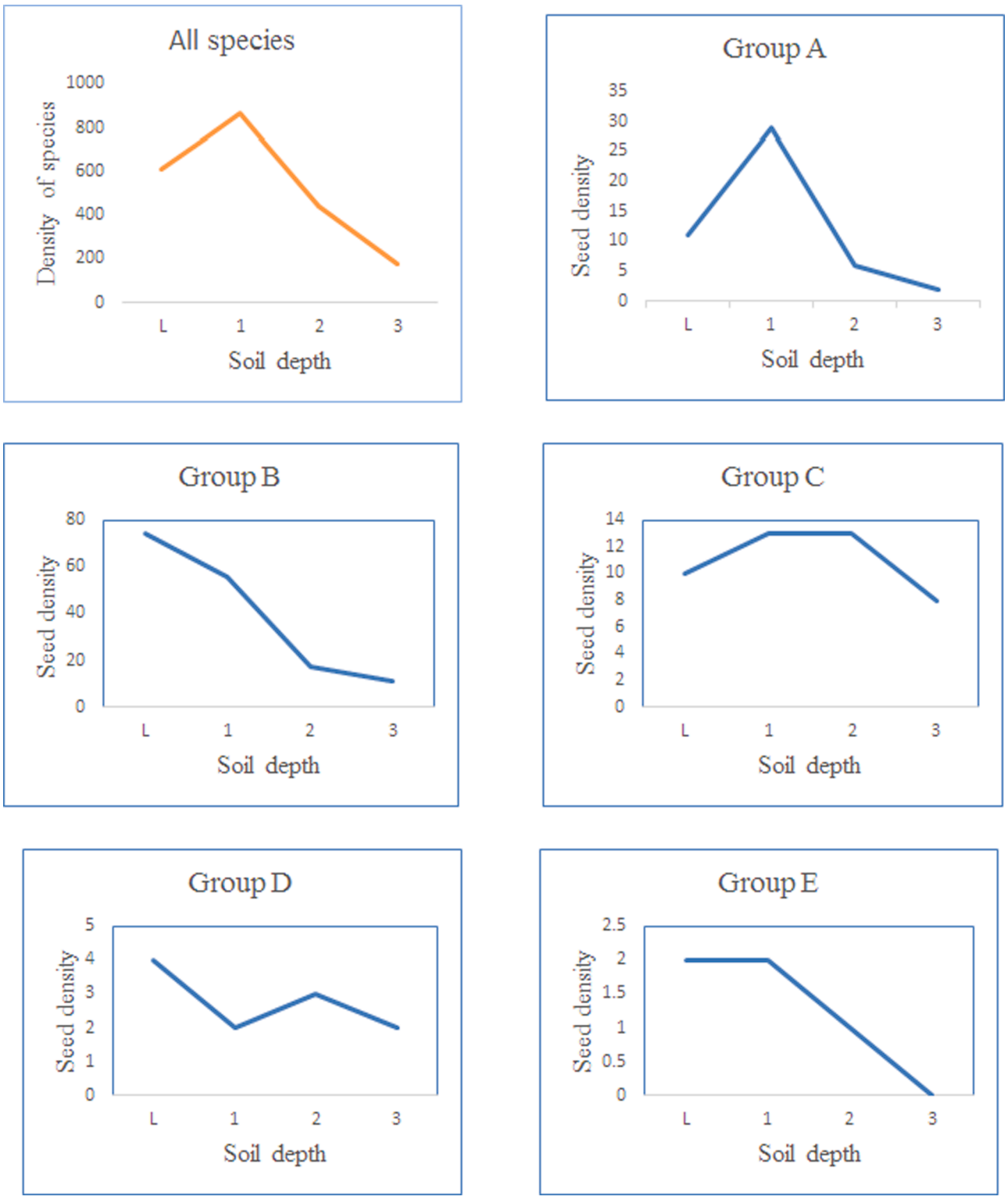

Fig. 4. Different trends of vertical (depth) distribution of seed densities from the soil seed bank in the riparian woodland. Group A: exhibited low densities of seeds in the litter layer, increasing densities in the first layer and, then, declining in the second and third layers. Group B: exhibited high densities of seeds in the litter layer and declining densities in the next layers. 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. 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 and 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.

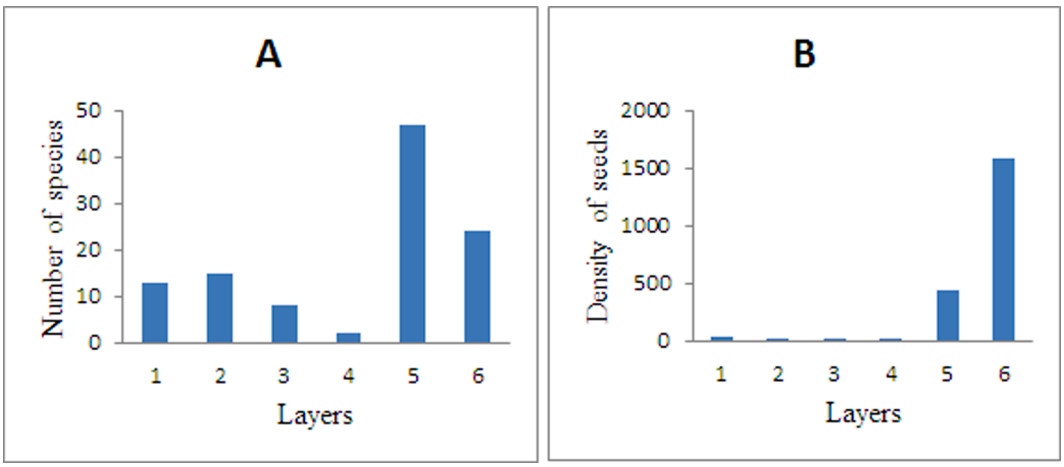

Fig. 5. A. Depth distribution from different soil layers and number of species along the Thamalakane River in the Okavango Delta, Botswana. 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, 4 = 6–9 cm, 5 = found in 2–3 layers and 6 = All layers. B. Depth distribution from different soil layers and density of seeds, 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	*Vachellia tortilis**	Fabaceae	29	17	4	1	51
2	*Combretum imberbe***	Combretaceae	35	1	0	0	36
3	*Berchemia discolor***	Rhamnaceae	15	7	1	1	23
4	*Grewia* sp.**	Malvaceae	2	0	0	0	2
5	*Philenoptera violacea***	Fabaceae	2	0	0	0	2
6	*Terminalia prunioides***	Combretaceae	2	0	0	0	2
7	*Colophospermum mopane***	Fabaceae	1	0	0	0	1
8	*Vachellia erioloba**	Fabaceae	0	0	0	1	1
9	*Sclerocarya birrea***	Anacardiaceae	0	0	1	0	1
		Total	**86**	**25**	**6**	**3**	**119**

*viable seeds, **non-viable seeds.

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 *Seeds of the Setaria verticilata-Amaranthus hybridus* community were found in all the soil layers. The distribution was as follows: 12 plots of litter layer, 13 plots of layer 1 (first layer), 9 plots of layer 2 (second layer) and 8 plots of layer 3 (third layer) out of 42 plots. This community was more different from *Cyperus longus-Fimbristylis dichotoma* community (T = -62) than it was from *Acanthospermum hispidum-Setaria sagittifolia* (T = - 43.00) and *Acanthospermum hispidum-Setaria sagittifolia* (T = - 23.00) communities (Table 6).

ii Seeds of the *Cyperus longus-Fimbristylis dichotoma* community were mostly found in layer 2 (36 plots out of 99) followed by layer 1 (34 plots out of 99), layer 3 (23 plots out of 99) and litter layer (10 plots out of 99). The *Cyperus longus-Fimbristylis dichotoma* community was most strongly separated from *Digitaria eriantha-Eclipta prostrata* community (T = - 69.00) while it was comparatively closely related to *Acanthospermum hispidum-Setaria sagittifolia* community in terms of species composition (Table 6).

iii In the *Digitaria eriantha-Eclipta prostrata* community seeds were also found in all the layers. Litter layer was most dominant with 36 plots followed by layer 3 with 23 plots out of a total of 101. Soil layers 1 and 2 had the least number of plots with each represented by 20 and 18 plots, respectively. See the two sections above in terms of statistical comparison on species composition.

iv The seeds in *Acanthospermum hispidum-Setaria sagittifolia* community were found almost exclusively in the litter layer . Out of a total of 12 plots in this community, 10 were for the litter layer while the remaining 2 were for layers 1 (1) and 2 (1).

4. Discussion

Soil seed banks, represented by all viable seeds and fruits present on or in the soil and associated litter/humus, exhibit variations in space as well as time and display both horizontal and vertical dispersion, reflecting initial dispersal onto the soil and subsequent movement (Simpson et al., 1989; Teketay, 2005a). They reflect partly the history of the vegetation and can play an important role in its regeneration or restoration after disturbances. Soil seed banks have been exploited to manage the composition and structure of existing vegetation and restore or establish native vegetation (van der Valk and Pederson 1989; Teketay, 2005b).

The results revealed that the TRWs can be characterized as possessing large populations of buried seeds of herbs, grasses, sedges (88% of the total species) and a few woody species (12%) in the soil. The dominance of herbaceous species in the soil seed banks of TRWs showed similarities with findings from several other studies undertaken elsewhere (e.g., De León Ibarra et al. 2019, Souza et al. 2016 Ma et al. 2014, Ma et al. 2011, Teketay and Granström 1995, Teketay 1998, 2005a, Tekle and Bekele 2000, Senbeta and Teketay 2001, 2002, Richter and Stromberg 2005, Lemenih and Teketay 2006, Wassie and Teketay 2006, Wang et al. 2009, Ayele 2014, Savadogo et al. 2016, Teklu and Bekele 2019, Mndela et al. 2020, Omomoh et al. 2020, Zida et al. 2020). The dominance of herbaceous species could be attributed to ease of dispersal by various agents, such as wind and water, because of their light weight.

It is interesting to note that of the 109 species that were encountered in the soil seed bank, eight were introduced plant species, from sixty-eight herbaceous, nineteen grass species, nine sedges and thirteen woody species (Table 2). Introduction of non-native species to the ecosystem, where they have not previously occurred, has been reported to cause or likely cause harm to human health, economy and environment (Richardson et al., 2000). Some exotic species have been introduced to new areas by birds, animals, water and wind dispersal (Herbold et al., 1986). Most exotic plant species can transform ecosystem functions (Richardson et al., 2000), resulting in biodiversity loss, altered ecosystem functioning and a changed capacity to provide services. They often dominate an environment and reduce the diversity of local species since they are aggressive competitors (Vitousek et al., 1997). Those that are highly invasive and strongly modify their

Table 5
Plant communities from soil seed bank along Thamalakane River.

Species	IV	P value
Setaria verticilata-Amaranthus hybridus		
Setaria verticillata	69.7	0.0002
Amaranthus hybridus	35.5	0.0002
Eleusine coracana	17.3	0.0286
Eragrostis cilianensis	3.9	0.1786
Alternanthera pungens	2.7	0.5429
Chamaesyce prostrata	2.3	0.7009
Portulaca oleraceae	1.7	0.7017
Sesuvium hydaspicum	1.7	0.6871
Solanum nigrum	1.7	0.6929
Sonchus asper	1.7	0.5601
Cyperus compressus	1.5	0.7590
Boerhavia coccinea	1.3	0.6207
Commelina benghalensis	1.3	0.7714
Triumfetta pentandra	1.2	0.9266
Eragrostis aspera	1.1	0.8586
Cyperus pectinatus	0.9	0.8178
Acanthospermum hispidum-Setaria sagittifolia		
Acanthospermum hispidum	84.1	0.0002
Setaria sagittifolia	15.4	0.0344
Abutilon angulatum	7.6	0.1112
Xanthium strumarium	6.6	0.1794
Justicia heterocarpa	5.9	0.2657
Bidens pilosa	4.7	0.1906
Panicum maximum	4.5	0.1542
Spermacoce sinensis	3.2	0.5119
Cyperus squarrosus	2.7	0.6607
Digitaria eriantha-Eclipta prostrata		
Digitaria eriantha	18.3	0.0288
Eclipta prostrata	12.5	0.0902
Urochloa mosambicensis	12.4	0.1682
Nesaea crassicaulis	11.8	0.0650
Heliotropium ovalifolium	8.2	0.1508
Phyllanthus purvulus	8.1	0.2190
Flaveria bidentis	6.6	0.0934
Achyranthes aspera	3.9	0.5693
Corchorus tridens	3.7	0.6123
Cyathula orthocantha	3.4	0.4515
Sesbania microphylla	2.9	0.6283
Cynodon dactylon	2.8	0.6755
Digitaria velutina	2.8	0.7165
Gomphorena celosioides	2.1	0.7690
Philenoptera violacea	1.0	1.0000
Cyperus longus-Fimbristylis dichotoma		
Cyperus longus	10.2	0.1310
Fimbristylis dichotoma	9.4	0.3057
Bulbostylis hispidula	6.5	0.4329
Eragrostis rotifer	4.6	0.3585
Ammania baccifera	3.5	0.6025
Mollugo cerviana	2.0	0.2673
Dactylectonium aegyptium	2.0	0.5767
Pycreus pelophilus	1.1	0.9244
Digitaria debilis	1.0	0.6063
Sida alba	1.0	0.6063
Terminalia prunioides	1.0	0.6031
Brachiaria deflexa	0.5	1.0000
Jamesbrittenia elegantissima	0.5	1.0000

environment are of greatest management concern as they must be controlled.

The species, family and genera richness values of all soil seed bank species (109 spp., 31 families and 87 genera) recorded in this study were higher than those recorded from riparian forests of the Paraguay River, distributed in 61 species, 24 families and 53 genera representing herbs, Cyperaceae and Poaceae, vines, shrubs and subshrubs and lianas (Kohagura et al., 2020), Pantanal wetlands (90 species, 22 families) (Bao et al., 2014), ephemeral wetland system in semi-arid Australia (77 species, 33 families) (James et al., 2007), Cooper Creek floodplain in Australia (56 species, 22 families) (Capon and Brock, 2006), Tibetan Plateau (57 species, 17 families) (Ma et al., 2014), Savanna woodland watering point in West Africa (30 species, 13 families and 21 genera) (Sanou et al., 2018), Alpine wetland on the Tibetan Plateau (82 species) (He et al., 2021) and degraded riparian zones in Southeastern Australia (55 species, 18 families) (Williams et al., 2008), and were lower than soil seed bank of a neotropical floodplain in the Pantanal wetlands (124 species representing herbs, graminoids and woody species (Souza et al., 2016). Neotropical riparian dry forests (142 species) (De León Ibarra et al., 2019), and Alpine wetland on the Tibetan Plateau (124 species, 27 families) (Ma et al., 2011).

The diversity value of the soil seed bank in TRWs (3.25) was lower than that reported from light livestock grazing sites (7.93) and very light pressure sites from a Savanna woodland watering point (7.85) in West Africa by Sanou et al., (2018).

The overall density (2101 seeds m^{-2}) of the seeds recovered from soil samples collected in the TRWs was much lower than densities from Tibetan Plateau (5419 seeds), Alpine wetland on the Tibetan Plateau (6436 seeds), Mexican riparian tropical dry forest (10,033 seeds), Neotropical floodplain (33,181 seeds) and Savanna woodland watering point in West Africa (3948 seeds).

Although there was considerable variation among species in the vertical distribution of their soil seed banks, the overall trend of depth distributions of the soil seed bank and number of species exhibited the highest densities in the upper 3 cm of soil and, then, gradually decreasing densities with increasing depth. This is consistent with several previous reports on the depth distributions of soil seed banks (Teketay and Granström, 1995; Teketay, 2005a; Teklu, 2014).

The seeds in the soil reflect partly the composition of the standing vegetation at present and partly the vegetation cover that existed in the past at the site. Soil seed banks of riparian corridors are very dynamic in space and time (Stromberg et al., 2008; De León Ibarra et al., 2019). They form a part of the existing flora at the site with a high potential as sources of regrowth in the event of any disturbance in the future (Teketay, 1998). The spatial distribution of seeds of different species varied greatly, both vertically and horizontally. These variations may reflect differences of species in terms of seed longevity in the soil, mode of seed dispersal, seed predation and, probably, differences in local edaphic conditions where seeds land (Teketay and Granström, 1995; Teketay, 1996, 1997a, 1998; Senbeta and Teketay, 2001, 2002; Senbeta et al., 2002; Ericksson et al., 2003; Matus et al., 2005; Mengistu et al., 2005).

Species forming soil seed banks are characterized by producing numerous small seeds, mechanisms for long-distance dispersal, formation of persistent soil seed banks and the capacity to remain viable in a dormant state for a long period of time (Whitmore, 1991; Teketay, 1998, 2005a; Thompson, 2000). In the present study, the fact that many species have seeds deeply distributed in the soil, e.g. *Kohautia virgata, Acanthospermum hispidum, Ammannia baccifera, Amaranthus hybridus, Nesaea crassicaulis, Eclipta prostrata, Flaveria bidentis, Phyllanthus parvulus, Heliotropium ovalifolium, Abutilon angulatum, Setaria verticillata, Urochloa mosambicensis, Cynodon dactylon, Digitaria eriantha, Setaria sagittifolius, Eleusine coracana, Digitaria velutina, Eragrostis aspera, Eragrostis sarmentosa, Bulbostylis hispidula, Cyperus longus, Fimbristylis dichotoma, Cyperus compressus* and *Vachellia tortilis* (refer to Table 2), suggests that the dormancy of seeds can be broken only in connection with disturbances (Teketay and Granström, 1995).

Table 7.

The accumulation of seeds in the soil is favoured by the dormancy of many of the seeds, which is caused by either the presence of embryo dormancy or impermeable seed coat or both (Leck et al., 1989; Teketay, 2005a; Wassie and Teketay, 2006). The seed dormancy in the species is controlled by several factors, including requirements for mechanical scarification (Ballard, 1973; Baskin and Baskin, 1985; Teketay, 2005a), both light and/or light with relatively high red to far-red ratio (no germination in darkness) (Pons, 1992) and alternating temperatures (Proberts, 1992), and only light/light with relatively high red to far-red ratio (no germination in darkness) (Baskin and Baskin, 1989; Baskin and Baskin, 1998).

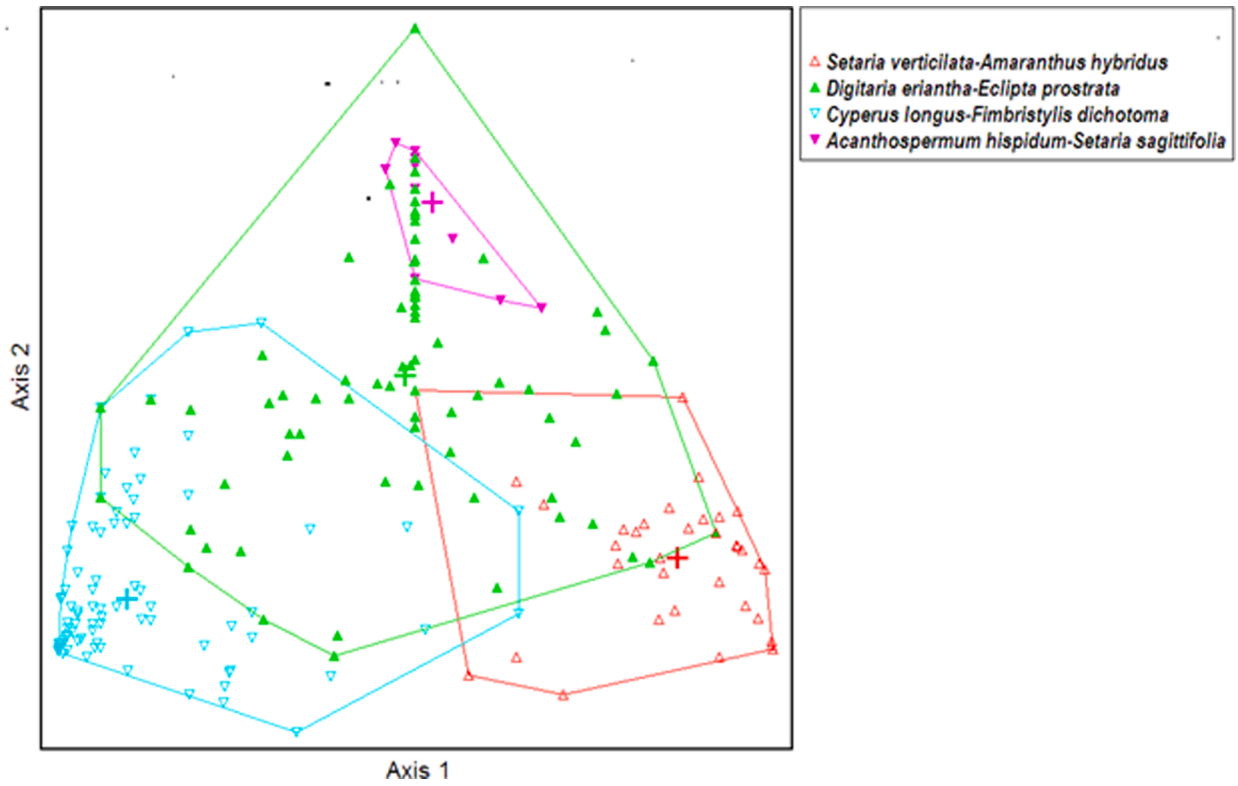

Fig. 6. Bray-Curtis plot of riparian soil seed bank plant communities along the Thamalakane River in the Okavango Delta, Botswana.

Table 6
MRPP pairwise comparisons of soil seed bank plant communities along Thamalakane River.

Plant communities	T	P value
SV-AH[1] vs DE-EP[2]	- 43.00	0.00001
SV-AH vs CL-FD[3]	- 62.00	0.00001
SV-AH vs AH-SS	- 23.00	0.00001
DE-EP[4] vs CL-FD	- 69.00	0.00001
DE-EP vs AH-SS	- 22.00	0.00001
CL-FD vs AH-SS	- 32.00	0.00001

[1] Setaria verticilata-Amaranthus hybridus.
[2] Acanthospermum hispidum-Setaria sagittifolia.
[3] Digitaria eriantha-Eclipta prostrata.
[4] Cyperus longus-Fimbristylis dichotoma.

Table 7
Variation of indicator values across different soil layers in the riparian woodland along the Thamalakane River (*L* = litter, 1 = 0–3 cm, 2 = 3–6 cm and 3 = 6–9 cm soil layers).

Species	L	1	2	3
Amaranthus hybridus	38.9[a]	-	26.9[a]	-
Setaria verticillata	80.7[a]	21.9	81.7[a]	53.1
Kohautia virgata	95.1[a]	14.6	46.4[a]	30.5
Abutilon angulatum	23.7[a]	66.1[a]	23.8	22.2
Acanthospermum hispidum	57.7[a]	21.7[a]	78.8[a]	-
Eragrostis rotifer	12.6	72.1[a]	-	-
Cynodon dactylon	5.7	27.7[a]	-	-
Bulbostylis hispidula	9.2	37.2[a]	-	25.0
Digitaria debilis	-	47.5[a]	-	-
Terminalia prunioides	-	67.8[a]	-	-
Gomphorena celosioides	10.1	43.6[a]	-	-
Cyperus pectinatus	-	35.3[a]	-	-
Digitaria eriantha	17.5	36.0[a]	-	-
Urochloa mosambicensis	20.8	-	92.9[a]	
Fimbristylis dichotoma	4.4	-	100.0[a]	79.7[a]
Heliotropium ovalifolium	8.0	-	50.0[a]	68.5[a]
Eclipta prostrata	11.0	10.4	35.3	100.0[a]

[a] Significantly different at $P < 0.05$.

There was a disparity in woody species composition between the soil seed bank flora and above-ground vegetation in the TRWs. Most of the woody component of the TRWs lacked reserves of seeds in the soil. Of the 49 woody species recorded in the standing vegetation of the TRWs (Tsheboeng et al., 2017), only 13 species (27%) were represented in the soil seed banks. Our findings concur with those of different authors (Amiaud and Touzard, 2004; Teketay, 1996, 1997a, 1998; Teketay and Granström, 1995; De Villiers et al., 2003; Ericksson et al., 2003; Senbeta et al., 2002; Senbeta and Teketay, 2001, 2002; Granström, 1982; Tekle and Bekele, 2000; Lemenih and Teketay, 2006; Mengistu et al., 2005; González-Rivas et al., 2009; Lu et al., 2010; Mukhongo et al., 2011; Legesse et al., 2018; Teklu and Bekele, 2019) who reported lower proportions of woody species in the soil seed banks. This result agrees with the results of other studies that reported a poor relationship between existing vegetation and underground seed reserves. This poor correspondence in species composition between seed bank and above-ground vegetation may be due to seed predation (Baskin and Baskin, 1998; Crowley and Garnett, 1999; Marone et al., 2000), reliance on vegetative reproduction (Baker, 1989) and lack of dormancy mechanisms (Esmailzadeh et al., 2011). The poor correspondence in species composition between soil seed banks and standing vegetation is also probably due to the great dynamism of seed banks close to watercourses (De León Ibarra et al., 2019). There are studies showing that spatial heterogeneity is a prevailing feature in riparian vegetation, in the standing vegetation and soil seed bank of both woody and herbaceous components.

The woody species recorded in this study, such as *Vachellia erioloba* and *V. tortilis,* are also favoured by disturbances for their regeneration since they possess seeds with hard seed coats that require scarification for germination (Teketay, 1996; Odirile et al., 2019). When the forests or woodlands are burnt, which is an annually occurring phenomenon in Botswana, temperatures often exceed 100 °C at and one centimeter

below the surface (Ewel et al., 1981; Uhl et al., 1981; Garwood, 1989; Teketay, 1998, 2005b). As a result, seeds of many species lying on the surface or buried in the upper soil layers are killed by the high temperature during the burn and their seed density could be either eliminated or severely reduced. On the other hand, the high temperatures favor germination of heat-resistant or heat-stimulated species, such as species of *Vachellia* and several other hard-seeded species, e.g. legumes.

Results reported from other studies (e.g. Teketay 1996, 1997b, Teketay and Granström, 1995), have revealed that seeds of several woody species are large and contain high moisture, indicative of adaptations to immediate germination and seedling establishment and survival under the canopy of forests. Moreover, the residence time of their seeds in the soil is relatively short compared with those of herbaceous species, which can maintain their viability for a long time (Teketay, 1998; Teketay and Granström, 1997a, b). Those seeds, which do not germinate are consumed by predators or succumb to attack by microorganisms. By immediate germination and establishment, many trees and shrubs form large populations of seedlings in the forest, and many of them are also capable of re-sprouting from damaged stems or roots (Foster, 1986; Teketay, 1997a). This implies that the sources of re-growth of woody species are totally dependent on the presence of the whole or a portion of the woody vegetation with mature individuals. In the event of disturbances, herbaceous species can regenerate from both the soil seed bank or seed rain while the woody species from pre-existing seedlings, coppice shoots or recently dispersed seeds or seed rain.

The fact that most of the dominant tree species in TRWs do not accumulate seeds in the soil suggests that regeneration of these species from seeds would be prevented by removal of mature individuals. Most species are relatively large seeded and apparently have poor long-distance dispersal, suggesting that restoration of TRWs would be difficult and slow to accomplish if they are destroyed. The ground flora has a better chance of natural recovery, because it has diverse soil seed bank, probably with higher seed longevity. Therefore, the future of the woody flora of TRWs seems to depend on the successful conservation of the remaining standing vegetation. These findings concur with those reported from similar studies elsewhere (Teketay and Granström, 1995; Teketay, 2005a; Senbeta and Teketay, 2002; Gnoumou et al., 2011). This has an important management implication in that the standing vegetation cannot be fully replaced by the seeds stored in the soil in the event of any natural or anthropological disturbances.

From a management point of view, knowledge on the soil seed bank is vital for conservation and restoration efforts of degraded habitats (Hegazy, 1996). Riparian vegetation along the Thamalakane River is exposed to human use, livestock grazing, land clearing for agriculture and cutting of trees for fencing fields and crops (Neelo et al., 2013). These activities may lead to the degradation of the riparian vegetation in this area as shown by unhealthy population structures and regeneration status of most of the woody species along the Thamalakane River (Tsheboeng et al., 2017; Teketay et al., 2016). Therefore, the soil seed bank would play a critical role towards replacing degraded extant vegetation (Strykstra et al., 1998).

5. Conclusions

Based on the results from this study, the TRWs can be characterized by possessing large populations of buried seeds of herbs, grasses and sedges. The results also revealed that only a few woody species were represented in the soil seed bank, and there is great disparity in the similarity of woody species composition between the standing vegetation and soil seed bank flora.

These results imply that the herbaceous flora has a better chance of natural recovery in the event of disturbances, owing to the diverse soil seed banks while the regeneration of woody species would be prevented by removal of mature individuals and their seedlings on the forest floor since most of them lack seed reserves in the soil. These results provide further evidences that consolidate the conclusions of previous studies on soil seed banks from other countries that the future existence of the woody species found in the TRWs depends on the conservation and sustainable utilization of the riparian woodlands.

There is still more research required on the life-history strategies of riparian woodland species along the Thamalakane River. For example, there is still lack of knowledge on seed production rates, mechanisms of seed dispersal, seed rain, seed germination behavior, seed longevity in the soil and status of seed predation of the riparian woodland species along the Thamalakane River. Future research should focus on these gaps, among other themes, in order to clearly understand the dynamics of TRWs and promote their sustainable management.

Declaration of Competing Interest

The authors declare that there is no conflict of interest associated with this publication.

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