Natural vegetation regeneration from soil seed banks in the cultivated edges of Sudd wetlands in Juba, Southern Sudan

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Abstract
Soil seed banks are important for regeneration of degraded wetlands ecosystems. The Sudd wetlands of Juba city have long been encroached for crop cultivation. Seedling germination was monitored in a greenhouse to establish possible natural regeneration in Mindiari, Rejaf and Roton wetlands in the Sudd. Sixty-four species germinated from the soil seed bank of which 12.5% were dominated by *Cyperus difformis* and *Typha capensis*. The findings showed that median wetland species richness in Mindiari was 1.5 (interquartile range = 0.75─3.5), Rejaf 2.5 (interquartile range = 1.0 ─ 4.0), Roton 3 (interquartile range = 1.0 ─ 5.0) while median Shannon-Wiener diversity was 1.5 (1.14 ─1.73), 1.43 (1.01─1.66), 1.15 (0.98─1.67) for Mindiari, Rejaf and Roton respectively. Both the median seed species richness and diversity were not significantly different among the study wetlands. The median of seed density (56.1) was significantly higher in Roton than in Mindiari (36.7) and Rejaf (29.4) wetlands. The NMDS results showed that species composition of Mindiari and Rejaf was different from Roton. It is concluded that growing crops in wetlands did not influence species richness and diversity but it reduced seed density and altered species composition. Although wetland species were not significantly different in the three-wetland categories, dominance of canopy species belonging to Typhaceae and Cyperaceae indicates that these species are resilient to cultivation and could facilitate natural regeneration of cultivated wetlands edges of the Sudd region in Juba. Further research should examine effect of cultivation duration and flooding regimes on soil seed bank species richness, diversity, and density and composition.

Introduction

Wetlands are usually viewed as suitable alternative arable lands for crop cultivation as they have reliable water and fertile soils (Verhoeven and Setter, 2010; Saha and Pal, 2019; Munishi and Jewitt, 2019). Increase in human population coupled with the growing demand for food production land has accelerated wetland conversion to farmlands resulting in wetland degradation and loss. About 33% of wetlands have been lost globally including 16% in Africa (Hu *et al.,* 2017). Cognizant of wetland degradation challenges, the Ramsar Convention, (1971) permits sustainable and non-destructive wetland uses including livestock grazing and wetland edge cultivation, which allows natural regeneration from soil seed banks (Ramsar Secretariat, 2013).

However, such regeneration is influenced by site characteristics, proximity to seed sources and intensity of wetland disturbances (Ma *et al.,,* 2014; Peralta *et al.*, 2016; Shi *et al.*, 2020). Several studies have examined disturbance intensity and natural regeneration of emergent macrophytes from soil seed banks in wetland ecosystems including studies in Australia (Brock, 2011; Grieger *et al.,,* 2019), Europe (Abernethy and Willby 1994, Klimkowska *et al.*, 2010; Lenzewski *et al.,,* 2020), Asia (Yang *et al.*, 2018; Chen *et al.*, 2020) and America (Keddy and Reznicek, 1996; Kottler and Gedan; 2020), which have affirmed that wetland soil seed banks are usually associated with high species richness. A study linking hydro period with vegetation response showed that wetland species richness and density was related to flood frequency (Battaglia and Collins, 2006; Shoemaker and Ervin, 2019). Other studies found no relationship between flood frequency, species richness and density in soil seed banks (Capon and Brock, 2006; Webb *et al.*, 2006; Stone *et al.*, 2018; Baskin, Baskin and Chester, 2019) or fewer species in low flood frequency zones (Capon, 2007). Other than flooding, human disturbances such as cultivation in wetlands have increased

around the world (McCartney *et al.*, 2010; Rebelo *et al.*, 2010; Chen *et al.*, 2018). Cultivation increases seed turnover rate in the soil seed bank (Baskin and Baskin, 2014) and influences soil seed bank species richness, diversity and density.

The process of wetland cultivation involves removal of vegetation to pave way to crop planting. Vegetation removal reduces species richness, diversity, density and alters composition of soil seed banks as the seed rain changes. On the other hand, sparing vegetation increases seed density through enhanced internal seed inputs to the soil seed bank (Brown and Cahill Jr., 2020). Therefore, the seed bank of least cultivated wetlands tend to have low species richness and diversity but high seed density. Meanwhile moderately and highly cultivated wetlands have limited or no vegetation, which increases chances for germination from the soil seed bank (Brown and Cahill Jr., 2020) and the seed bank, is usually species rich and diverse with low seed density. This implies that cultivation intensity influences natural vegetation regeneration from soil seed bank.

In Europe, Asia and America, studies of natural regeneration from soil seed banks in cultivated wetlands have produced mixed results. Some authors have reported species rich, diverse and abundant soil seed banks in formerly cultivated wetlands enabling natural regeneration (Touzard *et al.*, 2002; Bao, *et al.*, 2014; He *et al.*, 2020). These results imply that the soil seed bank reservoirs in wetlands are resilient during cultivation. In contrast, some studies have reported limited regeneration in cultivated wetlands with low species richness, diversity and density of seeds in the soil seed bank (Galatowitsch and van der Valk, 1996; Wang *et al.,* 2017: Salaria *et al.*, 2018). In Sub-Saharan Africa, studies of wetland regeneration from soil seed banks and disturbance by cultivation are limited and inconclusive. For example, Matayaya *et al.*, (2017) found that species richness was lower in conventional tillage plots in dambo wetlands in Zimbabwe. In East Africa, Gaudet (1977) found no influence of flooding on wetland regeneration

from soil seed banks in Lake Naivasha in Kenya. Whereas wetlands in other East African countries such as Uganda, Tanzania as well as the Sudd wetland of South Sudan have continued to experience increased degradation by cultivation (Kyalo and Heckelei, 2018; Msofe *et al.,* 2019; Kabiri *et al.,* 2020; Wehling, 2020), there is limited information on soil seed banks and wetland regeneration which provided the impetus to carry out this study.

Wetlands cover about 7% of the total area of South Sudan and vary in size with the Sudd as the largest wetland (African Development Bank, 2013). The Sudd wetland, associated with the Lake Victoria catchment, is the largest wetland ecosystem in the Nile basin and one of the largest tropical wetlands in the world. It experiences regular floods, which vary with season and rainfall. Habitats within the Sudd wetland consists of submerged and emergent macrophytes, floating and fringing vegetation, seasonally flooded and rain-fed grasslands and floodplain woodlands (Wilusz *et al.,* 2017). *Cyperus papyrus*, *Phragmites communis*, *Vossia cuspidata*, *Typha domingensis* and *Eichornia crassipes* (water hyacinth) are common along open water channels and dominate the permanent swamp areas, which are surrounded by floodplains and seasonally flooded grasslands characterized by *Oryza longistaminata* and *Echinochloa pyramidalis.* Previous wetland research in the area tended to focus on hydrological regime (Rebelo *et al.,* 2011; Sosnowski *et al.,* 2016; Sutcliff and Brown, 2018) and effects of hydrocarbon contamination on soils (Ruley *et al.,* 2019) while soil seed bank studies have largely been neglected thus curtailing deeper understanding of soil seed banks in the Sudd wetlands of South Sudan. Moreover, there has been limited research in wetlands in the surroundings of Juba City which are experiencing increasing human population growth estimated at 4.61% per annum (Fernando and Garvey, 2013). The local population is poor and 80% live on less than USD1 per day (Fernando and Garvey, 2013). The above scenario coupled with changing weather patterns and widespread localized droughts tends to accelerate the encroachment of wetlands for cultivation by the urban poor, which threatens their existence and the biodiversity. Therefore, knowledge of soil seed banks is crucial to broaden understanding of vegetation regeneration in the cultivated wetlands found on the fringes of Juba City. If the wetland vegetation is conserved and allowed to regenerate, inherent functions such as hydrological buffers and provision of food, water, construction materials and grazing areas will benefit the local people in the area. In addition, wetlands' aesthetic value will provide opportunities for nature-based tourism and conservation of the local cultures (Sanna and Eja, 2017; Zhou *et al.,* 2020).

Research on wetland regeneration resonated well with the recently declared United Nations (UN) 2021-2030 Decade on Ecosystem Restoration, which recognizes the need to restore degraded ecosystems such as wetlands throughout the world including South Sudan. Natural vegetation regeneration from soil seed banks would enable cultivated wetlands to regain their functions such as providing goods and service to people. However, natural vegetation regeneration relies mainly on soil seed banks (Saatkamp, Poschlod and Venable, 2014; Vadvik *et al.,* 2015).

The purpose of this study was to investigate the potential for natural vegetation regeneration from soil seed banks of cultivated wetlands in the surroundings of Juba City. The objective of the study was to assess soil seed bank species richness, diversity and density in wetlands differing in cultivation intensity.

Materials and Methods

Description of study site
Juba (4.859363°N; 31.571251°E) is located west of the River Nile at 457 m above sea level (Figure 1). It has a tropical wet and dry/savanna climate with the dry season in November to March, and the wet season from April to October. It has an average temperature of 27.8°C, and an annual average rainfall of 972.4 mm (Lomeling, 2020).

The city is situated between River Nile, and the Logwe (Rejaf West), Körök (Kujur) and Nyar Kenyi (Lado) mountains. The surrounding lowlands are prone to repeated flooding from River Nile, Luri River, and others (State of Environment Report, 2018). Juba is the political capital city of South Sudan and administrative headquarters of Central Equatoria State. The city is expanding and Mindiari, Rejaf and Roton wetlands (Figure1) have been encroached for settlements and agriculture. Mindiari wetland (2.48 km²) is located 7.3 km from Juba city; North West. It lies at 465 m asl and receives water from seasonal streams such as Luri and Kapuri and eventually drains into river Kriti. The dominant riparian vegetation includes sedges and grasses such as *Echinochloa* sp., *Justicia insularis*, *Cyperus rotundus*, *Carex pseudocyperus* and trees and shrubs such as *Grewia tenax, Balanites aegyptiaca, Acacia sieberiana* that are mostly found in the southern and eastern parts of the wetland. Fishing and harvesting of wild vegetables such as *Amaranthus sp.*, and *Cleome gynandra* (spider web plant) and collecting wild fruits, for example from *Grewia tenax*, are the main economic activities. In the past, the wetland was a major source of water for wildlife, cattle and goats, which mostly grazed on *Echinochloa* sp. However, increase in human population in and around Juba city has resulted in encroachment by crop cultivation and human settlements.

Rejaf wetland (0.526 km²) is located 10 km in the south east of Juba city; South East. It lies at 461m asl and receives water from River Kit during the rainy season. The dominant vegetation includes *Setaria megaphylla*, *Typha domingensis* and *Cyperus rotundus*. The western part of the wetland is covered by woodland dominated by *Acacia sieberiana* whereas the eastern part is dominated by *Balanites aegyptiaca* and *Ziziphus mauritanica*. There is moderate cultivation and livestock grazing on the edges. Roton is a permanent wetland covering 4.39 km² located 2.7 km north east of Juba city. It lies at 452 m asl and receives water from seasonal streams and rivers. It is located on the fringes of Juba International Airport and is the least cultivated due to restricted access. The dominant plant species include *Typha domingensis* and *Alopecurus* sp. and *Balanites aegyptiaca*.

In this study, extent of disturbance as spatial size of area cleared has been categorized as; large when most parts of the wetland is cultivated (Most), medium when moderate area of wetland is cultivated (Moderate) and small when least area of wetland is cultivated (Least) and herein represented in and denoted as Mindiari, Rejaf and Roton wetlands respectively (Figure 1).
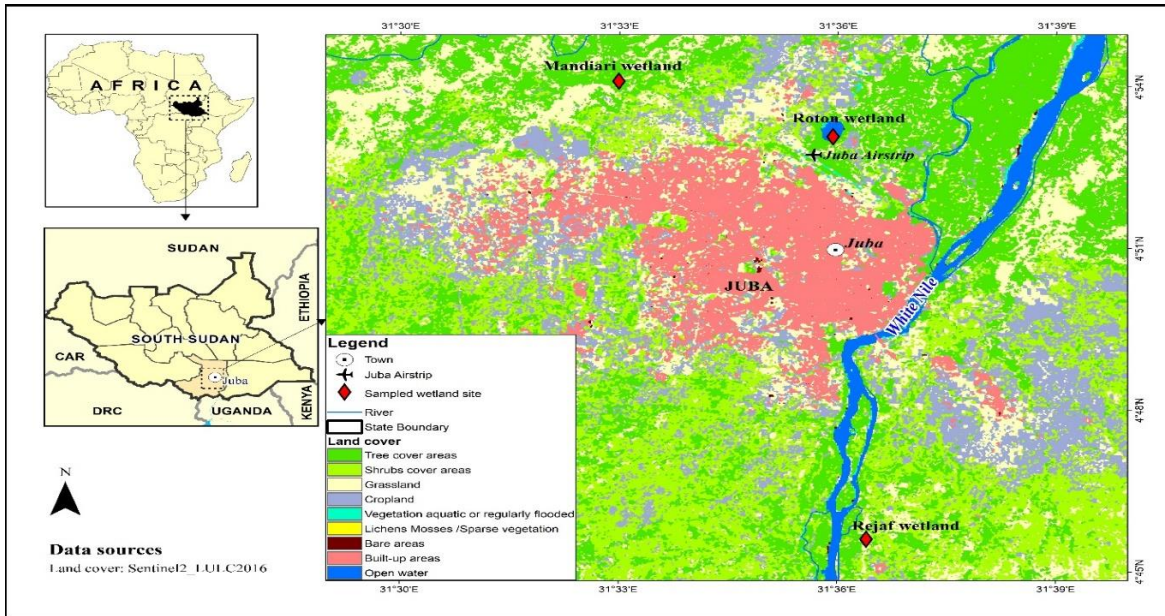
Figure 1. Location of Mindiari, Roton and Rejaf wetlands in the Sudd wetland system, South Sudan.

Materials and Methods

Soil seed bank sampling

Mindiari and Rejaf, and Roton wetlands representing most, medium and least intensely cultivated ecosystems respectively were sampled for soil seed bank and vegetation based on methods by Gross (1990) and Kent and Coker (1992). Three to five transects at a distance of 500 m and 100 m away from the edge of the wetland were established in each wetland depending on its size (Cooper *et al.*, 2006). Within each transect, six plots measuring 0.60 x 0.60 m were randomly established taking into account edge effects. Within each plot, five-soil samples were collected, one at each corner and one in the center using a soil core (12 cm depth and 4.5cm diameter). The soil sample was divided as follows: 2 cm top soil was placed in a separate envelope and the 10 cm soil (bottom) in another envelope. This procedure was repeated for the plots in each site and every time keeping the 2 cm layers soil together in one envelop and the 10 cm layer in another envelop. Every plot measuring 0.60 x 0.60 m had two composite soil samples consisting of 2 cm soil and 10 cm soil. The surface area sampled by the core was 15.9 cm^2 and volume of soil was 190.8 cm^3 thus in each plot 953.8 cm^3 of soil was collected. The soil samples were kept in sealed paper bags and stored for two months at room temperature (25°C) and ambient humidity (58%) to minimize infestation by pathogens such as moulds and to maintain seed viability (Baskin and Baskin, 2014).

Seed germination

A greenhouse germination experiment was set up, soil samples sieved in 2.0 mm mesh and spread in individual seed trays (30 cm x 27 cm) on a substrate of sand excavated from beneath Khor Romulah lake floor (assumed to contain no viable seeds). Ten extra trays containing sand only were included as control. The trays were watered daily using water collected from the River Nile and seed germination monitored for nine months until no seedlings emerged. Germinating seeds (seedlings) were identified and removed to allow germination to continue. Seedlings that could not be identified were replanted and identified later using the Flora of Tropical East Africa and RBG and East Africa Herbarium 1952-2012.

To determine species richness and diversity for understory and seed bank, the total number of species counted was taken to be the species

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richness while for species diversity the Shannon-Wiener Diversity Index (*H*) was calculated in Microsoft Excel using the following expression.

$$H = -\sum_{i=1}^{N} pi \ln pi$$

Where

Pi = proportion of total sample represented by species *i*

Obtained by dividing no. of individuals of species i by total number of individuals in sample.

S = number of species, = species richness

ln= natural logarithm

Seed density was computed by dividing seed abundance per plot by the volume of soil expressed in litres.

Data analysis
Data were analyzed in SPSS (version 20) and subjected to homogeneity of variance test to show whether all variables (species richness, diversity and density) measured deviated from normal. The results showed that all the variables deviated from normal hence Kruskal-Wallis (K-W) test was applied to show differences in soil seed banks from the three wetlands. The test of differences in medians were followed by Dunn-Bonferroni's pairwise post-hoc test and adjustment of significant values (Zar, 2009). Data were also subjected to Analysis of Similarity Species Composition using non-metric multidimensional scaling (NMDS) in Community Analysis Package (CAP 5) Software. NMDS dissimilarity matrix was generated using Bray-Curtis to show whether species were shared between cultivated and uncultivated wetlands. Bray-Curtis distances were computed from species abundance data that were log transformed (log_{10} x+1) to improve normality

(Henderson and Seaby, 2014). Species Similarity Percentage (SIMPER) was calculated to determine the contribution of species to the dissimilarity species composition under intensive wetland cultivation. No seedlings germinated from the control trays.

Results

Sixty four species germinated from the soil seed bank belonging to 21 families dominated by Poaceae, Cyperaceae, Phyllanthaceae, Typhaceae and Brassicaceae. These included 53 terrestrial, eight wetland, three species occurring in both wetland and terrestrial and one unidentified species. Forty-seven species germinated from Mindiari (most cultivated) wetland; which included six wetland species dominated by *Echinochloa colona* (L.) Link and forty-one terrestrial annual species dominated by *Phyllanthus niruri* L., *Mollugo nudicaulis* Lam. and *Anagallis arvensis* L. followed by *Eleusine indica* (L.) Gaertn. and *Eragrostis* sp. Wolf. Wetland soil from Rejaf (moderately cultivated) germinated 28 species including four wetland species dominated by *Typha capensis* (Rohrb.) N.E. Br. and *Cyperus difformis*. There were 24 terrestrial perennial and annual species dominated by *Phyllanthus niruri*. Fifty-one species germinated from the Roton (least cultivated) wetland soil including seven wetland species dominated by perennial species such as *Typha capensis, Cyperus difformis, Alopecurus sp.* L., and annual species like *Echinochloa colona*, *Portulaca* sp. L., *Phyllanthus niruri*, *Ocimum basilicum* L. and *Raphanus raphanistrum* L. These were also the dominant terrestrial annual species in Roton wetland. Terrestrial perennials namely *Brachiaria ruzinensis* Germ. and Evrard and *Cyperus rotundus* L. dominated all the three wetlands while two wetland perennial species *Cyperus difformis* and *Typha capensis* were dominant in the all three wetlands (Table 1).

Table 1.*Total abundance of wetland species recorded in the soil seed bank of most (Mindiari), moderate (Rejaf) and least (Roton) cultivated wetlands in Juba*

Cultivation intensity		Most	Moderate	Least
Species	Family	Mindiari	Rejaf	Roton
Alopecurus sp. L.	Poaceae	13	1	55
Cyperus difformis L.	Cyperaceae	73	52	373
Cyperus esculentus L.	Cyperaceae	1	-	3
Echinochloa colona (L.) Link	Poaceae	54	1	27
Ipomoea aquatica Forssk.	Convolvulaceae	-	-	2
Typha capensis (Rohrb.) N.E. Br.	Typhaceae	285	47	618
Typha domingensis Pers.	Typhaceae	-	-	16
Pulicaria crispa Sch. Bip.	Asteraceae	2	-	-

The dominant terrestrial perennial species included *Brachiaria ruzinensis*, *Cyperus rotundus* and *Eleusine indica* and annuals such as *Phyllanthus niruri*, *Anagallis arvensis* and *Raphanus raphanistrum*.
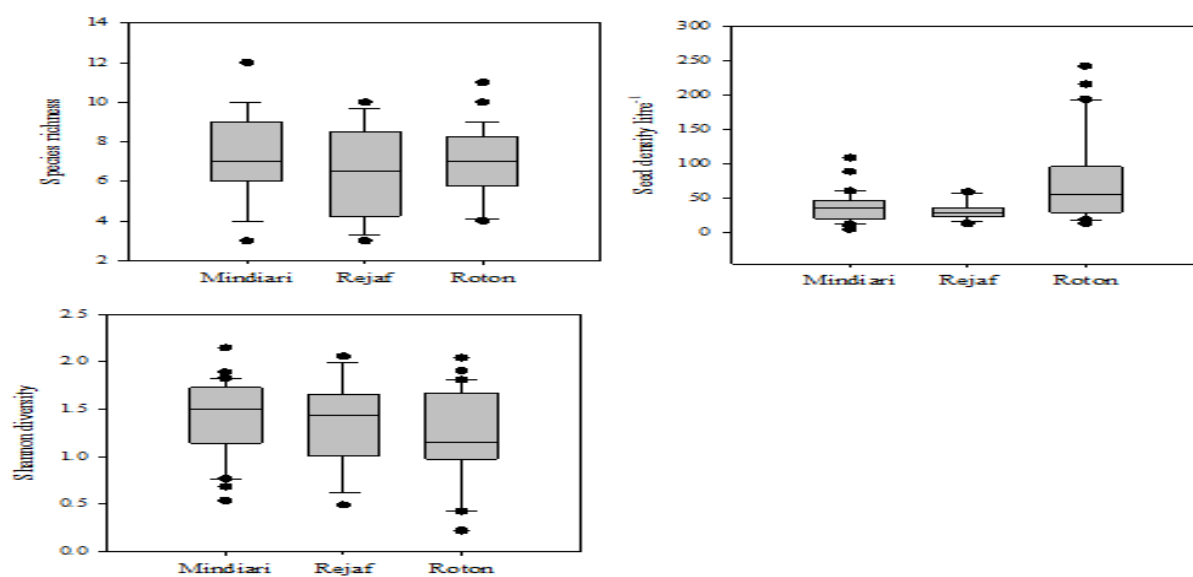

Figure 2. Species richness, Shannon diversity and density per litre of seeds from Mindiari, Rejaf and Roton wetlands in Juba. The thick line represents the median, the outer limits of the box represent first and third interquartile range.

The median species richness was similar in Mindiari (7) and Roton (7) and slightly lower in Rejaf (6.5) but not significantly different (K-W X^2_2 =2.577, $P > 0.05$). The median of Shannon-Wiener diversity was 1.5 in Mindiari wetland, 1.4 in Rejaf wetland and 1.2 in Roton wetland but was not significantly different (K-W X^2_2 =1.805, $P>0.05$). However, median of seed density (56.1) was significantly higher in Roton than in Mindiari (36.7) and Rejaf (29.4) (Figure 2).

Table 2. Seed density in top and lower soil layers in most (Mindiari), moderate (Rejaf) and least (Roton) cultivated wetlands

Wetland	Median per litre of top 2 cm soil layer	Median per litre of lower 10cm soil layer	Difference between top and lower layer Wilcoxon Z values
Mindiari	9.96	18.87	-2.70**
Rejaf	9.44	15.73	-1.29
Roton	31.98	19.40	-0.99

** $P < 0.01$

Fewer seeds were found in the top 2 cm soil profile of Mindiari and Rejaf wetlands. In Mindiari, the difference in median seed density between top and lower layers (top 2 cm layer = 9.96, interquartile range = 39.84, lower 10 cm l = 18.87, interquartile range = 92.26) was significant (Wilcoxon W = 363.60, P = 0.007). In Rejaf, median seed density (top 2 cm layer = 9.44, interquartile range = 48.23, lower 10 cm l = 15.73, interquartile range = 38.79), was not significant. Although the median seed density in top layer was relatively high in Roton wetland (top 2 cm layer = 31.98 interquartile range = 185.57, lower 10 cm = 19.40, interquartile range = 159.36) it was not statistically significant (Table 2).
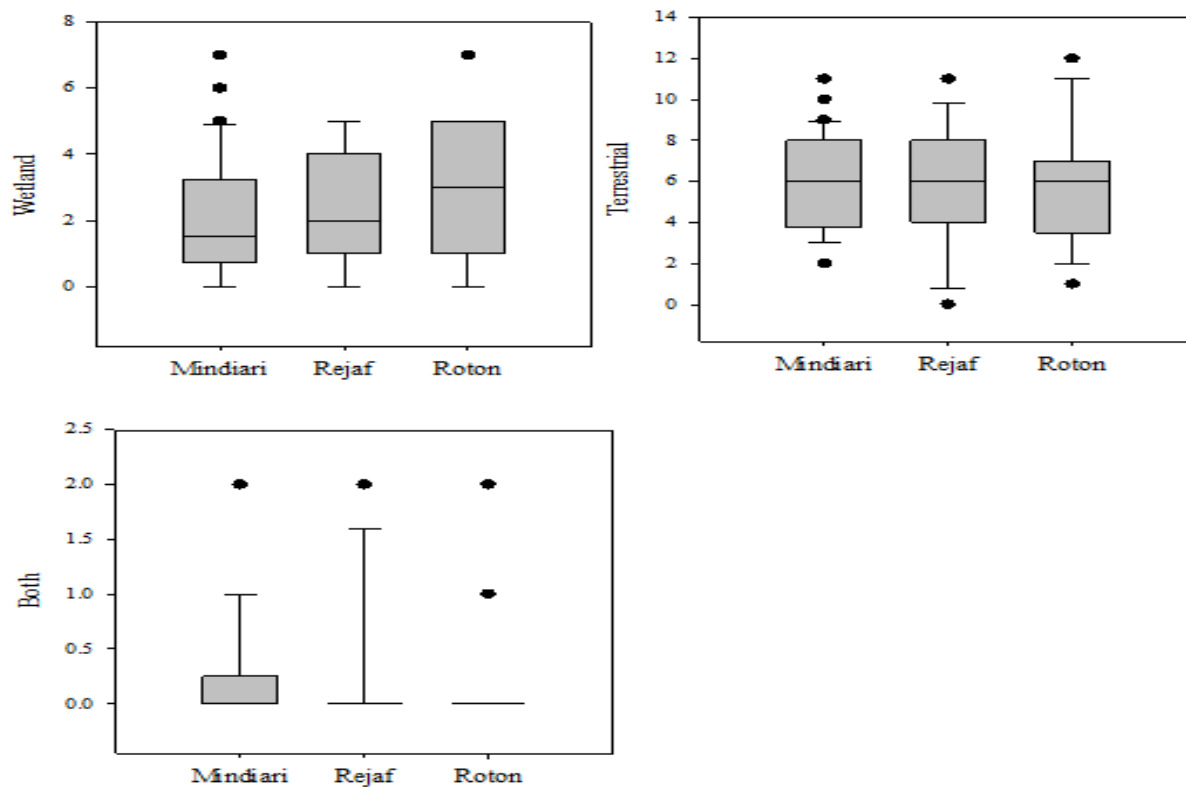
Figure 3. Soil seed bank species from Mindiari, Rejaf and Roton wetlands commonly found in wetland and terrestrial habitats.

The median of wetland species was slightly higher in the Roton wetland, but was not significantly different (K-W X^2_2 =2.515, P > 0.05). Terrestrial species were represented in equal proportions in soil seed banks of Mindiari, Rejaf and Roton wetlands as shown by similar medians (Figure 3). The median of terrestrial annual species was similar in Mindiari and Rejaf wetlands bout lower for Roton wetland (3.5) though not statistically significant. Median of terrestrial perennial species was slightly higher in Roton wetland (5.07) (K-W X^2_2 =2.577, P > 0.05) than Mindiari wetland (4.06) and Rejaf (4.03) though not significant (Figure 4). The median of families was also similar in Mindiari, Rejaf and Roton wetlands (K-W X^2_2 = 2.796, P>0.05).
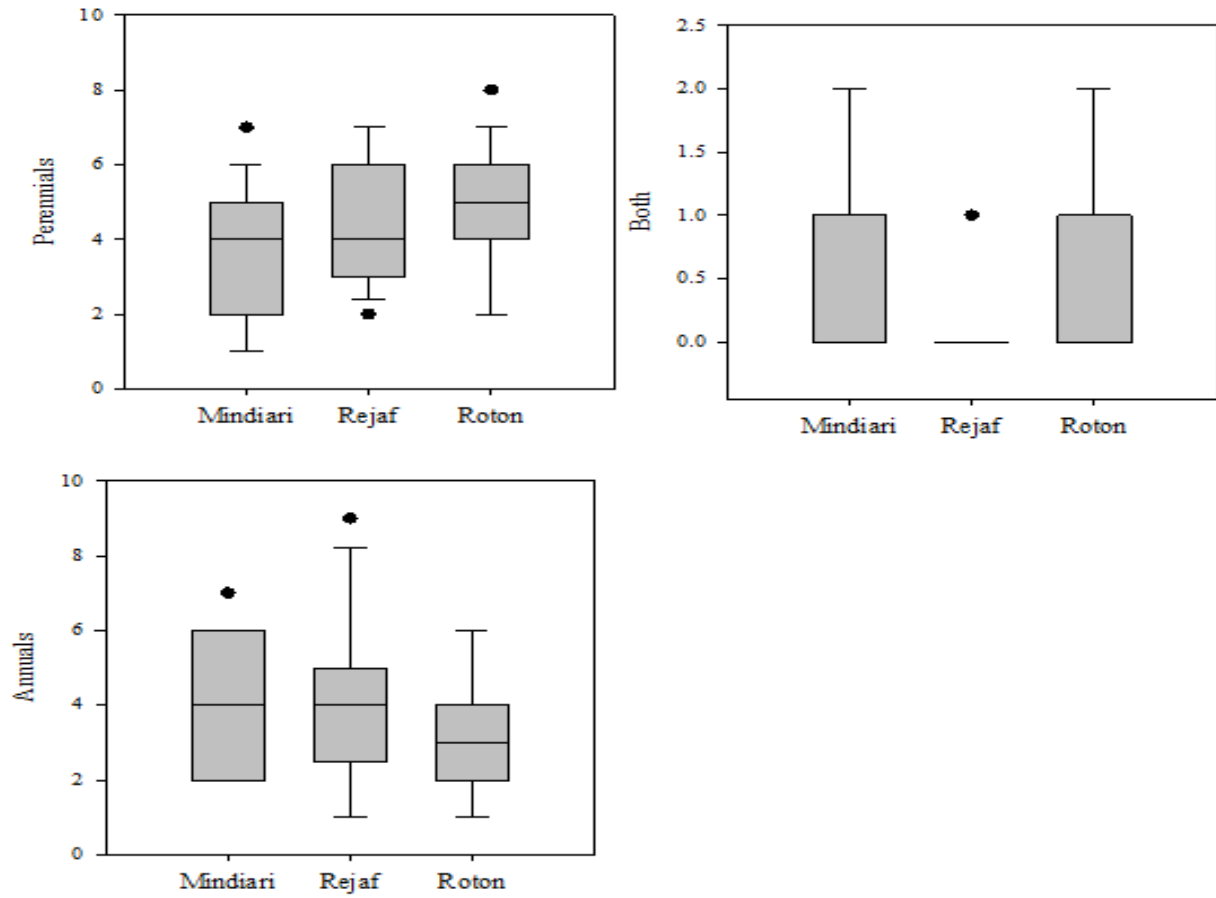
Figure 4. Life cycle of seeds from Mindiari, Rejaf and Roton wetlands.

Non woody species and sedges were similar in the three wetlands. Generally, woody species representation in the soil seed bank was scanty with only one terrestrial species (*Euclea divinorum* Hiern) germinating from the soil seed bank of Roton wetland (Figure 5).
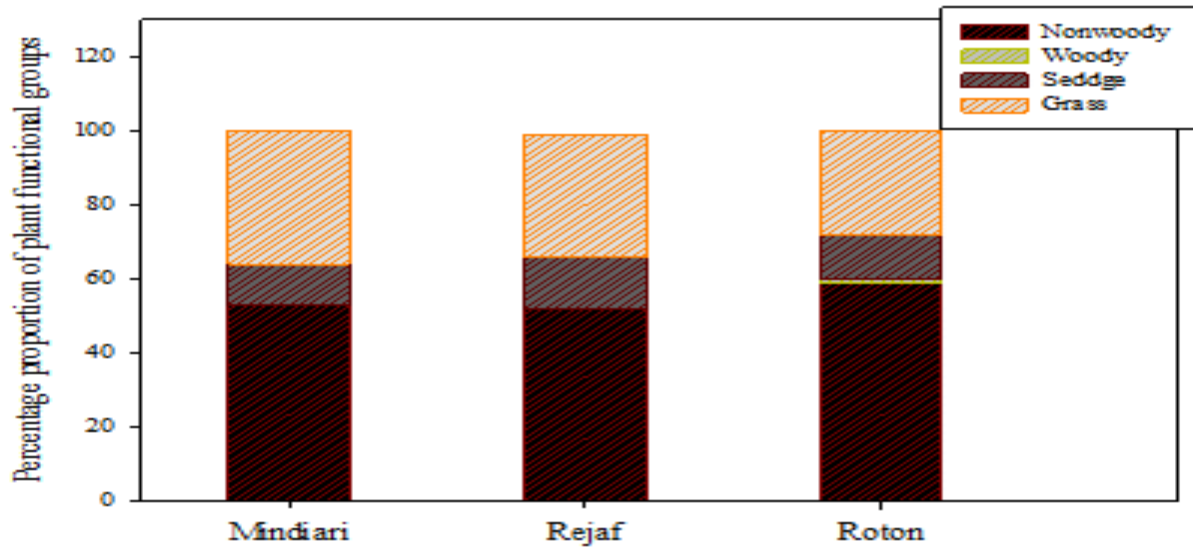
Figure 5. Proportion of plant functional groups in soil seed bank of Mindiari, Rejaf and Roton wetlands.

Results from two-dimensional NMDS ordination (iterations =200; stress = 0.15) showed that species composition of cultivated wetlands was different from uncultivated wetlands (Figure 6). This finding was augmented by results from SIMPER, which showed 97.38 dissimilarity between Mindiari and Rejaf wetlands. *Brachiaria decumbens*, *Digitaria longiflora*, *Cynodon nlemflehensis*, *Cynodon dactylon*, *Cyperus esculentus* and *Centurea inatongensis* tended to occur in wetlands that had been cultivated most and moderately occurred in Mindiari and Rejaf wetlands respectively (Figure 6).
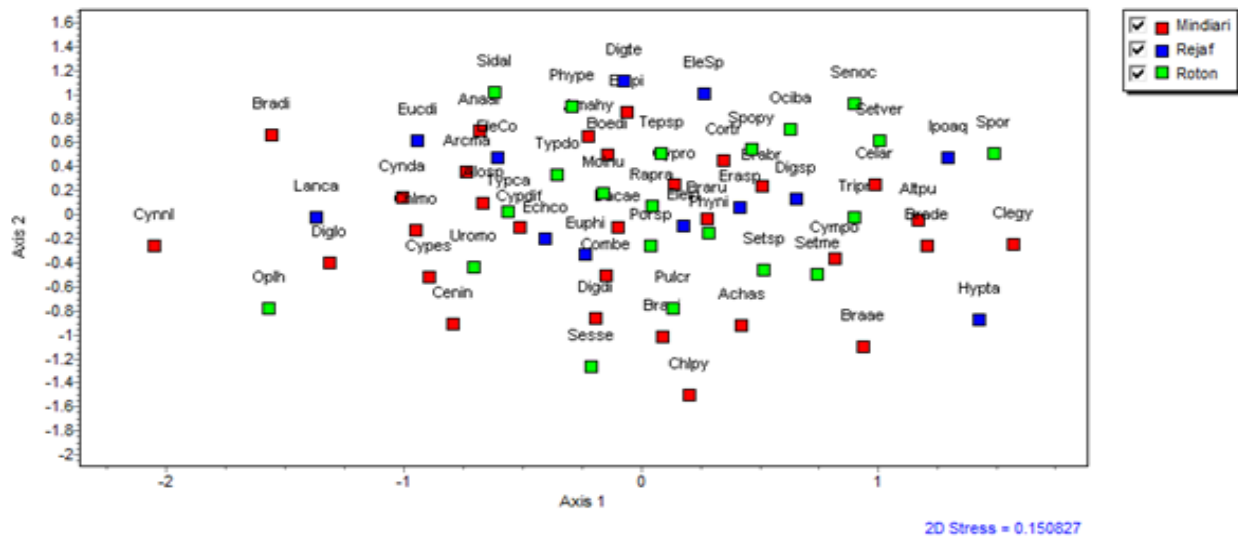

Figure 6. Axes 1 and 2 of the two dimensional NMDS ordination of soil seed bank species composition in most cultivated (Mindiari), moderately cultivated (Rejaf) and least cultivated (Roton) wetlands of Juba city

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Discussion

Results show that in total, 64 species germinated of which eight were wetland species. Species richness, diversity and number of terrestrial annual and perennial species was similar in all the three wetlands. While the median seed density was higher in Roton wetland and there were fewer seeds in the top 2 cm soil layer in Mindiari and Rejaf wetlands than in Roton wetland. Results from NMDS ordination showed that species composition of Mindiari and Rejaf was different from that of Roton wetland. Terrestrial species such as *Brachiaria decumbens*, *Digitaria longiflora*, *Cynodon nlemflehensis*, *Euclea divinorum*, *Cynodon dactylon*, and *Centurea inatongensis* were associated with Mindiari and Rejaf wetlands; representing most and least cultivated wetlands respectively. Wetland species such as *Typha capensis* and *Cyperus difformis* were associated with all the three wetlands.

These findings suggest that cultivation of wetlands has no influence on species richness and diversity. This did not support the prediction of high species richness and diversity in least cultivated wetland and low species richness in the heavily cultivated wetlands. Previous studies report mixed findings on species richness and diversity of soil seed banks in relation to the extent of wetland cultivation. Soil seed banks from cultivated wetlands may be species rich (Bao *et al*., 2014; Wang *et al*., 2016) or species poor (Middleton 2003; Amiaud and Touzard, 2004; Wang *et al*., 2015). Species that grow in wetlands require special adaptations to survive, grow and reproduce in a unique environment associated with waterlogging, frequent hydroperiod and heavy deposition of detrital matter (Shipley and Parent, 1991; Warwick and Brock, 2003; Fraser and Karnezis, 2005; Sakagami *et al*., 2020). However, human activities such as cultivation affects wetland hydrological regimes and water quality (Downs and Piégay, 2019) which influences plant growth in the wetlands (Dai *et al*., 2016; Byun, Nam and Kim, 2017; Hu *et al*.,

2020). Crop cultivation did not limit species richness and diversity in Mindiari and Rejaf wetlands which are classified as most and medium cultivated respectively. This might explain why species richness and diversity was similar in Mindiari, Rejaf and Roton wetlands irrespective of the extent of cultivation. At the same time, wetland soil seed bank species are known to be resilient (Ma *et al*., 2014) and survive episodes of cultivation (Galatowitch and van der Valk, 1996; Wang *et al*., 2016).

Seed density was lower and the top 2cm soil layer had fewer seeds in Mindriari and Rejaf wetlands. It appears that cultivation reduces the soil seed density as it destroys wetland vegetation through direct vegetation removal thus limiting seed rain (Brown and Cahill Jr., 2020). In addition, seed density declines in cultivated wetlands due to seed losses arising from reduced viability (Eldridge and Lunt, 2010), limited seed dispersal into the site (Soomers *et al*., 2013) or increased germination because of improved aeration and light availability (Baskin and Baskin, 2006). Many factors affect the rate of seed loss including longevity of seeds, duration of cultivation and type of wetland (Leck and Brock, 2000; Middleton, 2003).This finding is in agreement with previous studies on seed density of cultivated wetlands. For example, a study in the prairie pothole depression wetlands of North America revealed that wetlands used for corn and soybean cultivation had low seed density compared to uncultivated natural wetlands (Galatowitsch and van der Valk, 1996). Similarly, seed density was lower in wetlands reclaimed for soybean and paddy rice growing in Sanjiang, China (Wang *et al*. 2015).

This study indicates that the three wetlands have similar number of annual (primary wetland species) and perennial (secondary wetland species) germinating from the soil seed bank. It would be logical to expect more annual species to germinate from the soil seed bank of Mindiari and Rejaf wetlands since most annuals have small seeds, are easily buried and incorporated

into soil seed bank. However, this was not observed. Besides seed size, other factors influence seed availability in wetlands including dispersal mechanism, wetland type and seed predation (Chambers and MacMaho, 1994; van den Broek *et al.*, 2005 and Fraaije *et al.*, 2017). In terms of wetland vegetation regeneration, the findings are not in agreement with some of the previous studies. For instance, one of the earlier studies found that annuals such as *Amaranthus rudis* were more dominant in restored than undisturbed wetlands in the Canadian prairie pothole wetland ecosystems, while perennials such as *Leersia oryziodes* and *Phragmites australis* dominated undisturbed wetlands (Galatowitch and van der Valk, 1996). Another study revealed that restored Playa wetlands in America were dominated by mudflat annuals and lacked deep-rooted emerged perennial species associated with natural wetlands (Beas *et al.*, 2013). In this study, the dominant terrestrial annual species in Mindiari and Rejaf wetlands was *Phyllanthus niruri*, an annual species common in disturbed sites. Meanwhile *Echinochloa colona*; primary wetland species and *Cyperus difformis* and *Typha capensis*; secondary wetland species dominated the soil seed bank of all the wetlands. *E. colona* is an invasive species of seasonally flooded habitats, agricultural landscapes and pastures and has the potential to change species composition of wetland species (Zedler and Kercher, 2004; Hedja *et al.,* 2009; Andrew, 2018). This has negative implications on natural regeneration because invasive species impede natural regeneration of wetlands (Vilá *et al.*, 2011).

The NMDS results show that species composition of Mindiari (most disturbed), Rejaf (moderately disturbed) and Roton (least disturbed) wetlands was different, implying that cultivation influences species composition. Previous studies have shown that species composition in cultivated wetlands differed. For example, intact, restored and cultivated wetlands had different species composition with deep emergent invasive perennials and annuals associated with cultivated wetlands (Beas *et al.*,

2013). Similarly, species composition of natural wetland was different from that in the soybean and rice paddy fields (Wang *et al.*, 2015). In contrast, Bao *et al.,* (2014) reported similarity in plant species composition from seed bank of native and cultivated Pantanal wetland ecosystem probably due to flooding which acted as an environmental filter that restricted the establishment of invasive species such as *Urochloa humidicola* and favored growth of native species. Findings from this study also show that *Typha capensis* and *Cyperus difformis* occurred in all the three wetlands (Figure 6). High fecundity might explain the occurrence of these species in the seed bank of all the three wetlands. *Typha* species produce several tiny (<2 mm long) wind dispersed seeds which survive for long periods in the soil (van der Valk and Davis, 1976) and can regenerate by rhizomes (Redish, 1964). In many tropical wetlands, *Typha* sp. often forms dense canopy and excludes other wetland species (Keddy, 2010). *Cyperus difformis* is a prolific seed producer and completes vegetative and reproductive cycles in a short period of time (Holm *et al.*, 1977). The family Cyperaceae is a common weed in wetlands planted with agricultural crops including paddy rice in many countries (May, 1981) and might explain the dominance of these species that belong to this family in both wetlands. Since *Cyperus difformis* and *Typha capensis* were dominating, these species could play an important role in the UN Decade of Ecosystem Restoration (2021-2030) which calls for efforts to restore degraded ecosystem including wetlands.

Of the eight-wetland species, *Cyperus esculentus*, *Ipomoea aquatica* and *Pulicaria crispa* were the least represented in all the three wetlands. Many factors may explain this including species ability to from soil seed banks which is associated with seed longevity (Honda 2008; Phartyal *et al.,* 2019), changes in wetland water regime which influences recruitment (Shoemaker and Ervin, 2020) and germination conditions (Gonzalez and Ghermandi, 2012). These factors interactively explain low representation species in the seed banks and hence limit the potential of these

species to contribute to natural vegetation regeneration of these wetlands.

Conclusions and recommendations

In conclusion, the study has shown that growing crops in wetlands i) does not influence species richness and diversity; ii) negatively affects seed density; and iii) alters species composition. Although wetland species were not significantly different in the three-wetland categories, dominance of canopy species belonging to Typhaceae and Cyperaceae indicates that these species are resilient to cultivation and could facilitate natural regeneration of wetlands. However, low seed density of other species suggests that additional seeding might be required to facilitate regeneration of these species in Mindiari and Rejaf wetlands. Further studies are recommended to examine the effect of duration of cultivation and flooding regimes on

wetland soil seed bank species richness, diversity, density and composition in cultivated wetlands. If species such as *E. colona, T. domingensis* with low seed densities are to be assisted through seeding, more research on germination and survival of these species is vital.

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