

Dynamics of the Soil Seed Bank and Regeneration Potential of Hydromorphic Ecosystems in the North-Sudanian Zone of Burkina Faso

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Abstract

In a context of global change, understanding the regeneration potential of semi-arid hydromorphic ecosystems is crucial for their sustainable management. This study, conducted in Burkina Faso, aimed to characterize the soil seed bank (SSB) of three hydromorphic ecosystems, a rice field, a lowland and a gallery forest. The experimental design involved collecting soil samples within 12 plots of 100 m² at three soil layers (0 - 5 cm, 5 - 10 cm and 10 - 15 cm). In total, 936 soil samples were pooled into 36 composite soil samples and then incubated in a greenhouse for three months for seedling emergence. The data were used to determine SSB diversity and density, while multivariate analyses evaluated SSB similarity between the aboveground vegetation. The results revealed that SSB is composed of 37 species (36 herbaceous and 1 woody species) belonging to 23 families. The dominant families were Poaceae, Lamiaceae, and Rubiaceae. The gallery forest exhibited the highest species richness (31 species), while the rice field displayed the highest density (>10 seeds/dm³), dominated by ruderal species (*Ludwigia decurrens*, *Hyptis spicigera*). The vertical distribution of SSB density and species richness was homogeneous across the top 15 centimeters of soil. Multivariate analyses showed a strong similarity between the aboveground vegetation and the SSB within each floodplain ecosystem. Furthermore, these analyses highlighted that the germinable SSB structure (under greenhouse conditions) of these floodplain ecosystems is primarily driven by site-specific environmental factors rather than soil depth. These findings confirm the role of the SSB as a biological memory. Although agricultural intensification simplifies the flora, the natural regeneration po-

tential remains significant, providing concrete pathways for the sustainable management and restoration of critical semi-arid hydromorphic (floodplain) ecosystems in West Africa.

Keywords

Anthropization, Burkina Faso, Natural Regeneration, Soil Seed Bank, Wetlands

1. Introduction

The soil seed bank (SSB) holds considerable ecological importance for maintaining plant biodiversity. It serves as a primary source of natural re-establishment of vegetation following environmental disturbances, including anthropogenic pressures [1]. Indeed, the trajectory of natural regeneration and restoration in ecosystems degraded by human pressure heavily depends on the stock of viable seeds buried within the soil [2]. The SSB can also ensure the ecological resilience of plant communities subjected to flooding regimes [3]. Vegetation formations associated with rivers and watercourses are typically subjected to flooding regimes characterized by high heterogeneity and high species richness; however, they are currently undergoing massive destruction due to anthropogenic activities [4]. Research conducted on riparian flood meadows highlights the critical role of these ecosystems in their capacity to regenerate and reconstitute biodiversity [5] [6]. Within these riparian vegetation complexes, seasonal floods constitute major recurrent disturbances [7]. The seed bank in these environments is composed of the standing in-situ stock, the seed rain from neighboring vegetation, and seeds transported by the disturbance itself. During a flood event, erosive dynamics or fine sediment deposition vary substantially across space and time [7]. This phenomenon frequently strips the topsoil layer, which is subsequently covered by new allochthonous deposits left behind by high waters [7]. Although several studies on the SSB have been conducted in Burkina Faso to characterize regeneration dynamics in savannas and fallows [8]-[12], few studies have focused on evaluating seed banks within hydromorphic ecosystems. These ecosystems, despite being critical for ecological resilience and food security in semi-arid zones, suffer from a significant deficit in scientific data regarding their natural regeneration potential from the soil. To address this knowledge gap, the objective of this study is to contribute to the sustainable management of hydromorphic ecosystems in the North-Sudanian zone of Burkina Faso. Specifically, this study aims to: 1) evaluate the composition, diversity, density, and vertical distribution of the SSB across three hydromorphic ecosystems (a rice field, a lowland, and a gallery forest) in the large floodplain of Saria in the Nando Region of Burkina Faso; and 2) assess the degree of similarity and relationship between the SSB flora and the aboveground vegetation of these three ecosystems. To achieve the study's aims and objectives, the following hypotheses were formulated: a) the composition, diversity, density, and

vertical distribution of germinable SSB structure (under greenhouse conditions) in the SSB are significantly structured by the type of hydromorphic ecosystem (rice field, gallery forest, lowland) rather than by soil depth alone; and b) there is a strong floristic similarity between the SSB and the corresponding aboveground vegetation of each hydromorphic ecosystem.

2. Materials and Methods

2.1. Description of the Study Site

The study was conducted within plant communities of the floodplains in the village of Saria, located in the Boulkiemdé Province (Nando Region ex-Central-West Region, Burkina Faso) (Figure 1). The site is 23 km away from the city of Koudougou and 80 km from the Burkina Faso capital Ouagadougou [13]. Its geographical coordinates are 12°16'N latitude and 2°09'W longitude, with an average elevation of 300 m. The site is located within the North-Sudanian phytogeographical zone, characterized by an annual rainfall oscillating between 600 and 900 mm. The climate is typically Sudanian, featuring a long dry season (October to May) and a short rainy season (June to September). The dominant soils are ferric Lixisols [14]. These poor and leached soils are limited at depths ranging from 50 to 80 cm by an ironstone duricrust [15]. The local flora comprises annual herbaceous plants, trees, and shrubs [16]. The main woody tree species include *Parkia bi-globosa* (Jacq.) R.Br. ex G.Don, *Vitellaria paradoxa* C.F.Gaertn., *Adansonia digitata* L., *Tamarindus indica* L., *Lannea microcarpa* Engl. & Krause, and *Saba senegalensis* (A.DC.) Pichon. The shrub layer is dominated by *Guiera senegalensis* J.F.Gmel., *Combretum nigricans* Lepr. ex Guill. & Perr., and *Piliostigma reticulatum* (DC.) Hochst. [17]. The herbaceous layer is mainly characterized by widespread species such as *Andropogon gayanus* Kunth and *Cyperus rotundus* L [17].

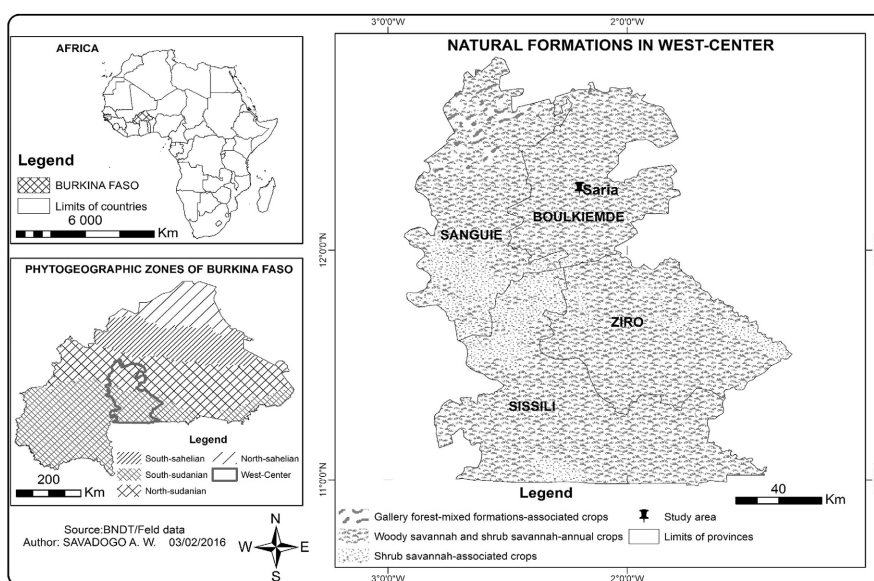


Figure 1. The study area is located in the Boulkiemdé Province, specifically within the Saria Agricultural Research Station.

2.2. Selection of Sampling Sites

The floodplain ecosystems targeted in this study correspond to lands characterized by a distinct hydromorphic regime. Three contrasting types of hydromorphic ecosystems were selected within the village lands of Saria: a rice field, a seasonally flooded lowland (bas-fond), and a gallery forest. These three sites were identified based on their topo-sequential position, seasonal water dynamics, and land-use practices, thereby providing a representative gradient of floodplain ecosystems found in the North-Sudanian phytogeographical zone.

The structural attributes, light availability, and level of human disturbance characterizing each site are summarized in **Table 1**.

Table 1. Structural characteristics and land-use intensity across the selected sampling sites.

Site/Physical variables	Rice field	Seasonally flooded lowland	Gallery forest
Flood regime and duration	Controlled to semi-controlled Temporary to prolonged flooding (3 to 5 months). Strict alternation of drying and submersion.	Natural and variable. Prolonged to permanent submersion (4 to 8 months). Fluctuations based on local floods.	Ephemeral to temporary. Occasional flooding during high water events (a few days to weeks). Saturated but well-drained soil.
Canopy cover	Open Cover: 0% (or limited to the rice herbaceous layer, <30%). Direct sunlight	Open to semi-shaded Cover: 10% to 40% (helophytes, tall grasses, and scattered bushes).	Closed Cover: 70% to 90% (trees and shrubs). Dense shade, low direct radiation.
Anthropogenic management practices	Intensive and recurring • Soil tillage (plowing, leveling) • Weeding (manual/chemical) • Fertilization (NPK/urea) • Biomass removal (ou <i>Biomass export</i>)	Low to moderate • Occasional extensive grazing • Occasional vegetation cutting • No direct soil tillage	Negligible to low • Minor harvesting • Absence of mechanical soil disturbance

2.3. Assessment of Aboveground Vegetation

To compare the plant communities emerging from the soil seed bank (SSB) with the existing aboveground (standing) vegetation, an exhaustive floristic inventory was conducted within a 2500 m² plot (50 m × 50 m) established at each selected site. For the woody layer, dendrometric surveys were performed. The total height and diameter at breast height (DBH) of each individual woody plant were measured using a graduated pole and a diameter tape, respectively. For multi-stemmed individuals branching below 1.30 m, the quadratic mean diameter (dm) was calculated using the following formula:

$$dm = \sqrt{\frac{1}{n} \sum_i^n di^2}$$

where di represents the diameter of the i -th stem, and n is the total number of measured stems for the individual. Woody individuals with a dbh ≥ 5 cm and a height greater than 1.5 m were classified as adult trees, whereas those with lower values were categorized as juveniles. The herbaceous layer was sampled within the same 2500 m² plots using the aligned point-quadrat method [18]. Readings were recorded along transect lines 200 m in length, noting the plant species intercepted by a fine pin every 2 m. This resulted in 100 reading points per transect.

2.4. Soil Seed Bank Sampling and Sample Collection

Soil samples were collected from the three different floodplain ecosystems at sampling depths of 0 - 5 cm, 5 - 10 cm and 10 - 15 cm [13]. Following a transect line, four (4) main plots of 100 m² (10 m $\times$ 10 m) were randomly established within each of the floodplain ecosystems. Twenty-five (25) subplots of 2 m $\times$ 2 m were demarcated within each main plot (Figure 2). Thirteen (13) of these subplots were systematically selected for sampling, ensuring an empty subplot was left between each sampled subplot [9]. Within the selected subplots, soil samples were taken from opposite ends of the diagonals and alternated from one row to another along the diagonals [9]. This resulted in a total of 26 sampling points per plot. Samples were collected using a knife and an auger with a depth of 5 cm [7]. In total, 78 soil samples (26 points $\times$ depths) were collected per plot. This represents a grand total of 936 individual samples (78 samples $\times$ 4 plots $\times$ 3 land types) across all three floodplain ecosystems. The samples from each plot and soil layer were then mixed to form a homogeneous composite sample. This process yielded 12 composite samples per floodplain ecosystem (4 plots $\times$ 3 depths), for a grand total of 36 composite samples across the entire study. Each plot-depth composite sample served as the experimental unit.

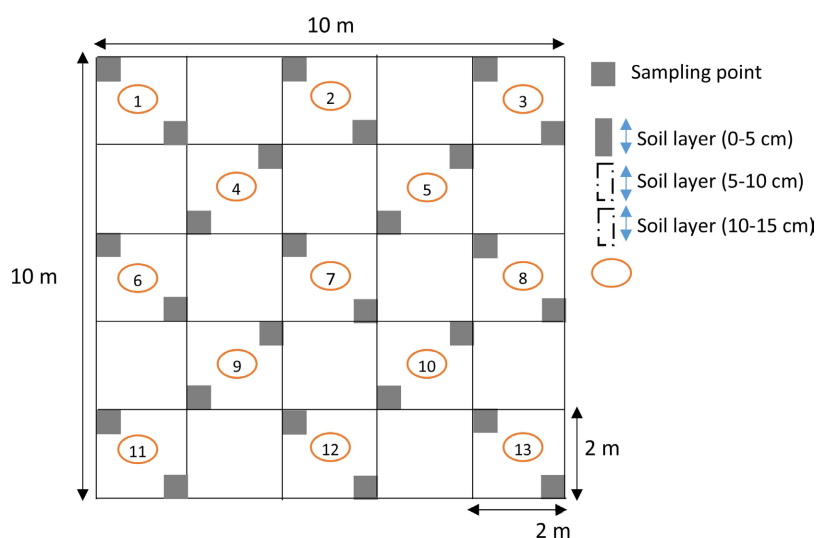


Figure 2. Soil sampling layout.

2.5. Soil Seed Bank Assessment and Germination Protocol

To facilitate sample identification, a coding system was established. The sampling sites were designated by the codes BAF for the lowlands (bas-fond), RIZ for the rice fields, and GAL for the gallery forest. These codes were followed by the labels P1, P2, and P3, corresponding to the soil horizons of 0 - 5 cm, 5 - 10 cm, and 10 - 15 cm depth, respectively. Finally, the subscripts R1, R2, R3, and R4 indicate the four replicates carried out for each treatment (**Figure 3**). The trays were placed on pallets inside the greenhouse to avoid any contact with a source of contamination. In addition, 10 trays containing sterilized sand were randomly distributed throughout the greenhouse to check for airborne contamination. Every week, all germination trays were monitored for emerging seedlings to estimate the germinable soil seed bank size. Emerging seedlings were identified (by species and biological type), counted, and removed. Those that were difficult to distinguish at the juvenile stage were left in the trays longer until they could be identified.

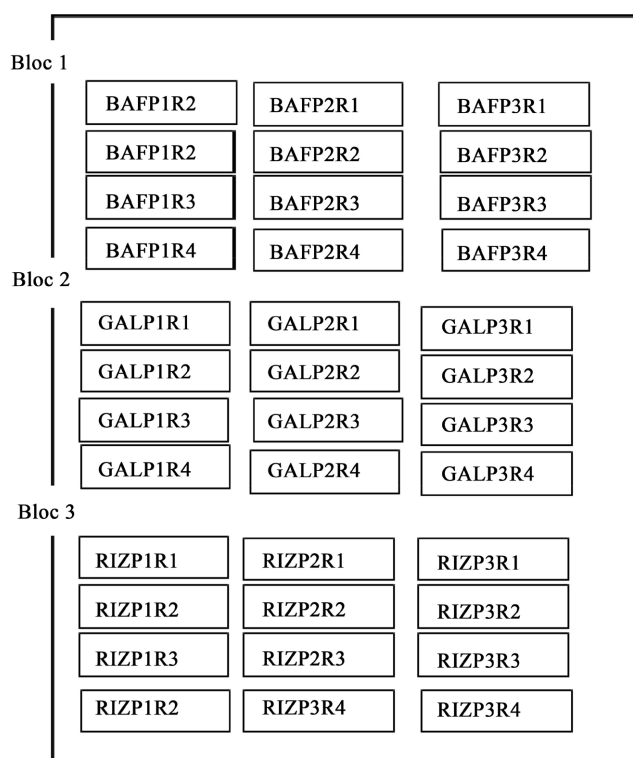


Figure 3. Experimental setup for the soil sample germination.

2.6. Data Analysis

Parameters related to species composition and vegetation structure, as well as soil seed bank (SSB) density and species richness, were subjected to a two-way analysis of variance (ANOVA) to assess the main effects of floodplain ecosystem type, soil depth layer, and their interaction term (Flooding site $\times$ Depth). Prior to ANOVA, normality and homogeneity of variances were verified. When significant main effects or interactions were detected ($p < 0.05$), pairwise post-hoc comparisons were

performed using Tukey's HSD test. Effect sizes were estimated using partial eta squared (η^2).

The number of germinated seeds and species richness were aggregated by floodplain ecosystem and soil sampling layer, and then converted into density (number of seedlings per dm^3) [11]. To evaluate the vertical seed distribution across the floodplain ecosystem, seedlings from each similar layer were combined to determine the density by sampling depth. Seedling density was calculated using the following formula:

$$\text{Seedling density} = 100 \times \frac{\text{Cumulative Number of seedlings}}{\text{Soil Volume per polypropylene}} \quad (1)$$

The Shannon index (H') and Pielou's evenness index (J') were used to assess species diversity and the even distribution of individuals within the SSB across the floodplain ecosystem and soil layers, respectively [19]. The Shannon index was calculated using the following formula:

$$H' = - \sum_{i=1}^S p_i \ln(p_i) \quad (2)$$

where S is the species richness, $p_i = n_i/N$, and $\ln$ is the natural logarithm [20]. Under this natural log formulation, H' is strictly bounded by $0 \leq H' \leq \ln(S)$. Pielou's evenness index (J') was determined using the formula: $J' = H'/\ln(S)$. [20].

Pielou's evenness index (E) was determined from the formula:

$$E = \frac{H}{H_{\max}} = \frac{H}{\log_2 S} \quad (3)$$

where $H_{\max}$ is the theoretical value of the maximum diversity that can be reached in each type of floodplain ecosystem. It measures the degree of species diversity in the SSB according to the floodplain ecosystem [21]. According to [17], this index is low when $E < 0.6$; medium when E is within the interval 0.6 to 0.70; and high when $E \geq 0.8$. The relationship between the specific compositions of the SSB of the types of floodplain ecosystem was evaluated by calculating the Jaccard similarity index according to the formula:

$$J = \frac{C}{a + b - c} \quad (4)$$

where a is the number of species shared between both ecosystems, b is the number of species unique to the first ecosystem, and c is the number of species unique to the second ecosystem. The corresponding Sørensen similarity index (Ss) is strictly derived using the identity $Ss = 2J/(1 + J)$.

In addition, the Sørensen index was applied to assess the similarity between the SSB of the different floodplain ecosystem. Both indices were calculated as follows:

$$\text{Jaccard similarity index (Sn): } Sn = \frac{S_{1,1}}{(S_{1,1} + S_{1,0} + S_{0,1})} \quad (5)$$

$$\text{Sørensen similarity index (Ss): } Ss = \frac{2c}{(2c + a + b)} \quad (6)$$

where $S_{i,1}$ = number of species common to two floodplain ecosystems/soil layers, $S_{0,1}$ = number of species unique to floodplain ecosystem $S_{0,1}$ / soil layer $S_{0,1}$. In the Sørensen formula, c = number of species common to the SSB and the above-ground vegetation, a = number of species present in the SSB, and b = number of species present in the vegetation survey. According to [7], these two indices fluctuate between 0 and 1, while the closer the result is to 1, the more similar the samples are. The relationships between the species composition of the SSBs and the aboveground vegetation across the floodplain ecosystems were analyzed using non-metric multidimensional scaling (NMDS). The ordination was performed on the floristic composition matrix, Sørensen distance as the dissimilarity metric. Prior to the analysis, abundance data were presence/absence transformed to downweight high-abundance species. The NMDS configuration was derived from multiple random starts (250 iterations) to avoid local minima and identify the optimal stable solution. Goodness-of-fit was assessed using Kruskal's stress value and Shepard diagrams.

The statistical significance of floristic compositional differences among ecosystem types and soil depth layers was formally tested using permutational multivariate ANOVA (PERMANOVA) based on the same distance matrix with 999 random permutations. All ordination and multivariate statistical analyses were performed using PC-ORD software (ver. 6.0).

To examine the relationships between taxon composition and external variables such as floodplain ecosystems and soil depths, canonical correspondence analysis (CCA) was selected using CANOCO software ver. 4.5 [22]. This technique detects patterns of variation in the germinable seed taxon data that can be “managed” by researchers and can be “best” explained by the observed external variables [23]. CCA ordains taxa using axes that are constrained to be linear combinations of the measured external variables, so that the relationship between the taxa and these variables is clearly visible. Thus, the ordination axes (representing the gradient of change in community composition) in CCA are extracted under the constraint that the axes are linear combinations of predefined external variables noted for each sample. To measure the association between species and external variables, we used the eigenvalue, which measures the magnitude of variation in species data explained by each axis, and therefore by the external variables [22].

3. Results

3.1. Floristic Composition and Vegetation Structure of the SSB across Floodplain Ecosystems

A total of 37 species were identified in the SSB across all three floodplain ecosystems. Herbaceous species largely predominated with 36 taxa, whereas only one woody species, *Sclerocarya birrea*, was recorded. The lowland (bas-fond) comprised 24 species, the gallery forest 31 species, and the rice field 23 species. These

species were distributed among 32 genera and 23 families (**Table 2**). *Spermacoce stachidea*, *Alysicarpus ovalifolius*, *Cyperus brevifolius*, *C. rotundus*, *Eragrostis tremula*, *Euphorbia hirta*, *Hexasepalum teres*, *Hyptis spicigera*, *Phyllanthus urinaria*, *Setaria viridis*, and *Spermacoce pusilla* were common to all three sites. However, species such as *Ipomoea eriocarpa*, *Ocimum americanum*, *Panicum dichotomiflorum*, *Sclerocarya birrea*, *Acmella uliginosa*, *Corchorus capsularis*, *Cyanthillium cinereum*, *Cyperus compressus*, *Desmodium triflorum*, *Euphorbia heterophylla*, *Hyptis alata*, *Hyptis suaveolens*, *Leucas martinicensis*, *Microchloa indica*, *Hibiscus cannabinus*, and *Echinochloa colona* germinated exclusively in either the lowland, rice field, or gallery forest. With 6 species, Poaceae was the most abundant family, followed by Lamiaceae and Rubiaceae, accounting for 13% each (**Table 2**). The proportion of annual herbs present in the SSB across all three sites accounted for 74% of the identified seeds, compared to 26% for perennials, which included one woody species (*Sclerocarya birrea*) (**Figure 4(a)**). Furthermore, five life forms (biological types) were recorded (**Figure 4(b)**), including Therophytes (74%), Chamephytes (3%), Hemicryptophytes (10%), Géophytes (10%) and Phanerophytes (3%).

Table 2. List of species that emerged from the SSB by floodplain ecosystem.

Species	Family	Lowland	Gallery forest	Rice field
<i>Ludwigia decurrens</i>	Onagraceae	11	0	251
<i>Spermacoce strachydea</i>	Rubiaceae	3	8	2
<i>Alysicarpus ovalifolius</i>	Fabaceae	1	3	2
<i>Bonnaya antipoda</i>	Linderniaceae	9	6	0
<i>Corchorus olitorius</i>	Malvaceae	7	8	0
<i>Cyanotis arachnoides</i>	Commelinaceae	1	13	0
<i>Cyperus brevifolius</i>	Cyperaceae	1	4	227
<i>Cyperus rotundus</i>	Cyperaceae	21	136	49
<i>Digitaria horizontalis</i>	Poaceae	3	0	1
<i>Eragrostis tremula</i>	Poaceae	13	21	6
<i>Euphorbia hirta</i>	Euphorbiaceae	2	12	3
<i>Hexasepalum teres</i>	Rubiaceae	43	19	12
<i>Hyptis spicigera</i>	Lamiaceae	8	1	117
<i>Ipomea eriocarpa</i>	Cuscutaceae	6	0	0
<i>Murdannia keisak</i>	Commelinaceae	5	1	0
<i>Ocimum americanum</i>	Lamiaceae	1	0	0
<i>Panicum dichotomiflorum</i>	Poaceae	5	0	0
<i>Phyllanthus urinaria</i>	Phyllantaceae	1	2	5
<i>Sclerocarya birrea</i>	Anacardiaceae	1	0	0
<i>Setaria viridis</i>	Poaceae	5	1	1

Continued

<i>Spermacoce pusilla</i>	Rubiaceae	1	5	1
<i>Mitracarpus hirtus</i>	Rubiaceae	1	1	0
<i>Acalypha indica</i>	Euphorbiaceae	0	3	0
<i>Acmella uliginosa</i>	Asteraceae	0	13	0
<i>Corchorus capsularis</i>	Malvaceae	0	2	0
<i>Cyanthillium cinereum</i>	Asteraceae	0	3	0
<i>Cyperus compressus</i>	Cyperaceae	0	63	0
<i>Desmodium triflorum</i>	Fabaceae	0	1	0
<i>Euphorbia heterophylla</i>	Euphorbiaceae	0	1	0
<i>Hyptis alata</i>	Lamiaceae	0	3	0
<i>Hyptis suaveolens</i>	Lamiaceae	0	0	6
<i>Leucas martinisensus</i>	Lamiaceae	0	2	0
<i>Microchloa indica</i>	Poaceae	0	23	0
<i>Physalis angulata</i>	Solanaceae	0	1	1
<i>Hibiscus cannabinus</i>	Malvaceae	0	0	5
<i>Echinochloa colona</i>	Poaceae	0	0	9
<i>Spermacoce radia</i>	Rubiaceae	0	2	4

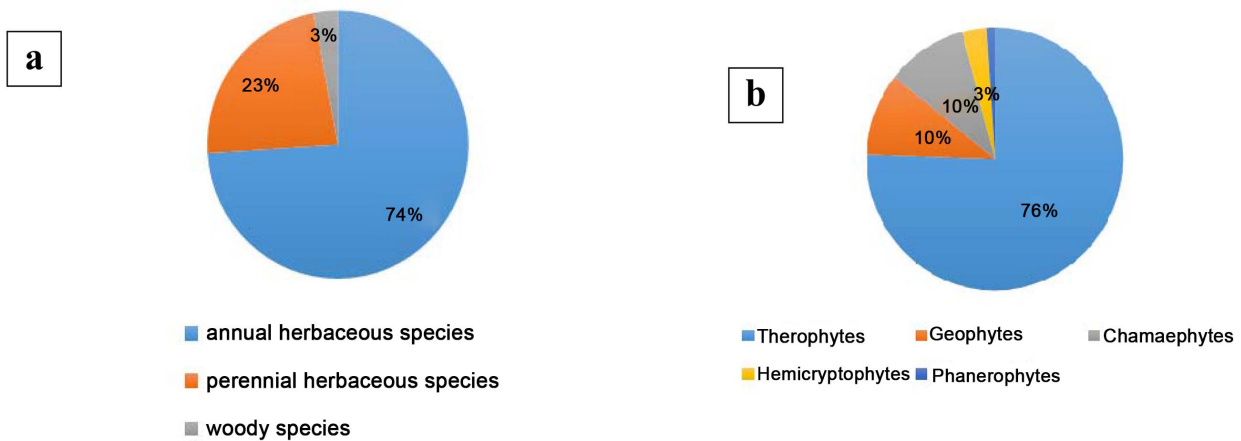


Figure 4. Species composition structure of the Soil Seed Bank (SSB) across all floodplain ecosystems.

3.2. SSB Diversity and Similarity across Floodplain Ecosystems

The gallery forest exhibited the highest species richness with 31 species identified in the SSB, followed by the lowland (24 species) and the rice field (23 species). Overall, the species diversity of the SSB across the three sites was moderate; however, the gallery forest was structurally the most diverse (Shannon index = 3.43), although the difference with the rice field (3.36) remained narrow. Furthermore, species dominance within the SSB was low across all three floodplain ecosystems. The lowland area was the most balanced site in terms of species abundance (Pié-

low's evenness index = 0.814). Conversely, evenness decreased in the gallery forest (0.660) and dropped even more sharply in the rice field (0.558) (**Table 3**). The similarity indices calculated between the different sites revealed a strong similarity between the lowland (bas-fond) and the rice field, with respective values of 0.45 (Jaccard) and 0.60 (Sørensen), indicating a high consistency between the SSB species of both sites. Between the lowland and the gallery forest, the similarity was moderate (0.37 and 0.53). Conversely, the gallery forest and the rice field displayed the lowest similarity (0.33 and 0.50), thus sharing fewer common species within their SSB (**Table 4**).

Table 3. Summary of soil seed bank (SSB) diversity indices across different floodplain ecosystems.

Floodplain ecosystems	Shannon-Wiener (H') index	Species' specific richness (S)	Simpson's Dominance Index (D)	Pielou's Evenness Index (E)
Lowland	2.59	24	0.917	0.814
Gallery forest	2.27	31	0.933	0.66
Rice field	1.75	23	0.951	0.558

Table 4. Jaccard and Sørensen similarity indices of the SSB across different floodplain ecosystems.

Similarity index	Floodplain ecosystems	Lowland
Jaccard similarity index (Sn)	Lowland	1
	Gallery forest	0,37
	Rice field	0,45
Sørensen similarity index (Ss)	Lowland	1
	Gallery forest	0.53
	Rice field	0.62

3.3. Effect of Floodplain Ecosystem on SSB Density

Regarding seed density among the floodplain ecosystems, a statistically significant main effect of ecosystem type was observed (**Table 5**; $F_{2,23} = 8.24$, $p = 0.002$, $\eta^2 = 0.42$). Post-hoc comparisons revealed a significant difference between the rice field and the remaining sites. Indeed, with a germinable seed density exceeding 10 seeds/dm³, the rice field was by far the most populated site in terms of SSB (**Table 5**). It was followed by the gallery forest and the lowland (bas-fond), both of which recorded mean densities below 5 seeds/dm³. Conversely, no significant difference was observed in the species richness of the germinable SSB across the different floodplain ecosystems.

Regarding vertical distribution, the effect of soil depth showed only a non-significant, marginal trend at the 5% significance level (**Table 5**; $F_{2,23} = 3.00$, $p = 0.0697$, $\eta^2 = 0.21$). Consequently, no significant differences were found among the SSB seed densities or species richness across the three evaluated depth layers (0 - 5 cm, 5 - 10 cm, and 10 - 15 cm). Furthermore, the interaction term between eco-

system type and soil depth was not statistically significant (**Table 5**; $F_{4,23} = 1.27$, $p = 0.3086$, $\eta^2 = 0.18$), confirming high vertical homogeneity within the SSB across all depth layers regardless of the ecosystem.

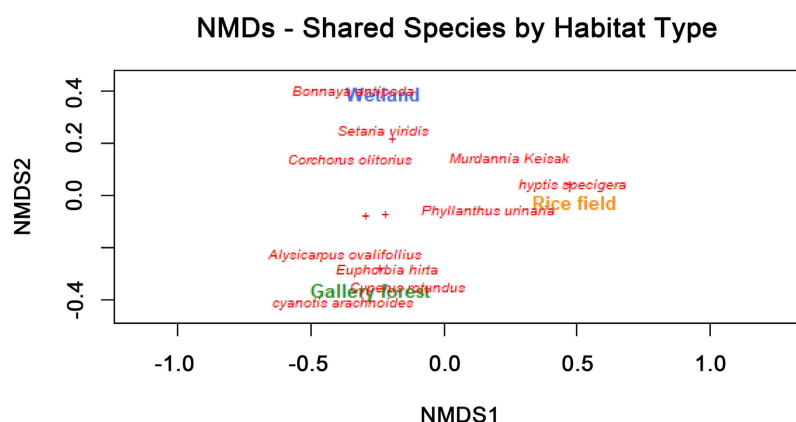
Table 5. Two-way ANOVA summary for the effects of ecosystem type and soil depth on the germinable soil seed bank characteristics.

Sources of variation	ddl	F	p-value	Effect size (η^2)
Site	2	8.24	0.002	0.42
Depth	2	3.00	0.0697	0.21
Site $\times$ Depth	4	1.27	0.3086	0.18

3.4. Relationship between SSBs and Aboveground Vegetation

Non-metric multidimensional scaling (NMDS) reveals distinct floristic similarities between the soil seed bank (SSB) and aboveground vegetation (AGV) across the three habitats stress = 0.0624; **Figure 5**). The rice field exhibited the highest community overlap with 15 shared species ($J = 0.556$, $S = 0.714$; SSB richness = 25, AGV richness = 17), driven by species such as *Hyptis spicigera*, *Phyllanthus urinaria*, and *Murdannia keisak*. In contrast, similarity between the seed bank and standing vegetation was markedly lower in the gallery forest ($J = 0.176$, $S = 0.300$; 9 shared species), characterized by *Cyperus rotundus*, *Euphorbia hirta*, *Alysicarpus ovalifolius*, and *Cyanotis arachnoides*, as well as in the lowland ($J = 0.119$, $S = 0.213$; 5 shared species), associated with *Bonnaya antipoda*, *Corchorus olitorius*, and *Setaria viridis*. Species near the center of the ordination space displayed a generalist character without strict habitat preference. Multivariate dispersion was homogeneous across factors (Betadisper: Compartment, $F_{1,10} = 0.0637$, $p = 0.8065$; Site, $F_{2,9} = 1.1526$, $p = 0.3800$), validating group variance assumptions. PERMANOVA confirmed that the interaction of Compartment and Site significantly structures community composition ($F_{4,7} = 3.2034$, $p = 0.001$), explaining 64.38% of the total variance ($R^2 = 0.6438$).

Canonical Correspondence Analysis (CCA) shows that the composition of the SSB is primarily structured by site type, with the effect of depth being more secondary. Axis 1 of the graph (**Figure 6**) clearly opposes the closed forest environment (gallery forest, on the left) to the open agricultural environment (rice field, on the right). The gallery forest is characterized by *Physalis angulata*, *Cyperus compressus*, and *Microchloa indica*, while the rice field is dominated by *Hyptis spicigera*, *Ludwigia decurrens*, *Corchorus capsularis*, and *Acalypha indica*. Axis 2 isolates the lowland (at the top) from the other two ecosystems, marked by specific species such as *Spermacoce* sp., *Panicum dichotomiflorum*, *Bonnaya antipoda*, and *Digitaria horizontalis*. The surface (P1) and intermediate (P2) layers more strongly influence the weed flora of the rice field (recent weeds), whereas the deep layer (P3) occupies a central position, reflecting a loss of floristic specificity at depth.



Site	SSB Richness	AGV Richness	Shared Species (a)	Jaccard (J)	Sørensen (S)
Gallery forest	26	34	9	0.176	0.300
Lowland	18	29	5	0.119	0.213
Rice field	25	17	15	0.556	0.714

NMDS STRESS = 0.0624. Betadisper (Compartment): Factor/Variable: Compartment; Test statistic (F): $F = 0.0637$; Degrees of freedom (df): 1, 10; p-value: $p = 0.8065$; Variance explained (R²): Diagnostic: Homogeneous dispersion ($p > 0.05$). Betadisper (Study Site): Factor/Variable: Study site; Test statistic (F): $F = 1.1526$; Degrees of freedom (df): 2, 9; p-value: $p = 0.3800$; Variance explained (R²): Diagnostic: Homogeneous dispersion ($p > 0.05$). PERMANOVA (adonis2): Factor/Variable: Compartment + Site; Test statistic (F): $F = 3.2034$; Degrees of freedom (df): 4, 7; p-value: $p = 0.001$; Variance explained (R²): $R^2 = 0.6438$; Diagnostic: Highly significant separation.

Figure 5. Relationship between the Soil Seed Bank (SSB) and aboveground vegetation using non-metric multidimensional scaling.

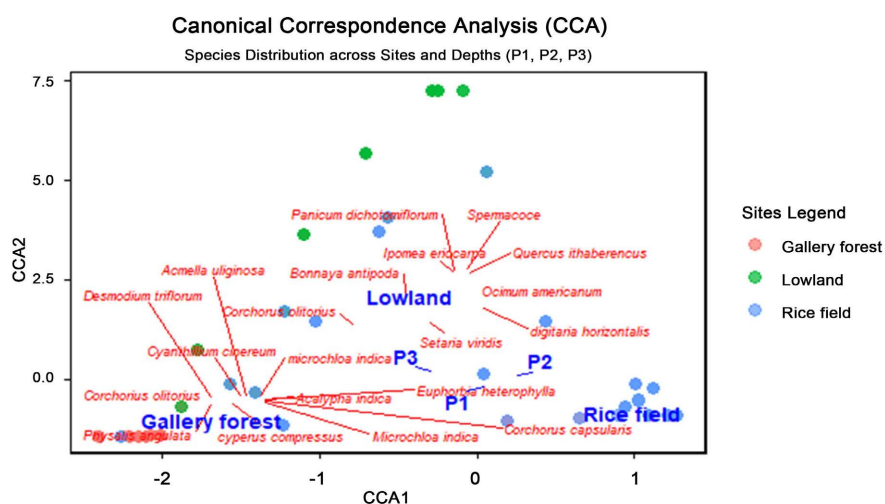


Figure 6. Effect of site and depth variables on the relationship between the Soil Seed Bank (SSB) and aboveground vegetation using CCA ($p < 0.05$).

4. Discussion

4.1. Composition of the Soil Seed Bank

The overall physiognomy of the studied SSB, characterized by a clear hegemony

of annual species, likely reflects an adaptation to hydrological disturbance cycles, aligning with models proposed by authors such as [24] and [25]. In disturbed environments, annual species tend to dominate because they invest their energy into massive seed production rather than perennial biomass. Furthermore, [26] and [7] demonstrated that in flood-prone areas, the water cycle acts as a key factor determining the composition of the SSB. Indeed, in these flood-prone environments, annuals survive the submersion phase as dormant seeds and then germinate rapidly as water levels recede. However, the emergence of *Sclerocarya birrea* indicates either a woody recolonization dynamic within the lowland or an exogenous seed input from unstudied neighboring environments. This highlights the complex exchanges between plateaus and lowland areas, which are certainly linked to surface runoff or other dispersal vectors. In fact, [27] notes that although *S. birrea* possesses a wide ecological amplitude, its presence in flooded zones remains rare. In this study, its occurrence could be explained by hydrochory (water dispersal) or zoochory (animal dispersal). The dominant botanical families identified were Poaceae, Lamiaceae, Rubiaceae, and Cyperaceae, which is consistent with the findings of authors like [11] and [28] in the savanna formations of the North-Sudanian zone of West Africa. The predominance of Poaceae and Cyperaceae can also be explained by the fact that these two families represent a classic signature of flooded ecosystems. According to [29], these families possess specialized tissues (aerenchyma) that enable them to survive in anoxic (oxygen-depleted) conditions. Additionally, [30] emphasizes that Cyperaceae produce seeds with thick seed coats capable of remaining viable in mud for several years, thereby forming a “biological memory” of the site. Herbaceous Lamiaceae operate as pioneer species [29]. Authors such as [31] classify them as “ruderals” that exploit the drawdown period (exondation) to germinate rapidly on bare, nutrient-rich soils. Regarding Rubiaceae, this family is highly diversified in tropical zones, showing a strong adaptive capacity along the fringes of flooded areas [32]. Although the gallery forest serves as a primary seed reservoir, the lowland appears to be the most structurally stable environment. Transition zones like gallery forests continuously receive seed fluxes from both the forest interior and surrounding savannas [33], while their tree canopy limits water erosion [34]. In contrast, the lowland which is subject to regular natural cycles (seasonal flooding without major anthropogenic disturbance) maintains a more balanced distribution of abundance within the SSB [35]. The drastic drop in evenness observed in the rice field reflects a “simplification” of the plant community driven by cropping practices, a phenomenon previously reported by authors like [36]. Indeed, ecological intensification in the rice field appears to favor a few highly competitive taxa at the expense of overall functional diversity. The fact that the lowland and the rice field share the highest number of species can be explained by the historical context, as most lowland rice fields are created by converting natural wetlands. According to [37], the “memory” of the SSB persists even after land conversion to agriculture. Furthermore, because these two environments are often adjacent or interconnected by the same drainage

network, seeds easily circulate via water transport [38]. Conversely, the low similarity between the gallery forest and the rice field illustrates a distinct functional divergence; agricultural intensification creates a hostile environment for forest species, while the dense shade of the gallery forest canopy limits the establishment of heliophilous (light-loving) crop weeds [39]. Furthermore, it should be noted that the seedling emergence method used in this study specifically characterizes the germinable soil seed bank under greenhouse conditions. Consequently, viable seeds that were dormant, quiescent, or required highly specific environmental triggers (such as seasonal submersion cycles or specialized lighting) may not have emerged during incubation, leading to a potential underestimation of the absolute total viable seed stock.

4.2. Vertical and Horizontal Distribution of Seeds in the Soil Seed Bank

The high density of the SSB in the rice field is a classic indicator of anthropogenic disturbance. Indeed, according to [37], cropland weeds such as certain Poaceae and Cyperaceae counteract the risks associated with tillage through phenomenal seed production, a phenomenon known as the “r-strategy” (characterized by rapid growth and high fecundity). This high SSB density in the rice field can also be explained by the fact that tillage and agricultural practices bury seeds deeper into the soil profile, thereby protecting them from predation and premature germination. Conversely, the low SSB density observed in the gallery forest reflects an equilibrium between seed input and consumption. According to [39], gallery forests harbor a more diversified fauna (including insects and rodents) that consumes a significant portion of the seeds dropped to the ground, which limits the total density of the SSB compared to more open environments. Similarly, the low seed density in the lowland is driven by natural dynamics; unlike the rice field where bunds retain water and sediments, the natural lowland undergoes active leaching and washing out of seeds [7]. The homogeneity of both species richness and seed density observed down to a soil depth of 15 cm across the three floodplain ecosystems of Saria constitutes a remarkable result. This pattern departs from the classic vertical distribution described by several authors, who state that SSB density and species richness are most prominent within the first five centimeters of the soil and decrease considerably with depth [11] [12] [28]. Although studies conducted in protected areas frequently demonstrate an exponential decline with depth [28] [40], our study was carried out in areas heavily subjected to anthropogenic activities (cultivated fields, fallows, pastures), which can redistribute seeds evenly across the different soil layers. Furthermore, this homogeneous distribution of seed density across depths could be linked to environmental factors such as surface runoff. Over time, successive overland flows may have deposited sediment particles containing seeds, gradually building up the top 15 centimeters of soil in these ecosystems. An identical trend was observed for species richness across the studied depths [7].

4.3. Relationship between the Soil Seed Bank and Aboveground Vegetation

The NMDS analysis revealed a strong floristic similarity between the SSB and the aboveground vegetation within each respective ecosystem (lowland, rice field, and gallery forest), suggesting that the SSB plays an active role in the short-term regeneration dynamics of these ecosystems. This well-defined spatial structure confirms that local environmental factors, specifically hydrological regimes and the level of anthropogenic disturbance, simultaneously dictate the composition of the standing flora and the accumulation of buried seeds. In open, wetland environments (lowlands and rice fields), the heavy representation of highly specialized species such as *Bonnaya antipoda*, *Hyptis spicigera*, and *Ludwigia decurrens* is explained by their strict adaptation to flooding cycles. These findings align with recent studies by [41] and [42], which demonstrate that areas subjected to alternating periods of drawdown and submersion select for a distinct suite of semi-aquatic or ruderal species characterized by massive seed production and dormancy cycles synchronized with seasonal floods. In contrast, the gallery forest clearly distinguishes itself from the other two floodplain ecosystems. Marked by species such as *Cyanotis arachnoides*, *Cyperus rotundus* and *Microchloa indica*, it demonstrates the “buffering” effect of the forest canopy. The canopy limits the encroachment of heliophilous (light-loving) species from adjacent cultivated fields and maintains a more stable SSB, typical of less disturbed tropical forest environments [43]. The central position of species like *Setaria viridis*, *Corchorius olitorius*, *Euphorbia hirta*, and *Murdannia keisak* on the ordination plot indicates that these species adapt to a broad ecological spectrum. Within the context of tropical agro-ecosystems, these taxa behave as opportunistic pioneers. Their simultaneous prevalence in both the SSB and the standing vegetation reflects a biotic homogenization of the landscape, which is frequently exacerbated by recurrent anthropogenic disturbances such as tillage in rice fields or livestock grazing [44] [45]. These generalist weeds share highly competitive functional traits, namely efficient dispersal mechanisms, long-term seed persistence in the soil [46], and the capacity for rapid emergence or germination immediately following a disturbance [47]. These optimal ecological attributes allow them to overcome local environmental barriers and constitute a shared floristic background across all three floodplain ecosystems.

Furthermore, the Canonical Correspondence Analysis (CCA) reveals that the composition of the SSB depends primarily on the ecosystem type (gallery forest, rice field, or lowland), whereas soil depth plays a much more secondary role. Consequently, macro-environmental drivers such as human activities and surface runoff water function as the primary determinants shaping the SSB structure [39]. Additionally, the vertical distribution of seeds across the soil profile depends closely on their lifespan within the soil matrix. As a result, the surface (P1) and intermediate (P2) layers predominantly contain recent agricultural weeds introduced by farming management. In contrast, within the deep layer (P3), the floris-

tic composition narrows down to ancient, persistent seeds capable of surviving in the soil for many years [43].

5. Conclusions

Land use dynamics directly influence the resilience of ecosystems through the regeneration potential contained in the soil seed bank (SSB). The objective of this study was to contribute to the sustainable management of hydromorphic ecosystems in the North-Sudanian zone of Burkina Faso. The results obtained allow us to validate our working hypotheses and bring essential insights into the dynamics of these floodplain environments. On one hand, the composition, diversity, and density of the SSB are strongly dictated by the type of hydromorphic ecosystem and the level of anthropisation. The rice field is distinguished by a high seed density but low evenness, testifying to a floristic simplification caused by cultural practices and the massive seed production strategy of weeds. Conversely, the natural lowland and the gallery forest maintain more stable and diversified SSB communities. Remarkably, the vertical distribution of richness and seed density proves to be homogeneous down to 15 cm of depth, departing from the classic decreasing profile, a phenomenon attributable to anthropogenic mixing such as ploughing or grazing, and to alluvial deposition dynamics during floods. These results confirm hypothesis (a), according to which the composition, diversity, density, and vertical distribution of the SSB depend on the type of hydromorphic environment (rice field, natural lowland, gallery forest). On the other hand, ordination analyses (NMDS and CCA) reveal a strong floristic similarity between the buried seed stock and the standing aboveground vegetation within each given ecosystem unit. In both the gallery forest and the natural lowland, the species composition of the soil seed bank closely mirrors the surrounding mature vegetation. Even in agro-ecosystems like rice fields, the SSB maintains a strong structural relationship with the local weed community, alongside persistent seeds of native wetland species. CCA confirms that the local hydrological regime and management mode are the primary drivers structuring both the soil seed bank and its corresponding aboveground canopy, far ahead of soil depth. This strong internal coherence confirms hypothesis (b), which stipulated that there is a high floristic similarity between the soil seed bank and the aboveground vegetation within each hydromorphic ecosystem type. However, the emergence of opportunistic and Generalist pioneer taxa across these environments reflects a trend towards biotic homogenisation under recurrent anthropogenic pressures. In terms of conservation, this study demonstrates that the SSB of the Saria floodplain possesses a strong biological memory and significant natural regeneration potential. The persistence of characteristic natural wetland species within rice field soils further indicates that these agro-ecosystems retain a latent ecological resilience.

Ensuring the sustainable management of these North-Sudanian hydromorphic ecosystems requires two crucial interventions:

- Limit uncontrolled agricultural intensification: Over-exploitation threatens to

disrupt the equilibrium of seed banks by permanently excluding specialized forest species in favor of ubiquitous weeds.

- Protect gallery forests: These habitats must be preserved to fulfill their indispensable role as biodiversity reservoirs and buffer zones against water erosion.

Finally, future research should build upon these findings by evaluating the actual viability of deep seeds through extended greenhouse germination tests, and by integrating seasonal analyses before and after floods to quantify the exact contribution of hydrochory to the annual renewal of this soil memory.

Authors Contributions

SD, SL, and HM formulated the theme, while SL facilitated the acquisition of funding for this study. SD and SL conducted the field research under the supervision of MH and SP. SD and SL performed the data analyses. SL and SP provided the sampling and collection equipment. SL, MH, ZD, and SP ensured the supervision of the research work throughout this study.

Conflicts of Interest

All authors declare that they have no competing interests.

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