Dispersal potential of herbaceous species according to climate, land use and habitat conditions in West African savannah

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Photo 1.
Diaspores of *Hyparrhenia rufa* (Poaceae) which disseminate by epizoochorous and anemochorous dispersal pattern.
Photo I. Zerbo.

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RÉSUMÉ

POTENTIEL DE DISPERSION DES PLANTES HERBACÉES SELON LES CONDITIONS CLIMATIQUES, D'UTILISATION DES TERRES ET D'HABITAT EN SAVANE OUEST-AFRICAINE

Les prévisions environnementales indiquent une vulnérabilité croissante de l'Afrique de l'Ouest aux effets des changements climatiques et d'utilisation des terres. Les plantes herbacées sont les plus sensibles à ces effets. La présente étude porte sur le potentiel de dispersion de différentes plantes herbacées afin d'évaluer leur résilience face à ces changements. Les données sur la composition de la végétation herbacée et les paramètres environnementaux ont été récoltés selon les gradients climatiques, d'utilisation des terres et d'habitat des zones de savane en Afrique de l'Ouest, de même que les diaspores de toutes les espèces herbacées rencontrées. Une description des traits des diaspores a été réalisée afin de documenter leur diversité au sein de la composition floristique herbacée en savane. Un diagramme de fréquence nous a permis d'identifier la variation des modes de dissémination des espèces d'une même famille afin de déterminer leurs potentiels de dispersion. La typologie des modes de dispersion a été établie à l'aide d'une méthode de classification hiérarchique, puis une analyse en composantes principales (PCA) a permis d'identifier les conditions environnementales expliquant leurs distributions. Nos résultats montrent que les diaspores des espèces herbacées peuvent se classer selon les types de fruits et de diaspores, la présence ou non d'hétérosporie, l'exposition des diaspores, le nombre de graines par diaspore, la morphologie des diaspores, la forme des diaspores et le mode de dispersion. Il existe six modes de dispersion pour la famille des poacées, la plus abondante en savane. Il existe plus d'un mode de dispersion pour la plupart des espèces, et celles dont le potentiel de dispersion est élevé (85,43 %) sont dominantes dans la végétation herbacée. Quatre groupes d'espèces herbacées ont été identifiés selon leur mode de dispersion. Les espèces potentiellement épizoochores et anémochores (39,25 % de la flore) sont davantage associées aux zones villageoises, indépendamment des conditions climatiques et d'habitat. Les espèces potentiellement endozoochores et dyszoochores (31,06 % de la flore) s'associent davantage aux habitats frais et secs en zone protégée dans le nord et le sud de la savane soudanienne. Les espèces potentiellement hydrochores (12,63 % de la flore) s'associent aux habitats humides mais sont plus fréquentes en zone sahélienne. Les espèces potentiellement autochores (17,06% de la flore) s'associent plutôt aux habitats de type *bowé* dans le sud de la zone soudanienne. Notre étude montre que toutes les espèces herbacées possèdent un potentiel de dispersion élevé, ce qui devrait favoriser leur permanence dans les savanes ouest-africaines malgré les changements climatiques majeurs qui s'annoncent.

Mots-clés : caractéristiques des diaspores, typologie des modes de dispersion, perturbation, diversité, changement climatique, Afrique de l'Ouest.

ABSTRACT

DISPERSAL POTENTIAL OF HERBACEOUS SPECIES ACCORDING TO CLIMATE, LAND USE AND HABITAT CONDITIONS IN WEST AFRICAN SAVANNAH

According to environmental predictions, West Africa is becoming vulnerable to the adverse effects of climate change and land use disturbance. Herbaceous vegetation is the most sensitive to these effects. To assess the potential of species to cope with these changes, this study investigated the dispersal potential of different herbaceous species. Data on herbaceous plant composition and environmental parameters were collected along climate, land use and habitat gradients in West African savannah areas, as well as the diaspores of all herbaceous species encountered. Their traits were described in order to document the diversity of diaspore categories in herbaceous savannah vegetation. Based on an occurrence diagram, variations in dissemination patterns within families were identified. The dispersal potential of each species was determined on the basis of their patterns of dispersal. A hierarchical classification method was used to establish a dispersal typology, and principal component analysis was applied to identify the environmental conditions that account for their patterns of dispersal. The results show that the diaspores of herbaceous species can be classified according to fruit type, diaspore type, presence of heterodiaspory, exposure of diaspores, number of seeds per diaspore, diaspore morphology, shape of diaspores and pattern of dispersal. Poaceae, the most abundant family in savannah areas, have six patterns of dispersal. Most species have more than one pattern, and species with high dispersal potential (85.43%) dominate the herbaceous vegetation. Four groups of herbaceous species were identified according to their dispersal patterns. Potentially epizoochorous and anemochorous species (39.25% of the flora) were more related to village areas independently of climatic conditions and habitat types. Potentially endozoochorous and dysozoochorous species (31.06% of the flora) were more related to fresh and dry habitats in protected areas of the North and South Sudanian zones. Potentially hydrochorous species (12.63% of the flora) were related to wet habitats but were more prominent in the Sahel, and potentially autochorous species (17.06% of the flora) were more related to *bowé* habitats in the southern Sudanian zone. Our study showed that all herbaceous species have good dispersal potential, which might enable them to persist in West African savannahs despite the severe climatic changes predicted.

Keywords: diaspore traits, dispersal group, disturbance, diversity, Climate change, West Africa.

RESUMEN

POTENCIAL DE DISPERSIÓN DE ESPECIES HERBÁCEAS SEGÚN LAS CONDICIONES DE CLIMA, USO DE LA TIERRA Y HÁBITAT EN LA SABANA DE ÁFRICA OCCIDENTAL

Las previsiones ambientales indican una creciente vulnerabilidad a los efectos del cambio climático y del uso de la tierra en África Occidental. Las plantas herbáceas son las más sensibles a dichos efectos. Este estudio investigó el potencial de dispersión de diferentes especies herbáceas para evaluar su resiliencia frente a estos cambios. Se recopilaron datos sobre la composición de la cubierta herbácea y los parámetros ambientales según los gradientes climáticos, de uso de la tierra y de hábitat de las zonas de sabana de África Occidental, así como las diásporas de todas las especies herbáceas halladas. Se realizó una descripción de las características de las diásporas para documentar su diversidad en la composición florística herbácea de la sabana. Mediante un diagrama de frecuencia se pudo identificar la variación de los modos de diseminación de las especies de una misma familia para determinar su potencial de dispersión. Se empleó un método de clasificación jerárquica para establecer la tipología de los modos de dispersión y el análisis de componentes principales (PCA) nos permitió identificar las condiciones ambientales que explican la distribución. Nuestros resultados muestran que las diásporas de las especies herbáceas pueden clasificarse según el tipo de fruto y de diáspora, la presencia o no de polidiasporia, la exposición de las diásporas, el número de semillas por diáspora, la morfología de las diásporas y el modo de dispersión. En la familia de las poáceas, la más abundante en la sabana, existen seis modos de dispersión. La mayoría de las especies tiene más de un modo de dispersión y las que tienen un alto potencial de dispersión (85,43%) dominan en la vegetación herbácea. Se identificaron cuatro grupos de especies herbáceas según sus modos de dispersión. Las especies potencialmente epizoócoras y anemócoras (39,25% de la flora) están más relacionadas con las tierras comunales, con independencia de las condiciones de clima o hábitat. Las especies potencialmente endozoócoras o disozoócoras (31,06% de la flora) están más relacionadas con hábitats frescos y secos de las áreas protegidas en el norte y sur de la sabana sudanesa. Las especies potencialmente hidrócoras (12,63% de la flora) se relacionan con hábitats húmedos, pero son más frecuentes en la zona saheliense. Las especies potencialmente autócoras (17,06% de la flora) están más bien relacionadas con los hábitats de tipo *bowé* del sur de la zona sudanesa. Nuestro estudio muestra que todas las especies herbáceas tienen un alto potencial de dispersión, esto debería favorecer su permanencia en las sabanas de África Occidental, a pesar de los importantes cambios climáticos previstos.

Palabras clave: características de las diásporas, tipología de los modos de dispersión, perturbación, diversidad, cambio climático, África Occidental.

Introduction

Sub-Saharan Africa, especially West Africa, is predicted to be one of the most vulnerable regions to the adverse effects of climate change and land use (Mc Clean *et al.*, 2005; Heubes *et al.*, 2013). All current change scenarii agree on biodiversity loss (Bellard *et al.*, 2012) and disorders of ecosystem functioning (Hooper *et al.*, 2005). In fact, changes in the functioning of geographical regions of approximately 81-97% and a loss of approximately 25-42% of 5,197 plant species in Sub-Saharan Africa have been predicted by 2085 (Mc Clean *et al.*, 2005).

However, plant species possess several adaptation strategies, including their dispersal patterns. Indeed, the diversity of diaspore traits implies that seed and fruit dispersal play a central role in plant geographic distributions (Howe and Miriti, 2004). Dispersules are thus the result of evolution and the adaptation of species to their environment (Pérez-Harguindeguy *et al.*, 2013). These dispersal strategies, favoured by natural selection, allow species to reach suitable habitats for their development, decrease competition among individuals, exchange individuals among populations and create new populations by colonizing new environments. Bille (1992) reported that in West Africa, the herbaceous layer of savannah vegetation produces more than 50 million of diaspores per hectare, of which 5 million germinate but only 800,000 develop into adult plants. Thus, selection acts to give rise to very variable cover according to the respective annual amount and distribution of rainfall (Bille, 1992).

Several studies have been carried out to show the importance of diaspore dispersal in sustaining plant diversity and ecosystem functioning processes in Europe, Asia, America and Australia (Heinken *et al.*, 2002; Nathan and Muller-Landau, 2000; Brederveld *et al.*, 2011). Some of these studies have demonstrated the dispersal potential of the species by wind (Nathan and Katul, 2005; Tackenberg *et al.*, 2003) or animals (Heinken *et al.*, 2002; Manzano and Malo, 2006; Tackenberg *et al.*, 2005; Will and Tackenberg, 2008). Weidema and Lindeijer (2001) showed that habitat fragmentation affects species dispersal processes. However, this field remains little explored in African savannahs, and, until now, there has been a lack of scientific information regarding species dispersal potentials.

In West Africa, studies based on seed dispersal are rare: Hovestadt *et al.* (1999) investigated dispersal patterns encountered in the forests of the national park of Comoé in Ivory Coast, and Devineau (1999) focused on seeds found in animal faeces in the Bondoukuy area in Burkina Faso. Therefore, due to the various threats to West African vegetation and the lack of scientific information on species dispersal potentials, it is necessary to study this aspect of functional ecology in order to highlight the impact of changes that occur in environmental conditions on the survival of species.

Furthermore, dispersal patterns are affected decisively by the main change scenario affecting biodiversity, such as habitat fragmentation, overexploitation, biological invasion or climate change (Mc Conkey *et al.*, 2012). Given that herbaceous vegetation is an important indicator of the changes that occur in environmental conditions (Devineau and Fournier, 2007), the study of herbaceous species diaspores is essential. For example, climate change and higher CO_2 concentrations increase grass community productivity (Polley *et al.*, 2014). However, in the future, this will cause major alterations in the community structure of grasslands (Christensen *et al.*, 2004), as elevated CO_2 improves photosynthesis in most C4 plants but causes the reverse effect in C3 plants (Lattanzi *et al.*, 2010). Moreover, for conservation needs, diaspore dispersal must be studied under all environmental conditions (Mc Conkey *et al.*, 2012). However, knowledge of dispersal potentials necessarily requires a deep understanding of diaspore types, but information regarding diaspore characteristics is lacking. Thus, this study aims to contribute to a better understanding of the ability of herbaceous species to cope with environmental disturbances in West African savannahs by studying their dispersal potentials.

Specifically, this study seeks to:

- analyse the diversity of dispersal traits of herbaceous species;
- examine dispersal patterns according to herbaceous plant families;
- analyse the dispersal potential of herbaceous species;
- define the dispersal groups of herbaceous species;
- determine the relationships between the dispersal groups and climate, land use and habitat conditions.

We will test the following assumptions:

- herbaceous species diaspores can be classified into several categories;
- dominant herbaceous families contain the highest numbers of dispersal patterns;
- herbaceous vegetation is dominated by species with high dispersal potential;
- different dispersal groups exist in the herbaceous layer of savannahs;
- each dispersal group is influenced by specific climate, land use and habitat conditions.

Photo 2.
Diaspores of *Triumffeta rhomboidea* which disseminate by epizoochorous dispersal pattern.
Photo I. Zerbo.

Materials and methods

Study sites

The study was conducted in Burkina Faso along a climatic gradient in three protected areas and their adjacent communal areas characterized by multiple human activities, including agriculture in its traditional form of shifting cultivation, industrialized permanent crop cultivation, grazing, and the collection of non-timber forest products for multiple purposes (Fontès and Guinko, 1995; Ouédraogo *et al.*, 2014). The three study areas are located in different phytogeographical zones, as described by Guinko (1984) as follows (figure 1):

- The sylvopastoral reserve and partial faunal reserve of the Sahel: located in the Sahel, the vegetation is dominated by shrub-savannahs and shrub-steppe (Fontès and Guinko, 1995). The average annual rainfall in the last three decades was 477.89 ± 114.68 mm. The annual average temperature over the same period was 29.95 ± 3.53°C. The soil types are dominated by tropical eutrophic brown soils on argillaceous material; ferruginous tropical soils, slightly percolated or percolated on sand, sandy-argillaceous and argillaceous-sandy material; and halomorphic soils with a degraded structure (solonetz on argillaceous-sandy material) (Sattran and Wenmenga, 2002).
- The Tapoa-Djerma area of the W National Park: located in the northern Sudanian zone and characterized by grassland, shrubs, trees, and woodland savannahs (Fontès and Guinko, 1995). The average annual rainfall in the last three decades was 795.68 ± 197.74 mm. The annual average temperature over the same period was 28.79 ± 2.48°C. The soil types consist of soils of erosion, poorly developed on gravel material, and ferruginous tropical soils, slightly percolated or percolated on sand, sandy-argillaceous and argillaceous-sandy material (Sattran and Wenmenga, 2002).
- The Southern Pama Partial Reserve of Fauna: located in the southern Sudanian zone and characterized by grassland, shrubs, trees, woodland savannahs and gallery forests (Fontès and Guinko, 1995). The average annual rainfall in the last three decades was 901.42 ± 163.41 mm. The annual average temperature over the same period was 27.5 ± 2.41°C. The soil types are composed of soils of erosion, poorly developed on gravel material; vertisols on alluvial or argillaceous material; and hydromorphic mineral soils to pseudo-gleys on materials of different textures (Sattran and Wenmenga, 2002).

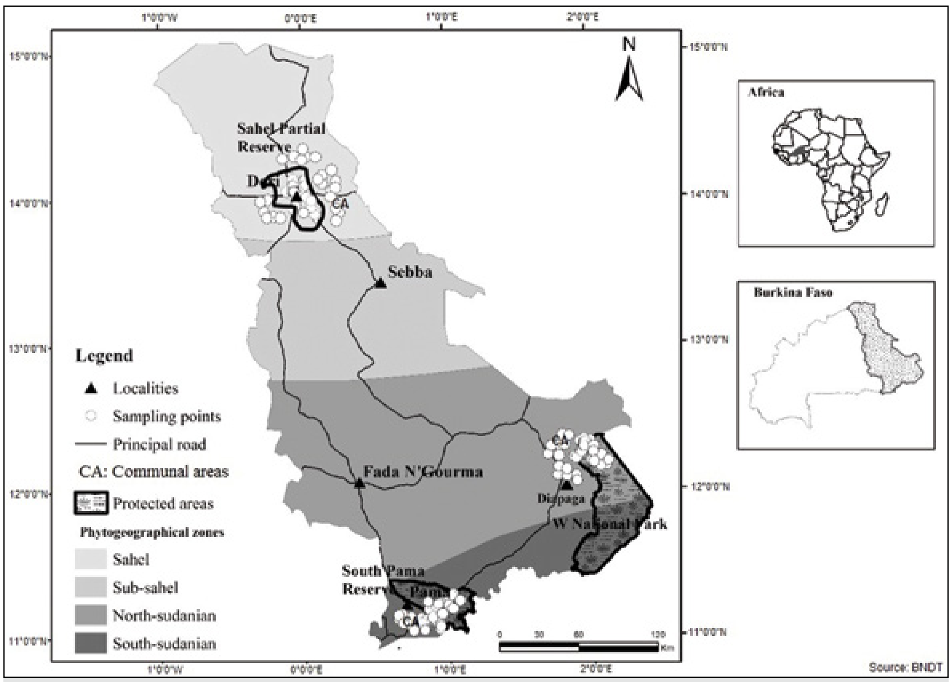


Figure 1.
Study area.

Data collection

Phytosociological data

In each study area (Sahelian, North Sudanian and South Sudanian), the herbaceous vegetation composition of two land use types (protected and communal areas) and four habitat types (bowé, i.e., "shallow soil on lateritic crusts", dry, fresh and wet) (table I) was sampled in 10 m × 10 m plots during the rainy season (September to November). In total, 240 plots were sampled (2 land use types × 4 habitats × 3 study areas × 10 replicates). In each plot, the percent cover of each herbaceous species was visually estimated using the method defined by Braun-Blanquet (1932).

Environmental data

In each plot, the environmental conditions (climate conditions, land use type and habitat type) were determined according to the phytogeographical area (Sahel, North Sudanian or South Sudanian), land use type (communal area or protected area) and habitat type (bowé, dry, fresh, wet) of each plot.

Diaspore data

Diaspore data were collected for all herbaceous plants during the period of fruit maturity. The floristic composition of the herbaceous savannah vegetation varied according to the climate zone, land use regime and habitat type (Devineau and Fournier, 2007; Zerbo *et al.*, 2016). Thus, according to their presence, for each herbaceous species, eight representative individuals were randomly selected regardless of the climate zone, land use type and habitat conditions, and diaspore data were collected on these individuals according to the standard protocol described by Knevel *et al.* (2005). The diaspores of each species were investigated in the laboratory using a magnifying glass and described according to the protocol used by Hintze *et al.* (2013) based on eight dispersal trait categories (table II).

Data analysis

Diversity of dispersal traits of herbaceous species

To determine the importance of each trait value in each dispersal trait category, the percentage of traits in each category describing diaspores was calculated for all herbaceous species. The eight categories concerned fruit type, diaspore type, heterodiaspory, exposure of diaspores, the number of seed per diaspore, diaspore morphology, shape of diaspores and dispersal pattern.

$$\textit{Percentage of trait/category} = \frac{\textit{(Number of species with a given trait)}}{\textit{(Total number of species)}} \times 100$$

A Kruskal-Wallis test at the significance threshold of 5% was used to assess the differences in the percentages of each category.

Dispersal patterns according to herbaceous plant families

The list of 302 herbaceous species was used to analyse the taxonomic diversity of the considered flora, and then a diagram of occurrence revealed the variation of each dispersal pattern by family.

$$\textit{Dispersal pattern occurrence/family} = \frac{\textit{(Number of species per dispersal pattern in the family)}}{\textit{(Total number of species in the family)}}$$

Dispersal potential of herbaceous species

The potential of a species to spread by wind (Tackenberg *et al.*, 2003) or animals (Tackenberg *et al.*, 2005; Will *et al.*, 2007) depends mainly on its external morphology (the presence of wings, hairs, or hooks). We defined the dispersal potential of a species based on the quantity of its dispersing means according to the morphological traits of its diaspores. This varies not only among species but also within a species based on its different dispersal patterns and therefore shows whether the dispersal capacity of the species is limited and whether environmental changes can be considered to be a threat to its survival. Thus, to characterize the dispersal potential of each species, we introduce an index called the "relative index of dispersal" (RID). The relative index of dispersal was calculated on the basis of the morphological traits of diaspores (nutrients, aerenchyma, appendages for transport by wind, elongated appendages, hooking appendages, mucilaginous surface, no specialization) describing the dispersing means (table II, section 5.1 to 5.7). Subsequently, each dispersal trait was ranked in terms of presence / absence data.

The relative index of dispersal was computed by species and dispersal pattern as follows:

- Step 1: relative index of dispersal by dispersal pattern ($RID_{pattern}$)

For each species, we calculated the ratio between the number of dispersing traits by dispersal pattern described per morphological trait (as a species can possess several traits that can indicate the same dispersal pattern) and the total number of dispersal means.

$RIDpattern = (\sum ni)/N$

where *ni* is the number of morphological trait categories indicating a given dispersal pattern, and N is the number of morphological traits.

- Step 2: relative index of dispersal by species ($RID_{species}$)

For each species, we summed the different relative indices of dispersal by dispersal pattern.

$RIDspecies = \sum RIDpattern$

where $RID_{pattern}$ is the relative index of dispersal by dispersal pattern.

The relative index of dispersal ranges from 0 to 1. A value close to 1 indicates a high dispersal potential. A value close to 0 expresses the reverse.

Species were subsequently classified on the basis of their relative index of dispersal into three classes of dispersal potential, where we supposed that a species with a relative index of dispersal higher than 50% possesses a large dispersal potential. The three classes of dispersal potential are:

-]0-25]: low dispersal potential,
-]25-50]: moderate dispersal potential,
-]50-100]: high dispersal potential.

In addition, we observed the variation in species proportions according to the number of dispersal patterns, which varied from 1 to 5. A Kruskal-Wallis test at the significance threshold of 5% was used to assess the differences within respective percentages of species within classes of dispersal potential and percentages of species with different numbers of dispersal patterns.

Table I.
Land use and habitat characteristics.

Habitats	Characteristic
Bowal habitat	Superficial lateritic crust and rocky soils (about 0 - 10 cm of deep)
Dry Habitat	Shallow lateritic or rocky soils (about 5 -15 cm of deep)
Fresh habitat	Ferralitic or Ferruginous, intermediate to deep soil (about 15 - 100 cm)
Wet habitat	Hydromorphic, intermediate to deep soil (about 10 - 120 cm)

Dispersal groups of herbaceous species

Based on the relative index of dispersal calculated by dispersal pattern ($RID_{pattern}$), we created a species dispersal matrix with dispersal patterns in rows and herbaceous species in columns (matrix 1). This matrix was submitted to a hierarchical classification method based on cluster analysis (Sorensen distance measure and flexible beta group linkage) to classify herbaceous species according to their dispersal pattern/type.

Relationships between the dispersal groups and climate, land use and habitat conditions

Based on vegetation data and environmental conditions, the abundance of each herbaceous species was used to express the weight of each dispersal pattern according to the environmental conditions (climate conditions, land use type and habitat type). This results in an occurrence matrix of dispersal patterns according the climate conditions (Sahel, North Sudanian and South Sudanian), land use type (protected area, communal area) and habitat type (bowé, dry and fresh, wet), where dispersal patterns occupy the rows and environmental conditions the columns (matrix 2). In addition, a principal component analysis (PCA) was then used to highlight the environmental factors that promote the expression of the different dispersal patterns. We examined the relationships between the dispersal patterns and the environmental conditions using the species dispersal matrix (matrix 1) as the main matrix and the occurrence matrix of dispersal patterns according environmental conditions (matrix 2) as the second matrix (Mc Cune and Grace, 2002). We used Pearson correlation to show relationships among dispersal patterns and among environmental conditions.

Results

Diversity of herbaceous species diaspore traits

Diaspores show the diversity of means used by species to disseminate in nature. At each level, the categories of diaspores vary significantly at $p < 0.05$ (table III).

Concerning the fruit type, herbaceous vegetation is dominated by herbaceous species with non-fleshy fruits (54.83%) followed by non-fleshy fruits with an upright aperture (29.59%) and non-fleshy indehiscent fruits with a lateral aperture (11.53%) (figure 2.a).

In regard to diaspore type, herbaceous species disseminate by fruits (59.78%) and seeds (39.25%) (figure 2.b and figures 3, 4, 5, 6 & 7).

Considering the number of seeds per diaspore, we predominantly encountered 50.47% of diaspores with only one seed, while 38.38% had 2 to 10 seeds (figure 2.c).

The external morphology of diaspores also varied considerably. The most encountered forms were diaspores with elongated appendages (34.86%), diaspores with hooked appendages (20.38%), diaspores with nutrient-containing structures (18.37%) and diaspores without specialization (15.55%) (figure 2.d & figures 3, 4, 5, 6).

Regarding the geometric shape of diaspores, the most abundant forms were spherical forms (43.75%), elongated flat forms (28.29%) and elongated forms (27.63%) (figure 2.e).

Concerning the dispersal pattern, we essentially found epizoochorous (23.57%), anemochorous (21.21%), endozoochorous (20.68%) and dysochorous species (19.54%) (figure 2.f and figures 3, 4, 5, 6).

Table II.
Description of diaspores.

Dispersal Traits Categories	Trait description	Value
1. Diaspore type	Morphological structure that acts as the diaspore, i.e. the dispersal unit.	Nominal: seed, fruit, infrutescence, fruit segment, pepo
2. Fruit type	Ecological characteristics related to seed release patterns	Nominal: non-fleshy indehiscent fruit, fleshy fruit, non-fleshy fruit with upright aperture, non-fleshy fruit with lateral aperture, explosive release mechanism, pepo (Cucurbitaceae)
3. Exposure	Exposition of the diaspore to dispersal vectors	Nominal: enclosed, covered partly, exposed
4. Heterodiaspory	Species with more than one diaspore type	Binary: presence (1); absence (0)
5. Diaspore morphology	State of diaspores surface	Nominal: Combination of 5.1; 5.2; 5.3; 5.4; 5.5; 5.6 & 5.7
5.1. Nutriments	Indicator for dysochory and endozoochory	Binary: presence (1); absence (0)
5.2. Aerenchym	Indicator for hydrochory and anemochory	Binary: presence (1); absence (0)
5.3. Flat appendages	Indicator for anemochory	Binary: presence (1); absence (0)
5.4. Elongated appendages	Indicator for anemochory and epizoochory	Binary: presence (1); absence (0)
5.5. Hooked appendages	Indicator epizoochory	Binary: presence (1); absence (0)
5.6. Mucilaginous surface	Indicator for epizoochory	Binary: presence (1); absence (0)
5.7. No specializations	Indicator for autochory	Binary: presence (1); absence (0)
6. Diaspore form	Form of the diaspore in categories	Nominal: Spherical, flat, elongated, elongated and flat
7. Dissemination	Dispersal pattern	Nominal: Combination of 5.1; 5.2; 5.3; 5.4; 5.5; 5.6 & 5.7
8. Seed per diaspore	Number of seeds per diaspore	Ordinal: 0 = no seed; 1 = one seed; 2 = 2-10 seeds; 3 = 11-100 seeds; 4 = 101-1000 seeds

The proportion of herbaceous species that produce a single diaspore (79.74%) largely exceeded those species producing several types of diaspores (20.26%) (figure 2.g).

The analysis of the mode of diaspore exposure shows that 46.10% of the herbaceous species possess exposed diaspores, 28.35% have partly covered diaspores, and 25.55% of the diaspores were enclosed within a pericarp (figure 2.h).

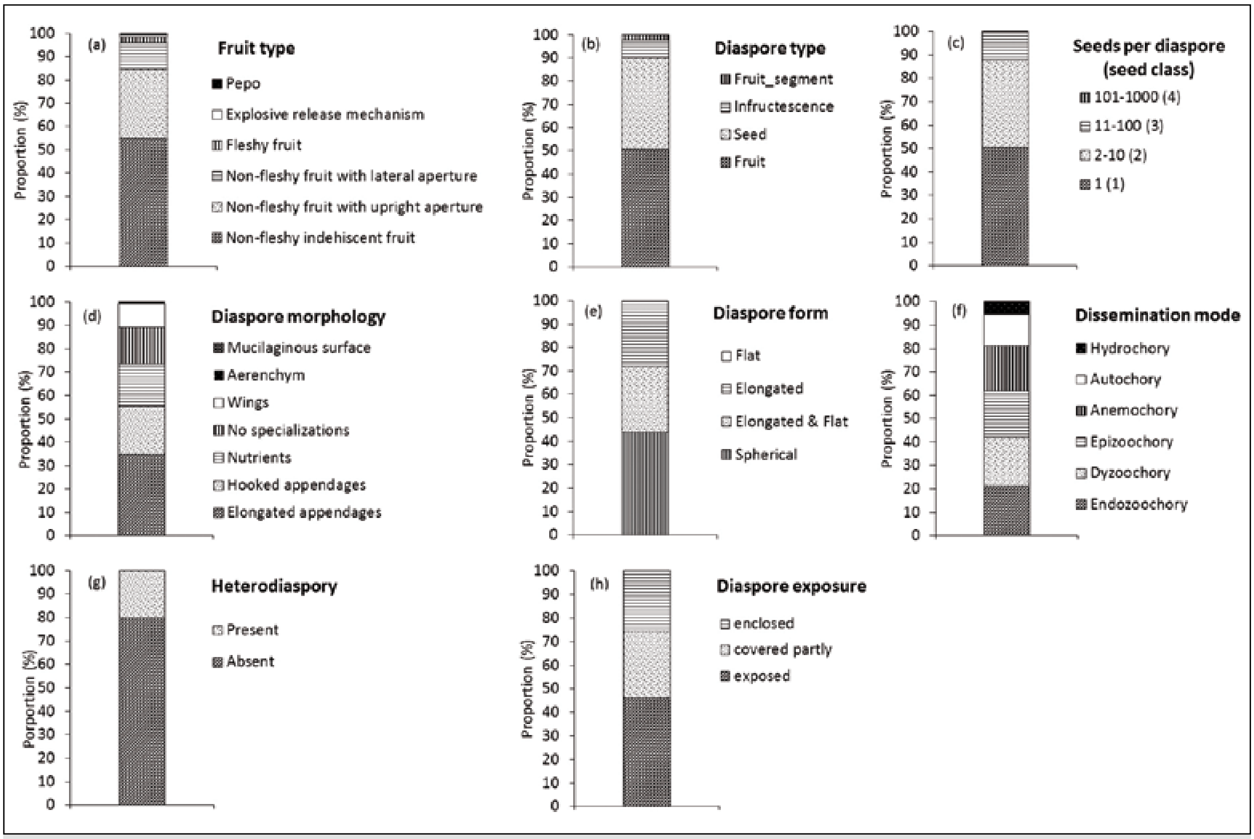


Figure 2.
Diaspore diversity based on (a) = type of fruit, (b) = type of diaspore, (c) = number of seeds per diaspore, (d) = surface of diaspores, (e) = form of diaspores, (f) = dispersal pattern, (g) = heterodiaspory, and (h) = exposure of diaspores.

Photo 3.
Diaspores of *Hyparrhenia smithiana* on parent plant which disseminate by epizoochorous and anemochorous dispersal pattern.
Photo Issouf Zerbo.

Table III.
Synthetic table of Kruskal-Wallis test results for diaspore categories.

Categories	d.f.	X²	P
Fruit type	5	348.47	‹ 0.0001
Diaspore type	3	160.52	‹ 0.0001
Heterodiaspory	1	132.71	‹ 0.0001
Diaspore exposure	2	58.32	0.0213
Seeds per diaspore	3	128.48	‹ 0.0001
Diaspore Morphology	6	254.11	‹ 0.0001
Diaspore Form	3	117.86	‹ 0.0001
Dissemination mode	5	45.17	0.03117

(a) *Acanthospermum hispidum* (Asteraceae): fruits

(b) *Zornia glochidiata* (Fabaceae): fruits

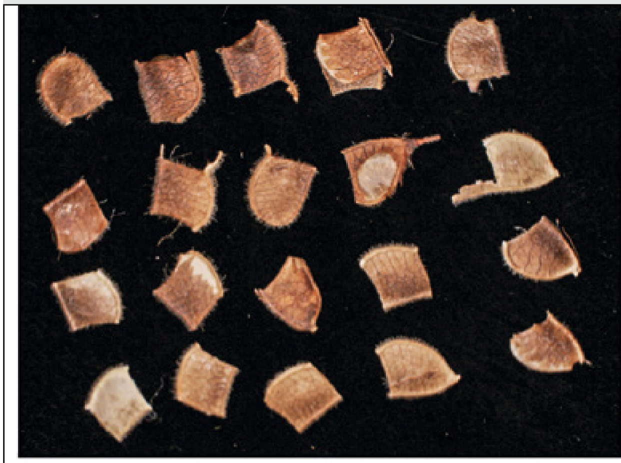
(c) *Achyrranthes aspera* (Asteraceae): fruits

(d) *Desmodium velutinum* (Fabaceae): fruit segments

(e) *Aspilia paludosa* (Asteraceae): seeds

(f) *Sida rhombifolia* (Malvaceae): seeds

Figure 3.
Some epizoochorous diaspores with hook appendages.



(a) *Desmodium hirtum* (Fabaceae): fruit segments

(b) *Desmodium hirtum* (Fabaceae): seeds

(c) *Alysicarpus ovalifolius* (Fabaceae): fruit segments

(d) *Alysicarpus ovalifolius* (Fabaceae): seeds

(e) *Sida alba* (Malvaceae): seeds

(f) *Sida alba* (Malvaceae): seeds

Figure 4.
Heterodiaspory in different species (epizoochory (a) and (e); endozoochory and dyszoochory (b), (c), (d), (f)).

(a) *Tephrosia bracteolata* (Fabaceae): seeds
(b) *Indigofera dendroides* (Fabaceae): seeds
(c) *Cyanotis lanata* (Commelinaceae): fruits
(d) *Ipomea eriocarpa* (Convolvulaceae): seeds

Figure 5.
Seed diaspores without specialization (dispersal pattern: dyszoochory, endozoochory).

(a) *Chloris pilosa* (Poaceae): fruits
(b) *Hackelochloa granularis* (Poaceae): fruits

Figure 6.
Fruit diaspores with short appendages in the Poaceae family (dispersal pattern: dyszoochory, endozoochory).

Figure 7.
Diaspores with long appendages in the Poaceae family (dispersal pattern: anemochory, epizoochory, dyszoochory, endozoochory).

Dissemination patterns according to herbaceous families

The considered flora includes 302 herbaceous species distributed among 152 genera and 39 families. This herbaceous flora is dominated by the Poaceae family (31.76%) followed by Fabaceae (13.18%), Cyperaceae (9.46%) and Malvaceae (6.42%) (figure 8).

The percentage of dispersal patterns ranged from 0 to 100% (figure 9). It was observed in this study that the most abundant families of herbaceous vegetation are those that contain the highest number of dispersal patterns. Thus, Poaceae was found to contain six dispersal patterns, of which the most important are anemochory, epizoochory, endozoochory and dyszoochory, with percentages ranging from 80 to 100%. The families characterised by five dispersal patterns were Acanthaceae, Cyperaceae and Polygalaceae, and those with four patterns were Asparagaceae, Convolvulaceae, Malvaceae and Fabaceae. Thirty-three percent of families contained species with three dispersal patterns, among which were Asteraceae and Rubiaceae. However, 27.27% of families are characterised by the absence of other dispersal patterns and are essentially autochorous. Among these were Antheriaceae, Araceae, Hypoxidaceae, Caryophyllaceae, and Pedaliaceae.

Dispersal potential of herbaceous species

The dispersal potential of species according to the number of dispersal patterns showed that most of the considered herbaceous species are equipped with multiple dispersal modes (figure 10.a). The number of dispersal patterns varied significantly ($X^2 = 296$; df = 4; p ‹0.0001), and species with 4 and 3 dispersal patterns were abundant.

The analysis of the dispersal potential on the basis of the relative index of dispersal revealed that species with high (38.08%) and moderate (47.35%) dispersal potential were the most abundant (figure 10. b) and represented 85.43% of the considered flora. The results also showed that there was a significant difference among the dispersal potentials of herbaceous species ($X^2 = 269.5$; df = 2; p ‹0.0001).

Dispersal groups of herbaceous vegetation

Based on the species dispersal index, hierarchical classification (figure 11) allowed the categorization of herbaceous species into four major dispersal groups:

▪ The group of potentially autochorous species (17.06% of the flora), including species such as *Evolvulus alsinoides* (L.) L., *Buchnera hispida* Buch.-Ham. ex D.Don, *Ammannia baccifera* L., *Cycnium tubulosum* (L.f.) Engl., *Sphenoclea zeylanica* Gaertn., *Leucas martinicensis* (Jacq.) R.Br. and *Albuca nigritana* (Baker) Troupin.

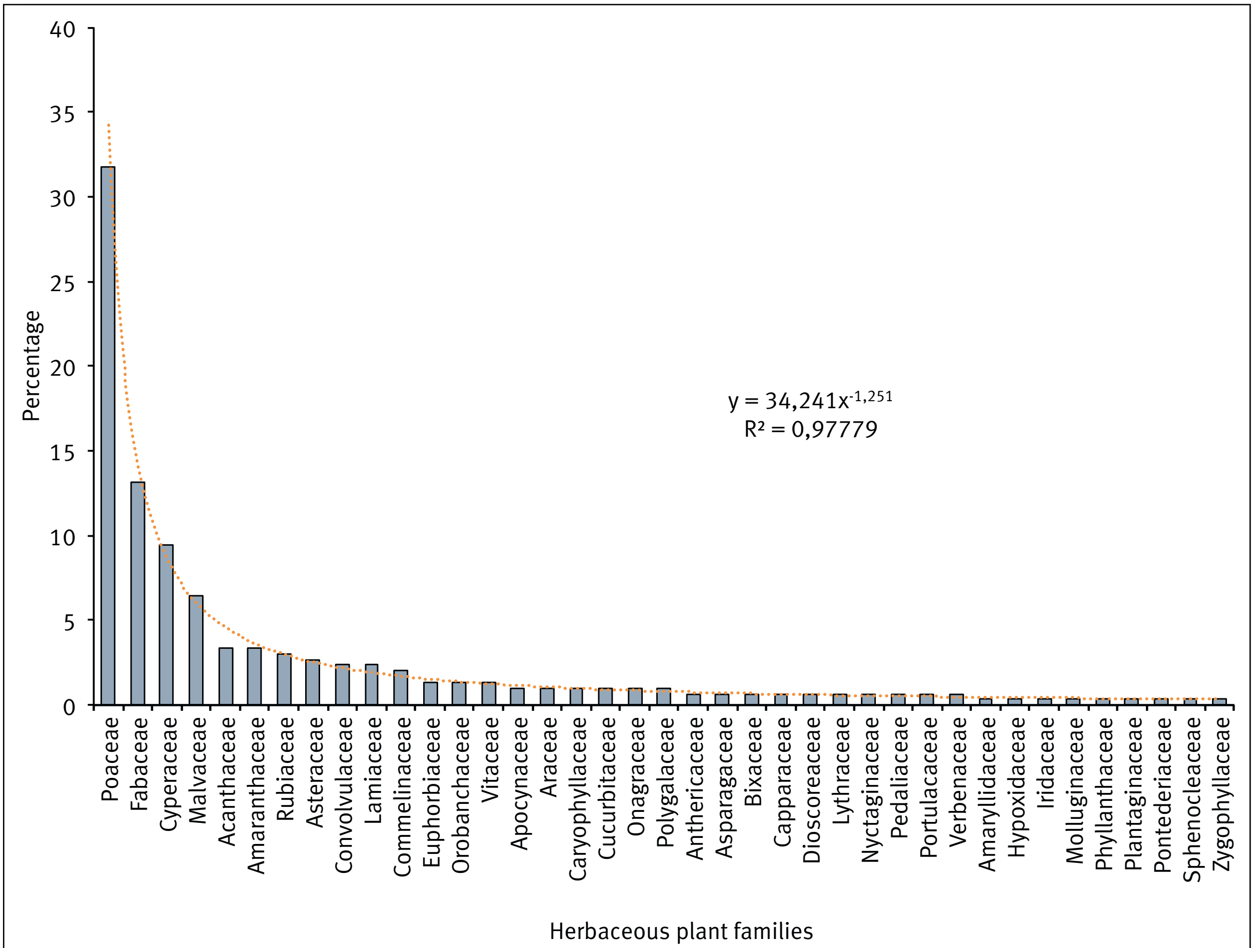


Figure 8.
Diagram of families of the considered flora.

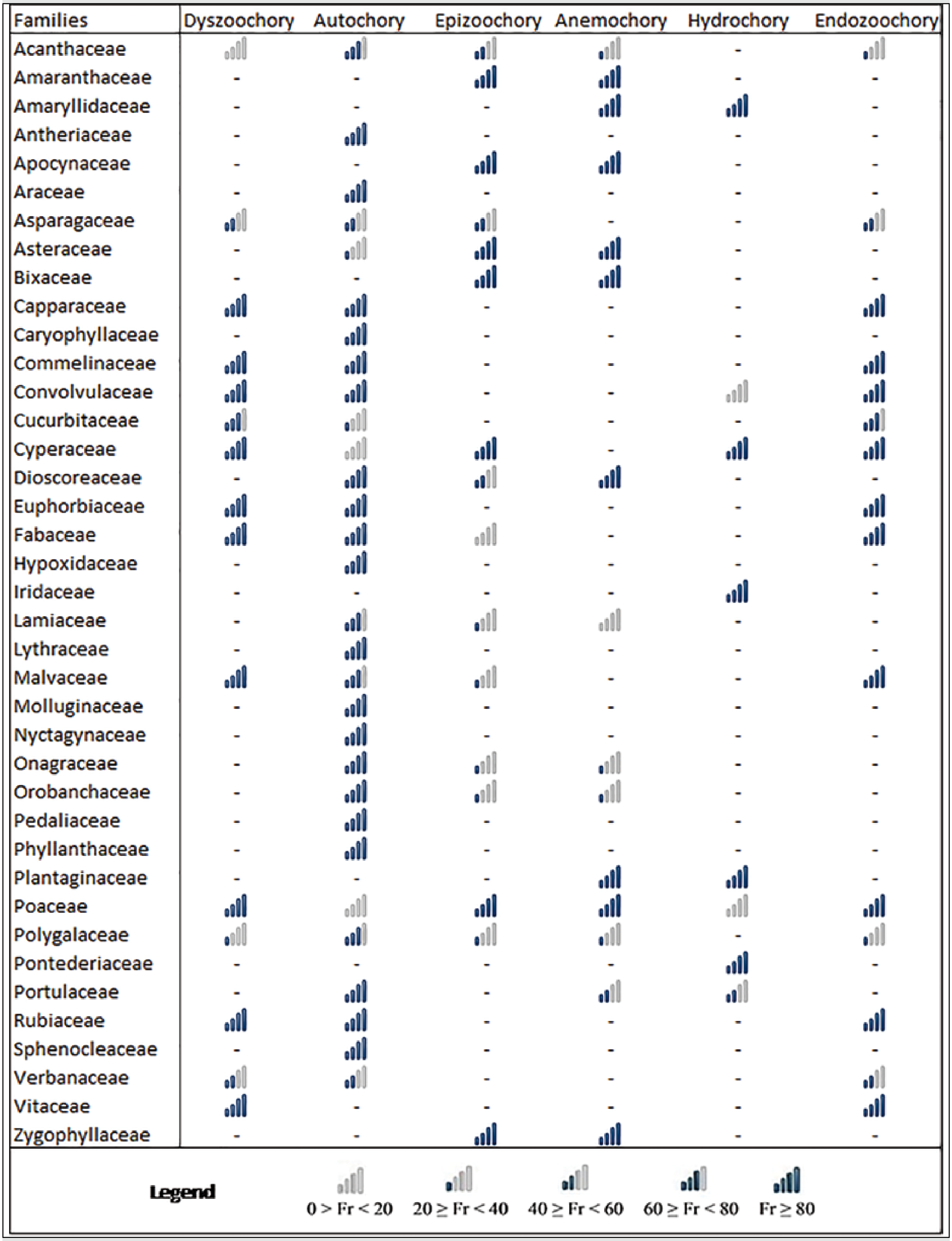


Figure 9.
Occurrence diagram of dispersal patterns by family.

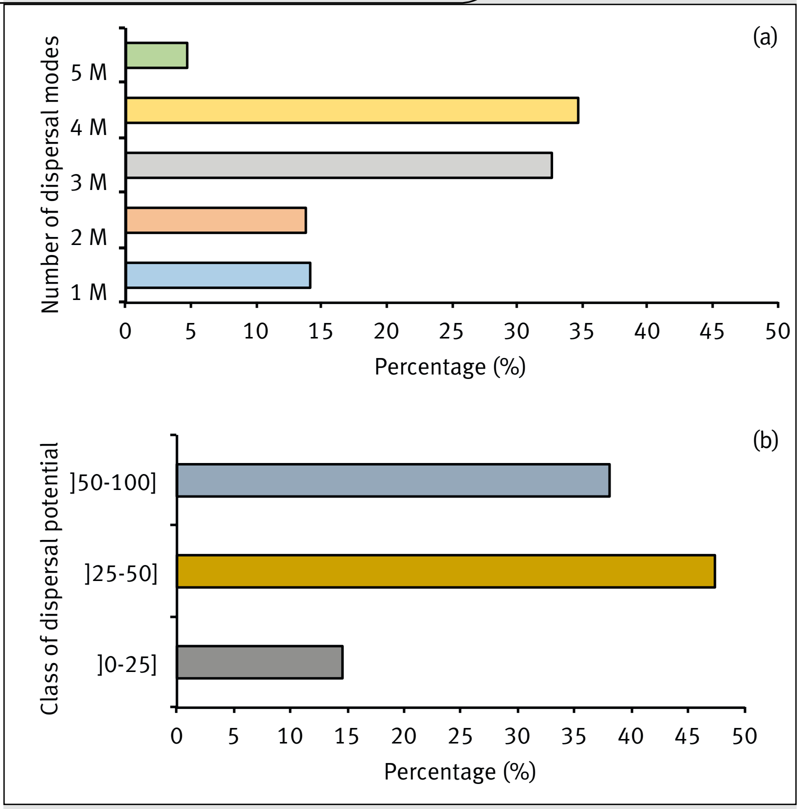


Figure 10.
Spectrum of the number of dispersal patterns and the dispersal potential of herbaceous species.
(a) Number of dispersal modes per species: (1M = 1 mode: 2M = 2 modes; 3M = 3 modes; 4M = 4 modes; 5M = 5 modes).
(b) Dispersal potential of all species: (]0-25] = Low dispersal potential;]25-50] = moderate dispersal potential ;]50-100] = High dispersal potential.

▪ The group of potentially epizoochorous and anemochorous species (39.25% of the flora), mainly including Poaceae species such as *Andropogon gayanus* Kunth, *Hyparrhenia involucrata* Stapf, *Aristida hordeacea* Kunth, *Euclasta condylotricha* (Hochst. ex Steud.) Stapf, *Cenchrus biflorus* Roxb. and *Pennisetum polystachion* (L.) Schult.; Fabaceae species such as *Zornia glochidiata* Rchb. ex DC.; Asteraceae species such as *Linzia purpurea* (Sch.Bip. ex Walp.) Isawumi; and Malvaceae species such as *Triumfetta rhomboidea* Jacq.

▪ The group of potentially endozoochorous and dysozoochorous species (31.06% of the flora), mainly containing seeds of Fabaceae species such as *Aeschynomene indica* L., *Tephrosia pedicellata* Baker, *Desmodium velutinum* (Willd.) DC., *Indigofera geminata* Baker, *Cassia absus* L. and *Vigna filicaulis* Hepper; Malvaceae species such as *Hibiscus asper* Hook f., *Corchorus tridens* L., and *Grewia cissoides* Hutch. & Dalziel; Rubiaceae species such as *Spermacoce stachydea* DC. and *Spermacoce radiata* (DC.) Hiern; and Poaceae species as *Panicum pansum* Rendle and *Hackelochloa granularis* (L.) Kuntze.

▪ The group of potentially hydrochorous species (12.63% of the flora), containing mostly Cyperaceae species such as *Cyperus podocarpus* Boeckeler, *Cyperus pustulatus* Vahl, *Schoenoplectus junceus* (Willd.) Lye, *Fuirena umbellata* Rottb., and *Lipocarpha albiceps* Ridl. and Poaceae species such as *Echinochloa stagnina* (Retz.) P.Beauv., *Panicum fluviicola* Steud. and *Acroceras amplectens* Stapf.

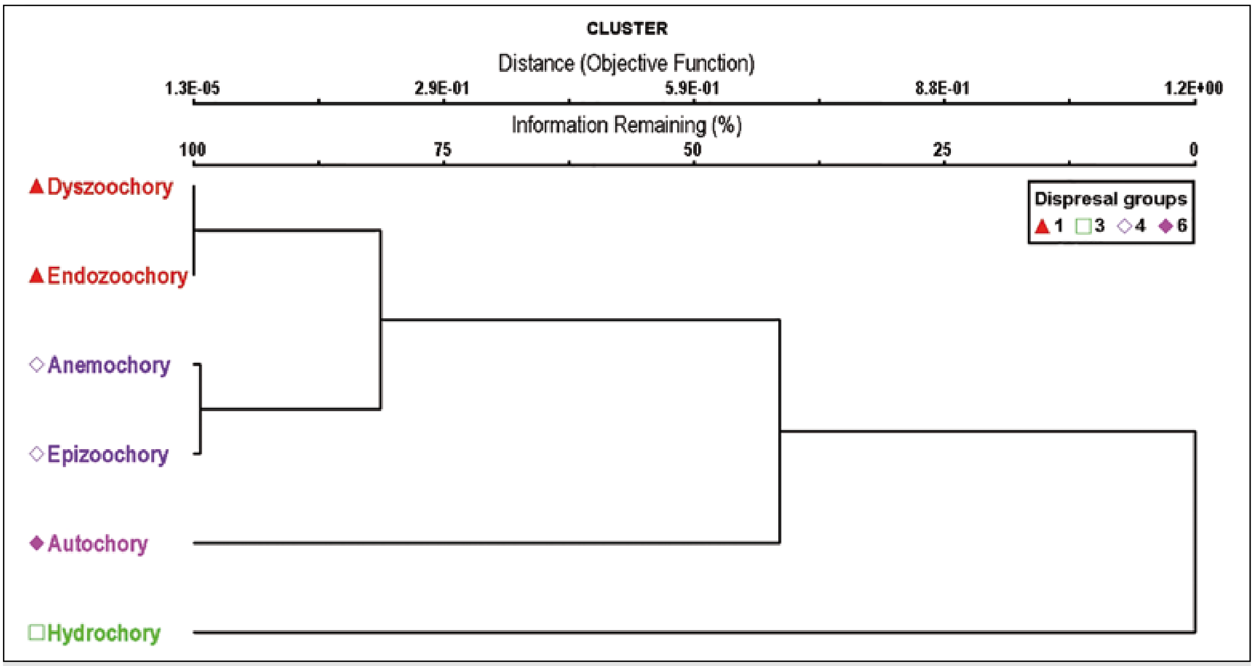


Figure 11.
Hierarchical classification of species by their predominant dispersal patterns.

Table IV.
Pearson correlations between dispersal patterns.

Modes	Dysochory	Endozoochory	Hydrochory	Anemochory	Epizoochory	Autochory
Dysochory	1					
Endozoochory	0.99***	1				
Hydrochory	-0.35***	-0.36***	1			
Anemochory	-0.44***	-0.44***	0.41***	1		
Epizoochory	-0.38***	-0.37***	0.13*	0.79***	1	
Autochory	-0.28***	-0.28***	-0.25***	-0.68***	-0.68***	1

*** Very highly significant; ** highly significant; * less significant.

Table V.
Pearson correlations among environmental conditions based on dispersal patterns.

	Climate conditions			Land use		Habitat			
	Sahel	North Sudanian	South Sudanian	Communal Area	Protected Area	Wet	Fresh	Dry	Bowal
Sahel	1								
North Sudanian	-0.16**	1							
South Sudanian	-0.20**	0.15**	1						
Communal Area	0.26***	0.09	0.05	1					
Protected Area	-0.09	0.40***	0.33***	-0.19**	1				
Wet	-0.07	0.17**	0.26***	0.05	0.06	1			
Fresh	0.05	0.25***	0.24***	0.06	0.39***	-0.18**	1		
Dry	0.14**	0.29***	0.19**	0.22**	0.22**	-0.19**	0.47***	1	
Bowal	0.10*	0.30***	0.25***	0.21**	0.31***	-0.13*	0.39***	0.59***	1

*** Very highly significant; ** highly significant; * less significant.

In addition, we noticed that there were strong positive and significant correlations on the one hand between dysozoochory and endozoochory (0.99%) and on the other hand between anemochory and epizoochory (0.79%) (table IV). There was a weak correlation between anemochory and hydrochory (0.44%).

Relationships between climate, land use, habitat conditions and dispersal groups

The output of the principal component analysis revealed the environmental factors that influence the dispersal potential of species. The eigenvalues of axes 1, 2 and 3 were, respectively, 6.27, 5.27 and 4.76, and the principal components explained 97.96% of the total variance in the data. Endozoochory and dyszoochory were mostly found in fresh and dry habitats and were most related to the protected areas of the North and South Sudanian zones (figure 12.a). Epizoochory and anemochory were more common in communal areas regardless of the climate and habitat conditions (figure 12.a, b & c). Hydrochory is more related to wet habitats and is more pronounced in the Sahel (figure 12.a.). Regarding autochory, it is more prominent in the South Sudanian zone, especially in bowé habitats (figure 12.a & c).

Based on their similarities in dispersal patterns, there were very highly significant positive correlations between bowé habitat and fresh habitat (r = 0.39) and between bowé habitat and dry habitat (r = 0.59) (table V). We also observed a highly significant positive correlation between protected areas and fresh habitat (r = 0.39) and between dry and fresh habitats (r = 0.47).

Discussion

Diversity of herbaceous species diaspore traits

The description of herbaceous flora diaspore traits allows them to be classified into eight categories. These eight categories reveal the diversity of dispersal modes employed by herbaceous species to disperse in savannah ecosystems. The diversity of diaspores verifies the central role played by seed dispersal in plant ecology (Howe and Miriti, 2004).

The dominance of indehiscent dry fruit diaspores is linked to the abundance of grass species in the savannah flora. Indeed, Poaceae is the most diversified family in savannahs (Becker and Muller, 2007; Bocksberger, 2012), and members of this family essentially disperse their fruits, which are achenes or caryopses and therefore indehiscent dry fruits (Poilecot, 1995 and 1999). In addition, this reflects the predominance of fruits and diaspores containing only one seed in the dissemination process in savannahs.

The dominance of diaspores with long appendages and hooking appendages indicates the abundance of epizoochorous and anemochorous species. This dominance of diaspores with long appendages and hooking appendages represents a benefit for the herbaceous flora, as it indicates the ability of long-distance dispersal (Kleyer *et al.*, 2008; Will and Tackenberg, 2008; Hintze *et al.*, 2013). Long-distance dispersal can favour mixing between populations and conveys the ability of species to cope with climate change as predicted in different climate change scenarios (Cain *et al.*, 2000; Manzano and Malo, 2006; Soons and Ozinga, 2005).

Moreover, diaspore exposure is a favourable asset for their spread because, in this case, they are accessible to most dispersing agents, such as wind and animals (Hintze *et al.*, 2013). Indeed, the potential of species to spread by wind (Tackenberg *et al.*, 2003) and animals (Tackenberg *et al.*, 2005; Will *et al.*, 2007) depends mainly on their external morphology (presence of wings, hairs, or hooks).

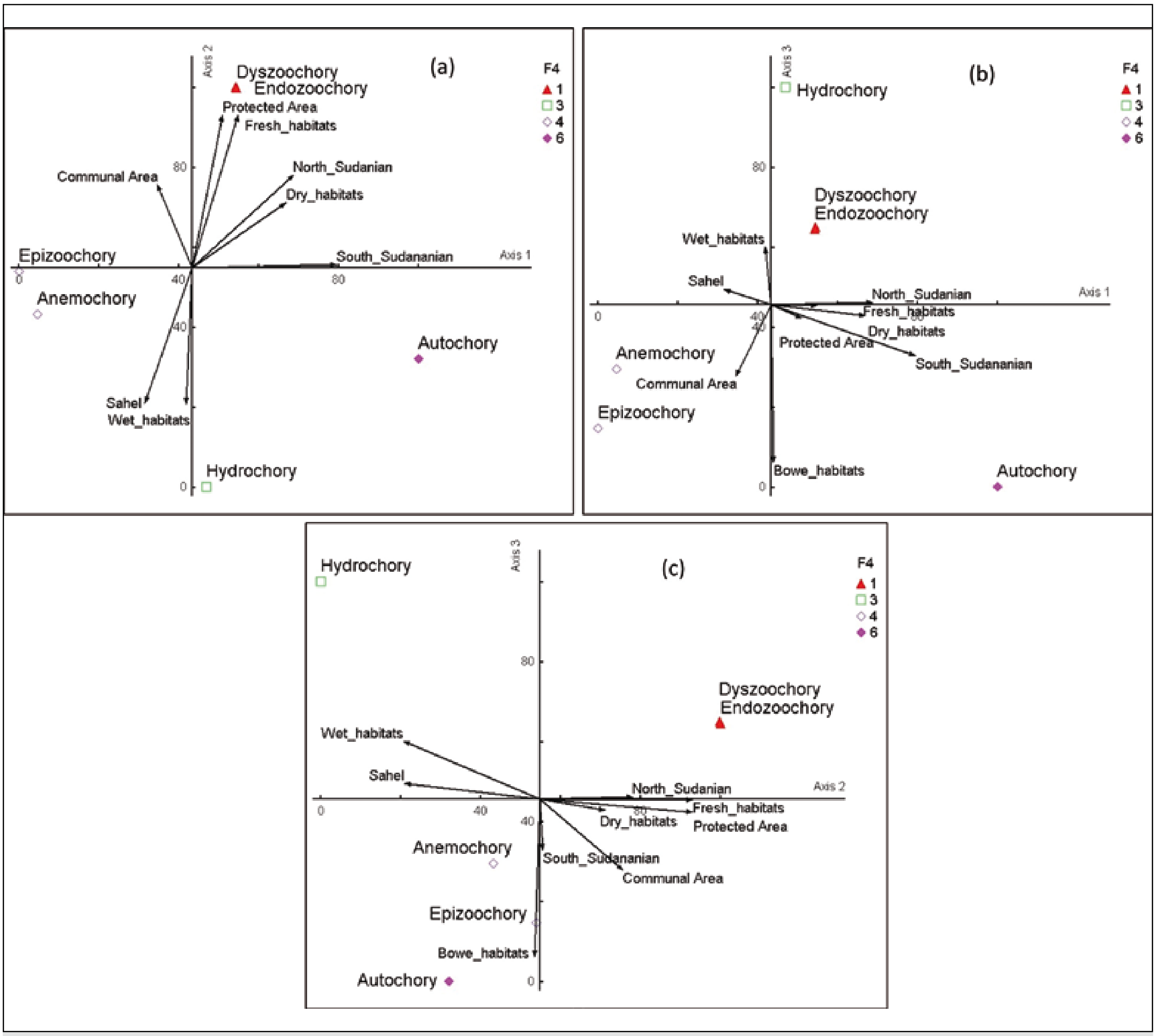


Figure 12.
Principal component analysis of dispersal patterns according to environmental conditions.

Variation in dispersal patterns among families

The considered flora was dominated by the Poaceae, Fabaceae, Cyperaceae, Malvaceae, Acanthaceae, Amaranthaceae, Rubiaceae and Asteraceae families. These families are the most encountered in herbaceous savannahs in West Africa (Becker and Müller, 2007; Assédé *et al.*, 2012; Zerbo *et al.*, 2016). Thus, the flora considered in this study is representative of the most common taxa found in West African savannahs and therefore expresses the essential categories and dispersal patterns of diaspores in West African terrestrial savannah ecosystems.

The Poaceae and Fabaceae families, which were the most important families in the herbaceous savannah vegetation, contain a large variety of dispersal patterns. This indicates the good adaptation of herbaceous species to savannah environments and therefore demonstrates the proper distribution of species with high dispersal potential in this environment. The good distribution of species with high dispersal potential is very important for the possible future changes because it enables gene flow between different populations (Nathan and Muller-Landau, 2000).

Dispersal potential of herbaceous species

The dominance of species with multiple dispersal patterns in the herbaceous flora reflects the high dispersal potential of herbaceous vegetation. This large presence of multiple dispersal patterns among species is a strong asset, as it is responsible for their expansion into areas that are far from the parent plant (Vander-Wall and Longland, 2004; Soons and Ozinga, 2005). Indeed, the possession by a species of multiple dispersal patterns, known as diplochory, presents different benefits for plant species (Vander-Wall and Longland, 2004). For example, diplochory increases the likelihood that a species will cross the barrier of massive seedling mortality related to the proximity to the parent plant and colonize habitats far from the parent plant (Vander-Wall and Longland, 2004). This allows the diaspores to reach favourable sites where the probability of seedling establishing is higher (Vander-Wall and Longland, 2004).

Herbaceous species dispersal groups and their relationships with climate, land use and habitat conditions

The herbaceous species were classified into four major groups according to their dispersal patterns. These four groups expressed the most likely dispersal patterns of the species. Some dispersal patterns are inseparable. Thus, most anemochorous species possess epizoochorous attributes, and endozoochorous species are also dysozoochorous. Indeed, whereas dysozoochory represents the transport of seeds with reserve substances for animals that end up being forgotten or lost, endozoochory represents the seeds that are ingested by animals and rejected (Kleyer *et al.*, 2008; Pérez-Harguindeguy *et al.*, 2013). Moreover, most species belonged to these two groups, and this showed that herbaceous species have high dispersal potential. Indeed, anemochory, epizoochory, endozoochory and dyszoochory are long-distance dispersal patterns (Soons and Ozinga, 2005; Nathan, 2006; Aparicio *et al.,* 2008). Devineau (1999) noted the importance of endozoochory in the dissemination of species of families such as Fabaceae, Rubiaceae and Malvaceae.

Despite the high dispersal potential of herbaceous species, our results show that dissemination processes are influenced by environmental factors. Indeed, environmental factors individually or collectively influence the dissemination process (Nathan and Katul, 2005; Mc Conkey *et al.*, 2012). The dominance of potentially epizoochorous and anemochorous species in communal areas can be explained by the fact that there is a strong anthropogenic influence in these areas. Indeed, Bille (1992) and Manzano and Malo (2006) reported that grazing represents an excellent mode for the dissemination of epizoochorous species. Moreover, landscapes transformed by agriculture and various activities undertaken by local people in communal areas contribute considerably to the exposure of the herbaceous vegetation because there are fewer woody species in this kind of vegetation. The low density of woody species in communal areas therefore promotes the transport of potentially anemochorous species by wind. Different authors have documented that the vegetation structure affects long-distance dispersal patterns by wind (Soons *et al.*, 2004). Nathan and Katul (2005) noted that the loss of leaves in forest environments improves the potential for species dispersal by wind. The abundance of anemochory and epizoochory in all climatic zones of our study can be explained by the fact that all communal areas of the savannahs are influenced by the same anthropogenic factors (Bille, 1992; Manzano and Malo, 2006). In contrast, in protected areas, where the density of woody species is high, because of the prohibition of human activities, anemochory and epizoochory are less pronounced. Moreover, the richness of wildlife (including mammal fauna, avifauna and entomofauna) in protected areas can explain the significant presence of dysozoochory and endozoochory in these areas. Ragusa-Netto (2006) also showed that the abundance of wild animals in protected areas was favourable for the dissemination of dysozoochorous and endozoochorous diaspores. Macrofauna participate actively in ecosystem diversity through endozoochory (Heinken *et al.*, 2002). Birds also play an important role in seed dispersal (Levey *et al.*, 2005). In addition, Hovestadt *et al.* (1999) found that in protected areas where vegetation was denser, anemochory was less important than dispersal patterns related to animals. Consequently, in regard to vegetation gradients, anemochory becomes more important when moving from closed to opened vegetation. Therefore, landscape fragmentation has promoted the diversification of dispersal traits by wind (Cramer *et al.*, 2007; Riba *et al.*, 2009). However, Vander-Wall and Longland (2004) noticed that the coat of animals accumulated a large quantity of diaspores even if they were initially dispersed by anemochory. More dispersal patterns were related to habitat conditions. This importance of the habitat in the dissemination process is related to the fact that the distribution and occurrence patterns of species in ecosystems highly depend on habitat types. Habitat fragmentation affects the process of species dissemination and therefore disrupts the preservation of biodiversity (Weidema and Lindeijer, 2001; Cramer *et al.,* 2007).

Conclusion

The diaspores of herbaceous species can be classified into eight categories according to the fruit type, the elements used as diaspores, the presence of heterodiaspory, the exposure of diaspores, the number of seeds per diaspore, the morphology of diaspores, the shape of diaspores and the dispersal patterns. The dominant dispersal patterns encountered in the study area are anemochory, epizoochory, endozoochory, dyszoochory, hydrochory and autochory. According to the results of our study, in West African savannah ecosystems, herbaceous species with multiple dispersal patterns and those with high dispersal potential are frequent. The most important families of the herbaceous vegetation are those having several modes of dispersal. The findings of this study reveal that herbaceous species can be grouped into four main dispersal groups, of which potentially epizoochorous and anemochorous species are closely related to communal areas regardless of the climate and habitat conditions, potentially endozoochorous and dysozoochorous species are more related to the fresh and dry habitats of protected areas located in the North and South Sudanian zone, potentially hydrochorous species are encountered in wet habitats but are more prominent in the Sahel, and potentially autochorous species are more related to bowé habitats in the South Sudanian zone. Herbaceous species generally have good dispersal potentials, which might enable them to persist in West African savannahs despite the predicted severe climatic changes.

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