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Spatial structure of *Xylopia aethiopica* (Dunal) A. Rich., in the Guineo-Congolean zone of Benin (West Africa)

Essè Florentin DISSOU^{1*}, Soufiyanou KARIMOU³, Agossou Brice Hugues TENTE² and Ismaïla TOKO IMOROU³

¹Département de Géographie et Aménagement du Territoire (DGAT), Faculté des Sciences Humaines et Sociales (FASHS), Université d'Abomey-Calavi (UAC) ; 03 BP 366 Cotonou-Jéricho, République du Bénin. ²Laboratoire de Biogéographie et Expertise Environnementale (LABEE), Département de Géographie et Aménagement du Territoire (DGAT), Université d'Abomey-Calavi ; BP 698 Abomey-Calavi, République du Bénin.

³Laboratoire de Cartographie (LaCarto), Département de Géographie et Aménagement du Territoire (DGAT), Université d'Abomey-Calavi ; 10 BP 1082 Cotonou-Houéyiho, Benin. * Corresponding author, E-mail: defloty21@gmail.com ; Tel. : (00229) 67310981

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ABSTRACT

Xylopia aethiopica is a spice widely consumed in sub-Saharan Africa for the medicinal virtues of its fruits and seeds, whose distribution in its natural habitat is compromised by anthropic pressure. The aim of this study was to characterize the spatial distribution of Xylopia aethiopica plants and the possible interactions (attraction, independence, repulsion) that exist between them under the direct or indirect influence of the environment in which they grow. Phytosociological surveys were carried out in habitats hosting Xylopia aethiopica in the Guineo-Congolean zone of Benin. The geographical coordinates of adult plants and seedling individuals of Xylopia aethiopica were collected in 50 m x 200 m rectangular plots. The results of the univariate analysis showed that the spatial distribution of adult plants and seedlings was significantly aggregated in the fields. However, a random distribution trend was noted among seedling individuals, due to anthropogenic environmental influences. In the semi-deciduous dense forest, adult plants were significantly aggregated, with a tendency towards random distribution over certain distances, whereas seedling individuals had a significant exclusively aggregated distribution. In the gallery forest, both adult plants and young individuals were significant aggregated. Bivariate analyses showed that in the fields and the semi-deciduous dense forest, spatial associations were positive (attraction) and there was a strong independence of seedling individuals from adult plants over certain distances. Moreover, spatial associations between adult plants and seedling individuals in gallery forest were exclusively positive (attraction). The results of this study could be useful for policies aimed at the sustainable conservation of vulnerable plant species in Benin.

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INTRODUCTION

The regional center of Guineo-Congolean endemism encompasses the equatorial and humid tropical forest domains of West and Central Africa, characterized by a dense forest vegetation, mosaics of secondary formations and savannas, and abundant rainfall (Huntley, 2023).

However, this forest belt is separated by the enigmatic phenomenon of the "Dahomey Gap", a mosaic of open forest and savannas that covers some 200 km from South East Ghana to South East Benin (Assi-Kaudihis, 2011; Salzmann and Hoelzmann, 2005; Nobime et al., 2009). In the Beninese part of the Dahomey Gap, Sinsin and Kampmann (2010) point out that the humid dense forest exists only in small islands, and the dry-land evergreen unit is completely absent. Furthermore, the flora and fauna of these forests are made up of species from either or both forest blocks, as well as species from different savannah zones (Sinsin and Kampmann, 2010; Neuenschwander et al., 2011). For example, two of the three endemic genera of the Sudanian region (Vitellaria and Pseudocedrela) have been recorded here, and in the Commune of Grand-Popo, where rainfall is often less than 900 mm/year, there are still a few Balanites aegyptiaca plants, a typical Sahelian species (Sinsin and Kampmann, 2010). In addition, the islands of humid dense forest are mainly home to wide-ranging Guineo-Congolese species, which are common in countries such as Côte d'Ivoire (western bloc) on one hand, and Cameroon (eastern bloc) on the other. Most of these species are threatened by extinction due to the small size of these relict forests, heavy human pressure and their unclassified legal status. The IUCN Red List for Benin has identified 106 plant species threatened with extinction belonging to 103 genera and 44 families. Among plant species, some are endangered, while others such as Xylopia aethiopica, which have taken refuge in the dense forest relics like the Lokoli swamp forest (Adomou, et al. 2009) are vulnerable (Neuenschwander et al., 2011).

some species such as *Xylopia aethiopica*, which have taken refuge in the dense forest relics similar to that of Lokoli (Adomou, et al. 2009)

The acquisition of reliable data on the extinction risks ecology, and spatial distribution of species is a prerequisite for understanding their population dynamics and developing effective management plans (Fandohan et al., 2008). Better still, a better understanding of species spatial organization patterns enables to pinpoint the nature of the ecological processes underlying their coexistence (Martinez et al., 2013; Li et al., 2014). It is in that light that the present study analyzed the spatial distribution patterns of Xylopia aethiopica (Dunal) A. Rich. in the Guineo-Congolean zone of Benin. Its main objective was to understand the ground distribution of adult individuals of Xylopia aethiopica and the possible interactions they have with their regenerations under the direct indirect influence of environmental or disturbances, on the one hand, or in the absence of disturbances, on the other.

MATERIALS AND METHODS Study area

The Guineo-Congolean zone of Benin is located in the south of the Benin Republic, formerly known as Dahomey. The name Dahomey refers to the Dahomean Gap, one of the most basic definitions of which is a dry corridor separating the West African rainforest into two blocks, Upper Guinea and Lower Guinea (Poorter et al., 2004). The study area thus corresponds to the southern part of the Dahomean-Gap in the present-day Republic of Benin. It lies between 6° 25' and 7° 30' N and between 1° and 3° 40' E (IUCN/BIODEV2030, 2021). The rainfall regime is bimodal, with two rainy and two dry seasons alternating throughout the year. From east to west in the Guineo-Congolean zone of Benin, rainfall varies from 900 mm (Grand-Popo) to 1300 mm (Pobè), with an average number of rainy days equal to 200, while temperatures vary from 25°C to 29°C within the zone. Relative humidity varies from 97% to 69%, and the Mangenot humidity index ranges from 3.9 in Aplahoué to 5.8 in Porto-Novo (Sinsin and Kampmann, 2010).

The Guineo-Congolean zone of Benin is dominated by deep, ferrallitic soils of low fertility, alluvial soils and Vertisols located in the Mono, Couffo and Ouémé valleys, and in the Lama depression. These soils are rich in clay, organic matter and mineral elements (MCVDD, 2022).

The phytogeographical breakdown of Benin (Adomou, 2005) divided it into four phytogeographical districts (Coastal, Pobè, Ouémé Valley and Plateau) on the basis of phytosociology in relation to climatic and pedological factors (Figure 1).

Data collection

The plant material considered in the present study was the individuals of *Xylopia aethiopica* found in the phytogeographic districts of the Guineo-Congolean zone of Benin, regardless of their phenological development.

Sampling

Investigations were carried out in different types of habitats (fields, dense semideciduous forest and degraded gallery forest) in the Guineo-Congolean zone of Benin. As the geographical position of the individuals of Xylopia aethiopica was not known in advance, a guide, native to each targeted village and with a good knowledge of the species and the village, was recruited. The Communes of the Plateau (Adja-Ouèrè, Ifangni, Kétou, Pobè, Sakété) and Ouémé (Adjarra, Adjohoun, Akpro-Missérété, Avrankou, Aguégués, Bonou, Dangbo, Porto-Novo, Sèmè-Kpodji) departments were prioritized as they recorded at least 80% of the frequency of citation. Next came the communes of Abomey-Calavi,

Allada and Ouidah in the Atlantic Department, with frequencies of 40%, 38% and 35% respectively.

A total of thirty-three sample points (plots) were investigated, unevenly distributed across the phytogeographical districts of the Guineo-Congolean zone of Benin. The plots were rectangular (50 m x 200 m) in shape, each covering an area of one hectare.

Collected data

The data collected were as follows:

- the geographical coordinates of all *Xylopia aethiopica* individuals found within the plots, regardless of their phenological stage;
- information on plot location (department, commune, arrondissement, village, station number) and ecological parameters (soil formation type, type, topographical situation, degree of anthropization, special observations).

Methods of treatment

The g(r) function is based on tree-tree distances and describes tree repulsion and aggregation at a given spatial scale r, using the expected number of trees found at spatial scale r from an arbitrary tree, divided by the model intensity (Wiegand and Moloney, 2014). Equation (a) is the pairwise correlation function g(r). It is the non-cumulative counterpart of Ripley's K-function represented by equation (b) (Erfanifard and Sterenczak, 2017). The Ripley's K-function is one of the most popular second-order summary statistics that expresses the expected number of additional points (trees) in a disk of radius r centered on a typical point (tree) of a model, previously used by Fajardo et al. (2015). It was also used by Toko Imorou (2020) in a study on spatial distribution of Triplochiton the scleroxylon in the Guineo-Congolese zone of Benin and Atindogbe et al. (2020). Due to its cumulative structure, Ripley's K-function is not easy to interpret and less present in the literature (Erfanifard and Sterenczak, 2017).

$$g(\mathbf{r}) = \frac{dK(r)}{(2\pi r)(dr)} \quad (a)$$
$$K(r) = n^2 |A| \sum_{i \neq j} \sum e_{ij}^{-1} I(u_{ij}) \quad (b)$$

where r is the radius of the disc (ring in g(r)), A is the area of the study plot, u_{ij} is the distance between the focal tree (i) and its neighboring tree (j), n is the total number of points in the point model, I (u_{ij}) is equal to 1 if $u_{ij} < r$ and 0 if not, and e_{ij} is the edge effect correction method. If g(r) > 1, then tree pairs are more abundant than the spatial mean at a spatial scale r, expressing tree aggregation. Conversely, if g(r) < 1, then it shows tree repulsion as tree pairs are less abundant than the spatial average at a spatial scale r. The univariate g(r) function under a null model of inhomogeneous Poisson processes was used because the exploratory analysis carried out on the plots studied revealed significant environmental heterogeneity of the stands studied (Getzin et al., 2008; Wiegand and Moloney, 2014).

Statistical analysis

The data collected, essentially consisting of points of presence of *Xylopia aethiopica*, (seedling individuals and adult plants) were initially entered to the Microsoft Office Excel 2019 spreadsheet. However, all analyses (univariate and bivariate) of the species' spatial distribution were respectively carried out using Paleontological Statistics software (package for education and data analysis, Hammer, July 2017, Past 3.16) and R 3.0.3 software.

Analyses were performed using the univariate pair correlation function g(r), as the most informative second-order distancedependent summary statistic for spatial pattern analysis, frequently used in ecological studies (Getzin et al., 2006; Petritan et al., 2015; Erfanifard and Sterenczak, 2017).

Univariate analysis is performed on individuals in one category (adult or regeneration), while bivariate analysis between the concerns interactions two categories. Considering a 95% confidence interval, the null hypothesis for univariate analyses is a random spatial distribution, while for bivariate analyses, the null hypothesis is spatial independence. Thus, the significance of an observed pattern deviating from the expected distribution under the null model was assessed by comparing the observed distribution function with the confidence interval generated by Monte Carlo simulations of the null hypothesis (Diggle, 2013).

In other words, it implies that when at a given scale the estimated model falls outside the confidence interval of the simulation, the null hypothesis was rejected at that scale. For univariate analyses, when the estimated model is above the upper bound of the confidence interval, this indicates an aggregated spatial character. When the estimated model is below the lower bound of the confidence interval, this indicates regularity. When the estimated pattern lies within the confidence interval, this indicates spatial randomness.

For a bivariate analysis, when the estimated model is aligned within the confidence interval, this indicates spatial independence, whereas when the model is located above or below the bounds of the interval, this indicates a positive association (attraction) and a negative association (repulsion) respectively. Spatial analyses were performed in the spatstat package (Baddeley and Turner, 2005) of the R 3.0.3 statistical software (R Core Team, 2014).



Figure 1: Location of the Guineo-Congolean zone of Benin.

RESULTS

Univariate analysis Spatial distribution of Xylopia aethiopica in fields

A total of twenty-four plots were established in the fields, representing 72% of the overall inventory area. Statistical analyses of the spatial distribution pattern of *X. aethiopica* in the fields showed significant levels of aggregation. Table 1 shows the results of some of the parameters analyzed for adult individuals and regeneration of *X. aethiopica*.

Analysis of the results presented in Table 1 showed that the average number of neighbors is 23.5 for adult individuals and 27.6 for seedling individuals. The results indicate a significant aggregated spatial distribution of adult individuals over a distance of more than 50 meters in the fields (Figure 2a). The density of aggregated individuals was observed over the first 10 meters (Figure 2b). A similar spatial pattern was observed for seedling individuals. However, as shown in Figure 2c, some minor exceptions were noted. Between 0 and 27 meters, the distribution was aggregative, while beyond 27 meters, the trend took the form of a random distribution. The density of agglomerated individuals ranged from 0 to 14 meters and from 19 to 24 meters (Figure 2d).

On the other hand, in some cases, such as the one illustrated in Figure 3, the distribution of regenerating individuals is significantly random. This confirms the trend observed above, as well as the null hypothesis of the research.

Figure 3 illustrates the random ground distribution of young *X. aethiopica* seedlings observed in a field over a distance of between 0 and 30 meters. The high density of seedlings was observed between 2.5 and 18 meters.

However, in this field, the density of adult *X*. *aethiopica* trees was zero, that is, there were no standing adult seedling individuals.

Spatial distribution of Xylopia aethiopica in dense semi-deciduous forest

Investigations in the semi-deciduous dense forest covered a total area of 5 ha, i.e. 15.15% of the total area investigated. Table 2 presents the results of the analysis of the distribution pattern of adult and seedling *X*. *aethiopica* individuals in the semi-deciduous dense forest.

Analysis of Table 2 shows the significance thresholds of an aggregated distribution for all adult and regenerating individuals. The average number of nearest neighbors is 25.66 for mother plants and 66.33 for regeneration. Figure 4 shows the relative distances between individuals in the same category.

The results revealed a significant aggregated spatial distribution of adult individuals over a distance of more than 300 meters (Figure 4a), with aggregation density globally concentrated between 10 and 12 meters (Figure 4b, f,h). The same spatial distribution pattern was observed for seedling individuals over a distance of 22 meters (Figure 4d), with an aggregation density less than or equal to 3 meters (Figure 4d).

Although the overall distribution of adult individuals was significantly aggregated, there were some non-significant trends towards a random distribution in some cases between 0 and 2 meters (Figure 4e) and over a distance of more than 15 meters (Figure 4g).

Spatial distribution of Xylopia aethiopica in degraded gallery forest

The total area covered by the investigations carried out in the gallery forest was 4 ha, that is, 12.12% of the total area investigated. Table 3 presents the results of the analysis of the distribution mode of adult and juvenile *X. aethiopica* in the gallery forest.

Analysis of Table 3 reveals that in the

gallery forest, adult and regenerating *X. aethiopica* plants are significantly distributed in an aggregated fashion. The average number of nearest neighbors is 10 for seedlings and 13 for regeneration. Analysis of Figure 5 shows the relative distances between individuals in the same category.

In terms of adult individuals, the distribution was significantly aggregated between 0 and 150 meters (Figure 5a). The density of aggregated adult individuals was concentrated between 0 and 2 meters, 6 and 8 meters and 9 and 10 meters (Figure 5b). For seedling plants, the spatial distribution was also aggregated over a distance ranging from 0 to over 120 meters, with a high density of individuals between 0 and 20 meters and between 30 and 34.9 meters (Figure 5c,d).

Bivariate analysis

Bivariate analysis indicated that associations between adult plants and seedling individuals of X. aethiopica varied from habitat to habitat (Figure 6). In some fields, positive spatial associations were detected between 0 and 27 meters (Figure 6a), while in other fields, strong independencies were observed over a distance between 0 and 25 meters overall (Figure 6b,c). The same findings apply to semideciduous dense forests. However, in semideciduous dense forest, positive associations extended over a relatively long distance of at 150 meters (Figure 6d). least while independent associations were observed over a distance of no more than 25 meters (Figure 6e,f). Concerning outside fields and semideciduous dense forests, the spatial associations of adult X. aethiopica individuals and their seedlings were exclusively positive (attraction). This interrelationship between adults plants and seedling individuals in gallery forest was observed over distances ranging from 0 to 20 meters, 0 to 8 meters and 0 to 79 meters respectively (Figure 6g,h,i).

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Categories	Number of	Mean density	Mean	Expected	Ζ	R	p (random)
	neighbors	(number of	distance	distance			:
		stems/ha)	(m)	(m)			
Adult plants	46	3,74E-03	3,2881	8,18	-7,7595	0,4020	8,52E-15
	28	0,0019505	6,1302	11,321	-4,6416	0,5414	3,46E-06
	10	0,0050505	3,1493	7,0356	-3,3417	0,4476	0,0008327
	10	0,0003858	7,9706	25,456	-4,1554	0,3131	3,25E-05
	23,5	-	-	-	-	-	-
Young plants	23	3,90E-03	4,5411	8,0054	-3,9703	0,56726	0,000071784
	31	0,010438	3,5882	4,894	-2,8421	0,73318	0,0044821
	31	0,020764	1,0967	3,4699	-7,285	0,31606	3,22E-13
	18	0,002726	4,8669	9,5764	-3,9915	0,50821	6,56E-05
	17	0,0012599	5,7962	14,086	-4,6421	0,41147	3,45E-06
	50	0,0044045	2,6675	7,5339	-8,7378	0,35407	2,38E-18
	15	0.0027322	10.812	9.5656	0.96507	1.1303	0.33451
	51	0.014182	1.2253	4.1985	-9.6747	0.29185	3.8623E-22
	23	0.0055288	1.2051	6.7244	-7.5304	0.17922	5.058E-14
	17	0.0011054	8.7465	15.039	-3.3002	0.5816	0.00096601
	27.6	_	_	_	_	_	_

Table 1: Results of the statistical analysis of the spatial distribution of X. aethiopica in the fields.



Figure 2: Spatial distribution, observed and expected distances of X. aethiopica in the fields.



Figure 3: Spatial distribution, observed and expected distances of *X. aethiopica* in the fields.

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Categories	Number of	Mean density	Mean	Expected	Z	R	p (random)
	neighbors	(number of	distance (m)	distance			:
		stems/ha)		(m)			
Adult plants	35	0,0082547	3,4184	5,5032	-4,2876	0,6211	1,806E-05
	14	3,67E-03	3,3067	8,2549	-4,2907	0,4005	1,78E-05
	28	4,36E-05	10,478	75,704	-8,7219	0,1384	2,74E-18
	25,66	-	-	-	-	-	-
Young plants	148	0,031732	1,0993	2,8068	-14,158	0,39167	1,67E-45
	14	4,17E-03	2,8647	7,746	-4,5107	0,36983	6,46E-06
	37	6,07E-05	6,1197	64,185	-10,527	0,0953	6,47E-26
	66,33	-	-	-	-	-	-

Table 2: Spatial distribution of X. aethiopica individuals in semi-deciduous dense forest.

Table 3: Spatial distribution of X. aethiopica in degraded gallery forest.

Categories	Number of neighbors	Mean density (number of stems/ha)	Mean distance (m)	Expected distance (m)	Z	R	p (random) :
Adult plants	10	1.9263E-05	5.3792	113.92	-5.764	0.0472	8.2157E-09
Young plants	13	0.00017789	13.267	37.488	-4.4566	0.3538	8.3251E-06



Figure 4: Spatial distribution, observed and expected distances of *X. aethiopica* in semi-deciduous dense forest.



Figure 5: Spatial distribution, observed and expected distances of *X. aethiopica* in the gallery forest.



Figure 6: Results of bivariate analysis.

DISCUSSION

Spatial distribution of adult plants and seedling individuals of *Xylopia aethiopica* within their habitats in the Guineo-Congolean zone

The present results showed that, although some differences were noted in certain habitat types for both adult and regenerating individuals of X. aethiopica, the most widespread distribution pattern in all habitats considered for the species is the aggregative distribution. This is to be expected, given that X. aethiopica is a barochorous species. The global spatial structure of X. aethiopica (aggregative distribution) then contrasts with the random spatial of Triplochiton scleroxylon (Toko Imorou, 2020) in the Guineo-Congolese region of Benin. These results also contrast with those of Glèlè Kakaï et al. (2009) in a study carried out on Pterocarpus erinaceus, which had an overall random distribution and a tendency to aggregate in the savannah and open forest of the Sudanian zone of Benin, and those of Fandohan et al. (2008) in a study carried out on three medicinal woody species in the Wari-Maro classified forest in Benin.

In the fields, a significant aggregated distribution of adult individuals and those of X. aethiopica regeneration was observed. The aggregated distribution was confirmed significantly at 100% for adult individuals. This means that, at the soil surface, they are arranged or gathered in groups. As for the seedlings, a random distribution was observed in a field marked by an absence of seed trees. It could therefore be deduced that the random distribution of regeneration in this field was due to an anthropogenic influence. Indeed, the distribution pattern observed in a field may result from the objectives pursued by the field operator.

Semi-deciduous dense forest is present in southern Benin in the form of islands witnessing the climax vegetation. The high number of neighbors for adult plants (25.66) and seedling individuals (66.33) in semideciduous dense forest means that seedling individuals of the species grows in clumps at the foot of seed trees after fruit drop and when these are not collected by man or moved by animals. This explains why all X. aethiopica distribution patterns are aggregated in semideciduous dense forest. Although there is a tendency towards a random distribution of adult individuals in some cases, this is not significant; in other words, the distribution pattern of X. aethiopica remains globally aggregated for both adult plants and seedling individuals. On the other hand, the observed tendency of adult individuals to a random distribution can be explained by strong interspecific competition in dense forest, which naturally reduces the density of X. aethiopica plants per hectare during its development. These results are similar to those of a study carried out on pine stands in Poland (Erfanifard and Sterenczak, 2017). Indeed, according to Kint et al. (2006) and Baudis et al. (2014), the shift from an aggregative to a random distribution of individuals is justified by differences in the competitive interactions of trees at various stages of their growth. Competition significantly influences the spatial distribution of trees at later stages of development.

In the gallery forest, all adult and seedling individuals of X. aethiopica have an aggregative distribution on the ground. This habitat, marked by the more or less permanent presence of water, is the preferred habitat of X. aethiopica (Orwa et al., 2009). Unfortunately, the gallery forest hosting X. aethiopica is degraded, which explains the low density of adult and regenerating individuals. For example, an average of 15% of mutilated or dead adults in a plot was found. The death of adult individuals is due to overharvesting of organs, notably bark and roots, and results in a drop in reproduction, which indirectly influences the species seedling density.

The apparent aggregation of spatial

distribution across all habitats is consistent with the typical spatial patterns of species found in humid rainforests (Condit et al., 2000; Xiang et al., 2011). The aggregative trend of X. aethiopica shown by the present study is similar to the behavior of Cola millenii and Dialium guineense individuals within a 10 m radius around their landmarks in secondary forests of southern Benin (Kakpo et al., 2018). According to Li et al. (2009) spatial aggregation could be attributed to several major mechanisms and processes, including dispersal limitation (Harms et al., 2001), reproductive behavior and habitat heterogeneity (Harms et al., 2001).

Interdependence between adult individuals and regeneration of *Xylopia aethiopica*

Bivariate analyses were carried out to establish interdependent relationships between adult plants and seedling individuals. The positive results revealed associations (attractions) in all the species' habitats. However, X. aethiopica seedlings were found to be independent of adult individuals in fields and semi-deciduous dense forests. In gallery forest, the positive associations show that the distribution of young individuals around the trees is indicative of greater seedling density in the immediate vicinity of the mother trees than away from them. This indicates that mature X. aethiopica trees promote the development of seedling individuals in their immediate vicinity (Glèlè Kakaï et al., 2009). In contrast, the independent relationships observed between seedlings and adult individuals in the field can be explained by anthropogenic influences. On the other hand, in semi-deciduous dense forest, this can be explained by the small size of the dense forest block, which imposes strong competition in this type of habitat.

Conclusion

The present study characterized the spatial distribution of adult plants and seedling individuals of *X. aethiopica* individuals in

different habitats of the species in the Guineo-Congolean zone of Benin. The main results showed that in the fields, the spatial distribution of adult individuals is significantly aggregative, while that of seedling individuals is both aggregative and random (due to anthropogenic environmental influences). In semi-deciduous dense forest, the distribution of adult trees is globally aggregated, with a tendency towards random distribution over certain observed distances. The distribution of seedling individuals is significantly aggregated in semi-deciduous dense forest. Finally, in gallery forest, both adult plants and seedling individuals are significantly aggregated. Analysis of the interdependent relationships between adult plants and seedlings individuals led to the conclusion that in fields and semideciduous dense forest, there were positive spatial associations (attraction) and strong independence of young individuals over certain distances. On the other hand, in the gallery forest, spatial associations between adult plants and seedling individuals of X. aethiopica were exclusively positive (attraction).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

EFD and SK conducted the study, collected the field data, carried out the statistical analyses and edited the manuscript. ABHT and ITI supervised the study and corrected the manuscript. All authors have read and approved the final version of the manuscript.

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