

Spatial distribution patterns of *Azelia africana* (Fabaceae – Detarioideae) in a tropical savanna of Benin: implications for management

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Background and aims – Understanding the spatial patterns and associations of tree species with their conspecific and heterospecific neighbours is critical for sustainable management of their stands. This study assessed the intra- and interspecific spatial structure of six life stages in *Azelia africana*, a keystone multipurpose and endangered tree species in a tropical savanna of Benin.

Material and methods – Three plots of 4 ha each were demarcated on three sites along a conservation gradient (hunting zone – core conservation zone). Individuals of *A. africana* (irrespective of their diameter at breast height) and heterospecific trees (dbh \geq 5 cm) were mapped. Tree spatial patterns and associations were determined using univariate and bivariate pair correlation functions. The distance to the nearest neighbour was further used to assess tree-to-tree distance.

Key results – We found variable spatial patterns across sites. In the core zone where wildlife density is high, most life stages had a random distribution. In contrast, in the hunting zone where wildlife density is low, the species spatial distribution changed from a predominantly aggregative pattern during early stages to a less aggregative or random spatial pattern for very large adults. Most pairs of life stages showed neutral associations, except for small and large adults, which had positive association between themselves on two sites. We also found that *A. africana* tree spatial distribution was unrelated to heterospecific trees.

Conclusion – We suggest that bush fire, seed dispersion, predation, and local environment would have contributed to the observed patterns.

Keywords – Pair correlation function; plant coexistence; plant-plant interactions; point pattern process; silviculture; tree-to-tree distance.

INTRODUCTION

Understanding tree species spatial pattern is central in plant population and community ecology (Zhang et al. 2010; Chu et al. 2014; Liu et al. 2014). Tree spatial patterns primarily inform on how plants are positioned naturally to each other in forest stands (Yuan et al. 2018). They are important in explaining ecological processes, species coexistence, and community structure (Martinez et al. 2010). The extent to

which plant individuals are aggregated or dispersed can also guide inference on how species use or share resources, and how they reproduce (Barot et al. 1999b; Condit et al. 2000). Finally, tree spatial patterns also provide vital information for managing natural stands through optimal planting techniques (Liu et al. 2014).

There is evidence that plant spatial patterns are governed by interactive effects of biotic and abiotic factors (McIntire & Fajardo 2009), because these factors determine

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neighbourhood competition, regeneration limitation, predation, habitat heterogeneity, and niche segregation. The abiotic factors are diverse, and include soil nutrient (Barot & Gignoux 2003), topographic variables (aspect, slope, elevation) (Bai et al. 2012; Chanthorn et al. 2013; Muvengwi et al. 2018), light requirement (Ledo et al. 2012), and fire occurrence and intensity (Chu et al. 2014; Riginos et al. 2015). Biotic factors include seed dispersal and predation (Barot et al. 1999b; Ledo et al. 2012), diversity of dispersers (Beckman & Rogers 2013; Harrison et al. 2013), herbivores feeding patterns and activities (Salako et al. 2019), conspecific and heterospecific competitive and facilitative interactions (Getzin et al. 2006; Metz et al. 2010; Uriarte et al. 2010; Jurinitz et al. 2013; Martínez et al. 2013), and association to ectomycorrhizal fungi (Sasaki et al. 2019). The magnitude of the importance of these factors is habitat and species specific.

Afzelia africana Sm. ex Pers. (Fabaceae – Detarioideae) is a keystone multipurpose tree species of Sudanian and Sudano-Guinean savannas, woodlands, and gallery forests in West Africa (Aubrèville 1959; Arbonnier 2004). Its timber is of good quality and highly priced on international markets (Mensah et al. 2016). It is an important medicinal tree used to treat various ailments (Houehanou et al. 2011; Balima et al. 2018; Partey et al. 2018). Trees of *A. africana* are also pruned to feed livestock during the dry season, when the herbaceous layer is not available for grazing (Amahowe et al. 2018). Its leaves are reported to be one of the most palatable to livestock in West Africa (Onana & Devineau 2002; Nacoulma et al. 2017). These multiple uses have resulted in the over-exploitation of the species, and this has considerably affected its natural populations, putting the species higher on the research agenda in West Africa. *Afzelia africana* is considered as vulnerable on the IUCN red list of threatened species (Hills 2020) but considered endangered in many countries (e.g. Benin) (Adomou et al. 2011).

Previous studies described the species population structure and associated drivers (Mensah et al. 2014; Assogbadjo et al. 2017; Nacoulma et al. 2017; Amahowe et al. 2018; Atanasso et al. 2019). There are consistent reports of poor natural regeneration and a recruitment bottleneck of the species even in protected areas (Sinsin et al. 2004; Bonou et al. 2009; Amahowe et al. 2018). Bationo et al. (2001) suggested this is linked to the sensitivity of the species seedling to fire, grazing, and drought stress that prevail in the Sudanian zone (Nacoulma et al. 2017; Amahowe et al. 2018). Despite research efforts and valuable information existing on the species, we still know little about *A. africana* intra- (i.e. within the species populations) and interspecific (i.e. between these populations and their neighbouring heterospecific trees) interactions. No study has explicitly addressed the species population ecology from a spatial perspective, despite the fact that additional insights could still be drawn from analysing intra- and interspecific spatial relationships.

The present study is guided by the need to understand how individuals of *A. africana* interact with their conspecific and heterospecific neighbours from the same and different life stages. Previous studies on tree spatial pattern suggest variation across life stages, with an overall trend of a

less intraspecific aggregation in adult trees (Barot et al. 1999a; Liu et al. 2014). A target species may also show neutral, positive, or negative spatial relationships with its heterospecific neighbours depending on their size (e.g. stem diameter class). Therefore, differences in species spatial patterns and associations should be considered when designing afforestation and developing conservation strategies (Chu et al. 2014).

Here, we used the pair correlation function approach, which is the derivative of Ripley's popular K function (Wiegand & Moloney 2004) to analyse the spatial relationship of *A. africana* conspecific and heterospecific trees in the Pendjari Biosphere Reserve in West Africa. Specifically, we assessed (i) the spatial relationship of *A. africana* individuals within each life stage, (ii) the spatial relationship of each life stage of *A. africana* with its conspecific neighbours from other life stages, (iii) the spatial relationship of each life stage of *A. africana* with its heterospecific neighbours of different size, (iv) and the pairwise distance between *A. africana* conspecific and heterospecific individuals within and across life stages.

MATERIAL AND METHODS

Study species

Afzelia africana is an evergreen tree, up to 40 m tall, with the trunk branchless for up to 20 m, usually straight and cylindrical, up to 150–200 cm in diameter, often with unequal, thick buttresses up to 1.5 m high (White 1986; Gérard & Louppe 2011). Fruits are thick and flat with bivalve pod of 10 to 15 cm long and 6 to 7 cm wide. Each pod contains up to ten ellipsoid or oblong-ellipsoid black seeds of 1.5 to 3 cm long. The seeds are covered by an orange aril at the base, which could play a role in their dispersal and predation (Bationo et al. 2000). Pods open violently to facilitate seed dispersal (Arbonnier 2004).

The species is characteristic of the transition zone between tree savannas and dense dry forests, and of the dense semi-deciduous forest in the humid regions of West Africa, showing an adaptation to various climatic conditions. However, it is most common in areas with annual rainfall of more than 900 mm. In drier regions, it is limited to sites with deep, well-drained but moist soils and to termite mounds. The species can grow on various soil types characterized by sandy or ferrallitic soils, steep slopes, as well as in depressions and in regularly flooded sites (Gérard & Louppe 2011). Regarding the light requirements, *A. africana* is considered as a non-pioneer light demander species (Hawthorne 1995).

In the driest sites, *A. africana* is fairly fire resistant, but in dense forest it appears to be susceptible even to occasional fires. Data suggest that *A. africana* woodlands are being threatened and invaded by more fire-tolerant species when they are burned (Gérard & Louppe 2011). Early life stages, namely seedlings, are very sensitive to fire, browsing, and drought (Hawthorne 1995). Young *A. africana* trees often develop poorly due to damage caused by animals such as antelopes or livestock that feed on the foliage and damage the terminal buds. The seedling stage is also susceptible to fungal and grasshopper attacks (Gérard & Louppe 2011;

Table 1 – Number of individuals mapped by site. †The first number corresponds to the number of solitary seedlings (respectively solitary saplings) and the second number corresponds to the number of clumps of seedlings (respectively clumps of saplings).

Site	Species	Seedlings [†]	Saplings [†]	Juveniles	Small adults	Large adults	Very large adults
Batia (hunting zone)	<i>A. africana</i>	38/31	49/122	4	92	93	14
	Heterospecific			14	182	80	29
Bondjagou (edge of core zone)	<i>A. africana</i>	37/58	7/9	2	43	102	67
	Heterospecific			2	37	50	8
Bali (core zone)	<i>A. africana</i>	28/64	4/3	0	24	64	27
	Heterospecific			5	82	24	0

Mensah et al. 2020). As such, individuals that have their terminal buds out of reach of browsing animals in the dry season are more likely to survive. Seeds are dispersed by large birds such as hornbills, which feed on the arils (Bationo et al. 2000). Similar to observations in the sister species *Afzelia bipindensis* (Evrard et al. 2019), rodents such as rats (*Proechimys* spp.) seem to be the main predators of *A. africana* seeds (Bationo et al. 2000). Some stocks of its seeds have been found in dead termitaria. More than 30 species of ectomycorrhizal fungi have been recorded as associated with *A. africana* (Gérard & Louppe 2011).

Study area

The Pendjari Biosphere Reserve (PBR) is located in the Sudanian zone between 0°30'–11°30'N and 0°50'–2°00'E in Benin. The PBR is divided into the Pendjari National Park (PNP, 2660 km²) which is the core zone of the reserve, i.e. completely protected and where only tourism activities are permitted, and the hunting zones of Pendjari (1750 km²) and Konkombri (251 km²) where hunting activities are permitted for tourists and occasionally for the local population. In the hunting zones, harvesting of non-timber forest products is also common. As a result, wildlife density is higher in the core zone (Sinsin et al. 2002, 2008). The hunting zones are further surrounded by a buffer zone where agricultural activities are controlled (Assédé et al. 2012).

The climate is characterized by one rainy season (May–October) and one dry season (November–April). Mean annual rainfall is 1000 mm with a mean annual temperature of 27°C. *Afzelia africana* is found in the reserve in both the hunting zones and the core zone, often as mixed natural stands. Most co-occurring species include *Vitellaria paradoxa* C.F.Gaertn., *Pterocarpus erinaceus* Poir., *Lannea acida* L., *Detarium microcarpum* Guill. & Perr., *Terminalia avicennioides* Guill. & Perr., *Isobertinia tomentosa* (Harms) Craib & Stapf, *Burkea africana* Hook., *Diospyros mespiliformis* Hochst. ex A.DC., *Tamarindus indica* L., and *Anogeisus leiocarpus* (DC.) Guill. & Perr. (Mensah et al. 2016; Atanasso et al. 2019).

The PBR, especially the National Park, is also home to most West African wild fauna including savanna elephant, roan antelope, savanna buffalo, waterbuck, common duiker, reedbuck, oribi, baboons, and carnivores such as lion, cheetah, leopard, side-striped jackal, and spotted hyena (Sokpon et al. 2008). As a savanna ecosystem, prescribed burns are commonly applied as management intervention to

improve the availability of herbaceous fodder to wildlife but also for tourism. These fires are set at the end of the rainy season, before the start of the dry season, and they are more frequent in the core zone than in the hunting zones (Grégoire & Simonetti 2010).

Sampling design and data collection

Three stands of *A. africana* populations in mixture with other species were identified and characterized along a core zone – hunting zone gradient in a preliminary study by Atanasso et al. (2019). These include Batia in the hunting zone of Pendjari, Bali in the core zone, and Bondjagou at the edge of the core zone. The stand in Bondjagou was the largest in terms of area (supplementary file 1). Density of adult trees (dbh ≥ 10 cm) of *A. africana* was twice as high in Batia and Bondjagou as in Bali. Density of regeneration (dbh < 10 cm) of *A. africana* was twice as high in Batia as in Bali and Bondjagou. Due to its location in a hunting zone, the site of Batia is more exposed to anthropogenic activities and has a smaller wildlife density than that of Bali in the core zone where wildlife density is higher. The Bondjagou site being at the edge of the core zone is characterized by intermediate wildlife density and human activities. Dominant heterospecific species differ among the sites (supplementary file 1). More details regarding differences in the floristic, density, and structural characteristics of the three sites can be found in Atanasso et al. (2019).

We established a 4 ha (200 m × 200 m) plot in each of the three stands for data collection. To facilitate tree identification and mapping, each plot was sub-divided into four contiguous bands of 50 m × 200 m. All individuals of *A. africana* (irrespective of their diameter at breast height) and heterospecific trees (dbh ≥ 5 cm, see supplementary file 2) were mapped. Starting with a reference tree, we measured distance between nearest neighbouring trees, dbh, total height, azimuth, and slope. Dbh was measured with Pi ribbon; tree total height was calculated using trigonometry relationship based on the distance from measurement spot to the tree (using penta-decameter) and the angle of its base and top (using clinometer); the azimuth was determined with a compass (Salako et al. 2019).

Data analysis

Individuals of *A. africana* and heterospecific species were categorized, on the basis of their dbh in the following life stages: seedlings (dbh ≤ 1 cm); saplings (1 cm < dbh ≤ 5

cm); juveniles (5 cm < dbh < 10 cm); small adults (10 ≤ dbh ≤ 25 cm); large adults (25 < dbh ≤ 40 cm); and very large adults (dbh > 40 cm) (Kanagaraj et al. 2011; Zhu et al. 2018). Heterospecific trees were only considered from the juvenile stage onward, resulting in four categories. We used these categories based on the hypothesis that spatial relationships would vary with tree size (Zhu et al. 2018). The number of individuals mapped per life stage on each site is summarized in table 1. Chi-square tests were used to examine whether the demographic structure of *A. africana* and that of other species was independent of the site.

The data on distance, azimuth, and slope were converted into *x* and *y* coordinates using Arpent 1.3.d. software (Lejeune 2001) (see fig. 1). Spatial relationships of trees were analyzed using the pair correlation function. The global pair correlation function *g* for a point pattern process of two types of objects *i* and *j* at a distance *r* is given by the following formula (Baddeley & Turner 2005; Baddeley et al. 2015):

$$g_{i,j}(r) = \frac{K'_{ij}(r)}{2\pi r}$$

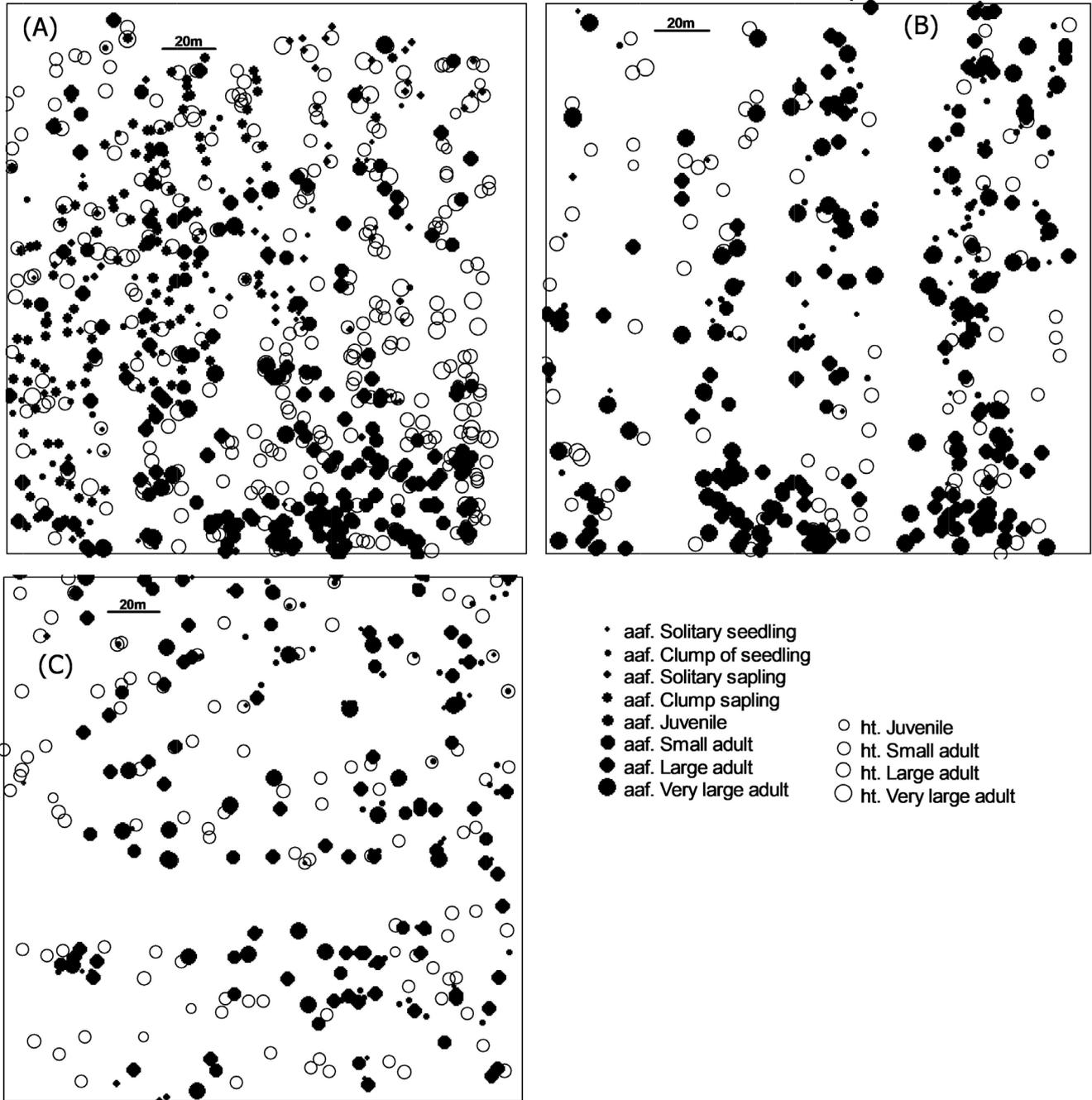


Figure 1 – Cartography of individuals mapped in the three sites. A. Site of Batia (hunting zone). B. Site of Bondjagou (edge of the core zone). C. Site of Bali (core zone). *aaf* stands for *A. africana* and *ht* for heterospecific.

where $K'_{ij}(r)$ is the derivative of the Ripley's K function $K_{ij}(r)$ (Ripley 1981). The spatial relationship between a life stage j (e.g. seedlings) and a life stage i (e.g. very large adults, taken as reference) in a radius r is given by $g_{ij}(r)$; when $i = j$, the analysis is univariate, and bivariate otherwise (Barot et al. 1999a; Baddeley & Turner 2005).

The above function was used to test whether the distribution of each mapped life stage of *A. africana* was random, aggregative, or regular (in the case of univariate spatial analysis), or whether the relationship between two life stages of *A. africana* (or between a life stage of *A. africana* versus a life stage of heterospecific trees) suggests spatial association i.e. positive relationship, repulsion i.e. negative relationship, or independence i.e. neutral relationship (in the case of bivariate spatial analysis) (Stoyan & Stoyan 1994).

The significance of any observed pattern that deviates from the null model of complete spatial randomness (univariate case) or spatial independence (bivariate case) was determined using the confidence envelopes based on 500 Monte Carlo simulations of the null model (Diggle 2003). For a given scale r , when $g(r)$ falls outside the simulation envelope (i.e. $\neq 1$), the null hypothesis of random distribution (and spatial independence in case of bivariate analysis) is rejected. For a univariate point pattern, $g(r) = 1$ indicates a random distribution or no pattern, while $g(r) > 1$ or $g(r) < 1$ indicates clumping and regularity, respectively. For a bivariate analysis, $g_{ij}(r) = 1$ indicates a spatial independence whereas $g_{ij}(r) > 1$ or $g_{ij}(r) < 1$ indicates a positive association (attraction) or a negative association (repulsion), respectively. The spatial analyses were conducted with the R package spatstat (Baddeley & Turner 2005) in the R statistical software v.3.3.3 (R Core Team 2017).

To assess the tree-to-tree distance, the `nndist` and `nncross` functions were used to compute the distance from each point to its nearest neighbour for univariate and bivariate point pattern analysis, respectively. Because the function g_{ij} is not symmetric (Barot et al. 1999a), both directions (i vs j and j vs i) were explored. Linear mixed effect models with a random intercept structure were fitted using `lmerTest` package (Kuznetsova et al. 2017) to test how the pairwise distance between any two individuals varied with the life stage. Explanatory variables in these models were “life stage” (fixed factor) and “site” (random factor). One model was run for univariate point pattern where the factor “life stage” refers to the life stages of *A. africana*. In the case of bivariate patterns, one model was run for each focal life stage (supplementary file 4). Here, factor “life stage” refers to life stages of *A. africana* in the case of conspecific bivariate point patterns, and to life stages of other species in the case of heterospecific bivariate patterns.

RESULTS

Demographic structure of *A. africana* and other tree species

Density of *A. africana* was higher in the hunting zone than in the two other sites (table 1). Density of heterospecific trees also showed a relatively similar trend. There was significant difference (Chi-square test, $\chi^2 = 208.697$, d.f. = 10, $p < 0.001$)

in the size class distribution of *A. africana* among sites (supplementary file 3A). The proportions of large and very large *Afzelia* adults were higher in the core zone (52%) and edge of the core zone (43%) than in the hunting zone (24%). Similarly, the proportion of *Afzelia* seedlings was higher in the core zone (29%) and edge of the core zone (43%) than in the hunting zone (13%). No juvenile was found in the core zone while its proportion in the two other sites was less than 1%, clearly showing a bottleneck of recruitment at this stage. The size class distribution of individuals of *A. africana* also differed significantly (Chi-square tests, $p < 0.0001$, see χ^2 values for all three sites in supplementary file 3B) from that of other species for all sites. Together, large and very large *Afzelia* adults were dominant ($> 50\%$) in all stands (supplementary file 3B). There were also more individuals of *A. africana* than the sum of all other species in the core and at the edge of the core zone, 68.8% and 50.9%, respectively (when considering only juveniles, small, large, and very large adults) (table 1).

Spatial pattern of *A. africana* conspecific and heterospecific trees

Figure 1 shows the location of the trees within each plot along with their life stage. The univariate analyses revealed that all life stages of *A. africana* had a random distribution at the edge of the core zone and in the core zone, except for small and large adults, which showed aggregative patterns within 0–6 m and 0–25 m radius, respectively, at the edge of the core zone (table 2). However, in the hunting zone, seedlings, saplings, small adults, and large adults of *A. africana* had aggregative distributions within 0–6 m, 2–8 m, 0–40 m, and 0–3 m radius, respectively, whereas very large *Afzelia* adults exhibited a random spatial distribution (table 2). The univariate spatial pattern could not be assessed for juveniles due to insufficient number of individuals (table 1).

The intraspecific bivariate analyses revealed spatial independence between all pairs of life stages of *A. africana* on all sites, except for small and large adults which showed a positive association at the edge of the core zone and in the hunting zone (table 2).

There was a spatial independence between individuals of *A. africana* and its heterospecific trees, irrespective of the life stages on all sites (table 3). An exception was found in the hunting zone where small adults had a positive association with heterospecific juveniles within 20–25 m radius and heterospecific large adults within 0–5 m radius (table 3).

Distances to nearest neighbours

Distance within life stages of *A. africana* – The distance to nearest neighbours varied significantly across life stages for the pooled data ($p < 0.001$, supplementary file 4) but also for each site (fig. 3A–C). For the pooled data (fig. 2D), on average, tree-to-tree distances were higher for regenerations, particularly juveniles, than for adult trees. Small and large adults were the closest individuals (fig. 2D). However, some variations were found across sites (fig. 2A–C). For example, tree-to-tree distance was higher among juveniles in the hunting zone (48.36 ± 5.04 , $n = 4$) than at the edge of the core zone (1.8 ± 0 , $n = 2$) (fig. 2B, C). Conversely, the tree-

Table 2 – Univariate (within a life stage) and bivariate (between pairs of life stages) spatial pattern of *A. africana* in three sites in the PBR. Bold font indicates univariate analyses and regular font intraspecific bivariate analyses. For the bivariate analyses, stages *i* were the focal points; a: aggregative; A: association; n: no pattern/spatial independence; NA: not applicable. Values in parentheses are the radii within which the pattern is observed.

Stages of <i>A. africana</i> (subject <i>i</i>)	Stages of <i>A. africana</i> (subject <i>j</i>)					
	Seedlings	Saplings	Juveniles	Small adults	Large adults	Very large adults
Site of Batia (hunting zone)						
Seedlings	a (0–6)	n	n	n	n	n
Saplings	NA	a (2–8)	n	n	n	n
Juveniles	NA	NA	NA	n	n	NA
Small adults	n	n	n	a (0–40)	A (2–30)	n
Large adults	n	n	n	A (2–25)	a (0–3)	n
Very large adults	n	NA	n	n	n	NA
Site of Bondjagou (edge of the core zone)						
Seedlings	n	n	NA	n	n	n
Saplings	NA	NA	NA	NA	NA	n
Juveniles	NA	NA	NA	NA	n	n
Small adults	n	n	n	a (0–6)	A (0–10)	n
Large adults	n	n	n	A (0–10)	a (0–25)	n
Very large adults	n	n	NA	n	n	n
Site of Bali (core zone)						
Seedlings	n	n	n	n	n	n
Saplings	NA	n	NA	NA	NA	NA
Juveniles	NA	NA	NA	NA	NA	NA
Small adults	n	n	NA	n	n	n
Large adults	n	NA	n	n	n	n
Very large adults	n	n	n	n	n	n

Table 3 – Interspecific bivariate spatial associations between *A. africana* and its heterospecific trees in three sites in the PBR. Heterospecific trees (*i*) were used as reference tree; A: association; n: random; NA: not applicable. Values in parentheses are the radii within which the pattern is observed.

Stages of heterospecific trees (subject <i>i</i>)	Stages of <i>A. africana</i> (subject <i>j</i>)					
	Seedlings	Saplings	Juveniles	Small adults	Large adults	Very large adults
Site of Batia (hunting zone)						
Juveniles	n	n	NA	A (20–25)	n	NA
Small adults	n	n	n	n	n	n
Large adults	n	n	n	A (0–5)	n	n
Very large adults	n	n	n	n	n	n
Site of Bondjagou (edge of the core zone)						
Juveniles	NA	NA	NA	NA	NA	NA
Small adults	NA	NA	n	n	n	n
Large adults	n	NA	n	n	n	n
Very large adults	n	n	NA	NA	n	n
Site of Bali (core zone)						
Juveniles	NA	NA	NA	NA	NA	NA
Small adults	n	NA	NA	n	n	n
Large adults	n	n	NA	n	n	n
Very large adults	n	n	NA	n	n	n

to-tree distance among saplings was four times shorter in the hunting zone (12.90 ± 1.81 , $n = 171$) than at the edge of the core zone (53.2 ± 7.38 , $n = 16$) and in the core zone (57.0 ± 30.1 , $n = 7$) (fig. 2A–C).

Distance between pairs of life stages of *A. africana* – Tree-to-tree distances of individuals of *A. africana* to their conspecific seedlings (focal life stage) varied significantly across life stages ($p < 0.001$, supplementary file 4, fig. 3A). Similar results were observed for saplings (supplementary file 4, fig. 3B), juveniles (supplementary file 4, fig. 3C), small adults (supplementary file 4, fig. 3D), large adults (supplementary file 4, fig. 3E), and very large adults (supplementary file 4, fig. 3F). In particular, small adults

and large adults were often the closest to individuals of other life stages (fig. 3). In contrast, saplings and juveniles were often the most distant to individuals of other stages (fig. 3). Saplings and juveniles were respectively two to five times more distant to large and very large adults than seedlings (fig. 3E, F).

Distance of *A. africana* individuals to heterospecific trees – Tree-to-tree distance of *A. africana* seedlings to heterospecific trees was significantly dependent on the stage of the heterospecific trees ($p < 0.001$, supplementary file 4, fig. 4A). Similar results were observed for other life stages (supplementary file 4, fig. 4B–F). The highest distances were to heterospecific juveniles followed by very large

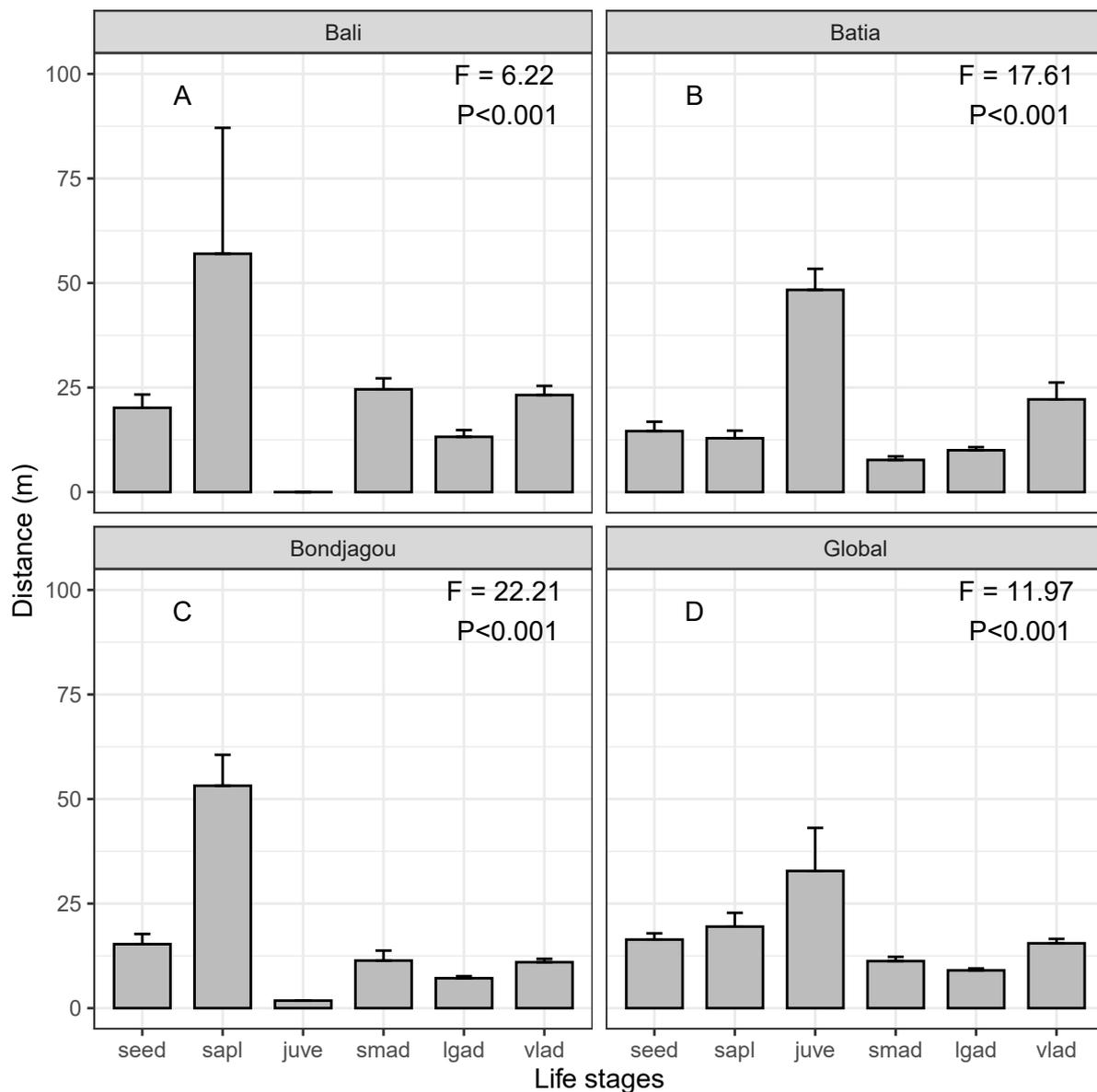


Figure 2 – Mean tree-to-tree distances among individuals of *A. africana* across sites and for pooled sites: variation across life stages. **A.** Site of Bali (core zone). **B.** Batia (hunting zone). **C.** Site of Bondjagou (edge of the core zone). **D.** All sites together. Seed = seedlings, sapl = saplings, juve = juveniles, smad = small adults, lgad = large adults, vlad = very large adults.

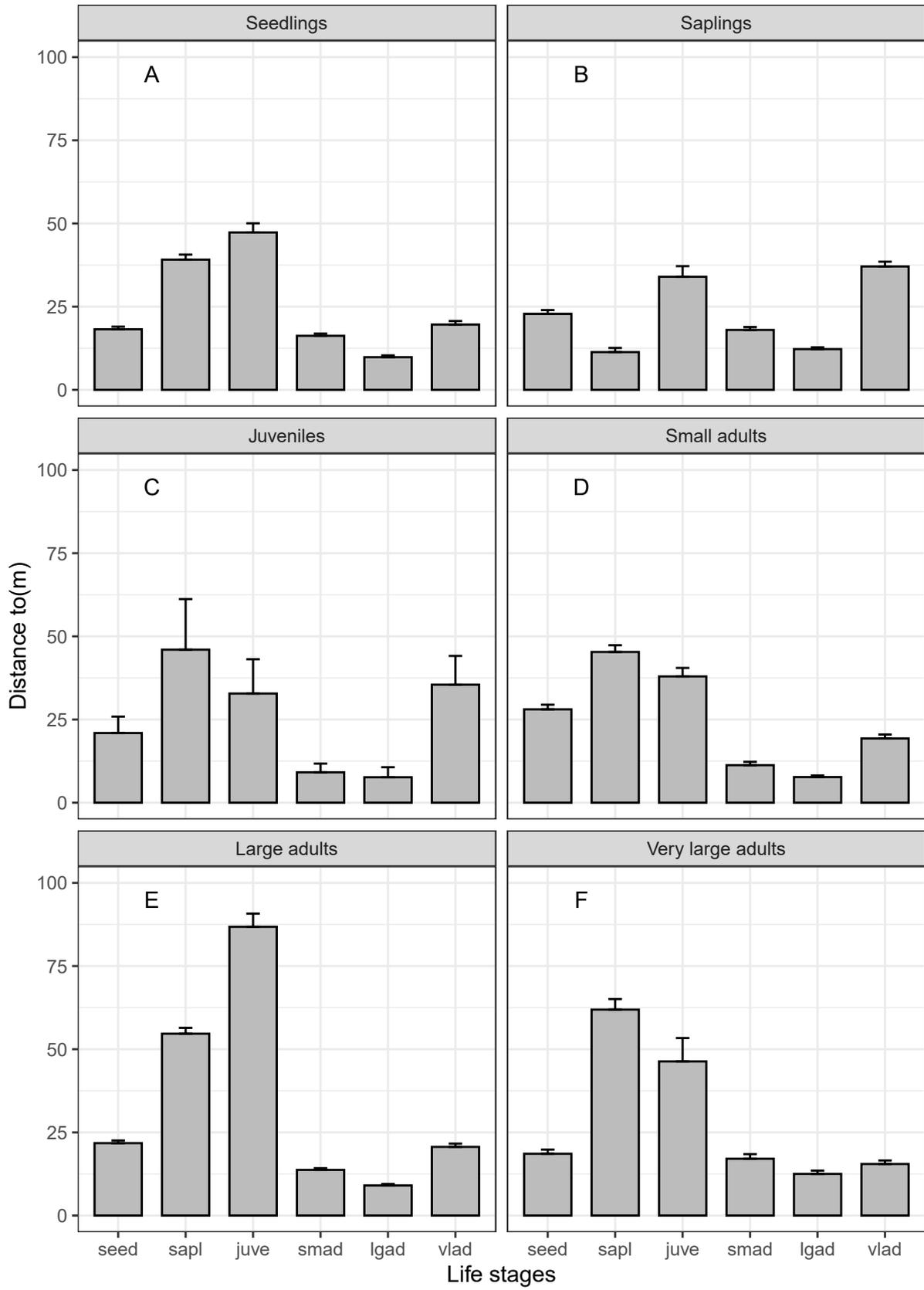


Figure 3 – Mean tree-to-tree distances of *A. africana* individuals of a stage *i* (A. Seedlings. B. Saplings. C. Juveniles. D. Small adults. E. Large adults. F. Very large adults) to their conspecific neighbours of stage *j* (seed = seedlings; sapl = saplings; juve = juveniles; smad = small adults; lgad = large adults; vlad = very large adults).

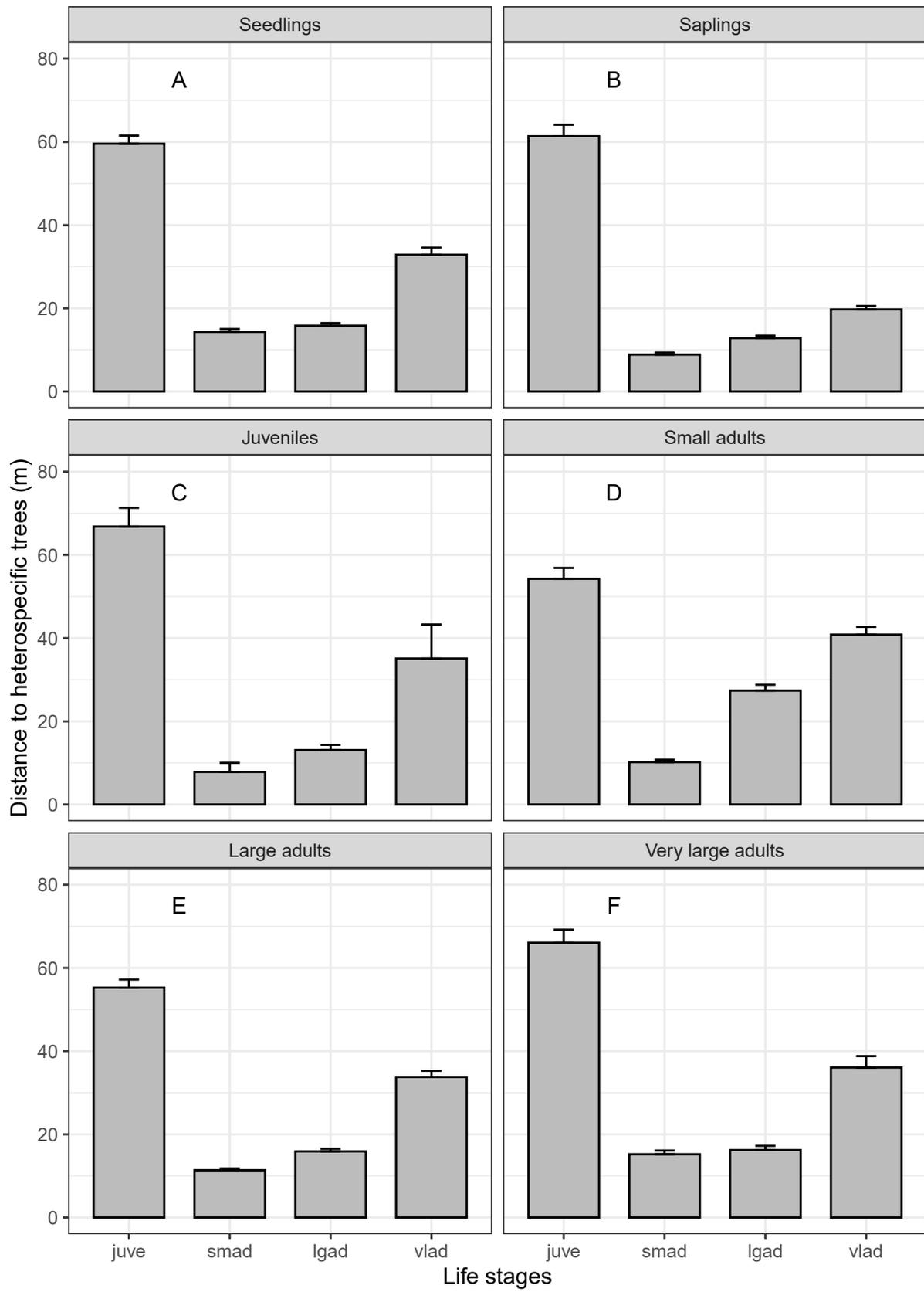


Figure 4 – Mean tree-to-tree distances of *A. africana* individuals of a stage *i* (A. Seedlings. B. Saplings. C. Juveniles. D. Small adults. E. Large adults. F. Very large adults) to their heterospecific neighbours of stage *j* (juve = juveniles; smad = small adults; lgad = large adults; vlad = very large adults).

heterospecific adults. The shortest distances were to small and large heterospecific adults, irrespective of the life stages of *A. africana* (fig. 4). Irrespective of their size, individuals of *A. africana* are often closer to small heterospecific trees than to larger ones (fig. 4).

DISCUSSION

Demographic structure of *A. africana*

Our results showed higher *A. africana* tree density in the hunting zone as compared to the edge of the core zone and the core zone, which could be linked to the low density of wildlife among which elephants (Atanasso et al. 2019). Our findings of less than 1% juveniles in all sites also support previous studies that consistently reported a recruitment challenge at juvenile stage (Sinsin et al. 2004; Bonou et al. 2009; Amahowe et al. 2018). Similar findings have been reported for Marula trees in South Africa where high elephant pressures have caused its sharp decline (Helm & Witkowski 2012). For *A. africana*, this trend has been attributed to the sensitivity of the species seedling to fire, grazing, and drought stress that prevail in the Sudanian zone (Nacoulma et al. 2017; Amahowe et al. 2018). Potential effects of several other factors such as natural enemies and competition have been extensively discussed in Atanasso et al. (2019) and Mensah et al. (2020).

Intraspecific spatial patterns

We found evidence for variable spatial patterns across sites. All life stages had random distribution in the core zone and at the edge of the core zone (except small and large adults that showed aggregative distribution). In the hunting zone, however, all life stages except for very large adults, had aggregative distribution. Browsing and trampling by elephants and other mammals, seed dispersion and predation, local topography, prescribed burns, and soil conditions can be offered to explain the among-sites variation.

The hunting zone has lower wildlife density, hence is exposed to lower animals browsing and trampling (Assédé et al. 2012). This low wildlife activity would entail limited disturbance, thereby favouring the survival of the species individuals. Guy (1989) and Tchamba & Seme (1993) reported that adult trees of *A. africana* are appreciated food species by elephants during their grazing, debarking, breaking, and uprooting activities. We actually found several signs of herbivore activity (e.g. broken branches, debarking, and grazing) on individuals of *A. africana* in the core zone, especially on young individuals, during our field investigations (also see Tehou et al. 2012).

The aggregative patterns observed for seedlings and saplings in the hunting zone can be attributed to high fruit/seed rain combined with reduced activities of predators (Jansen & Zuidema 2001). Hunting and anthropogenic activities in this zone might have also reduced the density of dispersers, and hence seed dispersal of *A. africana* (Trolliet et al. 2019). Limited seed dispersal and limited seed predation are therefore plausible explanations of the aggregative patterns of seedlings and saplings. This pattern seems to

have been maintained till the large adult stage, although with reduced intensity. Dispersal by birds and predation by rodents (Bationo et al. 2000), which are presumably higher in the core zone and at its edge, likely explain why we found a random spatial pattern across life stages for these two sites.

Environment heterogeneity has also been suggested to explain aggregative patterns in plants (Perry et al. 2009; Le et al. 2016). This might also be true in the hunting zone. Indeed, the greater range of the slope in the hunting zone (0–60%) compared to others sites (0–45%, table 1) might have favoured microtopographic features, such as depressions and runnels, creating seed traps that would have played a role in the maintenance of the aggregated structure (Chu et al. 2014).

Differences in historical frequency of fires across the sites could also partly contribute to the aggregative pattern observed in the hunting zone. Indeed, in areas where fires occur irregularly such as in the studied hunting zone, small trees tend to clump together, while in a continuous fire regime, small to large adult trees tend to exhibit random distributions due to fire-induced mortality (Svátek et al. 2018).

We also found spatially independent relationships between pairs of life stages of *A. africana* on all sites. Exception was noted between small and large adults that exhibited positive spatial relationships in the hunting zone and at the edge of the core zone, with larger clumps (2–30 m) in the hunting zone than at the edge of the core zone (0–10 m). This result suggests that intraspecific interactions across life stages may change across sites for conspecific individuals. It further highlights that *A. africana* can tolerate association with its conspecific of various size. There are insights that *A. africana* is associated with diverse ectomycorrhiza fungi (ECM) (Gérard & Louppe 2011). Even if no actual data exist on patterns of ECM across the study sites, this association can also contribute to some extent to the observed differences in life stages association across sites. In some ECM-associated species, associations between different life stages could actually result in large clumps of adults (Sasaki et al. 2019).

Interspecific spatial patterns

Our results showed spatial independence between pairs of life stages of *A. africana* and heterospecific neighbours in all sites except some marginally positive associations of small adults of *A. africana* with heterospecific juveniles and large adults in the hunting zone. Our data is however rather limited and these positive associations have to be tested with more data, for example by replicating plots in the studied sites. The independence of the distribution of *A. africana* vis-à-vis its heterospecific neighbours suggests that *A. africana* can be successfully grown in mixed plantations with its co-occurring species, as far as the pool of species planted share the same niche. In a previous studies, Atanasso et al. (2019) identified the ten most co-occurring species with *A. africana* in the Pendjari Biosphere Reserve as *V. paradoxa*, *P. erinaceus*, *L. acida*, *D. microcarpum*, *T. avicennioides*, *I. tomentosa*, *B. africana*, *D. mespiliformis*, *T. indica*, and *A. leiocarpus*. Mensah et al. (2014) also reported other species

such as *Boswellia dalzielii* Hutch., *Dialium guineense* Willd., and *Mimusops andongensis* Hiern as co-occurring with *A. africana* in a more humid semi-deciduous forest in southern Benin.

In our study, we pooled all heterospecific trees (supplementary file 2) and did not consider species-specific features, and this could be viewed as a limitation. Indeed, the spatial pattern may be different if we looked for particular species among heterospecific trees. Studies that separate each heterospecific species may provide additional insights and refine the conclusions of the present study.

Intra- and interspecific tree-to-tree distance

The scarcity of juveniles resulted in individuals of this stage being the most distant in the studied populations. The observed distances between individuals of each life stage are consistent with the trend in tree density; small and large adults were the most common and then the closest to each other. The Janzen-Connell hypothesis predicts that offspring standing far from their mother trees are likely to escape damage and successfully recruit. Therefore, saplings and juveniles are expected to be more distant to large-sized trees than seedlings are to large-sized trees (Janzen 1970; Connell 1971). We found that saplings and juveniles were respectively two to five times more distant to large and very large adults than seedlings. This is consistent with the Janzen-Connell hypothesis, as also reported by Amahowe et al. (2019) for *A. africana* in the W National Park, Benin. Nevertheless, we believe a more detailed study on survival chance of seedlings, saplings, and juveniles is needed to draw reliable conclusions.

Conclusion and implications for management

This study reveals that the *A. africana* tree spatial pattern varies from aggregative to random across sites, possibly due to a number of biotic and abiotic conditions that are site-specific. From a perspective of interspecific relationships, *A. africana* has generally showed a neutral relationship with heterospecific neighbours, suggesting that the species can be planted with other species in mixed plantations, e.g. *V. paradoxa* and *P. erinaceus*, which are among its most co-occurring species. However, the observed patterns in this study might not always apply to other *A. africana* natural habitats, e.g. dry forests, deciduous forests, or gallery forests, where competition for light is more intense. Long-term experiments would be needed to advance our understanding of the interactions of *A. africana* with its heterospecific neighbours and refining management recommendations. By encountering only six juveniles of the species, the study also corroborates previous findings on the species recruitment challenge, which implies a need for an artificial regeneration strategy and the enrichment of its natural stands. In such a strategy, particular attention should be given to the protection of the planted seedlings against biotic and abiotic stressors (see Mensah et al. 2020 for extensive discussion on data from a two-year monitoring in the study sites) to ensure a successful recruitment. Our findings also suggest that for artificial plantations of *A. africana*, careful attention

should be given to seedlings and saplings to ensure that they successfully recruit to the juvenile stage.

SUPPLEMENTARY FILES

Supplementary file 1 – Characteristics of the selected sites of *A. africana* (adapted from Atanasso et al. 2019).

<https://doi.org/10.5091/plecevo.2021.1713.2543>

Supplementary file 2 – List of species other than *A. africana* mapped in the plots and their abundance.

<https://doi.org/10.5091/plecevo.2021.1713.2545>

Supplementary file 3 – Population structure analysis of *A. africana* and other species across the three stands.

<https://doi.org/10.5091/plecevo.2021.1713.2547>

Supplementary file 4 – Variation of intraspecific and interspecific tree-to-tree distance across life stages: summary of the linear mixed models.

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