



Spatial distribution and interspecific association patterns between *Mansonia altissima* A. Chev., *Ceiba pentandra* (L.) Gaertn and *Triplochiton scleroxylon* K. Schum. in a moist semi-deciduous forest

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Abstract

• **Key message** *Mansonia altissima* A. Chev. has an aggregated distribution at the juvenile life stage that becomes random at the mature life stage. *Ceiba pentandra* (L.) Gaertn could play the role of nurse plant in the management of *M. altissima* populations providing them a moderate forest shade in large gaps for early growth. *M. altissima* and *Triplochiton scleroxylon* K. Schum. displayed independent distribution patterns.

• **Context** *M. altissima* is a species with economic value found in moist semi-deciduous forests of tropical Africa. The analysis of spatial distribution patterns can help to understand the ecology of this species in forest stands dominated by emergent pioneer tree species like *C. pentandra* and *T. scleroxylon*.

• **Aims** To assess the spatial distribution patterns of *M. altissima* and spatial relationships with *C. pentandra* and *T. scleroxylon* in their natural habitat.

• **Methods** We investigated the spatial patterns of the three species during three life stages; juvenile (immature trees), premature (trees with minimum flowering diameter) and mature (trees with minimum fruiting diameter). Diameter at breast height (DBH) was measured and geographical coordinates of trees were recorded within ten one-ha plots, divided into sixteen subplots (625 m²). We computed the L(r) function, normalized from Ripley's K(r) function to detect aggregated, random or regular distribution patterns.

• **Results** Aggregations were detected in juvenile and premature *M. altissima*. Size and scales of spatial aggregation were inversely proportional to the DBH size. *M. altissima* and *C. pentandra* displayed interspecific association patterns at the similar life stages. Both species were positively associated within a radius ≥ 3 m. No positive association was detected between *M. altissima* and *T. scleroxylon*.

• **Conclusion** Interspecific association patterns between *M. altissima* and *C. pentandra* suggest that *C. pentandra* could be used as a nurse tree in reforestation and management practices of *M. altissima* populations.

Keywords Life stages · Spatial distributions · Ripley's L-function · *Mansonia altissima* · *Ceiba pentandra* · *Triplochiton scleroxylon*

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Contributions of the co-authors

N. Bienvenue Kuiga Sourou and Towanou Houêchégnon have contributed to install the plots and to data collection in the forest and to database management. Christine A. I. N. Ouinsavi has supervised the work (data collection and analysis), review of drafts and manuscript improvements.

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1 Introduction

In a forest stand, spatial distribution of a species can be aggregated, random or regular (Du et al. 2017). These spatial distribution and association patterns of populations within plant communities are affected by various ecological or evolutionary processes such as niche segregation (Pielou 1962), habitat heterogeneity (Harms et al. 2001), differential predation (Janzen 1970; Connell 1971), neighborhood competition (Le et al. 2016; Getzin et al. 2006), dispersal limitation (Thioulouse et al. 1997), shade tolerance (Zhang et al.

2013), regeneration (Cheng et al. 2014) and life history of populations (Qi et al. 2016).

Numerous studies of spatial distribution patterns showed that in heterogeneous forest stands (in terms of diversity and size of individuals) a tree is in competition with its immediate neighbors to access nutritive resources (Liu et al. 2014; Barot et al. 1999; Connell et al. 1984) leading to changes in spatial distribution patterns of the species. Competitive effects are detected through significant positive correlations between the size of trees and segregation distances of immediate neighbors (Pielou 1962). However, immediate neighbors are not inevitably competitors during all life stages of a species. They can act as facilitators in species with different shade tolerances and growth forms (Ledo 2015). Agyeman et al. (2016) found that the richness and abundance of timber species seedlings and saplings are mainly due to the presence of facilitating pioneer tree species.

To understand spatial distribution patterns, spatial distribution indices like Blackman's index (Blackman 1942) and Green's index (Green 1966) were used for a long time. These indices are giving a general idea of the type of spatial distribution in a forest stand, but cannot inform both on aggregation scale and location of a tree among neighbors (distance between two objects). This information is important to know the spatial scales of plant associations with different life strategies (Omelko et al. 2018). It can be generated using Ripley's *K*-function (Ripley 1977) that is an efficient indicator of spatial patterns (Marcon 2010; Cressie 1993; Diggle 1983). Ripley's *K*-function allows the analysis of spatial distribution patterns at several spatial scales and the detection mixed processes (association and repulsion at some scales) (Fonton et al. 2012; Fajardo et al. 2006). Since reforestation with native species may strongly contribute to the regeneration or restoration of degraded forests (Omelko et al. 2018; Agyeman et al. 2016), such analyses are important in forest management since they could improve our understanding of the role of pioneer species in maintaining plant diversity. They should enable a reasoned choice about distances between conspecific or heterospecific trees for ecological restoration of habitats and sustainable management of threatened species.

Although *Mansonia altissima* (Malvaceae) has the status of least concern (Botanic Gardens Conservation International and IUCN SSC Global Tree Specialist Group 2018), *Mansonia altissima* var. *altissima* A. Chev. is an overexploited and endangered variety of economic value (African Regional Workshop 1998). It grows naturally in moist semi-deciduous forests of tropical Africa. It is known to be a non-pioneer light-demanding (Agyeman et al. 1999; Veenendaal et al. 1996) while seedlings are known to grow in forest shade (Gyimah and Nakao 2007; Hawthorne 1995). The species is hermaphrodite but seems to be pollinated by insects (Akinagbe et al. 2010). *M. altissima* is a popular West African timber tree that is also used as a substitute for American black walnut. It is popular for various uses in house building (Wédjangnon et al. 2016a), joinery as well as bark

extracts used in therapeutic and medicinal fields (Adeoti et al. 2016). In Benin, it is only found in one moist semi-deciduous forest where it is critically endangered (Wédjangnon et al. 2016b; Neuenschwander et al. 2011) due to human activities and land property conflicts. Thus, management, restoration and conservation of this species increasingly required. It coexists with several other large size heterospecific pioneer tree species such as *Ceiba pentandra* (L.) Gaertn. (Malvaceae) and *Triplochiton scleroxylon* K. Schum. (Malvaceae) in plant communities of moist semi-deciduous forests in Benin.

The spatial patterns of these species substantially differ according to their size (Ligot et al. 2019; De Madron 2003), age and reproductive stages (Ouédraogo et al. 2018). It is therefore important to take life stages into account, taking the diameter class as a surrogate of life stage (Omelko et al. 2018; Ledo 2015; Li et al. 2008). Thus, forest stands are conventionally divided into two groups: juveniles (<10 cm dbh) and adults (≥ 10 cm dbh). However, tree species have not the same growth rate, diameter size and reproductive size. Therefore, the knowledge of the biology (reproductive size, growth rate) of the studied species is an important criterion to define similar life stages. Some studies assessed the reproductive size (Ouédraogo et al. 2018; De Madron and Daumerie 2004) and growth rate (Ligot et al. 2019; De Madron 2003) of the three species. The reproductive size and growth rate vary strongly among these three species. *M. altissima* can fructify at 18 cm diameter while, the minimum fruiting diameter for *T. scleroxylon* is 45 cm (Ouédraogo et al. 2018). De Madron and Daumerie (2004) showed that the diameter of *M. altissima* intervenes only slightly in fruiting. In contrast, fruiting diameter for *T. scleroxylon* varies strongly across sites (Ouédraogo et al. 2018). Moreover, *C. pentandra* and *T. scleroxylon* grow faster than *M. altissima* with annual diameter increments ranging up to 3 cm year⁻¹ (Duvall 2011), 1.63 cm year⁻¹ (Ligot et al. 2019) and 0.93 cm year⁻¹ (De Madron 2003) respectively. The largest radial growth rate is reached for trees with a dbh below 20 cm in *M. altissima*, and between 20 and 60 cm in *T. scleroxylon* (Ligot et al. 2019).

The main objective of this work is to assess the spatial distribution patterns of *M. altissima* trees and spatial relationships with these two pioneer tree species. The following questions were addressed: what is the spatial distribution pattern of *M. altissima* during the different life stages of the species? How does *M. altissima* coexist with these two dominant pioneers in its habitat? How do association patterns change with life stages of the species?

2 Material and methods

2.1 Study area

This study was conducted in the moist semi-deciduous forest of Adakplamè (2°33' - 2°35' north and 7°27' - 7°29' east) in

the district of Kétou. The climate of this habitat is subequatorial. The rainfall is bimodal with about 1300 mm year⁻¹. The soil is weakly desaturated ferralitic above sandy-clay sediment, the clay contents of which increase according to depth. The vegetation is dominated by dense forest stands and some savannas and woodlands. This habitat that extends over 738 ha is a sacred grove. Its management is regulated by religious principles which are materialized across prohibitions, prescriptions and ritual practices. The dense forest stand constitutes a conservation area for several endangered species in Benin. Two plant communities were identified. One is dominated by *Ceiba pentandra* and *Mansonia altissima* and the second is dominated by *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel and *Triplochiton scleroxylon* (Amanouido et al. 2018). The presence of *C. pentandra*, *M. altissima* and *T. scleroxylon* is a positive indicator of soil fertility (Medjibe et al. 2011).

2.2 Sampling

The sampling design was constituted by ten (10) forest dynamics plots installed into two different plant communities (Amanouido et al. 2018). Each one-ha plot was divided into sixteen (16) consecutive subplots, 625 m² (25 m × 25 m). Previous investigations had shown that plots of one-ha size are reasonably suitable in the sudanian zone of Benin (Fonton et al. 2011).

2.3 Data collection

In each subplot, all juvenile individuals of *M. altissima*, *C. pentandra* and *T. scleroxylon* with a diameter ≥ 1 cm were measured with an electronic Vernier caliper (Kreator Stainless Hardened), while adult trees (trees with a circumference larger than 31 cm at 1.30 m above ground) were measured with a metric tape. The diameter measurement for adult trees of *C. pentandra* and *T. scleroxylon* was made above buttresses. The position of each tree was determined into

two orthonormal vectors whose origin was fixed to upper left corner of each subplot.

2.4 Data analysis

2.4.1 Distribution of trees in life stages

Diameter distribution models for the three species were established and adjusted to the Weibull distribution curve in order to estimate historical parameters (shape and scale) of diameter distribution within each population. The software Minitab 16 was used to perform this analysis. The DBH of trees were classed into three functionally similar life stages according to the biological variables such as minimum flowering and fruiting diameter (Ouédraogo et al. 2018), diameter limit and annual growth rate (Ligot et al. 2019; De Madron 2003).

Mansonia altissima: Juvenile (< 10 cm), Premature (10–20 cm), Mature (> 20 cm).

Triplochiton scleroxylon: Juvenile (< 40 cm), Premature (40–70 cm), Mature (> 70 cm).

Ceiba pentandra: Juvenile (< 50 cm), Premature (50–80 cm), Mature (> 80 cm).

Juveniles are immature trees. Prematures are trees with minimum flowering diameter. Matures are trees with minimum fruiting diameter.

2.4.2 Simulation of uni and bivariate spatial patterns

Ripley's K(r) function (Ripley 1977) is a reliable informer of the spatial pattern (Marcon 2010; Diggle 1983; Cressie 1993). It is commonly used in point process analysis to detect the spatial distribution of species in a plant community (Fonton et al. 2012; Condit et al. 2000). However, the interpretation of K(r) function is not very easy because of its reference value π^2 and its hyperbolic graphical representation. A normalized function of K(r) was then proposed by Besag (1977) whose reference value is 0 (Pelissier and Goreaud 2015). This normalized function

Table 1 Dendrometric characteristics of the three species in the moist semi-deciduous forest of Adakplamè

	N	n	DBHmin	DBHmax	Juvenile	Premature	Mature
<i>Mansonia altissima</i>	479	35	1.06	53.8	< 10 cm (53.4%)	10–20 cm (31.7%)	> 20 cm (14.8%)
<i>Triplochiton scleroxylon</i>	216	16	7.18	94.2	< 40 cm (31.5%)	40–70 cm (43.0%)	> 70 cm (25.5%)
<i>Ceiba pentandra</i>	152	9	5.43	143.2	< 50 cm (24.3%)	50–80 cm (52.6%)	> 80 cm (23.0%)

N: total number of trees; n: average number of trees per plot; DBHmin: minimum diameter at breast height; DBHmax: maximum diameter at breast height

noted $L(r)$ enables to stabilize the $K(r)$ function variance and makes it easy to interpret the curves. Indeed, spatial distribution and intra – interspecific association patterns of the target species were studied by computation of $L(r)$ function estimations (Besag 1977). Univariate spatial patterns were simulated for one object using $L_{11}(r)$ function while, bivariate spatial patterns were simulated for two various objects using intertype $L_{12}(r)$ function, which characterizes the spatial interaction between points of two different types (for example trees of two different species) within the same plant community (Diggle 1983). Confidence limits were computed under the null hypothesis of a complete spatial random distribution (CSR) with 199 Monte Carlo simulations (Besag 1977) and fifth lowest and highest values were used to build the simulation envelopes (Wiegand 2014). The process was repeated for various scales from 0 to 50 m. The theoretical values under the null hypothesis as well as confidence limits and CSR departure probabilities were estimated at 1 m intervals. Analyses were performed with Programita software (Wiegand and Moloney 2014).

Under these conditions, the distribution of an object is aggregated to scale r when the $L_{11}(r)$ function curve is positive (above confidence limits), it is regular when the function curve is negative (below confidence limits) and random when it is inside. Reciprocally, when the intertype function curve $L_{12}(r)$ is above or below or inside confidence limits, it respectively indicates the attraction, repulsion or independence of two objects.

3 Results

3.1 Dendrometric characteristics and diameter distribution models

Dendrometric characteristics of species are shown in Table 1. Modeled distribution of diameter for three species in the forest stand is shown in Fig. 1. *M. altissima* displays a lower diameter than both dominant pioneer tree species as indicated by the shape and scale of the diameter distribution. Weibull's distribution curve shows an exponential descending distribution for *M. altissima* and a bell-shape distribution for *C. pentandra* and *T. scleroxylon*. The shape parameter ranked between 1 and 3.6 showing the predominance of trees with low or middle diameter. The larger value of shape parameter for *T. scleroxylon* (1.81) and *C. pentandra* (2.34) compared to *M. altissima* (1.11), highlights the abundance of trees with smaller size in this population of *M. altissima* and the abundance of trees with higher size in populations of *C. pentandra* and *T. scleroxylon*. Individuals with DBH < 10 cm were almost lacking in *C. pentandra* (2 stems) and *T. scleroxylon* (5 stems).

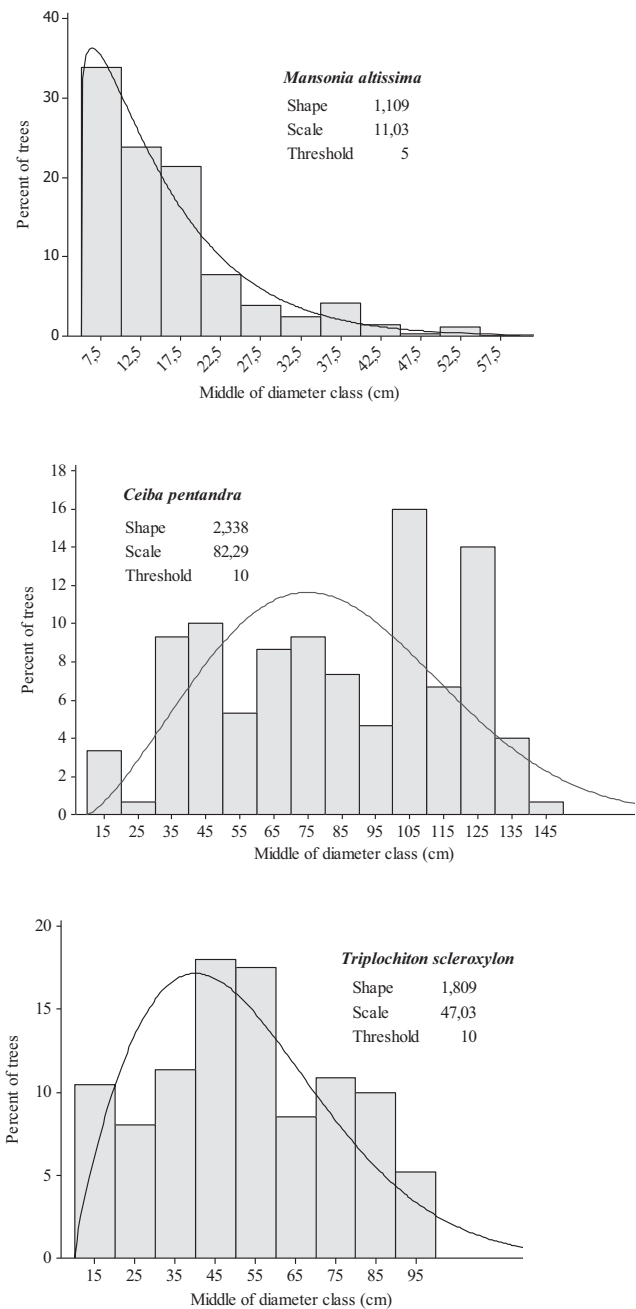
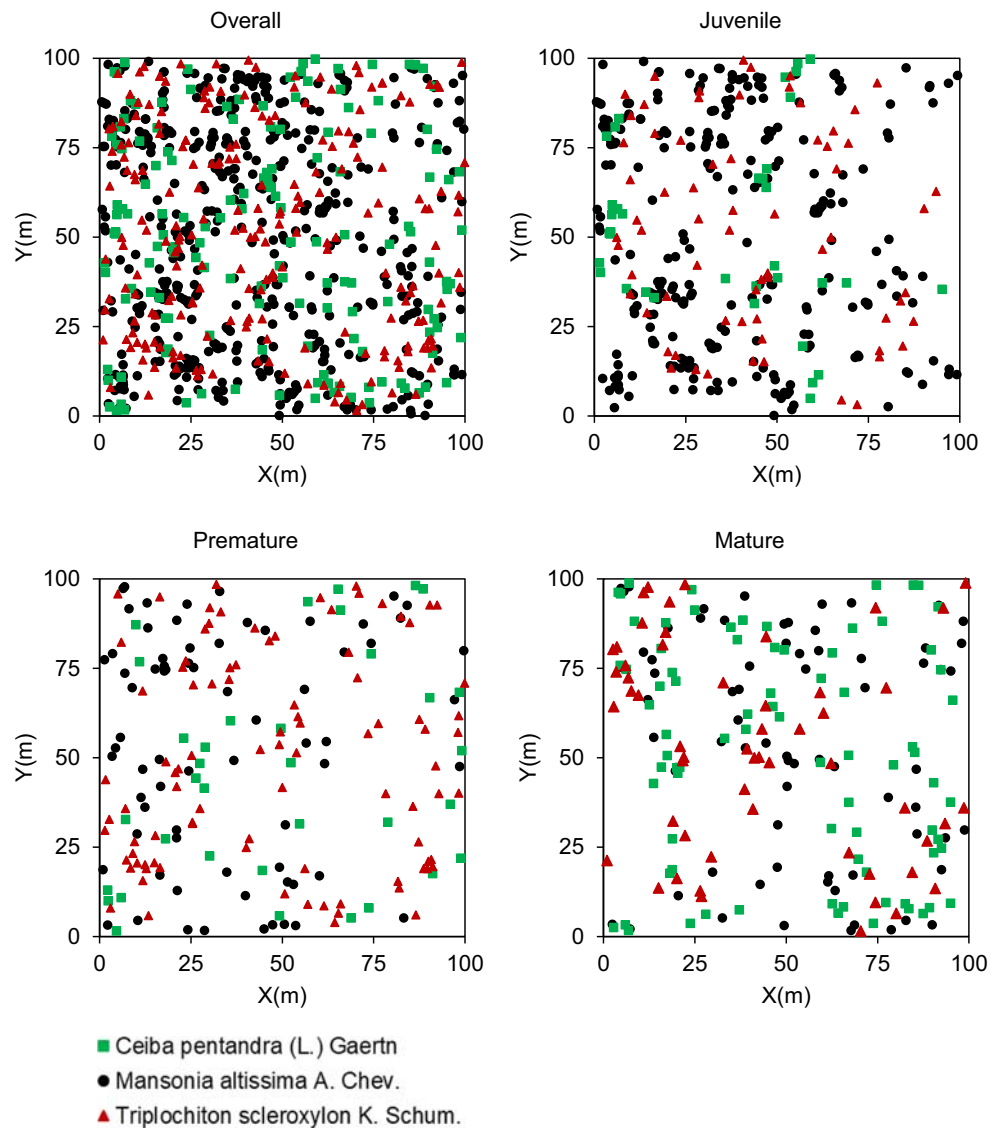


Fig. 1 Modeled distribution of diameter at 1.30 m above ground for *Mansonia altissima*, *Ceiba pentandra* and *Triplochiton scleroxylon* in the study area

3.2 Spatial distribution patterns of *M. altissima*

Distribution maps of the three species within 10 plots are shown in Fig. 2. Univariate analysis performed from location of *M. altissima* within each plot (100 × 100 m) showed an aggregated distribution of low intensity at scale 0–15 m (Fig. 3). However, when we consider the life stages separately, the spatial distribution of *M. altissima* varied in the three life stages (Figs. 2 and 3). In fact, juveniles of *M. altissima* display

Fig. 2 Spatial distribution patterns of *Mansonia altissima*, *Ceiba pentandra* and *Triplochiton scleroxylon* according to their life stages within a plot in the moist semi-deciduous forest of Adakplamè. The plot was selected in the conservation core area to avoid the influence of anthropogenic disturbance factors



an aggregated distribution at scale 0–14 m whose peak is located at 6 m while, premature trees display an aggregated distribution at scale 2–7 m and mature trees, a random distribution (Fig. 3).

3.3 Intraspecific association patterns of *M. altissima*

Bivariate analysis of spatial associations between life stages of *M. altissima* are shown in Fig. 4. Significant attractions of low intensity were observed between juvenile and premature and then premature and mature. In fact, juvenile and premature trees showed a positive attraction at scale 0–3 m with an attraction peak at 2 m while, premature and mature are positively associated to the spatial scales 2–6 m. On the other hand, the distribution of juvenile *M. altissima* was independent from mature trees (reproductive) with a repulsion trend at scale 5–12 m.

3.4 Interspecific association patterns between *M. altissima* and *C. pentandra*

Bivariate analyses of spatial association patterns between *M. altissima* and *C. pentandra* are shown in Fig. 5. Overall, *M. altissima* and *C. pentandra* showed an independent distribution patterns at all spatial scales (Fig. 5). However, positive attractions between *M. altissima* and *C. pentandra* occurred mainly among individuals from functionally similar life stages (or even life stage). Thus, juveniles of *M. altissima* and *C. pentandra* showed a significant positive association of lower intensity at scale 3–5 m and higher intensity over 45 m whereas negative attractions (repulsion) were observed among juveniles of *M. altissima* and both prematures and matures life stages of *C. pentandra*. *M. altissima* (juveniles) and *C. pentandra* (prematures) showed a repulsion at scale 15–23 m and 7–

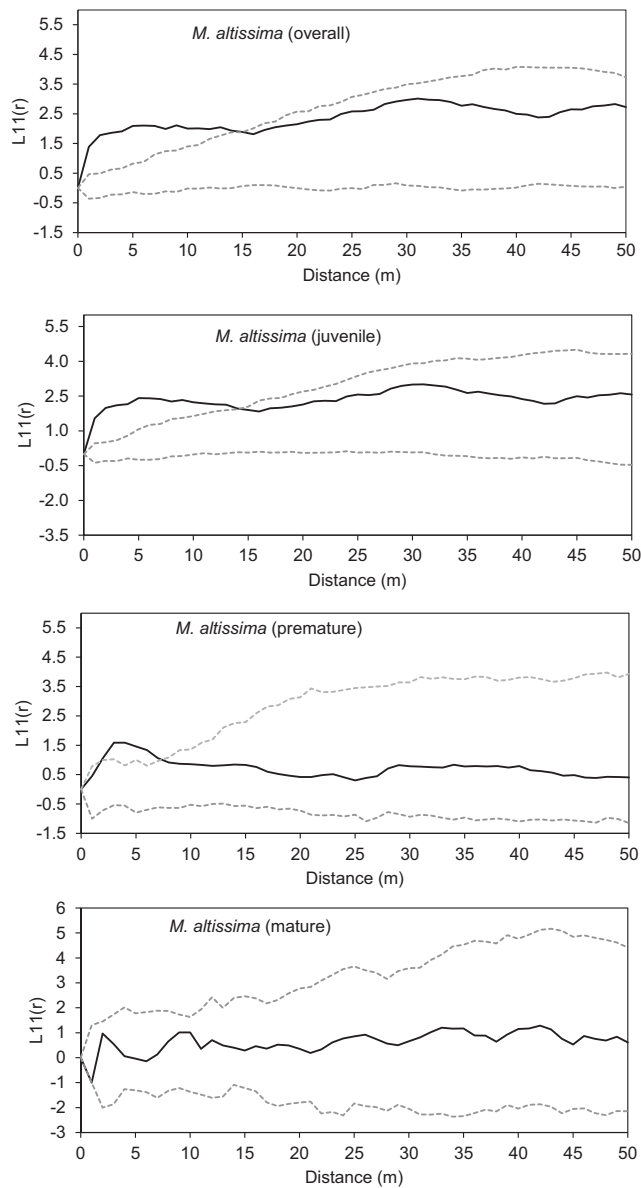


Fig. 3 Spatial distribution patterns of *Mansonia altissima* in the moist semi-deciduous forest of Adakplamè according to its life stages. Black curves are observed patterns and dotted lines are 95% confidence limits for 199 Monte Carlo simulations. Curves above upper limit show aggregate, curves below lower limit show regularity and curves within limits show random of the trees from same life stage

11 m for *M. altissima* (juveniles) and *C. pentandra* (matures).

3.5 Interspecific association patterns between *M. altissima* and *T. scleroxylon*

Bivariate analyses of spatial association patterns between *M. altissima* and *T. scleroxylon* are shown in Fig. 6. Overall, *M. altissima* displayed an independent distribution pattern from *T. scleroxylon* during the three life stages. Thus, the

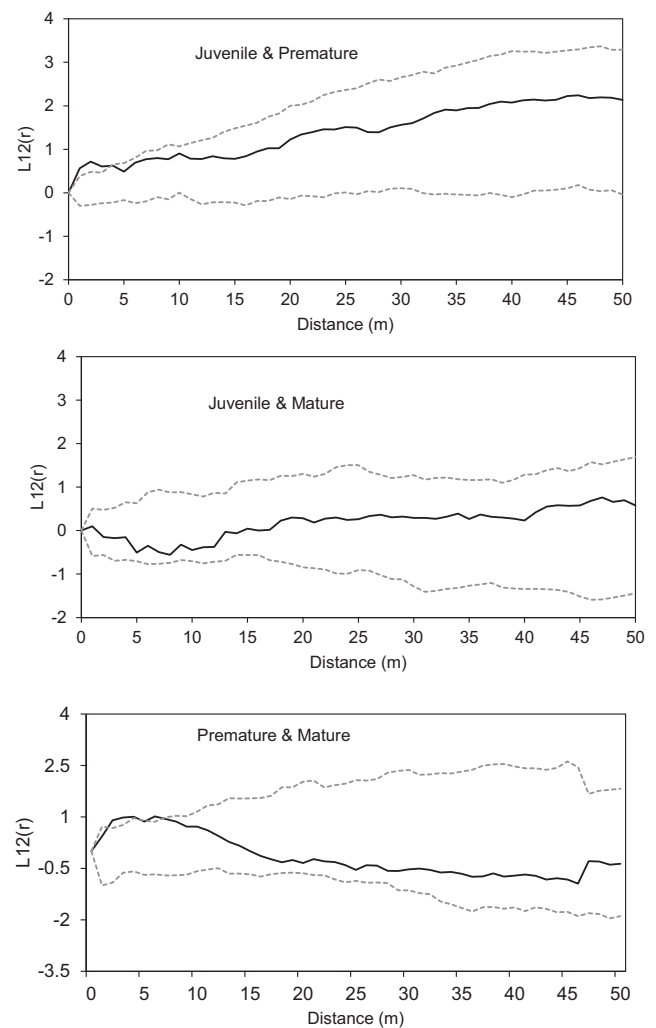


Fig. 4 Intra-species association patterns of *Mansonia altissima* in the moist semi-deciduous forest of Adakplamè. Black curves are observed patterns and dotted lines are 95% confidence limits for 199 Monte Carlo simulations. Curves above upper limit show association, curves below lower limit show repulsion and curves within limits show independence of the individuals with different life stages

distribution pattern of *M. altissima* did not depend on that of *T. scleroxylon* in the moist semi-deciduous forest.

4 Discussion

4.1 Diameter distribution and regeneration status of the three species

The diameter size of plant species in a forest stand follows two types of distribution; exponential descending and bell-shape distribution. These two types of distribution are often used to characterize the behavior of species (Dupuy et al. 1998). An exponential descending distribution is characteristic of typically sciaphilous species, while a bell-shape distribution is characteristic of typically heliophilous species (Dupuy et al.

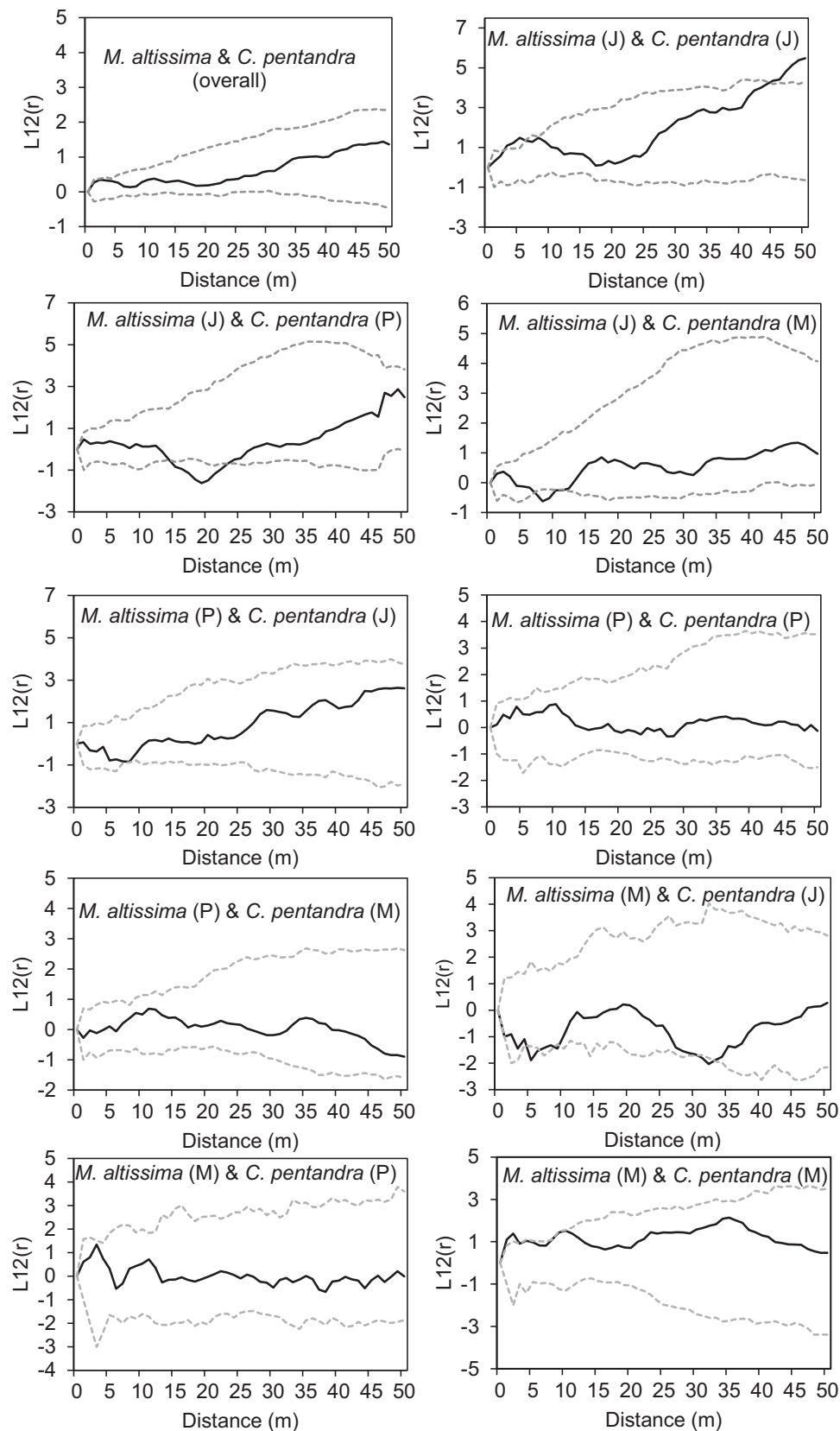
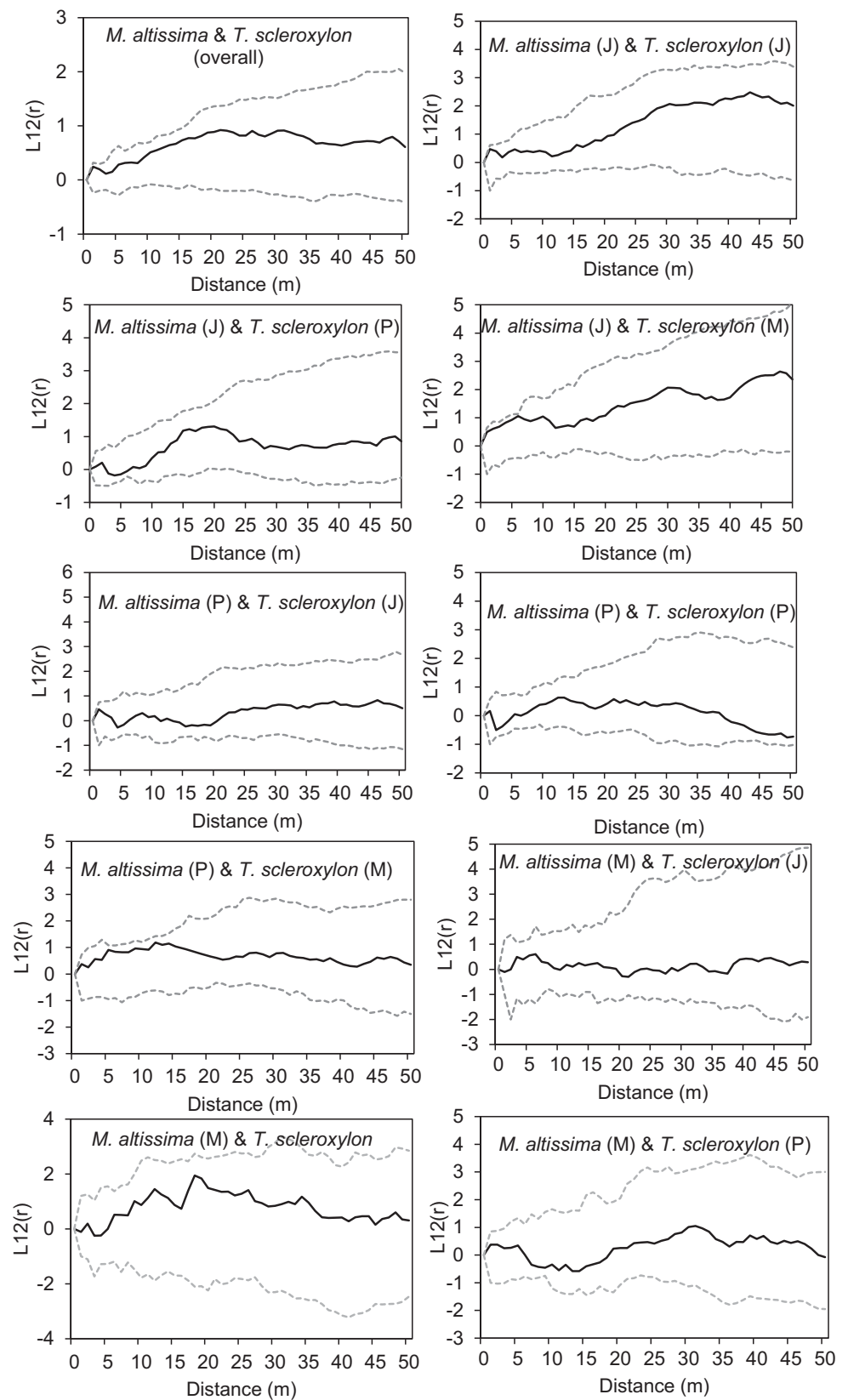


Fig. 5 Inter-species association patterns of *Mansonia altissima* and *Ceiba pentandra* in the moist semi-deciduous forest of Adakplamè according to their life stages. Black curves are observed patterns and dotted lines are 95% confidence limits for 199 Monte Carlo simulations. Curves above

upper limit show association, curves below lower limit show repulsion and curves within limits show independence of the two species. J, P, M denote juveniles, prematures and matures respectively

Fig. 6 Inter-species association patterns of *Mansonia altissima* and *Triplochiton scleroxylon* in the moist semi-deciduous forest of Adakplamè according to their life stages. Black curves are observed patterns and dotted lines are 95% confidence limits for 199 Monte Carlo simulations. Curves above the upper limit show association, curves below lower limit show repulsion and curves within limits show independence of the two species. J, P, M indicate juveniles, pre-matures and matures respectively



1998). *M. altissima* is a non-pioneer species (Veenendaal et al. 1996) whose seedlings are known to grow and establish in

forest shade during the first years (Gyimah and Nakao 2007; Hawthorne 1995). This change of ecological requirements

during the development of *M. altissima* seedlings may explain the abundance of juveniles comparatively with premature trees in the dense forest stand. The bell-shape distribution for *C. pentandra* and *T. scleroxyton* suggests poor regeneration.

The almost lack of regeneration (<10 cm dbh) for *C. pentandra* and *T. scleroxyton* reveals different life histories of these species compared to *M. altissima*. Populations of *C. pentandra* and *T. scleroxyton* are older than the population of *M. altissima* in the forest. Nevertheless, the reproduction of *T. scleroxyton* seems to be supra-annual with irregular fructifications (Palla and Louppe 2002; Jones 1974) which may further hamper its regeneration (Ligot et al. 2019). *C. pentandra* is known to be gap depending for its regeneration (Sokpon 1995). It has very few seedlings in dense forest stands as well as large gaps dominated by undergrowth species (Sokpon 1995). Particularly, *C. pentandra* is one of species that produce many seedlings, which are not able to live under dense canopies and require from first years both sunlight and large gaps where they can grow rapidly. So, the dense canopy of the forest could hamper the growth and survival of *C. pentandra* seedlings.

4.2 Spatial relationships between the three species in the forest

Tree species generally are less aggregated with increasing size-class (Zhang et al. 2013; Condit et al. 2000) suggesting that larger trees are more competitive than smaller ones (Zhang et al. 2013). It is also supported that when the competition is important, adult or mature trees are less aggregated than juvenile and premature trees due to the recruitment limit of adults among conspecific or heterospecific large trees (Murrell 2009). The ecological requirements of plants during their life stages can result in a competition at some life stages meaning a decrease of aggregation in large size-classes. It is the case of non-pioneer and light-demanding plants that emerge. The competition to access light resource after juvenile stage, should remove individuals that are nearby neighbors meaning a decrease of aggregation at premature and mature stages. It can increase distances between individuals with different life stages and mean random distributions (Du et al. 2017). The aggregated distribution of juveniles and premature *M. altissima* and random distribution of mature *M. altissima* in the forest could be due to the aggregation of smaller trees in forest shade and the change of requirements in light resource at the adult stage. After juvenile life stage, *M. altissima* requires light to emerge.

M. altissima displayed an independent distribution pattern between juvenile and mature trees. This distribution pattern confirms its status of non-pioneer and light-demanding. Thus, the growth conditions required for *M. altissima* at the mature stage would not facilitate seedling establishment and early

growth. Interspecific association patterns displayed in *M. altissima* and *C. pentandra* indicated that the functionally similar life stages are positively associated. *C. pentandra* particularly colonizes large gaps and becomes emergent in mature forest stands with larger growth rates (Duvall 2012). That would allow seedlings of *M. altissima* within periphery to find the forest shade required for their establishment and survival. This suggests that *C. pentandra* could play the role of nurse plant in the management of *M. altissima* populations to create a moderate shade and increase seedlings establishment and survival chance. Moreover, *C. pentandra* is an evergreen tree whose shade could facilitate or improve seedlings survival during the dry season. In contrary, *T. scleroxyton* is a deciduous tree. This could mean adverse conditions for seedlings survival during the dry season leading to the independent distribution patterns in *M. altissima* and *T. scleroxyton*.

5 Conclusion

Our study found interspecific associations between *M. altissima* and *C. pentandra*, which suggest that *C. pentandra*, as pioneer species, can play an important role in improving the establishment and survival conditions of *M. altissima* in plant communities. Therefore, *C. pentandra* could be used as a nurse tree in reforestation and management practices of *M. altissima* populations. The study provides a scientific basis for a reasoned choice of distances between the plants of *M. altissima* and *C. pentandra*. Silvicultural treatments such as thinning could be required after juvenile life stage to increase the survival and growth rates of *M. altissima*. *M. altissima* and *T. scleroxyton* displayed independent distribution patterns, which meant a lack of interaction between the two species in the three life stages. The results shown in this paper can also be implemented to more deeply elucidate the role of pioneer species in plant communities.

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Data availability The datasets generated and/or analyzed during the current study together with the associated metadata are available in the Advanced Ecological Knowledge and Observation System (AEKOS) portal (Wédjangnon et al. 2019) at <https://doi.org/10.25901/5dce7f2714885>

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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