Original article

Do isolated gallery-forest trees facilitate recruitment of forest seedlings and saplings in savannna?

Akomian Fortuné Azihou[*,1], Romain Glèlè Kakaï, Brice Sinsin

Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-Calavi (UAC), 01 BP 526 Cotonou, Benin

ABSTRACT

Facilitation is an ecological process that allows some species to establish in environments they can hardly afford in the absence of the process. This study investigated if the subcanopy of gallery-forest trees isolated in savanna is suitable for the early recruitment of forest woody species. We measured tree crown area as well as the density of seedlings and saplings of gallery-forest tree species beneath isolated trees and in the savanna matrix along 50 transects of 5-km long and 600 m wide located along four gallery forests. We then tested the nurse-plant effect and Janzen-Connell hypothesis beneath isolated trees. We also examined the relationships between the crown area and the density of seedlings and saplings. Among the eight identified tree species isolated in savanna, only *Daniellia oliveri* and *Khaya senegalensis* showed nurse-plant effect and promoted a significant, yet low early recruitment with a seedling-to-sapling survival of 0.044 and 0.578, respectively. The suitability of the subcanopy of isolated trees decreased with the recruitment progression and Janzen-Connell effects were absent. Seedlings had neutral association with the crown area of isolated trees which shifted to positive at the sapling stage. The species of the isolated tree and the crown area explained less than 20% of total variance, indicating that other predictive factors are important in explaining the nurse-plant effect observed in this study.

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1. Introduction

In tropical Africa, gallery forests are edaphic forests formed by a complex of riparian and temporary flooded forests located at the riversides in savannas characterized by a discontinuous tree canopy in a continuous grass layer (Aubréville, 1957; Natta, 2003; Scholes and Archer, 1997). The transition between gallery forest and savanna occurs over a relatively short distance but represents unique habitats and dynamic zones where ecological traits (e.g. water availability, fire occurrence, soil properties, species composition, tree density) undergo important changes over a relatively short period of time (Azihou et al., 2013; Geiger et al., 2011; Porensky, 2011). Gallery-forest and savanna dynamics are likely to be strongly controlled by demographic processes (Murphy and Bowman, 2012). In annually burned areas, gallery-forest species are excluded from savanna ecosystems at the seedling stage (Gignoux et al., 2009). However, a recent study has shown the existence of individual gallery-forest trees isolated in savanna despite

frequent fires (Azihou et al., 2013). Resisting disturbances in savanna is relatively easier for adult trees due to their large size, but more problematic for forest young individuals such as seedlings and saplings (Gignoux et al., 2009). As the savanna matrix is a less conducive environment for forest regeneration, successful establishment of gallery-forest seedlings and saplings could be limited to refuges provided by isolated trees canopies (Hennenberg et al., 2006). In fact, some studies carried out in harsh environments have shown trees to facilitate the germination and the growth of young individuals beneath their canopies thanks to increased shade (Kos and Poschlod, 2007), temperature buffering (Drezner, 2007), increased hydraulic lift (Armas and Pugnaire, 2005), amelioration of soil physical and chemical traits (Suzan-Azpiri and Sosa, 2006), effects on mycorrhizae and other soil microorganisms (Ouahmane et al., 2006) and concentration of animal activities below canopies which increases soil nutrients (Dean et al., 1999). However, most studies deal with positive plant−plant interactions in alpine and arid ecosystems. Stress amelioration by neighbouring plants in African savanna ecosystems considered as more productive has received less attention from ecologists. Biaou et al. (2011) evaluated the intensity of tree seedlings facilitation by nurse trees in mesic and dry woodlands in Benin. The authors found tree canopies to facilitate seedling survival, confirming that positive interactions also occur in plant communities of African woodlands.

* Corresponding author. Tel.: +229 98286317.
   E-mail addresses: fazihou@gmail.com (A.F. Azihou), gleleromain@yahoo.fr (R. Glèlè Kakaï), bsinsin@gmail.com (B. Sinsin).
[1] Mail: 01 BP 526 Cotonou, Benin.

This study investigated the possibility that isolated gallery-forest trees established in savanna facilitate the germination and growth of forest woody species beneath their canopies (Bruno et al., 2003; Duarte et al., 2006a). Isolated trees attract dispersers from their native habitat, increasing seed rain under their canopy. Such enhanced dispersal has been considered as a classic case of directed dispersal (Spiegel and Nathan, 2012; Wenny, 2001). Directed dispersal theory predicts that high seed deposition rate generates seed aggregations (Kwit et al., 2007; Schupp et al., 2002) that often develop into hotspots of high density-dependent mortality, possibly negating the advantage of favourable site characteristics (Russo and Augspurger, 2004; Schupp, 1995). Many studies demonstrated that seedlings are more likely to compete when they start to utilize environmental resources beneath nurse plants (Berger et al., 2008; Casper et al., 2003; Ramula and Buckley, 2009). A predicted consequence of such a competition is that the nurse-plant effect might not be beneficial for later life cycle stages (Schupp, 1995, 2007; Spiegel and Nathan, 2012). Several studies have documented nurse-plant effect to be positive when beneficiaries are young and small, and negative as the nursed species become older and larger (Nuñez et al., 2009; Padilla and Pugnaire, 2006; Tewksbury and Lloyd, 2001). Also, shade-tolerant and late-successional protégé species may respond more positively to nurse plant than shade-intolerant and pioneer species (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, it is not known whether density-dependent processes in reducing seed-to-adult survival beneath nurse plants canopies vary across different nurse plant species or between conspecific and heterospecific protégés. Empirical evidence of species-specific associations between beneficiaries and nurse plant canopies across different protégés species and life cycle stages is also limited.

This study assesses how the suitability of the subcanopy changes across establishment phases by testing the nurse-plant effect hypothesis and predictions of the directed dispersal hypothesis across seedling and sapling phases. A chronosequence approach (following a given cohort throughout the recruitment process) would have been ideal for this purpose (Spiegel and Nathan, 2012). However, this is unfeasible for most perennial plants in general and for our study system in particular. Therefore, we compared the transition rates between seedling and sapling cohorts along the recruitment process. This approach relies on the assumption that the observed seedling community is similar to the one that preceded the observed sapling community. Densities of seedlings and saplings as well as seedling-to-sapling survival were therefore computed to test if isolated gallery-forest trees in savanna carry larger beneficiary loads than the savanna matrix. The hypothesis that regeneration beneath isolated tree experiences high mortality from the seedling to the sapling stage was also tested. Then, changes in conspecific and heterospecific regeneration densities were evaluated to test the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970) throughout the recruitment trajectory. The Janzen-Connell hypothesis postulates that seeds and seedlings that occur at high density or close to adult conspecifics are more likely to be attacked by specialized natural enemies such as pathogens and insect herbivores (Connell, 1971; Janzen, 1970). As a consequence, heterospecific recruits resulting from seeds dispersed away from conspecific adults escape from Janzen-Connell effects and are expected to have higher seedling survival compared to recruits established under conspecific trees. Finally, it was assessed if the relationships between isolated trees canopies and abundance of beneficiaries change across seedling and sapling stages. These hypotheses were tested using field data collected in the Biosphere Reserve of Pendjari, Benin. The distinction of gallery forest and savannas (tree, shrub and grass savannas) follows the classification approach of the Yangambi conference (Aubréville, 1957). Because

gallery forest is not a specific vegetation type in Africa (Aubréville, 1957), gallery-forest trees species were identified following the distribution of tree species at the boundary of savanna and gallery forest described for the Biosphere Reserve of Pendjari in Azihou et al. (2013).

2. Material and methods

2.1. Study area

The fieldwork was carried out in the Biosphere Reserve of Pendjari, Benin (10°30′–11°30′N, 0°50′–2°00′E). The reserve covers an area of 4661 km^2 and is located in the sudanian zone with one rainy season (April/May to October) and one dry season (November to March). The mean annual rainfall is 1000 mm with 60% falling between July and September. The relative humidity varies between 17% and 99% during the year and the mean annual daily temperature is 27 °C. The annually burned vegetation is dominated by savannas intermingled with gallery forests along waterways (PAG2, 2005; Sokpon et al., 2008). Rocky outcrops, ferruginous and silty soils support savannas while gallery-forest soil is clayey. Some gallery-forest tree individuals are found isolated in savanna (Azihou et al., 2013).

2.2. Sampling design and data collection

Isolated gallery-forest trees were systematically sampled in savanna along 50 transects established along four rivers. A first 5-km transect was drawn at 400 m from river to sample all gallery-forest trees located in a band of 300 m from each side of the transect. A second 5-km transect was drawn at 1000 m from river, parallel to the first, to record data on all forest trees located at 700–1300 m from river. A gallery-forest tree was considered to be isolated in savanna if located further than 100 m from river (see Azihou et al., 2013 for details) and had no neighbour forest woody plant touching its crown. The total area where isolated trees were sampled was approximately 15000 ha. Each sampled individual was described by morphological traits (diameter at breast height, height and crown area).

The abundance of regeneration (dbh < 10 cm) was quantified at the subcanopy of isolated trees and compared with that of the adjacent savanna. For this, following the direction of the transect, a circular area outside the crown of the isolated tree was sampled, with the diameter equalling the corresponding isolated tree crown diameter. Each savanna plot was located away from the respective isolated tree by a distance equal to the crown diameter of the later (Duarte et al., 2006a). During the data collection, the regeneration of all woody species (both savanna and gallery-forest species) was counted and separated in two height classes: seedling ≤1.3 m and sapling >1.3 m which are respectively sensitive and able to survive fire (Gignoux et al., 2009). The regeneration of gallery-forest trees species was extracted from the entire data set according to the distribution of tree species at the boundary of savanna and gallery forest described in Azihou et al. (2013). Species nomenclature follows the Flora of Benin (Akoegninou et al., 2006). Data were collected in the dry season after the annual vegetation fire to ensure that seedlings and saplings recorded have survived at least one fire event.

2.3. Data analysis

All statistical analyses were carried out within the R statistical environment (R Core Team, 2012). To test the nurse-plant effect of isolated trees, the R package Coin was used to perform the analysis of variance by randomization (Manly, 2007) with two factors

(habitat, species of the isolated tree). The randomization test was used instead of a two-way analysis of variance because the sampling of seedlings and saplings in the savanna was dictated by the location of the isolated trees and may not be representative of the whole savanna matrix. Through this procedure, the density of seedlings and saplings beneath the crown of various isolated tree species was compared with that of the adjacent savanna.

The survival from seedling to sapling was estimated from the average seedling-to-sapling ratio (the ratio between sapling density and seedling density) (Spiegel and Nathan, 2012). Species recorded only at the sapling stage were removed from the data set prior to computing the seedling-to-sapling ratio. The one sample T-test was performed on the seedling-to-sapling ratio to test the early persistence of seedlings beneath each isolated tree species and in the savanna matrix. The true mean was set to 0, a value that indicates a failure of seedlings to develop into saplings. The same procedure was used to test the significance of the seedling-to-sapling ratio for all species recorded in the regeneration community.

To test the Janzen-Connell hypothesis beneath isolated trees, the paired T-test was performed to compare density and seedling-to-sapling ratio between conspecific and heterospecific regeneration.

The relationships between the crown area and the number of seedlings and saplings beneath isolated trees were examined using linear mixed effects models (function lme, Pinheiro and Bates, 2000). The existence of a random effect in the data according to the species of isolated trees was investigated by fitting the unconditional means model (Singer and Willett, 2003). The intra-class correlation (ICC) was respectively 0.09 and 0.34 indicating that 9% and 34% of the total variance could be explained by the species of isolated trees at the seedling and the sapling stages. These results suggest that linear mixed effect modelling is more appropriate than fitting a common regression to all species of isolated tree. Therefore, the random slope and intercept model was used by allowing slopes to vary across species. The crown area was incorporated in all models as a fixed factor and the species of the isolated trees as a random factor. Individual isolated trees of same species constituted the pseudo-replication in the experimental design. To estimate the relative proportions of variances that the crown area and the species of isolated trees explain, varpart command of the R package vegan was used.

The species-specific associations between the crown area of isolated trees and protégés species at seedling and sapling stages were examined using the wascores function in the vegan library. This function computed the average value of crown area for all isolated trees beneath which a species occurred, weighted by species abundance. The scores help to identify for each recruitment phase which protégés species have the highest abundance under isolated trees with largest crown area. The negative binomial regression was then run on the abundance of seedlings and

saplings to examine whether a beneficiary species had a positive, neutral or negative association with crown area.

3. Results

3.1. Nurse plant-effect of isolated gallery-forest trees established in savanna

During the survey, eight isolated gallery-forest tree species were recorded in tree, shrub and grass savannas (Table 1). The gregarious species *Daniellia oliveri* was the most abundant species, with 60% of sampled individuals. The second more abundant species (20%) was *Khaya senegalensis*. Vertebrate dispersed species were *Vitex doniana*, *Diospyros mespiliformis*, *Parkia biglobosa* and *Tamarindus indica*, representing only 8% of total abundance.

The nurse-plant effect varied among isolated tree species (Table 2). The analysis of variance by randomization showed a significant interaction between the species of the isolated tree and the habitat (subcanopy versus savanna) at both seedling and sapling stages ($P = 0.0026$ and $P = 0.0002$, respectively). For example, isolated individuals of *D. oliveri* and *K. senegalensis* had significantly higher seedling and sapling loads beneath their canopy than the savanna matrix. However, the density of seedlings and saplings was similar in the savanna matrix and the subcanopy of *V. doniana* and the 'Others group' formed by *D. mespiliformis*, *P. biglobosa* and *T. indica*. Isolated individuals of *Anogeissus leiocarpa* had higher seedling load than the savanna but similar density of saplings. Isolated *Pterocarpus erinaceus* trees showed the opposite trend to that of *A. leiocarpa*. The survival ratio was significantly higher than zero beneath *D. oliveri*, *K. senegalensis*, and the 'Others group' trees, with mean ratio values of 0.044, 0.578 and 0.465, respectively. However, for isolated individuals of *A. leiocarpa*, *P. erinaceus* and *V. doniana*, this parameter was not significantly different from zero. The seedling-to-sapling survival ratio increased 7 times (from 0.031 to 0.218; $P = 0.0008$) from savanna to isolated trees subcanopies.

3.2. Diversity and early recruitment of gallery-forest species beneath isolated trees

Seventeen gallery-forest woody species were found as seedling and sapling beneath isolated trees (Table 3). *D. mespiliformis* was the most abundant seedling and sapling species found under isolated tree crowns (Table 3). Among the seedlings, *K. senegalensis* was the second most abundant species and *D. oliveri* the third. For saplings, *A. leiocarpa* and *T. indica* were respectively the second and the third most abundant species. At seedling and sapling stages, other species represented less than 1% of total abundance. In general, the density of regeneration decreased from the seedling to the sapling stage except for *A. leiocarpa* and *P. erinaceus*. Four species

Table 1
Diversity and morphological characteristics of isolated gallery-forest trees sampled in savanna ecosystems of the Biosphere Reserve of Pendjari, Benin.

Isolated tree species	Botanical family	n	Mean plant diameter ± SE (cm)	Mean plant height ± SE (m)	Total crown area (m^2)
Daniellia oliveri	Leguminosae-Caesalpinioideae	55	75.21 ± 3.35	17.79 ± 0.56	8194.86
Khaya senegalensis	Meliaceae	18	92.38 ± 4.09	24.45 ± 1.13	7485.04
Anogeissus leiocarpa	Combretaceae	7	41.83 ± 3.49	14.81 ± 0.76	755.72
Pterocarpus erinaceus	Leguminosae-Papilionoideae	4	44.85 ± 3.20	13.80 ± 1.48	498.19
Vitex doniana	Verbenaceae	3	49.67 ± 5.10	14.25 ± 1.69	311.28
Others		4	66.78 ± 16.80	14.04 ± 1.55	839.32
Diospyros mespiliformis	Ebenaceae				
Parkia biglobosa	Leguminosae-Mimosoideae				
Tamarindus indica	Leguminosae-Caesalpinioideae				
Total		91			18084.41

n refers to number of sampled individuals; SE, standard errors. Species nomenclature follows the Flora of Benin (Akoegninou et al., 2006).

Table 2
Mean values of the density of seedlings and saplings (individuals per m^2) and seedling-to-sapling ratio at the subcanopy of isolated tree species and in the savanna matrix of the Biosphere reserve of Pendjari, Benin.

Isolated tree species	Seedlings		Saplings		Survival ratio[a]	
	Subcanopy	Savanna	Subcanopy	Savanna	Subcanopy	Savanna
Daniellia oliveri	0.063a	0.017b	0.003a	0.0002b	0.044*	0.030[ns]
Khaya senegalensis	0.065a	0.002b	0.017a	0.0007b	0.578*	0.050[ns]
Anogeissus leiocarpa	0.097a	0.001b	0.022a	0.004a	0.330[ns]	NA
Pterocarpus erinaceus	0.117a	0.000a	0.034a	0.000b	0.568[ns]	NA
Vitex doniana	0.711a	0.000a	0.044a	0.022a	0.308[ns]	NA
Others[b]	0.242a	0.000a	0.091a	0.004a	0.465*	NA
Overall	0.098a	0.011b	0.014a	0.002b	0.218*	0.031[ns]

*: survival ratio significantly higher than 0 (one sample t-Test).
[ns]: survival ratio not significantly different from 0 (one sample t-Test).
NA: observation units where the survival ratio could not be computed due to the absence of seedlings.
[a] Values of survival ratio are only computed for observation units where seedlings are observed.
[b] Species forming the 'Others group': Diospyros mespiliformis, Parkia biglobosa and Tamarindus indica.

(K. senegalensis, D. oliveri, Borassus aethiopum, Syzygium guineense) were not recorded at the sapling stage. The survival ratio of Cassia sieberiana, Sarcocephalus latifolius and P. biglobosa did not significantly differ from zero. However, seedlings of A. leiocarpa, D. mespiliformis, Feretia apodanthera and T. indica had survival ratio significantly higher than zero, with ratio values of 0.917, 0.365, 0.366 and 0.202, respectively.

3.3. The Janzen-Connell effects beneath isolated trees

Both conspecific and heterospecific regenerations were found under the canopy of isolated trees. The density of heterospecific regeneration was higher than that of conspecific regeneration, for both seedling and sapling stages (Fig. 1). Indeed, heterospecific regeneration represented 77% and 80% respectively of seedling and sapling density beneath isolated trees. When considering the diversity of heterospecific regeneration by dividing their abundance by the number of species, the density of conspecific seedling and sapling became similar to those of single heterospecific protégé ($P = 0.30$ and $P = 0.50$, respectively). From the conspecific to the heterospecific regeneration, the seedling-to-sapling survival ratio significantly increased from 0.116 to 0.143 ($P = 0.0015$).

3.4. Species-specific association between isolated tree crown area and beneficiary species

Seedlings had no association with the crown area of isolated trees (Table 4). Indeed, the abundance of seedlings under three isolated tree species (A. leiocarpa, D. oliveri, P. erinaceus) increased with the crown area (Fig. 2A), whereas the number of seedlings under two species (K. senegalensis, V. doniana) decreased with the crown area. This trend was also expressed by the contrasting responses of groups of seedlings. Seedlings of D. oliveri had weighted scores lower than the mean crown area and seemed to suffer from crown area (Fig. 2B). In the opposite, seedlings of D. mespiliformis, T. Indica and S. latifolius seemed to benefit from crown area and had weighted average higher than the mean crown area. Between these groups, seedlings of B. aethiopum, A. leiocarpa, F. apodanthera, C. sieberiana, S. guineense, P. biglobosa and K. senegalensis had neutral association with crown.

The abundance of saplings was positively associated with the crown area of isolated trees, and this pattern was consistent across the five isolated tree species (Table 4, Fig. 3A). In addition, most of sapling species occurred under isolated tree with crown larger than the mean crown area (Fig. 3B). Saplings of P. biglobosa, S. latifolius, T. indica and D. mespiliformis had positive association with crown, whereas saplings of A. leiocarpa, P. erinaceus, C. sieberiana and F. apodanthera had neutral association with crown.

At seedling and sapling stages, the crown area and the species of isolated trees explained less than 20% of variation (Table 4), indicating that other factors may influence the species-specific association between isolated trees and the regeneration of gallery-forest species beneath their canopy.

Table 3
Seedlings and saplings density (individuals per m^2) and survival ratio of species forming the regeneration community beneath isolated gallery-forest trees sampled in savanna ecosystems of the Biosphere Reserve of Pendjari, Benin.

| Species	Botanical family	Seedlings		Saplings		Survival ratio[a]
		Mean density	%	Mean density	%	
Diospyros mespiliformis	Ebenaceae	0.0239	36.06	0.0060	48.88	0.365*
Khaya senegalensis	Meliaceae	0.0132	19.95	0.000	0.000	0.000[mu]
Daniellia oliveri	Leguminosae-Caesalpinioideae	0.0075	11.27	0.000	0000	0.000[mu]
Feretia apodanthera	Rubiaceae	0.0058	8.76	0.0011	8.97	0.366*
Borassus aethiopum	Arecaceae	0.0053	7.93	0.000	0.000	0.000[mu]
Tamarindus indica	Leguminosae-Caesalpinioideae	0.0049	7.43	0.0014	10.76	0.202*
Cassia sieberiana	Leguminosae-Caesalpinioideae	0.0020	3.09	0.0005	4.04	0.291[ns]
Anogeissus leiocarpa	Combretaceae	0.0014	2.09	0.0023	18.83	0.917*
Syzygium guineense	Myrtaceae	0.0009	1.42	0.000	0.000	0.000[mu]
Sarcocephalus latifolius	Rubiaceae	0.0008	1.17	0.0004	3.59	0.167[ns]
Parkia biglobosa	Leguminosae-Mimosoideae	0.0002	0.33	0.0002	1.79	0.750[ns]
Pterocarpus erinaceus	Leguminosae-Papilionoideae	0.0001	0.17	0.0003	2.24	NA
others		0.0002	0.33	0.0001	0.90	NA
Antidesma venosum	Euphorbiaceae					
Ficus ovata	Moraceae					
Oncoba spinosa	Flacourtiaceae					
Vitex chrysocarpa	Verbenaceae					
Vitex doniana	Verbenaceae					
Total		0.0662	100	0.0123	100	NA

[mu]: survival ratio equals to 0 over all observation units and used as true value of mean to perform the one sample t-test.
*: survival ratio significantly higher than 0 (one sample t-test).
[ns]: survival ratio not significantly different from 0 (one sample t-test).
NA: the survival ratio could not be computed for group of species or individual species that lack seedlings.
[a] Values of survival ratio are only computed for observation units where seedlings are observed.
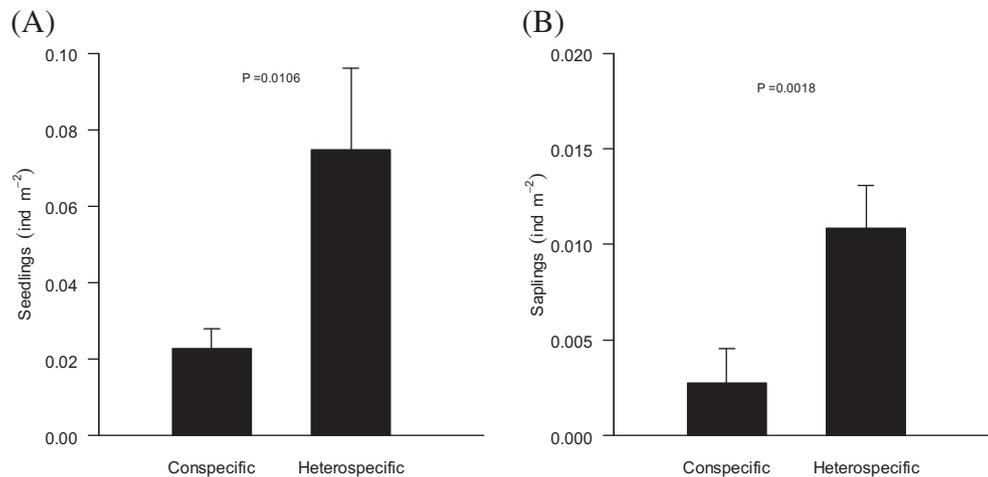
Fig. 1. Conspecific and heterospecific regeneration density beneath isolated gallery-forest trees. (A) seedlings (dbh < 10 cm; height ≤ 1.3 m); (B) saplings (dbh < 10 cm; height > 1.3 m). Vertical lines above bars indicate standard errors. P-value generated by the paired T-test.

4. Discussion

We provide evidence for the nurse-plant effect but only for *D. oliveri* and *K. senegalensis*. Such evidence is however lacking for *V. doniana*, *D. mespiliformis*, *P. biglobosa* and *T. indica* whereas isolated *A. leiocarpa* and *P. erinaceus* trees were respectively suitable for seedlings or saplings only. Morphological traits (diameter, height and large crown) that attract vertebrate dispersers may explain the success of *D. oliveri* and *K. senegalensis* as nurse plants. The large crown of these isolated trees could result in increased shade (Kos and Poschlod, 2007), loss of grass and reduction of fire intensity and flame length (Hoffmann et al., 2012) and protection of seedlings and saplings from burning contrary to the flammable savanna matrix (Collin et al., 2011). The nurse-plant effect of *D. oliveri* and *K. senegalensis* accords with the findings of Biaou et al. (2011) who found that seedling survival is greater under tree canopy compared with open fields in African woodlands. It highlights the facilitative role of nurse trees on tree seedling establishment in their optimum habitat (Biaou et al., 2011) and in harsh environment of African savanna as investigated in this study. Other studies on the nurse-plant effect also reported more individuals of woody species under the canopy of isolated trees than in the open field in a pasture (Holl, 2002; Slocum, 2001) or in grassland (Duarte et al., 2006a).

Interestingly, the two species (*D. Oliveri* and *K. senegalensis*) forming 80% of isolated trees were the tallest suggesting that plant height might be a good predictor of long distance dispersal (Thomson et al., 2011), the underlying mechanism of tree isolation. However, the ingression of gallery-forest trees in savanna by the recruitment of seedlings beneath isolated trees may be a very slow process given the low values of seedling survival ratio.

The general trend of decreasing density from the seedling to the sapling stage supports the hypothesis of high mortality beneath isolated trees along the recruitment trajectory. Indeed, no sapling of *K. senegalensis*, *D. oliveri*, *B. aethiopum* and *S. guineense* was recorded in the field. Saplings of *C. sieberiana*, *S. latifolius* and *P. biglobosa* were scarce. Few seedlings of *A. leiocarpa*, *D. mespiliformis*, *F. apodanthera* and *T. indica* developed into saplings. Regenerations of these species are able to survive disturbances (fire, herbivory) through resprouts. These results support the view of Gignoux et al. (2009), according to which the resprout stage is an obligate step for establishment and early persistence of tree seedlings in annually burned savannas. For example, *D. mespiliformis* was the most abundant seedling and sapling species beneath isolated trees in the savanna. This species produces a large number of small, purplish and perfumed vertebrate-dispersed berries, mainly from August to November (Akoegninou et al., 2006), when baboons forage near gallery forest to avoid fire in savanna. Moreover, *D. mespiliformis* is a slow-growing species that can persist in an annually burnt savanna through seedling sprouting or root suckering. Successful dispersal, associated with the tolerance of the species to stressful environmental conditions could explain the abundance of *D. mespiliformis* beneath isolated trees in savanna.

This snapshot study does not allow us to identify the process responsible for the mortality or assess their relative importance that may vary among recruitment phases. For instance, density-dependent predation might be important at the seed phase, while allelopathy might be more important at the seedling phase, and competition more pronounced at sapling and late establishment phases (Spiegel and Nathan, 2012). The reduction of regeneration density across the recruitment trajectory, congruent with the prediction of the directed dispersal hypothesis (Schupp, 1995, 2007; Spiegel and Nathan, 2012), may alter the nurse-plant effect, making it difficult to observe. Savanna is actually a less conducive environment for forest species. So, enhanced seed arrival under isolated trees is a case of directed dispersal to a safer site (isolated tree subcanopy) (Spiegel and Nathan, 2012). Therefore, seedling mortality occurring beneath isolated trees is of minor importance compared to the exclusion of forest species from the savanna at the seedlings stage (Gignoux et al., 2009).

No support was found for the hypothesis that Janzen-Connell effects extirpate conspecific seedlings and saplings from the

Table 4
The result of the linear mixed effects (LME) models for number of seedlings and saplings in relation to crown area and isolated tree species. R^2 values (percentage values) of the crown area and isolated tree species are derived from a separate variation partitioning analysis.

| Beneficiary groups	Direction of the effect	Variation partitioning	LME modelling		
		R^2	dfs	F	P
Seedlings	No effect	Crown area: 11 Tree species: 0.5	82	0.0004	0.984
Saplings	Positive	Crown area: 12 Tree species: 4	82	6.0291	0.016
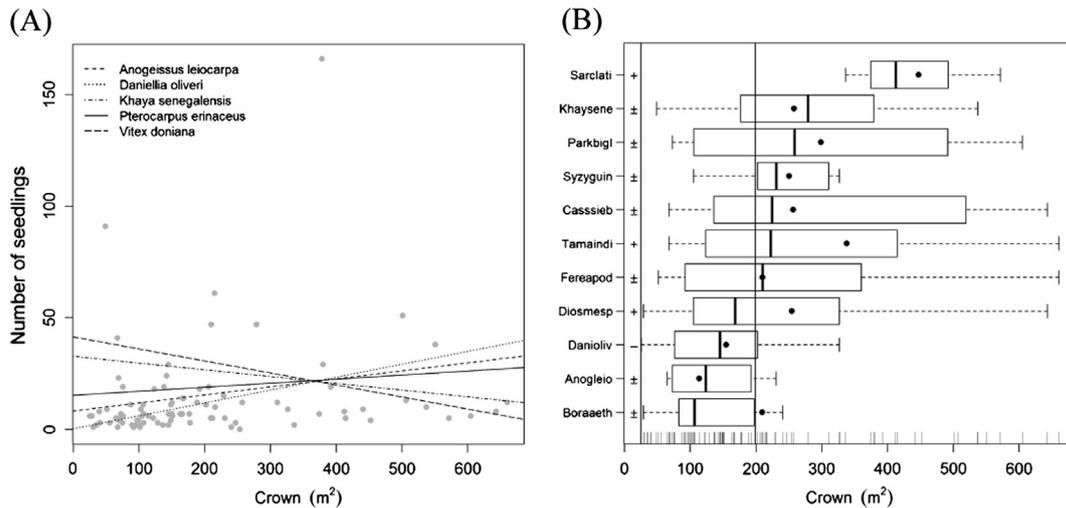
Fig. 2. Relationship between crown area and abundance of seedlings (dbh < 10 cm; height ≤ 1.3 m) beneath isolated gallery-forest trees. (A) Scatter plot of the number of seedlings − crown area relation. The prediction lines for the abundance of seedlings under each of the five isolated tree species are drawn based on the intercept and slope of crown area taken from the linear mixed effects models. (B) Weighted averages scores for species recorded at the seedling stage. In boxplot images, the middle lines represent the median and outer line quartiles, whereas points indicate weighted averages. The boxplot are based on presence data only, but weighted averages are based on the original quantitative information. Boxes are arranged by medians. The species codes are the first four letters of the genus and species (see below for full names). The direction of the relationship (±) to the crown area is indicated after the species code. The vertical line indicates mean crown area. Full species names: Sarclati = *Sarcocephalus latifolius*, Khaysene = *Khaya senegalensis*, Parkbigl = *Parkia biglobosa*, Syzyguin = *Syzygium guineense*, Casssieb = *Cassia sieberiana*, Tamaindi = *Tamarindus indica*, Fereapod = *Feretia apodanthera*, Diosmesp = *Diospyros mespiliformis*, Danioliv = *Daniellia oliveri*, Anogleio = *Anogeissus leiocarpa*, Boraaeth = *Borassus aethiopum*.

subcanopy of isolated trees. Indeed, the densities of heterospecific regenerations, considered individually, were similar to those of conspecific seedlings and saplings. This suggests that the dispersers carrying conspecific seeds beneath isolated trees facilitate the escape of seeds from natural enemies prevalent in area with high density of conspecific adults (Hirsch et al., 2012). Because heterospecific regeneration consisted of sixteen species, enhanced recruitment beneath isolated trees will result in the development of small forest patches in savanna. This process, which is more congruent with a strategy of community ingression in new

environments than population spread, has been recorded in Araucaria forest expansion over grassland in south Brazil (Duarte et al., 2006b, 2007).

Seedlings had no association with isolated-trees crown area. Indeed, seedlings represent post-dispersal phase, a process where the only role of isolated trees is to attract dispersers (Duarte et al., 2006a; Spiegel and Nathan, 2012). However, the abundance of saplings increased under larger crowns. Increase in canopy effects from seedling stage to sapling suggests that isolated trees play limited role in early establishment of forest species but are crucial
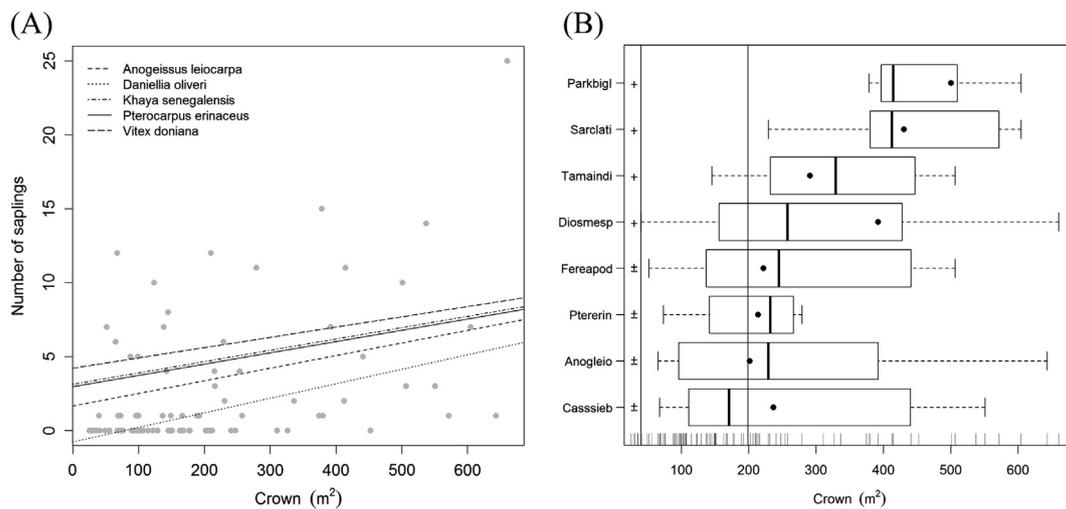
Fig. 3. Relationship between crown area and abundance of saplings (dbh < 10 cm; height > 1.3 m) beneath isolated gallery-forest trees. (A) Scatter plot of the number of saplings − crown area relation. The prediction lines for the abundance of saplings under each of the five isolated tree species are drawn based on the intercept and slope of crown area taken from the linear mixed effects models. (B) Weighted averages scores for species recorded at the sapling stage. In boxplot images, the middle lines represent the median and outer line quartiles, whereas points indicate weighted averages. The boxplot are based on presence data only, but weighted averages are based on the original quantitative information. Boxes are arranged by medians. The species codes are the first four letters of the genus and species (see below for full names). The direction of the relationship (±) to the crown area is indicated after the species code. The vertical line indicates mean crown area. Full species names: Parkbigl = *Parkia biglobosa*, Sarclati = *Sarcocephalus latifolius*, Tamaindi = *Tamarindus indica*, Diosmesp = *Diospyros mespiliformis*, Fereapod = *Feretia apodanthera*, Ptererin = *Pterocarpus erinaceus*, Anogleio = *Anogeissus leiocarpa*, Casssieb = *Cassia sieberiana*.

for their persistence in savanna. Despite the canopy effect, some beneficiary species failed to persist beneath isolated trees as saplings indicating that the characteristics of beneficiary species may also be a contributing factor to tree persistence (Yang et al., 2010). Indeed, shade-tolerant and late-successional species may respond more positively to nurse plants than shade-intolerant and pioneer species (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). In the current study, species that failed to persist as saplings may be shade intolerant or of high palatability for herbivores (Kitajima and Poorter, 2010). In the other hand, species recorded as seedling and sapling may have some similarities with shade tolerant species which allow them to persist beneath isolated trees. Indeed, shade tolerant species tend to have tougher leaves (Kitajima and Poorter, 2010), a defence trait against herbivores (Coley and Barone, 1996), have relatively high mass partitioning to carbohydrate storage, which could enable recovery from damage (Kobe, 1997; Myers and Kitajima, 2007), and higher tissue density and fibre content (Alvarez-Clare and Kitajima, 2007), which could provide resistance to damping off (Augspurger and Kelly, 1984) and other mortality agents. Seedlings of shade-tolerant and shade-intolerant species could be observed beneath isolated trees because shade-induced mortality has not filtered out shade intolerant species, which would be expected in the larger and older size classes (Comita et al., 2010; Kobe and Vriesendorp, 2011).

The main limitation of this study may be related to the methodological approach of comparing cohorts rather than following a chronosequence approach. Especially, this is more relevant to the determination of the seedling-to-sapling survival where different subsets of data were used to exclude isolated trees and savanna plots with regeneration species recorded at only sapling stage without seedlings. We also have some observations where the number of saplings was higher than the number of seedlings; thus violating our assumption by providing "saplings recruited from imaginary seedlings". These rare observations might have noteworthy effects on our conclusions if more prevalent.

5. Conclusions

According to our results, among gallery-forest trees isolated in savanna, only *D. oliveri* and *K. senegalensis* trees facilitate the establishment and early recruitment of forest regeneration beneath their crown. The suitability of the subcanopy as a colonization site decreased from the seedling to the sapling stage. There is no evidence of extirpation of conspecific seedlings and saplings beneath isolated trees by Janzen-Connell effects. The relationship between the crown area and density of seedlings and saplings is positive, neutral or negative, depending on the identity of the species and the development stage. The consistency of the results across many isolated tree and regeneration species is indicative of the strength of facilitation as a driving force of species coexistence. However, more than 80% of the variation within the data remains unexplained by the species of isolated trees and the crown area. Further studies are needed to investigate potential additional factors underlying facilitative interactions in savanna ecosystems.

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