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Influence of tree clumps on vegetation dynamics and resilience in a west African humid savanna submitted to annual fires

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Abstract

Annual fires shape humid savanna dynamics, yet their interaction with heterogeneous vegetation structures remains poorly understood. This study examines how tree clumps influence vegetation dynamics in the fire-prone savanna of Lamto (Côte d'Ivoire), testing the hypothesis that these formations locally alter fire regimes, creating micro-habitats that facilitate species survival and forest tree establishment. We sampled fifty tree clumps (>9 trees each), comparing understory (internal) zones with adjacent external areas (5 m perimeter). Vegetation structure, fire behavior, tree health, and plant community composition were quantified. Results reveal a protective "umbrella effect" of tree clumps. Understory zones exhibited lower grass height and biomass, leading to significantly reduced flame heights compared to external areas. This fire mitigation enhanced species richness beneath tree clumps, supporting savanna species (*Piliostigma thonningii*, *Crossopteryx febrifuga*), along with juvenile regeneration of forest and exotic species (*Elaeis guineensis*, *Ceiba pentandra*, *Azadirachta indica*). External zones were dominated by pyrophilic grasses (*Hyparrhenia sp.* 88%), while understories featured less flammable assemblages. Tree health (*Bridelia ferruginea*) was superior under tree clumps, confirming their protective function. Tree clumps function as critical fire refuges, attenuating fire intensity and creating niches for fire-sensitive species within the savanna matrix. They serve as resilience nuclei and potential drivers of forest expansion. However, exotic species colonization within refuges raises concerns about invasion vulnerability. Preserving these keystone structures is essential for maintaining biodiversity and ecosystem processes in West African savannas under global change.

Keywords: Guinean savanna; Tree clumps; Fire regimes; Spatial heterogeneity; Forest regeneration; Conservation

1. Introduction

Savannas cover approximately 20% of the Earth's land surface and are ecosystems characterized by the coexistence of a continuous grass layer and a more or less discontinuous tree layer [1]. This coexistence, long perceived as paradoxical, is maintained by complex interactions between climatic factors, edaphic conditions, and disturbances (fires, herbivory) [2]. At the global scale, annual precipitation below 650 mm directly constrains tree biomass, while above this threshold, fire and herbivory become the primary regulators of tree density [3].

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In West African humid savannas (> 900 mm/year), fire is recognized as an essential driver maintaining the savanna-forest equilibrium. Long-term fire exclusion experiments conducted over several decades show that in the absence of fire, these savannas transition to dense forest within a few decades [4]. Fire primarily acts by limiting tree recruitment: it maintains young individuals at a "sapling stage" where above-ground parts are regularly burned, delaying their growth until they reach a refuge size (> 2-3 m) allowing them to escape fire-induced mortality [5]. This demographic "bottleneck" mechanism is fundamental to understanding woody population dynamics in savannas [6]. However, the savanna is not a homogeneous matrix. The spatial heterogeneity of vegetation, characterized by complex tree-grass interactions, has been the submit of numerous studies [7]. This heterogeneity is particularly manifested by the presence of tree clumps (or tree islands), defined as aggregations of trees with overlapping crowns [8]. These dense structures locally modify microclimatic conditions and resource availability (light, water, nutrients) [9].

Recent work conducted in southern and central Africa highlights the key functional role of these tree clumps in forest expansion processes. [10] showed that species capable of forming tree clumps possess particular functional traits, notably thicker bark, conferring both fire resistance and tolerance to seasonal drought. These tolerant pioneer species act as facilitators: by establishing under the canopy of isolated trees, they create favorable conditions for the establishment of more sensitive forest species, thus initiating a process of tree clump coalescence toward closed forest formation [11].

Furthermore, [12] identified a critical woody biomass threshold (40 Mg ha^{-1}) beyond which the grass layer is sufficiently reduced to break the grass-fire feedback loop, allowing irreversible forest expansion. This hysteresis phenomenon suggests that savannas and forests could represent alternative stable states, whose transition is mediated by the emergence of dense tree clumps [3,13].

In the Lamto savanna (Côte d'Ivoire), a reference site for the study of West African humid savannas, the dynamics of tree clumps and their role in ecosystem resilience to annual fires remain insufficiently documented. Yet these structures could constitute critical fire refuges, influencing long-term vegetation trajectories [14]. By locally modifying the fire regime, tree clumps create micro-habitats favorable to tree species regeneration, including forest and exotic species, as observed in other African contexts [15].

This study aims to assess the impact of tree clumps on vegetation dynamics in the Lamto savanna submitted to annual fires. By comparing under-tree clump and around-tree clump areas, we test the hypothesis that these structures act as fire refuges by locally modifying fuel biomass and fire intensity. More specifically, we seek to: (i) quantify differences in vegetation structure (grass height and biomass, canopy openness) between under-clump and around-clump areas; (ii) assess fire intensity through flame height; (iii) analyze the diversity and abundance of tree and herbaceous species and (iv) characterize the health status of dominant trees. These results will allow a better understanding of the role of tree clumps as resilience nuclei and potential anchor points for savanna dynamics in a context of global change.

2. Materials and Methods

2.1. Study site

The study was conducted in the Lamto Reserve (6°9'-6°13' N, 4°57'-5°15' W), a 2500 ha protected area located in Côte d'Ivoire, within the forest-savanna transition zone of West Africa. The climate is humid tropical with a sub-equatorial regime, characterized by a mean annual rainfall of 1200 mm [16] and a mean annual temperature of 27°C. The year is divided into four seasons: a long dry season (November to February), a long rainy season (March to July), a short dry season in August, and a short rainy season (September to October).

The vegetation is typical of Guinean savannas, with a discontinuous tree layer dominated by *Borassus aethiopum* Mart., *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth., *Piliostigma thonningii* (Schum.) Milne-Redh., *Bridelia ferruginea* Benth., *Cussonia arborea* Hochst. ex A. Rich., and *Annona senegalensis* Pers. [17]. The herbaceous layer is mainly composed of perennial tussock grasses from the genera Hyparrhenia, Andropogon, and Loudetia [18], covering approximately 15% of the soil surface, with the remainder consisting of bare soil [19]. Herbaceous biomass at the beginning of the long dry season averages 6.61 ± 1.94 $Mg.ha^{-1}$ in open areas, but is only 4.47 ± 1.37 $Mg.ha^{-1}$ under tree clumps, where it tends to disappear beneath the densest formations [20].

Since 1962, the Lamto savanna has been submitted to an annual controlled fire regime, generally ignited in the middle of the dry season (January), making it a reference site for studying fire-vegetation dynamics interactions in West Africa [19].

2.2. Sampling design

Fifty tree clumps were randomly selected within the reserve. Each tree clump was defined as a grouping of at least nine trees with overlapping crowns, following the definition of [8] (Figure 1). This minimum size was chosen to ensure a sufficiently dense structure to allow studying fire protection effects. The geographic coordinates of each tree clump were recorded using a Garmin 12 GPS.

Figure 1 Tree clumps in the shrubby savanna of Lamto

For each tree clump, two contrasting zones were delineated (Figure 2):

- Internal zone (under-clump): corresponding to the vertical projection of the tree clump canopy.
- External zone (around-clump): a 5 m wide peripheral band extending from the canopy edge, representing the adjacent savanna matrix directly influenced by the tree clump.

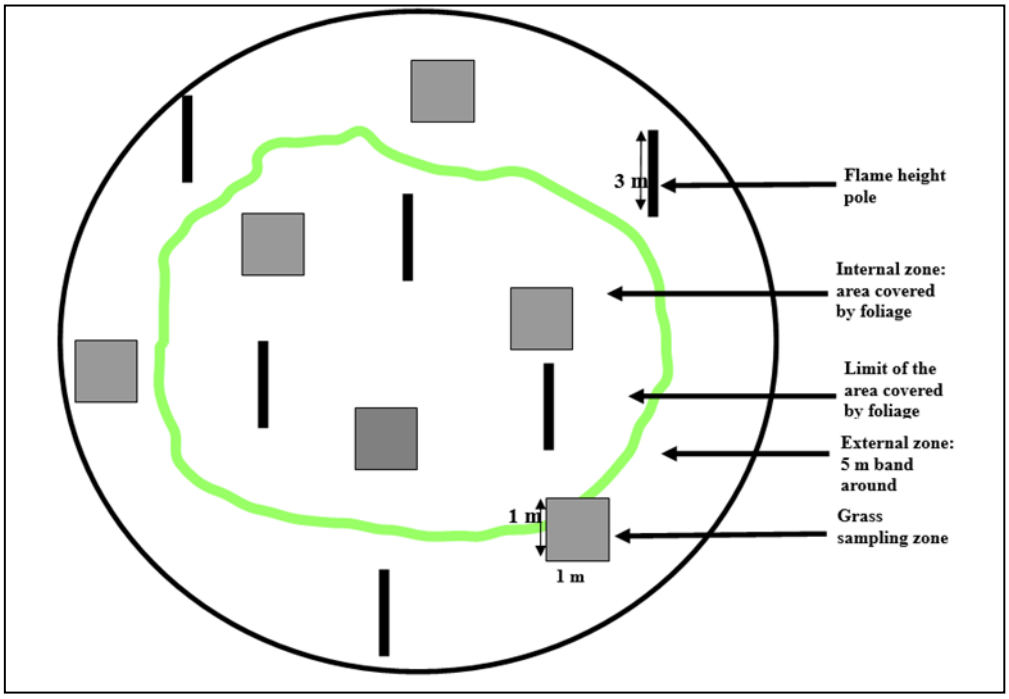

Figure 2 Sampling design under clump and around clump

(**Internal zone:** area covered by the foliage of the tree clump; **External zone:** 5 m limit defined around the clump; **Gray square:** corresponds to the grass sampling area, 1 m per side)

2.3. Vegetation structure measurements

2.3.1. Herbaceous layer and litter characteristics

Herbaceous layer height was measured using a herbometer (Figure 3). Three random measurements were taken in each zone (internal and external) per tree clump.

Herbaceous biomass was estimated by complete harvesting within three 1 m^2 quadrats randomly distributed in each zone. Samples were weighed fresh in the laboratory (Scout Pro 200 g electronic balance), then dried at 65°C to constant weight to determine dry biomass (expressed in $g.m^{-2}$). In the same quadrats, all litter (dead organic matter not included in live biomass) was collected and weighed after drying.

Species composition and relative abundance of herbaceous species were visually assessed in each zone, distinguishing between:

- Dominance zones (a single species representing >75% of the cover);
- Mixed zones (co-dominance of several species).

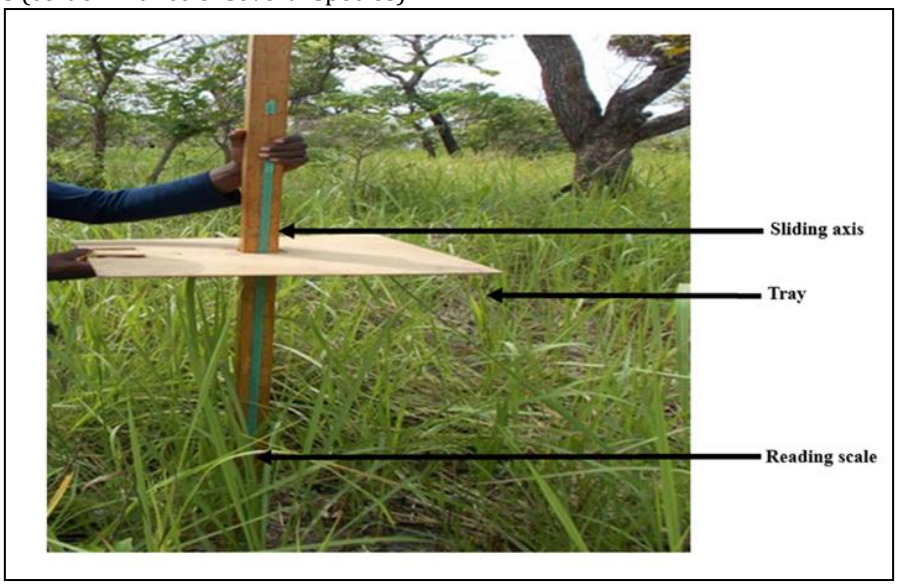

Figure 3 Herbometer (sliding axis and tray)

2.3.2. Canopy openness

Figure 4 Hemispherical photograph of a clump

Canopy openness was estimated from hemispherical photographs taken under each clump (n = 3 photos per tree clump, totaling 150 photos). Photographs were taken before sunrise to avoid artifacts related to direct sunlight [21], using a Coolpix 990 digital camera (Nikon) equipped with an FC-E8 hemispherical lens (Nikon), mounted on a tripod 1 m above the ground. Images were analyzed using ImageJ software (version 1.48k+dfsg). The threshold for separating sky and vegetation was determined manually in a consistent manner by a single operator to minimize bias [22]. Distortion of the FC-E8 lens is negligible (< 3%; [23] (Figure 4).

2.4. Fire regime characterization

Fire intensity was assessed indirectly by measuring flame height, using the instrumented stake method. Stakes 3 m in height were graduated every 10 cm with heat-sensitive paper adhesive tape. Six stakes were installed per tree clump: three in the internal zone and three in the external zone. Immediately after fire passage (the annual controlled fire in January), the maximum flame height reached was determined for each stake by measuring the distance from the ground to the last visible burn mark on the adhesive tape.

2.5. Floristic and demographic inventories

An exhaustive inventory of tree species was conducted in each zone (internal and external). For each individual, the species was identified on site or, in case of doubt, from samples collected for subsequent laboratory identification. Individuals were classified into four developmental stages:

- Seedlings (< 50 cm height, no signs of resprouting);
- Resprouts (individuals originating from resprouting after fire, height < 1.3 m);
- Juveniles (height > 1.3 m, but diameter at breast height (DBH) < 5 cm);
- Adults (DBH ≥ 5 cm).

Species diversity was characterized by species richness (number of species) and relative abundance (frequency of occurrence) in each zone.

2.6. Tree health assessment

Fire impact on trees was assessed using two visual indicators for all tree individuals (juveniles and adults):

- Crown condition (Good condition: dense and green foliage, normal architecture; Poor condition: crown dieback, broken, dry, or burnt main branches).
- Trunk condition (Good condition: intact bark, no injuries; Poor condition: burnt or missing bark, hollow, split, or fire-scarred trunk).

2.7. Statistical analyses

All statistical analyses were performed using R software [24]. Data normality and homogeneity of variances were verified beforehand (Shapiro-Wilk test and Levene's test). Analyses of variance (ANOVA) were used to compare internal and external zones for normally distributed continuous variables (flame height, herbaceous biomass, litter biomass). When normality conditions were not met, the Wilcoxon-Mann-Whitney test was applied (herbaceous height). The relationship between canopy openness and herbaceous layer characteristics (height, biomass) was analyzed using linear regression (lm function). Frequency comparisons (herbaceous composition, crown condition, trunk condition) were performed using Fisher's exact test. Alpha diversity (species richness) was compared between zones using a Student's t-test.

Results are presented as means ± standard deviation, with a significance threshold set at $\alpha = 0.05$.

3. Results

3.1. Effect of tree clumps on fire regime

Flame height, used as a proxy for fire intensity, was significantly higher in external areas (around clumps) than under clumps (204.6 ± 77.96 cm versus 159.8 ± 46.08 cm; ANOVA, $F_{1,98} = 12.21$, $p < 0.001$). This approximately 22% reduction in flame height under dense tree cover suggests a direct protective effect of tree clumps on the fire regime.

3.2. Characteristics of the herbaceous layer and litter

3.2.1. Herbaceous biomass

Herbaceous biomass was significantly higher in external areas (0.723 ± 0.14 kg.m^{-2}) than under clumps (0.426 ± 0.08 kg.m^{-2}) (ANOVA, $F_{1,98} = 149.8$, $p < 0.001$). This difference represents a 41% reduction in fuel biomass under clumps, which helps explain the decrease in fire intensity observed in these areas.

Linear regression analysis revealed a significant positive relationship between herbaceous biomass and flame height under clumps ($F_{1,48} = 8.58$, $p = 0.005$, $R^2 = 0.15$), indicating that local variations in fuel load directly influence fire intensity.

3.2.2. Herbaceous layer height

Mean grass height was significantly lower under clumps (36.61 ± 7.89 cm) than in external areas (56.70 ± 8.45 cm) (Wilcoxon test, $W = 2450$, $p < 0.001$, $n = 50$). This 35% reduction in herbaceous cover height under clumps confirms the shading and competitive effect exerted by the tree canopy.

3.2.3. Litter biomass

Unlike herbaceous biomass, litter biomass did not differ significantly between internal and external areas (0.053 ± 0.017 kg.m^{-2} under tree clumps versus 0.048 ± 0.036 kg.m^{-2} outside tree clumps; ANOVA, $F_{1,98} = 1.97$, $p = 0.16$). However, a non-significant trend toward slightly greater litter accumulation under tree clumps was observed (Figure 5).

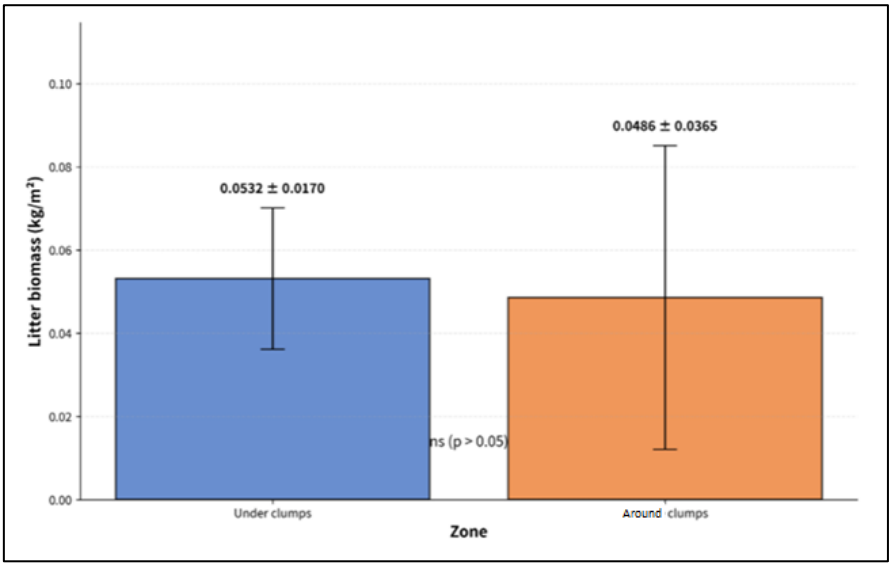

Figure 5 Comparison of litter biomass between under-clump and around-clump zones (Mean ± standard deviation)

3.2.4. Herbaceous community composition and structure

Analysis of herbaceous layer composition revealed marked contrasts between the two zones (Figure 6). *Hyparrhenia* sp. was largely dominant in external areas, where it represented 88% of the herbaceous cover. Under clumps, this dominance was strongly reduced, with only 32% of under-cover areas dominated exclusively by *Hyparrhenia* sp. *Imperata cylindrica* was present only under clumps, where it dominated in 24% of cases and was co-dominant in an additional 12%. *Loudetia simplex* was rare and always in mixtures, with 6% external areas. Herbaceous mixtures (*Imperata cylindrica* and *Hyparrehnia* sp.) were more frequent under clumps (44%) than in external areas (6%), indicating greater spatial heterogeneity and a release from dominance by pyrophilic species under woody cover.

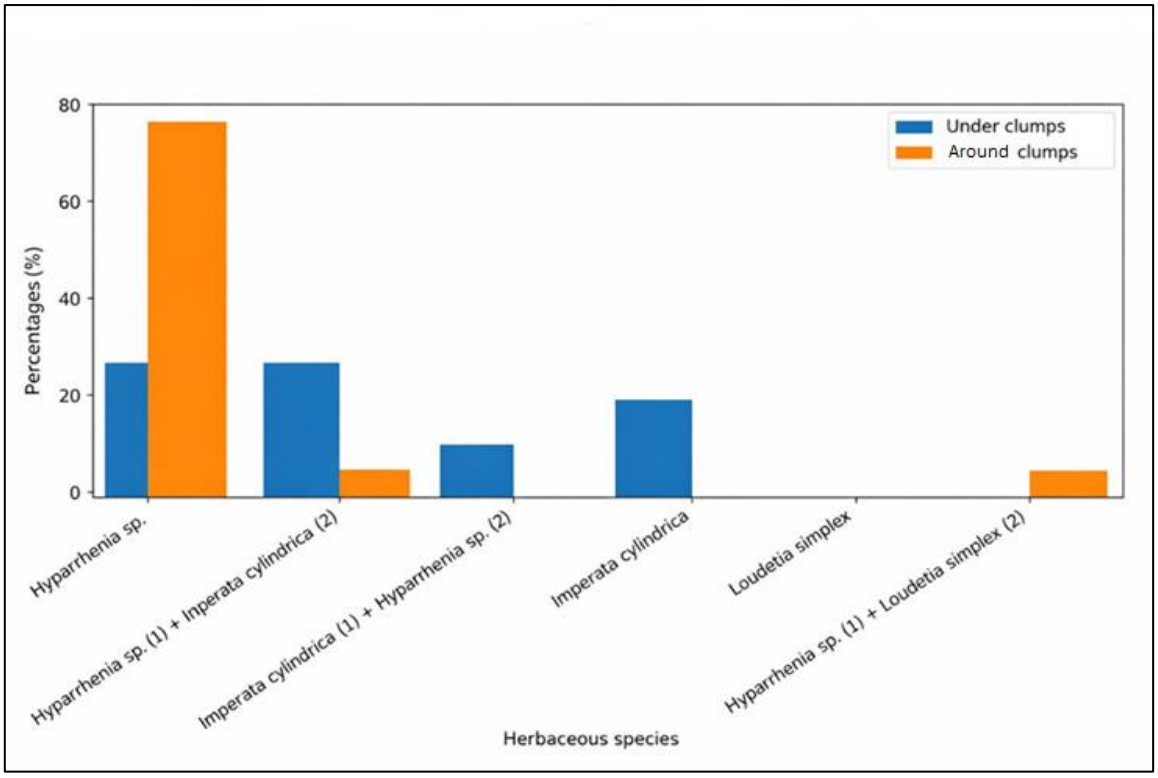

Figure 6 Space occupancy proportions of the herbaceous layer by main species under clumps and around clumps (1=dominant specie; 2= second dominant specie)

3.3. Canopy openness

Mean canopy openness under clumps was 39.85 ± 5.82%, indicating moderately dense tree cover allowing substantial understory light penetration.

Linear regression analysis showed a significant relationship between canopy openness and grass height ($F_{1,48} = 6.24$, $p = 0.016$, $R^2 = 0.11$) as well as herbaceous biomass ($F_{1,48} = 5.87$, $p = 0.019$, $R^2 = 0.10$) under clumps. This relationship was particularly pronounced when the herbaceous layer was well-developed (height > 40 cm), but disappeared when grass was sparse (height < 30 cm), suggesting a threshold effect in the light-grass interaction under cover.

3.4. Floristic composition and diversity of tree communities

3.4.1. Species richness and abundance

The floristic inventory recorded 20 tree species belonging to 20 genera and 17 families across all tree clumps. Mean species richness was significantly higher under clumps (8.2 ± 2.1 species per tree clump) than in external areas (4.3 ± 1.8 species; Student's t-test, $t = 9.84$, $p < 0.001$), confirming the role of tree clumps as tree biodiversity hotspots.

The dominant savanna species were *Piliostigma thonningii* (27.7% of individuals), *Cussonia arborea* (20.9%), *Bridelia ferruginea* (20.6%), and *Crossopteryx febrifuga* (13.3%). Other common woody species were present at lower abundances: *Terminalia schimperiana* (5.9%), *Borassus aethiopum* (4.7%), *Annona senegalensis* (2.6%), *Lannea barteri* (1.9%), *Pterocarpus erinaceus* (1.7%), *Vitex doniana* (0.4%), *Psorospermum febrifugum* (0.2%), and *Zanthoxylum zanthoxyloides* (0.2%) (Figure 7).

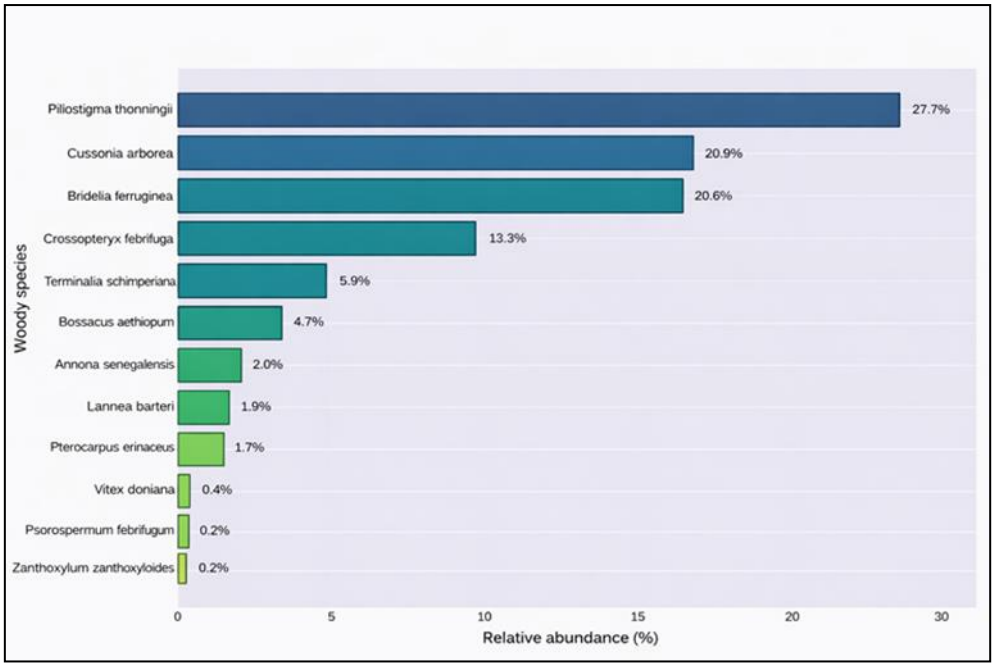

Figure 7 Relative abundance of main tree species in Lamto tree clumps

3.4.2. Recruitment of forest and exotic species

Remarkably, several non-typical savanna species were recorded exclusively under clumps and only at the seedling stage (Table 1): forest species (*Ceiba pentandra*, *Ficus sur*, *Elaeis guineensis*, *Phoenix reclinata*) and exotic species (*Azadirachta indica*, *Psidium guajava*, *Cassia* sp). Furthermore, the invasive exotic species *Chromolaena odorata* was observed as rootstocks in 58% of tree clumps, confirming the function of these structures as preferential establishment sites for non-native species.

Table 1 Forest and exotic species recorded exclusively under tree clumps at the seedling stage

Species	Family	Type	Status
Ceiba pentandra	Malvaceae	Tree	Forest
Elaeis guineensis	Arecaceae	Palm	Forest
Ficus sur	Moraceae	Tree	Forest
Phoenix reclinata	Arecaceae	Palm	Forest
Azadirachta indica	Meliaceae	Tree	Exotic
Psidium guajava	Myrtaceae	Shrub	Exotic
Cassia sp.	Fabaceae	Shrub	Exotic
Chromolaena odorata	Asteraceae	Herbaceous	Invasive exotic

3.5. Health status of dominant trees

3.5.1. Crown condition

Analysis of crown condition revealed significant differences between zones for two dominant species (Table 2). For *Bridelia ferruginea*, the proportion of individuals with crowns in good condition was significantly higher under tree clumps (69.2%) than in external areas (30.1%) (Fisher's exact test, $p < 0.001$, odds ratio = 0.25), indicating strong protection against fire-induced damage. For *Piliostigma thonningii*, the trend was similar but less pronounced, with 87.1% of individuals in good condition under clumps compared to 74.5% outside clumps (Fisher's exact test, $p = 0.007$, odds ratio = 0.45).

In contrast, for *Crossopteryx febrifuga*, *Terminalia schimperiana*, and *Cussonia arborea*, no significant differences were observed between the two zones ($p > 0.05$), suggesting higher intrinsic fire tolerance of these species or lower crown sensitivity.

Table 2 Comparison of crown condition of dominant tree species between under-clump and around-clump areas

Species	Under clump (%)	Around clump (%)	p-value	Odds ratio
Bridelia ferruginea	69.2	30.1	< 0.001	0.25
Piliostigma thonningii	87.1	74.5	0.007	0.45
Crossopteryx febrifuga	78.3	75.6	0.68	-
Cussonia arborea	82.5	80.1	0.72	-
Terminalia schimperiana	76.9	74.3	0.81	-

3.5.2. Trunk condition

Analysis of trunk condition showed contrasting results according to species (Table 3). For *Bridelia ferruginea*, the proportion of undamaged trunks (intact bark) was significantly higher under tree clumps (63.2%) than in external areas (27.2%) (Fisher's exact test, $p < 0.001$, odds ratio = 0.25), confirming the particular vulnerability of this species to fire. For the other dominant species (*Crossopteryx febrifuga*, *Cussonia arborea*, *Piliostigma thonningii*, *Terminalia schimperiana*), no significant differences were observed between zones ($p > 0.05$), these species generally having well-protected trunks (thick bark) or being less sensitive to direct fire damage.

Table 3 Comparison of trunk condition (intact bark) of dominant tree species between under-clump and around-clump areas

Species	Under clump (%)	Around clump (%)	p-value	Odds ratio
Bridelia ferruginea	63.2	27.2	< 0.001	0.25
Piliostigma thonningii	91.4	89.7	0.63	-
Crossopteryx febrifuga	88.6	87.1	0.79	-
Cussonia arborea	85.3	84.8	0.92	-
Terminalia schimperiana	79.8	78.4	0.88	-

4. Discussion

4.1. Tree clumps as modulators of fire regime: umbrella effect and reduction of fuel load

Our results clearly demonstrate that tree clumps significantly modify local combustibility conditions and fire intensity. The 41% reduction in herbaceous biomass and 35% reduction in grass height under tree clumps, compared to external areas, is consistent with previous work conducted at Lamto [25] and in other African savannas [26]. This decrease in the herbaceous layer is mainly explained by shading induced by the tree clump canopy, which limits photosynthesis and grass development [27].

The positive relationship we highlighted between herbaceous biomass and flame height ($R^2 = 0.15$, $p = 0.005$) confirms that fuel reduction under tree clumps directly leads to a decrease in fire intensity. Flame height, reduced by 22% under tree clumps (160 cm versus 205 cm), is a reliable indicator of fire intensity, widely used in the literature [28; 29]. This attenuation of fire intensity under tree clumps has major implications for vegetation dynamics, as it increases the survival probability of young trees and promotes their recruitment, a central mechanism in spatial models of savanna dynamics [7].

The absence of a significant difference in litter biomass between internal and external areas, despite a trend toward slightly greater accumulation under tree clumps, corroborates the observations of [8]. This similarity is explained by

different sources: litter under tree clumps comes from both trees (leaves, branches) and residual grasses, while in external areas, it is almost exclusively of herbaceous origin.

4.2. Role of canopy openness in regulating the herbaceous layer

Mean canopy openness (39.85 ± 5.82%) indicates that Lamto tree clumps do not form a continuous and closed canopy, but rather a light-permeable structure. The significant relationship between canopy openness and herbaceous layer characteristics (height, biomass) when the latter is well-developed suggests a threshold effect in the light-grass interaction. This result is consistent with the work of [27], who showed a linear relationship between herbaceous biomass and canopy openness measured by hemispherical photographs. The disappearance of this relationship when grass is sparse (< 30 cm) indicates that beyond a certain shading level, other factors (root competition, litter quality) become predominant in limiting herbaceous development.

4.3. Tree clumps as refuges for tree biodiversity and drivers of forest dynamics

The significantly higher species richness under tree clumps (8.2 species versus 4.3 in external areas) confirms their role as biodiversity hotspots within the savanna matrix. This observation is consistent with the work of [30] and [31] who described the floristic composition of the Lamto savanna.

4.3.1. Recruitment of forest and exotic species

The exclusive presence under clumps of forest species (*Ceiba pentandra*, *Elaeis guineensis*, *Ficus sur*, *Phoenix reclinata*) and exotic species (*Azadirachta indica*, *Psidium guajava*, *Cassia* sp.) at the seedling stage constitutes a major result of this study. These species, not adapted to fire, find in clumps a micro-habitat refuge where fire intensity is reduced, allowing their temporary establishment. [32] had already observed these species in experimental plots near the Lamto camp, but our study demonstrates that their establishment is strictly limited to the fire-protected zones that tree clumps constitute.

The presence of *Chromolaena odorata*, an invasive exotic species, in 58% of tree clumps raises important questions about the vulnerability of these ecosystems to biological invasions. This species, known for its ability to colonize disturbed environments and modify fire regimes [33], could benefit from the protection offered by tree clumps to establish and potentially spread, constituting a threat to savanna integrity.

4.3.2. Distribution of dominant tree species

The dominance of *Piliostigma thonningii*, *Cussonia arborea*, *Bridelia ferruginea*, and *Crossopteryx febrifuga* in tree clumps reflects their adaptation to fire-prone savanna conditions, as described by [30]. The presence of woodland species (*Terminalia schimperiana*, *Lannea barteri*, *Pterocarpus erinaceus*, *Zanthoxylum zanthoxyloïdes*) and wetland species (*Ficus sur*) under clumps confirms the role of these structures as ecological diversification islands.

4.4. Differential protection of tree species against fire

4.4.1. Vulnerability of Bridelia ferruginea

The most striking observation concerns *Bridelia ferruginea*, which shows a dramatic improvement in its health status under tree clumps: the proportion of individuals with crowns in good condition increases from 30% in external areas to 69% under cover, and that of undamaged trunks from 27% to 63%. This species appears to be particularly sensitive to fire and thus fully benefits from the protective effect of tree clumps. [8] suggested that fire protection in tree clumps, a mechanism reinforcing aggregation for sensitive species, also applies to resistant species. Our results confirm this hypothesis and identify *B. ferruginea* as a species whose population dynamics are strongly dependent on the presence of micro-refuges.

4.4.2. Relative resistance of Piliostigma thonningii and other species

For *Piliostigma thonningii*, the improvement in crown condition under tree clumps (87% vs. 75%) is significant but less marked, suggesting higher fire tolerance. This species, known for its thick bark and ability to resprout after fire [34], appears less dependent on refuges for its survival.

The absence of significant differences for *Crossopteryx febrifuga*, *Cussonia arborea*, and *Terminalia schimperiana* indicates that these species possess fire resistance traits (protective bark, architecture, resprouting capacity) that allow them to maintain good health status even in external areas. These results are consistent with the work of [35] on differential resistance of woody species to fire.

4.5. Modification of the herbaceous community under clump influence

The transition from an herbaceous community dominated by *Hyparrhenia* sp. in external areas (88%) to a mosaic including *Imperata cylindrica* and mixtures under tree clumps reflects a profound change in ecological conditions. *Hyparrhenia* sp., a pyrophilic species adapted to full light conditions, is disadvantaged by shading under tree clumps [20]. Conversely, *Imperata cylindrica*, with its deep rhizome system, would be more competitive for water and nutrient acquisition in a shaded and potentially drier environment under cover [36].

This replacement dynamic could have long-term consequences for the fire regime: *I. cylindrica* being generally considered less flammable than *Hyparrhenia* sp. [37], its expansion under tree clumps could reinforce the fire protection effect and accelerate the transition toward denser formations.

4.6. Implications for savanna-forest dynamics and ecosystem resilience

Our results provide new insights for understanding transition mechanisms between savanna and forest in West Africa. They confirm the role of tree clumps as resilience nuclei and potential anchor points for savanna dynamics, consistent with recent theoretical models [3,13].

By attenuating fire intensity, tree clumps create favorable conditions for (i) The survival and recruitment of sensitive species (*B. ferruginea*); (ii) The establishment of forest species not adapted to fire; (iii) The modification of the herbaceous community toward a less flammable facies.

These processes could, in the long -term, lead to tree clump coalescence and progressive forest expansion, as observed in other African contexts [38,11]. However, the presence of invasive exotic species in these refuges tempers this perspective and underscores the need for ecological monitoring.

5. Conclusion

This study demonstrates that tree clumps play a key functional role in the dynamics of the Lamto humid savanna submitted to annual fires. By significantly reducing the biomass and height of the herbaceous layer under their cover, these structures locally attenuate fire intensity, as evidenced by the 22% reduction in flame height. This umbrella effect creates distinct micro-environmental conditions that profoundly modify vegetation: the herbaceous community shifts from dominance by pyrophilic species toward a mosaic including less flammable species; woody diversity is twice as high under tree clumps, with a dramatic improvement in the health status of sensitive species; above all, the exclusive presence of forest and exotic species seedlings reveals the function of these tree clumps as "nurseries" for species not adapted to fire. These observations support the hypothesis that savannas and forests constitute alternative stable states, whose transition is mediated by structures such as tree clumps which, by attenuating fire, create recruitment windows for woody species and potentially accelerate the coalescence of wooded islands toward forest formation. However, the presence of invasive exotic species in a significant proportion of tree clumps tempers this perspective and underscores the need for research on the impact of these invasions on successional dynamics. From an applied perspective, the preservation of these key structures appears crucial for maintaining the biodiversity and resilience of West African savannas in the face of global change, as these tree clumps act as fire refuges and potential nuclei for forest dynamics.

Compliance with ethical standards

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Disclosure of conflict of interest

The authors declare no conflicts of interest.

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