



Structure, long-term dynamics, and demography of the tree community

Jacques Gignoux, Sébastien Barot, Jean-Claude Menaut, Roger Vuattoux

► To cite this version:

Jacques Gignoux, Sébastien Barot, Jean-Claude Menaut, Roger Vuattoux. Structure, long-term dynamics, and demography of the tree community. Luc Abbadie, Jacques Gignoux, Xavier Le Roux, Michel Lepage. 2007, Ecological studies 179. bioemco-00136592

HAL Id: bioemco-00136592

<https://hal-bioemco.ccsd.cnrs.fr/bioemco-00136592>

Submitted on 14 Mar 2007

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Structure, Long-Term Dynamics, and Demography of the Tree Community

Jacques Gignoux, Sébastien Barot, Jean-Claude Menaut, and Roger Vuattoux

18.1 Introduction

In this chapter, we study the population and community dynamics of the major tree species of the most common savanna type in Lamto, the *Andropogoneae* shrub savanna (see Sect. 5.2). The most frequent tree species are: *Borassus aethiopum*, *Bridelia ferruginea*, *Crossopteryx febrifuga*, *Cussonia arborea* and *Piliostigma thonningii*. Of these, only the palm tree *Borassus* can be considered as a true tree species since it can reach 20 m in height; the other species are smaller and never grow over 10-12 m. These five species will be the main subject of our study since they comprise 90% of tree individuals. Another species, *Annona senegalensis*, is very common in *Andropogoneae* savannas, and although it can develop a real (small) tree morphology, it never grows over 3 m in burned savannas. Other less frequent, true tree (up to 15-20 m in height) species will sometimes be examined in this chapter: *Terminalia shimperiana*, *Zanthoxylum zanthoxyloides*, *Lannea barteri*, *Vitex doniana*, *Pterocarpus erinaceus* and *Ficus sur*. These species are usually rare in the savanna, but can be locally abundant in fire-protected sites like rocks and dense tree clumps: *Terminalia shimperiana* often dominates savanna woodlands.

Tree dynamics is driven by competition for resources and fire. As fire intensity varies considerably in space (Sect. 4.5), as nutrient availability is low in the savanna except in some rich patches (Sect. 4.3), and as the seed dispersal distances of trees are small ([12]; Gignoux, unpublished data), the population dynamics of trees is linked to the spatial structure of the ecosystem. For these reasons, we examine in this chapter tree population dynamics in relation to population spatial structure.

18.2 Factors influencing tree population dynamics

18.2.1 Competition for resources

Despite the high rainfall and the leafless state of trees during the dry season in Lamto [50], water stress can occur for tree species with a shallow rooting



Fig. 18.1. Typical *Loudetia simplex* grass savanna (top) and Andropogoneae tree savanna (bottom). Notice the presence of trees only on small mounds and on the rocky outcrop in the *Loudetia* savanna, and the presence of trees scattered everywhere in the Andropogoneae savanna (photographs by S. Barot and J. Gignoux).

depth, e.g., *Crossopteryx febrifuga*, during the dry season [48]. Konaté et al. [47] measured a slower leaf fall for *Crossopteryx febrifuga* trees growing on termite mounds, which are spots of higher shallow water availability, than for trees growing in the open; this difference was absent for a deep rooted species like *Cussonia arborea*. On the contrary, water affects community dynamics when it is too abundant, e.g., in the hydromorphic soils of flat areas dominated by the grass *Loudetia simplex* (Sect. 5.2). In these areas, tree survival seems impossible except on mounds located above the water table (Fig. 18.1). However, there is evidence that water stress in these areas is even stronger than in the Andropogoneae savannas.

The soils of Lamto are characterized by a very low average nutrient availability ([26] and Sect. 4.3), but are locally nutrient rich at different

scales: termite comb chambers and grass rhizospheres concentrate nitrogen ([2, 1] and Sect. 15.6). Termite activity is concentrated in mounds of various size, visible in the landscape. Termite mounds usually have a random or regular spatial pattern [11]. Trees are spatially associated to termite mounds [11] and are more numerous on mounds than in the open [1]. Apparently, the soil of termite mounds, more nutrient-rich and with a higher water storage capacity, is able to support higher tree density than the surrounding savanna. Tree clumps, even without mounds, are also more nutrient-rich than the surrounding savanna ([55] and Sect. 8.2).

Finally, competition for light is probably important, at least in dense tree clumps. As trees of the same species may be clumped or individually scattered (Fig. 18.1), trees of the same developmental stage can experience very different light conditions.

The major characteristic of resources in Lamto is the heterogeneity of their spatial distribution: whereas no resource seems to be the main driver of the whole ecosystem, the three resources described here influence competition between trees, at least at some places or during some periods of the year. As a consequence, we expect population and community dynamics to be intimately linked to the spatial structure of the ecosystem. Tree demographic parameters (survival rates, growth rates, fecundity, etc.) should be different for trees growing on a mound, in a tree clump, or in the open.

18.2.2 Fire and the definition of demographic stages

Fire prevents tree invasion, as 40 years of protection from burning have demonstrated in Lamto [72, 73, 27]. This led to the conclusion that fire was the major factor explaining the existence of Lamto savannas in climatic conditions where rainforests could survive [54].

Other arguments support the idea that fire is a major driving force of tree communities in Lamto: the dominant savanna tree species all show a very high resistance to fire, based on a high resprouting ability for dicotyledon trees [39] and on a very good bud protection for *Borassus* palm trees [71].

Like forest trees, adult savanna trees can resist fire through adaptations like a thick bark [42, 61] and a high resprouting ability from belowground organs. But the regularity of savanna fire, the low flame height, and the short time of exposure to flame (Sect. 4.5) give adult trees other possibilities of resistance: leaf fall occurring during the dry season minimizes the chance of a crown fire; once a tree overgrows the grass stratum, most of its buds are located above flame height [32]. There is evidence that low intensity fires kill smaller stems, but not taller ones in fire-tolerant species [57]. Before young trees can reach the safe zone above the grass layer, they have to survive within the fuel bed where fire intensity is highest [24]. Therefore, fire objectively defines a recruitment stage, where a tree acquires a perennial, fire-resistant trunk instead of producing resprouts each year from belowground organs, like a grass tuft. Based on average flame height, Menaut and César [52] considered

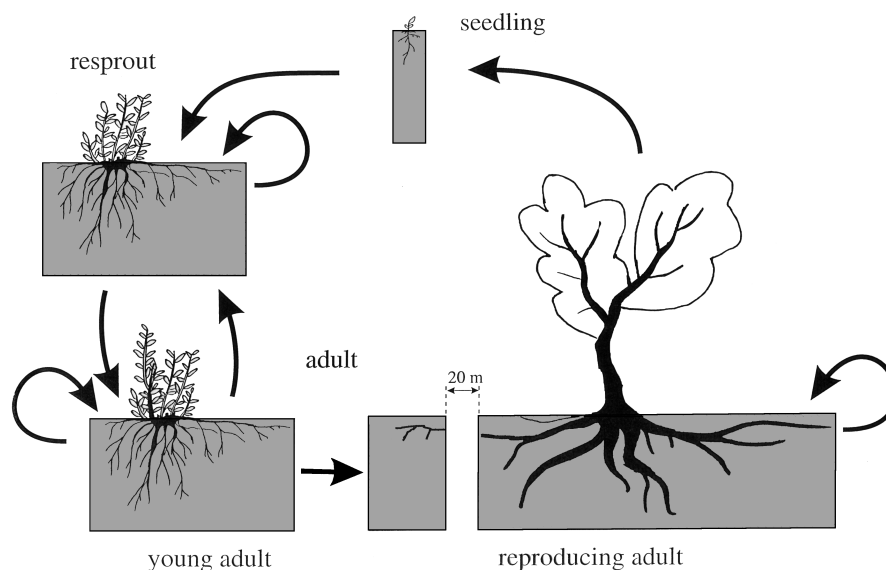


Fig. 18.2. Definition of demographic stages based on morphological traits (fire scars). Perennial parts of the trees are in black and annual parts are in white. Seedlings are identified by the presence of cotyledons or their small size together with the absence of record at their location at the previous census. Resprouts have a perennial belowground system and an annual aboveground systems, i.e., all stems or their tallest stem bear no fire scars. Adults (either young or reproducing) have a perennial aboveground system, i.e., their tallest stem bears fire scars.

a 2 m tall limit for defining the young and adult stages. Through a detailed study of fire resistance in *Crossopteryx febrifuga* and *Piliostigma thonningii*, Gignoux et al. [39] demonstrated that this limit actually varied among species: *Crossopteryx* can recruit as soon as it reaches 25 cm and will almost certainly build a trunk when taller than 65 cm, while *Piliostigma* cannot recruit before 100 cm and will almost certainly recruit when 225 cm tall.

It is possible to see on all individual trees (except palms) the scars left by fire (Fig. 18.2). This was used as a basis for classifying trees in meaningful demographic stages, since tree age cannot be assessed simply by ring counting (growth rings are irregular (unpublished data by Menaut)). Unburned stems can be distinguished from burned ones, since burned stems always have their killed top remaining during most of the wet season. This enables one to classify trees as adults when they have a perennial trunk (2 years old) or as resprouts when they only have annual stems; intermediate cases exist when both annual and older stems are present: they have been classified as resprouts or adults according to whether their tallest stem was an annual stem or an older stem.

Cussonia has a particular architecture (Leeuwenbergs model [43]) and does not branch before it reaches 2-3 m in height; but the leaf scars are visible on the stems and tend to be closer to each other at the end of the growing season, so that it is possible to count the number of growing seasons on young (1-5 years) stems and apply the same stage classification as for the other species.

18.3 Spatial patterns of tree species

Spatial pattern analysis relies on the hypothesis that it is possible to infer some conclusion about the processes leading to the observed patterns simply by analyzing these patterns [49]. Problems arise from the fact that it is usually difficult to find a single cause for a pattern: many processes can often explain the same pattern. However, Barot [11] argues that with a carefully chosen set of hypotheses and appropriate data, it is possible to draw some conclusions on the underlying processes (or at least to screen out processes) from the observed patterns. As for the grass population patterns (Sect. 17.2), we analyzed the spatial pattern of trees using Diggle's and Ripley's methods [29, 66] with a software developed by Gignoux [38]. Our set of hypotheses to interpret spatial patterns is as follows:

- Competition leads to regularity within a population and to spatial inhibition between populations [62, 3, 60].
- Plants should be aggregated and associated to nutrient-rich patches if they are nutrient-limited [58, 15].
- Different stages within a population have different requirements and can have different spatial patterns.
- Low dispersal distance generates aggregated patterns [45, 6].
- Due to lower fuel (grass phytomass) loads in tree clumps, fire sensitive species should tend to have a clumped pattern [53, 67].

The spatial data set comprises 7 plots of increasing tree density where all plants were mapped (Table 18.1). Other data sets (transects by Bonvallot et al. [17] where all trees, soil depths, and an indication of the grass cover, were mapped) were not included in this analysis because of the conspicuous gradient in tree density linked to topographic position observed. We expect fire intensity to be lower on the highest density plots, and competition for light and nutrients to increase with tree density.

18.3.1 Spatial distribution of tree species

The patterns presented here have been inferred from works by Gignoux et al. [37, 40] on *Crossopteryx febrifuga*, *Piliostigma thonningii*, *Cussonia arborea*, and *Bridelia ferruginea*, on a detailed study of *Borassus aethiopum* populations [11], and on original results (Tables 18.2 and 18.3).

Table 18.1. Savanna plots used for spatial pattern analysis and demographic studies: “Tree demography” plots were set up in May 1969 and were censused in 1970, 1973, 1975, 1989, May 1991, Dec. 1991, May 1992, Dec. 1992, May 1993, Dec. 1993, 1994 and 1995. All trees > 2 m in height were mapped, tagged, and measured over the 1969 to 1989 period; all smaller individuals were added in the following censuses. “Spatial pattern” studies: All trees > 1 m were mapped on plots PL-PP; Only *Borassus* palms were mapped on plot PM. “Long term dynamics” plots: All trees (incl. seedlings) were counted every 3 years from 1965. Fire regimes: unb., unburned; l.f., late fires; exc., except.

Study	Year	Plot	Name/ location	Type	Fire treatment	Size (m)	Surface (ha)
Tree (Menaut, Dauget, Gignoux, Lahoreau)	1969	A	Plateau	AS	yearly	50 × 50	0.25
	to	C	Savane Gruyère	AS	unb. 64-69	50 × 50	0.25
	2003	G	Virage glissant	AS	yearly	50 × 50	0.25
		H	Maison du garde	SW	yearly	50 × 50	0.25
		I	Seaux à Barbault	AS	yearly	50 × 50	0.25
Spatial pattern (Barot)	1994	PL/TS3	Plateau	AS	yearly	150 × 140	3.50
		BA	Barrière	SW	yearly	150 × 150	2.25
		PP/GS2	Pont de Paris	LS	yearly	200 × 250	5.00
Demography of <i>Borassus</i> (Barot)	1995	GS1	Savane du Rocher	LS	yearly	150 × 250	3.75
	to	PP/GS2			as above		
	1999	TS1	Savane du Rocher	AS	yearly	200 × 200	4.00
		TS2	Piste du Sud	AS	yearly	128 × 250	3.20
		PL/TS3			as above		
Long-term dynamics (Vuattoux)	1965	1	Mare Portères	LS	yearly	50 × 50	0.25
		2	Pont de Paris	AS	l.f. 64-66	50 × 50	0.25
	2002	3	Campement	AS	unb. 62-	50 × 50	0.25
		4	Piste de Zougoussi	AS	unb. 64-65	50 × 50	0.25
		5	Marigot salé	LS	unb. 64-69	50 × 50	0.25
		6	Non brûlé en brûlé	AS	unb. 66-	50 × 50	0.25
					exc. 85, 89	50 × 50	0.25
		7	Terres noires	AS	unb. 62-	50 × 50	0.25
					exc. 67	50 × 50	0.25
		S	Sismographe	SW	yearly	50 × 50	0.25
Tree/grass interactions (Mordelet)	1989	PM	Piste du Sud	AS	yearly	100 × 230	2.30

Results presented here concern plots of Andropogoneae savanna with different tree densities. Plots H and BA have a high tree density (savanna woodland) and plot G is a shrub savanna evolving toward a savanna woodland. Except for *Borassus aethiopum*, results concern only >2 m individuals.

The overall spatial pattern of adult trees (all species together) is aggregated on all savanna plots, even in savanna woodlands (plots H and BA). Three groups of species can be distinguished based on the overall spatial pattern of adult trees:

Group 1: Species with a random spatial pattern on all plots, whatever the density of trees: *Crossopteryx febrifuga* and *Borassus aethiopum*. For

Table 18.2. Number of the various mapped items (adult trees, termite mounds, and rocky outcrops) on the spatial pattern analysis plots. Spatial analyses were performed only when sample size was ≥ 9 .

Mapped item	Plot						
	A	C	G	H	I	PL	BA
<i>Annona senegalensis</i>	3	1	1	6	21	5	23
<i>Borassus aethiopum</i>	6	12	3	3	5	25	20
<i>Bridelia ferruginea</i>	7	12	22	39	18	66	534
<i>Crossopteryx febrifuga</i>	17	17	23	13	29	163	124
<i>Cussonia arborea</i>	11	7	14	60	10	113	88
<i>Piliostigma thonningii</i>	2	9	3	90	1	9	129
<i>Pterocarpus erinaceus</i>	0	0	8	1	0	4	20
<i>Terminalia shimperiana</i>	1	1	1	61	2	12	248
All trees	47	59	75	310	88	404	1289
Termite mounds	—	—	—	—	—	48	18

Borassus, this result was confirmed from analysis for another plot of 100×230 m of shrub savanna (mapped in 1990 by P. Mordelet, 1993, and analyzed by Gignoux [37]).

Group 2: Species with an aggregated pattern at high tree density (in savanna woodlands) and a random pattern at low density: *Annona senegalensis*, *Piliostigma thonningii*, *Terminalia shimperiana*.

Group 3: Species with a random or aggregated pattern, without a clear relation between the change in pattern and tree density: *Cussonia arborea*.

Bridelia ferruginea could be classified either in group 1 or 2, since it has a random pattern on almost all plots except the BA plot, where it has an aggregated pattern and reaches its highest density; however, its pattern becomes random in the H plot, where tree density is maximal.

From our hypotheses, very fire-resistant species should have a random pattern, relatively independent from the presence of clumps, because they have no advantage in recruiting in such safe sites. We can therefore classify species of the group 1 (*Crossopteryx* and *Borassus*) as good candidates for being very fire-resistant. Since *Bridelia* also tends to have a random pattern in low tree density, e.g., most fire-prone plots, we can also suspect it of being a very resistant species; its tendency toward aggregation when fire conditions become milder is probably explained by another trait than fire resistance. All the other species would then be more fire-sensitive.

Competition for light is expected to cause an increase in regularity of the patterns from initially aggregated patterns to random and even regular patterns as time goes on. However, none of the species here shows such a change in pattern with increasing density, except maybe *Bridelia* when comparing plots BA and H: it is probable that on plot H, forest species are further in the process of outcompeting savanna species than on BA. *Bridelia* could then be classified as a relatively fire-resistant species sensitive to competition for light.

Table 18.3. Summary of spatial pattern and spatial association test results: For each item, three tests were run (based on Diggle's G and F functions and on Ripley's K function for spatial patterns, and on the $G_{1,2}$, the $G_{2,1}$, and the $K_{1,2}$ functions for spatial associations), and the conclusion of the tests (decision made as in [11]) is shown for each class of mapped items on each plot as: A for aggregation or spatial association; - for random pattern or spatial independence; R for regular pattern or spatial repulsion; empty cell when the tests could not be performed because of a too small sample size.

Mapped item	Plot						
	PL	A	C	G	I	BA	H
Spatial pattern analyses							
All tree species	A					A	
<i>Annona senegalensis</i>					-	A	
<i>Borassus aethiopum</i>	-		A			-	
<i>Bridelia ferruginea</i>	-		-	-	-	A	-
<i>Crossopteryx febrifuga</i>	-	-	-	-	-	-	-
<i>Cussonia arborea</i>	A	-		A	-	A	A
<i>Piliostigma thonningii</i>	-		A			A	A
<i>Pterocarpus erinaceus</i>				-		A	
<i>Terminalia shimperiana</i>	-					A	A
Termite mounds	R					-	
Spatial association analyses							
<i>Annona</i> × <i>Crossopteryx</i>					-	-	
<i>Annona</i> × <i>Borassus</i>						-	
<i>Annona</i> × mounds						-	
<i>Borassus</i> × <i>Crossopteryx</i>	-		A			-	
<i>Borassus</i> × mounds	A					-	
<i>Bridelia</i> × <i>Crossopteryx</i>	A		-	-	A	-	-
<i>Bridelia</i> × <i>Borassus</i>	R		-			-	
<i>Bridelia</i> × mounds	A					-	
<i>Crossopteryx</i> × mounds	A					-	
<i>Cussonia</i> × <i>Crossopteryx</i>	A	A		A	A	-	A
<i>Cussonia</i> × <i>Borassus</i>	A					-	
<i>Cussonia</i> × mounds	A					A	
<i>Piliostigma</i> × <i>Crossopteryx</i>	-		-			-	-
<i>Piliostigma</i> × <i>Borassus</i>	-		R			-	
<i>Piliostigma</i> × mounds	A					A	
<i>Terminalia</i> × <i>Crossopteryx</i>	-					-	A
<i>Terminalia</i> × <i>Borassus</i>	-					-	
<i>Terminalia</i> × mounds	-					-	

For the other species, the aggregated pattern can be the result of grouping within nutrient-rich areas or to fire sensitivity favoring recruitment within tree clumps or to low dispersal distances combined with a relatively constant juvenile mortality. Spatial association analyses help to sort out among these hypotheses.

18.3.2 Association to environment heterogeneities

Spatial association tests [28] were used to distinguish between specific attraction of one species by another and average or symmetric association, i.e., association where no species can be pointed out as dependent from the other.

Nutrient-rich patches

Mounds, that are nutrient-rich patches, were mapped on two plots (PL and BA). Termite mounds have a regular spatial pattern in the low tree density savanna and a random pattern in the savanna woodland. Some tree species are associated to mounds, while others are not:

- *Cussonia* and *Piliostigma* are spatially attracted by mounds on both plots.
- *Bridelia* and *Borassus* are attracted by mounds in the open savanna, but not in the savanna woodland.
- *Terminalia* and *Crossopteryx* are independent from mounds on both plots. On the only plot where the analysis could be done, *Annona* also seems to be independent of mounds.

Since tree clumps and termite mounds are nutrient-rich patches, we can classify *Terminalia*, *Crossopteryx*, and maybe *Annona* as species not strongly nutrient demanding, *Cussonia* and *Piliostigma* as nutrient-demanding species (since they always need to grow close to a mound), and *Bridelia* and *Borassus* as intermediate species, since their need to be close to a mound in the open savanna vanishes when tree density, and, from our hypotheses, average nutrient richness, increase.

Fire-safe sites

We can confirm the supposed high fire resistance of *Crossopteryx febrifuga* and *Borassus aethiopum* by checking whether they constitute kernels of clumps for more sensitive species on the lower density plots (PL to I).

- *Crossopteryx* and *Borassus* are independent from each other, confirming their high fire resistance.
- *Annona*, *Piliostigma*, and *Terminalia* are independent of *Crossopteryx* or *Borassus*, in the plots PL to I where fire intensity is higher because of lower tree densities. This suggests that these species have an aggregated pattern not because of their fire sensitivity, but for some other reason.
- *Cussonia* is systematically associated to *Crossopteryx* and *Borassus*, suggesting that it needs protection from fire to recruit successfully.

Our results at this stage do not enable us to validate the clump formation mechanism proposed by Menaut et al. [53], partly because reality is more complex than model assumptions (i.e., fire is not the only cause of tree aggregation). We would require more detailed analysis based on tree size and grass presence to check whether tree recruitment is favored in grass-free areas.

Dispersal

Crossopteryx and *Terminalia* are anemochorous, *Borassus* and *Piliostigma* are barochorous (with a possible secondary dispersal by animals), and *Bridelia*, *Cussonia*, and *Annona* are apparently zoochorous (Menaut, personal observations). All these dispersal modes should generate clumped patterns of seedlings, but these might evolve later to less aggregated patterns.

The spatial pattern of seedlings and resprouts of *Bridelia*, *Crossopteryx*, *Cussonia*, and *Piliostigma* is aggregated on plots A, C, G, H, and I [37], suggesting very low dispersal distances for all these species. *Borassus* seeds are never dispersed further than 10 m away from the mother tree [12], even though Vuattoux observed in the 1960s secondary dispersal of *Borassus* seeds and transport on mounds or rocks by baboons, now extinct from the area (Vuattoux, personal observation).

The spatial patterns of seedlings is aggregated for all species, as expected for short dispersal distances. However, this initial pattern can be later modified by differential mortality or recruitment rates linked to local environment. In extreme cases like *Borassus*, those processes can lead to a random pattern of adults [11]. We should therefore expect that the pattern of seedlings resulting from seed dispersal shows little relation with the spatial pattern of adults.

18.3.3 Case study: *Borassus aethiopum*

A detailed study of the spatial pattern of *Borassus* has been performed by Barot et al. [11, 8]. This palm tree is dioecious and shows a marked senescence period where fecundity declines [9]. The spatial pattern of 3 different stages (seedlings, juveniles, adults, split into males and females) revealed the following:

- There is a strong competition between seedlings and between juveniles for recruitment; females have a negative (direct or indirect) influence on their own offsprings survival [12]; intraspecific competition increases when tree density increases.
- All classes of *Borassus* palms are nutrient demanding; adults are loosely associated to nutrient-rich patches (mounds and tree clumps) thanks to an efficient root foraging strategy [56], while juveniles and seedlings are closely associated to nutrient-rich patches; association distances decrease with demographic stage, adult females being sometimes independent of patches while most seedlings grow in nutrient-rich patches.
- There is a discrepancy between the spatial pattern and the location of adults and juveniles, which is apparently due to a complex set of interactions between at least four processes: seed dispersal, negative effect of females on juveniles, the need for juveniles to be close to a nutrient-rich patch, and density-dependent mortality of juveniles within a clump of juveniles.

- Male and female palms have different spatial patterns, which can be explained only by a difference in nutrient requirement associated to reproduction costs: from the results, females should have a higher nutrient demand and have developed a more efficient root foraging strategy than males. This results in females being independent of nutrient-rich patches while males are associated to them. The cause of this pattern could be differential survival of sexes or environment-induced sex.

From those results, a spatialized scenario of the life cycle of *Borassus* was proposed [8]: (1) short distance seed dispersal initiates clumps of seedlings around mother palms; (2) the recruitment and survival of seedlings are higher near nutrient-rich patches and far from the mother palm, leading to a weaker aggregation and association to female adults at older stages; (3) when the mother dies, juveniles from the periphery of the clumps have the highest chance to recruit as adults because they suffer less competition than juveniles from the center of the clump; (4) as time goes on, only one adult remains per former clump of juveniles, and the pattern of adults more or less reflects that of clumps (random), with a weak association to nutrient-rich patches thanks to the root foraging ability of adult *Borassus*.

18.3.4 Conclusion: Vital attributes of savanna trees inferred from their spatial patterns

The interpretation of spatial pattern and association analyses is not straightforward because of the inherent ambiguities of our set of assumptions. For example, the aggregated pattern of *Cussonia* and *Piliostigma* at high densities could be due to important nutrient requirements as well as low fire resistance. Their random pattern at low density would tend to indicate a good fire resistance, but the systematic association of *Cussonia* to *Crossopteryx* and *Borassus* would rather indicate sensitivity to fire. A parsimonious interpretation would be to consider *Piliostigma* as more resistant to fire than *Cussonia*, based on the overall set of results and not on a single particular result. Experiments on fire resistance as already performed for two other species [39] would enable one to decide between those two hypotheses.

From the simple analyses of spatial pattern and spatial association presented so far, we can infer major properties (i.e., some vital attributes as defined by Noble and Slatyer [59]) of savanna tree species, as follows:

Competition between adult trees apparently plays only a minor role in the savanna, since thinning is only observed for one species (*Bridelia*) in the highest density savanna woodland plot; all other species either show no change in spatial pattern with increasing tree density, or a change opposite to what the competition hypothesis predicts (more aggregation as density increases).

We can roughly classify tree species on a scale of fire resistance on the basis of their spatial pattern, with *Crossopteryx* and *Borassus* as the most fire resistant, then *Bridelia* as a less resistant species, and *Cussonia*, *Piliostigma*, *Annona*, and *Terminalia* as the most fire-sensitive species. An independent study

of individual tree resistance to fire [39] effectively proved that *Crossopteryx* was much more fire resistant than *Piliostigma*.

We can also classify the major tree species on a scale of nutrient demand, with *Cussonia* and *Piliostigma* being the most nutrient demanding, *Bridelia* and *Borassus* nutrient demanding only in the open savanna, but not in the richer savanna woodland areas, and *Crossopteryx*, *Annona*, and *Terminalia* showing no evidence of nutrient limitation.

These results and the detailed study of *Borassus* illustrate the interest of spatial analyses for the integrated study of an ecosystem like Lamto, which has an obvious structure at all scales. This clearly showed that demography in Lamto savannas is influenced by and influences spatial pattern in a complex way that needs to be taken into account in modeling exercises addressing the question of the stability of the ecosystem.

18.4 Tree population dynamics

Three datasets constitute our main information on tree community dynamics in Lamto (Table 18.1):

Seven plots (labeled 1 to 7 and S) were set up in 1965 by Vuattoux in various savanna facies and under various fire regimes. Trees were counted by species and stage on these plots every 3 years until 1998, so that a detailed demographic analysis is not possible, but the long-term dynamics of the plot is documented.

Five plots (labeled A, C, G, H, I) were set up in 1969 by Menaut and César, where all trees have been mapped, tagged, and measured in 1969, 1970, 1973, 1975, 1989, and yearly since 1991 (twice a year in 1991-1993). These data can be used for the estimation of demographic parameters for adults on the 1969-1989 period, and also for smaller trees (including seedlings) afterward.

Five plots (labeled GS1, PP/GS2, TS1, TS2, PL/TS3, BA) were set up by Barot and S. Konaté and censused yearly between 1995 and 1999 for a detailed study of *Borassus aethiopum* [11].

18.4.1 Long-term dynamics

Comparison of treatments of the long-term dynamics study (Table 18.1 and Fig. 18.3) provides insights on the major forces driving the ecosystem [72, 73, 27]:

1. Under the normal fire regime, the tree community did not seem stable: tree density increased by 20-50% in the “standard” *Andropogoneae* savanna plots (plots A, G, and I), by 600% in the *Louvetia* savanna plot (plot 1), and by 50% in the high density plots (plots S and H). Only these

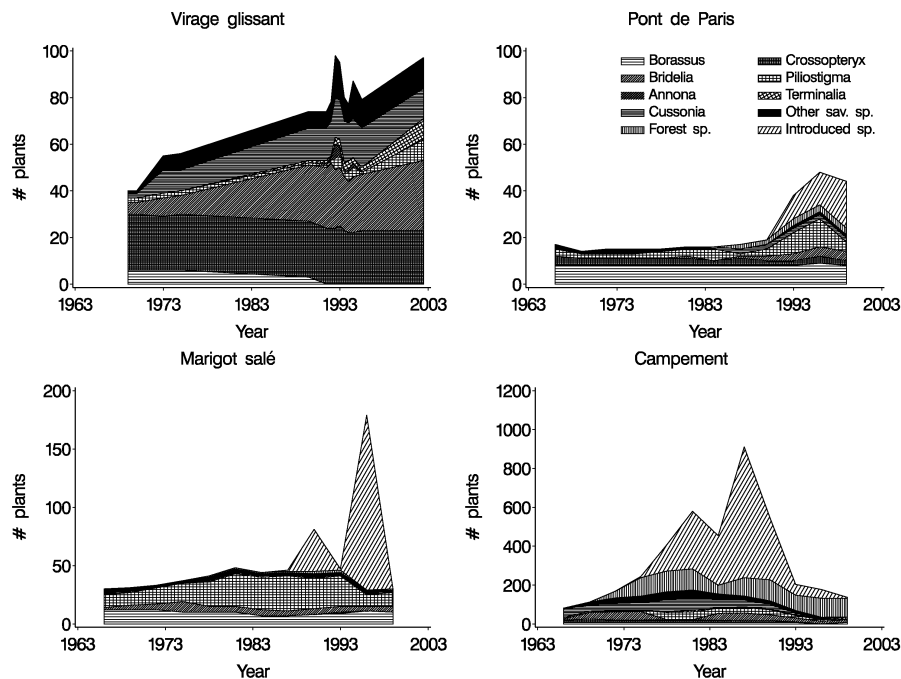


Fig. 18.3. Dynamics of tree numbers on four 0.25 ha plots (Table 18.1). Fire treatments: plot “Virage glissant,” annually burned; plot “Pont de Paris,” 3 years of late fires (1964-66); plot “Marigot salé,” protected from fire during 4 years (1964-65, 1968-69); plot “Campement,” protected from fire over 40 years (after [72, 73, 27] and unpublished data by R. Vuattoux).

latter plots were invaded by other species: fire-sensitive savanna species like *Terminalia shimperiana* and *Ficus sur*, the invading weed *Chromolaena odorata* [35], and forest species [25]. In the other plots, increase in density was mainly due to *Piliostigma thonningii*, *Cussonia arborea*, *Annona senegalensis*, and *Bridelia ferruginea*.

2. In savannas unburned for a few years (C, 4, and 5), the same conclusions hold. On plot 5, the increase in *Piliostigma* can be linked to fire protection. The later decrease of the population indicates a relatively short life span (< 30 years) for this species under the normal fire regime, since numbers are now equal to their initial values in 1965.
3. In the 3-year late burned plot (plot 2), there was a decrease in tree density just after the treatment for all species except *Borassus aethiopum* and *Crossopteryx febrifuga*; *Piliostigma thonningii* started to recover after 10-15 years; *Bridelia ferruginea* and *Cussonia arborea*, absent from the plot in 1965, started to invade it roughly at the same period. The time lag

between the end of the late fire treatment and the recruitment of new adults gives a duration of the juvenile/resprout stage of 10-15 years for the main savanna species.

4. Unburned savannas (Plots 3, 6, 7) had a qualitatively identical evolution, with slight quantitative differences. A succession started with fire protection, where savanna species already present first invaded the plot, *Bridelia ferruginea* and *Ficus sur* being the fastest invaders, followed by *Cussonia arborea* and *Piliostigma thonningii*; other more fire-sensitive savanna species like *Terminalia shimperiana* then took the advantage, followed by species growing in humid areas, forest-savanna edge species, and true forest species starting to invade 6-12 years after fire protection. After 15 years, *Borassus aethiopum* and *Crossopteryx febrifuga* (which both showed very little response to fire protection) started to decline. This overall pattern was disturbed by the introduced weed *Chromolaena odorata*, which apparently slowed down the invasion by forest species [35]. The timescale of this succession also depended on the distance of the plot to the source of forest species seeds (gallery forests). Accidental fires had little effect on the succession once started, whereas major droughts seemed to be important.

These long-term data enable one to infer savanna species habits compatible with that of the analysis of their spatial patterns: *Crossopteryx* and *Borassus* appear as the most fire-resistant species, able to grow in any type of savanna under any fire regime (including late fires), and decrease in density only when tree density increases (in savanna woodlands or unburned savanna). The other major savanna species (*Annona*, *Bridelia*, *Cussonia*, and *Piliostigma*) are able to increase in density even in the normal fire regime although they seem to have much more fluctuating numbers. They quickly take advantage of any reduction of fire severity or frequency, but they decrease under a late fire regime. Other rarer savanna species like *Terminalia shimperiana*, *Pterocarpus erinaceus*, and *Ficus sur* only invade when fire is excluded, either temporally or spatially. These patterns are consistent with the vital attributes inferred from the spatial pattern analyses.

The behavior of the main savanna species is also consistent with the predictions of Gignoux et al. [39]: (1) there should be a trade-off between competitive ability for resources and fire resistance and (2) fire-sensitive trees should recruit either in clumps or in cohorts. Indeed, the most fire-resistant *Crossopteryx* and *Borassus* never increase in numbers when fire is excluded, while the more fire-sensitive *Annona*, *Bridelia*, *Piliostigma*, and *Cussonia* all respond to fire protection by increasing in numbers; they are later excluded by the even more fire-sensitive savanna and forest species. This strongly supports the existence of a trade-off between individual growth rate (competitive ability) and fire resistance. Furthermore, *Annona*, *Bridelia*, *Piliostigma*, and *Cussonia* densities fluctuate under the normal yearly fire regime, while

Borassus and *Crossopteryx* are much more stable. These fluctuations can be interpreted as cohort recruitment events linked to less intense fires, as suggested in hypothesis 2.

Although there is no difference in the increase in tree density between Andropogoneae savannas and savanna woodlands under a normal fire regime (all plots except plot I increase by ca. 50% over 25 years), there is an important qualitative difference: fire-sensitive species (first *Terminalia shimperiana* and *Ficus sur*, then edge and forest species) appear in the densest parts of the plots, apparently initiating a succession like that observed in the unburned savanna plots. The mechanism explaining this evolution in dense plots is probably that hypothesized by Gignoux [36] and Menaut et al. [53]: when tree density locally increases, some dense tree clumps may appear at random (due to the initial pattern of the tree community); once a clump is established, it becomes a fire safe site where the recruitment of fire-sensitive species is possible. This idea seems confirmed by the comparison of plots G and I. These plots had different densities in 1969 (156 ha⁻¹ trees for G and 300 for I). Plot I remained a typical open savanna, with a slight increase in density over 25 years (352 ha⁻¹ trees in 1992), while plot G seems to evolve toward a savanna woodland, with the invasion of *Pterocarpus erinaceus* and *Terminalia shimperiana*, fire-sensitive savanna species. This difference can be explained only by the fortuitous coalescence of 2-3 smaller clumps on plot G, a random event that did not happen on plot I although the initial spatial patterns was quite similar (Fig. 18.4).

Gautier [34] estimated from the comparison of aerial photographs taken in 1962 and 1989 that the density of savanna trees had doubled in Lamto over this period. Possible explanations are (1) a change in the rainfall regime (a deficit in rainfall has been observed over the same period (Sect. 3.5)) or (2) a change in the fire regime due to the imposed date of fires at the heart of the dry season since the set up of the Lamto reserve in 1962. Hypothesis 1 would mean that the Guinea savannas are more sensitive to the water balance than expected given their high rainfall and average water availability, and that tree density increases when rainfall decreases. Hypothesis 2 would mean that Guinea savannas need some variations in the date of fires to be stable: trees normally invade the savanna, but are prevented from doing so by occasional late fires which, although usually less intense than mid-season fires, are more harmful to adult trees because of their phenological stage. Hypothesis 2 seems confirmed by the results of the plot 2. It also has the advantage of explaining the overall increase in density observed in the region of Lamto (not only in the reserve): the increase in human population is expected to reduce the occurrence of late fires. Since people tend to light fires for safety reasons (Sect. 4.5) early in the dry season, the probability that areas remain unburned until the end of the dry season decreases with human density.

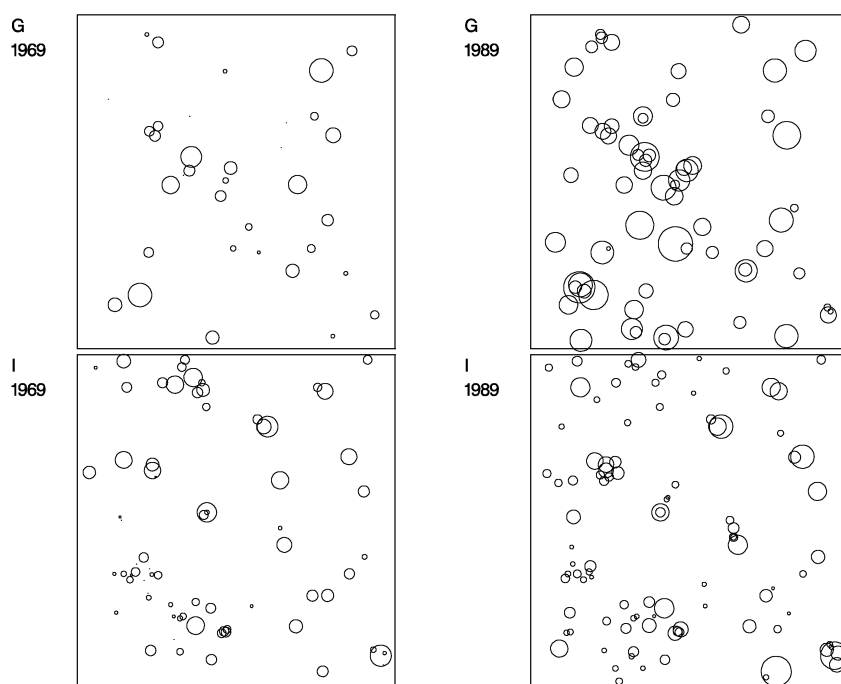


Fig. 18.4. Maps of two savanna plots censused in 1969 and 1989. Plots are 50×50 m. Circle surface equal to tree crown surface. Only >2 m high trees have been mapped (J.M. Dauget and J.C. Menaut, unpublished data).

18.4.2 Size structure of tree populations

Main tree species

The best measure of tree size in Lamto savannas is probably basal circumference for adult trees, since trunks are rarely straight and branch at a low height. The four main species (*Bridelia*, *Crossopteryx*, *Cussonia*, *Piliostigma*; Fig. 18.5) have very different population structures. *Bridelia* has a classical population structure, with many small individuals and few large ones. *Piliostigma* and *Cussonia* have similar structures, but the structure is not identical at all on most plots: the mode of the distribution moves toward higher classes across time on plot H (where the invasion by other species is important), but also on plots A, G, and I for *Cussonia*. This is consistent with the results of the previous section, suggesting that for the species *Cussonia*, *Piliostigma*, and *Bridelia*, recruitment is linked to temporal variations in fire severity and produces cohorts of relatively even-sized individuals. *Crossopteryx* population has a particular structure with very flat histograms with almost the same numbers of individuals in all classes. Since only >2 m individuals were considered to draw the histograms, this simply means that

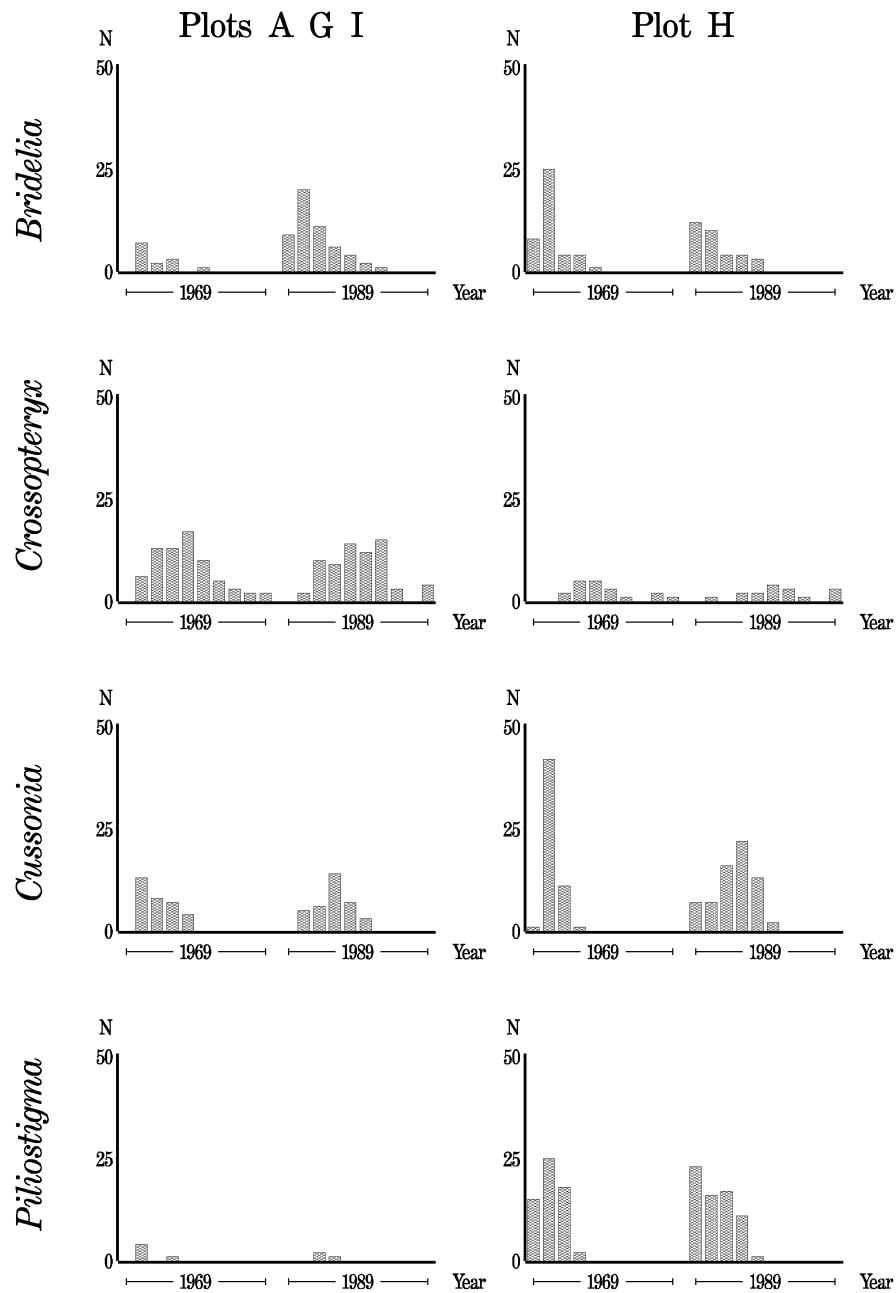


Fig. 18.5. Histograms of basal circumference for the four main species (*Bridelia*, *Crossopteryx*, *Cussonia*, and *Piliostigma*) over the 1969-1989 period on plots A, G, H, and I. Circumference in classes of 20 cm from 0-20 to 180-200 cm; frequency in numbers (J.C. Menaut and J.M. Dauget, unpublished data).

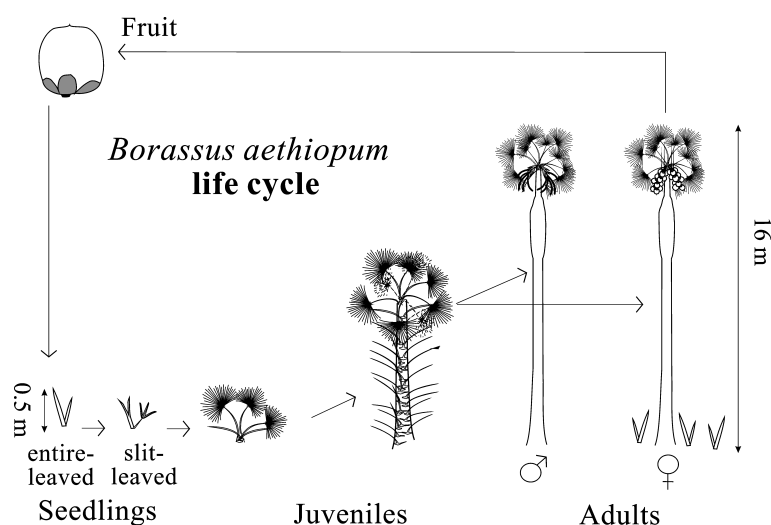


Fig. 18.6. Schematic diagram of *Borassus aethiopum* life cycle.

recruitment to the adult stage occurs long before 2 m for *Crossopteryx* (i.e., only the tail of the distribution is observed) and around 2 m for the other species. This again is fully compatible with the spatial pattern analyses of the previous section and the analysis of fire resistance of Gignoux et al. [39].

Case study: The population structure of *Borassus aethiopum*

Barot [9] defined four stages for *Borassus*: Entire-Leaved seedlings (EL-seedlings), Slit-Leaved seedlings (SL-seedlings), juveniles, and adults (Fig. 18.6). Germination is remote-tubular [71] so that seedlings are buried about 40 cm deep in the soil by the cotyledonary axis that extends downward. In both seedling stages and in the younger juveniles, the terminal bud is far below ground level: this defines the establishment phase. EL-seedlings have one or two elongated entire leaves. SL-seedlings have one or two leaves that are slitted a few times. Juveniles and adults have the same fan-shaped, induplicate and costapalmate leaves. Petioles of dead leaves remain on juveniles stems. In a few years, these petioles fall down, a swelling appears on the stem, and sexual maturity is reached.

Most seedlings die before reaching the adult stage (Fig. 18.7), as in most tree species [44]. The distribution of juveniles and adults classified according to their height is strongly bimodal (Fig. 18.8): there are very few juveniles in the 2–8 m height class. This could be due to (1) temporal variations of survival and recruitment rates (the population would be far from the stable stage distribution, and some decades ago, juveniles could have suffered from an exceptionally sharp mortality event due to some disturbance) or (2) size-dependent growth rate of juveniles (if juveniles of the intermediate height

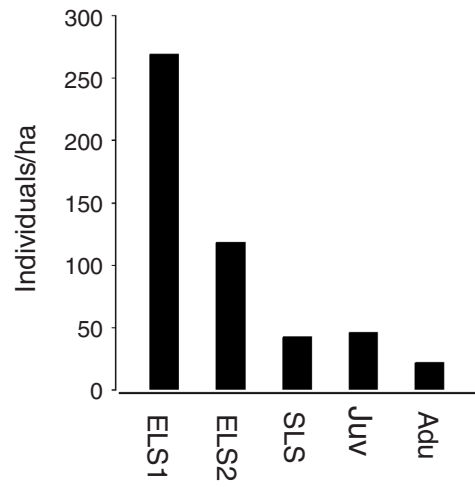


Fig. 18.7. Palm density by stage (EL S1, one leaf Entire Leaved Seedling; EL S2, two leaves Entire Leaved Seedling; SLS, Slitted Leaved Seedling; Juv, Juvenile; Adu, Adult). Individuals of 4 plots (17.5 ha all together) were pooled together (S. Barot, unpublished data).

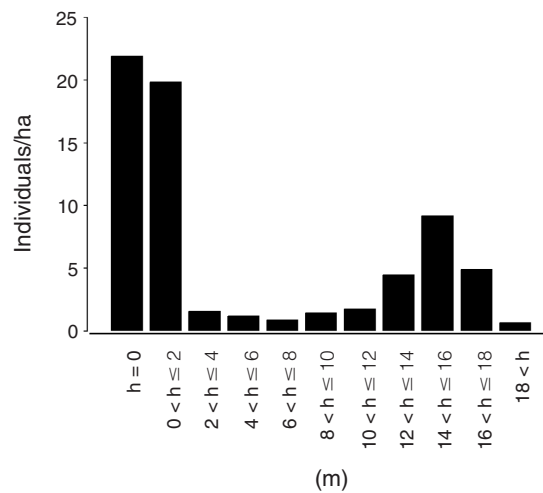


Fig. 18.8. Adult and juvenile palm density by height class. Individuals of 4 plots (17.5 ha all together) were pooled together (S. Barot, unpublished data).

classes grow faster than smaller juveniles, these classes will be less represented in the population) [46]. Since there is no hint of a past important disturbance and since it has been proved that the taller a juvenile is, the faster it grows [9], the second hypothesis seems to be the more likely. This is supported by the study of *Borassus* demography (see below): the palm population seems to be close to the stable stage distribution.

18.4.3 Demographic parameters

Although substantial data already exist for estimating the main demographic parameters of trees, no comprehensive analysis has been performed yet. We report here the few available estimates, plus a detailed case study of the palm tree *Borassus aethiopum*.

Main tree species

Survival - Seedling survival was estimated from the censuses of plots A-I and from experiments where seedlings were planted in an annually burned savanna (Table 18.4, from [37]). This experiment was designed to test the effect of tree cover on seedling growth and survival. Seedlings were planted in the field between grass tufts, under a tree clump or in the open; they were protected against rodent predation. There is a clear difference between species, and apparently no difference between treatments, suggesting that the relatively small tree clumps chosen were not big enough to cause a reduction in fire intensity. The survival of *Piliostigma* seedlings is strikingly high given their small size. At the seedling stage, *Piliostigma* has a higher survival than *Bridelia*, maybe because of a higher investment into belowground organs (Sect. 5.4).

Indications of adult and resprout stages life span is provided by the long-term dynamic data (Fig. 18.3): on plot 5, *Piliostigma* numbers start to increase 5 years after the end of fire exclusion, suggesting a duration of the resprout stage of at least 5 years, and adults recruited at this time are now slowly declining, suggesting a life span of the adult stage in this

Table 18.4. Experiment on seedling survival: numbers of alive seedlings. 20 seedlings of *Bridelia ferruginea* and *Piliostigma thonningii* were planted in the field in May 1992, under a tree clump and in the open, with a protection against rodent predation (after [37]).

Species	Treatment	Number of seedlings alive			
		Sept. 92	Oct. 93	Oct. 94	Oct. 95
<i>Bridelia</i>	Cover	20	18	6	5
<i>ferruginea</i>	Open	20	20	7	6
<i>Piliostigma</i>	Cover	20	20	20	19
<i>thonningii</i>	Open	20	20	20	20

species of 20-30 years, which is remarkably short. These conjectures would need further work to be confirmed.

Growth - Using data of two unburned plots measured by Menaut between 1969 and 1975 [51], Gignoux [36] estimated an empirical growth equation for adult trees of the shape:

$$\frac{dD^2H}{dt} = G D^2 \left(1 - \frac{D H}{DH_{max}} \right) (1 - \alpha N),$$

where D is basal diameter in cm, H is total height in cm, G is the intrinsic growth rate, DH_{max} is the maximal value of the DH product in cm^2 , α is a competition factor, and N is the number of crown-overlapping neighbors (Table 18.5). This equation was derived from Botkin et al. [18] and enables one to estimate tree maximal height and basal diameter. The analysis was performed for all species mixed. The estimated value for the competition parameters leads to a reduction of growth by 55% when a tree has 5 crown-overlapping neighbors, explaining the poor competitive ability of savanna trees in shaded conditions.

Reproduction and germination - From preliminary analyses of the long-term demographic data, the average recruitment rate into the adult population for the four main species is around $4 \text{ ha}^{-1} \text{ y}^{-1}$. Ponce de Leon Garcia [64] studied the germination ecophysiology of *Bridelia* and *Piliostigma*, germination of the other two main species being very difficult to obtain. These two species display tegumentary inhibition of germination (they need scarification to germinate). *Bridelia* seeds are still able to germinate after 5 years of storage, a relatively long life span compared to most tropical forest species. Seedlings of some species are apparently subject to heavy predation in their early stages, e.g., by rodents for *Piliostigma* and by crickets for *Cussonia* (unpublished field observations by Gignoux and Simioni).

Resistance to fire - Based on architectural descriptions of trees, César and Menaut [24] distinguished two main strategies enabling young trees to resist fire:

1. “Hide-and-resprout” strategy: As temperature rise is very low or negligible in the soil, young individual trees can survive by resprouting each year from belowground storage structures. To recruit into the adult population, such resprouts have to successfully establish a fire-resistant perennial trunk which will allow further growth in height the

Table 18.5. Estimates of adult growth equation parameters. Non-linear adjustment, all effects significant, $R^2 = 0.39$ (after [36]).

Parameter	Estimate	Standard error
G	53	4
DH_{max}	36000	2000
α	0.16	0.02

following year. This is achieved only when belowground structures are strong enough to produce between two successive fires (in some cases, this can be as short as one growing season only) a trunk (i) reaching a height where the terminal buds are able to resist the existing fire conditions and (ii) thick enough at its base to resist the high fire intensity existing in the fuel bed.

2. “Stay-and-resist” strategy: Young individuals can also survive by directly building an aerial fire-resistant structure (i.e., a thick trunk with a fire-protecting bark) enabling it to resist all fire conditions.

Gignoux et al. [39] have demonstrated that fire resistance resulted from the interaction of at least three properties defining a continuous set of strategies: (1) intrinsic resistance of stems, linked to bark properties; (2) specific trunk profile; (3) growth rate between two successive fires. Some species, like *Crossopteryx febrifuga*, are able to resist through a high intrinsic resistance and a thick trunk, while others like *Piliostigma thonningii* rely on a fast growth between fires. These differences should result in different spatio-temporal patterns of recruitment probabilities and probably affect tree dynamics through interactions with competition, which is consistent with the spatial patterns and long-term dynamics reported here.

Case study: The demography of *Borassus aethiopum*

Results presented here are based on a detailed demographic study based on a series Lefkovitch matrix population model presented in Sect. 19.2 [9, 14, 13, 10].

Demographic parameters - The model was based on the demographic stages defined in the previous section. Parameters were estimated for the populations of 2 plots (PP/GS2 and TS2: Table 18.1) for the period April 1995-April 1997 for SL-seedlings ($n = 369$), juveniles ($n = 423$), and adults ($n = 80$). Fecundity and EL-seedling survival and recruitment rates were estimated from the offspring of 6 females (999 EL-seedlings) during the period April 1996-April 1997 [12].

Death rate is U-shaped (respectively for the 4 stages 0.0930, 0.0100, 0.0065, 0.0400) as for probably most trees [74]. Juveniles seem to be the individuals the less likely to die. Recruitment rates are relatively high for seedlings (0.015 and 0.17) and much lower for juveniles (0.0035). Fecundity has been estimated as 28 seedlings produced per female per year.

Estimates of palm age - Mean age of palms (mean age of residence in the original paper), mean age at recruitment, and mean remaining life span were calculated [22] for each stage as well as their standard deviation (Table 18.6). The recruitment of juveniles into the adult population occurs very late, when juveniles are in average 116 years old. Adults then reproduce for a relatively short period since the mean remaining life span of adult is 25 years and since the mean age in the adult stage is 140

Table 18.6. Mean age, mean age of recruitment, and mean remaining life span for *Borassus* individuals of each stage. σ , standard deviation (after [14], with permission of Cambridge University Press).

Variable	EL-seedlings	SL-seedlings	Juveniles	Adults
y (mean age)	9.26	14.81	114.81	139.81
$\sigma(y)$	8.74	10.09	100.01	102.96
τ (mean age of recruitment)	-	10.26	15.81	115.81
$\sigma(\tau)$	-	8.74	10.09	100.01
Ω (mean remaining life span)	24.30	108.26	108.75	25.00
$\sigma(\Omega)$	53.97	101.63	101.25	24.49

years. The mean remaining life span is nearly the same for SL-seedlings (108 years) and juveniles (109 years). Individuals of these 2 stages behave quite in the same way: they both have very high survival rates, and the recruitment rate between the 2 stages is relatively high. Standard deviations values are close to the mean ages values. Thus, according to the model hypothesis, individuals can have very different temporal life histories and individuals in the same stages may have very different ages.

Senescence - Number of leaves, fecundity [9], and survival probability decrease with adult age, indicating a senescence period. The particularity of this senescence is that it seems to start just when sexual maturity is reached: adult number of leaves is maximum for the younger adults that have just recruited. The adult stage seems to be globally a senescent stage. Senescence is known for some tree species [74] and other palm trees [30, 21] but we do not know any other comparable senescence as strong as in *Borassus*, and beginning nearly as soon as individuals begin to reproduce.

Conclusion: The demographic strategy of *Borassus* - The demographic strategy of *Borassus* was compared to available results for other palm tree species: *Podococcus barteri* [20], *Astrocaryum mexicanum* [63], and *Rhopalostylis sapida* [31]. There was no proof of senescence in any of those (forest) species [9]. The estimates of stage ages computed for all the species reveal a much longer reproductive life for all the other species: they spend more than half of their life span reproducing, while *Borassus* only reproduces during a third of its life [14, 10]. The fact that *Borassus* is a savanna palm whereas the three others are forest palms could have played a role in the divergence of their life histories since the two kinds of ecosystem do not provide the same constraints. In forest, competition for light plays a very important role: it is an offspring-size-beneficial habitat [16]. In humid savannas, competition between trees is less intense, at least for adult palms that almost never grow close to each other [11], and competition, if any, is more likely to be for nutrients. Fire is also likely to have played an important evolutionary role in savannas and other fire-prone ecosystems [19, 68, 39].

Conclusion: Tree dynamics and demographic strategies

There is substantial evidence that the tree community in Lamto is unstable: trees are slowly but surely invading the savanna, both by an increase in savanna tree density [34] and a progression of gallery forest edges over the savanna [33]. The only estimate of a population asymptotic growth rate we have (for *Borassus*) is consistent with those descriptive results (population doubling in 20 years with the estimated value). There is enough data available to assess that the fluctuating numbers of some of the main species, probably linked to temporal fire variability, do not hide this long-term trend.

The scarce information we have so far on the demographic strategies of the main species show surprising facts: relatively short life spans for the main tree species (< 30 years for the adult stage and < 15 years for the resprout stage), and an original life cycle with a quick senescence for the palm tree *Borassus*. At the moment, we lack a comprehensive comparative study of the demographic strategies of all the major tree species of Lamto to propose any sound explanation for these particularities.

However, if demographic analysis results are consistent with the long-term trend, they do not explain it or provide any mechanism explaining it. Some results indicate that the long-term trend could be due either to (1) a change in the fire regime causing a change in tree recruitment patterns and (2) an effect of tree aggregation (i.e., comparison of the fate of plots I and G: Fig. 18.4). We explored this question through (1) analyses of the links between spatial structure of the ecosystem and population dynamics (next section) and through (2) modeling studies of the tree demography in relation to the major factor apparently constraining their recruitment, fire (Chap. 19).

18.5 Discussion: The interaction of demography and spatial patterns and its effect on savanna stability

The studies conducted so far on tree dynamics at Lamto illustrate once more the great complexity of this dynamics in savanna ecosystems, even without explicitly considering the problem of tree-grass interactions (Chap. 8). As demonstrated by fire exclusion experiments, fire effectively shapes Guinea savannas by selecting the species able to survive in these extreme conditions, but among the community of fire-resistant species, it becomes a secondary factor affecting their demography. Spatial pattern analyses showed that for two dominant species (*Crossopteryx* and *Borassus*), fire was not a problem, and for some other ones, nutrients were at least as important. This is supported in Lamto by the fact that only late fires are able to maintain tree populations, normal fire being unable to prevent tree invasion. For the less fire-resistant savanna species (*Piliostigma*, *Cussonia*, *Annona*, *Bridelia*), we observe fluctuating numbers in the long term, unstable population structures, and heterogeneous or clumped spatial patterns, as in other savanna systems

[65, 69]. Although the exact reason for these fluctuations is not known, it is certainly not due to herbivores as in [65] given the low herbivore load in Lamto (Chap. 10), but more probably to fire, as previously hypothesized [39].

The second most important regulator of tree populations appears to be nutrients, which are characterized in Lamto by a very heterogeneous distribution: nutrients are concentrated in patches, which provides a key for analyzing spatial patterns. Nutrient patchiness (together with fire protection and short-distance seed dispersal) contributes to the formation of clumps associated to those patches, a cause often invoked to explain clumped patterns [67, 23] but never evidenced as here. We observe here these clumps for adult trees, but the studies of Barot clearly demonstrated that different stages in the same species could have different nutrient requirements, or different abilities to capture nutrients just because of their sizes: patterns within a species could complicate the picture. Furthermore, a detailed study of the fate of *Borassus* seedlings as a function of distance to their mother or to nutrient-rich patches [12] shows that the key assumption of matrix population models, that demographic parameters are homogeneous within a stage, is not fulfilled in Lamto because these parameters depend on the spatial pattern of the population.

Since water is probably not the main limiting factor in Lamto (Sects. 4.2, 3.2 and 18.2), the last factor affecting tree patterns and dynamics is competition for light. Little evidence of self-thinning has been found, except for young stages in the *Borassus* study [11], as in many other savanna systems [23, 70].

The key input of the studies of tree dynamics conducted at Lamto is the demonstration that ecosystem heterogeneity, tree demography, and spatial patterns are closely linked: over the initial patchiness of soil nutrients, demography, through the differences in seed dispersal, survival at different stages, and fire resistance of different species, adds a second layer of patchiness that eventually reinforces the initial patchiness, tree clumps becoming nutrient-rich and fire-protected patches. This feedback of tree demography on spatial pattern and environmental heterogeneity is apparently able to produce nursing effects comparable to those documented in other savannas [5, 4, 7] and lead to a local invasion by trees even under a normal fire regime as observed on plots H and G and modeled by Gignoux et al. [41]. In such a case, large clumps would constitute stable features of the landscape, even if they start randomly.

There are many unanswered questions left: there is still a dispersal problem in *Borassus* (how can the life cycle be accomplished when favorable sites for seedlings and adults are different?); the effect of fire on seedling survival and resprout recruitment has been studied at the individual level, but the response of the population has not been studied; seed dispersal is a key factor linking pattern and demography and is worth a detailed study; a comprehensive and comparative analysis of spatial pattern and demography of the major tree species, such as that performed for *Borassus*, is needed to understand the determinants of the demographic strategies of savanna tree species; linking functioning and dynamics is also necessary to understand the link between

recruitment fluctuations and climate. Most of this work involves long-term processes and thus requires a substantial modeling effort to be achieved.

References

1. L. Abbadie, M. Lepage, and X. Le Roux. Soil fauna at the forest-savanna boundary: Role of termite mounds in nutrient cycling. In P.A. Furley, J. Proctor, and J.A. Ratter, editors, *Nature and dynamics of forest-savanna boundaries*, pages 473–484. Chapman & Hall, London, 1992.
2. L. Abbadie, A. Mariotti, and J.C. Menaut. Independence of savanna grasses from soil organic matter for their nitrogen supply. *Ecology*, 73(2):608–613, 1992.
3. J. Antonovics and D.A. Levin. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, 11:411–452, 1980.
4. S. Archer. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, USA. *Journal of Biogeography*, 17:34, 1990.
5. S. Archer, C. Scifres, C.R. Bassham, and R. Maggio. Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Monographs*, 58(2):111–127, 1988.
6. C.K. Augspurger. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps and pathogens. *Ecology*, 65(6):1705–1712, 1984.
7. P.W. Barnes and S. Archer. Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: Implications for patch dynamics. *Oecologia*, 105(4):493–500, 1996.
8. S. Barot. *Interactions entre répartition spatiale, hétérogénéité environnementale et démographie: Cas du palmier Rônier dans une savane humide de Côte d'Ivoire*. Ph.D. thesis, Université de Paris 6, Paris, 1999.
9. S. Barot and J. Gignoux. Population structure and life cycle of *Borassus aethiopum* Mart.: Evidence of senescence in a palm tree. *Biotropica*, 31(3):439–448, 1999.
10. S. Barot, J. Gignoux, and S. Legendre. Matrix models and age estimations in plants. *Oikos*, 96:56–61, 2000.
11. S. Barot, J. Gignoux, and J.C. Menaut. Demography of a savanna palm tree: Predictions from comprehensive spatial pattern analyses. *Ecology*, 80(6):1987–2005, 1999.
12. S. Barot, J. Gignoux, and J.C. Menaut. Seed shadows, survival and recruitment: How simple mechanisms lead to the dynamics of population recruitment curves. *Oikos*, 86:320–330, 1999.
13. S. Barot, J. Gignoux, and J.C. Menaut. Neighborhood analysis in a savanna palm: Interplay of intraspecific competition and soil patchiness. *Journal of Vegetation Science*, 14:79–88, 2000.
14. S. Barot, J. Gignoux, R. Vuattoux, and S. Legendre. Demography of a savanna palm tree in Ivory coast (Lamto): Population persistence and life history. *Journal of Tropical Ecology*, 16:637–655, 2000.
15. S.W. Beatty. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology*, 65(5):1406–1419, 1984.
16. M. Begon, J.L. Harper, and C.R. Townsend. *Ecology - Individuals, populations and communities*. Blackwell Scientific Publications, Boston, 1986.

17. J. Bonvallot, M. Dugerdil, and D. Duviard. Recherches écologiques dans la savane de Lamto (côte d'ivoire): Répartition de la végétation dans la savana préforestière. *La Terre et la Vie*, 1:3–21, 1970.
18. D.B. Botkin, J.F. Janak, and J.R. Wallis. Some ecological consequences of a computer model of forest growth. *Journal of Ecology*, 60:849–871, 1972.
19. R.A. Bradstock and T.D. Auld. Soil temperatures during experimental bushfires in relation to fire intensity: Consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology*, 32(1):76–84, 1995.
20. S.H. Bullock. Demography of an undergrowth palm in littoral Cameroon. *Biotropica*, 12(4):247–255, 1980.
21. R.L. Chazdon. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. *Biotropica*, 24(1):43–51, 1992.
22. M.E. Cochran and S. Ellner. Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs*, 62(3):345–364, 1992.
23. P. Couteron and K. Kokou. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology*, 132:211–227, 1997.
24. J. César and J.C. Menaut. Analyse d'un écosystème tropical humide: La savane de Lamto (Côte d'Ivoire). II. Le peuplement végétal. *Bulletin de Liaison des Chercheurs de Lamto*, S2:1–161, 1974.
25. J.M. Dauget and J.C. Menaut. Evolution sur vingt ans d'une parcelle de savane boisée non protégée du feu dans la réserve de Lamto (Côte d'Ivoire). *Candollea*, 47:621–630, 1992.
26. J. Delmas. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire): Premier aperçu sur les sols et leur valeur agronomique. *La Terre et la Vie*, 21(3):216–227, 1967.
27. J.L. Devineau, C. Lecordier, and R. Vuattoux. Evolution de la diversité spécifique du peuplement ligneux dans une succession préforestière de colonisation d'une savane protégée des feux (Lamto, Côte d'Ivoire). *Candollea*, 39:103–134, 1984.
28. P.J. Diggle. On parameter estimation and goodness-of-fit testing for spatial point patterns. *Biometrics*, 35(0):87–101, 1979.
29. P.J. Diggle. *Statistical analysis of spatial point patterns*. Mathematics in Biology. Academic Press, London, 1983.
30. N.J. Enright. Age, reproduction and biomass allocation in *Rhopalostylis sapida* (Nikau Palm). *Australian Journal of Ecology*, 10:461–467, 1985.
31. N.J. Enright and A.D. Watson. Population dynamics of the Nikau palm, *Rhopalostylis sapida* (Wendl. et Drude), in a temperate forest remnant near Auckland, New Zealand. *New Zealand Journal of Botany*, 30:29–43, 1992.
32. P.G.H. Frost and F. Robertson. The ecological effects of fire in savannas. In B.H. Walker, editor, *Determinants of tropical savannas*, volume 3 of *Monograph series*, pages 93–140. International Council of Scientific Unions Press, Miami, FL, 1985.
33. L. Gautier. Contact forêt savane en Côte d'Ivoire centrale: Evolution de la surface forestière de la réserve de Lamto (sud du V baoulé). *Bulletin de la Société Botanique de France*, 136(3):85–92, 1989.
34. L. Gautier. Contact forêt-savane en Côte d'Ivoire centrale: Evolution du recouvrement ligneux des savanes de la réserve de Lamto (sud du V baoulé). *Candollea*, 45:627–641, 1990.

35. L. Gautier. *Contact forêt-savane en Côte d'Ivoire - Rôle de Chromolaena odorata (L) dans la dynamique de la végétation*. Doctorat, Université de Genève, Genève, 1992.
36. J. Gignoux. *Modélisation de la dynamique d'une population ligneuse - Application à l'étude d'une savane africaine*. M.Sc. thesis, Institut National Agronomique Paris-Grignon, Paris, 1988.
37. J. Gignoux. *Modélisation de la coexistence herbes/arbres en savane*. Ph.D. thesis, Institut National Agronomique Paris-Grignon, Paris, 1994.
38. J. Gignoux. *SPASTAT: Un logiciel pour l'analyse de répartitions spatiales par les méthodes de Diggle et Ripley*. Ecole Normale Supérieure, Paris, 1994.
39. J. Gignoux, J. Clobert, and J.C. Menaut. Alternative fire resistance strategies in savanna trees. *Oecologia*, 110(4):576–583, 1997.
40. J. Gignoux, C. Duby, and S. Barot. Comparing the performances of Diggle's tests of spatial randomness for small samples with and without edge-effect correction: Application to ecological data. *Biometrics*, 55(1):156–164, 1999.
41. J. Gignoux, J.C. Menaut, I.R. Noble, and I.D. Davies. A spatial model of savanna function and dynamics: model description and preliminary results. In D.M. Newbery, H.H.T. Prins, and N.D. Brown, editors, *Dynamics of tropical communities*, volume 37 of *Annual symposium of the BES*, pages 361–383. Blackwell Scientific Publications, Cambridge, 1998.
42. A.M. Gill and D.H. Ashton. The role of bark type in relative tolerance to fire of three central Victorian eucalypts. *Australian Journal of Botany*, 16:491–498, 1968.
43. F. Hallé and R.A.A. Oldeman. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson, Paris, 1970.
44. P.A. Harcombe. Tree life tables. *BioScience*, 37(8):557–568, 1987.
45. H.F. Howe and J. Smallwood. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13:201–228, 1982.
46. M.A. Huston and D.L. DeAngelis. Size bimodality in monospecific populations: a critical review of potential mechanisms. *The American Naturalist*, 129(5):678–707, 1987.
47. S. Konaté, X. Le Roux, D. Tessier, and M. Lepage. Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. *Plant and Soil*, 206:47–60, 1999.
48. X. Le Roux and T. Bariac. Seasonal variation in soil, grass and shrub water status in a West African humid savanna. *Oecologia*, 113:456–466, 1998.
49. S. A. Levin. The problem of pattern and scale in ecology. *Ecology*, 73(6):1943–1967, 1992.
50. J.C. Menaut. Chutes de feuilles et apport au sol de litière par les ligneux dans une savane préforestière de Côte d'Ivoire. *Bulletin d'Ecologie*, 5:27–39, 1974.
51. J.C. Menaut. Evolution of plots protected from fire since 13 years in a Guinea savanna of Ivory coast. In *Actas Del IV Symposium Internacional De Ecologia Tropical*, pages 541–558, Panama, 1977.
52. J.C. Menaut and J. César. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology*, 60(6):1197–1210, 1979.
53. J.C. Menaut, J. Gignoux, C. Prado, and J. Clobert. Tree community dynamics in a humid savanna of the Côte d'Ivoire: Modelling the effects of fire and competition with grass and neighbours. *Journal of Biogeography*, 17:471–481, 1990.

54. Y. Monnier. *Les effets des feux de brousse sur une savane préforestière de Côte d'Ivoire*, volume 9 of *Etudes Eburnéennes*. Ministère de l'Education Nationale de Côte d'Ivoire, Abidjan, 1968.
55. P. Mordélet, L. Abbadie, and J.C. Menaut. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Côte d'Ivoire). *Plant and Soil*, 153:103–111, 1993.
56. P. Mordélet, S. Barot, and L. Abbadie. Root foraging strategies and soil patchiness in a humid savanna. *Plant and Soil*, 182:171–176, 1996.
57. D.A. Morrison. Some effects of low-intensity fires on populations of co-occurring small trees in the Sydney region. *Proceedings of the Linnean Society of New South Wales*, 115:109–119, 1995.
58. J.J. Mott and A.J. McComb. Patterns in annual vegetation and soil microrelief in an arid region of Western Australia. *Journal of Ecology*, 62:115–125, 1974.
59. I.R. Noble and R.O. Slatyer. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, 43:5–21, 1980.
60. D.L. Phillips and J.A. MacMahon. Competition and spacing patterns in desert shrubs. *Journal of Ecology*, 69:95–115, 1981.
61. M.A. Pinard and J. Huffman. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology*, 13:727–740, 1997.
62. E.C. Piélou. The use of plant-to-plant distances for the detection of competition. *Journal of Ecology*, 50:357–367, 1962.
63. D. Piñero, M. Martínez-Ramos, and J. Sarukhán. A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *Journal of Ecology*, 72:977–991, 1984.
64. L. Ponce de Leon Garcia. *L'écophysiologie de la germination d'espèces forestières et de savane, en rapport avec la dynamique de la végétation en Côte d'Ivoire*, volume 1 of *Travaux des chercheurs de Lamto*. Ecole Normale Supérieure, Paris, 1982.
65. H.H.T. Prins and H.K. Van der Jeugd. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology*, 81:305–314, 1993.
66. B.D. Ripley. *Spatial statistics*. John Wiley & Sons, New York, 1981.
67. J.J. San José, M.R. Fariñas, and J. Rosales. Spatial patterns of trees and structuring factors in a *Trachypogon* savanna of the Orinoco Llanos. *Biotropica*, 23(2):114–123, 1991.
68. A.L. Schutte, J.H.J. Vlok, and B.E. Vanwyk. Fire-survival strategy - A character of taxonomic, ecological and evolutionary importance in fynbos legumes. *Plant Systematics and Evolution*, 195(3-4):243–259, 1995.
69. C.M. Shackleton. Demography and dynamics of the dominant woody species in a communal and protected area of the Eastern Transvaal Lowveld. *South African Journal of Botany*, 59(6):569–574, 1993.
70. C. Skarpe. Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science*, 2:565–572, 1991.
71. P.B. Tomlinson and E.C. Jeffrey. *The structural biology of palms*. Clarendon Press, Oxford, 1990.
72. R. Vuattoux. Observations sur l'évolution des strates arborée et arbustive dans la savane de Lamto (Côte d'Ivoire). *Annales de l'Université d'Abidjan, Série E*, 3(1):285–315, 1970.

73. R. Vuattoux. Contribution à l'étude de l'évolution des strates arborée et arbustive dans la savane de Lamto (Côte d'Ivoire). Deuxième note. *Annales de l'Université d'Abidjan, Série C*, 7(1):35–63, 1976.
74. A. Watkinson. Plant senescence. *Trends in Ecology and Evolution*, 7(12):417–420, 1992.