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Establishment and early persistence of tree seedlings in an annually burned savanna

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Summary

1. In severely disturbed habitats, the onset of resprouting as a persistence strategy might be problematic for tree species which do not accumulate sufficient reserves before the first disturbance event. This is due to the trade-off between the growth of reserves required to recover after disturbance and that of photosynthetic tissues.
2. In humid savannas, fire prevents trees from invading the whole landscape and nearby gallery forests have a completely different floristic composition. We test if the variations of survival during the first years of a young tree's life can explain the exclusion of forest species and the dominance pattern within savanna species.
3. Every six months for four years, we censused all seedlings and resprouts in 1 ha area of an annually burned savanna, to estimate their seasonal survival rates. We used capture–recapture statistical models to control for the probability of missing seedlings in the tall grass.
4. There were two main distinct patterns of survival among seedlings: 'fire-responding' species showed a 20–80% decrease in survival during the dry season, interpreted as mainly due to fire; 'drought-responding' species showed 20–80% variations in survival positively correlated to early-growing-season rainfall.
5. Yearly averaged survival probabilities of seedlings ranged between 0.10 and 0.63, reaching 0.850–0.996 for > 3-year-old resprouts of savanna species. Forest species showed no increase in survival with age.
6. A 4-year-survival-probability analysis showed that forest species were excluded from the savanna at the seedling stage. No parameter of the early survival curve related to the abundance of savanna species at the adult stage.
7. *Synthesis*. Savanna tree species follow two mutually exclusive main patterns of early survival probably related to fire and early-wet-season drought. The exclusion of forest species is consistent with a build up of reserves that is too slow due to the growth-resistance trade-off. We conclude from these findings that the use of resprouting as a persistence strategy is heavily constrained by disturbance frequency and imposes strong trade-offs on plant growth strategy.

Key-words: Disturbance, fire, persistence niche, resprouting ability, seedling survival, tree demography, tropical savanna

Introduction

As long-lived species, trees require particular adaptations to achieve their demographic cycle in frequently and intensely disturbed habitats. Whereas resisting disturbances is relatively easy for adult trees due to their large size, it is more problematic for young individuals such as seedlings and saplings. The concept of the persistence niche (Bond & Midgley 2001) emphasizes that in frequently disturbed habitats the survival of seedlings and saplings relies on resprouting, in order to persist in spite of recurrent removal of some or all above-ground biomass. The ability to resprout relies on stored reserves that are protected from disturbance effects. This has two important consequences:

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1 A *resistance-growth trade-off*: Resources allocated to reserves are diverted from other important functions such as growth in height and leaf construction, both crucial in competition for light (Chapin *et al.* 1990). Investing into reserves is investing into survival, that is, securing future growth, to the detriment of current growth. A delicate adjustment of the resource allocation strategy in response to the timing of disturbance events must be reached, similar to the adjustment between the persistence strategy – resprouting or heavy seed production – and the frequency and intensity of disturbance discussed by Bellingham & Sparrow (2000) for larger trees.

2 A *latency time to persistence*: Building up a sufficient reserve takes time. A newly germinated seedling will be unable to resprout before it has accumulated enough reserves. Therefore, the timing of disturbance events relative to the rate of reserve accumulation and the date of germination determines whether resprouting is efficient in helping seedlings to survive and persist. In particular, passing the first disturbance event encountered by a seedling is a prerequisite to enter the persistence stage.

Because of these two constraints, acquiring the ability to persist and surviving the first disturbance event in a frequently disturbed habitat might be as difficult for a seedling as is the recruitment from the persistence, resprout stage to the adult stage. Whereas the latter barrier has been identified and studied for a long time (Bond & Midgley 2001; Bond & Keeley 2005), the former barrier has been less studied although it could be equally critical for the population dynamics of a species. Our aim in this paper is to explore the way tree seedlings of different species survive to their first disturbance event and successfully establish at a resprout stage, thus able to persist under a rather extreme disturbance regime.

Savannas constitute a good example of disturbed systems which is stressful for trees. According to a recent meta-analysis at the scale of the African continent (Sankaran *et al.* 2005), and to a global vegetation modelling exercise (Bond *et al.* 2005), at least half of tropical savanna and grassland ecosystems owe their very existence to perturbations such as fire and herbivory in areas where otherwise climate would permit the maintenance of forests. These large-scale findings are in accordance with field experiments of fire exclusion conducted in wet savannas around the world (Dereix & N'guessan 1976; San José & Fariñas 1983, 1991; Devineau *et al.* 1984; Swaine *et al.* 1992; Bowman & Panton 1995; Russell-Smith *et al.* 2003), which demonstrate that fire exclusion is quickly followed by the invasion of trees and the establishment of a forest, and with the numerous reports of bush encroachment following perturbations in the grazing regime (Hobbs & Huenneke 1992) or in the natural population dynamics of herbivores (Prins & Van der Jeugd 1993).

At the wettest end of the climatic gradient where savannas can be found, fires are very frequent (they usually occur every year) and intense (Gignoux *et al.* 2006a; Russell-Smith & Edwards 2006). Savanna trees resist fire through repeated resprouting: the tops of young individuals are killed every year, but their below-ground part survives and produces new stems (Gignoux *et al.* 1997; Archibald & Bond 2003; Wright & Clark 2007). In essence, their growing habit is not different from that of the surrounding perennial grasses. Young trees can be caught in this 'fire trap' (Bond & Midgley 2001; Bond & Keeley 2005) for several decades, waiting for the 'Great Day' where they will have accumulated enough reserves to produce a sprout able to resist fire, either because of its vigour or because of a temporary decrease in fire intensity. Although there are some differences in resistance to fire among species (Gignoux *et al.* 1997), the resprout stage is an obligate step for all species, because they all start as small seedlings with no below-ground reserves. The main difference between species lies in the size at which they can escape the fire trap, with some species never escaping and relying on the limited seed production resprouts are capable of (Menaut & César 1979; Gignoux, personal observation).

Most savannas are intermingled with gallery forests that are of a completely different floristic composition than the savanna tree community (Gautier 1989; Meave & Kellman 1994; Hoffmann & Franco 2003; Hennenberg *et al.* 2005; Nangendo *et al.* 2006). The exact mechanism by which fire excludes these species is unknown: many forest trees are able to resprout after cutting (de Rouw 1993; Marrinan *et al.* 2005) and their seedlings can be found in the adjacent savanna (Hoffmann *et al.* 2004; Gignoux *et al.* 2006b). Forest-tree seedlings are less resistant to water stress than savanna-tree seedlings (Hoffmann *et al.* 2004) and by far less able to survive fire (Hoffmann 2000); their establishment success in the savanna is correlated to the amount of available water (Bowman & Panton 1993). Wet-season dry spells also affect survival of forest-tree species (Engelbrecht *et al.* 2006). Since gallery forest-tree species invest much less in their root system than savanna species (Gignoux 1994; Hoffmann *et al.* 2004), their exclusion from the savanna might be due to the growth-resistance trade-off resulting in less resistance to both drought and fire. Fire is also known to decrease savanna seedling survival (Setterfield 2002), with a possible interaction with dry-season water shortage and early wet-season dry spells (Hoffmann 1996; Higgins *et al.* 2000).

The aim of this paper is to study the pattern of seedling survival at an early stage, during the onset of resprouting, in a humid savanna with yearly fires. We use data from four successive years and a biannual sampling regime in order to account for interannual and seasonal variability of survival and work on all tree species encountered in a natural ecosystem in order to span the whole range of possible initial growth strategies. We address the following questions:

1 Are the different species more sensitive to interannual variation in rainfall, or to the seasonal effect of fire?

2 Are some groups of tree species, like forest and rare savanna species, excluded from the system because of their inability to pass the first fire?

3 Does the pattern of early survival correlate with the hierarchy of abundances of common savanna tree species?

To test the hypotheses, we examined the patterns of variation in survival within stages, between stages and the persistence of resprouts in the 'long term', that is, over the four years of the study.

Table 1. Study species. All species were studied individually except those of groups IV and V which were treated as a single guild for statistical analyses

	Group	Species	Family
I	Dominant savanna species	*Bridelia ferruginea* Benth.	Euphorbiaceae
		Crossopteryx febrifuga (Afzel. ex G. Don) Benth.	Rubiaceae
		Cussonia arborea Hochst. ex A. Rich.	Araliaceae
		Piliostigma thonningii (Schumach.) Milne-Redhead	Caesalpiniaceae
II	Species present as resprouts only	*Annona senegalensis* Pers.	Annonacea
		Psorospermum febrifugum Spach	Hypericaceae
III	Savanna woodland species	*Pterocarpus erinaceus* Poir.	Fabaceae
		Terminalia shimperiana Planch. ex Benth.	Combretaceae
IV	Other savanna species	Eight species studied as a whole (Table S1)	
V	Gallery forest species	18 species studied as a whole (Table S1)	

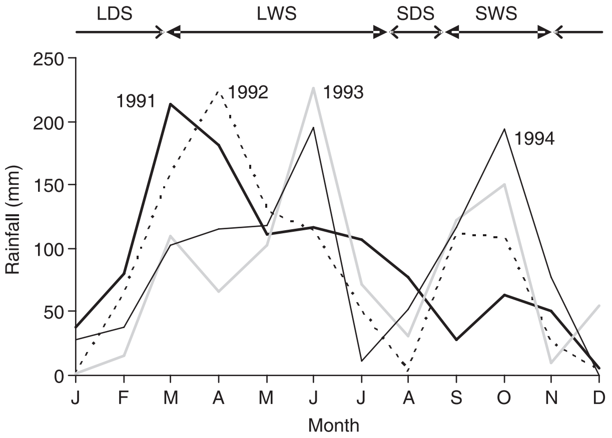

Fig. 1. Monthly rainfall at the Lamto Research Station (Côte d'Ivoire) over the years 1991–1994 with long wet season (LWS), long dry season (LDS), short dry season (SDS) and short wet season (SWS). Data kindly provided by the Lamto geophysical station.

Methods

STUDY SITE

The study was conducted in the Lamto Natural Reserve in Côte d'Ivoire (06°13′ N, 05°02′ W), which consists of a mosaic of Guinea savannas and gallery forests (Abbadie *et al.* 2006). Rainfall follows a bimodal seasonal distribution with the main dry season from December to January, the short dry season occurring in August (Fig. 1), and an average yearly rainfall of 1169 mm. During the study period (1991–1994), annual rainfall was low, ranging from 959 to 1071 mm (Fig. 1). The vegetation of Lamto savannas is composed of perennial Andropogoneae bunch grasses, small dicotyledonous trees and tall palm trees (Menaut & César 1979). The tree cover is very variable (from 0% up to 75%) and averages 15–20%, with 250 stems ha^{-1} (Menaut & César 1979). Due to the high rainfall, the grass standing crop can reach 1000 g dry wt m^{-2} at the end of the growing season (Menaut & César 1979). The average height of grass often exceeds 1.5 m from August to December, with spikes reaching more than 2 m. The Lamto reserve is managed to maintain the fire regime typical for most of the Guinean zone, with intense yearly fires occurring during the dry season. Fire is deliberately set every year around 15 January. As a result, most (> 80%) savanna ecosystems of the reserve are burnt every year; by contrast, gallery forests never burn. The ecotone between the two formations is very sharp (commonly 2 m wide). In this savanna, the recruitment of resprouts to the adult stage, is generally considered to occur when they reach 2 m in height, which is roughly equivalent to average flame height (Menaut & César 1979; Gignoux *et al.* 2006b) and maximum resprout size (Gignoux *et al.* 1997).

STUDY SPECIES

In order to sample the whole range of possible strategies of initial development, we studied the seedlings and young resprouts of all tree species found in the savanna, classified into five abundance groups (Table 1). Given their lower density, two sets of species were lumped for statistical analyses into two guilds: a guild comprising all the less common savanna tree species (eight species) and a guild comprising all forest species (18 species) (see Table S1 in Supporting Information). From now on, we refer to these eight single species and two groups of species as guilds, even though some of them actually consist of one species only.

BIANNUAL TREE CENSUSES

In order to isolate the effect of fire from the effect of climate on seedling survival, the ideal sampling design would have been to census trees just before the fire and just after it. Unfortunately, this was not possible because fire occurs during the dry season, when seedlings are leafless (and often stemless, being reduced to a root system and a little stump) and their status (dead or alive) can be uncertain. Our compromise was to undertake a sampling at the end of the wet season, before most young trees were leafless, and a further sampling after the beginning of the wet season, where new seedlings had germinated and older ones had started to resprout. This maximized our chance of finding new and previously marked seedlings, but resulted in fire and dry-season effects on survival being confounded. From 1991 to 1994, four censuses were conducted during the long wet season (June 1991, June 1992, July 1993 and July 1994) and three at the beginning of the long dry season (December 1991, November 1992 and December 1993) in four 50 × 50 m permanent plots. The position of all seedlings and resprouts was marked with a fire-resistant stainless steel label attached to a 50-cm stake. We avoided trampling grass tufts as these strongly affect the growth of young tree individuals by competing for light, water and nutrients (Scholes & Archer 1997). At each census, we recorded species and life-history stage and scored dead plants (label, but no plant in the vicinity).

DEMOGRAPHIC STAGES

Young individuals were sorted into two different demographic stages: seedlings (S) and resprouts (R). We defined resprouts as individuals > 1-year old and with stem height ≤ 2 m. While seedlings is an implicit age class with only < 1-year old individuals, resprouts is a heterogeneous class with regard to age. We further divided the resprouts into three age-classes: 1 year < age < 2 years (R_1), 2 years < age < 3 years (R_2), and age > 3 years (R_3). Classes R_1 and R_2 were made of individuals previously marked as seedlings and subsequently continuously tracked; class R_3 comprised 3-year-old individuals previously marked as R_2 plus non-seedling individuals of unknown age present at the first census, assuming exactly 1- or 2-year-old resprouts would be a minority in this initial population (Lahoreau *et al.* 2004). Non-seedling individuals seen after the first census were classified as R_3, assuming they were most likely resprouts that had been missed before. All individuals older than one growing season were irreversibly marked by the annual fire. The identification of seedlings in the field was based on the following criteria:

1 Presence of one or two cotyledons or cotyledon remains;

2 Small size *and* no visible sign of having been through a fire. We noticed the following recurrent characteristics of resprouts: at the time of the censuses, well into the rainy season, resprouts are usually taller than seedlings; seedlings tend to occur in cohorts of similar appearance; burnt individuals have a thicker and stiffer stem than seedlings; and most of them have a small dead stem or stump at their base.

3 For all censuses but the first one, absence from the previous records.

4 For the December censuses only, a previous record as seedling since no fire had happened between the June and December censuses.

A total of 4606 seedlings and resprouts were tracked. The number of marked seedlings varied greatly over the three years studied (800 in June 1991, 1358 in June 1992 and 325 in July 1993). Seedlings recorded in June were around 4-months old, except for *Cussonia* (1-month-old, Lahoreau, personal observation).

MARK—RESIGHTING—RECOVERY MODELLING

During censuses, we encountered problems detecting plants or marks: (i) the tall and dense tufts of grass sometimes hid seedlings, resprouts or tagged stakes; and (ii) the tree species studied were deciduous, it was therefore also not always possible to determine if leafless individuals were alive or dead when censuses were done at the start of the long dry season. In a previous methodology paper on the same data (Lahoreau *et al.* 2004), we estimated that the probability of detecting seedlings and resprouts averaged 0.88 ± 0.15 (mean ± SE) and 0.92 ± 0.10, respectively, and that the probability of detecting dead individuals averaged 0.71 ± 0.25. As unencountered plants may lead to biased estimates of survival (Kéry & Gregg 2003; Lahoreau *et al.* 2004), we applied mark–reencounter models commonly used in animal studies (e.g. Lebreton *et al.* 1992; Williams *et al.* 2001). We used models which explicitly take into account the detection probabilities of both alive and dead individuals (Burnham 1993; Catchpole *et al.* 1998), conventionally named resighting and recovery probabilities in animal studies. These models are known as mark–resighting–recovery (MRR) models. The parameters of the models were estimated with a maximum likelihood method implemented in the MARK software (White & Burnham 1999). The general statistical model applied to our data was (MARK notation):

$$S(a4 - t\ /\ t\ /\ t\ /\ t)\ p(a4 - t\ /\ t\ /\ t\ /\ t)r(t)$$

where S, the survival probability, depends on age class a (four age classes), and on time for each age class; p is the resighting probability; and r is the recovery probability. The model was fitted to data after correction by a species-specific variance inflation factor (Lahoreau *et al.* 2004). Models for resighting probabilities were age- and time-dependent, while models for recovery probabilities were time-dependent (Lahoreau *et al.* 2004). The detailed technical aspects of the models applied to our data are explained in Lahoreau *et al.* (2004).

MODEL FITTING PROCEDURE: TEMPORAL AND AGE VARIATION OF SURVIVAL

We fitted MRR models including effects of season, plant age and year on survival probabilities separately for each species (Table 2 and Table S2). We selected best models based on the Quasi-Akaike Information Criterion ($QAIC_c$) (Burnham & Anderson 1998) (Table S2). Season, age and year effects were interpreted as follows:

1 *Seasonal effect*: We called *wet-season survivorship* S_D, the survival probability estimated over the July–December period; and *dry-season survivorship* S_J, the survival probability estimated over the January–June period. The dry season survivorship S_J actually measures the survival during most of the long dry season (December–February), the survival of fire (occurring in January) and the survival during the first months of the long wet season (March–June) (Fig. 1). The wet-season survivorship S_D actually measures the survival during the end of the long wet season (July–August), the short dry season (generally in August) and the short wet season (September–November) (Fig. 1).

2 *Age effect*: Age classes (S, R_1, R_2, R_3) were used in all models. They were lumped together when no difference in survival between successive age classes was detected, in order to reduce the number of model parameters.

3 *Year effect*: We tested for three patterns of year dependency (Table 2): survival probabilities were either different at all dates (model Y1), different at the June census and equal at the December census (model Y2), or were different at the December census and equal at the June census (model Y3).

INTERPRETATION OF YEAR AND SEASONAL EFFECTS ON SURVIVAL PROBABILITIES

Rainfall is the main driver of primary production in this tropical ecosystem (Gignoux *et al.* 2006b), and as such is a good indicator of interannual climatic variability. When a significant year effect was detected (i.e. cases Y1–Y3 above), we fitted an alternative MRR model including the effect of either dry- or wet-season rainfall in replacement for the year effect (Table S3). For S_D, the amount of rainfall was calculated over the July–November period. For S_J, the amount of rainfall was calculated over the February–June period to take into account only rainfall influencing the survival and resprouting of young individuals (young trees were leafless in December and January). This was done for seedlings only. When S_D and S_J showed a seasonal effect on survival (model S1 in Table 2), or when it was visible on the graphs that the year variability comprised a part of seasonal variability (e.g. in models Y1–Y3), we computed the absolute and relative decrease in mortality in June compared to December from the averages of probabilities in these seasons.

Table 2. Mark–resighting–recovery models tested on seedling and resprout survival for each species

	Models			
Effect studied	Code	Short name	Terms included/ hypotheses tested	Interpretations
Age class	A1	4 age classes	S, R_1, R_2, R_3	Rate of increase in survival between stages can be discussed
	A2	3 age classes	S, R_1, R_2R_3 or S, R_1R_2, R_3	As above
	A3	2 age classes	S, $R_1R_2R_3$	As above
	A4	1 age class	$SR_1R_2R_3$	No difference between S and R
Year variability	Y1	Full year dependency	$S_D(y)$, $S_J(y)$	Interannual and seasonal variability in survival
	Y2	'dry season' variability	$S_D(.)$, $S_J(y)$	Effect of dry season/early wet season rainfall or variations in fire intensity on survival
	Y3	'wet season' variability	$S_D(y)$, $S_J(.)$	Effect of wet season rainfall on survival
Seasonal variability	S1	seasonal difference	$S_D(.) \neq S_J(.)$	If $S_D > S_J$: fire + dry season drought effect
	S2	constant survival	$S_D(.) = S_J(.)$	No effect of fire or rainfall on survival

Notes: S_D: wet-season survivorship (over the July–December period); S_J: dry-season survivorship (over the January–June period). Age classes: S: seedling, R_1: 1-yr < age < 2-yr, R_2: 2-yr < age < 3-yr, R_3: age > 3-yr resprout. Hypotheses tested: $S_D(y)$ or $S_J(y)$: year-dependency, $S_D(.)$ or $S_J(.)$: constancy over years.

ESTIMATION OF THE PERSISTENCE ABILITY

To assess whether seedlings had successfully entered the persistence, resprout stage, we used two different approaches. First, we examined the dynamics of survival probability of a seedling experiencing successive fires in the study. Of particular interest was the point where young individuals reached a plateau of high survival probability (> 0.9), therefore reaching a stage with an expected persistence time of 10 years (Barot *et al.* 2002). Second, we estimated the probability of successful establishment into the resprout stage over the duration of the study period ('long term' survival). Using the best models arising from the selection procedure, we calculated for each species the probability that a seedling survived the four years of the sampling period and became a 4-year-old resprout (i.e. reached the R_3 stage), using averages of S_D and S_J over years for each age-class, as an indication of longer term survival.

Results

The model selection procedure consistently resulted in lumping of some of the demographic stages (Table S2). For all guilds, with the exception of 'forest species', seedlings showed different responses to resprouts. The best models for savanna species guilds (groups I–IV in Table 1) were always lumped: the R_2 class was lumped with either R_1, or R_3, or with both, so that we were able to classify resprouts of these species into two groups, 'young' and 'old' resprouts, respectively. This is not suggestive of an unreliable identification of the R_2 individuals since classification into this stage is automatic at two years after the seedling stage.

PATTERNS OF TEMPORAL VARIATION OF SURVIVAL WITHIN STAGES

For seedlings, only three patterns of temporal variation were found among the five possible (Table 2): full year dependency (model Y1) for three guilds, dry-season variability (model Y2) for two guilds and seasonal difference (model S1) for the remaining five guilds (Fig. 2 and Table S2). For resprouts, the dominant pattern of resprout survival was one of constant survival (Fig. 3 and Table S2). Only young resprouts of *Annona* and *Bridelia* showed a different pattern: *Annona* showed wet-season variability (Y3 pattern in Table 2), and *Bridelia* showed seasonal difference (S1 pattern in Table 2). There was a significant, positive relationship between dry-season survivorship S_J and the cumulative rainfall for the corresponding period for four of the five guilds showing year-to-year variability in S_J (Fig. 4a and Table S3). By contrast, there was no significant relationship between the wet-season survivorship S_D and the cumulative rainfall at the end of the wet season for the three guilds showing year-to-year variability in S_D (Fig. 4b and Table S3), except for *Bridelia* where the relation was negative. The wet-season survivorship S_D was greater than the dry-season survivorship S_J for the guilds showing seasonal difference in survival, except for *Psorospermum* (Fig. 2 and Table 3). The absolute decrease in survival probability between the fire season and the rainy season ranged between 0.16 and 0.58. This meant a relative decrease of survival probability of 19–82%.

CHANGES IN SURVIVAL PROBABILITY OVER TIME AND DEMOGRAPHIC STAGES

Survival probability increased with age: the yearly averaged survival probability of young and old resprouts was always greater than that of seedlings and young resprouts, respectively (Table 4 and Fig. 5). The only exception was 'forest species', for which no increase in survival with age was noticed. On average, the 'safe zone' with a yearly survival probability higher than 0.9 was reached after the second fire for *Crossopteryx*, *Piliostigma and Psorospermum*, after the third fire for *Terminalia* and *Pterocarpus*, after the fourth fire for *Annona*, *Bridelia*, *Cussonia* and 'other savanna species', and never for 'forest species' (Table 4). These figures changed dramatically when variability in seedling survival, either

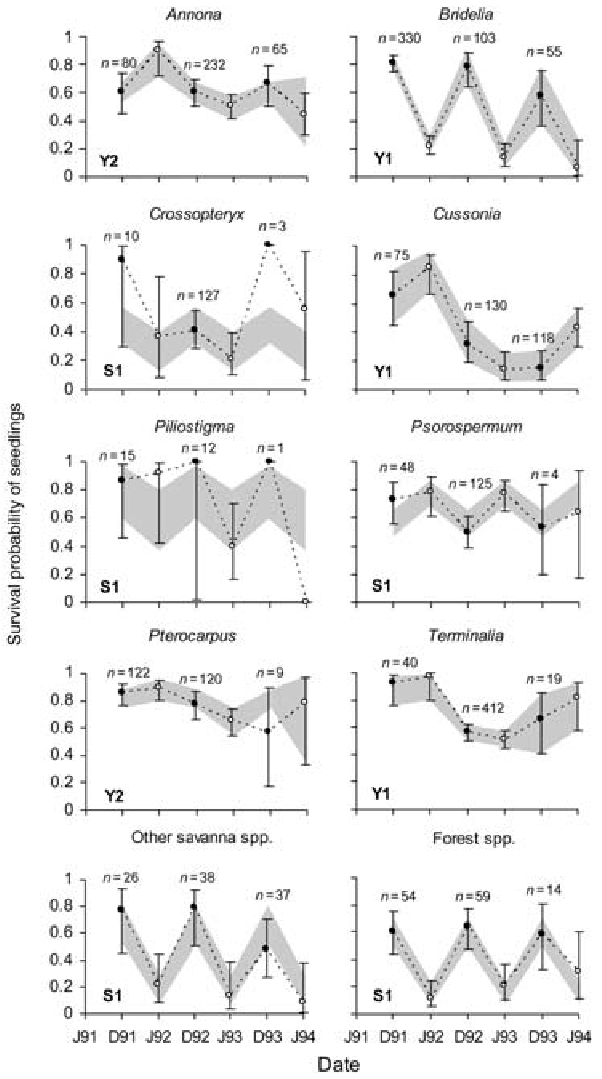

Fig. 2. Temporal variation of seedling survival probabilities for the 10 species guilds in the moist and fire prone savanna of the Lamto Research Station (Côte d'Ivoire). Solid symbols: S_D, survival over the July–December period (D, December). Open symbols: S_J, survival over the January–June period (J, June). Error bars represent the 95% confidence intervals of survival probabilities estimated with the most complex model, that is, S_D and S_J year-dependent (model Y1 in the Table 2). Grey areas represent the 95% confidence intervals of survival probabilities estimated with the best-fit model, whose code is specified in the lower-left corner of the graphs (Table 2 and Table S2). *n* is the number of seedlings found in June of the studied year.

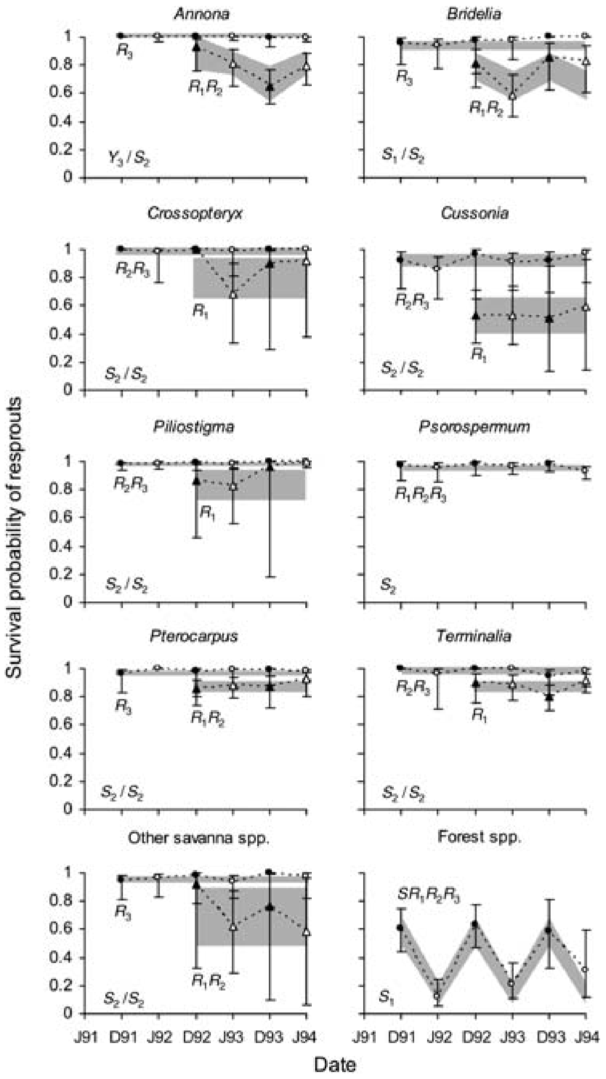

Fig. 3. Temporal variation of resprout survival probabilities for the 10 species guilds in the moist and fire prone savanna of the Lamto Research Station (Côte d'Ivoire). Legend as for Fig. 2. Age classes: *S*: seedling, R_1: 1-year < age < 2-years, R_2: 2-years < age < 3-years, R_3: age > 3-years resprout. R_1R_2, R_2R_3, $R_1R_2R_3$ and $SR_1R_2R_3$ mean that, respectively, [R_1 and R_2], [R_2 and R_3], [R_1, R_2 and R_3] and [S, R_1, R_2 and R_3] were clumped.

yearly or seasonal, was considered. Considering their average survival curve, guilds showing interannual variations in survival do not reach the safe zone before their third fire (Fig. 5, dotted lines, and Table 4). But if we take into account that the variation in survival at the seedling stage is linked to the rainfall pattern, seedlings are able to reach the safe zone even before their first fire in high rainfall years. By contrast, guilds showing seasonal variations in survival only gain one year or show no improvement when shifting from their lower survival curve to their upper survival curve (except possibly *Piliostigma*, but the uncertainty in the survival estimate is large) (Fig. 5, dashed curves). The final average yearly survival probabilities reached by R_3 resprouts were very high (Table 4), with only two guilds having survival probabilities lower than 0.9 (*Cussonia* and 'forest species'). The highest survival probability (0.995) was that of *Annona*, which corresponds to an expectancy of persistence time in this stage of 191 years (Barot *et al.* 2002).

LONG-TERM SURVIVAL

Different patterns of variation of survival probabilities at the seedling and resprout stages can produce similar long-term survivorships if antagonistic effects cancel out, hence the present analysis. Seedlings of *Pterocarpus*, *Piliostigma*, *Terminalia* and *Psorospermum* had the highest probability of surviving over the four years of the study (Fig. 6): 0.46, 0.42, 0.39 and 0.35, respectively. For *Annona*, *Crossopteryx*, 'other

Table 3. Differences in survival between seasons for species showing a seasonal effect on survival of seedlings or resprouts, and relative decrease in survival $(S_J - S_D)*100/S_D$

Stage	species	S_D	S_J	$S_J - S_D$	% decrease
Seedlings	*Bridelia**	0.72	0.14	–0.58	–82
	Crossopteryx	0.45	0.25	–0.20	–44
	Piliostigma	0.91	0.61	–0.30	–33
	Psorospermum	0.57	0.77	0.20	+35
	Other savanna sp.	0.66	0.16	–0.50	–76
Young resprouts	*Bridelia*	0.83	0.67	–0.16	–19
All	Forest sp.	0.61	0.17	–0.44	–72

Notes: S_D: wet-season survivorship; S_J: dry-season survivorship. *averaged over the three years of the study period.

Table 4. Average yearly survival probability and number of fires survived before reaching the 'safe zone' with survival probability > 0.9 (visually computed from Fig. 5). In Fig. 5, the average number of fires considers the fitted curve (lower curve when there are two), and the best case considers the first time (1) an error bar, or (2) the upper fitted curve when there are two, reaches the 0.9 survival zone

	Yearly average survival probability			Number of fires before survival probability > 0.9	
Species	Seedlings	Young resprouts	Old resprouts	Average	Best case
Annona	0.39	0.65	0.995	4	1
Bridelia	0.10	0.55	0.941	4	3
Crossopteryx	0.11	0.72	0.990	2	2
Cussonia	0.18	0.29	0.850	3–4	1
Piliostigma	0.56	0.78	0.983	2	0
Psorospermum	0.44	0.93	0.927	2	1
Pterocarpus	0.63	0.78	0.966	3	1
Terminalia	0.55	0.77	0.962	2–3	0
Other savanna sp.	0.11	0.53	0.932	4	3
Forest sp.	0.11	0.11	0.107	∞	∞

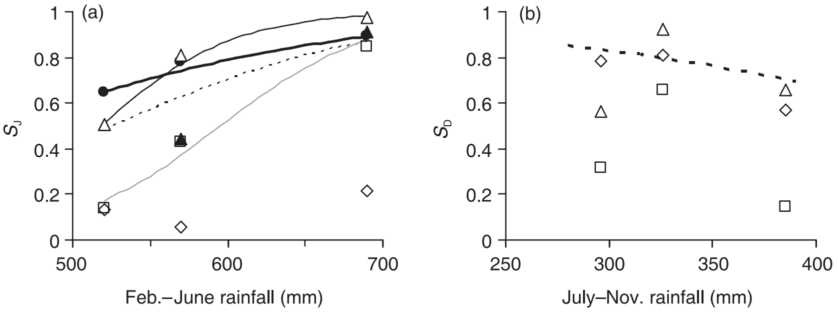

Fig. 4. Survival probabilities of seedlings as a function of rainfall, for the species with year-to-year variability on (a) dry-season survival S_J or on (b) wet-season survival S_D in the moist and fire prone savanna of the Lamto Research Station (Côte d'Ivoire). Symbols represent survival probabilities estimated with the year-dependent MRR models for *Annona* (▲), *Bridelia* (◇), *Cussonia* (□), *Pterocarpus* (●) and *Terminalia* (△). Lines represent the dependence of survival on rainfall as predicted by rainfall-dependent MRR models (Table S3): *Annona* (······), *Bridelia* (......), *Cussonia* (—), *Pterocarpus* (—) and *Terminalia* (—).

savanna species', *Cussonia* and *Bridelia*, these probabilities were only 0.13, 0.05, 0.04, 0.04 and 0.03, respectively. 'Forest-species' seedlings only had a 0.0001 probability of surviving four years, and they were the only species showing no stabilization of their survival probability with time. It took between two and three years for all other guilds to reach a plateau in survival probability.

Discussion

The range of annual survival probabilities obtained here (0.1–0.63, Table 4) is comparable to survival probabilities obtained for other savanna trees (Hoffmann 2000; Radford *et al.* 2001; Setterfield 2002; Williams 2004), for savanna perennial grasses (Silva & Castro 1989; Silva *et al.* 1990; O'Connor 1991; Garnier & Dajoz 2001), for temperate forest trees (de Steven 1991; del Val *et al.* 2007) and for tropical rainforest trees (Henkel *et al.* 2005; Paz *et al.* 2005; Queenborough *et al.* 2007). For all species in our study, except 'forest species', the survival probability reaches a plateau after 2–3 years (Fig. 5) where survival is comparable to adult survival probabilities, if not higher (Hochberg *et al.* 1994; Watson *et al.* 1997; Hoffmann & Solbrig 2003). This clearly demonstrates that the resprout stage is a persistence stage *sensu* Bond & Midgley (2001).

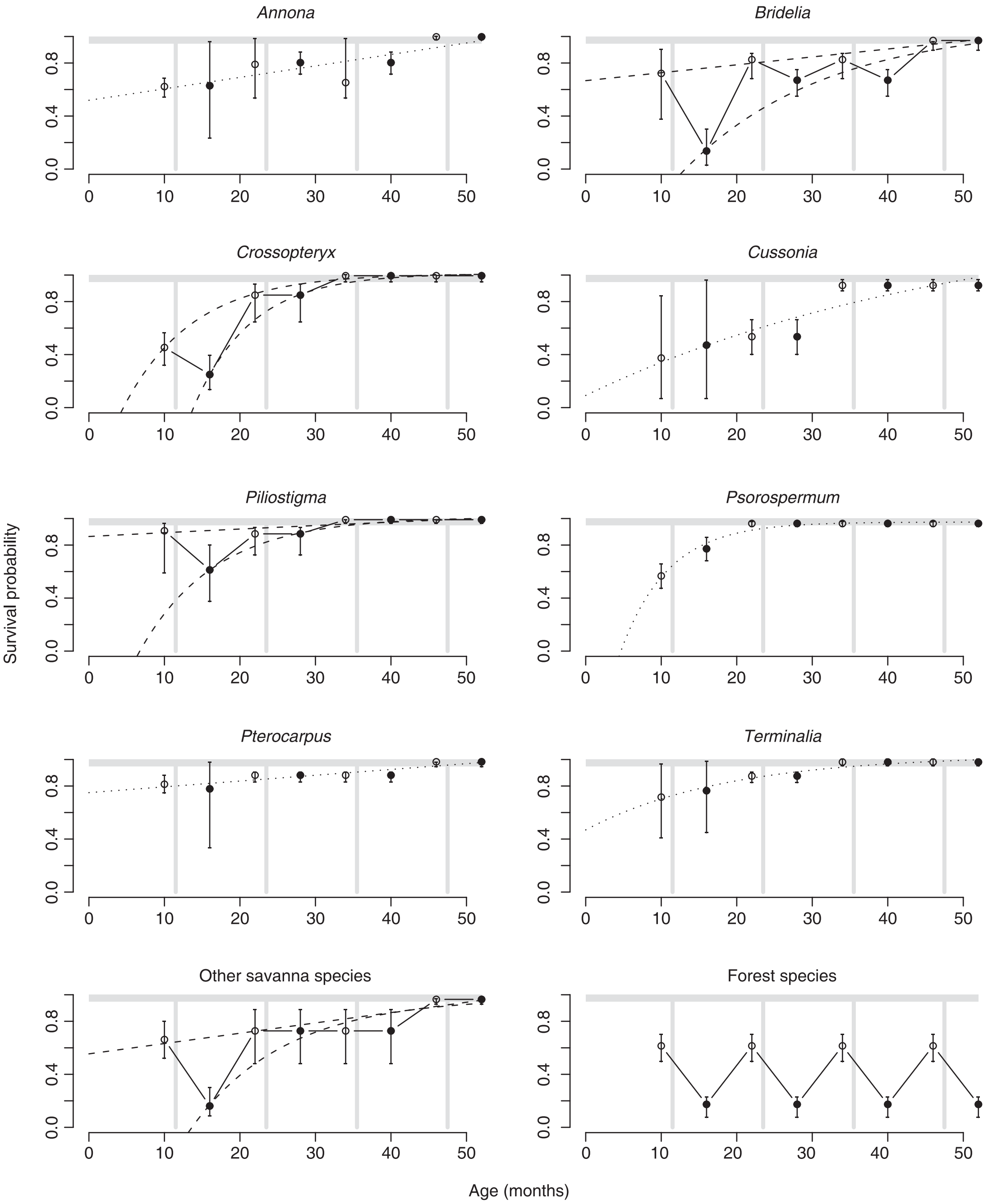

Fig. 5. Dynamics of survival probability during the first years of a tree's life. Open symbols: S_D; Solid symbols: S_J. Stages were converted to age in months assuming that seedlings had emerged four months before the first census. Fire occurrence is indicated by vertical grey lines. Probability estimates for a single stage were averaged over the study period when variable. Error bars report the confidence intervals estimated from the models of Figs 2 and 3. The grey-shaded area at the top of the graphs represents the 'safe zone' where yearly survival probability is above 0.9, granting a minimal life expectancy of 10 years. Two types of graphs were drawn: (i) for species showing year-to-year variations in survival at the seedling stage (patterns Y1 and Y2: *Annona*, *Cussonia*, *Psorospermum*, *Pterocarpus*, *Terminalia*), a single model (dotted line) was fitted to data and the error bars represent the widest possible variation in survival, as affected by rainfall or simple year-to-year variation; and (ii) for species showing seasonal variations in survival at the seedling stage (pattern S1: *Bridelia*, *Crossopteryx*, *Piliostigma*, 'other savanna species' and 'forest species' – shown with a solid line linking symbols), two models were fitted when possible (dashed lines), (i) the top line was fitted on the S_D data to estimate the background 'wet season' survival rate; and (ii) the bottom line was fitted on the S_J data to estimate the comparatively lower 'dry season' survival rate. Models used were either an asymptotic model with equation $y = a(1 - e^{-b(x-c)})$ where y is survival probability, x is age in months and a, b and c are parameters or, when convergence was not achieved, a simple regression line. Details of statistical fits are not shown as these models were only used as a visual help to differentiate patterns.

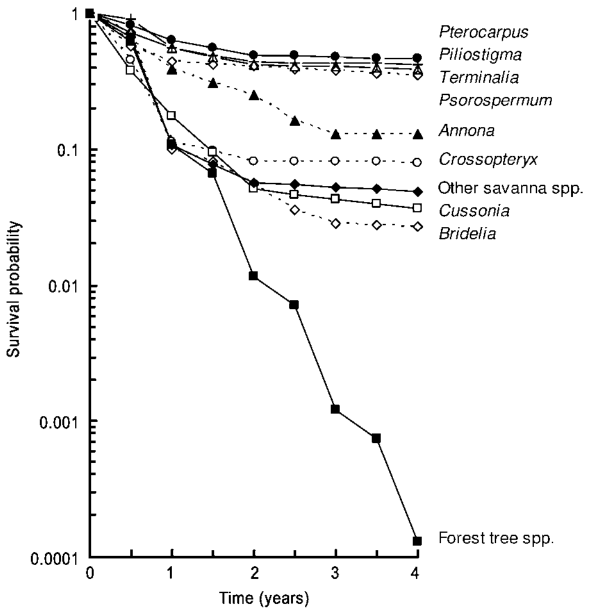

Fig. 6. Long-term cohort survival of 4-month old seedlings for the 10 species guilds in the moist and fire prone savanna of the Lamto Rresearch Station (Côte d'Ivoire).

Furthermore, the species studied here show responses to environmental factors that are specific to savannas and may explain the exclusion of forest tree species and the pattern of abundances of savanna tree species.

THE RELATIONSHIP OF SEEDLING AND YOUNG RESPROUT SURVIVAL TO FIRE AND CLIMATE

We identified a very clear dichotomy between two main patterns of seedling survival (Fig. 2). Seedlings either displayed strong seasonal variation in survival, oscillating between a high and a low survival, or interannual variation in survival, always related to rainfall. *Bridelia* was the only guild to display both patterns. A positive response of dry-season survival S_J to rainfall during the early wet season (Fig. 4) can only be a response to early-wet-season drought or dry spells, because fire intensity, the alternative possible source of interannual variation, could not be related to rainfall events occurring *after* the fire. We can thus state that guilds responding to early-wet-season rainfall are more affected by drought than by fire. On the other hand, an oscillating pattern with a high wet-season survival S_D and a low dry-season survival S_J could be due to the long drought during the dry season or to fire. Fire is more likely to be responsible for this pattern because: (i) if drought played a role, then we would expect a positive response to rainfall as in the previous case; and (ii) all savanna tree species studied here are deciduous species, and hence in a dormant state during the long dry season (Simioni *et al.* 2003). Our parsimonious interpretation is that (i) an oscillating pattern is mainly caused by fire; and (ii) a negative response to early-wet-season rainfall is mainly caused by dry spells occurring during this period. Further testing is required to properly disentangle the confounded effects of fire and drought on seedling survival. A factorial fire-irrigation experiment, using the same demographic approach as in this study, would provide greater insights. Plots that remained unburned during one year would be subject to drought mortality only, while irrigated and burned plots would be subject to fire mortality only. Other approaches for assessing whether seedlings are alive just after the fire could also be considered, for example, heavy irrigation just after fire to induce faster regrowth or destructive sampling of subsets of seedlings to examine if their tissues are alive.

Contrary to all other rainfall-responding guilds, *Bridelia* showed a decrease in survival with increasing rainfall over the late wet season (Fig. 4). This may result from a high sensitivity to competition with grass which reaches 100% cover in May–June (Menaut & César 1979). In wetter years, grass biomass actually builds up more quickly (Gignoux *et al.* 2006b; Le Roux *et al.* 2006) and could increase competition for light, affecting the survival of *Bridelia* seedlings. Competition with grass could also explain the inverted oscillation pattern of *Psorospermum* (Fig. 2) given that this species would be so sensitive to competition for light that it actually better survives the dry season drought and the fire than the competition with fully grown grass over the second half of the year.

Based on these premises, we classified our guilds in three (non-exclusive) groups:

1 Fire-sensitive guilds, which can be ranked according to the difference between their wet-season and dry-season survival probabilities (Table 3) on a scale of increasing fire sensitivity: *Bridelia* (young resprouts) < *Crossopteryx* < *Piliostigma* < 'forest species' < 'other savanna species' < *Bridelia* (seedlings).

2 Early-wet-season (EWS) drought-sensitive guilds (*Annona*, *Cussonia*, *Pterocarpus*, *Terminalia*). Water stress only occurred during this period (Le Roux *et al.* 2006), and wet-season water shortage was reported to negatively affect seedling survival or establishment in a modelling study (Higgins *et al.* 2000) and an experiment in the Brazilian cerrado (Hoffmann 1996).

3 Guilds sensitive to competition with grass (*Bridelia* and *Psoropsermum*).

We consider reaching a 'safe zone' where yearly survival is above 0.9 as a proxy for entering the persistence stage given that average persistence time in this stage is at least 10 years (Barot *et al.* 2002). EWS drought-sensitive guilds seem to rely on climate variability for successful recruitment into the persistence, resprout stage. On average, the least fire-sensitive guilds (*Crossopteryx* and *Piliostigma*) do better than the EWS drought-sensitive guilds in quickly reaching the safe zone, but they are slower in high-early-rainfall years. The most fire-sensitive guilds (*Bridelia*, 'other savanna species' and 'forest species') do worse in any case.

The growth-resistance trade-off predicts that fire-resistant species should be more sensitive to competition. However, our competition-sensitive group of guilds contains one of the most fire-sensitive guilds (*Bridelia*). Instead, the two dominant and apparently exclusive patterns are the EWS drought-sensitive and fire-sensitive patterns. Investing into below-ground storage organs theoretically might provide resistance to fire as well as to EWS drought. Sensitivity to drought and to fire are often correlated in tropical tree seedlings (Bowman & Panton 1993; Hoffmann *et al.* 2004). Our results do not support the growth-resistance trade-off. The mechanism that determines the two survival syndromes is unknown but could be related to root architecture. There is weak support for this given the contrasted root morphologies and water extraction strategies of *Cussonia* and *Crossopteryx* (César & Menaut 1974; Le Roux & Bariac 1998), however, the topic requires further investigation.

ARE GROUPS OF TREE SPECIES EXCLUDED FROM THE SYSTEM BECAUSE OF THEIR INABILITY TO SURVIVE THE FIRST FIRE?

Seedlings of 'forest species' had a relatively high survival during the wet season, suggesting that forest tree species could establish in savannas, as it has occurred in other areas (Bowman & Panton 1993). By contrast, their survival probability was among the lowest during the dry season and early wet season. The apparently more stressful open-light environment in savannas, causing greater water stress (Hoffmann *et al.* 2004) or nutrient limitation (Bowman & Panton 1993), has often been proposed to explain the lower survival of forest-tree seedlings, but fire almost always kills forest tree seedlings (Bowman & Panton 1993; Hoffmann 2000; Hoffmann *et al.* 2004).

'Forest species' were the only species to show no increase of survival probability at resprout stages and their survival probability never reached a plateau (Fig. 5). As a consequence, fewer than one in 10 000 'forest-species' seedlings survive as long as four years, compared with approximately 200 seedlings of those savanna species with the lowest long-term survival (Fig. 6). If fires were suppressed, our estimates of 'forest-species' seedling and resprout survival would predict a 4-year survival probability of 0.02, that is, equivalent to all other savanna tree species. 'Forest species' are thus characterized by an inability to build up a resistance to fire over time, unlike savanna tree species, including those which had very low initial survival probabilities (e.g. *Crossopteryx*, Fig. 5). Our results confirm previous demographic studies comparing seedlings or resprouts of forest and savanna trees, conducted in Brazilian and Australian savannas (Hoffmann 2000; Fensham *et al.* 2003), highlighting the considerable influence of fire on the composition of these plant communities (Trapnell 1959; Hoffmann *et al.* 2004). In the absence of fire, forest tree species might rapidly invade savannas, as it has been shown in many fire protection experiments (e.g. Brookman-Amissah *et al.* 1980; Devineau *et al.* 1984; Swaine *et al.* 1992) and suggested in recent larger-scale studies (Bond *et al.* 2005; Sankaran *et al.* 2005).

The absence of any stabilisation of survival at the resprout stage for forest tree species means that latency time of these species, or the time needed to build up reserves in order to resist the first disturbance event at the seedling stage, is longer than the time between two successive fires; otherwise, the reserves accumulated after one growing season would give resprouts an advantage compared to seedlings and we should observe an increase in survival with time. Latency times could theoretically be estimated from curves such as those in Fig. 5 (latency time is equal to the x-intercept of the lower survival curve for guilds having two curves), but the uncertainty in our survival estimates and in the extrapolation of the curve makes this practically impossible in our case. An experiment designed to measure latency time would allow estimation of the fire-return interval needed for forest trees to invade the savanna. The latency time best explains the major difference in survival patterns observed between forest and savanna tree species. It creates a threshold effect: if the latency time is shorter than the time to the first fire, the seedlings can survive; if it is longer, they cannot survive. The exclusion of forest species from the savanna at the very first stage of their life is easily explained by a latency time that is too long relative to the high fire-frequency observed in Lamto. Forest species are well known for investing much less in their root system than savanna species (Hoffmann & Franco 2003; Hoffmann *et al.* 2004), hence the long latency time is probably due to the growth-resistance trade-off.

DOES THE PATTERN OF EARLY SURVIVAL CORRELATE WITH THE HIERARCHY OF ABUNDANCES OF SAVANNA SPECIES?

The demographic parameters studied in this paper (seedling survival probability (Fig. 2 and Table 4), resprout survival (Fig. 3 and Table 4), long term survival (Fig. 6), type of variability (to fire or to rainfall: Figs 2 and 5)) provide a framework for classifying tree species guilds. None of these classifications matches the abundance groups of Table 1, recorded at the adult stage. For example, (i) two of the dominant species had the lowest survival probabilities at the seedling stage (*Bridelia* and *Crossopteryx*). Walters and Milton (2003) also found this reversed dominance between the juvenile and adult tree stage for two *Acacia* species in a South African savanna; (ii) individuals of the species with the highest resprout survival probability, *Annona*, are often trapped in the resprout stage and very rarely recruit as > 2 m trees (Table 4); (iii) *Cussonia*, a dominant species at the adult stage, has the lowest resprout survival probability of savanna guilds (Table 4); and (iv) three of the dominant species showed variations in seedling survival in response to fire and only one in response to rainfall.

Inability to predict adult abundance from early life survival parameters is probably because adult tree abundance depends more on other factors, like the recruitment from the resprout stage to adult trees. Successful recruitment to the resprout stage is necessary for species maintenance in the savanna community but successful recruitment from the resprout stage to the adult stage is required for a species to achieve dominance. Those species that do not recruit beyond the resprout stage are caught in the fire trap.

Therefore, savanna species could be classified into three groups: (i) excluded forest species that are unable to pass the first disturbance event and hence to *enter* the resprout stage – only present as < 1-year old seedlings (group V, Table 1);

(ii) a first subset of savanna species that are able to pass this first barrier, but are seldom able to *exit* the resprout stage successfully as adults – mostly present as resprouts (group II); and (iii) a second subset of 'true' savanna species that are able to both enter and exit the resprout stage and recruit as adult trees under the fierce disturbance regime of savannas – dominant in the adult tree community (groups I and, possibly, III).

These patterns hold as long as a high-frequency fire regime (one fire per year), characteristic of Lamto savannas, is maintained. A single year without a fire has dramatic impacts on seedling and tree recruitment in Lamto savannas, which can explain the occasional appearance of adult trees of group II or the switch of portions of the landscape to savanna woodlands (group III species). Furthermore, in areas where fire is excluded, because grass has been excluded through competition for light in densely wooded areas, forest species tend to invade and out-compete savanna species. Both cases have been observed in Lamto (Gignoux *et al.* 2006b).

Conclusion

Our key findings are (i) the existence of two alternative patterns of seedling survival, suggesting differing sensitivities to fire and early-wet-season water shortages; (ii) the exclusion of forest species from the savanna at the seedling stage because of a structural inability to stabilize their survival probability at the following resprout stage, and (iii) the absence of a simple relation between savanna species abundances and early life survival patterns. Result (i) is not related to the growth-resistance trade-off hypothesized earlier, but might arise instead from differences in root architecture, a hypothesis which requires further investigation. Result (ii) supports the existence of the resistance-growth trade-off and of a latency time to persistence. Further understanding would require specific experiments aimed at precisely measuring and comparing the allocation strategies of forest and savanna species, and estimating the latency time using, for example, experimental burnings of seedlings of known age. Result (iii) recalls that the life cycle of savanna trees is complex due to the interaction of the species growth and development strategies and the existing disturbance regime.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Species composition of the 'forest species' and 'other savanna species' guilds.

Table S2. Modelling survival probabilities per age-class for the 10 species with S_D, survival over the July–December period and S_J, survival over the January–June period.

Table S3. Modelling survival probabilities of seedlings as a function of rainfall for the species with year to year variability.