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Alternative fire resistance strategies in savanna trees

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Abstract Bark properties (mainly thickness) are usually presented as the main explanation for tree survival in intense fires. Savanna fires are mild, frequent, and supposed to affect tree recruitment rather than adult survival: trunk profile and growth rate of young trees between two successive fires can also affect survival. These factors and fire severity were measured on a sample of 20 trees near the recruitment stage of two savanna species chosen for their contrasted fire resistance strategies (*Crossopteryx febrifuga* and *Piliostigma thonningii*). *Crossopteryx* has a higher intrinsic resistance to fire (bark properties) than *Piliostigma*: a 20-mm-diameter stem of *Crossopteryx* survives exposure to 650°C, while *Piliostigma* needs a diameter of at least 40 mm to survive. *Crossopteryx* has a thicker trunk than *Piliostigma*: for two trees of the same height, the basal diameter of *Crossopteryx* will be 1.6 times greater. *Piliostigma* grows 2.26 times faster than *Crossopteryx* between two successive fires. The two species have different fire resistance strategies: one relies on resistance of aboveground structures to fire, while the other relies on its ability to quickly re-build aboveground structures. *Crossopteryx* is able to recruit in almost any fire conditions while *Piliostigma* needs locally or temporarily milder fire conditions. In savannas, fire resistance is a complex property which cannot be assessed simply by measuring only one of its components, such as bark thickness. Bark properties, trunk profile and growth rate define strategies of fire resistance. Fire resistance may interact with competition: we suggest that differences in fire resistance strategies have important effects on the structure and dynamics of savanna ecosystems.

Key words *Crossopteryx febrifuga* · *Piliostigma thonningii* · Recruitment · Fire temperature · Humid savanna

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Introduction

Fire is increasingly being recognized as a major disturbance affecting all ecosystems in the world, even those that had not seemed fire-prone, such as humid tropical forests (Whitmore and Burslem 1996). Through ecosystem fragmentation and change in fire regimes, human activity causes formerly fire-free ecosystems to come into contact with fire-prone ones, enabling even mild fire to spread into former fire-free (and hence very sensitive) ecosystems (Uhl and Kauffman 1990). In savannas, trees do not normally burn, but most offspring, saplings and young individuals suffer from the running fires, which destroy almost all the aboveground grass phytomass and lead to the apparently stable coexistence of grasses and trees (Menaut 1983). Most studies apply at the stand level and do not explain the mechanisms of fire resistance, which must be studied at the scale of the individual plant.

Fire is more intense in wet savannas than in dry savannas, where lower water availability leads to lower grass, i.e. fuel load, production. Fire is thus expected to control tree/grass interactions in wet savannas (Frost et al. 1986). In West Africa, it has been hypothesized that the maintenance of wet savannas at latitudes where climatic conditions are favourable to rainforests is due to fire (Monnier 1968). Fire has been shown to prevent tree invasion in a number of fire exclusion experiments: unburnt savannas quickly evolve to densely wooded formations, where savanna tree species are eventually displaced by forest species (Vuattoux 1970, 1976; Brookman-Amissah et al. 1980; Devineau et al. 1984; San Jose and Fariñas 1991; Swaine et al. 1992). Surprisingly, apart from these ecosystem-level experiments, few studies on the direct effect of fire on individual savanna trees have been conducted to analyse the mechanism by which fire affects tree populations. Even for forests, studies addressing the question of fire resistance of individual trees are rare (Gill and Ashton 1968; Vines 1968; Uhl and Kauffman 1990). Most studies usually deal with seed germination (Auld and O'Connell 1991; Ernst 1991; Moreno and Oechel 1991b; Pierce and Cowling 1991; Granström and Schimmel 1993; Lamont et al. 1993; Tyler 1995), tree survival (Moreno and Oechel 1991a; Glitzenstein et al. 1995), or resprouting (Gratani and Amadori 1991; Kauffman 1991; Ab Shukor 1993; Morrison 1995), and grass recovery (Silva and Castro 1989; Robberecht and Defossé 1995).

Savanna fires are frequent, usually occuring every 1–5 years in wet savannas (Frost and Robertson 1985). Fuel load typically ranges between 2.0 and 10.0 tha^{-1} (Hopkins 1965; Lacey et al. 1982; Stronach and MacNaughton 1989; Menaut et al. 1991; Mordelet 1993). The fire front is narrow and moves quickly: temperature measurements using thermocouples show that any given point is usually exposed to temperatures above 100°C for less than two minutes (Monnier 1968; Stronach and MacNaughton 1989; Miranda et al. 1993). Flame height is usually 2–3 metres high (Frost and Robertson 1985), although very variable. During fire, maximum temperatures are usually encountered between 0 and 50 cm above the ground (Pitot and Masson 1951; Miranda et al. 1993). In the soil, temperature rise quickly becomes negligible with depth, with no significant rise below 5 cm (Coutinho 1982; Bradstock and Auld 1995). Savanna fires can be considered as relatively mild compared to forest fires (Bessie and Johnson 1995). They burn the grass layer and the young trees included in it, leaving adult trees alive, affecting only tree recruitment and not adult survival.

Like forest trees, adult savanna trees can resist fire through adaptations such as thick bark and high ability to resprout from belowground organs. But the regularity of savanna fire, the low flame height, and the short time of exposure to flame give adult trees other possibilities of resistance: leaf fall occuring during the dry season minimizes the chance of a crown fire; once a tree overgrows the grass stratum, most of its buds are located well above the flames, where the vegetal matter is not ignited and hardly heated (Frost and Robertson 1985); thick stems have a higher survival in low-intensity fires than small stems in fire-tolerant species (Morrison 1995).

Before young trees can reach the "safe" zone above the grass layer, they have to survive within the fuel bed where fire intensity is concentrated. Based on architectural descriptions of trees, César and Menaut (1974) have 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 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 (1) reaching a height where the terminal buds are able to resist the existing fire conditions, and (2) thick enough at its base to resist the high fire intensity 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.

The aim of our study was to measure the response of young trees to fire in natural conditions, in order to help understanding how fire affects tree recruitment and which mechanisms are able to produce the architectural differences observed by César and Menaut (1974). We conducted a field experiment to measure the ability of young trees of two different species to resist fire, by measuring the height of the part of their trunk still alive after fire in relation to the temperature profile near their trunks. Data from a demographic study of tree populations were used to produce estimates of the maximum height a tree can reach between two successive fires.

Methods

Study site and characteristics

All the data were collected at the Lamto Research Station, in Côte d'Ivoire (West Africa: 5°02′W, 6°13′N; site description in Menaut and César 1979). Lamto savannas are located at the edge of the rainforest (annual rainfall *c.* 1200 mm). They are burnt every year. The main vegetation type in Lamto is a tree/shrub savanna. The maximum height of the grass stratum at the date of the fire is *c.* 2 m.

We selected two of the four dominant tree species (which account for *c.* 90% of the cover) for this experiment: *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. (Rubiaceae), and *Piliostigma thonningii* (Schum.) Milne-Redhead (Cesalpiniaceae). These species have pronounced resprouting abilities (J. Gignoux, unpublished work). Recruitment of all tree species was observed to occur when trees overgrew the grass layer, i.e. when they reached a height of 2 m, because fire conditions are milder for the buds above this height (Menaut and César 1979).

Piliostigma seems to behave according to the hide-and-resprout strategy, while *Crossopteryx* seems to follow the stay-and-resist strategy (César and Menaut 1974). Barks are relatively thin for fire-resistant species [mean and SE at ground level, $N = 5$: 8.2 ± 0.7 mm for *Crossopteryx* and 8.1 ± 0.8 mm for *Piliostigma*; see Gill and Ashton (1968) and Brookman-Amissah et al. (1980) for comparison].

Data collection

Demographic data

We used these data to estimate the maximal size that resprouts can reach within one growing season.

The data were collected on five 0.25-ha savanna plots of shrubby savanna where all individual trees (including seedlings and very small individuals) were mapped, tagged and measured (height, number of stems) in December 1992, just before the fire. The data are part of a long-term demographic study of the savanna trees in Lamto. For all species, fire scars on perennial stems enable to distinguish the stems of the year from older ones. Three stages were thus defined for all tree species: (1) *seedlings* (defined by the presence of cotyledons, or the appearance on a previously vacant place correlated with small size), (2) *resprouts* (individuals with no aboveground perennial structures), and (3) *adult trees* (individuals with aboveground perennial structure, i.e. with a trunk resisting fire). We were interested in the acquisition of a trunk by the tree enabling it to resist fire without having to resprout from its base: this corresponds exactly to the recruitment from resprout to adult stage.

Experiment on resistance of trees to fire

Tree sample

This experiment was conducted on 20 small *Crossopteryx* trees and 20 small *Piliostigma* trees. The trees were chosen in the savanna surrounding one of the plots of the demographic survey (systematic sampling on size and architecture criteria: individuals should be around 2 m in height, and preferably with a young perennial trunk, since between-year fire variability might delay the successful establishment of such a trunk; this last constraint resulted in samples with different average heights for the two species). *Crossopteryx* trees were between 1.1 m and 2.6 m high (measured to the nearest 10 cm), and all *Piliostigma* trees were between *c*. 2 m and 3 m.

Measure of fire severity

We used temperature to characterize fire because it is the easiest variable to measure (Hobbs et al. 1984), and because our purpose is not to precisely characterize fire physics, but simply to obtain a record of its intensity as experienced by the plants. The cost associated with the great number of measurements needed precluded the use of thermocouples. We used thermo-sensitive paints, pencils and stickers to measure temperature.

An iron pole equipped with thermal tags was placed next to every tree, as near to the trunk as possible, but without direct contact. Six thermal tags were attached with an aluminium wire to each pole, at six different heights: 0, 25, 50, 80, 130 and 200 cm. The choice of these heights was based on the well-established fact that maximum temperatures are usually encountered between 0 and 50 cm above the ground (Pitot and Masson 1951; Miranda et al. 1993). The tags were set at least 5 cm apart from the pole, and had only one contact point with the wire, to minimize direct heat transfer from the pole to the tags. Thermal tags consisted of 2 × 8 cm, 0.8-mm-thick pieces of aluminium marked with thermo-sensitive stickers, pencils and paints (Thermax). These thermo-sensitive markers show an irreversible colour change at fixed temperatures. Different markers were used in order to span the whole range of temperatures from *c*. 30°C to 660°C (melting point of aluminium). There were 14 temperature changes: 77°C, 99°C, 120°C, 165°C, 195°C, 245°C, 295°C, 315°C, 335°C, 360°C, 450°C, 505°C, 595°C, and 620°C. The colour change included an exposure time component: a higher temperature is needed to cause a colour change when the duration of exposure is shorter (Hobbs et al. 1984). We considered this time effect as negligible, because our measurement scale was accurate only to the nearest 20°C at best, and because exposure times were always short (never more than 5 min) compared to the time scale studied by the manufacturer (5 min–1 h). Temperature changes indicated by different markers (stickers vs. pencils and pencils vs.paints) were sometimes (but rarely) inconsistent, due to differences in response times (pencils and stickers). Temperatures were recorded as soon as possible after the fire (the longest delay was 48 h).

Grass phytomass (fuel load) before the fire was 4.4 t ha^{-1} (Le Roux, unpublished work).

Measure of tree resistance

At the individual tree level, the ability to survive fire depends on the protection of living tissues and the ability to rebuild destroyed tissues. The protection of buds and cambium in fire-resistant tree species depends on various bark properties, but bark thickness seems to be the most significant one (Vines 1968, Vines 1981; Uhl and Kauffman 1990). However, observations of savanna species from the Guinean bioclimatic zone show that the most fire-resistant species do not necessarily have the thickest barks (Brookman-Amissah et al. 1980). There is also a size effect in fire-resistance: small stems have a higher mortality than big stems (Morrison 1995). This effect of size can be explained only in two ways:

1. Stem diameter is positively correlated with bark thickness, and is just an indirect measure of it.
2. For stems of a small diameter exposed to fire on all sides, the cambium is not only directly heated through the bark, but also heated by energy coming through the stem from the opposite side. The bigger the stem, the lower this effect is. Big stems therefore need either a longer duration of exposure to flame or a higher flame temperature than small stems for the cambium to reach the lethal temperature, even if bark thickness is equal.

In both cases (and because a negative correlation between stem diameter and bark thickness is most unlikely), stem diameter is enough to measure tree resistance. As bark thickness measurements depend on drilling a core from the plant, which could affect its resistance to fire, we used stem diameter as the variable measuring resistance to high temperatures. At the height of the thermal tags, trunk diameters were measured to the nearest millimetre using a calliper rule.

Three months after the fire, at the beginning of the growing season, the height of the attachment of the highest living branch (hereafter referred to as *regrowth height*) was recorded for every tree, as well as the diameter of the trunk corresponding to this height (*regrowth diameter*).

This experiment was conducted during the 1992–1993 dry season.

Statistical analyses

We used regression analysis, covariance analysis, and nonlinear function fitting. All the analyses were performed with the SAS statistical package (PROC GLM, PROC REG, PROC NLIN procedures; SAS Institute 1990).

Results

The main effect of fire on small trunks is to kill the cambium of the tip of the stem beyond a certain diameter, or above a certain height – the regrowth height. Trees can limit the portion of the stem affected by cambial death by (1) having a high “intrinsic” resistance, i.e. by some special adaptation of the bark (thickness or composition), (2) having a thick stem, i.e. with an open top angle if the stem is considered conical, (3) having a high growth rate enabling them to reach a large diameter within one growing season.

We addressed these points by (1) building species-specific lethal temperature curves, (2) building species-specific height × diameter relations, and (3) estimating the difference between the two species in maximum size reached by resprouts in one growing season. Such data enabled us to determine the relation between tree size, fire temperature, and regrowth height after fire for each species.

Lethal temperature curves

At each measurement point along a stem, we can classify the stem as alive or dead by comparing the height of the measurement point to the tree's regrowth height. Dead measurement points higher than the first dead point (counted from the base of the trunk) were discarded, because they died from a cause other than the temperature they suffered (they died because a lower point of the trunk suffered a lethal temperature). This resulted in a group of live measurement points which resisted the temperature they experienced, and a group of dead points which died from exposure to a lethal temperature (Fig. 1).

In each temperature class we searched for the diameter separating the group of dead points from the group of live points. For simplicity, we used the median between the maximum diameter of the dead points and the minimum diameter of the live points as the lethal diameter at a given temperature. The lethal temperature curve is then computed as the regression line over these midpoints (Fig. 1): at high temperatures (650°C), a *Piliostigma* stem needs a diameter almost twice the size of a *Crossopteryx* stem to resist fire. *Crossopteryx* thus has a higher intrinsic resistance to fire than *Piliostigma.*

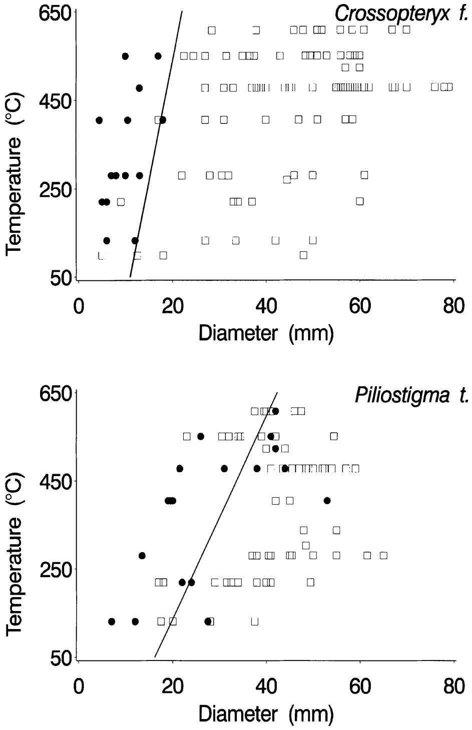

Fig. 1 Lethal temperature curves of *Crossopteryx* and *Piliostigma.* *squares* measurement points still alive after fire *dots* measurement points that died because of the temperature they endured. The *line* is the regression of diameter against temperature separating the two groups of points (regression on the midpoints of the maximum-diameter dead point and the minimum-diameter live point at each temperature). Regression for *Crossopteryx*: diameter = 10 + 0.0186 temperature ($R_2 = 0.36$; $F = 2.84$ with 1 and 5 *df*; $P = 0.1530$); for *Piliostigma*: diameter = 14 + 0.0436. Temperature ($R_2 = 0.75$; $F = 17.96$ with 1 and 6 *df*; $P = 0.0055$). These regressions are only a way to demonstrate the separation between the two groups of points on the graph, and are not intended to be predictive

Trunk profiles of each species

For a given trunk size, a particular profile (relationship between height along stem and sectional diameter) may induce a higher fire resistance than another. We performed an analysis of covariance with sectional diameter (dependent) as a function of height along stem (covariate), species, and individual (Table 1). If the height × diameter relationship is species-specific, we expect no significant variation of the slope with the individual, but a significant variation with species. Intercepts can vary with individuals, as they only measure tree size (basal diameter).

If the whole data set is used, all effects are significant, meaning that the height × diameter profile is species-specific, but also depends on the individual (Table 1). However, many trees in our sample had irregularities at the base of their trunk. We therefore repeated the analysis without the ground-level data (height along stem > 0), and the significant effect of individual on slope vanished in both species (Table 1).

The estimated slopes of the height × diameter regressions (± SE) were −0.0317 ± 0.0012 for *Crossopteryx* and −0.0196 ± 0.0007 for *Piliostigma.* These slopes are species-specific constants describing trunk profiles, i.e. they describe shape independently of size. From these values, estimates of the half-top angle of the trunk idealized as a cone (more meaningful than slope

Table 1 Height/diameter relationship for trees in the experiment on resistance to fire. Sectional diameter was the dependent variable, height along stem (*H*) the covariate, and species (*S*) and individual tree (*SI*, individual nested into species) the two factors. A first analysis included all data, and a second one included heights above ground level only (because many trees had an irregular profile at their base, due to root insertion). Results of the second analysis were confirmed by two separate analyses, performed on each species separately, where all effects are significant but the HI effect ($F = 1.63$ with 19 and 53 *df*, $P = 0.0816$ for *Crossopteryx*; $F = 1.05$ with 19 and 60 *df*, $P = 0.4236$ for *Piliostigma*)

Analysis	Source of variation	Sum of squares	*Df*	*P*
All heights	Intercept	3155	1	0.0001
	S	79	1	0.0001
	SI	87	38	0.0001
	H	622	1	0.0001
	HS	63	1	0.0001
	HSI	38	38	0.0010
	Residual	74	153	
	Total	4243	233	
Heights > 0 only	Intercept	1623	1	0.0001
	S	25	1	0.0001
	SI	33	38	0.0001
	H	343	1	0.0001
	HS	25	1	0.0001
	HSI	14	38	0.0653
	Residual	29	113	
	Total	2616	193	

since this angle directly measures stem "thickness") can be computed [the angle is equal to $tg^{-1}(-\text{slope}/2) \cdot 180/\pi$]: 0.91° for *Crossopteryx* and 0.56° for *Piliostigma*. *Crossopteryx* individuals have a thicker stem, i.e. a basal diameter equal to 1.6 times that of a *Piliostigma* of the same height: this should render *Crossopteryx* a more fire-resistant species.

Size reached by resprouts in one growing season

From the demographic data, we can estimate the size (measured as total height) distribution of the resprouts of both species (Fig. 2). The total height of resprouts is a measure of their growth rate, because they lack a perennial stems: their stems are less than 1 year old.

We can measure the ratio of the growth rates of both species by measuring the distance between the two height distributions of resprouts. To measure this distance, we performed a linear regression between all the 5% quantiles of the distributions of both species ($R^2 = 0.96$; $F = 516$ with 19 and 1 *df*; $P = 0.0001$; intercept non-significant: $t = 0.135$; $P > 0.05$). The slope of this regression is an estimate of the ratio of the growth rates of resprouts of both species (slope estimate: 2.26 with 95% confidence interval ± 0.12; Fig. 2).

A *Piliostigma* resprout grew on average 2.26 times faster than a *Crossopteryx* resprout. *Piliostigma* might thus be able to compensate for its poorer intrinsic resistance and less fire-resistant trunk shape by growing faster than *Crossopteryx*.

Estimation of potential regrowth height

So far, we have found that (1) *Crossopteryx* has a higher intrinsic fire resistance than *Piliostigma* (Fig. 1); (2) a *Crossopteryx* tree has a thicker trunk than a *Piliostigma* tree of the same height (Table 1); (3) *Piliostigma* resprouts have a higher growth rate than *Crossopteryx* resprouts (Fig. 2). To compare the resistance to fire of the two species, we have to take into account the interactions between the three fire-resistance components. For both species, we tried to summarize our results by predicting regrowth height as a function of tree size, fire severity, and controlling for growth rate differences.

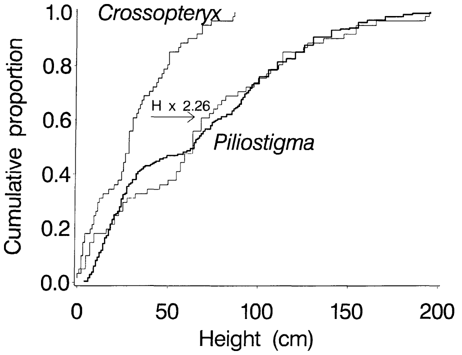

Fig. 2 Comparison of the distributions of the total heights of *Crossopteryx* and Piliostigma resprouts (demographic data). Resprouts are defined as individuals with no perennial stems. Their height therefore represent a measure of growth rate *Thick line* distribution of *Piliostigma* resprout total heights, *thin lines* distribution of *Crossopteryx* resprout total heights, and distribution of *Crossopteryx* resprout total heights multiplied by 2.26, which is an estimate of the difference in the growth rates of the species. This coefficient has been estimated as the slope of the regression of all the 5% quantiles of *Piliostigma* distribution against the 5% quantiles of *Crossopteryx* distribution

We used the estimates from the previous sections to compute a predicted regrowth height as a function of tree total height and temperature at ground level (Fig. 3): this is an estimate of the maximum possible regrowth height (possibly reduced by high fire temperatures occuring above ground level). These maximum regrowth heights allow us to define a recruitment threshold for both species (tree total height above which there is a chance of having a positive regrowth height) and to compare their resistances to fire. We controlled for the difference in growth rates by comparing *Crossopteryx* trees with *Piliostigma* trees that were 2.26 times taller.

We also estimated the proportion of trunk volume lost through fire for both species [by assuming that the trunk is a cone and using the estimated top angles, the volume of burnt trunk is equal to $(4\pi/3) \cdot (H - H_R) \cdot H_R^2 \cdot tg^2\alpha$ where H is total height, H_R is regrowth height, and α is the half top-angle of the trunk). From Fig. 3:

1. *Crossopteryx* trees are more resistant to very high temperature: a maximum-size resprout (100 cm) will have a positive regrowth height whatever the temperature, while a maximum-size *Piliostigma* resprout (226 cm) will have to resprout from its base at very high temperatures.
2. There is a recruitment threshold defined as the size below which no recruitment is possible whatever the temperature: *c*. 25 cm in height for *Crossopteryx* and *c*. 90 cm for *Piliostigma*.
3. At comparable sizes, *Crossopteryx* trees always lose less trunk volume (biomass) through fire than *Piliostigma* trees.
4. At low fire temperatures (< 200°C), tall *Piliostigma* individuals will have higher regrowth heights than comparable *Crossopteryx* individuals, although they still lose more trunk volume through fire.

Discussion

Our aim in this study was to understand the mechanism that give savanna trees the ability to resist very frequent fires.

Fire "resistance": a complex concept

Our results demonstrate that for small individuals, resistance to fire depends on a combination of traits (intrinsic resistance due to bark properties, stem profile and growth rate between fires) which can vary across species.

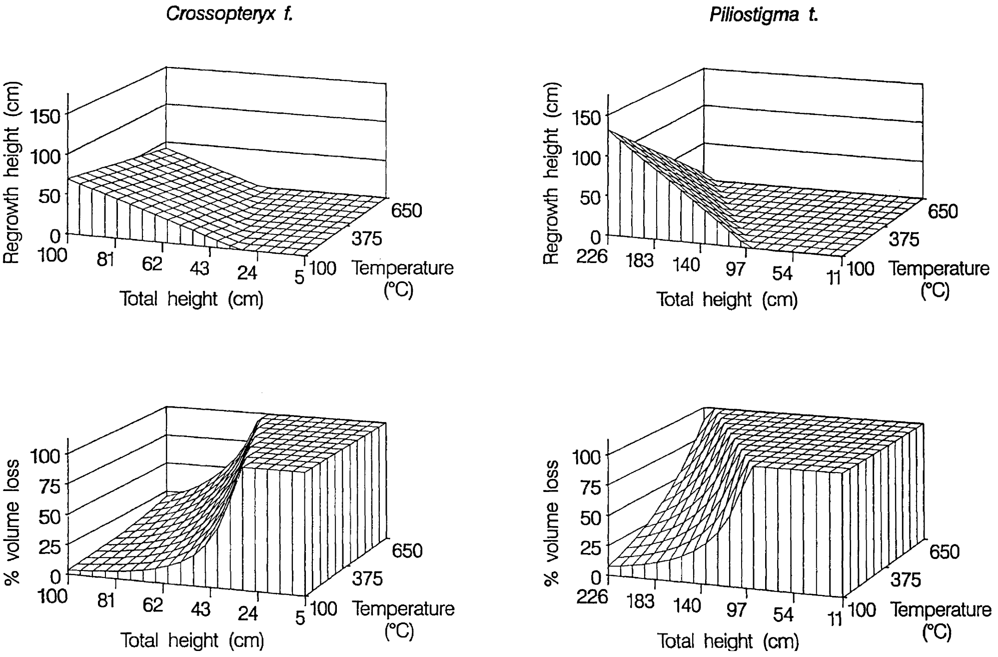

Fig. 3 Maximum regrowth height and percentage of volume lost through fire for *Crossopteryx* and *Piliostigma* trees as a function of their total height before fire and fire temperature at ground level. The scale of heights for *Piliostigma* was calculated by multiplying that of *Crossopteryx* by 2.26, which is an estimate of the ratio of the growth rates of the two species (Fig. 2). This insures that the same positions on the x-axis refer to trees at the same development stage in both species, although they are of different sizes. The regrowth height was computed from the lethal temperature curve (Fig. 1) and the assumption of a conical shape of the trunks, with their top angle fixed for each species (0.91° for *Crossopteryx* and 0.56° for *Piliostigma*; see text for the estimation of these angles). The conical shape hypothesis imposes the following relations: $\text{volume} = (\pi/3) \cdot \text{height} \cdot (\text{diameter})^2$, and $\text{diameter} = 2 \cdot \text{height} \cdot tg(\text{top angle})$. The percentage of volume lost is simply the ratio of the remaining living volume after fire (frustum of cone limited by regrowth height) to the volume before fire (cone of height equal to tree height)

Here, *Crossopteryx* has a higher intrinsic resistance than *Piliostigma* (Fig. 1), a thicker trunk for the same height (Table 1), and half the growth rate of *Piliostigma* (Fig. 2). The resulting effect of these differences is only visible in the complete picture (Fig. 3) where all components of fire resistance are considered: only then can we state that *Crossopteryx* is more resistant to fire than *Piliostigma* (because it is able to recruit in a wider range of fire conditions).

This is true for individual trees at (or close to) the recruitment stage only: other components of the fire/plant interaction, like survival to fire at the seedling stage, spatial variability of fire behaviour, date of the fire relative to tree phenology suggest that fire resistance should also be studied at the population/community level. *Crossopteryx* is more resistant than *Piliostigma* at the individual level, but we will have to conduct demographic analyses (estimation of the survival of seedlings and resprouts) to check that this is still true at the population level.

Resistance strategies

Resistance can be described by four continuous variables (Fig. 3): fire temperature at ground level, tree total height, ratio of species growth rates, and tree regrowth height after fire. Many combinations of relationships between these variables are possible and constitute a continuum of fire resistance strategies, among which those of *Crossopteryx* and *Piliostigma* are two particular cases: both are able to survive and recruit in a savanna that is burnt annually, but they use different strategies, as César and Menaut (1974) hypothesized from architectural descriptions.

Trees adapted to severe, infrequent fires (forest fires) usually rely either on survival (Glitzenstein et al. 1995), which depends directly on bark thickness (Vines 1968), or on reproduction by seeds – fire-enhanced germination, serotinity, and so on (Auld and O'Connell 1991; Moreno and Oechel 1991b, 1992; Pierce and Cowling 1991; Granström and Schimmel 1993; Bradstock and Auld 1995; Tyler 1995). Basal resprouting seems to be associated with less severe fires or cultivation-associated fires where the vegetation is cut before being burnt (Kauffman 1991; Moreno and Oechel 1991a; de Rouw 1993; Sampaio et al. 1993). By contrast, resistance to very frequent savanna fires seems to depend mainly on resprouting ability, the trait effectively measured by our four variables (Lonsdale and Braithwaite 1991; Morrison 1995). Our results are consistent with such a pattern of resistance to mild frequent fires by resprouting, contrasting with resistance to severe unfrequent fires by survival or reproduction by seed.

Fire resistance and savanna dynamics

If fire is the driving force of humid savanna ecosystems, as experiments of protection from burning tend to demonstrate, differences between fire-resistance strategies might have an important effect on savanna structure and dynamics, and be of great evolutionary significance (Schutte et al. 1995).

Due to its trunk profile (Table 1), *Crossopteryx* loses proportionally less wood biomass than *Piliostigma* (everything else being equal; Fig. 3) during a fire. If *Piliostigma* "wastes" biomass compared to *Crossopteryx*, it also grows faster when fire is excluded or less intense (for example in dense tree clumps where grass is excluded: Mordelet 1993). *Crossopteryx* seems to be able to recruit even in the worst fire conditions, while *Piliostigma* is able to take advantage of any decrease in fire intensity, either in time or in space (a good example of a risk-avoiding versus a risk-taking strategy). We can thus expect *Piliostigma* to be either associated to safe sites, or to recruit in cohorts the years of low fire intensity: different spatial and temporal patterns of recruitment are expected as a result of differences in fire-resistance strategies, and should be visible in population structure and spatial pattern.

We can easily imagine complex interactions between these two species: *Crossopteryx* recruits anywhere in the savanna thank to its high resistance to fire. By chance, some individuals are sometimes grouped and cause a local decrease in grass biomass, which will be a favourable site for the recruitment of the more fire-sensitive *Piliostigma*. The latter then outcompetes *Crossopteryx* thank to its faster growth rate. We could check this scenario with simulation models derived from Hochberg et al. (1994) or Menaut et al. (1990). Further complexity (still testable with a simulation model) can arise from the existence of possibly highly heterogeneous fire conditions, even when the fuel bed is homogeneous (Menaut et al. 1990; Beer 1991).

Conclusion

Fire resistance at the individual level depends on a combination of traits (a strategy), which will result in patterns of recruitment and mortality at the population level. Different species can have very different strategies for comparable fire resistances. As some traits involved in fire resistance (trunk profile and growth rate) also influence competitive ability, interactions of fire resistance with competition and fire variability are expected to have an influence on savanna structure and dynamics at the community/ecosystem level. To demonstrate this, we intend to analyse other existing data on (1) the survival and recruitment patterns observed at the population level, and (2) the impact of fire variability in space and time on these patterns.

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