

The dynamics of hollowing in annually burnt savanna trees and its effect on adult tree mortality

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Abstract Savanna trees often display significant hollows due to the combined action of fire and termites (N'Dri et al., *J Trop Ecol* 27:269–278, 2011). Observations have shown that internal cavities caused by termites in tree stems often result in external hollows under annual fire regimes, and it is quite possible that such hollows/fire interaction may increase the probability of trunk or big branch breakage and/or tree mortality. A study of individual tree and branch mortality as a function of prior termite and fire damage was undertaken in a West African savanna (Lamto, Côte d'Ivoire) where most of the trees naturally have

hollows in their stems due to termite and fire interaction. Our goal was to examine the dynamics of hollowing and to determine whether hollowing significantly affected tree mortality. Branch and whole plant mortality were quantified for dominant tree species according to their initial hollow state and height. Four different responses were obtained depending on tree species: (1) mortality increased with cavity severity and tree size (*Piliostigma thonningii*), (2) mortality depended on tree size only (*Bridelia ferruginea*), (3) no mortality even after being hollowed by termites and externally damaged by fire (*Crossopteryx febrifuga*, the species with the highest proportion of individuals with hollows yet the greatest background survival time, 14 ± 2 years) and (4) high mortality, but few hollow trees suggesting a weak resistance to hollowing (*Cussonia arborea* which was insensitive to all the factors examined in this study). For species resistant to hollowing, tree mortality was rare; alternatively, for species prone to hollowing, whole trees died quickly and before the most severe hollow classes could be observed. Long-term demographic data yielded population-level mortality estimates of adult trees at least four times lower in fire-exclusion zones than that in fire-prone areas. Because hollow dynamics interact with fire in affecting adult mortality of some dominant tree species, fire management is important for a sustainable woody component of these savannas.

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Introduction

Savannas are characterized by the coexistence of a continuous understory of C₄ grasses and a scattered overstorey of trees (Scholes and Archer 1997; House et al. 2003). Savannas are dynamic ecosystems, able to switch from grass-dominated to tree-dominated in a short time (e.g. van Langevelde et al. 2003; Favier et al. 2004). Such shifts in dominant physiognomy may have important consequences for nature conservation, cattle farming, availability of arable land, carbon sequestration and may even cause carbon sink ecosystems to become carbon sources, depending on rainfall (Jackson et al. 2002). In arid and semi-arid savannas, tree cover is controlled largely by mean annual rainfall (Sankaran et al. 2005). In most tropical savannas with annual rainfall above 650 mm, tree cover is controlled mainly by disturbances, such as fire and herbivory (Sankaran et al. 2004). In fact, fire has been identified as the main factor delaying or slowing down tree invasion in wet savannas of West Africa (Monnier 1968; Devinaux et al. 1984; Swaine et al. 1992), southern Africa (Bond and Keeley 2005), South America (San José and Farinas 1991) and Australia (Russell-Smith et al. 2003), where climate would otherwise allow the natural occurrence of closed forests.

Savanna fires are much less intense than closed-canopy forest fires, and savanna tree species are much more fire tolerant than forest species at the adult stage (Hoffmann et al. 2003; Cochrane 2003; Lloret et al. 2005). The impact of fire on adult savanna trees is often considered negligible (e.g. Higgins et al. 2000, 2007; Hoffmann and Solbrig 2003), in spite of experimental evidence of a role of fire in adult mortality alone (Williams et al. 1999; Hoffmann and Solbrig 2003; Lehmann et al. 2008, 2009; Prior et al. 2009; Smit et al. 2010) or interaction with elephants (Moncrieff et al. 2008) or termites (Werner and Prior 2007; Werner et al. 2008). This is in contrast to the generally accepted harmful effect of fire on seedlings (Setterfield 2002; Fensham et al. 2008; Gignoux et al. 2009; Williams 2009; Chidumayo 2012) and saplings or resprouts (Hoffmann 1996; Gignoux et al. 1997; Bond and Midgley 2001; Hoffmann and Solbrig 2003; Prior et al. 2010; Werner and Franklin 2010; Bond et al. 2012; Werner 2012; Werner and Prior 2013). Because annual mortality is usually low among mature trees, even small changes could have important accumulative impacts on tree population dynamics. Mortality of mature trees could be

an important and overlooked factor in the rapid shifts among grassland, savannas and closed-canopy forests.

Many savannas (e.g. West African or North Australian savannas) have few large herbivores. Insects, particularly termites, are the principal consumers of plant biomass (Josens 1972; Braithwaite 1990; Noble et al. 2009). Termites are a major component of these ecosystems (Abbadie et al. 1992; Tano 1993; Konaté et al. 2003; Traoré and Lepage 2008; Petts et al. 2009; Stein et al. 2009). We previously demonstrated that whereas termites were responsible for the formation of internal hollows in trunks in Western African savanna, fire was responsible for the formation of external hollows (N'Dri et al. 2011). When an internal hollow is opened to the outside, the tree trunk's mechanical strength is weakened and the risk of breakage and mortality increases (Mattheck et al. 1994; Whitford and Williams 2001). Further, if the tree is then exposed to fire, the debarked dead wood puts the tree at greater risk of destructive burning. In addition, further rapid increase in the size of a hollow is expected once the internal hollow has been opened to the outside. Thus, there is a chain of events begun with internal termite hollowing, external exposure, trunk and/or big stem breakage and ending when fire becomes the proximal cause of death of the adult tree.

Relating the direct effects of disturbances (here, fire and termites) to demographic parameters (here, mortality) are important for understanding the dynamics of tree populations in savannas. In this paper, we examine whether the formation and evolution of hollows through termite and fire interaction are related to trunk and branch breakage and to tree mortality. We addressed the following questions: (1) hollow dynamics: do the internal cavities caused by termites in tree stems develop or change under the ambient fire regime and if so, in what way? (2) Tree mortality: is adult tree mortality a function of hollow dynamics? (3) Species: do tree species respond differently to hollow dynamics? (4) Fire dynamics: do the probabilities of breakage and tree mortality increase with fire intensity or frequency?

Materials and methods

Study area

The study site was located in shrubby and woody savannas of the Lamto Reserve (6°13' N, 5°02' W), a

forest-savanna transition zone in central Côte d'Ivoire. The average annual rainfall is $\sim 1,200$ mm. The climate is sub-equatorial with four seasons annually (two dry and two wet seasons). Lamto Reserve is managed with a fire regime typical of most of the Guinean zone, with intense annual fires occurring during the dry seasons. Three different savanna types are differentiated by tree cover (Gautier 1990) and the main grass species: (1) grassy savanna dominated by the perennial grass *Loudetia simplex* (Nees) C. E. Hubbard (tree cover $<7\%$), (2) shrubby savanna dominated by grasses of the Andropogonae tribe (e.g. *Andropogon* spp., *Hyparrhenia* spp.) and (3) woody savanna, a sparsely covered woodland (tree cover $>62\%$) with sparse C_4 grass understorey.

The savanna woodland experiences fires of lower intensity than those in the other savanna types, due to reduced grass biomass and fuel load under trees (Mordelet and Menaut 1995; N'Dri et al. 2012). The major tree species are shrubby, usually <10 m high, and are considered to be adult when they reach 2 m in height, which also corresponds to the average flame height.

More than 90 % of the woody layer is composed of four species: *Bridelia ferruginea* Benth. (Phyllanthaceae), *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. (Rubiaceae), *Cussonia arborea* Hochst. ex A. Rich. (Araliaceae), and *Piliostigma thonningii* (Schum.) Milne-Redhead (Caesalpiniaceae; Menaut and César 1979). The shrub *Annona senegalensis* Pers. (Annonaceae) is very common, but rarely outgrows the grass layer. The small tree, *Terminalia schimperi* Hochst. (Combretaceae) is slightly taller than the four dominant species, but is usually confined to savanna woodlands. *C. febrifuga* is very frequently deformed or hollowed ($>95\%$ of >2 m individuals, N'Dri et al. 2011) and was the subject of more detailed observations and measurements than the other species.

Datasets

Hollow dynamics and tree mortality (dataset 1)

In 2006, we tagged, measured the height and checked for hollows in all trees greater than 2 m in height of the six tree species (named above). In shrubby savanna, approximately 1,400 trees were sampled in a $250\text{ m} \times 100\text{ m}$ transect. Hollow type was recorded (cf. below and as defined in N'Dri et al. 2011). In 2010,

we re-sampled all tagged trees including tree mortality, since the 2006 sample. Further, hollow type was recorded in resamples of *C. febrifuga* to determine the temporal development of hollows.

Hollow dynamics and main branch breakage in C. febrifuga (dataset 2)

Average adult tree mortality of *C. febrifuga* had been estimated earlier (Hochberg et al. 1994) at 2 % per year, but we found no mortality in our census. Because trees tend to 'die progressively' after a long senescence period (e.g. Barot and Gignoux 1999), we conducted an interim census in 2008 (dataset 2) to help monitor senescence by recording the breakage or loss of large tree parts of individuals >2 m in height. On each of 241 individual trees on eight $200 \times 20\text{ m}$ transects, main branches were tagged and the external opening size (length and width), if any, was recorded. We considered main branches as either (1) branches whose diameter was at least one third of the main trunk diameter (as in Archibald and Bond 2003) or (2) individual trunks for multi-stemmed individuals (including 'stems' resulting from the splitting of a previously wider trunk). All individuals were re-sampled for main branch mortality in 2010.

Long-term adult mortality under three fire regimes (datasets 3 and 4)

To further understand the mechanisms of tree mortality, we took advantage of a long-term monitoring dataset of trees (Gignoux et al. 2006), extending from 1969 to 2002 (34 years), to estimate the mean adult mortality of the dominant tree species (dataset 3). These data were recorded from five $50\text{ m} \times 50\text{ m}$ plots, four in the shrubby savanna (more intense fire) and one in a woody savanna (less intense fire). Although these data did not include observations of tree cavities, they were conducted under different fire regimes which, as we know from N'Dri et al. (2011), result in different cavity types and intensities. Thus, these data could provide an insight into the long-term outcomes of detailed hollow dynamics extracted from datasets 1 and 2. In each plot, all trees >2 m in height were sampled in 1969, 1970, 1973, 1975, 1989, 1991–1995 and 2002. There were two censuses per year in 1991–1993.

To estimate the fire impact on mortality of the dominant tree species, two other 50 m × 50 m plots were protected from fire from 1962 (dataset 4), and were censused, respectively, in 1969, 1970, 1973 and 1975, and in 1973, 1975 and 1978 (Gignoux et al. 2006). Censuses were discontinued because the increase in tree numbers prevented access to the plots at the end of the experiments. For these datasets, mortality rates estimated between two successive censuses were standardized to annual mortality rates, census dates being rounded to the nearest month. This enabled us to estimate standard errors for these mortality rates.

Typology of hollows/cavities

Following (N'Dri et al. 2011), adult *C. febrifuga* trees were classified into four cavity classes (datasets 1 and 2): (1) undamaged or healthy trees (UTs), (2) piped trees, where the heartwood of the tree had been removed by termites with no external opening except for a few dead branches (PTs), (3) externally damaged trees (EDTs) when an external wound, crack or split caused the exposure of heartwood or of the internal cavity if the tree was already piped and (4) split trees (STs, Fig. 1), where the growth of the cavity caused the trunk to split into two or more parts. For the other tree species (dataset 1), we classified cavities as large or small based on their extent along the trunk: cavities occupying less than one quarter of the total trunk length ($C_{1/4}$) were classified as 'small', and longer cavities were classified as 'large' (C_{+}).

Transitions between cavity classes

The form of fire–termite interactions depends on the timing of fire relative to the state of the tree, as described by N'Dri et al. (2011): (1) termites may enter trees through naturally broken branches. On a healthy tree, fire may cause the appearance of broken branches or small areas of exposed dead wood facilitating termite entry to the trees. Fire thus enhances the entry and effect of later termite action on healthy trees. (2) Once termites have entered the trunk, they create internal hollows or piping (PT), but restrict their action to heartwood and do not cause trunk opening. At this point, termites thus have no interactive effects of fire on the tree. (3) Unless the internal cavity is very large, a single fire will not cause



Fig. 1 An example of a split trunk (ST) of *Crossopteryx febrifuga* caused by an increase in size of the internal cavity

an external opening, but successive fires may cause some areas of the trunk to die. Although termites, as light-avoiding insects, would not expose the internal cavity to full light, a low intensity fire might be enough to expose a termite cavity to the outside. Fire and termites thus interact to open the cavity and form a deep external opening. As shown below, the consequences for trunk and stem breakage and for mortality of the tree differ, depending on the cavity type.

Over the 4-year observation period of the first census (dataset 1), we expected the following transitions for *C. febrifuga*: (1) UTs may be piped (PT) by termites; due to fire, (2) PTs may be externally damaged (labelled EDTs), (3) EDTs may split into two or more parts (ST) and (4) STs may break and die. Based on wood density and the strength of wood in general (Mattheck and Kubler 1995), UTs and PTs are resistant to breakage, EDTs are less resistant and STs even less resistant to breakage; in particular, a stem of a ST leaning towards its barked side cannot reduce its lean through further growth and is doomed to lean and eventually fall (Mattheck and Kubler 1995). We thus expected a higher mortality due to breakage of these latter categories compared to the former ones; in the case of STs, only part of the trunk may break and die (Fig. 2), hence our census of main branches instead of whole trees only.

These data were used to construct a four stage transition matrix (Caswell 1986, 1989; Barot et al. 2000) based on the tree damage cycle illustrated in Fig. 3. Transition probabilities were calculated based on the observed frequencies of trees in the different categories in 2008 and 2010. Based on these stage-based transition probabilities (P_s), we used the formulas of Cochran and Ellner (1992) in the general case of a population classified into n stages, simplified by Barot et al. (2002) to calculate the mean time spent $E(X_s)$ by individuals in each stage.

$$E(X_s) = 1/(1 - P_s).$$

In the second census (dataset 2), cavity shape (length and width) was expected to influence the probability of branch breakage. Long-term mortality of the different tree species was estimated the two savanna types (shrubby and woody) to determine the effect of fire on tree mortality (dataset 3) and the sensitivity of the different tree species to fire (dataset 4).

Statistical analyses

All analyses were accomplished with R software (R Development Core Team 2011). For dataset 1, analysed



Fig. 2 An example of a *Crossoteryx febrifuga* with a broken main branch due to a split stem

by a 2×2 contingency table, we used Fisher’s Exact Test. Since hollow classification in dataset 1 was hierarchical for *C. febrifuga*, we performed three Fisher’s Exact Tests, to check if (1) the proportion of hollowed trees had changed over time (sampling period T_0 vs. T_{+4}), (2) whether, among hollowed trees, the proportion of internal (PT) versus external (EDT) hollows had changed over time and (3) among EDTs, if the proportion of externally hollowed, but unsplit versus split trees (ST) had changed over time.

None of the *C. febrifuga* died over the 4 years of the study (we had expected ~ 18 deaths for 241 trees based on Hochberg et al. 1994 estimates of 2 % per year), but data on mortality of main branches made possible analysis of stem mortality. We used generalised linear models (GLMs) with binomial error distributions and a logit link functions to analyse the likelihood of branch breakage (dataset 2).

For all tree species except *C. febrifuga* (dataset 1), we used GLMs with binomial error distributions and logit link functions to analyse mortality rates by cavity

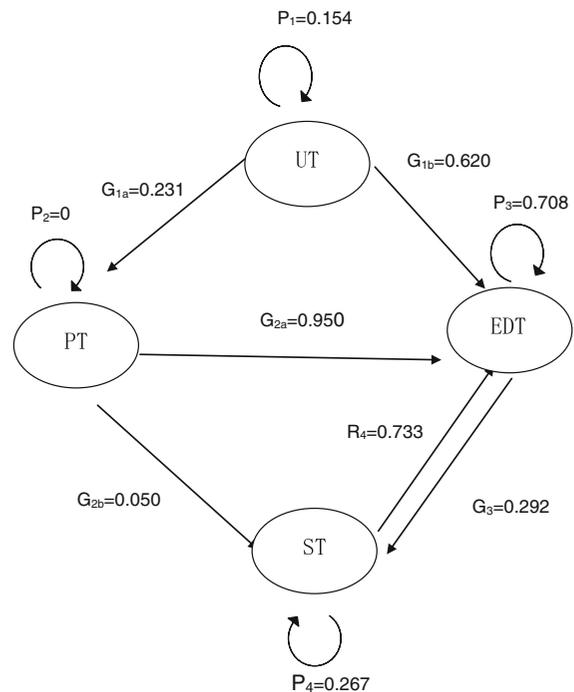


Fig. 3 The tree damage dynamics cycle in a *C. febrifuga* population. *UT* undamaged tree, *PT* piped tree, *EDT* externally damaged tree, *ST* split tree, P_i probability of remaining in the current stage, G_i probability of transition to a more damaged state, R_i probability of reverting to a less damaged state. Probabilities shown were estimated over a 4-year period

type (UT, $C_{1/4}$, C_+ and ST) after 4 years. Separate models were developed for each tree species. Because the opening of internal cavities is caused by fire (N'Dri et al. 2011), we expected a positive correlation between fire intensity and tree mortality. We analysed the mortality of adult trees in different savanna types subject to different fire treatments (datasets 3 and 4) with GLMs with binomial error and logit link functions.

Results

Hollow dynamics

After 4 years (dataset 1, Fig. 4), almost all (84 %) of the initially undamaged *C. febrifuga* trees exhibited cavities (Fisher's Exact Test, $P = 0.0052$, odds ratio = 0.1357). Almost all (95 %) individuals with pipes exhibited external openings (Fisher's Exact Test, $P < 0.0001$, odds ratio = 0.0966). The number of externally damaged individuals (EDT) almost tripled over the 4 years (Fisher's Exact Test, $P = 0.0054$, odds ratio = 0.3644). No tree death was recorded. Based on the transition matrix between damage classes (Fig. 3), the probability of persistence within the EDT stage was three times higher than the probability to remaining in any other stage. For all stages except EDT, transition rates to other stages were high (Fig. 3). Almost all (73 %) STs retrogressed to EDTs, often by losing one or more of their stems so that only one remained (Fig. 3).

Effect of hollows on main branch mortality

Only three of 241 *C. febrifuga* individuals died after 2 years (dataset 2) and they were all EDTs. The probability of branch breakage as a function of branch diameter, cavity length and cavity width and all their second order interactions increased with branch diameter ($P(\chi^2_1) < 0.001$), cavity width ($P(\chi^2_1) = 0.020$), and decreased with the interaction between branch diameter and cavity length ($\chi^2_1 = 415.23$, $P(\chi^2) = 0.012$).

Mortality of trees as a function of initial state and height

Whole tree mortality of *P. thonningii* increased significantly across the hierarchy of cavity types (UT, $C_{1/4}$,

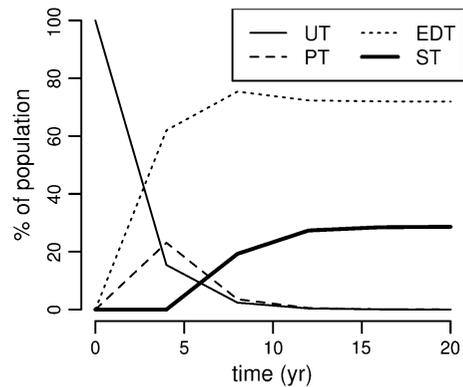


Fig. 4 Simulation of the transition matrix for hollow dynamics of Fig. 3 for the species *Crossopteryx febrifuga*, starting from a population where 100 % of trees are undamaged. UT undamaged tree, PT piped tree, EDT externally damaged tree, ST split tree. There is no mortality or recruitment in this model

C_+ and ST, dataset 1; $\chi^2_3 = 58.99$, $P = 0.009$) and with height ($\chi^2_1 = 22.28$, $P < 0.001$). Mortality of *B. ferruginea* increased with tree height only ($\chi^2_1 = 24.01$, $P = 0.04$). Mortality rates were low for *C. arborea* and no significant associations with tree state or height were detected. We did not examine *A. senegalensis* and *T. schimperiana* because of small sample sizes. *C. febrifuga* also showed no relationships with state or height because no trees died.

Long-term mortality of tree species

The long-term (34 years) mean mortality rate (Table 3, dataset 3) was different among the tree species ($\chi^2_5 = 1,281.94$, $P < 0.001$) and savanna types ($\chi^2_1 = 1,369.72$, $P < 0.001$). The highest mortality was observed for *C. arborea* and the lowest for *C. febrifuga* (Table 3). For all species except *T. schimperiana* and *C. arborea*, mortality was always higher in the woody savanna than in the shrubby savanna where fires were more common, in spite of large year-to-year variability. Nine years after fire exclusion began, mortality rates for all tree species were very low (Table 3, dataset 4).

Discussion

We firstly discuss the chain of events pertaining to tree hollowing by termites and subsequent fires that can ultimately cause tree death, including the dynamics of

hollows and the relationship between hollow types and branch breakage and/or tree mortality. Further, we discuss the difference in responses among species, as well as the long-term effect of fire intensity and fire exclusion on adult tree mortality.

Dynamics of hollows on trees under the ambient fire regime

In general, fire contributes to termite hollow exposure and to the later degradation of trunks until the trunks finally split (N'Dri et al. 2011). This was consistent with the finding of Mattheck and Kubler (1995) who pointed out that opening a pipe through a lateral slit weakens the mechanical resistance of the trunk much more than the initial piping of a solid stem. For *C. febrifuga*, damage severity tends to increase with time (Figs. 3, 4). Most of the STs had lost one or more stems, but nevertheless, those with only two 'trunks' (actually one trunk split into two parts) often reverted to a secondary EDT stage. This phenomenon may partly explain why this morphological stage (EDTs originating from PTs and STs) exhibits a longer residence time: a single individual may enter this hollow stage more than once during its lifetime (Fig. 3). We have shown, at least for *C. febrifuga*, that the dynamics of hollows development under the ambient fire regime are consistent with the scenario suggested by N'Dri et al. (2011).

Relation between piping and tree breakage/mortality

Breakage of large hollow branches may cause an entire tree to fall (Whitford and Williams 2001; Banks et al. 2011). In our 4-year study, however, no trees of *C. febrifuga* died, even though individual stems were damaged and died, a result similar to other studies where whole tree mortality rates following fire were low compared to stem mortality (Rutherford 1981; Trollope 1996; Williams et al. 1999; Holdo 2005). The frequency of branch breakage was correlated with the size of hollows on EDTs; branches with wide open cavities broke most often.

The data on these savanna trees support the hypothetical scenario proposed by N'Dri et al. (2011) that: (1) termites enter trees through naturally broken branches and pipe the heartwood of trees without causing trunk breakage, (2) fire then causes the external

opening of the pipe, (3) and this makes the tree much more susceptible to breakage and finally, (4) any mechanical agent like strong winds or large animals (both infrequent in our study site), and/or leaning of the tree trunk and its canopy (very frequent in our study site) promotes the progressive removal of exposed dead wood by successive fires. Whereas N'Dri et al. (2011) documented the respective roles of termites and fire in hollow formation, we show here that the different types of hollow may ultimately result in increased breakage or death of trunks and main branches. Further, we have demonstrated that this effect is stronger in some species than in others (below).

Differences in mortality among tree species

In spite of the high incidence of hollowing (85 % of >2 m individuals), often in its most extreme form (ST), the mortality rate of *C. febrifuga* was low (no whole tree death observed after 4 years) compared to, for example, *P. thonningii* whose individuals die quickly once externally damaged (17 % of mortality of hollow individuals: Table 2). Because *C. febrifuga* is very fire resistant, it acquires a perennial trunk at a smaller size than other species such as *P. thonningii* (Gignoux et al. 1997). Its trunk is therefore exposed to termite action earlier in its life cycle than that of other species which annually resprout for a longer period of time. This allows termites to pipe these trees at an earlier age than other species (N'Dri et al. 2011). But because this species is one of the most fire resistant species of the Lamto savanna (Gignoux et al. 1997) and presumably has very high resistance to breakage, in spite of being badly damaged by fire and termites. Most *C. febrifuga* individuals were in a damaged state in the field in each of our surveys, including one where individuals persisted in the externally damaged stage for an average of 14 ± 2 years. Such frequent occurrence of this species in a damaged state reflects its high tolerance of trunk and stem breakage with regard to whole-tree mortality.

In contrast, *P. thonningii* behaved in a more predictable fashion; in this species, mortality increased with the extent of tree damage (Table 1). We thus observe few damaged trees of this species in the field because they die quickly if damaged. Similarly, *C. arborea* also die soon after being damaged and few individuals are observed at different hollow stages (Table 1), whereas *B. ferruginea* and *C. arborea* are relatively insensitive to hollowing (Table 2).

Table 1 Annual mortality rate (%) per species and cavity type after 4 years (dataset 1)

Species	<i>Annona senegalensis</i>	<i>Bridelia ferruginea</i>	<i>Crossopteryx febrifuga</i>	<i>Cussonia arborea</i>	<i>Piliostigma thonningii</i>	<i>Terminalia schimperiana</i>
Cavity types						
Undamaged trees (UT)	15.91 % (<i>N</i> = 6)	3.18 % (<i>N</i> = 33)	0.00 % (<i>N</i> = 13)	6.94 % (<i>N</i> = 60)	4.46 % (<i>N</i> = 36)	1.02 % (<i>N</i> = 25)
Cavities occupying less than 1/4 of the total trunk height (<i>C</i> _{1/4})	0.00 % (<i>N</i> = 2)	1.27 % (<i>N</i> = 20)	0.00 % (<i>N</i> = 10)	9.64 % (<i>N</i> = 3)	14.06 % (<i>N</i> = 22)	0.00 % (<i>N</i> = 3)
Cavities occupying more than 1/4 of the trunk (<i>C</i> ₊)	ne (<i>N</i> = 0)	0.00 % (<i>N</i> = 16)	0.00 % (<i>N</i> = 34)	0.00 % (<i>N</i> = 1)	24.02 % (<i>N</i> = 6)	0.00 % (<i>N</i> = 0)
Split trees (ST)	ne (<i>N</i> = 0)	0.00 % (<i>N</i> = 2)	0.00 % (<i>N</i> = 32)	ne (<i>N</i> = 0)	100 % (<i>N</i> = 1)	ne (<i>N</i> = 0)

Number of individuals at *t*₀ in parentheses

ne None trees in this category so cannot estimate mortality

The estimated long-term mortality rates corroborated our 4-year study, confirming that *C. febrifuga* had the lowest mortality rate, whereas *P. thonningii* exhibited the highest mortality in annually-burned savanna (Table 3). Interestingly, there is a negative relationship among the dominant species (Fig. 5) between adult tree long-term mortality in the shrubby savanna (Table 3) and the overall frequency of hollowing. This is counterintuitive: the more damaged trees there are in a population, the lower the overall adult mortality rate. Damage extent is therefore not an indication of the susceptibility of a species to agents of mortality, but may in fact indicate the relative tolerance of a species to these mortality agents.

Effect of fire intensity/frequency on adult tree mortality

When fire is excluded, mortality rates drop quickly and spectacularly for all species (Table 3). The commonly observed increase in tree population size where fire is excluded is not only due to better recruitment, but also to improve adult survival in the absence of fire. The latter is compelling support for the negative effect of fire on adult tree mortality, although it does not indicate the mechanism of mortality.

In a woody savanna, where fire intensity is low, the increased mortality of adults in most species is contrary to studies elsewhere and to expectations based on the results of our hollow-dynamics analysis. However, in a woody savanna, tree density is high, and we suggest that mortality there is affected more by

Table 2 Annual mortality rate (%) by tree damage state over 4 years

Tree species	Annual mortality (%)	
	Hollow	Undamaged
<i>Bridelia ferruginea</i>	1 % (<i>N</i> = 38)	3 % (33)
<i>Cussonia arborea</i>	7 % (<i>N</i> = 4)	7 % (60)
<i>Piliostigma thonningii</i>	17 % (<i>N</i> = 29)	4 % (36)

Number of individuals is in parentheses

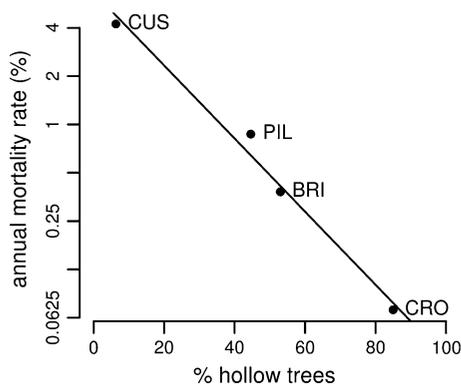
competition among the trees than by fire intensity. Indeed, the two species (*C. arborea* and *T. schimperiana*) for which there was no increase in mortality, were the larger and faster growing species in the field. This suggests a trade-off between growth rate (an expression of competitive ability in a densely wooded savanna) and fire resistance (Gignoux et al. 1997).

Conclusion

Cavities initially caused by termites and exposed by fires (N'Dri et al. 2011) clearly cause an increase in the likelihood of trunk and/or stem damage in later life stages in an annually burnt savanna, as is exemplified by *C. febrifuga*. There is a significant correlation between the size of hollows (external openings) and the probability of branch breakage. However, there was no evidence of increased whole-tree mortality in *C. febrifuga* (or with type of trunk damage) in contrast to *P. thonningii* which showed a significant increase in

Table 3 Annual mortality rates (%) of trees species calculated (a) over 34 years in two savanna types and (b) over 9 years in fire exclusion sites

	<i>Annona senegalensis</i>	<i>Bridelia ferruginea</i>	<i>Crossopteryx febrifuga</i>	<i>Cussonia arborea</i>	<i>Piliostigma thonningii</i>	<i>Terminalia schimperiana</i>
After 34 years						
Shrubby savanna	0.11 ± 0.39	0.38 ± 0.84	0.07 ± 0.14	4.23 ± 3.17	0.87 ± 1.61	0.41 ± 1.01
Woody savanna	2.82 ± 6.92	2.93 ± 3.3	2.97 ± 7.77	1.96 ± 1.92	1.53 ± 0.97	0
After 9 years						
On fire exclusion sites	0	0	0	0.32 ± 0.55	0.22 ± 0.38	0

**Fig. 5** Relationship between the proportion of hollow adult trees in a species and the mean annual mortality rate. Regression is significant ($F_{1,2} = 139.18$, $P = 0.007$, $R^2 = 0.99$). Note the y axis is on the \log_2 scale

mortality with more external openings. Across all dominant tree species, the likelihood of mortality of adult trees in response to trunk damage yielded greatly contrasting tolerances and responses to hollows and/or fire: one did not suffer any mortality, in others mortality was driven by tree size, or by hollow severity and one did not respond to any factor. Further, in a species sensitive to hollowing, trees in the most severe hollow classes died too quickly to be observed; in a species resistant to hollowing, death events were very rare. In sum, the responses (mortality) were very species specific. That fact, in addition to a weak negative correlation between adult mortality and the proportion of damaged trees observed in the field, makes it impossible to make general statements about relationship between hollow severity and mortality for a savanna as a whole. In any case, however, fire exclusion causes a spectacular decrease in mortality during the first years of exclusion, but in the long term, mortality increases because of competition with fast

growing, fire-sensitive species. This suggests a trade-off between fire resistance and rapid growth (Bond et al. 2012).

Our results are contrary to many theoretical and simulation models which assume that adult tree mortality in savannas are insensitive to fire. Our analysis shows that, for some species, hollows resulting from the joint action of termites and fire (N'Dri et al. 2011) do affect tree survival. The damage caused by either factor alone is probably insufficient to affect stem or branch mechanical resistance to breakage, but the joint action of fire and termites produces hollows and STs, which are more susceptible to breakage, ultimately leading to death of the individual.

If many trees in a particular savanna are in a breakage-sensitive stage, severe fires or strong winds may cause a mortality peak in adult tree populations, possibly causing abrupt shifts in tree cover. We suggest this may contribute to the high variability of tree densities among areas with similar local climate and soil conditions observed in many savannas around the world. The weakening of trees' mechanical resistance at the adult stage in savanna trees, by making their populations sensitive to even small environmental changes and local but intense events, may ultimately cause these ecosystems to respond very quickly to climate change and fire regime.

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