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# Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically

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**Abstract.** Although the demography of woody plants in savannas has long been shown to be due to many factors, there still is no consensus as to the relative importance of the top-down processes of fire and herbivory, nor on how fire and herbivory affect plant demography. We review the recent literature and suggest that further progress depends on the following: (i) a demographic framework with clear terminology and which focuses on recruitment, transitions and mortality, (ii) an understanding of mechanisms of how fire actually damages plants and how plants survive and out-grow this damage, mainly through height, bark thickness or diameter growth, (iii) an understanding of how losses in biomass due to herbivory may affect plant demography and, (iv) a consideration of interactions between fire and herbivory. Our synthesis suggests (i) strong recruitment limitation as well as some evidence of transition limitation by both fire and herbivory, (ii) that in some cases herbivory alone, notably by elephants and impala, can be more significant than fire alone, on woody plant population size, (iii) that fire and herbivory together are a lethal combination for woody plants and, (iv) that differences in strategies and responses of savanna plants to fire and herbivory are poorly explored.

### Introduction

Research in savannas is presently very active globally, yet a unified view of the dynamics of woody plants in savannas has been slow to emerge, especially concerning the role of fire and/or herbivory and at which demographic phase their impact is most important. For example, regarding the specific role of elephants on tree dynamics in Kruger National Park (KNP) in South Africa, Shannon *et al.* (2008) only focussed on larger size classes and noted 60% use of trees by elephants in their study area, of which 7% of trees had died. Despite this high mortality and an absence of any data on recruitment, they nevertheless invoked several other factors such as herbivory, fire, drought, diseases and plant senescence as contributory drivers of tree death. Similarly, for Australian savannas the focus has also been on larger size classes and several environmental effects have been evoked to explain tree dynamics and demography, such as fire (Williams *et al.* 1999; Lehmann *et al.* 2008, 2009; Prior *et al.* 2009), as well as herbivores, such as termites (Williams *et al.* 1999; Werner *et al.* 2008). The multiple factors involved and difficulty of experimentally identifying the key drivers of woody plant dynamics in savannas is typical of the current literature. Here, we review recent developments in understanding savanna dynamics by focusing on mechanisms and demographic consequences, especially of mesic savannas. We consider how

fire and herbivory may influence plant demography separately, as well as synergistically. In Africa, for instance, fire typically kills only small stems and elephants directly have an impact on medium-sized trees. However, acting synergistically, elephants and fire may kill trees larger than each could kill individually. The same may apply to the termite–fire interaction in Australia.

Understanding woody plant dynamics is important from both a theoretical and management perspective. Also, understanding woody plant dynamics is essential for facilitating an evolutionary perspective on woody plant strategies, such as what are the important plant traits, trade-offs and life-histories. There has been little research on evolutionary strategies of savanna plants of the form of, for instance, how African and Australian ‘*Acacia*’ species differ either within or between continents? Understanding comparative ecology is essential to inform modelling exercises which almost all typically consider only one generalised plant type or species and even just one size class (e.g. Higgins *et al.* 2000).

### How fire damages plants: death of canopy, xylem, phloem or cambium?

How fire kills the aboveground canopy and stems of plants (known as top-kill) has been poorly explored and is generally considered to be caused by fire damaging the cambium (Bond and

van Wilgen 1996). Cambium necrosis, a consequence of a reasonable period of heating to 60°C, can be modelled in relation to fire and stem properties (e.g. Jackson *et al.* 1999; Michaletz and Johnson 2007). Studies indicate that the degree of necrosis is scaled with bark thickness (McArthur 1968; Hengst and Dawson 1994; Gignoux *et al.* 1997; Hoffmann *et al.* 2003). Stem thickness is not as important because wood has low thermal conductivity and therefore not much heating of cambium is from heat passing inwards from the less intense leeward side and even from the more intense windward sides. Bark moisture content also is relatively unimportant because moisture increases both thermal conductivity and heat capacity. Also, leafless trees will experience greater heat convection to aerial buds than will leafy trees, because of less interception of heat by leaves. However leafed-out trees may suffer greater leaf loss lower in the canopy. Although the factors causing cambium death are now known (see summary in Michaletz and Johnson 2007), the link between cambium death and top-kill is not clear. Cambium death should merely prevent redifferentiation of new vascular tissue and thus should have a delayed post-fire impact on stem mortality. However, stems die rapidly after being burned.

Alternatively, fires may cause phloem death (i.e. ring-barking) and this should over time cause root starvation. This eventually would lead to canopy death by dehydration. Ring-barking, or stem girdling, which interrupts phloem connectivity, typically takes months or even years to cause stem death, so fires probably inflict more damage on the stem than mere ring-barking. If cambium necrosis occurs, phloem necrosis can be assumed to have occurred because it is more exposed to heat damage, although the reverse may not be true. However, since stem death after fire is experienced within days, weeks or months after fire, this calls into question whether cambium or phloem death is the main determinant of top-kill. This leaves xylem damage and hydraulic malfunction, which subsequently leads to canopy dehydration, as a further potential cause of top-kill.

Several lines of evidence point to top-kill (death of aboveground parts) after fire being due to more than cambium, phloem or canopy death. Ducrey *et al.* (1996) applied electrically heated pads to the base of *Pinus halepensis* stems and thereafter used various eco-physiological measurements to predict eventual stem death. Trees that were heated across 100% of the stem width died within 1–5 months, whereas those that suffered 37–78% stem circumference heating, all survived. All the trees that later died experienced immediate significant water stress (such as lower and declining sap flux density). However, electrical resistance (an indication of vigour) of the cambium was unaffected after heating and declined only just before these trees died. Ducrey *et al.* (1996) speculated that stem death could come from a range of causes including heat-induced cavitation of xylem and increased rates of air seepage through heat-damaged bark. Since water under negative pressure would be very prone to cavitation, it is likely that temperatures far lower than lethal temperatures (~60°C) could damage xylem.

Balfour and Midgley (2006) experimentally burned the crown or stem of saplings of a typical savanna species. They showed that burning the canopy while protecting the stem did not cause top-kill. Resprouting occurred epicormically within the canopy. In contrast, heating the stem while protecting the canopy damaged the xylem and caused immediate wilting followed by top-kill.

Further evidence that hydraulic damage causes top-kill comes from studies of frost damage. The pattern of frost damage matches that of fire damage (smaller stems suffer the greatest mortality, species resistant to fire also resist frost), frost and fire and frost and elephants act synergistically (Holdo 2006). Also frost impacts are rapid (within a month; Holdo 2006), again suggesting that stem death is not due to frost damage of cambium.

Fires also have an impact on subsequent plant growth rates compared with unburned plants (Murphy *et al.* 2009), suggesting that all fires will have at least some impact. Whether this impact is due to loss of canopy by scorching (Murphy *et al.* 2009), or due to damage of the hydraulics of the stem or even a combination of all of these, is unclear. The reduction in growth could be real or it could be due to the loss of stem thickness because of burning-off of bark (e.g. of fibrous-barked trees). The best correlate of plant-mortality response to fire is bark thickness (e.g. Hoffmann *et al.* 2009). Again, this suggests that damage to the stem is more important than damage to plant canopies. Murphy *et al.* (2009) indicated that evergreen eucalypts have faster post-fire growth rates than do deciduous eucalypts. If fires have an impact on eucalypts by scorching canopies, then we would expect evergreen canopies to be more prone to fire impacts than deciduous canopies. In summary, we apparently do not yet understand the mechanism of how fires damage and kill savanna plants. For example, whether the magnitude of fire damage to woody plants correlates with plant moisture stress at the time of the fire? Understanding this mechanism should be important in understanding evolutionary strategies, in defining the appropriate size classes for modelling analyses and may also open up possibilities for fire management.

### Evolutionary responses to fire regimes

Plants evolve to fire regimes, especially the mean and variance in intensity and frequency. Gignoux *et al.* (1997) made the first attempt at determining different evolutionary strategies based on *Crossopteryx febrifuga* (C) and *Ptilostigma thonningii* (P), which have different fire-resistance strategies – C relies on resistance of aboveground structures to fire, whereas P relies on its ability to quickly rebuild aboveground structures. They showed that a stem of C had the same intrinsic fire resistance as a stem of P of double the size. Unfortunately, they did not present relative (i.e. in relation to stem diameter) bark thickness, although presumably C had greater relative bark thickness than P. They also showed that the diameter growth rate of P was 1.4 times that of C. These two variables together revealed that C is superior to P under a regime of frequent fires (intrinsic resistance is more important than growth rates), whereas under a regime of less frequent fires, the species relative fire resistance is reversed.

Further perspectives on evolutionary strategies have come from the analysis of differences between forest and savanna species. Many of these comparisons would also apply at the level of within-savanna comparisons. Hoffmann *et al.* (2003) and Hoffmann and Franco (2003) noted a greater relative bark thickness of savanna species than related forest species. However, relative bark thickness does not predict fire response, whereas absolute bark thickness does. Absolute bark thickness is a function of the relative bark thickness (% of stem diameter) and stem diameter growth rates. Further analysis is

needed to determine whether savanna and forest species of the same age would differ in absolute bark thickness. A reason why savanna species have evolved relatively thick bark (e.g. Hoffmann *et al.* 2009) is because their diameter growth rates are slower than those of forest species.

Regarding other differences between savanna and forest species, Hoffmann *et al.* (2003) showed greater size (height) at maturity for forest than for related savanna species. Hoffmann and Solbrig (2003) noted that subshrub species achieved maturity within a year after fire despite top-kill, whereas trees were not reproductive despite lower levels of top-kill.

Most savanna species are vigorous basal resprouters; however, in instances where resprouting may occur from the stem as well as the base, these epicormic buds must also survive the fire. There is considerable variation in the ability to resprout epicormically. For example, Burrows (2002) and Burrows *et al.* (2008) have shown how specialised some Australian species (mainly in the Myrtaceae) are in terms of bud protection and development. In some extreme cases, meristematic tissue and strands even occur within the xylem. It remains to be seen whether Australian plants are unusual in this respect and whether this explains unusual aspects of Australian savannas. For example, high adult plant persistence should be traded-off against poor recruitment (Bond and Midgley 2001).

Damage to bark, whether by fire or herbivores, is an important disturbance that plants have evolved to respond to. Romero *et al.* (2009) removed a section of bark from a range of *Quercus* species. In the absence of fire, this removal nevertheless caused xylem decay below the section as well as, to a lesser or greater degree, decay upwards and downwards from the removed section. They showed that the different species responded to this damage by either regrowing bark to close this wound or by compartmentalising and sealing-off the xylem below the wound. Their analysis demonstrated different biogeographic patterns in the evolutionary responses of plants to stem damage. In some fire-prone ecosystems, species closed wounds whereas in others they limited the spread of xylem decay subsequent to bark removal. The response of trees to bark damage, whether due to herbivores or fire, is thus a further axis of differentiation of savanna plants.

On the basis of the above-cited work of Hoffman, Gignoux and others, the basic axes of differentiation of savanna and fire-prone forest species are now well known. There are three important life-history trait axes that separate tree species in fire-prone savannas, including (1) relative bark thickness, (2) diameter growth rates and (3) size at maturity. Diameter growth and relative bark thickness could be collapsed into bark thickness growth rates. This would allow some relatively thin-barked species to nevertheless match the fire-proofing of thick-barked species, within a given inter-fire period. Unfortunately, bark thickness cannot be reflected in a single number (such as % of stem) because its relationship with stem size differs among species in both slope (Jackson *et al.* 1999) and intercept. However, since ground fires in savannas affect mainly the smaller stems, a possible solution is to consider bark thickness growth rates to a standard bark thickness (e.g. Jackson *et al.* 1999), such as the period of time taken to achieve a bark thickness of 1 cm. Further analysis is needed to determine the relative importance of each and how they vary within continents

(e.g. arid v. mesic savannas) and between continents (e.g. Australian v. African mesic savannas).

### Savanna demography: terminology and methods

We believe that progress towards understanding savanna dynamics needs a clearer demographic, including terminology and framework. Demography concerns changes in both population *size* (numbers) and population *structure* (e.g. age classes, genetics). Midgley and Bond (2001) drew attention to the many demographic hurdles/bottlenecks facing savanna plants. They noted that only some of these hurdles may change population size (i.e. cause birth or death of individuals) and that it was rare for ecologists to show population-size impacts of a particular hurdle. For example, insect seed predators and large-herbivore seed consumers could potentially influence population size (see review in Or and Ward 2003), although we still do not know whether African savanna species are seed limited (i.e. whether the addition of seeds causes an increase in population size). Similarly, herbivores may influence reproductive output by lowering flowering or seed-set (e.g. Goheen *et al.* 2007; Young and Augustine 2007) and herbivores may influence seed dispersal (e.g. elephants, Dudley 2000). Even given seed or seedling limitation, the question remaining is 'would an increase in seedlings alone influence the population size of woody savanna plants'. The likelihood is that they would not. This is because the next transition, from seedling to resprout, is so intense (Gignoux *et al.* 2009; Williams 2009), owing to the impact of fire, herbivores and drought. An increase in population size thus requires both seedling recruitment and the absence of fire and herbivory.

Most woody savanna plants are highly persistent resprouters (Bond and Midgley 2001) and therefore unlike disturbance-sensitive species (reseeders), net population size changes less than population structure, in response to disturbance. The three dominant demographic phases for resprouting plants can be summarised as (1) recruitment, (2) transitions and (3) mortality of established plants. *Recruitment* refers to the processes that lead to the production of new plants (seedlings). This phase concerns plants <1-year old and not able to resprout yet. This phase is under-researched and potentially a bottleneck because resprouting is generally traded-off against recruitment (Bond and Midgley 2001). *Transitions* refer to processes that influence the diameter or height of already established plants and could include progression (increases in size), regression (decreases in size) and changes in the numbers of stems per individual plant. Transitions do not influence population size, although they may influence cover and size. *Mortality* would include processes that cause a decrease in population size by deaths of an individual, not just the death of stems. In our framework, top-kill or stem death followed by resprouting would not be termed mortality. Resprouting, whether from base or stem, would not be called recruitment. Prior *et al.* (2009) considered recruitment to mean an increase in stems >1.5 m in height and mortality to merely mean stem death (top-kill) not whole plant death. With their terminology, a stable savanna population could nevertheless have recruitment exceeding mortality. We suggest that an improved terminology will avoid these problems.

Because all plants experience demographic bottlenecks, the question is what are the unique demographic bottlenecks of woody plants in savannas? The potentially unique aspect of their demography, given the prevalence of resprouting, is the recruitment bottleneck and importance of transitions for small plants to fire-proof or herbivore-proof size classes (Higgins *et al.* 2000; Midgley and Bond 2001; Bond 2008). The key questions would be as follows: which data would show transition limitation, which are the important transition size classes and which processes determine transitions?

The first crucial need is data on the smallest size classes; however, this size class is typically ignored in demographic studies. Is there evidence that the smallest size class has individuals of various ages, reflecting repeated fire-induced regressions to the ground level? Interpretation of the numbers, or proportions, of individuals in the smallest size class is difficult because in resprouters, aboveground size and underground lignotuber size may be unrelated (e.g. Fensham and Bowman 1992). Thus, an accumulation of stems in the smallest height or diameter size class may reflect both the processes of recruitment and reversion. Skowno *et al.* (1999) and Balfour and Midgley (2008) attempted to circumvent this problem by comparing aboveground and belowground (lignotuber) size. On the basis of the assumption that belowground size is a better correlate of age than is aboveground size, they showed a relative absence of recruits and therefore an accumulation of reverting or stationary stems.

Is there evidence of a particular minimum size class above which plants do not regress after fire? Surprisingly, there have been few explicit tests of the demographic transitions hypothesis. Lehmann *et al.* (2009) recently analysed the demographic structure of four Myrtaceae in an Australian savanna. They lumped size-class information for several sites and suggested that at this scale, there was no evidence of a demographic bottleneck. They argued that the >10-cm diameter at breast height (dbh) size class represents a demographic transition above which trees are fire-tolerant. If correct, this suggests that Australian savanna trees may spend >50 years in a fire danger zone because they argue that trees grow in dbh  $\sim 2 \text{ mm year}^{-1}$ . Given that fires burn here several times a decade, the system should have few large trees and a large preponderance of trees in the smallest size class. This does not seem to be the situation, given the rather flat size-class distributions in Lehmann *et al.* (2009).

There are several problems with their analysis. First, they ignored the smallest size class (<1.5 m tall), which we have argued above is central to demonstrating a transitions bottleneck. Second, the analysis of lumped size-class distributions is difficult for many reasons. This includes the influence of bin size on size-class distribution shapes (Niklas *et al.* 2003) and the impact of variation of in post-fire age on interpretation of size-class distributions (Balfour and Midgley 2008).

Many studies of savanna dynamics use remote sensing (such as aerial photographs). Remotely sensed data are generally not refined enough to tell whether changes in woody plant cover are due to changes in rates of recruitment, mortality or transitions. For example, Asner *et al.* (2009) used Lidar to demonstrate strong impacts of herbivores on vegetation structure in KNP. In particular, they noted a decline in tall trees. Again, the

remote information is not refined enough to indicate whether herbivores influence plant population size (by actually causing mortality) or population structure (by causing reversions in size). As will be seen in the section below on bush encroachment, analyses of savanna woody plants dynamics often lacks precise information on rates of recruitment, transition and mortality, so as to be able to determine which rate is most limiting.

### Recruitment: the role of animals

Seedlings are easily killed by leaf/stem consumption because of their poorly developed resprouting ability. Because of size and energetic constraints, it is likely that small browsers consume more seedlings than larger species. This is seen in the herbivore-rich community of African savannas, where small-sized browsers have been found to be able to limit tree dynamics (Augustine and McNaughton 2004). In particular, impala may dramatically impair tree recruitment (e.g. along the Chobe riverfront, Botswana; Moe *et al.* 2009), with cohorts of trees escaping this control during epidemics that reduce herbivores, as argued by Prins and Van Der Jeud (1993) for *Acacia tortilis* in Lake Manyara or Sharam *et al.* (2006) for *Euclea* establishment in the Serengeti. Larger bulk grazers may also consume seedlings while grazing. Trampling effects are also potentially locally important. Also, because area trampled increases with herbivore body size, large bulk feeders may also have this further impact on recruitment levels (Cumming and Cumming 2003; Thompson Hobbs and Searle 2005).

Browsing effects on recruitment may vary, with changes in surrounding herbivore resources brought by adult trees, because no herbivore population can survive on seedlings alone. Is seedling consumption more intense at low tree density? Does seedling consumption decrease with distance to adult trees? Interestingly, in some situations the negative demographic impacts of herbivores (seedling consumption and trampling), appear to have been counterbalanced by some positive effects (increased seed dispersal and processing, reduced grass competition, reduced fire), and increased woody cover appears to have occurred despite high herbivore presence (e.g. Roques *et al.* 2001). This is the phenomenon of a bush encroachment on highly stocked pastoral or ranching areas. However, because there is often no data on actual levels of recruitment (e.g. in Roques *et al.* 2001), it is possible that bush encroachment can also be caused by increases in transitions.

### Recruitment: the role of fire

Recruitment is infrequently observed and studied (Fensham *et al.* 2008) and most studies indicate that it is a bottleneck for savanna plants. Even for extremely fire-tolerant eucalypts, percentage survival of seedlings beyond the first fire is low (Setterfield 2002). Fensham *et al.* (2008) thus considered the impact of limited recruitment to be more important on eucalypt demography, than is the impact of fire on established plants. They investigated the response of young (<1 year for glasshouse-grown plants) eucalypt seedlings in relation to water stress and fire. Interestingly, water stress was more detrimental than burning, although the combined impact of fire and water stress drastically increased mortality from 0 to  $\sim 80\%$  in some cases. The other important aspect of the present study is the demonstration

that lignotubers grow very slowly ( $<0.2\text{ cm}^2$  in a year in a glasshouse). Therefore, how long would it take a savanna tree to achieve a height of 2 m in the face of persistent disturbance and seasonal drought? Gignoux *et al.* (2009) estimated that this period could be as long as 10 years for savanna species in an annually burned African savanna. Williams (2009) showed strong recruitment bottleneck for the eucalypt (*Corymbia clarksoniana*), with seedlings being found only after wet years. Gignoux *et al.* (2009) recently documented very low levels of success for seedlings of both savanna (2%) and forest (0.01%) species, and argued that the high levels of mortality in the recruitment niche, mainly owing to fire, is the main factor keeping forest species out of the savanna.

### Transitions: the role of animals

Here we ask whether browsing affects plant demography? We have concentrated on vertebrate herbivores, whereas Andersen and Lonsdale (1990) and Andersen (1991) investigated the role of insect herbivores, notably seed predation and stem-hollowing by termites and ants, in Australian savannas. Fensham and Bowman (1992) argued that termites damage and destroy eucalypt lignotubers. Browsing by vertebrates apparently has a very low impact on individual tree mortality after the seedling stage, unless other conditions arise (drought, fire) or where the herbivore densities are very high. Generally, trees are highly resilient to even strong pulses of short-term herbivory because they are vigorous resprouters.

Browsing can reduce tree height growth by a combination of reduced resource availability because of loss of leaves and direct browsing of leader shoots. In some species, whole tree architecture may be modified because of lateral branch regrowth following the release of apical-meristem dominance, after browsing. Thus, drastic height growth reduction may be observed (Augustine and McNaughton 2004; Staver *et al.* 2009) and this may significantly reduce transition rates (Barnes 2001; Staver *et al.* 2009). Browsed trees may be more likely to suffer from canopy damage during fires. However, as discussed above, stem diameter and bark thickness may be more important than height in determining tree sensitivity to fire. Very little is known about how diameter growth is affected by browsing, with both positive (Dharani *et al.* 2009) and negative (Augustine and McNaughton 2004) impacts having been reported. Much of the literature on browsing concentrates on browser effects on biomass and plant response to, and compensation for, loss of biomass. In savannas, where height or diameter is the crucial correlate of plant fitness, the manner in which a browser affects plant biomass may be of little relevance compared with the way it affects plant fitness. Thus, a small loss of biomass to browsing may nevertheless strongly influence flowering, seed-production and dispersal.

African elephants, *Loxodonta africana*, represent an exceptional case of herbivores that can cause backward height transitions and significant mortality of trees, especially of species with low coppicing ability (e.g. Jacobs and Biggs 2002), and thus influence distribution patterns of sensitive or targeted tree species (e.g. Edkins *et al.* 2008). Elephants could also indirectly affect transitions by facilitating browsing by other browsers. When trees browsed by elephants suffer high mortality (non-resprouting),

elephant foraging may then open up landscapes and facilitate the spread of fire (Dublin *et al.* 1990). However, resprouting is the typical response of savanna plants and elephants avoid thickets caused by resprouting. Therefore, elephants may convert woodlands to shrublands, rather than to grasslands.

African savannas are unique because many areas still have the full faunal compliment, especially the larger animals. Inter-continental comparisons of the determinants of woody plant dynamics in savanna is thus complicated by the extinction of large endemic animals on other continents. Large herbivores are not entirely absent from other continents and, in some cases, invasive species have had an influence on the savanna structure (Petty *et al.* 2007). For example, in tropical north Australia the impact of large populations of feral buffalo (*Bubalus bubalus*) on the savanna woodlands are equivocal, with some reporting severe impact with little recruitment of juvenile trees into the canopy because of the indirect effects of grazing (Petty *et al.* 2007), whereas others have demonstrated a positive indirect effect of buffalo on the height growth by reducing the competitive regime for juvenile trees (Werner *et al.* 2006). However, both studies are in agreement that buffalo initiate a cascade of effects by changing ground-level biomass, which change competitive relationships and fuel loads, which then have an impact on tree growth and demography (Werner 2005; Werner *et al.* 2006).

### Transitions: the role of fire

The two determining aspects of fire regime that impinge on woody plants are the fire intensity and fire frequency. Fire size, especially the occurrence of large fires, may also be important (Williams and Bradstock 2008), as may a preponderance of small fires. Fire frequency and fire intensity are assumed to be negatively correlated. For example, Higgins *et al.* (2000) modelled decreasing fire intensity with increasing fire frequency, by incorporating a grass carry-over term. There remains some debate as to whether savanna fire frequency and intensity are negatively correlated (Midgley *et al.* 2006). For example, variability in summer rain dominates the size of the fuel loads for the fires of the following winter and thus carry-over from the previous year may be a relatively unimportant contributor to fuel loads compared with the amount of summer rains. Also, a more frequent fire regime is more likely to encompass wet years with high fuel, than will a less frequent regime. This would make it difficult to determine the impact of fire frequency independently from fire-intensity effects in fixed burning-period experiments, such as those analysed in Higgins *et al.* (2007).

The term 'escape height' (Higgins *et al.* 2000) is used to describe the height (typically 2–3 m) a plant must reach to escape the so-called fire-trap and thus avoid top-kill. Once escape height is reached, the stem does not get reset to the base after being burned. A dominant question in savanna ecology is 'what growth rates and fire-free interval is needed for plants to reach escape height'. Rapid height gain after basal resprouting, in the absence of fire for a few years, would allow woody plants to achieve a size greater than that in the fire-damage zone. This then is an expected mechanism that savanna plants could use to escape fire damage (Higgins *et al.* 2000). Thus, Archibald and Bond (2003) suggested that some *Acacia* species grow as slender poles to achieve fire-escape height rapidly.

There are several problems with the 'escape height-fast growth rate' hypothesis. First, damage to leaves and the canopy by the heat plume extends the danger zone considerably beyond that of canopy charring, to one of canopy scorching. This means that for escape to be possible for a basal resprout, extremely long fire-free periods are required. Second, top-kill and basal resprouting are two end-points of a continuum for plants that survive a fire. The intermediate response occurs in some plants; they resprout from the stem. Gignoux *et al.* (1997) termed the height at which sprouting occurred from the stem, as the 'regrowth height'. For example, a study of *Acacia karroo* in South Africa suggested that it frequently sprouts from the stem (Balfour and Midgley 2008). This helps it incrementally to increase in size, rather than being reset by each fire, and thus acquire an escape diameter despite the frequent local fire regime (Balfour and Midgley 2008). Baxter and Getz (2008) allowed plants to regress a size class following damage. Holdo (2007) also allowed damaged stems to resprout from a regrowth height. Resprout height is not well documented in the Australian literature. Williams (2009) argued that individuals of *Corymbia clarksoniana* (Myrtaceae) that were taller than 1.5 m, regrew from the stem not the base.

Third, if the main impacts of fire are on the stem, especially within 1 m of the ground where savanna fires are most intense, then escape height is a misnomer. Being rooted to the ground, trees cannot escape fire by growing tall, they escape fire impacts by having thick bark. Being tall may reduce fire damage to the canopy, although canopy damage does not cause top-kill (Balfour and Midgley 2006).

Growth rates of trees after fire, as well as information on regrowth heights, are therefore crucial in determining post-fire size-class distributions. Regarding height growth rates, many modelling exercises have noted that height growth rate is a sensitive parameter (e.g. Higgins *et al.* 2000). However, given the above discussions on the importance of bark thickness, the questions then arises, whether the height growth is more important than diameter or bark thickness growth? The pertinent parameter appears to be bark thickness growth rates because many studies have shown that fire excludes forest species from savanna, despite their faster growth rates than for savanna species. Hoffmann *et al.* (2009) argued that in South American savannas, forest species are kept out of the savanna by virtue of having thin bark (~20% of the relative bark thickness of savanna species). They showed that fires in savanna produce higher char heights than forest fires, but that forest species still suffered greater top-kill per stem. For the same study system, Rossatto *et al.* (2009) found that forest species grew (diameter growth) faster than did savanna species. This does not necessarily mean that forest species acquire thicker bark than savanna species. Forest species grow faster than savanna species in Australia, and also here they are presumably excluded from savannas by fire impacts. Prior *et al.* (2004) showed that monsoon dry forest had faster growth rates than open forest (=savanna). The point is that it is not growth rates *per se* that predict where trees from different forest types occur in a landscape. Other factors such as bark growth rates, regrowth height and fire resistance (variability in the ability to resprout) are critical in predicting which species occur in fire-prone areas. This information is not generally available.

Higgins *et al.* (2000) argued that height growth of <60 cm year<sup>-1</sup> in a 1000-mm annual rainfall environment in KNP resulted in a very low tree cover. Baxter and Getz (2008) used 30 cm year<sup>-1</sup> but also showed for KNP that varying height growth rates from 30 to 60 cm year<sup>-1</sup> drastically increased woody cover. Growth rates appear to be surprisingly low in Australia. Prior *et al.* (2006) found that under a regime of frequent late dry season fires, juveniles (<1.5 m) of the dominant Myrtaceae species, such as *Eucalyptus tetradonta* and especially *Eucalyptus miniata*, had faster rates of height growth than did non-Myrtaceae species, whereas height growth rates were low (0.17–0.3 m year<sup>-1</sup> v. -0.01–0.12 m year<sup>-1</sup>). Given the high fire frequency in Australian savannas, and the slow growth rates, it is not clear how trees out-grow fire impacts.

Part of the problem may be that growth rates of savanna trees are difficult to determine, or interpret, for several reasons. First, growth rates may vary with time since fire. Immediate post-fire sprouting growth rates are high, but they decline with time and thus cannot be easily extrapolated across the post-fire period (e.g. Prior *et al.* 2004; Balfour and Midgley 2008). Second, growth rates depend on size classes involved. Thus, Hanan *et al.* (2008) showed that impacts of fire are more 'buffered' if size-specific information for just two tree size classes is used, whereas model responses show 'bursting' behaviour if no size-specific information is used.

Third, growth rates may themselves be influenced by the fire. For example, in the absence of fire many Australian non-Myrtaceae species appeared to grow rapidly, whereas growth rates among Myrtaceae species remained stable and low (Russell-Smith *et al.* 2003). Murphy *et al.* (2009) made the point that fires depress subsequent growth rates of trees (compared with unburned trees) and thus increase the time period small trees may be damaged by fires. Frequent low-intensity fires may thus have the same accumulated impact on trees as infrequent higher-intensity fires. If there is a trade-off between fire frequency and intensity, then fire impacts would be relatively invariant. This has implications for interpretation of fire-frequency experiments. For example, increases in biomass in the absence of fire may be due to increased recruitment but they may also be due to increases in growth rates, and thus transitions, in the absence of fire. The low biomass of savannas is therefore partially due to the way the fire suppresses growth rates and how fire mortality and plant regression overwhelm gross growth.

A major puzzle then is why eucalypts dominate Australian savannas because their growth rates are low (generally <20 cm year<sup>-1</sup> in height for small individuals, and <0.2 cm year<sup>-1</sup> in dbh) (Prior *et al.* 2004, 2006; Cook *et al.* 2005; Murphy *et al.* 2009; but see Fensham and Bowman 1992) and lower than for non-Myrtaceae, such as *Acacia* species. They are also lower than the above rates of 30–60 cm in height growth indicated for African savanna trees. Prior *et al.* (2004) argued that for the apparently slower-growing Myrtaceae to dominate the tree stratum of Australian savannas, they must have greater longevity than do other species. The basic argument is that because they do not have better transition rates or recruitment rates, for some unknown reason this must be balanced by longer life-spans (i.e. lower rates of adult senescence). Savanna tree life spans are poorly known and plant senescence is a poorly understood topic. It remains to be seen just

how eucalypts achieve such large size (and presumed longevity because they are apparently not fast-growing) in a disturbance-prone ecosystem. Midgley and Kruger (2000) argued that senescence in fire-prone Cape fynbos is due to mechanical failure (longer-lived and taller plants need to have low ratios of crown diameter to stem diameter). More recently, Rossatto *et al.* (2009) showed that forest trees have greater growth rates than do savanna trees and that this may be because forest trees have larger and denser canopies for a given stem diameter, than do savanna trees. On the basis of this argument, the expectation would be that eucalypts have relatively small crowns per stem diameter. There are thus several possible solutions to the eucalypt paradox, including the following: (1) eucalypts have faster growth rates as juveniles (i.e. when size is controlled for, eucalypts are fast growing), (2) eucalypts are stronger resprouters (e.g. more deeply buried buds) and therefore they regress less than other guilds with each fire, (3) eucalypts, although not necessarily having relatively thick bark, may have faster bark growth rates, (4) eucalypts have unique allometries that allow them to avoid mechanical failure, and (5) growth rates have been incorrectly calculated (see below).

Growth-rate data in the literature can be difficult to interpret for several reasons. First, there is the problem of including or ignoring the large negative direct fire impacts on growth such as stem death and stem regression. Prior *et al.* (2006) detected a large number of negative growth rates (stem size was reduced by fire). They excluded the larger negative values in their analyses, as well as all stems that died. This may be unrealistic. Species A may be more fire-sensitive than Species B (say 60% stem mortality *v.* 10% for equal-sized stems but with thicker bark in Species B). After a fire on two similar populations, the mean size and growth rates of surviving stems of Species B may thus appear to be less than in Species A, because more stems of Species A suffered shrinkage or damage and thus smaller growth. Survivors of Species A may have very high growth rates, because this species may allocate fewer resources to persistence. The point though is that the predicted size-class distributions after a future fire would not just be a function of the mean growth rates determined from fire survivors. Second, extrinsic influences on growth rates (such as shade or competition) are more likely to reduce mean growth rates in potentially fast-growing species than in slow-growing species. In this case, it is the upper percentiles of growth rates, not the mean growth rate, that is important. For example, Fensham and Bowman (1992) noted extremely fast growth rates (from 1 m tall to 4 m in 1 year) for a breakaway *Eucalyptus miniata* individual, several years after surrounding trees were removed. For extremely fire-tolerant species, the strongest impact of fire on recruitment, could therefore be via an impact on canopy mortality.

Murphy *et al.* (2009) drew attention to the impact that burning has on reducing savanna C stores by influencing subsequent growth rates. However, the strongest impact fires have on savanna basal area and thus of carbon storage, is by influencing mortality rates of large trees, because most of the basal area is contained in a few large trees. Savannas typically have low basal area (e.g. 8.4 m<sup>2</sup> ha<sup>-1</sup> in Murphy *et al.* 2009) and low rates of stem increment (e.g. 0.2 cm year<sup>-1</sup> in Cook *et al.* 2005; Murphy *et al.* 2009). Thus, the loss of just one stem of 50 cm dbh per hectare would negate all annual gross growth. Factors that influence

mortality rates of large trees thus become more crucial than factors that influence growth rates of survivors. The combined impact of fire and termite hollowing is crucial in this regard in Australia (Williams *et al.* 1999; Cook *et al.* 2005) and elephants and fire in Africa.

The low basal area of Australian savannas is especially mystifying to African ecologists, given the large size local eucalypts achieve, the relatively closed canopy, the high rainfall (>1500 mm), the warm tropical temperatures of the area and the relative absence of vertebrate herbivores. Bond (2008) drew attention to the impact of fire on depressing the realised carrying capacity of savannas. This suggests that competitive interactions in savanna, should be weak. Therefore, the observation of strong release of sprouts after canopy (overwood) removal (Fensham and Bowman 1992), and negative correlations between sapling proportions and basal area in Australian savannas (e.g. Lehmann *et al.* 2009), are surprising because basal area appears to be so low in any event.

### Fire *v.* herbivory as determinant of woody plant demography

By using field data from African savannas, Sankaran *et al.* (2008) suggested that after mean annual precipitation, fire (fire frequency) was more important than herbivory in determining woody plant cover (see also Bucini and Hanan 2007). Bond (2008) considered fire to be the crucial disturbance agent in savannas. However, recently Higgins *et al.* (2007) reported the results of a four-decade burning program across several landscapes in the KNP, and which varied in frequency and seasonality. They suggested that neither fire frequency nor fire season affected woody plant density or small tree (<2 m tall) dominance. Landscape contexts had effects larger than fire effects. In only one landscape did fire exclusion have an apparent effect; here, both total numbers of woody plants and woody biomass increased, although these also increased in the burned plots in this landscape.

The surprising findings of Higgins *et al.* (2007) may have been in part because the KNP fire experiment had problems. Marked trees were not followed and so it was not clear whether we were detecting changes in recruitment, transitions, mortality or whether the results merely reflected differences in growth rates. In one landscape where the fire exclusion increased the estimated woody biomass, there was an estimated >10 t ha<sup>-1</sup> more biomass in fire-exclusion plots than in the burned plots, but with an increase of only 0.3 t ha<sup>-1</sup> year<sup>-1</sup> over the duration of the experiment. Because woody biomass strongly depends on the presence of large trees, small differences in the occurrence of large trees in their sample plots (<500 m<sup>2</sup>) strongly affected per hectare estimates of biomass. For example, 15-m trees were estimated to weigh 520 kg and 10-m trees to weigh 185 kg. A single extra tree of these dimensions per sample plot would equate to 10.4 t ha<sup>-1</sup> and 3.7 t ha<sup>-1</sup>. Similarly, biomass of plots is far more sensitive to large-tree mortality than to small-tree emergence (death of one 15-m tree in 40 years would equal biomass estimates of 170 new escapees of 2-m height). Also, impacts of fixed fire regimes in landscapes of different productivity may be dominated by productivity responses, not fire responses. For example, biomass could be higher in mesic areas because, although fire impacts are

similar (e.g. % top-kill), surviving plants grow faster after fires in mesic areas. Also critically, Higgins *et al.* (2007) did not consider the role of herbivory, nor the interaction between fire and herbivory, as determinants of woody biomass. For example, grazers may be attracted to post-fire patches and thus reduce subsequent fuel loads, woody plant recruitment or transitions. If browsers are preferentially attracted to certain landscapes, their impacts may over-ride fire impacts in these landscapes. This information is critical for understanding fire regimes and plant responses. Redfern *et al.* (2006) showed for KNP that most browsers (giraffe, kudu) were attracted to the resource-rich basalt areas, as were some grazers (zebra, wildebeest), whereas elephants and buffalo also occurred on nutrient-poor substrates.

In contrast to the above studies, other recent modelling exercises have suggested that herbivory, especially by elephants, is more important than fire (Baxter and Getz 2005, 2008; Holdo 2007), even for KNP. Holdo (2007) presented one of the most comprehensive models containing both fire and herbivory (and frost). It was locally validated (growth rates, mortality rates) for a semiarid savanna (i.e. more arid than parts of KNP). His simulations suggested that herbivory by elephants is far more important than fire (or frost) in determining the basal area of trees. Holdo (2007) is also notable in that he considered interactions between various factors. For example, frost and fire strongly interacted to reduce woody basal area. All interactions with elephants were strong, with a combination between elephants, frost and fire being almost fatal for trees, especially for elephant-favoured species. The three-way interaction would virtually eliminate the woody biomass from the area within 50 years, even when assuming no increase in elephant density. Baxter and Getz (2005) also provided broad models that consider the role of fire, herbivory and climatic variation on tree abundance. They suggested that fire was relatively unimportant and that elephant densities of 1 ha<sup>-1</sup> would eliminate woody plants within a century. Woody plants decline monotonically with densities of just 0.5 elephants km<sup>-1</sup>. The large decline of woody plants within kilometres of the Chobe River (Mosugulo *et al.* 2002) is associated with herbivory. Fire has declined in this area, probably because of both elephants and impala reducing fuel loads (Mosugulo *et al.* 2002). Recently, Asner *et al.* (2009) used herbivore exclosures to argue that herbivory, mainly by elephants, strongly affects vegetation structure. However, Asner *et al.* (2009) provided no fire information for the exclosures, nor any data on the inter-action between fire and herbivory outside of exclosures. Unfortunately, there are almost no experiments that have controlled for the impact of fire and herbivory, as well as the interaction between them. These would be expensive experiments.

Bush encroachment, the thickening up of woody components of savannas, should provide insights into savanna woody plant demography but unfortunately it also suffers from a plethora of factors, especially herbivory *v.* fire. Global factors may also be important, such as those involving the differential impacts of global CO<sub>2</sub> fertilisation on increased C3 woody plant growth (see Bond 2008 for recent review). Although bush encroachment is common across the planet (Berry and Roderick 2006; Bond 2008), encroachment is not global, nor always by C3 plants and is not always recent (i.e. in concert with rising CO<sub>2</sub>). For instance, only some sites in KNP have experienced increases in

woody plants (Higgins *et al.* 2007). The nutrient-rich basalts of KNP have experienced >60% decline of woody cover in recent times (Eckhardt *et al.* 2000), presumably because browsing is more intense there (Redfern *et al.* 2006). In Australia, Lehmann *et al.* (2008) detected rather small changes in plant cover or basal area across a 40-year period in a mesic savanna. This lack of increase may be because of the frequent fire regime (>50% of the area burns annually). Fensham (2008) also documented highly stable woody structure in eastern Australian savannas. Fensham *et al.* (2005) argued that fire and grazing variables did not explain increased cover in east Australian savanna in the second half of the 20th century, but that the less intense droughts of this period did.

Some encroaching species in savannas are CAM succulents, such as dense extensive stands of exotic *Opuntia* in KNP (Lotter and Hoffmann 1998) and indigenous *Euphorbia* in Queen Elizabeth Park (Midgley 2009). The photosynthetic rate of C4 and CAM plants would not benefit by CO<sub>2</sub> fertilisation as much as would that of C3 woody plants. Succulents would, however, benefit from declining fire frequencies. Regarding the time scale of bush encroachment, Silva *et al.* (2008) noted that gallery forest expansion into South American cerrado was initiated several thousand years ago. Few generalisations emerge regarding the causes of bush encroachment. More research is needed into ways of reducing it, especially through use of increased fire intensity and/or browsing.

### The synergistic role of fire and animals on tree demography

Herbivores can influence both the fire regime (such as intensity), as well as fire impacts on woody plants (such as reducing growth rates, and thus transitions). Herbivores are themselves affected by fire regimes (e.g. Klop and Prins 2008) and are attracted to burned areas (Archibald and Bond 2004). Okello *et al.* (2008) even hypothesised that elephants may be attracted to post-burn areas and thus should be considered a fire-mortality agent.

Another important aspect of fire–herbivory synergy may arise from herbivore-driven bark damage. Analysis of aerial photographs shows a general decline in large trees (>5 m) in KNP (Eckhardt *et al.* 2000). Most of these trees were beyond the size that either elephants or fire could topple. Although elephants typically do not routinely ring-bark trees, even removal of small bits of bark, especially within 1–2 m of the ground, could increase fire damage. Moncrieff *et al.* (2008) noted the significant impact of bark removal on post-fire responses of trees. Thus, an elephant–fire synergy supplies a mechanism for the fire mortality of large trees. Yeaton (1988) suggested that porcupine damage of stems allows fire to gradually incinerate and hollow out trees, predisposing them to toppling. Porcupine damage may also exacerbate fire effects, causing cambium necrosis, girdling and xylem damage, and not just the gradual incineration, and then toppling, of stems. Even horning of woody stems by grazers (wildebeest) in Serengeti is considered to be an important determinant of woody vegetation structure (Estes *et al.* 2008). In a further example from tropical savannas in Australia, tree-piping by termites indirectly increases the mortality of larger trees (>30 cm DBH) by making them more vulnerable to fire (Williams *et al.* 1999; Werner and Prior 2007). There may also be positive feedback; hydraulic damage due to fires progressively

facilitates wood incineration and the eventual toppling of large trees. Finally, the way different tree species respond to damage by regrowing their bark or reducing stripping with brittle bark may be an important savanna trait, to match bark thickness.

Because grazers can influence fuel loads, grazers may indirectly influence tree demography by potentially influencing fire frequency or intensity (Van Langevelde *et al.* 2003; Petty *et al.* 2007; Bowman *et al.* 2008), with e.g. an increase in grazing pressure leading to an increase in trees. Van Langevelde *et al.* (2003) invoked a complex model relating fire frequency, fire intensity and herbivory, soil moisture regimes and the 'tree–grass rooting niche' hypothesis to the cover of trees. Recently, Holdo *et al.* (2009) modelled the likely impacts of fire, elephants (mixed-feeder) and wildebeest (grazer) on the tree cover. Their results suggested that the presence of wildebeest reduces fire impacts. This then facilitates trees, whereas the presence of elephants and fires causes a strong decline in trees. This is some support for the 'high grazer–low fire–high tree abundance' hypothesis; however, it is not clear whether this is due to increases in recruitment or transitions. Evidence is needed to demonstrate the link between the increase in grazing and an increase in tree recruitment. Adult trees would largely be out of reach of the moisture influence of grasses or fire impacts and therefore the 'high grazing–high tree' hypothesis may be caused by increases in transitions. The 'tree–grass rooting niche' hypothesis is largely discredited (Scholes and Archer 1997), suggesting limited impacts of grasses on established trees. Riginos (2009) recently argued that the presence of grasses influences both growth and transitions of a savanna *Acacia* species. Many intensely grazed areas of East Africa remain open grasslands. This is probably due to impacts of small browsers such as impala on recruitment.

### Summary

Much remains to be discovered in savannas and in many cases modelling needs greater biological input, demographic clarity and to encompass more savanna plant strategies. How savanna trees survive fires remains poorly understood and a full demographic analysis of any savanna tree species remains to be done. Does over-grazing cause bush encroachment? Is this by increasing transitions or recruitment? Why are Australian eucalypts so large and how do they achieve this large size? The unravelling of the separate impacts of fire and herbivory is necessary but both difficult and expensive and should ideally involve a range of species and cross the arid–mesic savanna divide.

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