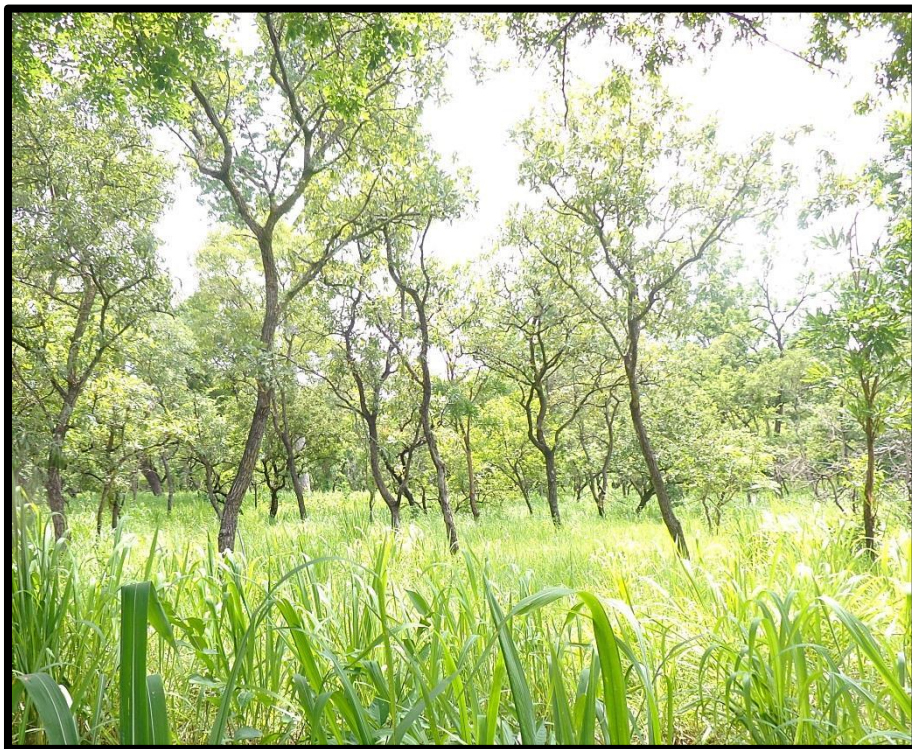


**PLAYING WITH FIRE:
INVESTIGATING SUPPRESSION AND
RESISTANCE THRESHOLDS
IN TROPICAL WEST AFRICAN FOREST SEEDLINGS
ACROSS A SAVANNA-FOREST TRANSITION**



*Submitted in partial fulfilment of the requirements for the degree of
Master of Science in Environmental Change and Management,
University of Oxford.*

Candidate number: 164654

Word count: 14 999

CONTENTS

	p
Abstract.....	1
General introduction.....	2
Literature review and background for hypotheses.....	4
Aims and hypotheses.....	20
Methods.....	22
Results.....	37
Discussion.....	54
Concluding remarks and management implications.....	70
References.....	72
Appendix.....	87
Acknowledgements.....	93

ABSTRACT

Forest and savanna represent two alternative ecosystem stable states. Shifts between states are not easily reversible. Fire can determine state shift, with shifts from savanna to forest occurring when trees cross the fire suppression or resistance threshold. This study investigated these thresholds in the seedlings of five tropical forest tree species across a forest-savanna transition in West Africa. The fire suppression threshold was not found. Below a threshold of 30% canopy openness herbaceous biomass decreased, however fire was not suppressed nor seedling survival increased. The fire resistance threshold was found. Seedlings taller than a threshold 380mm had a higher survival rate through fire than shorter seedlings. Trade-offs between growth traits and ability to recover from fire were observed across all species. *Bombax buonopozense*'s allocation patterns favoured fire recovery and it survived especially well in the savanna vegetation type, making it an excellent indicator species for forest encroachment into mesic tropical West African savannas.

GENERAL INTRODUCTION

Many of the responses of ecosystems to environmental change are characterised not by gradual linear behaviour but by thresholds and abrupt transitions from one stable state to another (Beisner *et al.*, 2003). Tropical forest and savanna are two such ecosystems (Hirota *et al.*, 2011; Staver *et al.*, 2011a), with the transition between them providing an interesting model system for investigating how and why such thresholds occur. Whether a forest or savanna state exists at a point in space and time is determined by the interaction between fire, climate, resources, and species traits (Hoffmann *et al.*, 2012). Shifts of state from savanna to forest, or vice versa, as a result of climate change or fragmentation, are neither smooth nor easily reversible (Staver *et al.*, 2011a).

The switch in states from savanna to forest, or forest encroachment, is an important process of tropical environmental change that has been well documented in several southern African savannas (Wigley *et al.*, 2009) as well as multiple regions in tropical Africa (Mitchard *et al.*, 2009; Mitchard & Flintrop, 2013). Furthermore, according to global circulation models, under climate change predictions alone the savannas of West Africa are predicted to contract by 2050 with tree cover predicted to increase by 1 - 10 % in large parts of Benin, Burkina Faso, Côte D'Ivoire, Ghana, and Togo (Heubes *et al.*, 2011). Forest encroachment into savanna will be further enhanced if fire and herbivory are suppressed (Mayer & Kahlyani, 2011; Hopkins 1992, Swaine *et al.*, 1992) and if atmospheric carbon dioxide increases and favours the growth of trees over herbaceous plants (Dai *et al.*, 1993; Ogren, 1984).

Savannas are fire maintained ecosystems while forests are ecosystems largely unaffected by fire (Hoffmann *et al.*, 2012). Fire driven tipping points, or thresholds, are likely to exist in savanna and once crossed will lead to the system shifting to forest (Hoffmann *et al.*, 2012). Understanding these thresholds is vitally important to effectively monitor and manage these important ecosystems as these thresholds are likely to be affected by current and future global and local environmental change (Bond & Midgley, 2012; Hoffmann *et al.*, 2012; Archibald *et al.*, 2005). As it stands, we are on the cusp of several fire-driven thresholds in many of the world's woody biomes, including savanna, as a result of changing climate and human management (Adams, 2013). This study will investigate these fire driven thresholds in a tropical African savanna-forest transition zone.

LITERATURE REVIEW AND BACKGROUND FOR HYPOTHESES

What are forests and savannas and why do they matter?

Tropical forests have a closed canopy of trees with an understory but no continuous herbaceous layer (Hoffmann *et al.*, 2012). Tropical savannas have a discontinuous tree layer which lies within a continuous C4 herbaceous layer (Lehmann *et al.*, 2014; Veenendaal *et al.*, 2014). Tropical forests are largely unaffected by regular fire (Hoffmann *et al.*, 2012), while drier forests are affected only by occasional ground fires (Bond & Van Wilgen, 1996). Tropical savannas, however, as a result of their continuous herbaceous fuel layer, are one of the most fire prone ecosystems in the world (Mouillot & Field, 2005), with 2.6 million km² of savanna burning in Africa each year (Schultz *et al.*, 2008).

Tropical savannas and forests are both globally important ecosystems. The tropical forest biome contributes 33% to total global land surface metabolic activity and gross primary productivity (Malhi, 2012). These forests are valuable both for their roles in carbon and water cycling and their extensive biodiversity (Malhi, 2012). The savanna biome covers 20% of the earth's land surface and contributing 25% to total global gross primary productivity (Beer *et al.*, 2010) and 30% to global net primary production (Scholes & Archer, 1997; Field *et al.*, 1998; Archibald *et al.*, 2013). It covers large regions of tropical and subtropical Africa (Bond & Midgley, 2000), is currently home to one fifth of the human population, and sustains most of the global megafauna population (Scholes & Archer, 1997). The transition between savannas and forests is important as, especially in Africa and South America, many people depend on it for the ecosystem services it provides, such as land for grazing and

agriculture (Skarpe, 1991). Changes affecting the savanna, the forest, or the transition between the two will thus have direct socio-economic consequences.

Alternative stable states, hysteresis and thresholds

Forest and savanna are alternative stable states (Hirota *et al.*, 2011; Staver *et al.*, 2011a). The theory of alternative stable states is that in the same geographical area two or more different stable ecosystem states may exist at different times (Holling, 1973; Scheffer *et al.*, 2001; Dent *et al.*, 2002). The analogy most often used to describe alternative stable state theory is that of a ball in a basin, next to adjacent basins, with each basin representing an alternative stable state of that ecosystem (Beisner *et al.*, 2003, **Figure 1**). If perturbed, the ball can move up the sides of its current basin, and if sufficient perturbation occurs it can roll into the adjacent basin, representing a shift from one stable state to another. The ball, or ecosystem, is more likely to roll into the other basin, or shift states, under repeated perturbations to the system or if perturbations are more extreme (Beisner *et al.*, 2003). The degree of difficulty the ball experiences in switching basins is determined by the steepness of the edges and the size of the basin, and the ability to resist changing basins, or states, is referred to as “ecological resilience” (Beisner *et al.*, 2003; Peterson *et al.*, 1998).

Associated with the idea of changing states is the idea of hysteresis, or irreversibility, and tipping points, or thresholds. Hysteresis is why it is easy for a ball to roll downhill into a steep basin, but much more difficult to roll out. In an ecological context, hysteresis means that while a system may be resilient to perturbations up to a point,

once a threshold is crossed and a state shift has occurred, far greater perturbations may be required to return it to the previous state (Beisner *et al.*, 2003). The threshold that, if crossed, leads to this irreversible state shift is called a tipping point.

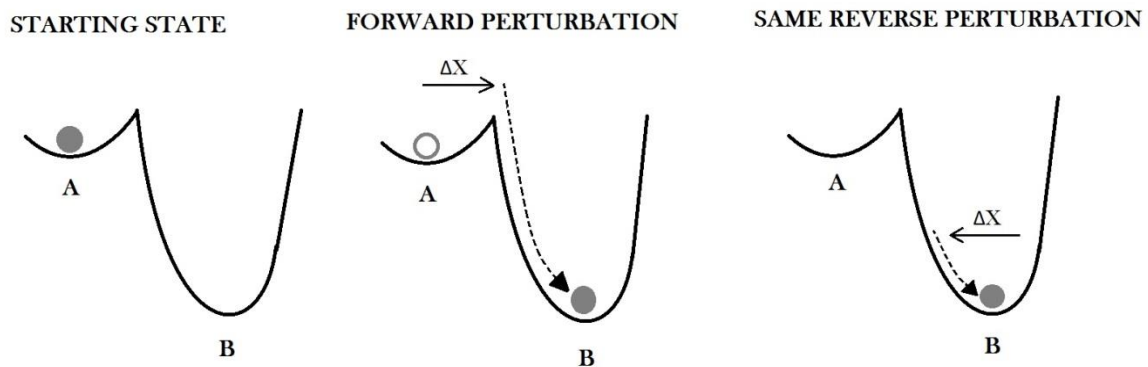


Figure 1: Simplified ball-in-basin model of the theory of alternative stable states and hysteresis. Alternative states “A” and “B” are the two basins, the current state of the system is the grey ball. A perturbation of size X it may push the ball from one state to another, however the same perturbation of size X cannot return it to the previous state (hysteresis). [Figure based on Beisner *et al.*, 2003].

The theory of alternative stable states, especially as it applies to savanna and forest ecosystems, has recently been questioned. Veenendaal *et al.* (2014), after looking at floristic and structural patterns of forest-savanna transitions across tropical areas in Africa, South America and Australia, found a much less marked transition between these two states than expected. This implies a continuum between these two states rather than a discontinuum or sudden state shift, thus providing some evidence against the alternative stable states hypothesis (Veenendaal *et al.*, 2014). Hanan *et al.* (2014) also suggest that evidence of the presence of alternative stable states may

be an artefact of errors in remote sensing products. Despite this recent controversy, there still remains ample support for the theory of alternative stable states in savanna-forest transitions (*inter alia* Hoffmann *et al.*, 2012; Hirota *et al.*, 2011; Staver *et al.*, 2011a; Sankaran *et al.*, 2005) and therefore this framework still remains relevant.

Climate, especially rainfall, plays an important role in determining whether a system is forest or savanna

The distribution of savanna across the globe is largely defined by precipitation, with mesic savannas being wetter than arid savannas (Lehmann *et al.*, 2011). Both effective rainfall (mean annual precipitation–potential evapotranspiration) and rainfall seasonality (dry season length) are important for determining where the transition from savanna to forest occurs (Lehmann *et al.*, 2011). Globally, the transition from forest to mesic savanna is most likely to occur where effective rainfall is less than 570mm, as long as the rainfall is seasonal (dry season exceeding five months) (Lehmann *et al.*, 2011). The transition from shrubland/thicket type forest to arid savanna is less predictable and varies between continents (Lehmann *et al.*, 2011). As a result of being wetter and more productive, mesic savannas have increased herbaceous biomass and therefore higher fuel loads than their drier, less productive arid counterparts (Hoffmann *et al.*, 2012; Bond *et al.*, 2003, 2005; Sankaran *et al.*, 2005; Higgins *et al.*, 2000). Mesic savannas, such as those of tropical West Africa,

therefore burn more regularly and with higher intensity than arid savannas (Bond *et al.*, 2003, 2005; Sankaran *et al.*, 2005; Higgins *et al.*, 2000).

One of the biggest differences between savanna and forest is their difference in above-ground biomass, which is largely determined by tree biomass (Sankaran *et al.*, 2005). Forests have closed canopies and therefore a higher tree biomass than savannas (Sankaran *et al.*, 2005). Tree biomass and formation of a closed canopy is largely determined by rainfall (Sankaran *et al.*, 2005; Lehmann *et al.*, 2011). When mean annual precipitation (MAP) is below ~650mm, tree biomass and thus canopy closure is limited by water availability (Sankaran *et al.*, 2005). Despite this, above ~650mm MAP tree biomass is often below the climate determined potential, where a high tree biomass and closed canopy is not always observed, despite there being enough water to provide for it (Sankaran *et al.*, 2005; Bond *et al.*, 2005).

Other factors, including fire, also play an important role in determining whether a system is forest or savanna

When the tree biomass and degree of canopy closure of a system is below the climatically determined potential, the ecosystem is said to be under “consumer control” (Bond *et al.*, 2005; Bond & Keeley, 2005). “Consumer control” is where a consumer, such as fire or herbivory, consumes part of the biomass in an ecosystem, causing the ecosystem to not reach its climate-determined biomass potential (Bond *et al.*, 2005). The discrepancy between actual and potential biomass is often so pronounced that it is estimated that closed canopy forest would double its current global range if “consumer control” was not present (Bond & Keeley, 2005).

Savannas are an excellent example of consumer controlled ecosystems, as they often have a lower biomass than their climatic potential as predicted by precipitation (Sankaran *et al.*, 2005 in Higgins *et al.*, 2007). This discrepancy between actual and potential biomass is extremely pronounced in savannas in the wetter regions of Africa, and, since these are some of the most frequently burnt ecosystems in the world, fire is often invoked as a key “consumer” in these systems (Bond & Keeley, 2005). Fire has been shown to be a factor playing a pivotal role in reducing tree cover in West, East, and Southern African savannas where mean annual precipitation is above ~650mm (Sankaran *et al.*, 2008). Fire, therefore, is a key driver in determining whether forest or savanna is the current stable state of an ecosystem.

How fire maintains savanna: the fire-trap hypothesis

In the past, models for tree-herbaceous layer coexistence in savannas were often implicitly equilibrium based, for example the root niche-separation hypothesis (Walter, 1971) that postulated that trees and grasses coexisted by separating their rooting depths and therefore their water sources. More recent hypotheses draw on non-equilibrium models where savannas are seen as dynamic and often unstable systems (Scholes & Archer, 1997; Bond & Midgley, 2000). One of the primary tree-herbaceous layer coexistence non-equilibrium theories is the “fire-trap” hypothesis (Bond, 2005; Bond *et al.*, 2005; Sankaran *et al.*, 2005; Higgins *et al.*, 2000; Hoffmann, 1999).

Fires in savanna typically burn the herbaceous layer, with trees not tall enough to escape the flames experiencing top-kill (whole or partial death of above-ground biomass) (Trollope, 1984; Glitzenstein *et al.*, 1995; Williams *et al.*, 1999; Higgins *et al.*, 2012). Top-kill in savannas seldom leads to whole plant death (Bond & Van Wilgen, 1996; Hoffmann *et al.*, 2009; Werner & Franklin, 2010), therefore repeated top-kill by fire leads to a demographic bottleneck with a large number of trees unable to reach canopy height (Bond & Keeley, 2005; Bond & Von Wilgen, 1996; Higgins *et al.*, 2012). Trees therefore persist for many years within the herbaceous layer, resprouting vigorously but never reaching escape height (Bond & Midgley, 2001; Higgins *et al.*, 2007). This phenomenon is known as the “fire-trap”, and acts as a mechanism to prevent canopy closure in savannas via repeated top-kill of smaller trees and more infrequent killing of entire trees in extreme events (Hoffmann *et al.*, 2012; Williams *et al.*, 1999; Hoffmann & Solbrig, 2003; Holdo, 2005; Higgins *et al.*, 2007). There are only two ways trees can escape the fire-trap: by crossing the “fire resistance” or “fire suppression” threshold.

Crossing either the fire suppression or fire resistance threshold facilitates the encroachment of forest into savanna

The “fire suppression” threshold acts on an ecosystem level and occurs when trees grow at such a density or large enough that the canopy closes and excludes fire (Hoffmann *et al.*, 2012; **Figure 2**). Under a closed canopy, the understory fuel layer is reduced due to lack of light. Light is often a limiting factor in forests, and decreased light can result in dramatic decreases in the success of herbaceous plants by decreasing photosynthetic capacity (Sims & Pearcy, 1989). The resulting

decrease in biomass of the herbaceous fuel layer combined with the moister, less windy microclimate associated with a closed canopy results in decreasing fire frequency and intensity as fire requires fine dry fuels to spread (Biddulph & Kellman, 1998; Uhl & Kauffman, 1990; Ray *et al.*, 2005; Hoffmann *et al.*, 2012) (**Figure 2**). The fire suppression threshold occurs at the point when canopy openness is low enough to decrease herbaceous biomass sufficiently to suppress fire (Hoffmann *et al.*, 2012, **Figure 3**).

The “fire resistance” threshold acts on the scale of individuals and occurs when trees grow large enough to no longer experience top-kill by fire (Hoffmann *et al.*, 2012; **Figure 2**). Increased size increases bark thickness as bark thickness is dependant on stem diameter (Hedge *et al.*, 1998). Thicker bark has an insulating effect during fire, protecting the xylem and phloem transport systems from being damaged, therefore enabling photosynthates and water to continue to be transported between root and shoot (Higgins *et al.*, 2012; Gill & Ashton, 1968; Bauer *et al.*, 2010). Bark also functions to protect the tree from top-kill as, if it is moist with water, it can prevent ignition during fire as a result of its higher heat capacity (Gill & Ashton, 1968; Higgins *et al.*, 2012). Increased tree size, specifically height, also helps prevent top-kill during fire by raising the fire-sensitive canopies, and thus the majority of the photosynthetic material, out of the flames, preventing them from reaching critical temperatures (Higgins *et al.*, 2012; Gill & Ashton, 1968; Bauer *et al.*, 2010). Stem diameter, height, and bark thickness are good predictors as to whether a tree will be top-killed by fire or not (Hoffmann *et al.*, 2012). Only certain individual trees ever manage to get big enough to escape fire, and these tend to be the individuals with growth rates exceeding the mean growth rate of the species (Wakeling *et al.*, 2011).

The fire resistance threshold occurs at the point where the diameter, a proxy for bark traits, or height of a tree is associated with a dramatic decrease in top-kill by fire (Hoffmann *et al.*, 2012, **Figure 3**).

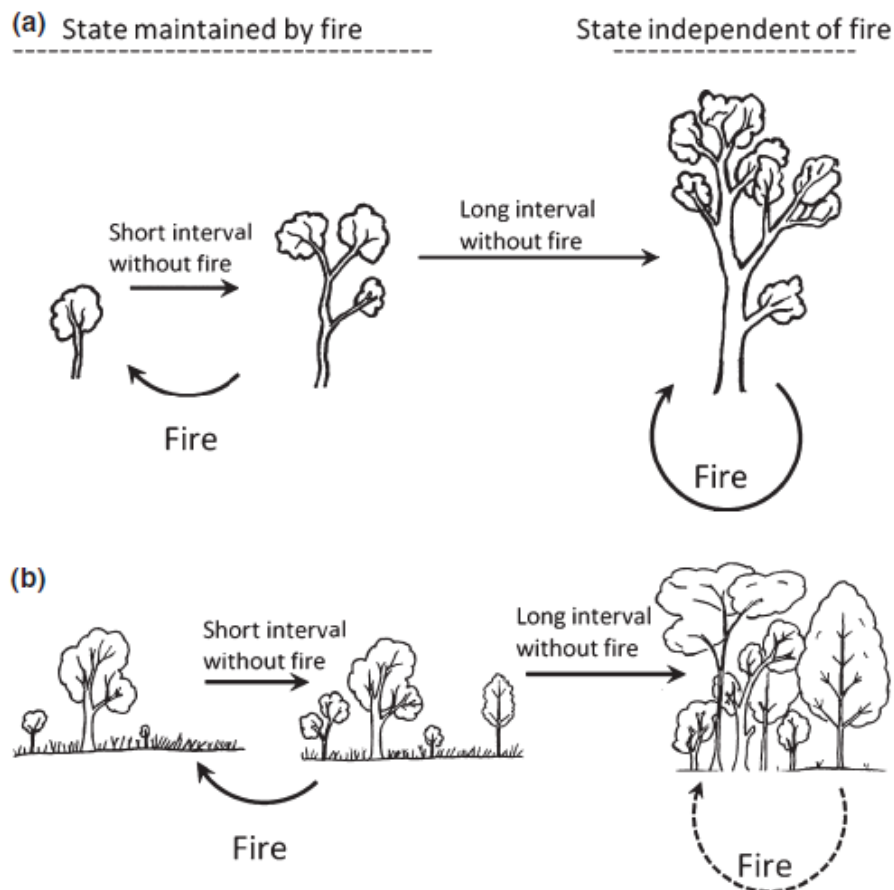


Figure 2: Trees can overcome the fire-trap and shift from a state maintained by fire (eg. savanna) to one independent of fire (eg. forest) by crossing a) the fire resistance threshold or b) the fire suppression threshold. In (a) saplings are unable to grow big enough to avoid top-kill by fire and therefore the system remains in a fire maintained state, however if the interval between fires is long enough then saplings have sufficient time to grow large enough to be able to resist top-kill by fire and the state shifts to one independent of fire. In (b) saplings are unable to grow mature crowns that overlap sufficiently to close the canopy and restrict the growth of the herbaceous fuel layer and therefore the system remains in a fire maintained state, however if the interval between fires is long enough then saplings are able to form closed canopies and therefore restrict herbaceous fuel and suppress fire (broken arrow) and the state shifts to one independent of fire. [Figure: Hoffmann *et al.*, 2012].

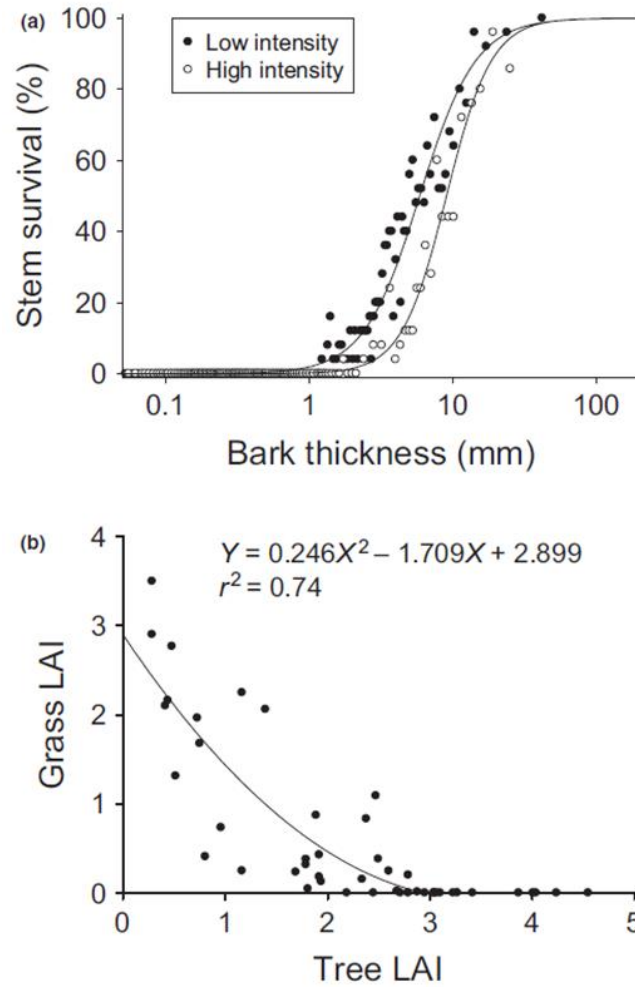


Figure 3: a) The fire resistance threshold, represented as the decreased probability of top-kill above a certain bark thickness in high and low fire intensities and b) the fire resistance threshold, represented by the decreasing grass leaf area index (LAI) with increasing tree LAI. (Data from Brazilian Cerrado) [Figure: Hoffmann *et al.*, 2012].

The encroachment of forest into savanna represents a shift between alternative stable states and is facilitated by the crossing of either the fire resistance or suppression threshold. Once either threshold is crossed the state shift is self-enforcing due to positive feedbacks (Lehmann *et al.*, 2011). Having a closed canopy that suppresses fire further promotes the growth of trees which further closes the

canopy and suppresses fire; and trees that grow large enough to resist top-kill by fire will continue, even under repeated fire, to resist top-kill by fire.

Global environmental change drivers can determine whether a forest or savanna state occurs by interfering with these thresholds

The time taken to cross either the fire suppression or fire resistance threshold is critical (Hoffmann *et al.*, 2012). Factors that increase or decrease this time can therefore have effects on tree density (Hoffmann *et al.*, 2012) and ultimately lead to a switch from savanna to forest or vice versa (**Figure 4**). Changes in climate and resources, which are often global scale processes, can thus have local effects and determine whether a system is forest or savanna.

Atmospheric carbon dioxide (CO₂) is important in determining the time taken to reach either threshold as increased CO₂ can enhance plant growth (Kgope *et al.*, 2010), particularly in trees (Dai *et al.*, 1993; Ogren, 1984). Palynological and isotopic evidence shows that the boundaries between forest and savanna are not constant but shift through time (Kershaw, 1992; Desjardins *et al.*, 1996; Schwartz *et al.*, 1996; Sanaiotti *et al.*, 2002). Historically, some of the largest scale changes in vegetation cover have been associated with changes in atmospheric CO₂ (Wills & McElwain, 2002). In greenhouse experiments, African Acacia seedlings showed increased photosynthesis, total stem, total stem diameter, shoot dry weight, and root dry weight under increased CO₂ concentrations, implying that CO₂ has a direct effect on these seedlings' ability to recruit in savanna systems (Kgope *et al.*, 2010).

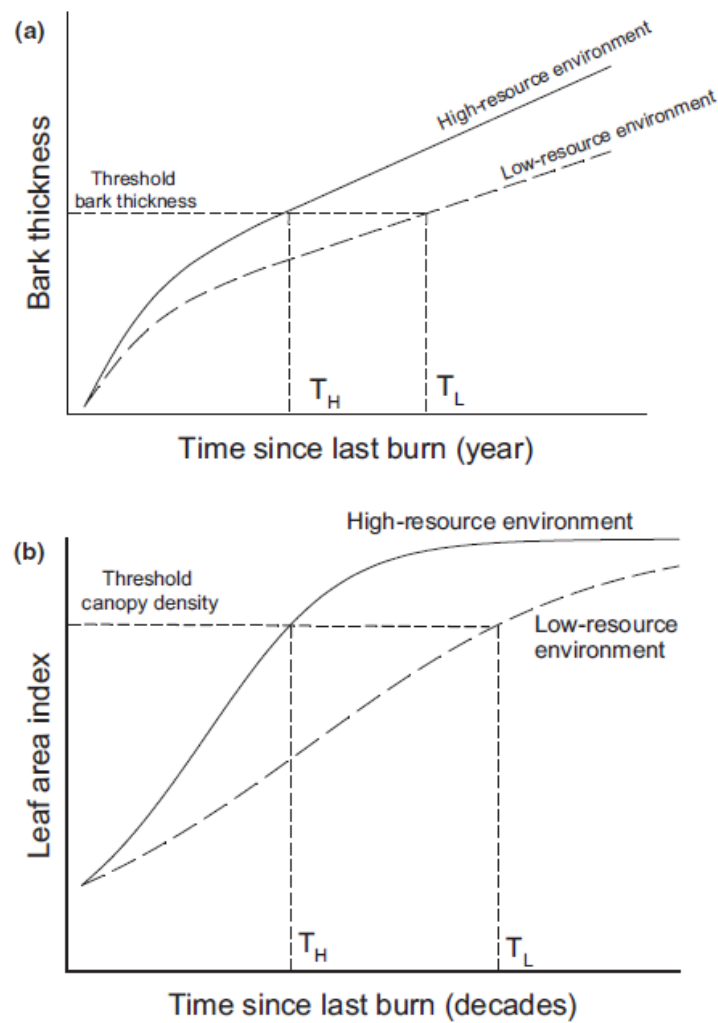


Figure 4: Increased resource availability can decrease the time taken to cross either the a) fire resistance or b) fire suppression threshold by increasing growth rate and rate of canopy closure respectively. [Figure: Hoffmann *et al.*, 2012].

Increased atmospheric CO_2 enhances tree success in savannas as the growth benefit it confers onto trees, which are C3, is relative more than it confers onto herbaceous plants, which are C4 (Dai *et al.*, 1993; Ogren, 1984). Plants that do C4 photosynthesis are less likely to photorespire than plants that do C3 photosynthesis (Dai *et al.*, 1993; Ogren, 1984). Photorespiration is the wasteful process whereby oxygen instead of the preferred CO_2 is reduced by the photosynthetic enzyme

Rubisco and is more likely to occur when atmospheric CO₂ is lower, as the decreased CO₂ concentration means that there is proportionally more oxygen in the air entering the stomata of the leaf (Dai *et al.*, 1993; Ogren, 1984). When atmospheric CO₂ increases, photorespiration decrease, conferring a growth benefit to plants as photosynthesis becomes more efficient. Since C4 plants, including the herbaceous layer of savanna, are evolved to experience little photorespiration at most CO₂ concentrations, this benefit is felt more strongly by C3 plants, such as the trees of savanna (Dai *et al.*, 1993; Ogren, 1984). Increased CO₂ in the atmosphere has therefore been suggested to have the ability to enhance tree seedling growth rate, therefore enabling more individuals to escape the fire-trap, promoting forest encroachment into savanna (Bond & Midgley, 2012).

Crossing the fire resistance threshold is associated with allocation trade-offs and these can determine which species lead the encroachment of forest into savanna

Linked to the fire resistance threshold is the idea of allocation trade-offs. Allocation trade-offs are not uncommon in plants, with the way resources are allocated to above- and below-ground biomass being an adaptive trait, with trade-offs existing between above- and below-ground resource capture (Tilman, 1988; Brouwer, 1962; Thornley, 1972; Bloom *et al.*, 1985). In scrub species these trade-offs are well documented, with carbon allocation in species that have carbon storage organs indicating that resources are either devoted to growth, specifically post fire recovery, or reproduction, specifically seed production (Bond & Midgley, 2001). In woody shrub seedlings, allocation patterns and trade-offs may even affect competitive ability

(Clarke & Knox, 2009). For example, in woody shrubs growing in grassy communities, species that recovered from fire by resprouting as opposed to releasing seeds allocated more to roots than their reseeding counterparts and were therefore less affected by above-ground competition with grasses (Clarke & Knox, 2009).

Trade-offs between ability to compete and ability recover from fire have been found in comparisons of savanna and forest tree species. The difference in processes governing forest and savanna biomes mean that the tree species associated with each biome are not usually the same, and therefore the communities have different species traits and thus different responses to fire (Bowman, 2000; Hoffmann *et al.*, 2003, 2005, 2009; Ratnam *et al.*, 2011; Gotsch *et al.*, 2010; Rossato *et al.*, 2009). Savanna tree species tend to have a carbon expensive life history strategy, investing heavily in increasing root carbohydrates (Hoffmann *et al.*, 2004), root biomass (Hoffmann & Franco, 2003), and bark (Hoffmann *et al.*, 2012). High investment below-ground means that these trees have an extensive energy store, enabling them to effectively resprout after top-kill by fire and quickly regrow their lost photosynthetic material (Hoffmann, 2000). Forest species, having evolved where fire was not as strong a selective pressure, tend to have up to three fold thinner bark than savanna species, meaning that they have to reach much larger sizes than savanna species to avoid being top-killed by fire (Hoffmann *et al.*, 2012; Hoffmann *et al.*, 2003). Forest seedlings growing in savanna therefore experience higher rates of top-kill than savanna species (Hoffmann *et al.*, 2009). This difference in survival is partially offset by forest trees growing faster than savanna trees when both are growing in savanna conditions, making them superior competitors and able to reach escape height faster

than savanna trees (Hoffmann *et al.*, 2012; Rossato *et al.*, 2009). These trade-offs have been documented in congeneric pairs of savanna and forest tree species, where there was greater allocation of resources to coarse roots in savanna species than their forest counterparts, a trait that helped them recover more effectively from fire as they had an increased sprouting ability (Hoffmann & Franco, 2003). Furthermore, tree species in tropical savannas that were from mesic savannas allocated more to roots than those from arid savannas, presumably because fire is more frequent in these environments (Tomlinson *et al.*, 2012).

The differences in allocation patterns seen in forest and savanna tree species is evidence that trade-offs between competitive ability and ability to recover from fire exist. Since allocation trade-offs can be adaptive traits (Tomlinson *et al.*, 2012), savanna tree species in fire-prone environments generally favour fire recovery allocation patterns and forest tree species in low-light, competitive environments generally favour allocation patterns that increase competitive ability (Hoffmann *et al.*, 2012). Plants with similar leaf properties therefore have different growth rates if one is allocating resources below ground in anticipation of resprouting after fire and one is not (Bond & Midgley, 2001). The inability of forest tree species to deal with fire is one of the primary factors decreasing their success in savanna environments (Hoffmann *et al.*, 2004, 2012), limiting the ability of forest to encroach upon savanna. Following this logic, forest tree species that exhibit allocation patterns most like savanna species, favouring recovery from fire rather than competitive ability, are more likely to succeed in savanna environments and thus lead the encroachment of forest into savanna.

Current knowledge gaps

The fire-trap hypothesis has been studied in Southern African arid savannas in savanna tree species (Wakeling *et al.*, 2011; Staver *et al.*, 2009) and in gallery forest and savanna tree species in Brazil (Hoffmann *et al.*, 2012; Hoffmann *et al.*, 2009), where it was found to apply to observational data. Both the fire suppression and fire resistance threshold theories were developed in the Cerrado region of Brazil using Brazilian gallery forest and savanna tree species (Hoffmann *et al.*, 2012). The fire suppression threshold has been demonstrated in the Venezuelan savanna-forest transition (Biddulph & Kellman, 1998) and the fire resistance threshold in South African arid savanna tree species (Higgins *et al.*, 2012). This study is novel as neither the fire-trap nor its associated thresholds have been studied in tropical mesic forest tree species, and there has been no study in the northern hemisphere African tropics, which appears to be a very active region of widespread forest encroachment into savanna (Mitchard & Flintrop, 2013).

AIMS AND HYPOTHESES

Aims

This study aims to investigate the fire-trap hypothesis across a tropical forest-savanna transition. Specifically, it will investigate aspects of the fire resistance threshold and the fire suppression threshold in five West African tropical forest tree species.

Hypotheses

- i) The fire suppression threshold exists in this system, therefore below a threshold of canopy openness, decreased canopy openness will be accompanied by a decrease in herbaceous biomass and this will be accompanied by a decrease in fire.
- ii) Decreased herbaceous biomass will be associated with increased tree seedling survival as a result of fire being suppressed by lack of fuel.
- iii) The fire resistance threshold exists in these tree seedlings; therefore a threshold of pre-fire size (diameter and height) in seedlings will be associated with a marked increase in seedlings' post-fire survival.
- iv) Trade-offs between competitive ability, as measured by growth, and ability to recover from fire, as measured by below-ground starch storage capacity, exist in these tree seedlings.

An experimental approach was taken to examine the thresholds, where plant traits were studied over time in a natural environment, in order to best incorporate as

much of the natural variation that occurs in the system as possible and therefore make the results as representative of the true-life situation as possible.

The study used seedlings as opposed to mature trees as the fire-trap acts on seedlings. Allocation patterns and trade-offs in seedlings are important to understand as they can drastically influence survival and therefore community structure (Clarke & Knox, 2009). Seedlings are also the most sensitive life stage to environmental impacts (Bond, 2008; Van Langeveelde *et al.*, 2011).

The choice of forest as opposed to savanna species was made as aspects of the fire-trap have been examined in savanna seedlings species (eg. Kgope *et al.*, 2010; Higgins *et al.*, 2012; Staver *et al.*, 2009) but not forest seedlings species. Furthermore, when savanna is encroached upon by forest, the invasion tends to come from forest species invading savanna as opposed to savanna species closing the canopy (Bowman & Fensham, 1991; San José & Fariñas, 1991; Swaine *et al.*, 1992; Russell-Smith, 2004; Hennenberg *et al.*, 2005; Pinheiro & Monteiro, 2006; Geiger *et al.*, 2011), as savanna species often don't have a high enough leaf area index (LAI) to form a closed canopy (Hoffmann *et al.*, 2012). Forest species that grow in the forest-savanna transition zone or that occur in both biomes are particularly important as they often represent the first stages of forest expansion (Geiger *et al.*, 2011), and thus some of our study species fit this description as well.

METHODS

Study Site

The study took place in Ghana, West Africa. Ghana has ten vegetation types according to White's vegetation map of Africa (White, 1983; **Figure 5**). Broadly, these are rain forests, swamp forests, woodlands, forest-grassland mosaics and mangroves.

The study took place in Kogyae Strict Nature Reserve (SNR) (**Figure 5**). Kogyae SNR is 386km² and is situated in the north-eastern part of the Ashanti region of Ghana. Kogyae SNR lies on the border between Guinea-Congolian rainforest of the drier type and mosaic of lowland rainforest rain forest and secondary grassland (White, 1983), with the large majority of its area falling into the latter (**Figure 5**). Kogyae SNR is one of only two protected areas in Ghana that cover the transitional vegetation zone between savanna and forest, making it an ideal study site for this experiment.

There are 105 vascular plant species in the reserve, with 57 of these being trees (Ghana Wildlife Department, 1994). The savanna in Kogyae SNR is made up of tall tussocky grasses and medium to short trees, usually with corky bark (Ghana Wildlife Department, 1994). The trees are widely spaced and do not form a closed canopy. The forest in the reserve is transitional forest, and is made of two sub-communities (Ghana Wildlife Department, 1994): transitional forest towards the true forest zone in the south-eastern part of the reserve (Ghana Wildlife Department, 1994) and the

transitional forest towards Guinea savanna woodland, covering about a third of the reserve (Ghana Wildlife Department, 1994).

The effects of large mammal herbivory in the study area were negligible.

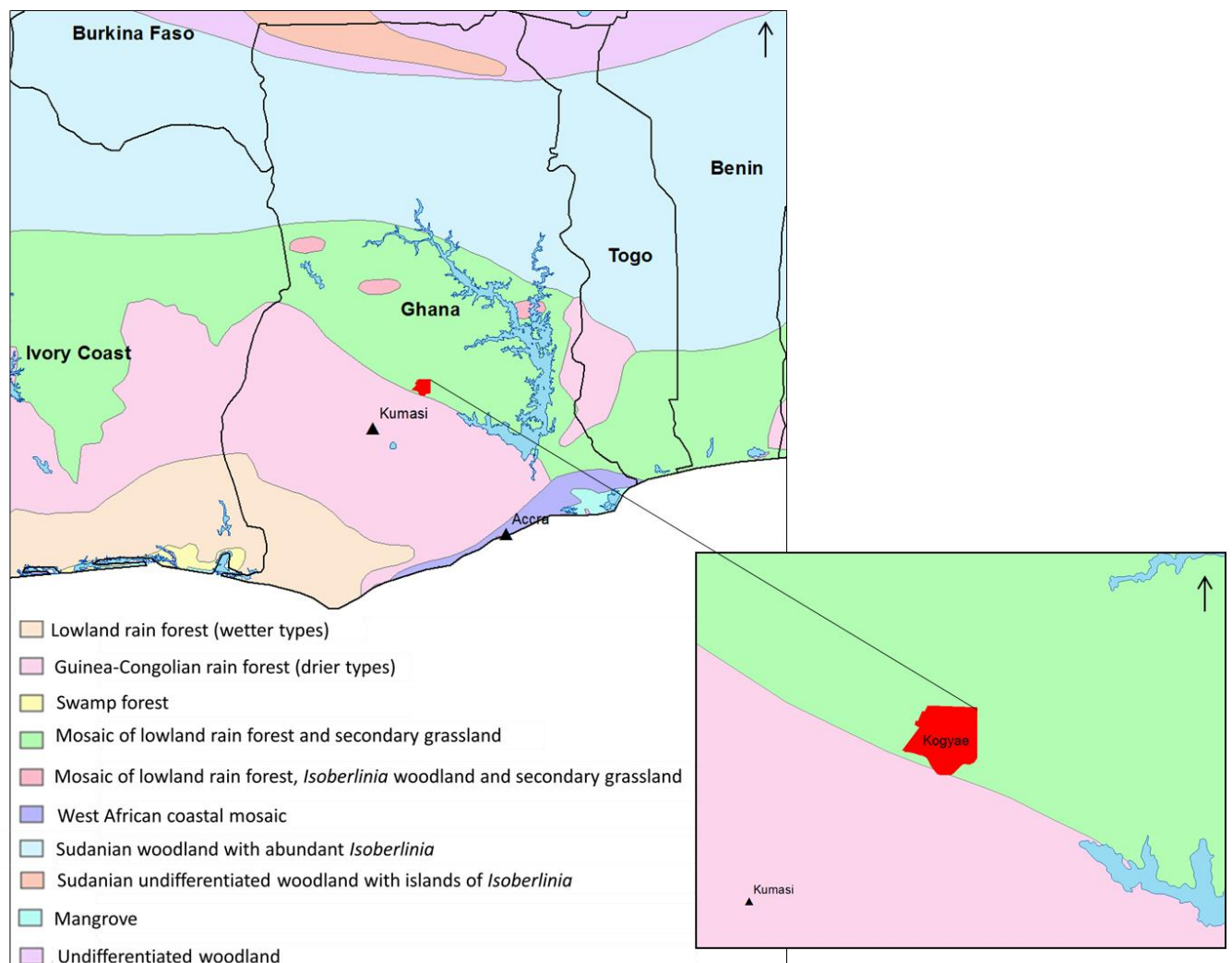


Figure 5: Location of the Kogyae Strict Nature Reserve (shown in red) in Ghana, West Africa where the study took place. Colours represent different vegetation types according to the classification by White (1983). Major Ghanaian cities are labelled with a filled triangle, the large lake (shown in blue) running along the right side of Ghana is Lake Volta.

Study species

Five tropical West African forest tree species were chosen: *Nauclea diderrichii*, *Khaya ivorensis*, *Terminalia superba*, *Triplochiton scleroxylon* and *Bombax buonopozense*.

Nauclea diderrichii (family Rubiaceae), or the Opepe or African Peach, grows in moist evergreen and transitional-to-moist semi-deciduous forests and is found throughout the tropical rainforest in West Africa, with its range extending to Angola (Orwa *et al.*, 2009). It is a light demanding species, regenerating in forest gaps and openings (Orwa *et al.*, 2009). It is particularly successful in freshwater swamp to lowland forest transitions (Orwa *et al.*, 2009).

Khaya ivorensis (family Meliaceae), or African mahogany, is found in semi-deciduous lowland rainforests that have a short dry season, generally preferring moist valley sites (Orwa *et al.*, 2009). It is a light demanding species although seedlings are shade tolerant (Orwa *et al.*, 2009). Its range covers coastal West Africa, mostly in the rainforests but extending into dry forests (Orwa *et al.*, 2009).

Terminalia superba (family Combretaceae), or Limba, grows in deciduous forests and high secondary forest areas with a dry season of four months, however does not respond well to long dry spells (Orwa *et al.*, 2009). It is tolerant to occasional flooding and very sensitive to fire (Orwa *et al.*, 2009). It is a light demanding, pioneer species (Orwa *et al.*, 2009).

Triplochiton scleroxylon (family Sterculiaceae), or Wawa or African Whitewood, is a deciduous tree, found mostly in forest at low and medium altitudes in the mosoonal equatorial forest belt (Orwa *et al.*, 2009). It grows in the semi-deciduous moist forest, and notably in the transition zone between forest and moist savanna (Orwa *et al.*, 2009). It is also characteristic of drier or more disturbed areas (Orwa *et al.*, 2009). Its range covers much of West Africa, from Guinea to DRC and from Gabon to Nigeria (Orwa *et al.*, 2009). It is a pioneer species (Orwa *et al.*, 2009).

Bombax buonopozense (family Bombaceae), or Wild Kapok or Wild Silk Cotton Tree, has seedlings that grow rapidly, up to 3m in the first two years (Oyen, 2011). It occurs throughout the dense forests of Guinea, usually at low elevations, and usually in primary rainforest, secondary forest, gallery forest and swamp forest (Oyen, 2011). Its range extends into drier areas, such as wooded savanna, coastal thicket, and grasslands, however it is much rarer here (Oyen, 2011).

Study design

Twenty-four 10m x 10m (100m²) plots were set up in Kogyae SNR with eight plots in each vegetation type: savanna, transition zone, and forest (**Figure 5**). Forty seedlings were planted in each plot, eight seedlings of each of the five study species. Seedlings were grown from seed in identical nursery conditions, were three months old when planted, and were planted randomly and equidistantly in the plots. When seedlings were planted all of the above-ground herbaceous cover was removed in order to minimise above-ground competition during the seedlings' establishment phase.

Seedlings were planted in June 2013 and the study ran over the course of a year until June 2014, when all surviving seedlings were uprooted. Fire burnt the majority of the plots in February 2014. The fire was not deliberately set as part of the study, but occurs annually in this area, usually due to local bush management and hunting practises.

Seedlings' ecophysiological measurements

The height, stem diameter at ground level, and number of leaves of each surviving seedling was recorded. These measurements were done five times during the study: three times before fire (June and September 2013 and January 2014) and twice after (April and June 2014). The number of surviving seedlings was recorded at each time step. All surviving seedlings were uprooted in June 2014 and root length was measured.

After uprooting, all leaves on each seedling were scanned on a CanoScan LiDE110 (Canon) flatbed scanner at 300dpi. Total leaf area of each seedling was calculated from these images in MATLAB (2014) using an algorithm specifically developed for this purpose (Neyret, unpublished data). The algorithm went through each image and subjected it to a thresholding process in order to differentiate leaf area from the background. Each leaf area then had its area calculated in pixels and converted to cm^3 . After scanning, seedlings were dried in a 70°C oven for a minimum of 48 hours before root, stem, and leaf dry weights were recorded.

Upon uprooting, seedlings were placed immediately into sealed bags with a piece of wet paper towel to prevent excess transpiration. Within six hours of uprooting all seedlings were microwaved at 800W for 30s in order to kill them (Hoch, 2014, personal communication). Seedlings were then separated into root, leaf, and stem material and analysed for starch content following the protocol of Duranceau *et al.* (1999) and Damesin *et al.* (2013) with minor changes (**Appendix**). Since many seedlings were very small, their volumes proved difficult to determine and thus seedlings material was collated into categories. Materials that were of the same tissue type (root, stem, leaves), the same species, the same vegetation type (forest, savanna, mixed), and the same fire treatment (burnt, unburnt) were collated together and analysed as one sample. Despite this, certain samples were still present in quantities too small to be analysed for starch concentration. Where enough material was available, all collated samples were analysed in triplicate. In total, 159 starch concentration analyses were performed. Measures were taken to ensure that each starch analysis was as independent as possible.

Aside from the basic ecophysiological measurements done between June 2013 and April 2014, which were performed by field assistants, all ecophysiological measurements and analyses, including starch analyses, were performed by me.

Herbaceous biomass and canopy openness

Herbaceous biomass in each plot was recorded at the time of the seedlings being harvested (June 2014). This was done using a disc pasture meter following the method described by Dorgelöh (2002). A disc pasture meter is a round lightweight

disc about 50cm in diameter with a rod running through the middle which it can move freely up and down. When gently placed onto herbaceous vegetation, the settling height of the disc on the vegetation has a linear relationship with the biomass of the vegetation (Dorgelöh, 2002). Therefore, after calibrating the disc, the settling height of the disc can be used to estimate herbaceous biomass in the plots. At each plot ten disc pasture readings were taken, the average of these ten readings was used to calculate herbaceous biomass per plot using a calibration equation.

To determine the calibration equation five 50cm x 50cm (0.25 m²) plots were marked out in each vegetation type, these were outside of the study plots and so were independent measures. In each of these plots, four disc pasture meter settling height readings were taken and the mean settling height calculated. The entire plot was then harvested of all of its above-ground herbaceous biomass, which was then weighed. A sub-sample of this biomass was also weighed before being dried at 70°C for 48 hours and weighed again. These measurements could then be used to calculate the relationship between mean disc settling height and dry herbaceous biomass (Mg per m²) and thus work out the calibration equation to be applied to all plots (Dorgelöh, 2002).

In order to determine the level of canopy openness at each plot, hemispheric pictures were taken in November 2013 using a Nikon E4500 camera with a fisheye lens on a tripod mounted at 1.50m at 180°. These pictures were used to calculate canopy openness (%) using Gap Light Analyser imaging software according to Frazer *et al.* (1999).

Herbaceous biomass measurements and calculations were done by me, canopy openness measurements were done by field assistants.

Precipitation

The nearest meteorological station to Kogyae SNR is in Ejura (25km away). Kogyae SNR has two rainy seasons between May and October, with precipitation peaking in June and September.

Total precipitation was recorded at the meteorological station in Ejura. Due to unforeseen technical issues, precipitation data was only available from September 2013. Precipitation data was missing between 17 April 2014 and 27 May 2014. The total precipitation for this period was therefore estimated by applying a mean total daily precipitation amount to each missing day. The mean used for this was the mean daily total precipitation of the fifteen preceding and proceeding days on either side of the missing data period (i.e. the mean of 2-16 April 2014 and 28 May-10 June 2014).

Fire

Fire occurred in Kogyae SNR on 2nd February 2014 at 15:00. At the time of the fire, the wind speed was 1.13 m.s^{-1} , the air temperature was 33.5°C , and the relative humidity was 12%.

Area burnt of each plot was calculated as the mean of three independent visual estimates. Plots that had more than 30% of their area burnt in the fire were considered to be “burnt” and plots with less than this amount were considered to be “unburnt”. All three vegetation types had burnt and unburnt plots. Seedlings that were planted in plots that burnt are classified as “burnt seedlings” while seedlings grown in unburnt plots were classified as “unburnt seedlings”.

Fire temperature was estimated using 16 different temperature sensitive paints painted on an iron rod at 30cm from the ground. The paints liquefied and changed appearance at maximum temperatures of 107, 149, 204, 253, 302, 343, 399, 454, 510, 566, 621, 649, 704, 760, 816 and 927 °C, therefore the maximum temperature at 30cm above ground could be determined. Flame height was determined using pieces of cotton tied at 30cm intervals up an iron pole, burnt cotton at a given height indicated that flames reached at least that high.

After the fire, all three vegetation types had plots that were classified as “burnt”. “Burnt” plots experienced no significant difference in burning temperature at the 30cm from ground level (Chi-squared, $X^2=2$, $df=2$, $p>0.05$). Flame height was less than 30cm, with the lowest piece of cotton at 30 cm above ground remaining unburnt after fire.

Fire measurements were performed by field assistants.

Data analysis

Herbaceous dry biomass at the time of seedling harvest was estimated by applying a calibration equation to the mean settling height of a disc pasture meter in each plot (**Figure 6**). The equation was determined via linear regression. The calibration points (five in each vegetation type) were well fitted to a linear model, with the model explaining 93% of the variation between points ($R^2=0.93$, $p<0.001$, **Figure 6**). Significant differences in this biomass between vegetation types was assessed using an analysis of variance (ANOVA) test, which was appropriate as the data were normally distributed (Sokal & Rohlf, 1995). Post-hoc Tukey HSD tests on the ANOVA revealed where significant differences between vegetation types lay in a pairwise manner (Sokal & Rohlf, 1995).

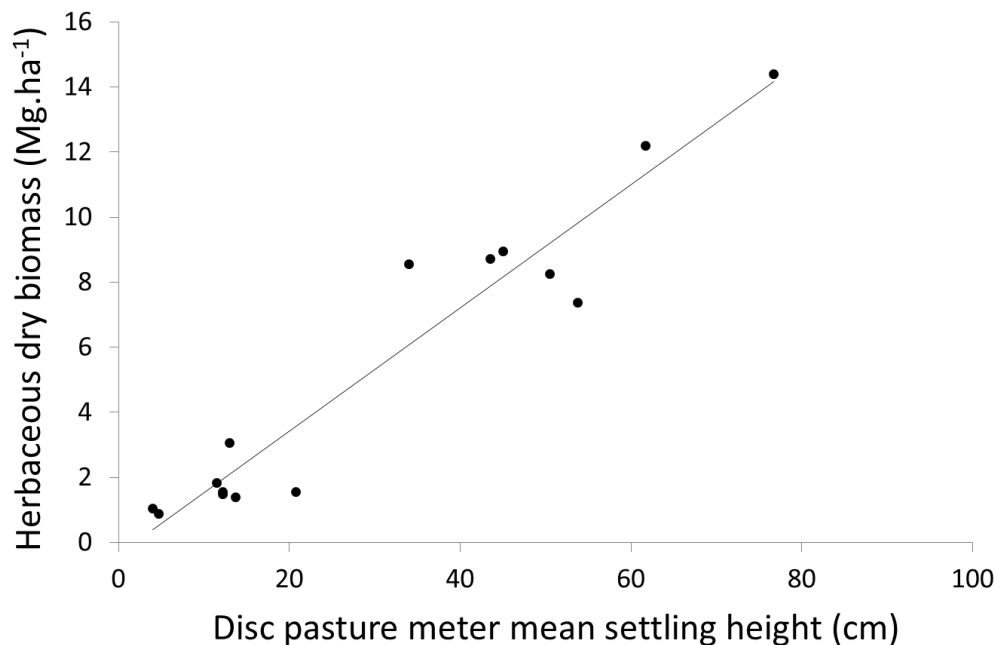


Figure 6: Calibration of the disc pasture meter across savanna, forest, and mixed vegetation types. Each point represents a calibrated sample. Five calibration samples were taken in each vegetation type. The line shows the calibration equation: $y = 0.1894x - 0.3625$ (linear regression, $R^2 = 0.93$, $p<0.001$).

Canopy openness measurements were also assessed similarly to the herbaceous biomass measurements using an ANOVA test and post-hoc Tukey HSD tests as the data were also normally distributed (Sokal & Rohlf, 1995). The relationship between herbaceous biomass and % seedling survival in each plot was assessed using a Spearman's rank correlation test as the response variable was not normally distributed even under transformation (Sokal & Rohlf, 1995).

Measured traits of all surviving seedlings were compared between species using one Kruskal-Wallis test per trait (Sokal & Rohlf, 1995). The Kruskal-Wallis test was chosen as the data were non-normal and often the sample size was small, therefore an ANOVA would have been unsuitable (Sokal & Rohlf, 1995). The trait variables assessed were: height, diameter, number of leaves, leaf dry mass, root dry mass, stem dry mass, specific root length ($\text{root length} / \text{root dry mass}$), root to shoot ratio ($\text{root dry mass} / (\text{stem} + \text{leaf dry mass})$), leaf starch concentration, root starch concentration, stem starch concentration, and specific leaf area ($\text{leaf area} / \text{leaf dry mass}$).

Survival of seedlings was compared between burnt and unburnt treatments overall as well as for each species and each vegetation type. The G-test was chosen for this as it compares observed vs expected frequencies for multiple factors (Sokal & Rohlf, 1995). The G-test involved comparing counts of observed seedling survival for each burning treatment (burnt and unburnt) to expected values. This was done fifteen times, one test of burnt vs unburnt seedling survival per species per vegetation type.

Expected survival frequencies were calculated manually in burnt and unburnt plots across all vegetation types according to the formula:

$$\begin{aligned} & \text{expected number of surviving seedlings in burnt savanna} \\ &= \left(\frac{\text{total number of surviving seedlings in savanna}}{\text{total number for seedlings planted in savanna}} \right) \\ &\times (\text{number of seedlings planted in burnt savanna plots}) \end{aligned}$$

The total G-value was then calculated as the sum of G-values for the fifteen individual G-tests above in order to determine whether there was a significant difference between burnt and unburnt seedling survival across all vegetation types. (Sokal & Rohlf, 1995). The pooled G-value of each vegetation type was calculated by summing the G-values of the comparisons between burnt and unburnt for each vegetation type to determine whether or not there was a significant difference between burnt and unburnt survival frequencies in each vegetation type (Sokal & Rohlf, 1995). The heterogeneity G-value was calculated to test whether or not the pooled G-value was appropriate to use, with significance ($p < 0.05$) indicating that it is inappropriate to use the pooled G-value as sample sizes are too different from one another (Sokal & Rohlf, 1995). The heterogeneity G-value was non-significant, therefore the pooled G-value was appropriate to use (heterogeneity-G=18.63, df=12, $p > 0.05$, **Appendix Table 1**).

Starch concentrations for each tissue type (leaf, stem, and root) were compared between species, between vegetation types and between burnt and unburnt treatments. This was done using a factorial ANOVA in order to determine which factors had a significant effect on starch concentrations of each seedling (Sokal & Rohlf, 1995). The factorial ANOVA was chosen as the data and the residuals

complied with the ANOVA assumption of having a normal distribution after \log_n transformation (Sokal & Rohlf, 1995). A post-hoc Tukey HSD test on this factorial ANOVA was performed to establish which factors (species, vegetation type, fire treatment) and which interactions between factors had a significant effect on starch concentrations for each tissue type (Sokal & Rohlf, 1995). For this analysis, the three replicates, where available, for the collated starch samples were used as independent measures.

The surviving proportion of seedlings, taken to be the number of surviving seedlings at each time period divided by the total number of seedlings planted at time zero, was also examined across species using line plots with 95% confidence intervals around the mean. These survival rates were compared by inspection to patterns of total precipitation.

In order to determine which variables explained survival, a principle components analysis (PCA) was done on all surviving seedlings' measured traits (Sokal & Rohlf, 1995). In addition to the measured variables, each seedling was also categorised by vegetation type and species, therefore the PCA was able to disentangle which measured variables contributed to survival in which vegetation types and for which species. In the final presentation of results, all superfluous (those that explained very little of the variation in the seedlings) or repetitive (those that were used to derive other variables) variables were removed. The variables shown in the PCA were examined using boxplots; significant differences between burnt and unburnt seedlings of each species for each of these variables were determined using

Kruskal-Wallis tests as the data were non-normal and the sample size small (Sokal & Rohlf, 1995).

Traits to compete (growth related traits) and traits to recover from fire (starch related traits) were plotted against one another to assess whether a trade-off was present or not. Evidence of a trade-off was considered to be where growth traits were favoured and fire recovery traits reduced or vice versa. Evidence of seedlings that displayed strength in both competitive traits and fire recovery traits were taken to indicate that a trade-off was not present. To look for evidence of the fire-trap in the seedlings, pre-fire height and diameter measurements of all seedlings alive just before the fire were sorted into size class bins. The associated percentage of seedlings that survived the fire in each size class was then calculated. These results were plotted in a histogram, where sharp increases in survival above a certain size class in burnt seedlings indicated the fire-trap's presence. Due to low sample sizes, this approach was unfortunately not suited to analysis by species.

To examine how pre-fire traits may determine survival through fire on a species level, burnt seedlings across all vegetation types were examined by species. Significant differences in pre-fire height and diameter between seedlings that survived fire and those that died after fire for each species were determined using Kruskal-Wallis tests. The Kruskal-Wallis test was used as the data was not normally distributed and sample sizes were small, therefore an ANOVA or T-test would have been inappropriate (Sokal & Rohlf, 1995).

All analyses were done in R v3.1.1 (R core team, 2014). In all statistical tests, overall differences were noted significant when $p < 0.05$ unless otherwise stated.

RESULTS

In the savanna, all but one of the eight plots was classified as burnt by fire, compared to six of eight in the forest and five of eight in the mixed vegetation types.

Herbaceous biomass increased with an increase in canopy openness, up until a threshold canopy openness of 30%, above which there was relatively little increase in herbaceous biomass despite canopy openness' continued increase (**Figure 7**). Forest and certain plots in the mixed vegetation type displayed increased herbaceous biomass with increased canopy openness, while the remaining mixed plots and the savanna plots did not show this, with large increases in canopy openness not being associated with increases in herbaceous biomass (**Figure 7**).

There was a significant relationship between herbaceous biomass and seedling survival, with an increase in herbaceous biomass being associated with an increased seedling survival rate (**Figure 8**). Seedling survival count was highest in the savanna with 41 out of the original 320 seedlings surviving the entire year, followed by mixed (36 surviving) and forest (14 surviving) vegetation types (**Table 1**). Savanna had significantly higher herbaceous biomass than forest and significantly higher canopy openness than forest and mixed vegetation types (**Figure 9**). The mixed vegetation type was not significantly different to forest or savanna with respect to herbaceous biomass, and was not significantly different from forest with respect to canopy openness (**Figure 9**). The mixed plot had the highest variability in herbaceous biomass however had the lowest variability in canopy openness (**Figure 9**).

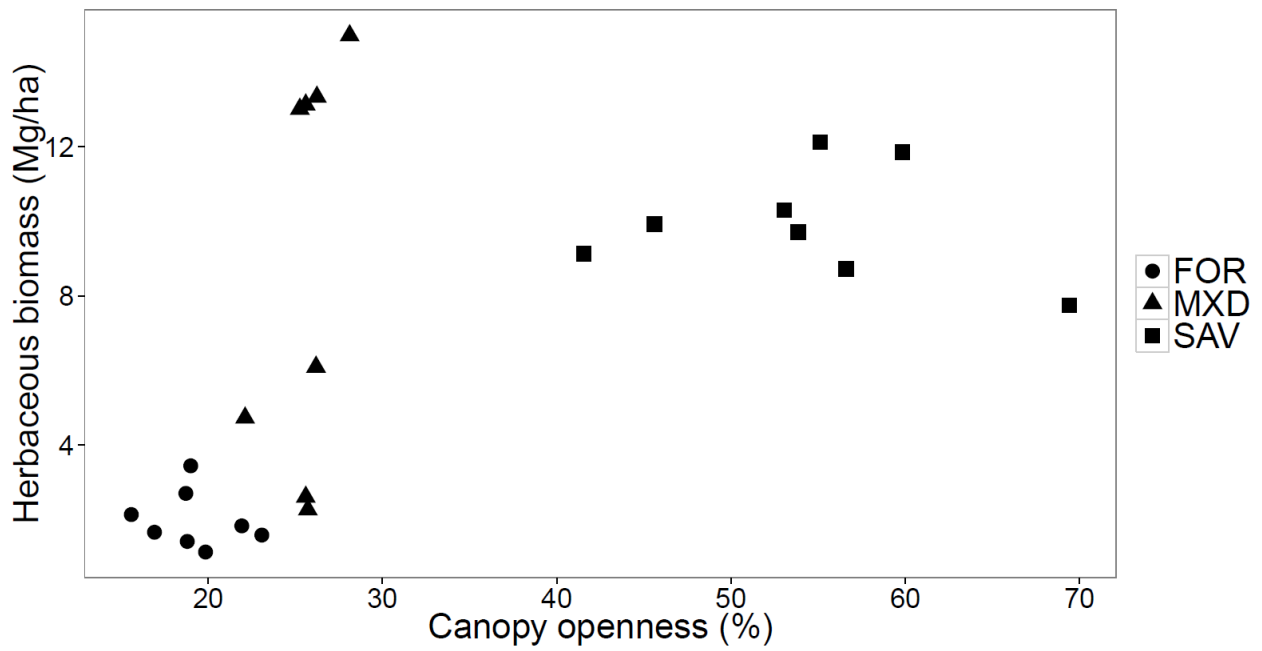


Figure 7: Canopy openness and herbaceous biomass across the three vegetation types [forest (FOR), mixed (MXD) and savanna (SAV)].

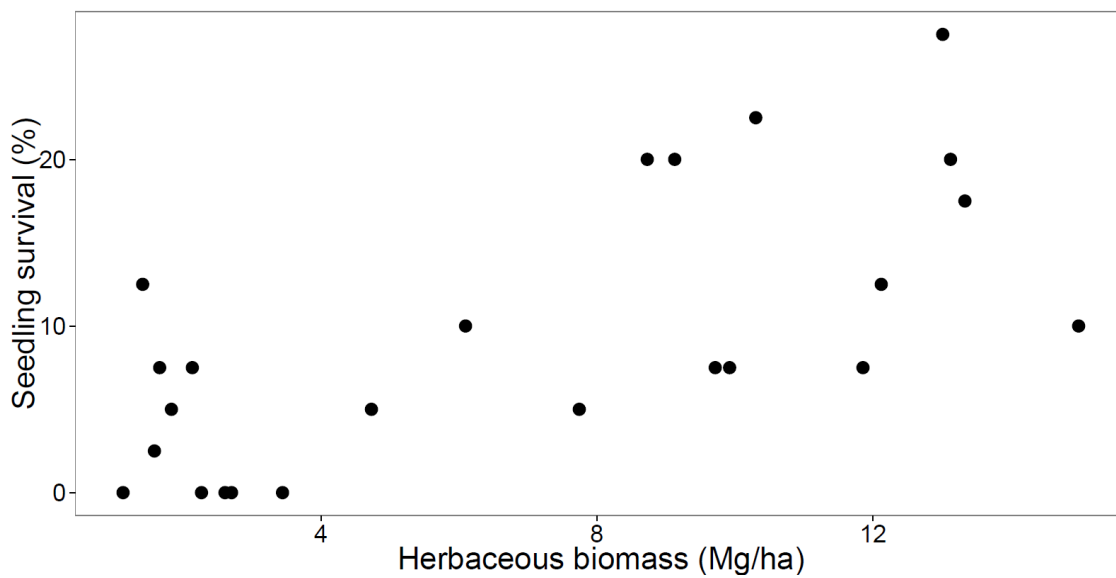


Figure 8: Relationship between seedling survival and herbaceous biomass per plot in all vegetation types (Spearman correlation test, $Rho=0.63$, $p<0.001$).

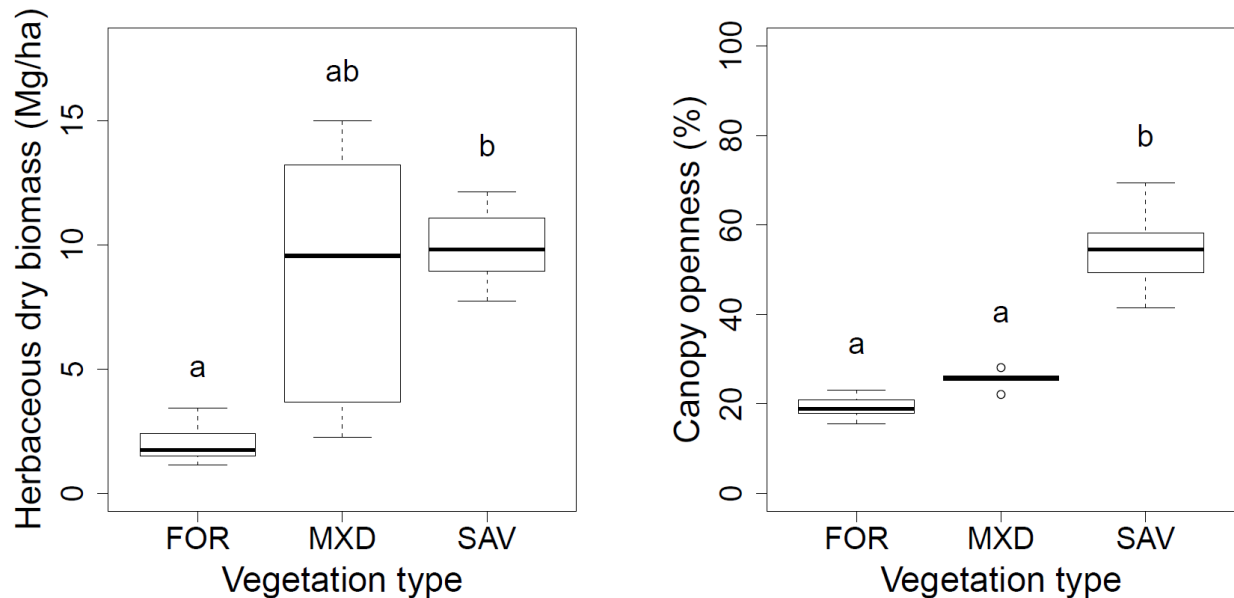


Figure 9: Herbaceous biomass as determined by the mean of ten disc pasture meter settling height readings per plot and canopy openness as determined by hemispheric photographs across forest (FOR), mixed (MXD) and savanna (SAV) vegetation types. Different letters indicate a significant ($p < 0.05$) difference between the vegetation types according to a Tukey HSD post-hoc test on an ANOVA.

Overall, there was a significant difference in number of surviving seedlings between burnt and unburnt plots (G-test, $G=44.6$, $df=15$, $p < 0.0001$, **Table 1 and Appendix Table 1**). According to total survival counts, more seedlings died when they were burnt than unburnt (**Table 1**). Furthermore, there was a significant difference between seedling survival in burnt and unburnt plots in forest and in mixed vegetation types, however no significant difference in savanna (**Table 1 and Appendix Table 1**). In forest plots, *K.ivorensis* was the only species to have a significant difference in survival rate between seedlings in burnt and unburnt plots (**Table 1**). The opposite is true for the mixed vegetation type, which has its significant difference in survival rate between burnt and unburnt seedlings driven by all surviving species except *K.ivorensis* (**Table 1**).

Table 1: Seedling survival (number of seedlings surviving and percentage of total seedlings originally planted) in each vegetation type for burnt and unburnt plots. Red values indicate significant ($p<0.05$) difference between burnt and unburnt seedling survival rates according to a G-test (Appendix Table 1). The last column shows the totals for each species, the last two rows the totals for each vegetation type and burnt and unburnt plots in each. The bottom right hand corner shows the total number of seedlings that survived the entire year (=91) and the top right hand corner how this total was proportioned between burnt and unburnt. Species are: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Vegetation types are: forest=FOR, mixed=MXD and savanna=SAV.

N of each sp planted		FOR		MXD		SAV		burnt=49 unburnt=42
		burnt 48	unburnt 16	burnt 40	unburnt 24	burnt 56	unburnt 8	=192*5spp=960
BB	N survival	2	1	3	10	23	4	=43
	% survival	4	6	13	42	41	50	=22
KI	N survival	0	2	1	1	3	2	=9
	% survival	0	13	4	17	5	25	=5
ND	N survival	0	0	0	0	0	0	=0
	% survival	0	0	0	0	0	0	=0
TS	N survival	0	1	3	8	2	0	=14
	% survival	0	6	13	33	4	0	=7
WW	N survival	4	4	3	7	5	2	=25
	% survival	8	25	13	29	9	25	=13
		=6 (3%)	=8 (10%)	=10 (5%)	=26 (22%)	=33 (12%)	=8 (20%)	
		tot=14 (1%)		tot=36 (4%)		tot=41 (4%)		=91

In the burnt plots, seedlings falling into a greater pre-fire size class for both height and diameter had a greater percentage survival post-fire (**Figures 10 a and b**). Specifically, seedlings with a pre-fire height greater than 380mm had a greater survival rate than those with a shorter pre-fire heights (**Figure 10 a**). In the unburnt plots, only increased diameter was associated with an increase in survival, with increased height not associated with an obvious increase in survival (**Figures 10 c and d**). When examining these traits by species, *T.superba* and *B.buonopozense* seedlings that survived the fire were significantly taller than those that died in the fire (**Figure 11**). *T.superba* seedlings that survived the fire also had a significantly

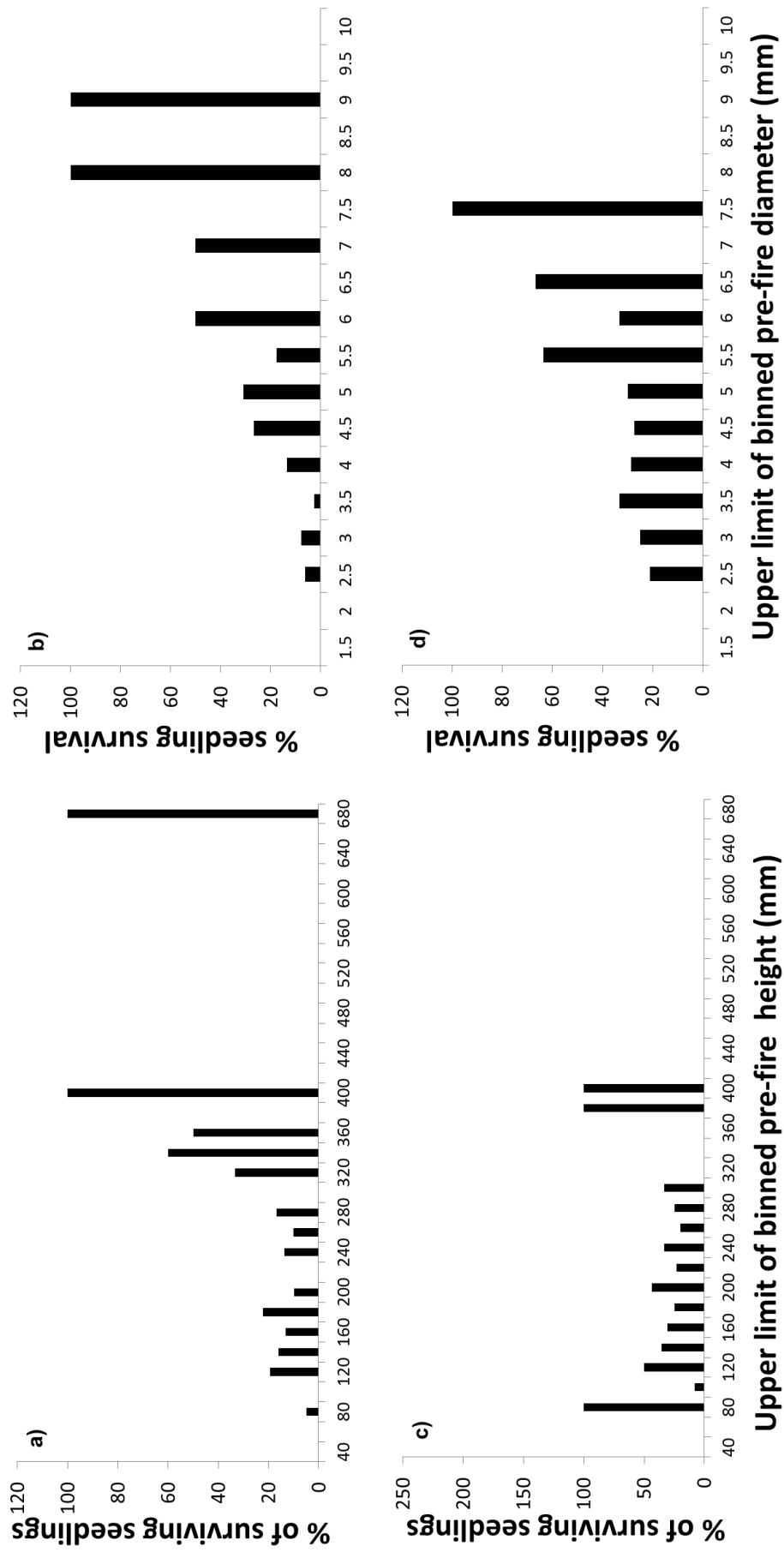


Figure 10: Histograms showing the percentage of post-fire survival associated with a size bin (upper limit of bin shown) of pre-fire height (a and c) or diameter (b and d) for burnt (a and b) and unburnt (c and d) seedlings.

greater diameter than those that died in the fire (**Figure 11**). No other significant differences in pre-fire traits between seedlings that survived the fire and those that died in the fire were found (**Figure 11**).

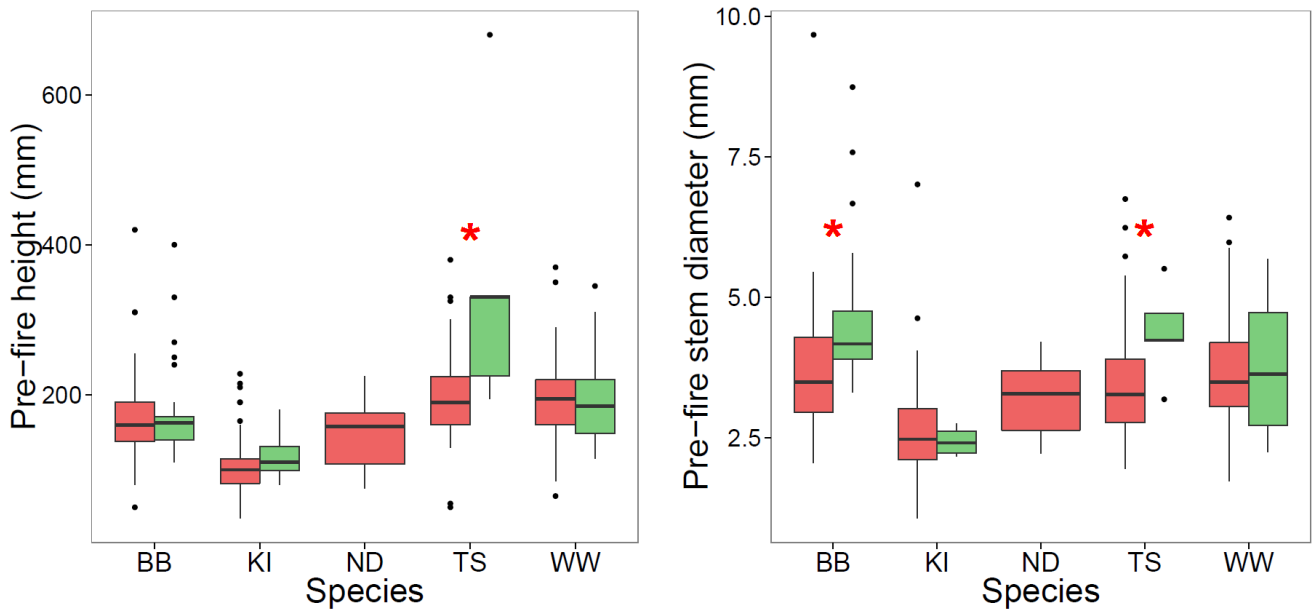


Figure 11: Pre- fire traits of seedlings that survived the fire and those that died after the fire. Boxplots show the median and interquartile range in the box, whiskers show the 95% confidence interval of the median, outliers are shown as individual points. Species are: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Note that all of ND died in the fire so there were no surviving seedlings. Red stars indicate significant difference ($p < 0.05$) between burnt and unburnt individuals for each species as determined by a Kruskal-Wallis test.

At the time of harvesting, 91 of the original 960 planted tree seedlings were alive (**Tables 1 and 2**). *B.buonopozense* had the highest number of surviving seedlings with 43 out of the original 192 that were planted surviving, followed by *T.scleroxylon* with 25, *T.superba* with 14 and *K.ivorensis* with 9 (**Table 2**). *N.didderichii* had no

surviving seedlings. At the time of harvest *T.superba* seedlings were significantly taller and had more leaves than the other species (**Table 2**). *K.ivorensis* had significantly lower root mass and root starch concentration than the other species (**Table 2**). *K.ivorensis* also had a significantly higher specific root length than the other species, which was the result of shorter roots that had a lower dry mass than the other species (**Table 2**). All four of the surviving species had significantly different root starch concentrations from one another, with *B.buonopozense* having the highest, followed by *T.scleroxylon* and then *T.superba*, with *K.ivorensis* having the lowest (**Table 2**).

Leaf starch concentration in surviving seedlings had 75% of its variability explained by species, vegetation type and whether or not it was burnt (factorial ANOVA, adjusted $R^2 = 0.75$, $F=8.8.34$, $df=18$. $p<0.0001$). Species had the most significant effect on leaf starch concentrations (post-hoc Tukey HSD, $F=15.30$, $df=3$, $p<0.0001$). The interaction between vegetation type and species also had a highly significant effect on leaf starch concentration (post-hoc Tukey HSD, $F=6.41$, $df=6$, $p<0.0001$). Whether a seedling was burnt or not had a significant effect on leaf starch concentration (post-hoc Tukey HSD, $F=4.40$, $df=1$, $p<0.05$) as did the interaction between burning treatment and species (post-hoc Tukey HSD, $F=6.16$, $df=3$, $p<0.005$). Leaf starch concentration was significantly higher in burnt than unburnt seedlings (**Figure 12**). Seedlings grown in savanna had significantly higher leaf starch concentrations than those grown in mixed, with seedlings grown in forest showing no significant difference in leaf starch concentration to seedlings grown in either of the other vegetation types (**Figure 12**). *B.buonopozense* had significantly higher leaf starch concentrations than all other species (**Figure 12**). *K.ivorensis* had

significantly lower leaf starch concentrations than all other species (**Figure 12**).

T.superba and *T.scleroxylon* had intermediate leaf starch concentrations that were not significantly different from each other (**Figure 12**).

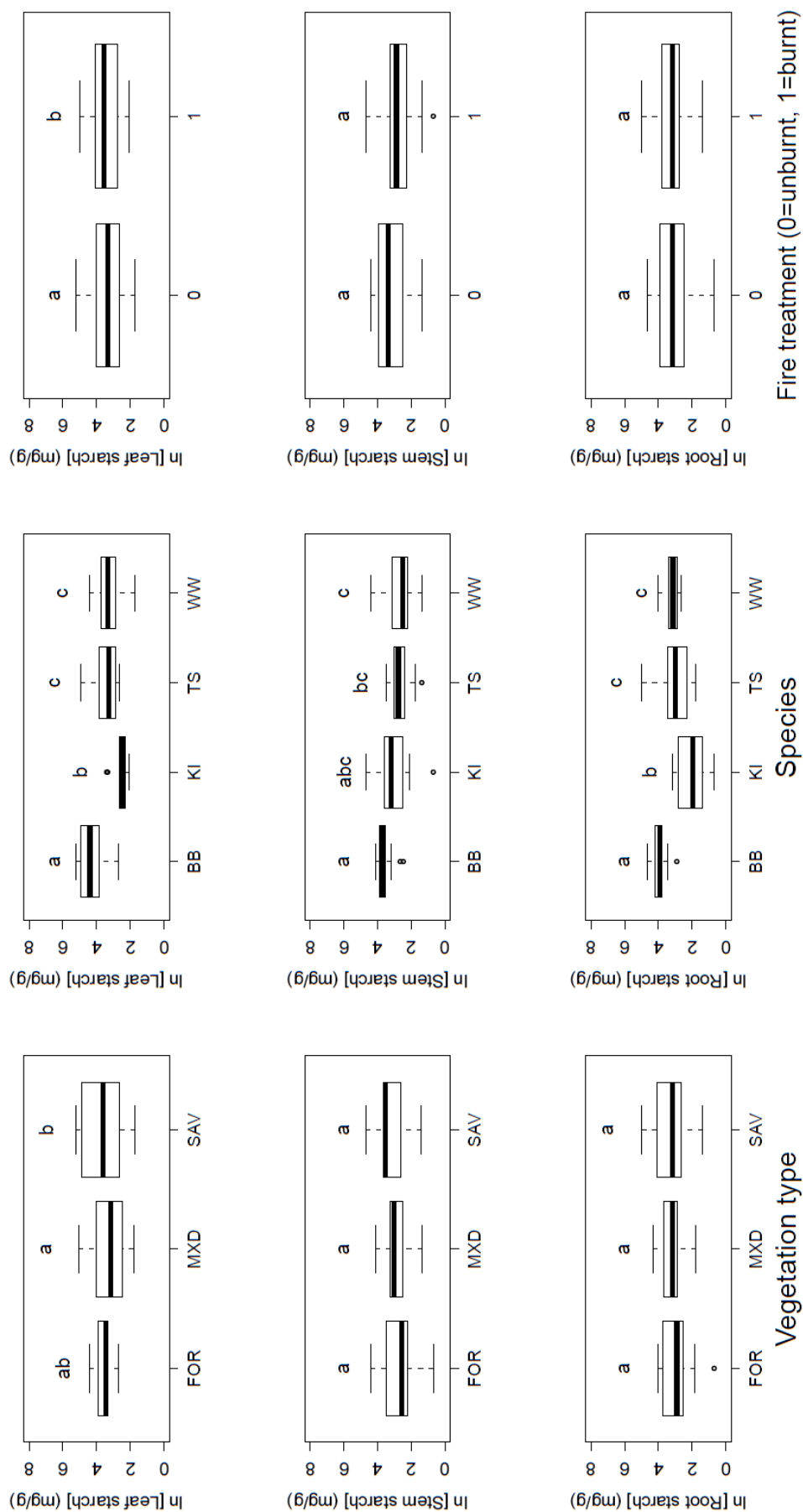
Table 2: All variables measured in all seedlings that survived until harvest. In total, 91 of the original 960 seedlings survived. The number of surviving seedlings of each species is shown in the top row (n=x). Species are: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Vegetation types are: forest=FOR, mixed-MXD, savanna=SAV. The data did not fit a normal distribution therefore the median and interquartile range are shown. Shared letters next to the median value indicate that species are not significantly different ($p < 0.05$) from each other for that variable according to a non-parametric Kruskal-Wallis test.

	BB (n=43)	KI (n=9)	TS (n=14)	WW (n=25)
Height (mm)	150 b (70-210)	110 b (90-128)	282 a (140-570)	150 b (80-365)
Diameter (mm)	4.4 a (3.7-6.1)	3.4 b (2.2-4.4)	4.6 a (4.4-6.2)	4.4 ab (2.2-6.6)
Number of leaves	5 c (4-7)	5 c (4-6)	16 a (11-25)	8 b (5-17)
Leaf dry mass (g)	0.17 a (0.07-0.37)	0.08 a (0.05-0.5)	0.73 a (0.10-2.00)	0.30 a (0.03-1.30)
Stem dry mass (g)	0.26 b (0.05-0.46)	0.13 b (0.08-0.29)	0.65 ab (0.23-2.11)	0.32 a (0.05-1.47)
Root dry mass (g)	0.77 a (0.46-1.20)	0.36 b (0.28-0.54)	1.04 a (0.60-1.80)	0.63 a (0.37-1.12)
Specific root length (mm/g)	242.54 b (184.17-367.54)	473.6 a (373.34-532.68)	235.24 b (166.41-325.44)	261.06 b (177.36-405.41)
Root:Shoot (g)	1.43 a (0.84-3.67)	1.63 ab (0.42-3.93)	0.63 b (0.32-1.71)	0.82 ab (0.41-4.40)
[Leaf starch] (mg/g)	95.4 a (95.4-107.3)	16.0 c (5.35-22.95)	17.1 b (17.1-46.4)	20.4 b (17.6-33.8)
[Root starch] (mg/g)	56.4 a (56.4-63.5)	10.7 d (8.05-11.0)	16.5 c (16.5-18.6)	30.5 b (24.8-30.7)
[Stem starch] (mg/g)	38.8 a (38.8-49.5)	29.5 a (25.6-58.6)	20 b (14.7-20.0)	18.6 b (12.0-30.1)
Specific leaf area (cm ² /g)	255.46 a (202.93-298.48)	223.78 a (200.89-247.36)	252.96 a (126.90-305.13)	322.62 a (84.66-363.42)

Stem starch concentration in seedlings had 28% of its variability explained by species, vegetation, and whether or not it was burnt (factorial ANOVA, adjusted $R^2=0.28$, $F=2.12$, $df=18$, $p<0.05$). Species was the only factor that significantly explained the difference in stem starch concentrations between seedlings (post-hoc Tukey HSD, $F=3.60$, $df=3$, $p<0.05$). *B.buonopozense* had significantly higher stem starch concentrations than *T.superba* and *T.scleroxylon*, but not *K.ivorensis* (**Figure 12**). *K.ivorensis* also did not differ significantly in stem starch concentrations to any of the other species and *T.superba* and *T.scleroxylon* did not differ significantly from each other in stem starch concentrations (**Figure 12**).

Root starch concentration in seedlings had 60% of its variability explained by species, vegetation type and whether or not it was burnt (factorial ANOVA, adjusted $R^2=0.60$, $F=5.11$, $df=18$, $p<0.0001$). Species was the only factor that significantly explained the difference in root starch concentrations between seedlings (post-hoc Tukey HSD, $F=22.64$, $df=3$, $p<0.0001$). *B.buonopozense* had significantly higher root starch concentrations than all the other species (**Figure 12**). *K.ivorensis* had significantly lower root starch concentrations than all other species (**Figure 12**). *T.superba* and *T.scleroxylon* had intermediate root starch concentrations that were not significantly different to each other (**Figure 12**).

A decrease in precipitation during the dry season (October to December 2013) was accompanied by a decrease in seedling survival, with a large proportion (approximately 50%) of seedlings dying before fire occurred (**Figure 13**). For the period before the fire, *N.diderrichii* showed the sharpest decrease in survival, with survival reaching zero following the fire (**Figure 13**). Both *T.superba* and *K.ivorensis*



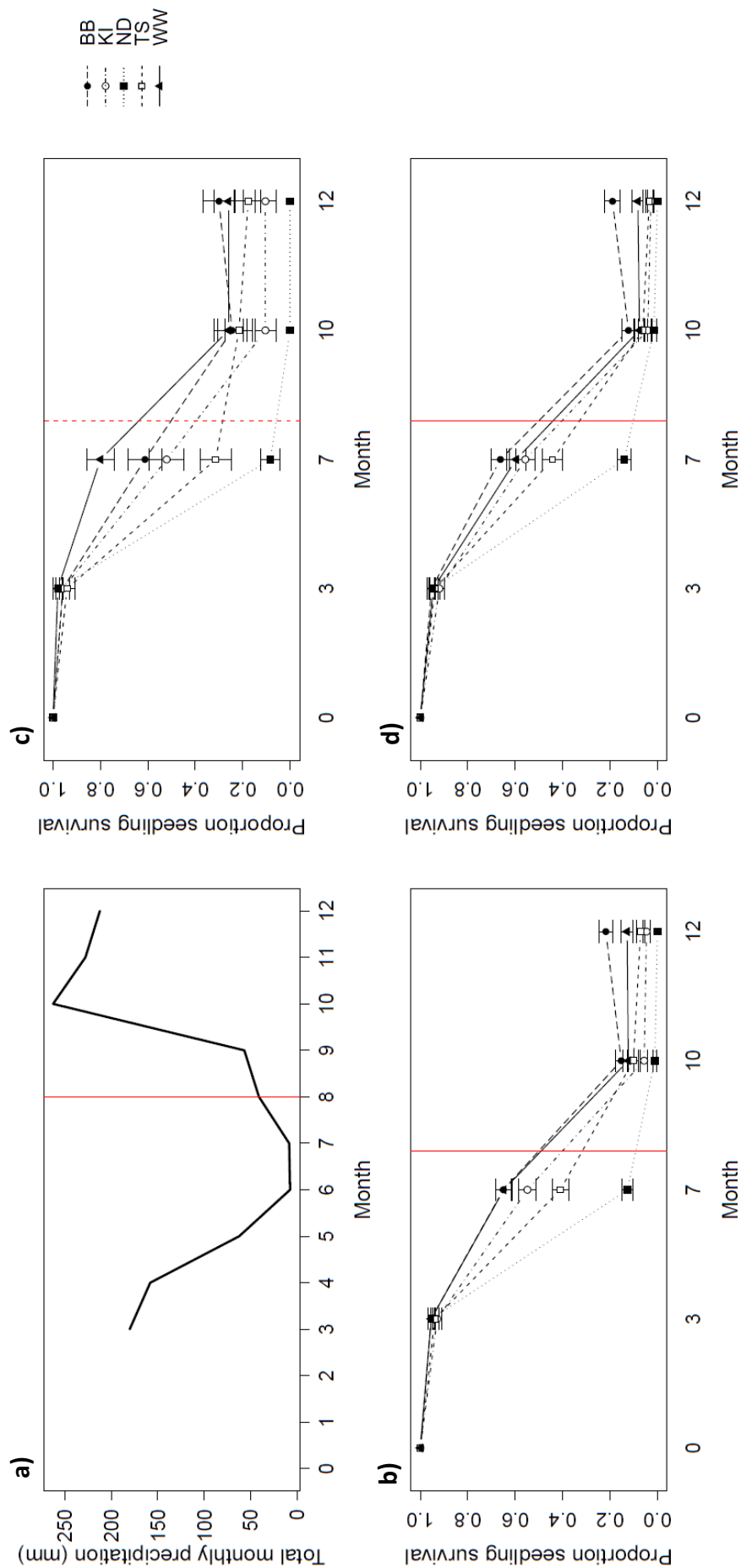


Figure 13: a) Precipitation over the year from June 2013 (month 0) to June 2014 (month 12). b) Total proportion of surviving seedlings across all species over this time period, as well as total proportion of surviving seedlings in unburnt (c) and burnt (d) plots. Species names are: BB=*B. buonopozense*, KI=*K. ivorensis*, ND=*N. diderichii*, TS=*T. scleroxylon* and WW=*W. wrightii*. Month number is relative to the month of planting, with planting month=0 and harvesting month=12. The red line shows when fire burnt some of the plots, in (c) the dotted line shows when fire came but indicates that these seedlings were not burnt. Error bars show 95% confidence intervals around the mean.

showed large decreases in survival before the fire, but not as extreme as *N.diderrichii* (**Figure 13**). *B.buonopozense* and *T.scleroxylon* had the highest survival rates before the fire (**Figure 13**). After fire, seedlings that were burnt continued to show decreased survival until April. After April, survival stopped declining as sharply, and even increased in *B.buonopozense*, indicating resprouting. This decreased mortality was associated with an increase in precipitation. At the time of harvesting in June 2014, burnt seedlings of *K.ivorensis*, *T.superba*, and *T.scleroxylon* all had similar surviving proportions, which were lower than the proportion of *B.buonopozense* that survived. After fire, seedlings that were not burnt also show a continued decrease in survival. This decrease, however, was not as extreme the decrease seen in burnt seedlings (**Figure 13**). At the end of one year (June 2014) the unburnt seedlings showed more of a difference in proportion surviving between species than the burnt seedlings (**Figure 13**).

The first axis of the principle component analysis (PCA), which explained 35.7% of the variation in traits between seedlings, separated seedlings surviving in the three vegetation types, with the split between forest and mixed being particularly well drawn out (**Figure 14**). The second axis of the PCA, which explained 21.7% of the variation in traits between seedlings, separated seedlings surviving in savanna from other vegetation types (**Figure 14**). In addition to separating seedlings based on vegetation type, the first two axes also separated species from one another (**Figure 14**). This separation of species coincided closely with the separation based on vegetation type: *B.buonopozense* survived very well in the savanna, *K.ivorensis* survived the best in the forest and *T.scleroxylon* and *T.superba* survived mostly in mixed and forest vegetation types (**Figure 14**). *B.buonopozense*'s survival in the

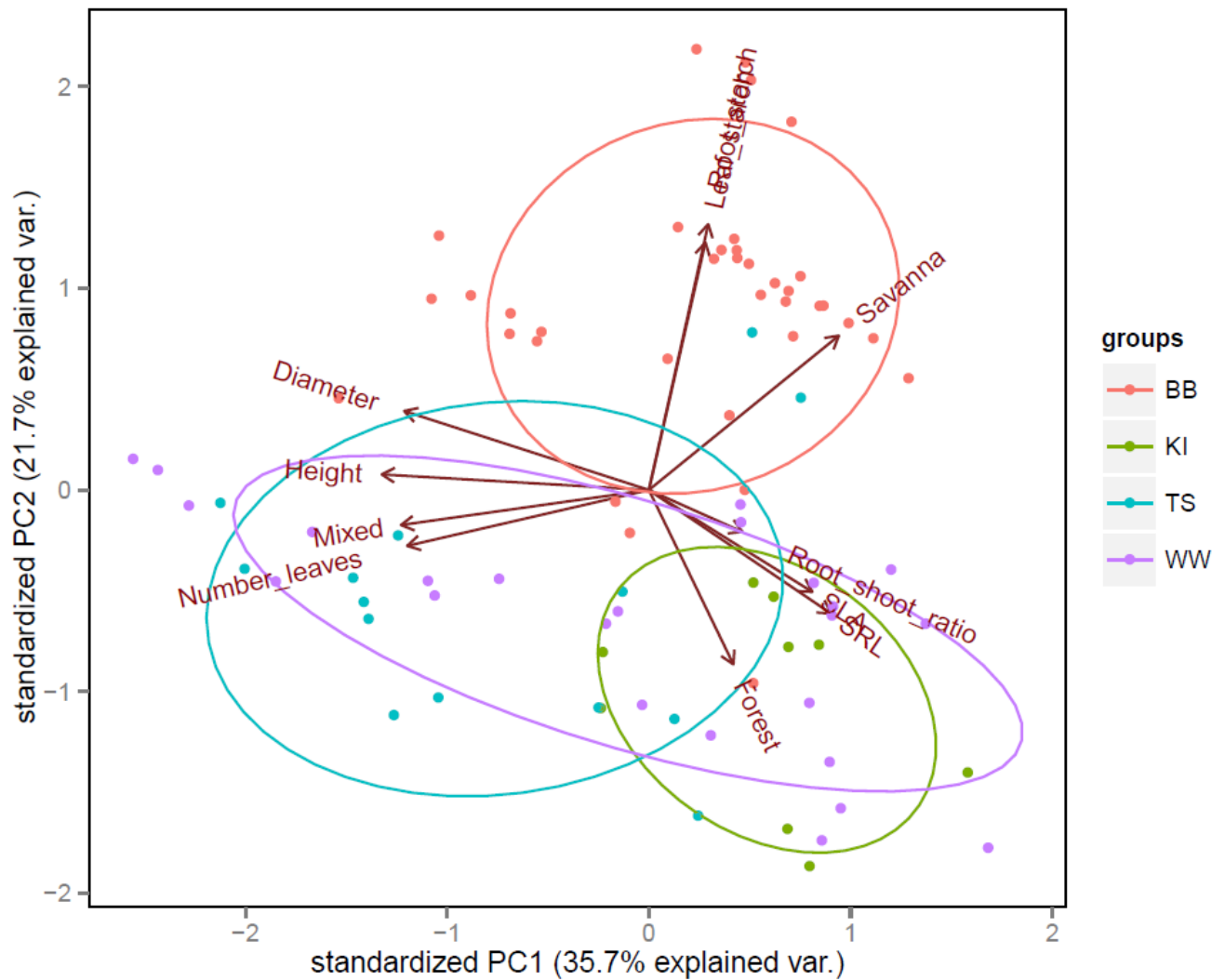


Figure 14: Results of a principle components analysis of all surviving seedlings. Principle components (PC's) 1 and 2 cumulatively explain 57.4 % of the variation within the data. Variables included were: leaf starch concentration, root starch concentration, root:shoot (g:g), specific leaf area (SLA) (cm^2/g), specific root length (SRL) (mm/g dry weight), diameter, height, and number of leaves. A variable to indicate vegetation type was also added (forest/mixed/savanna) so differential survival across vegetation types could be seen. Species names are: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Ellipses around species were drawn using cluster analysis. Overlapping labels at the 12 o'clock position are for root and leaf starch concentrations, whose vectors lie almost in exactly the same position.

savanna was strongly driven by its starch properties, with leaf and root starch concentrations being strong predictors of survival (**Figure 14**). The survival of *K.ivorensis* in the forest was strongly driven by biomass variables, specifically specific root length, root to shoot ratio and specific leaf area (**Figure 14**). Survival of *T.scleroxylon* and *T.superba* in the mixed vegetation type was driven by size variables, specifically number of leaves, height and diameter (**Figure 14**).

To closer examine potential trade-offs that occurred between traits to cope with fire, such as increased root starch concentrations, and traits to compete, such as growth and resource capture related traits, pairwise comparisons of the traits used in the PCA were plotted (**Figure 15**). Points falling in the top right hand corner of any plot indicated that trade-offs did not exist for that trait comparison as seedlings displayed strength in both traits. None of the comparisons showed this behaviour, indicating that trade-offs between fire recovery traits and competition traits existed. Specifically, trade-offs between root starch concentration and root to shoot ratio, specific leaf area, seedling height, stem diameter, and number of leaves were evident (**Figure 15**). In all trade-offs, *B.buonopozense* showed preferential allocation to fire tolerance traits (higher root starch concentrations) (**Figure 15**). In addition to these trade-offs being present between species they were also present within species, with individuals of the same species showing either a preference for allocation to root starch concentration or to competitive or growth traits, but not to both (**Figure 15**).

In order to establish whether recovery post-fire had occurred in burnt seedlings, traits between burnt and unburnt seedlings as measured at the time of harvest were compared for each species (**Figure 16**). All species showed no difference in height

between burnt and unburnt seedlings except *B.buonopozense*, whose burnt seedlings were significantly shorter when unburnt (**Figure 16**). *B.buonopozense* also had significantly lower above-ground biomass in burnt than unburnt seedlings (**Figure 16**). As a result, *B.buonopozense* also had significantly higher root to shoot ratios in burnt than unburnt seedlings (**Figure 16**). There was no significant difference in diameter, specific leaf area or specific root length between burnt and unburnt seedlings for any species (**Figure 16**). *B.buonopozense* had the highest proportion of surviving seedlings that showed evidence of resprouting (**Appendix Table 2**).

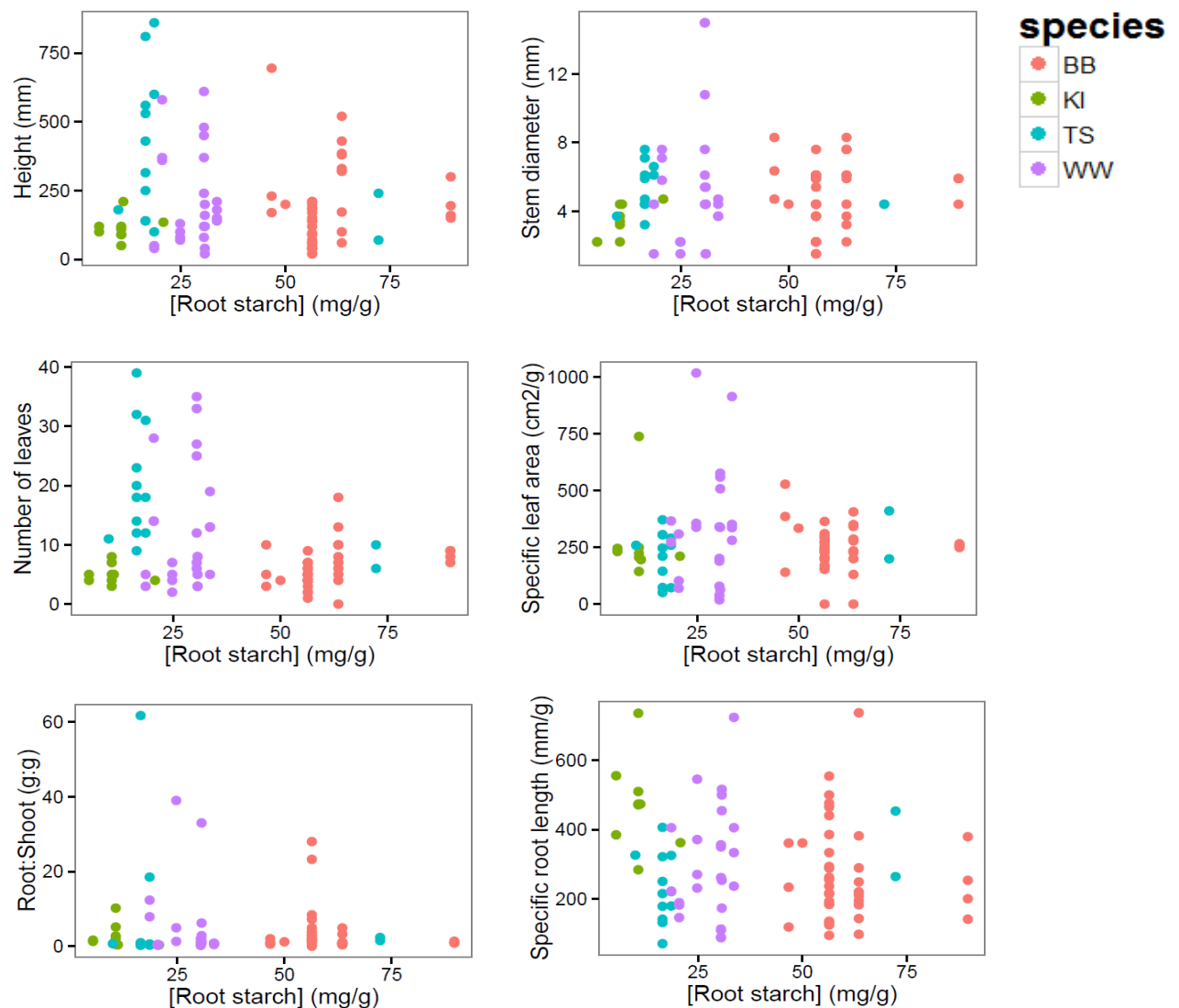


Figure 15: Potential trade-offs between root starch concentrations (a trait related to recovery from fire) and various growth and resource capture traits (traits that affect competitive ability). Different colours represent different species; each point represents a single surviving seedling and the traits it possessed at the time of harvesting. Species names are: BB=*B. buonopozense*, KI=*K. ivorensis*, ND=*N. diderrichii*, TS=*T. superba* and WW=*T. scleroxylon*.

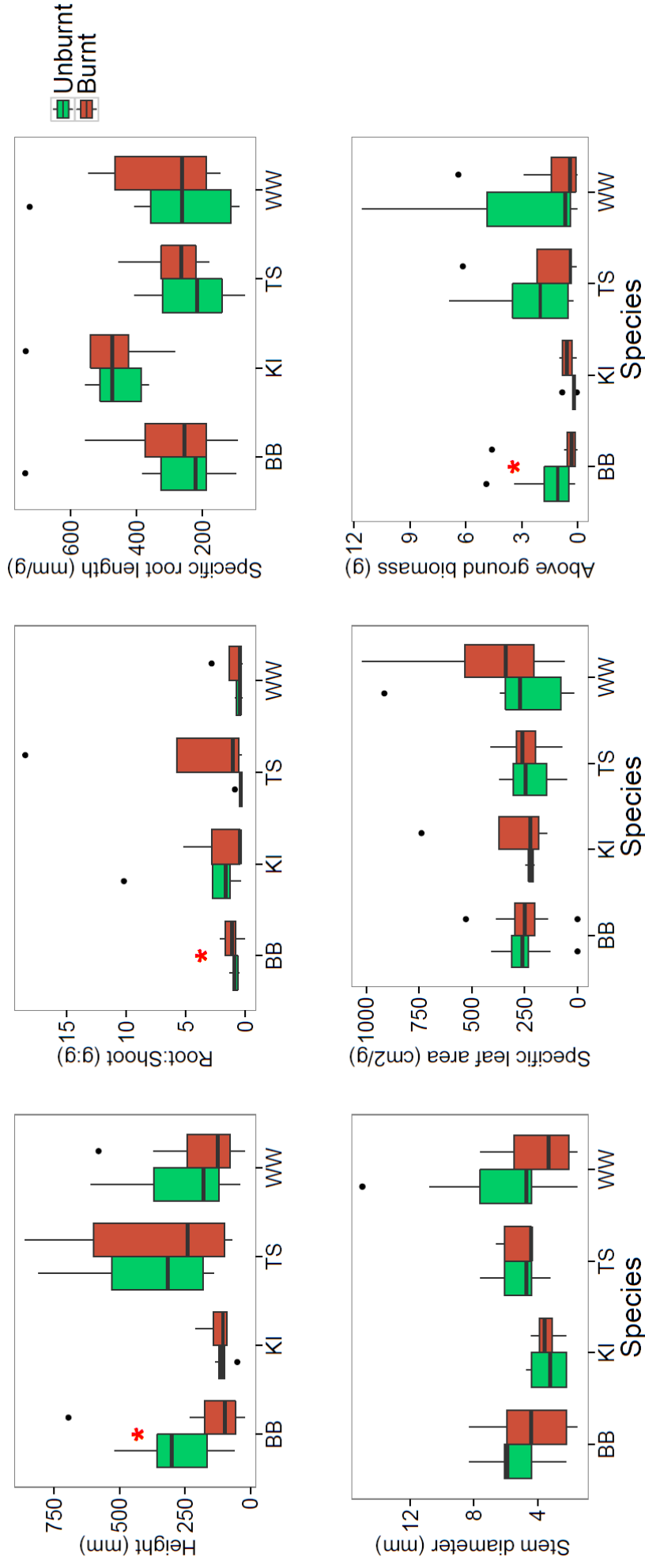


Figure 16: Differences in traits between burnt and unburnt seedlings that survived from June 2013 to June 2014. Boxplots show the median and interquartile range in the box, whiskers show 95% confidence interval of the median, outliers are shown as individual points. Red stars indicate significant difference ($p < 0.05$) between burnt and unburnt seedlings for each species as determined using a Kruskal-Wallis test. Species names are: BB=*B. buonopozense*, KI=*K. ivorensis*, ND=*N. diderrichii*, TS=*T. superba* and WW=*T. scleroxylon*. Note that the root:shoot plot excludes individuals that showed evidence of resprouting as these individuals were extreme outliers.

DISCUSSION

This study examined the fire-trap hypothesis in West African tropical forest tree seedlings. Aspects of the fire resistance and fire suppression thresholds were tested in order to gain insight into the processes likely to affect whether a savanna or forest stable state is present at a point in space and time. Limited support was found for the hypothesis that the fire suppression threshold existed in this system, while the hypothesis that decreased herbaceous biomass would be associated with increased tree seedling survival was disproved altogether. Support for the hypothesis that the fire resistance threshold exists in this system was found, as well as the hypothesis that trade-offs between competitive ability and ability to recover from fire existed.

A threshold of canopy openness existed, below which herbaceous biomass decreased, however fire was not suppressed by this decrease

The fire suppression threshold is the point at which canopy openness is low enough to decrease herbaceous biomass sufficiently to suppress fire (Hoffmann *et al.*, 2012; Biddulph & Kellman, 1998; Hennenberg *et al.*, 2006). The first hypothesis tested was that the fire suppression threshold exists in this system and that therefore below a threshold of canopy openness, decreased canopy openness will be accompanied by a decrease in herbaceous biomass and this would be accompanied by a decrease in fire.

The results supported part of the first hypothesis in that there was evidence that below the threshold of 30% canopy openness a decrease in herbaceous biomass

occurred. The forest vegetation type had the lowest canopy openness and also the lowest the herbaceous biomass. This is as expected as the decreased canopy openness decreases light reaching the forest understory, which decreases herbaceous growth as its C4 photosynthesis' metabolic cost is too high to cope with low light conditions (Sage & Kubien, 2003). These findings can be compared to those of Hoffmann *et al.* (2012) which led to the initial development of the fire suppression threshold hypothesis. Hoffmann *et al.* (2012) demonstrated that increased tree leaf area index (LAI), as a measure of canopy openness, of trees in the Brazilian Cerrado was associated with decreased grass LAI, which is related to herbaceous biomass (**Figure 4**). The results are novel, however, as they show a clear threshold of canopy openness at 30%, below which herbaceous biomass decreases with a decrease in canopy openness.

Despite this, the results do not support the first hypothesis fully as the decreased canopy openness and associated reduced herbaceous biomass in the forest plots did not suppress fire. Despite having a more closed canopy and less herbaceous biomass, more plots were burnt in the forest than the mixed vegetation type. This indicates that despite the reduced herbaceous biomass in the forest reducing fuel load, a critical minimum fuel threshold to suppress fire was not reached. A possible cause of this is litter fall from the canopy increasing fine fuel load, the presence of which facilitates the spread of fire (Biddulph & Kellman, 1998).

While the results did not support of the fire suppression threshold hypothesis, they did not necessarily refute it. Though the plots in the study did not reach low enough levels of canopy openness and herbaceous biomass to suppress fire, the threshold

may still exist. The results from this study are novel as, despite other studies finding that fire suppression occurred below 50-55% canopy openness (Archibald *et al.*, 2009; Pueyo *et al.*, 2010; Staver *et al.*, 2011b), this study found no suppression of fire even below 30% canopy openness.

Contrary to expectation, increased herbaceous biomass was associated with increased seedling survival

The second hypothesis stated that decreased herbaceous biomass would be associated with increased tree seedling survival as a result of fire being suppressed by lack of fuel. Decreased herbaceous biomass has been shown to suppress fire due to the decrease in fine fuel available to facilitate the spread of fire (Biddulph & Kellman, 1998; Hoffmann *et al.*, 2012). Decreased fire is an effective means to increase seedlings survival, especially in forest tree seedlings as these are especially sensitive to top-kill by fire as a result of their relatively thin bark (Hoffmann *et al.*, 2012). Decreased herbaceous biomass also acts to increase seedling survival by decreasing competition between herbaceous biomass and tree seedlings as herbaceous biomass suppresses tree seedling growth, especially in the establishment phase (Menaut *et al.*, 1990; Jeltsch *et al.*, 1997).

Contrary to the expectation of the second hypothesis, results indicated that increased herbaceous biomass was associated with increased seedling survival. Savanna, with high herbaceous biomass, had the highest percentage of surviving seedlings (4%). Conversely the forest, with low herbaceous biomass, had the lowest

percentage of surviving seedlings (1%). Non-fire factors are likely influencing survival rates as although survival was lower in burnt than unburnt plots, burnt savanna plots had greater seedling survival rates than unburnt forest plots (12% in burnt savanna vs 10% in unburnt forest).

Light is a non-fire factor that likely affects survival. Increased canopy openness was associated with increased herbaceous biomass, likely as a result of increased light reaching the understory. Light is often a limiting resource in forest environments, and one of the primary factors reducing herbaceous biomass in the understory (Sage & Kubien, 2003). The same increased access to light that enhances herbaceous biomass in savanna environments may also be enhancing seedlings survival in this vegetation type. Increased light functions to increase seedlings survival as it increases non-structural carbohydrate concentrations (which includes starch) in tropical tree seedlings (O'Brien *et al.*, 2014), which increases seedling survival through drought (O'Brien *et al.*, 2014) and fire (Miyashita & Kellman, 1986; Canadell & López-Soria, 1998; Chapin *et al.*, 1990; Iwasa & Kubo, 1997; Bowen & Pate, 1993; Hoffmann *et al.*, 2003; Olano *et al.*, 2006).

Increased non-structural carbohydrate (NSC) concentrations increases tropical tree seedling survival during drought as these NSC concentrations help tropical tree seedlings maintain osmoregulation and hydraulic function during times of water deficit (O'Brien *et al.*, 2014). Tropical tree seedlings that enter into a drought period with increased NSC concentrations maintain higher stem water potentials and sustain their NSC concentrations during the drought better than seedlings that entered the drought with reduced NSC concentrations (O'Brien *et al.*, 2014). The

ability of increased NSC concentrations to enhance seedling survival through drought explains the increased survival of tree seedlings in the savanna compared to other environments, as the significantly higher canopy openness increased the light available to the seedlings, allowing them to accumulate more NSCs.

Increased NSC concentration also help increase tropical tree seedlings survival through fire. Below-ground NSCs, or starch, reserves are essential for recovery and growth post fire (Hoffmann *et al.*, 2009). Species who survive fire are at an advantage if they have immediate access to stored NSCs with which to power the new growth until enough photosynthetic area has been recovered that the plant can start supporting itself in that way (Miyanashi & Kellman, 1986; Canadell & López-Soria, 1998; Chapin *et al.*, 1990; Iwasa & Kubo, 1997; Bowen & Pate, 1993; Hoffmann *et al.*, 2003, Olano *et al.*, 2006). Stored NSCs are so vital in the post-fire recovery process that pre-fire NSC concentrations actually determine the ability of trees to survive fire and how well they grow after being burnt (Bowen & Pate, 1993; Kays & Canham, 1991). It is as a result of this relationship between NSC concentrations and fire recovery ability that seedlings of savanna tree species, having to deal with much more frequent fire than forest tree species seedlings, have much higher total NSCs than forest tree species seedlings (Hoffman *et al.*, 2004). The ability of increased NSC concentrations to enhance seedling survival through fire explains the increased survival of tree seedlings in the savanna compared to other environments, as the significantly higher canopy openness increased the light available to the seedlings, allowing them to accumulate more NSCs.

Another cause of reduced survival in the forest plots may have been the nature of the fire in these areas. While it was not explicitly tested in this study, the litter fall from the canopy that facilitated the spread of fire in forest may have also allowed fire to burn more slowly as its moisture content was likely higher as a result of the increased humidity that accompanies decreased canopy openness in the forest (Biddulph & Kellman, 1998). This slower burning may cause more damage to seedlings by exposing them to increased temperatures for a longer period of time, therefore increasing top-kill. Despite this, unburnt forest seedlings still had a lower survival rate than seedlings in unburnt savanna or mixed, reinforcing that non-fire factors such as light are still important in determining seedling survival rate.

Evidence of the fire resistance threshold was found, with *T.superba* and *B.buonopozense* most strongly exhibiting this threshold response in survival rates

The fire resistance threshold is the point at which a tree seedling escapes the fire-trap, with its increased size decreasing its probability of being top-killed by fire (Hoffmann *et al.*, 2012). Fire is an important factor controlling seedling survival in all vegetation types, with significantly more seedlings dying in burnt than unburnt plots. The fire resistance threshold can be found by comparing pre-fire traits of seedlings that survived fire to those that died in the fire. The third hypothesis stated that this threshold existed in the system and that a threshold of pre-fire size (diameter and height) in seedlings would be associated with a marked increase in post-fire survival.

Stem diameter, height, and bark thickness are good predictors as to whether a tree will be top-killed by fire or not (Hoffmann *et al.*, 2012). Differences in relative bark thickness are particularly important for fire resistance (Midgley *et al.*, 2010) with the limited success of forest species in fire-prone savanna environments attributed to their increased rates of juvenile mortality as a result of thinner bark (Hoffmann *et al.*, 2009). In addition to predicting likelihood of top-kill, height is also a good indicator of how well a tree will recover from fire (Schutz *et al.*, 2009). For example, in African savanna *Acacia* trees that were under 3m tall, taller trees had bigger roots, increasing shoot growth post-fire (Schutz *et al.*, 2009).

Seedlings that fell into a greater pre-fire height size class showed an increase in survival compared to those that fell into a smaller pre-fire height class. This pattern was not observed in unburnt seedlings, and therefore indicates that the fire-trap hypothesis is true for seedling height, and that being taller conferred an advantage to seedlings subjected to fire and increased their likelihood of survival. Evidence for the fire resistance threshold was found for height, with seedlings taller than 380mm showing a marked increase in survival rate. These findings can be compared to those of Hoffmann *et al.* (2012) from the Brazilian Cerrado that led to the initial development of the fire resistance threshold hypothesis. The results are novel, however, as they show support for the fire resistance threshold existing for seedling height, while it has only previously been demonstrated for bark thickness (**Figure 4**).

The same patterns were not seen for diameter, where increasing diameter class conferred seemingly equal advantages to burnt and unburnt seedlings, with both showing increased survival with increased size. This indicates that diameter in these

small seedlings has not yet reached the fire resistance threshold, but rather that seedlings with larger diameters may be more successful in capturing resources.

In examining species individually for evidence of the fire-trap, both *T.superba* and *B.buonopozense* show evidence for its existence. In *T.superba*, seedlings that survived the fire were both taller and had a greater diameter than seedlings that died in the fire. Similarly, *B.buonopozense* seedlings that survived the fire had a greater diameter than those that died in the fire.

There was evidence of trade-offs between competitive ability (i.e. growth and resource capture traits) and ability to recover from fire (i.e. starch concentration traits)

Trade-offs between competitive ability and ability to recover from fire were hypothesised to exist. Since allocation trade-offs can be adaptive traits (Tomlinson *et al.*, 2012), it was predicted that there would be allocation trade-offs between fire recovery traits, such increased starch concentrations in roots, and competitive advantage traits relating to growth and resource capture, such as height and specific leaf area.

Allocation trade-offs in plants are common, and allocation trade-offs between competitive ability and dispersal ability (Sevenster & van Alphen, 1993; Rees, 1995; Westoby *et al.*, 1996) as well between competitive ability and colonisation ability (Levins & Culver, 1971; Horn & MacArthur, 1972; Levin & Paine, 1974; Hastings, 1980, Tilman, 1994) are well documented. Most commonly, allocation trade-off

patterns have been studied where the underlying trade-off is one where an investment in resprouting ability, or below-ground starch reserves, has been associated with a decline in investment in reproductive ability (Bellingham & Sparrow, 2000). The trade-off between investment in below-ground starch reserves and above-ground growth has not been demonstrated in tropical forest tree seedlings, and therefore the results of this study are novel.

Allocation patterns in seedlings indicated that trade-offs existed between growth and resource capture traits, which may enhance competitive ability, and starch concentration traits, which may enhance ability to cope with fire. There was an absence of any seedlings exhibiting both high root starch concentrations and great height, diameter, number of leaves, specific leaf area or root to shoot ratio. The implication of this is that seedlings are either allocating resources to below-ground starch storage in large root biomass, or to growing tall and big and capturing more light to increase photosynthesis and competitive ability. *B.buonopozense* showed this trade-off clearly, having the highest root starch and leaf starch concentration of all the surviving seedling species but not exhibiting greater growth and resource capture traits, such as height, stem diameter, number of leaves, specific leaf area or specific root length. Conversely, the other species had lower root and starch concentrations than *B.buonopozense*, but were often superior to *B.buonopozense* in other growth traits such as height or number of leaves (eg. *T.superba* was taller than *B.buonopozense* and had more leaves).

The principle components analysis (PCA) further examined these trade-offs and how they may be influencing survival. The first two principle components clearly separate

the tree species from one another and the species separate clearly according to which vegetation type they survived the best in. *B.buonopozense* survived well in savanna, *K.ivorensis* survived well in forest, and *T.scleroxylon* and *T.superba* survived well in mixed and forest environments. The enhanced survival of different species in different vegetation types and a lack of species that survive well in all three vegetation types implied that trade-offs were present in these seedlings, with different allocation strategies causing differential survival of species in different vegetation types.

The PCA showed that seedlings surviving in savanna did so based on leaf and root starch concentrations, traits that allowed them to recover from fire. Species that survived well in mixed environments did so on the basis of growth and resource capture or competition traits, such as height, diameter and number of leaves. Similarly, species that survived in forest also did so based on competition traits, however these were more biomass based, such as specific root length, specific leaf area and root to shoot ratio. These results indicate that fire drives survival in savanna, while competition drives survival in mixed and forest environments. The existence of trade-offs is not unexpected as trade-offs are a central part of the life history strategy of plants in frequently disturbed areas, with trade-offs between damage avoidance and resprouting ability observed across a wide range of woody plants (Vesk, 2006).

The existence of these trade-offs mean certain forest species may be better poised to encroach into savanna than others

Encroachment of forest into savanna is a process occurring in savannas worldwide (Archer, 1995; van Auken, 2000; Roques *et al.*, 2001, Moleele *et al.*, 2002). It has been specifically noted in tropical African savannas (Mitchard *et al.*, 2009; Mitchard & Flintrop, 2013) and in the southern hemisphere African savannas (Wigley *et al.*, 2010; Buitenwerf *et al.*, 2012). The encroachment of forest into savanna is not simply a matter of closing the canopy, but is also a change in species composition as savanna tree species have a lower leaf area index than forest species, and therefore are not be able to develop a closed canopy (Hoffmann *et al.*, 2005). Understanding which forest species are able to succeed in savanna is thus crucial if encroachment of forest in savanna is to be monitored and managed effectively.

A model that may explain how forests encroach into savannas is the “storage effect” (Warner & Chesson, 1985; Chesson & Huntly, 1989), whereby reproductive potential is stored between generations in the large number of small trees trapped in the fire-trap that are able to recruit strongly when conditions become favourable. The “storage effect” hypothesis hinges on the fact that under appropriate fire regimes forest species will be unable to encroach into savanna, and under fire suppression the opposite is true. This importance of fire in maintaining the savanna ecosystem is demonstrated well in fire suppressed savanna systems, for example in a Brazilian savanna under fire suppression forest tree species accounted for more than one third of all seedlings in the savanna and 14% of the adult trees, indicating that under continued fire suppression the forest would continue encroaching into the savanna (Geiger *et al.*, 2011).

Following the logic of the “storage effect”, forest tree species that survive better in savanna environments are able to build up a larger store within the grass layer, making them better poised to encroach upon savanna when conditions are suitable for the fire-trap to be overcome. Fire is one of the most important factors controlling tree success in savannas (Bond, 2008; Staver *et al.*, 2011a), therefore greater ability survive frequent fire is a distinct advantage to trees growing in a savanna environment. Forest species seedlings are rare in regularly burnt savanna (Hoffmann *et al.*, 2012), but more abundant when fire is suppressed (San José & Fariñas, 1991; Geiger *et al.*, 2011), suggesting that fire is limiting their success in the savanna (Hoffmann *et al.*, 2012, 2004). Furthermore, under fire suppression the recruitment of forest species can exceed that of savanna species in savanna, with forest tree species being especially common at forest-savanna border, indicating that under continued fire suppression forest will encroach into savanna (San José & Fariñas, 1991; Russell-Smith, 2004; Geiger *et al.*, 2011).

The observed trade-off patterns that allowed *B.buonopozense* to have greater survival rates in the savanna than other species both before and after fire indicate that this species has the potential to lead the encroachment of forest into savanna. *B.buonopozense* was the most successful species in the study, it had the highest number of surviving seedlings and most these survived in the savanna, despite this being the most extensively burnt of the vegetation types. *B.buonopozense* also had the highest root and leaf starch concentration, with the PCA linking these to its increased survival in the savanna. Starch accumulation was a trait that allowed it to survive and recover effectively from fire (Miyanashi & Kellman, 1986; Canadell &

López-Soria, 1998; Chapin *et al.*, 1990; Iwasa & Kubo, 1997; Bowen & Pate, 1993; Hoffmann *et al.*, 2003, Olano *et al.*, 2006), it also would have contributed to the increased pre-fire survival rate of this species by increasing its ability to survive drought (O'Brien *et al.*, 2014). *B.buonopozense* also showed a higher ability to resprout than the other species, which would have further enhanced its survival in this frequently burnt environment.

B.buonopozense also shows remarkable ability to recover from fire. Within five months of fire, *B.buonopozense* seedlings that were burnt show no significant difference to unburnt seedlings in diameter, specific leaf area or specific root length. Furthermore, root starch concentration was not significantly affected by whether or not seedlings were burnt, indicating that in addition to biomass recovery post-fire, in this same short time period starch reserves had also been replenished. Similarly fast rates of recovery have been reported for a fire-adapted African savanna *Acacia* tree species, where root starch concentrations in burnt trees reached the levels of unburnt trees within a year after fire (Schutz *et al.*, 2009). This places *B.buonopozense* in a good position to deal with repeated fire, an essential if this forest species is to survive in the frequently burnt savanna (Hoffmann *et al.*, 2012).

The encroachment of forest into savanna represents a shift from one stable state to another (Lehmann *et al.*, 2011; Ray *et al.*, 2005; Bowman, 2000). The ability, therefore, of seedlings to cross either the fire resistance or fire suppression threshold is vital, as once either threshold is crossed positive feedbacks within the system make reverse shifts to the previous state both difficult and unlikely (Lehmann *et al.*, 2011). Woody thickening and encroachment of forest into savanna has already been

reported in various southern African savannas, and here it has been attributed to global drivers such as increased atmospheric carbon dioxide and not to local drivers such as land use change (Wigley *et al.*, 2010; Bond & Midgley, 2012). It therefore it remains a relevant issue for the mesic West African savannas pre-emptive monitoring of this would be wise. Considering *B.buonopozense*'s success in savannas as well as its preferential allocation to fire recovery traits, it is a species ideally poised to flourish in the frequently burnt savanna if the right conditions prevail. These factors, combined with *B.buonopozense*'s ability to grow in the transition zone between forest and savanna, make it a prime candidate as an indicator species of forest encroachment into savanna in mesic West African savannas.

Non-fire factors, such as drought, are also likely important for seedling survival

Drought and herbivory are important drivers of open canopies in savanna, often acting in a way similar to fire (Hoffman, 2012). In fact, fire and drought are the two most important constraints in seedlings development in the Brazilian Cerrado (Hoffmann, 2000). Forest seedlings may be specifically vulnerable to the effects of drought, and changes in precipitation regimes as a result of climate change have already been shown to be causing dieback of tropical forests across the globe (Potts, 2003; Phillips *et al.*, 2010; Andregg *et al.*, 2012; Chaot *et al.*, 2012).

The sharp decrease in survival seen in all seedlings before the fire and in unburnt seedlings after the fire indicates that fire alone is not responsible for the lack of

success of these species. Drought is a likely cause of this as a strong association was found between decreased total precipitation and lower seedling survival. Drought is not an uncommon challenge for savanna tree species, and savanna seedlings tend to have a deeper taproot that develops quickly at a young age to help with drought tolerance by providing access to water at deeper levels (Rizzini, 1965; Moreira, 1992; Oliveira & Silva, 1993; Hoffmann, 2000). Forest seedlings do not have this ability, and the lower survival of forest than savanna seedlings when both are grown in a savanna environment has been attributed to drought stress (Hoffman *et al.*, 2004).

B.buonopozense and *T.scleroxylon* show the highest survival rates before the fire, when drought may have possibly been the factor most affecting survival. These two species had higher leaf starch concentrations than *T.superba*, which shows a lower pre-fire survival rate, suggesting that the ability of *T.scleroxylon* and *B.buonopozense* to accumulate starch may be helping them survive through drought conditions, as carbohydrates are important for drought tolerance (O'Brien *et al.*, 2014). The better ability to deal with drought before the fire allowed them to both have a higher number of seedlings go into the fire, but also a higher number survive the fire.

Possible improvements and future research opportunities

This study did well to examine how certain tropical forest tree species fit into the fire-trap hypothesis. However, a larger sample size with more species would make the tests even more powerful. The incorporation of savanna species as well as forest

species would be advised. Measures to specifically test the effect of drought on the seedlings, such as soil moisture measurements, would allow for more conclusions on factors affecting seedlings survival to be drawn. Similarly, including herbivory exclosures could provide fascinating results as field observations indicated that insect herbivory was widespread. Splitting the plots into those with no grass biomass, i.e. reducing competition, may also be helpful for determining what the greater survival of seedlings in savanna could possibly be attributed to.

CONCLUDING REMARKS AND MANAGEMENT IMPLICATIONS

This study found evidence for the fire suppression threshold in this system to a certain degree. A threshold canopy openness of approximately 30% existed, below which herbaceous biomass decreased with a decrease in canopy openness. However, this decreased herbaceous biomass was associated with neither the suppression of fire nor the increased survival of seedlings, with fire burning many low herbaceous biomass plots and seedlings survival increasing with increasing herbaceous biomass. Evidence for the fire resistance threshold was found, with seedlings with a pre-fire height above 380mm showing an increased post-fire survival rates. Trade-offs between competitive ability and ability to recover from fire were found both within and between species, with no individuals able to allocate extensive resources to both simultaneously. Allocation trade-offs in *B.buonopozense* increased its survival rate in savanna as it was the most equipped to deal fire and drought as a result of its high starch concentrations.

The implication of these fire thresholds being present, to varying degrees, in this West African tropical system is that this system is vulnerable to state shift. Following alternative stable states theory, the presence of thresholds in this system implies that once a threshold has been crossed a state shift from forest to savanna will occur and will not be easily reversible. Since global scale environmental drivers, such as increasing atmospheric carbon dioxide, can cause trees to cross these thresholds faster, effective monitoring is essential in order to be able to pre-emptively manage this system and avoid loss of the savanna biome. According to this study,

B.buonopozense is a species whose increased success in savanna systems may be a warning sign of encroachment of forest.

Once early signs of encroachment have been noted, the management of these systems in order to maintain both states of the ecosystem can be effectively accomplished by altering the fire regime of the area using the knowledge about thresholds in these forest species. However whether or not these systems should be managed to maintain both forest and savanna or not is a matter widely debated. While both ecosystem states have value, environmental change may make management of these states futile. Recent findings indicate that the effects of increasing atmospheric carbon dioxide will override the effects of alternative stable states theory across tropical and subtropical Africa, resulting in many alternative stable state ecosystems that are tree dominated or herbaceous layer dominated becoming deterministically tree dominated in the future (Moncrieff *et al.*, 2014).

REFERENCES

- Adams, M. A. (2013) Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. Forest Ecology and Management, 294: 250-261.
- Anderegg, W., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D.L., Field, C.B. (2012) The roles of hydraulic and carbon stress in a widespread climate-induced forest die-back. Proceedings of the National Academy of Science USA, 109: 233-237.
- Archer, S. (1995) Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience, 2: 83–99.
- Archibald, S., Bond, W. J., Stock, W. D., Fairbanks, D. H. K. (2005) Shaping the landscape: Fire-grazer interactions in an African savanna. Ecological Applications, 15: 96-109.
- Archibald, S., Roy, D., van Wilgen, B., Scholes, R. (2009) What limits fire? An examination of drivers of burnt area in Southern Africa. Global Change Biology, 15: 613-630.
- Archibald, S., Lehmann, C.E.R., Gómez-Dans, J.L., Bradstock, R.A. (2013) Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Science U.S.A., 110: 6442-6447.
- Bauer, G., Speck, T., Blomer, J., Bertling, J., Speck, O. (2010) Insulation capability of the bark of trees with different fire adaptation. Journal of Materials Science, 45: 5950-5959.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F.I., Papale, D. (2010) Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate. Science, 329: 834-838.
- Bellingham, P.J. & Sparrow, A.D. (2000) Resprouting as a life history strategy in woody plant communities. Oikos, 89: 409-416.
- Beisner, B.E., Haydon, D.T., Cuddington, K. (2003) Alternative Stable States in Ecology. Frontiers in Ecology and the Environment, 1: 376-382.

Biddulph, J. & Kellman, M. (1998) Fuels and fire at savanna-gallery forest boundaries in southeastern Venezuela. Journal of Tropical Ecology 14: 445-461.

Bloom, A.J., Chapin, F.S., Mooney, H.A. (1985) Resource limitations in plants – an economic analogy. Annual Review of Ecology and Systematics, 16, 363-392.

Bond, W. J. & Keeley, J. E. (2005) Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution, 20: 387-394.

Bond, W. J. & Midgley, G. F. (2012) Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philosophical Transactions of the Royal Society B-Biological Sciences, 367: 601-612.

Bond, W. J. & Van Wilgen, B.W. (1996) Fire and Plants (Population and Community Biology Series 14). London: Chapman and Hall.

Bond, W. J. (2005) Large parts of the world are brown or black: a different view on the 'green world' hypothesis. Journal of Vegetation Science, 16: 261-266.

Bond, W. J., & Midgley, G. F. (2000) A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology, 6: 865-869.

Bond, W. J., & Midgley, J. J. (2001) Ecology of sprouting in woody plants: The persistence niche. Trends in Ecology & Evolution, 16: 45-51.

Bond, W.J. (2008) What limits trees in C₄ grasslands and savannas? Annual Review of Ecology, Evolution, and Systematics, 39: 641-659.

Bond, W.J., & Midgley, G.F. (2012) Carbon dioxide and the uneasy interactions of trees and savannah grasses. Philosophical Transactions of the Royal Society B-Biological Sciences, 367: 601-612.

Bond, W.J., Midgley, G.F., Woodward, F.I. (2003) What controls South African vegetation – climate or fire? South African Journal of Botany, 69: 79–91.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. New Phytologist, 165: 525–538.

Bowen, B.J. & Pate, J.S. (1993) the significance of root starch in post-fire shoot recover of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). Annals of Botany, 72: 7-16.

Bowman, D.M.J.S. (2000) Australian Rainforests: Islands of Green in a Land of Fire. Cambridge: Cambridge University Press.

Bowman, D.M.J.S., Fensham, R.J. (1991) Response of a monsoon forest-savanna boundary to fire protection, Weipa, northern Australia. Australian Journal of Ecology, 16: 111-118.

Brouwer, R. (1962) Nutritive influences on the distribution of dry matter in the plant. Netherlands Journal of Agricultural Science, 10: 399-408.

Buitenwerf, R., Bond, W.J., Stevens, N., Trollope, W.S.W. (2012) Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver. Global Change Biology, 18: 675-684.

Canadell, J. & Lopez-Soria, L. (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Functional Ecology, 12: 31-38.

Chapin, F.S., Schulze, E.D., Mooney, H.A. (1990) The ecology and economics of storage in plants. Annual Review of Ecology, Evolution and Systematics, 21: 423-447.

Chesson, P.L. & Huntly, N. (1989) Short term instabilities and long-term community dynamics. Trends in Ecology and Evolution, 4: 293-298.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Field, T.S., Gleason, S.M., Hacke, U.G., Jacobson, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne A.E. (2012) Global convergence in the vulnerability of forests to drought. Nature, 491: 752-755.

Clarke, P. J. & Knox, K. J. E. (2009) Trade-offs in resource allocation that favour resprouting affect the competitive ability of woody seedlings in grassy communities. Journal of Ecology, 97: 1374-1382.

Dai, Z., Ku, M.S.B., Edwards, G.E. (1993) C4 photosynthesis- The CO₂-concentration mechanism and photorespiration. Plant Physiology, 103: 83-90.

Damesin, C., Bazot, S., Fresneau, C. (2013) Soluble sugar and starch extractions from plant tissues for isotope analysis. URL: [http://www.publish.csiro.au/prometheuswiki/tiki-pagehistory.php?page=Soluble sugar and starch extractions from plant tissues for isotope analysis&preview=8&preview=](http://www.publish.csiro.au/prometheuswiki/tiki-pagehistory.php?page=Soluble+sugar+and+starch+extractions+from+plant+tissues+for+isotope+analysis&preview=8&preview=) [12 May 2014].

Dent, C.L., Cumming, G.S., Carpenter, S.R. (2002) Multiple states in river and lake ecosystems. Philosophical Transactions of the Royal Society B-Biological Sciences, 357: 635-45.

Desjardins, T., Carneiro, A., Mariotti, A., Chauvel, A., Girardin, C. (1996) Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic carbon. Oecologia, 108:749–756.

Dorgelöh, W.G. (2002) Calibrating a disc pasture meter to estimate above-ground standing biomass in Mixed Bushveld, South Africa. African Journal of Ecology, 40: 100-102.

Duranceau, M., Ghashghaie, J., Badeck, F., Deléens, E., Cornic, G. (1999) Delta 13C of CO₂ respired in the dark in relation to delta 13C of leaf carbohydrates in *Phaseolus vulgaris* L. under progressive drought. *Plant, Cell and Environment*, 22: 515-523.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science, 281: 237-240.

Frazer, G.W., Canham, C. D., Lertzman, K. P. (1999) Gap Light Analyzer (GLA). Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs Millbrook: Institute of Ecosystem Studies.

Geiger, E. L., Gotsch, S. G., Damasco, G., Haridasan, M., Franco, A. C., Hoffmann, W. A. (2011). Distinct roles of savanna and forest tree species in regeneration under fire suppression in a Brazilian savanna. Journal of Vegetation Science, 22: 312-321.

Ghana Wildlife Department (1994) Kogyae Strict Nature Reserve: Development and Management Plan. Accra: Ghana Wildlife Department.

Gill, A.M. & Ashton, D.H. (1968) Role of bark type in relative tolerance to fire of 3 central Victorian Eucalypts. Australian Journal of Botany, 16, 491–498.

Glitzenstein, J.S., Platt, W.J., Streng, D.R. (1995) Effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. Ecological Monographs, 65: 441-476.

Gotsch, S.G., Geiger, E.L., Franco, A.C., Goldstein, G., Meiner, F.C., Hofmann, W.A. (2010) Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees. Oecologia, 163: 291-301.

Hanan, N.P., Tredennick, A.T., Pridhodko, L., Bucini, G., Dohn, J. (2014) Analysis of stable states in global savannas: is the CART pulling the horse? Global Ecology and Biogeography, 23: 259–263

Hastings, A. (1980) Disturbance, coexistence, history, and competition for space. Theoretical Population Biology, 18: 363-373.

Hedge, V., Chandran, M.D.S., Gadgil, M. (1998) Variation in bark thickness in a tropical forest community of Western Ghats in India. Functional Ecology, 12: 313–318.

Hennenberg, K. J., Goetze, D., Minden, V., Traore, D., Porembski, S. (2005) Size-class distribution of *Anogeissus leiocarpus* (Combretaceae) along forest-savanna ecotones in northern ivory coast. Journal of Tropical Ecology, 21: 273-281.

Heubes, J., Kuehn, I., Koenig, K., Wittig, R., Zizka, G., Hahn, K. (2011) Modelling biome shifts and tree cover change for 2050 in West Africa. Journal of Biogeography, 38: 2248-2258.

Higgins, S. I., Bond, W. J., Combrink, H., Craine, J. M., February, E. C., Govender, N., Lannas, K., Moncrieff, G., Trollope, W.S.W. (2012) Which traits determine shifts in the abundance of tree species in a fire prone savanna? Journal of Ecology, 100: 1400-1410.

Higgins, S. I., Bond, W. J., February, E. C., Bronn, A., Euston-Brown, D. I. W., Enslin, B., Govender, N., Rademan, L., O'Regan, S., Potgieter, A.L.F., Scheiter, S., Sowry, R., Trollope, L., Trollope, W.S.S. (2007). Effects of four decades of fire manipulation on woody vegetation structure in savanna. Ecology, 88: 1119-1125.

Higgins, S.I., Bond, W.J., Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. Journal of Ecology, 88: 213–229.

Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M. (2011) Global Resilience of Tropical Forest and Savanna to Critical Transitions. Science, 334: 232-235.

Hoch (March 2014) Personal communications about how best to store seedlings in the field prior to starch analysis.

Hoffmann, W. A. (2000) Post-establishment seedling success in the Brazilian Cerrado: A comparison of savanna and forest species. Biotropica, 32: 62-69.

Hoffmann, W. A. (1999) Fire and population dynamics of woody plants in a Neotropical savanna: matrix model projections. Ecology, 80: 1354-1369.

Hoffmann, W. A., Adasme, R., Haridasan, M., de Carvalho, M. T., Geiger, E. L., Pereira, M.A.B., Gotsch, S.G., Franco, A.C. (2009) Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. Ecology, 90: 1326-1337.

Hoffmann, W.A. & Franco, A.C. (2003) Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically-independent contrasts. Journal of Ecology, 91: 475-484.

Hoffmann, W.A. & Solbrig, O.T. (2003) The role of topkill in the differential response of savanna woody plants to fire. Forest Ecology and Management, 180: 273-286.

Hoffmann, W.A. (2000). Post-establishment seedling success in the Brazilian cerrado: A comparison of savanna and forest species. Biotropica, 32: 62-69.

Hoffmann, W.A., da Silva, E.R., Machado, G.C., Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C. (2005) Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna. Oecologia, 145:307-316.

Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lee Lau, O., Haridasan, M., Franco, A. (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters, 15: 759-768. .

Hoffmann, W.A., Orthen, B., Franco, A.C. (2004) Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. Oecologia, 140: 252-260.

Hoffmann, W.A., Orthen, B., Nascimento, P.K.V. (2003) Comparative fire ecology of tropical savanna and forest trees. Functional Ecology, 17: 720-726.

Holdo, R.M. (2005) Stem mortality following fire in Kalahari sand vegetation: effects of frost, prior damage, and tree neighbourhoods. Plant Ecology, 180: 77-86.

Holling, C.S. (1973) Resilience and stability of ecological systems. Annual Review of Ecology and Systematics, 4: 1-24.

Hopkins, B. (1992) Ecological processes at the forest-savanna boundary. In: Furley, P.A., Procter, J., Ratter, J.A. (eds) Nature and dynamics of forest-savanna boundaries. London: Chapman and Hall. pp 21-33.

Horn, H.S. & MacArthur, R.H. (1972) Competition among fugitive species in a harlequin environment. Ecology, 53: 749-752.

Iwasa, Y. & Kubo, T. (1997) Optimal size of storage for recovery after unpredictable disturbances. Evolutionary Ecology, 11: 41-65.

Jeltsch, F., Milton, S.J., Dean, W.R.J., van Rooyen, N. (1997) Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. Journal of Vegetation Science, 8: 177-88.

Kays, J.S. & Canham, C.D. (1991) Effects of time and frequency of cutting on hardwood root reserves and sprout growth. Forest Science, 37: 524-536.

Kershaw, A.P. (1992) The development of rainforest-savanna boundaries in tropical Australia. In: Furley, P.A., Procter, J., Ratter, J.A. (eds) Nature and dynamics of forest-savanna boundaries. London: Chapman and Hall. pp 255–271.

Kgope, B. S., Bond, W. J., Midgley, G. F. (2010) Growth responses of African savanna trees implicate atmospheric [CO₂] as a driver of past and current changes in savanna tree cover. Austral Ecology, 35: 451-463.

Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., Hutley, L.B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.D.J.S., Bond, W.J. (2014) Savanna vegetation-fire-climate relationships differ among continents. Science, 343: 548-552.

Lehmann, C.E.R., Archibald, S.A., Hoffmann, W.A., Bond, W.J. (2011) Deciphering the distribution of the savanna biome. New Phytologist, 191: 197-209.

Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species. Proceedings of the National Academy of Sciences USA, 6:1246–1248.

Levin, S.A. & Paine, R.T. (1974) Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences USA, 71: 2744-2747.

Malhi, Y. (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. Journal of Ecology, 100: 65–75.

MATLAB 2014a (2014). Natick: The MathWorks Inc.

Mayer, A.L., Kahlyani, A.H. (2011) Grass trumps trees with fire. Science, 334: 188-189.

Menaut, J., Gignoux, J., Prado, C., Clobert, J. (1990) Tree community dynamics in a humid savanna of the Coted'Ivoire: modelling the effects of fire and competition with grass and neighbors. Journal of Biogeography, 17: 471-481.

Midgley, J.J., Lawes, M.J., Chamaille-Jammes, S. (2010) Savanna woody plant dynamics: the role of fire & herbivory, separately & synergistically. Australian Journal of Botany, 58: 1–11.

Mitchard, E.T.A. & Flintrop, C.M. (2013) Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982-2006. Philosophical Transactions of the Royal Society B- Biological Sciences, 368: 1-7.

Mitchard, E.T.A., Saatchi, S.S., Gerard, F.F., Lewis, S.L., Meir, P. (2009) Measuring Woody Encroachment along a Forest–Savanna Boundary in Central Africa. Earth Interactions, 13: 1-29.

Miyanishi, K. & Kellman, M. (1986) The role of root nutrient reserves in regrowth of two savanna shrubs. Canadian Journal of Botany, 64:1244-1248.

Moleele, N.M., Ringrose, S., Matheson, W., Vanderpost, C. (2002) More woody plants? The status of bush encroachment in Botswana's grazing areas. Journal of Environmental Management, 64: 3-11.

Moncrieff, G.R., Scheiter, S., Bond, W.J., Higgins, S.I. (2014) Increasing atmospheric CO₂ overrides the historical legacy of multiple states biomes in Africa. New Phytologist, 201: 908-915.

Moreira, A.G. (1992) Fire protection and vegetation dynamics in the Brazilian Cerrado. Ph.D. dissertation. Harvard University, Cambridge, Massachusetts.

Mouillot, F., Field, C.B. (2005) Fire history and the global carbon budget: a fire history reconstruction for the 20th century. Global Change Biology, 11: 398-420.

Neyret, M. (unpublished data). MATLAB code for calculating leaf area from scanned images.

O'Brien, M.J., Leuzinger, S., Philipson, C.D., Tay, J., Hector, A. (2014) Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. Nature Climate Change, 4: 710-714.

Ogren, W.L. (1984) Photorespiration: pathways, regulation, and modification. Annual Review of Plant Physiology, 35: 415-442.

Olano, J.M., Menges, E.S., Martinez, E. (2006) Carbohydrate storage in five resprouting florida scrub plants across a fire chronosequence. New Phytologist, 170: 99-105.

Oliveira, P.A.E. & Silva, J.C.S. (1993) Reproductive biology of two species of *Kielmeyera* (Guciferae) in the Cerrados of central Brazil. Journal of Tropical Ecology, 9: 67-79.

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., Anthony, S. (2009) Agroforestree Database: a tree reference and selection guide version 4.0. Kenya: World Agroforestry Centre.

Oyen, L.P.A. (2011) *Bombax buonopozense* P.Beauv. Record from PROTA4U. Brink, M. & Achigan-Dako, E.G. (eds). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, Netherlands. <http://www.prota4u.org/search.asp> [20 August 2014].

Peterson, G., Allen, C.R., Holling, C.S. (1998) Ecological resilience, biodiversity and scale. Ecosystems, 1: 6-18.

Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E. A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T. R., Blanc, L., Bonal, D., de Oliveira, Á. C. A., Chao, K.-J., Cardozo, N. D., da Costa, L., Feldpausch, T. R., Fisher, J. B., Fyllas, N. M., Freitas, M. A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E., Keeling, H., Killeen, T. J., Lovett, J. C., Meir, P., Mendoza, C., Morel, A., Vargas, P. N., Patiño, S., Peh, K. S.-H., Cruz, A. P., Prieto, A., Quesada, C. A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J. W., Sonké, B., Thomas, A. S., Stropp, J., Taplin, J. R. D., Vásquez, R., Vilanova, E. (2010) Drought-mortality relationships for tropical forests. New Phytologist, 187: 631-646.

Pinheiro, M.H.O. & Monteiro, R. (2006) Contribution of forest species to the floristic composition of a forested savanna in South-eastern Brazil. Brazilian Archive Of Biology and Technology, 49: 763-774.

Potts, M. (2003) Drought in a Bornean everwet rain forest. Journal of Ecology, 91: 467-474.

Pueyo, S., De Alencastro Graça, P.M.L., Barbosa, R.I., Cots, R., Cardona, E., Fearnside, P.M. (2010) Testing for criticality in ecosystem dynamics: the case of Amazonian rainforest and savanna fire. Ecology letters, 13: 793-802.

R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL :<http://www.R-project.org/>.

Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E.R., Anderson, M.T., Higgins, S.I., Sankaran, M. (2011) When is a 'forest' a savanna, and why does it matter? Global Ecology and Biogeography, 20: 653-660.

Ray, D., Nepstad, D. & Moutinho, P. (2005) Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. Ecological Applications, 15: 1664–1678.

Rees, M., & Westoby, M. (1997) Game-theoretical evolution of seed mass in multi-species ecological models.

Oikos, 78: 116–126.

Rissini, C.T. (1965) Experimental studies on seedling development of Cerrado woody plants. Annals of the Missouri Botanical Garden, 52: 410-426.

Roques, K.G., O'Connor, T.G., Watkinson, A.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology, 38: 268-280.

Rossatto, D.R., Hoffmann, W.A. & Franco, A.C. (2009) Differences in growth patterns between co-occurring forest and savanna trees affect the forest– savanna boundary. Functional Ecology, 23: 689-698.

Russell-Smith, J. (2004) Rain forest invasion of eucalypt-dominated woodland savanna, iron range, north-eastern Australia: I. Successional processes. Journal Biogeography, 31: 1293-1303.

Sage, R. & Kubien, D. (2003) Quo vadis C4? An ecophysiological perspective on global change and the future of C4 plants. Photosynthesis Research, 77: 209–225.

San José, J.J. & Farinãs, M.R. (1991) Temporal changes in the structure of a Trachypogon savanna protected for 25 years. Acta Oecologica, 12: 237-247.

Sanaïotti, T.M., Martinelli, L.A., Victoria, R.L., Trumbore, S.E., Camargo, P.B. (2002) Past vegetation changes in Amazon savannas determined using carbon isotopes of soil organic matter. Biotropica, 34: 2–16.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N. (2005) Determinants of woody cover in African Savannas. Nature, 438: 846–849.

Sankaran, M., Ratnam, J., Hanan, N. (2008) Woody cover in African savannas: The role of resources, fire and herbivory. Global Ecology and Biogeography, 17: 236-245.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C., Walker, B. (2001) Catastrophic shifts in ecosystems. Nature, 413: 591-596.

Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savanna. Annual review of Ecology and Systematics, 28: 517-544.

Schultz, M.G., Heil, A., Hoelzemann, J.J., Spessa, A., Thonicke, K., Goldammer, J.G., Held, A.C., Pereira, J.M.C., van het Bolscher, M. (2008) Global wildland fire emissions from 1960 to 2000. Global Biogeochemical Cycles, 22: 1-17.

Schutz, A.E.N., Bond, W.J., Cramer, M.D. (2009) Juggling carbon: Allocation patterns of a dominant tree in a fire-prone savanna. Oecologia, 160: 235-246.

Schwartz, D., Floresta, H., Mariotti, A., Balesdent, J., Massimba, J.P., Girardin, C. (1996) Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (^{13}C and ^{14}C) study. Oecologia, 106: 516–524.

Sevenster, J.G. & van Alphen, J.J.M. (1993) A life history trade-off in *Drosophila* species and community structure in variable environments. Journal of Animal Ecology, 62: 720–736.

Sims, D.A. & Pearcy, R.W. (1989) Photosynthetic characteristics of a tropical forest understory herb, *Alocasia macrorrhiza*, and a related crop species, *Colocasia esculenta* grown in contrasting light environments. Oecologia, 79: 53-59.

Skarpe, C. (1991) Impact of Grazing in Savanna Ecosystems. Ambio, 20: 351-356.

Sokal, R.R. & Rohlf, F.J. (1995) Biometry: the principles and practice of statistics in biological sciences. New York: WH Freeman and Company.

Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J., Waldram, M. S. (2009) Browsing and fire interact to suppress tree density in an African savanna. Ecological Applications, 19: 1909-1919.

Staver, A.C., Archibald, S., Levin, S.A. (2011a) The Global Extent and Determinants of Savanna and Forest as Alternative Biome States. Science, 334: 230-232.

Staver, A. C., Archibald, S., Levin, S. (2011b). Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. Ecology, 92: 1063-1072.

Swaine, M.D., Hawthorne, W.D., Ogle, T.K. (1992) The effects of fire exclusion on savanna vegetation at Kpong, Ghana. Biotropica, 24:166–172.

Swaine, M.D., Hawthorne, W.D., Ogle, T.K. (1992) The effects of fire exclusion on savanna vegetation at Kpong, Ghana. Biotropica, 24: 166–172.

Thornley, J.H.M. (1972) A balanced quantitative model for root: shoot ratios in vegetative plants. Annals of Botany, 36: 431-441.

Tilman, D. (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton: Princeton University Press.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. Ecology, 75:2-16.

Tomlinson, K.W., Sterck, F.J., Bougers, F., da Silva, D.A., Barbosa, E.R.M., Ward, D., Bakker, F.T., van Kaauwen, M., Prins, H.T.H., de Bie, S., van Lengevelde, F. (2012) Biomass partitioning and root morphology of savanna trees across a water gradient. Journal of Ecology, 100: 1113-1121.

Trollope, W.S.W. (1984) Fire in Savanna. In: de Booyesen, P.V., Tainton, N.M. (eds) Ecological effects of fire in South African ecosystems. Berlin: Springer. pp 149-177.

Uhl, C. & Kauffman, J.B. (1990) Deforestation, fire susceptibility and potential tree responses to fire in the eastern Amazon. Ecology, 71: 437–449.

van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics, 31: 197-215.

van Langevelde, F., Tomlinson, K., Barbosa, E.R.M., de Bie, S., Prins, H.H.T., Higgins, S.I. (2011) Understanding tree-grass coexistence and impacts of disturbance and resource variability in savannas. In: Hill, M.J. & Hanan, N.P. (eds) Ecosystem Function in Savannas: Measurement and Modelling at Landscape to Global Scales. Boca Raton: CRC Press. pp 257–271.

Veenendaal, E.M., Torello-Raventos, M., Feldpausch, T.R., Domingues, T.F., Gerard, F., Schrodte, F., Saiz, G., Quesada, C.A., Djangbletey, G., Ford, A., Kemp, J., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Ratter, J.A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., Villarroel, D., Schwartz, M., Yoko Ishida, F., Gilpin, M., Nardoto, G.B., Affum-Baffoe, K., Arroyo, L., Bloomfield, K., Ceca, G., Compaoare, H., Davies, K., Diall, O.A., Fyllas, N.M., Gignoux, J., Hien, F., Johnson, M., Mougou, E., hoernaux, P., Killeen, T., Metcalfe, D., Miranda, H.S., Steininger, M., Sykora, K., Bird, M.I., Grace, J., Lewis, S., Phillips, O.L., Lloyd, J. (2014) Structural, physiognomic and aboveground biomass variation in savanna-forest transition zones on three continents. How different are co-occurring savanna and forest formations? Biogeosciences Discussions, 11: 4591–4636. ,

Vesk, P.A. (2006) Plant size and resprouting ability: trading tolerance and avoidance of damage? Journal of Ecology, 94: 1027-1034.

Wakeling, J. L., Staver, A. C., Bond, W. J. (2011) Simply the best: The transition savanna saplings to trees. *Oikos*, 120: 1448-1451.

Walter, H. (1971) Ecology of tropical and subtropical vegetation. Edinburgh: Oliver and Boyd.

Warner, R.R. & Chesson, P.L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. American Naturalist, 125: 769-787.

Werner, P.A. & Franklin, D.C. (2010) Resprouting and mortality of juvenile eucalypts in an Australian savanna: impacts of fire season and annual sorghum. Australian Journal of Botany, 58: 619–628.

Westoby, M., Leishman, M., Lord, J. (1996) Comparative ecology of seed size and dispersal. Philosophical Transactions of the Royal Society B- Biological Sciences, 351:1309–1318.

White, F. (1983) The vegetation of Africa: a descriptive memoir to accompany the NESCO/AETFAT/UNSO vegetation map of Africa by F.White. In: Natural Resources Research Report. Paris: UNESCO. pp 1-66.

Wigley, B.J., Bond, W.J., Hoffman, M.T. (2010) Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology, 16: 964-976.

Wigley, B.J., Cramer, M.D., Bond, W.J. (2009) Sapling survival in a frequently burnt savanna: mobilisation of carbon reserves in *Acacia karroo*. Plant Ecology, 2003: 1- 11.

Williams, R.J., Cook, G.D., Gill, A.M., Moore, P.H.R. (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. Australian Journal of Ecology, 24:50–59.

Willis, K. J. & McElwain, J. C. (2002) The evolution of plants. Oxford:Oxford University Press.

APPENDIX

Starch extraction

Since many seedlings were very small, their volumes proved difficult, thus seedlings material was collated into categories. Material that was from the same section of the seedlings (root, stems, leaves), the same species, the same vegetation type, and the same fire treatment (high, low) were collated together and analysed as one sample. Despite this, certain samples were still present in quantities too small to be analysed. Where enough material was available, all collated samples were analysed in triplicate.

Collated samples were ground into a powder in a kitchen spice grinder with a special attachment for grinding very small quantities of spice without waste. Root samples were specifically difficult to grind finely and so samples were passed through a 500 micron sieve to ensure no especially large pieces contaminated the powder. The grinder was cleaned and dried thoroughly between samples to avoid contamination. Samples were stored in a 40°C oven to avoid excess uptake of water vapour in the air.

Approximately 50 mg of each collated sample was placed into a 2 ml Eppendorf tubes, the exact weight of the sample was recorded (the scale used was accurate to 0.0001 g). 1 ml of water was added to each tube before vortexing on high speed for 30 s and placed in a freezer for 10 min before being vortexed again for 30 s and back in the freezer for 10 min. It was ensured that samples were not freezing during their time in the freezer, and if they seemed to be cooling to the point of solidifying

they were removed from the freezer. Samples were then centrifuged at 10 000 g in an Eppendorf Centrifuge 5415C for 10 min. The supernatant was then removed carefully with a capillary Pasteur pipette and discarded. The remaining pellets were stored in a -15 °C freezer overnight.

The next morning the frozen pellets in their tubes were put onto ice and 1 ml of ethanol was added using an automatic pipette. Samples were then vortexed on high speed for 30 s. Many pellets were not completely dissolved after 30 s and so these samples were vortexed until the pellet completely dissolved. Samples were then placed in a 70 °C oven for 10 min before being cooled down again in a freezer for 10 min and then centrifuged for 10 min at 10 000 g in the same centrifuge as before. The supernatant was then discarded in a similar as manner as before. These steps were repeated until the supernatant looked clear (i.e. not green because of chlorophyll), this was twice for root, three times for stem, and 4 – 6 times for leaf material. Washed pellets were stored overnight in a -15 °C freezer.

The next day the pellets in their tubes were put on ice and 1 ml of 6M HCl was added using an automatic pipette. The tubes were vortexed on high speed for 30 s and then an additional 0.5 ml of HCl was added to the tubes. The tubes were cooled for 1 h in a 4-5 °C fridge. The samples were then centrifuged for 20 min at 10 000 g in the same centrifuge as before. The supernatant was then transferred carefully into a 50 ml plastic centrifuge tube using Pasteur pipettes in a similar manner as before. Care was taken to clean pipettes using water carefully between samples to avoid contamination. 1 ml of 6M HCl was then added to the tubes with the pellets in them before they were vortexed on high speed for 30 s. A further 0.5 ml was then added to

the tubes before they were cooled for 1 h in a 4-5 °C fridge and centrifuged again for 20 min at 10 000 g in the same centrifuge as before. The supernatant was again recovered in a similar manner and added to the same 50 ml tube. 1 ml of 6M HCl was added to each 50 ml tube to make the total HCl volume per tube 4 ml. 16 ml of methanol was then added to each tube (giving a ratio of 1 part 6M HCl to 4 parts methanol) and all 50 ml tubes were vortexed. The 50 ml tubes were stored in a 4-5 °C fridge over the weekend.

The 50ml plastic tubes were centrifuged at 10 000 g for 10 min at 5 °C (Sorval SS-34 centrifuge) The supernatant was then removed and discarded using a Pasteur pipette as before. All of the remaining starch in the tube was transferred to a pre-weighed 2 ml Eppendorf tube using a Pasteur pipette. The 50 ml tubes were rinsed with methanol and each time this rinsing methanol containing starch was added to the same 2 ml Eppendorf as the starch, this was done until all starch was removed and the 2 ml mark was reached on the Eppendorf tube. Care was taken to not leave any starch behind. The 2 ml tubes containing methanol and starch were centrifuged at 16 000 g for 10 min in the same Eppendorf centrifuge as before. The supernatant was then carefully removed and discarded using a Pasteur pipette. The 2 ml tubes were then left open in a 50 °C oven for 60 min until the methanol had evaporated. The tubes were then closed left for 15 min and re-weighed with the dried starch inside. In this manner the starch content of each sample could be determined gravimetrically (mg starch per g plant material = ((weight of 2 ml tube with dried starch – weight of empty 2 ml tube weight) / original sample weight)*1000).

Note: 159 samples were processed in four days working very long hours. The speed of processing is almost entirely dependent on how many samples the centrifuge can spin at a time.

Appendix Table 1: Results of G-tests performed on the observed frequencies of seedling survival in burnt and unburnt plots in Table 1. Values in red indicate a significant difference between observed and expected frequencies for burnt vs unburnt in that comparison. Species names are coded as follows: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Vegetation types are coded as follows: forest=FOR, mixed-MXD and savanna=SAV. Total G is the sum of G-values for each individual comparison, indicating whether across all vegetation types and all species there was a significant difference between burnt and unburnt seedling survival frequencies. Pooled G is the sum of the G-values of the comparisons between burnt and unburnt for each vegetation type. Heterogeneity G is the G-value that tests whether or not the pooled G-value is appropriate to use, in this case it is not significant ($p>0.05$) indicating that underlying sample sizes are not different enough from one another that the pooled G-value would be inappropriate.

G test for burnt v unburnt

Species	Veg Type	G-value	df	p-value
BB	FOR	0.10	1	0.747
BB	MXD	8.39	1	0.004
BB	SAV	0.13	1	0.723
KI	FOR	16.64	1	0.000
KI	MXD	0.13	1	0.719
KI	SAV	2.39	1	0.122
ND	FOR	0.00	1	1.000
ND	MXD	0.00	1	1.000
ND	SAV	0.00	1	1.000
TS	FOR	2.77	1	0.096
TS	MXD	5.62	1	0.018
TS	SAV	0.53	1	0.465
WW	FOR	2.30	1	0.065
WW	MXD	4.33	1	0.037
WW	SAV	1.28	1	0.258
Total G		44.617	15	0.000

Pooled G test

FOR	fire/unburnt	6.511	1.000	0.005
MXD	fire/unburnt	17.863	1.000	0.000
SAV	fire/unburnt	1.612	1.000	0.204
Pooled G		25.986	3.000	0.000
Heterogeneity G		18.631	12.000	0.098

Appendix Table 2: Number of burnt seedlings that showed evidence of resprouting at the time of harvest in June 2014. Species names are coded as follows: BB=*B.buonopozense*, KI=*K.ivorensis*, ND=*N.diderrichii*, TS=*T.superba* and WW=*T.scleroxylon*. Vegetation types are coded as follows: forest=FOR, mixed-MXD and savanna=SAV.

		FOR		MXD		SAV		sum
		resprouting	no resprouting	resprouting	no resprouting	resprouting	no resprouting	
BB	Count	2	0	1	2	17	6	28
	% of total surviving	100	0	33	67	74	26	
KI	Count	0	0	0	1	1	2	4
	% of total surviving	0	0	0	100	33	67	
ND	Count	0	0	0	0	0	0	0
	% of total surviving	0	0	0	0	0	0	
TS	Count	0	0	0	3	1	1	5
	% of total surviving	0	0	0	100	50	50	
WW	Count	4	0	0	3	3	2	12
	% of total surviving	100	0	0	100	60	40	
		6	0	1	9	22	11	
		6		10		33		49

ACKNOWLEDGEMENTS

First and foremost I would like to thank my supervisors: Dr Yadvinder Malhi and Dr Imma Oliveras for their valuable input and unwavering support throughout this project. I would also like to thank Mr George K.D. Ametsitsi at the Forestry Institute of Ghana (FORIG) for his incredible support in Ghana during my fieldwork. My fieldwork was made infinitely easier with the assistance of Mr Yinye Kwaku, Mr Isaac Sarpong, and the staff of the Wildlife Division of Kogya Strict Nature Reserve. Dr Stephen Adu-Bredu and Mrs Gloria Djagbletey from FORIG and Dr Sam Moore from Oxford University were also extremely helpful in the planning, fieldwork and data acquisition stages of the project. I would like to thank Mr José Medina-Vega and Dr Elmar Veenendaal from Wageningen University for all for their input and support during the later stages of the project. Finally I would like to thank the British Ecological Society for funding the project, The Santander Travel Grant for funding my fieldwork expenses, and The Skye Foundation (South Africa) for funding my entire year at Oxford University.