Carbon Cycling, Fire and Phenology in a Tropical Savanna Woodland in Nhambita, Mozambique

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Declaration

I declare that this thesis has been composed by myself and has not been submitted for any other degree. The work described is my own, except where otherwise indicated.

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June 2009

Abstract

In the savanna woodlands of Southern Africa, locally know as miombo, carbon cycling is poorly quantified and many of the key processes remain obscure. For example, seasonal constraints on productivity and leaf display are not well understood. Also, fire is known to be a key process, with around 50% of the annual global area burned occurring in Africa, but detailed understanding of its ecological effects is lacking. Land use change and woodland degradation are changing the structure and functioning of these tropical woodlands, which cover 2.7 million km² of Southern Africa and provide ecosystem services which support the livelihoods of over 100 million people.

In this thesis I quantify the major carbon stocks of the woodlands in Nhambita Regulado, Gorongosa District in Sofala Province, Mozambique. I also examine processes that affect these stocks, including fire and clearance for agriculture. Furthermore, I quantify the seasonal cycle of leaf display, and its relationship to climate.

I conducted a series of experimental burns and found that fire intensity was strongly related to rates of top-kill and root stock mortality. Top-kill rates decreased as tree diameter increased up to 10 cm DBH. After this point increased size did not affect top-kill rates, possibly because of accumulated wounds and rottenness. I then extrapolated these results to long term predictions of tree populations and carbon stocks by modelling the interactions of fire, mortality and tree growth. The model was able to successfully predict woody vegetation structure at two sites with known fire regimes, including a 50-year fire experiment in Marondera, Zimbabwe. The results show that annual fires in miombo suppress all woody vegetation. Low intensity fires every 2.5 years are required to maintain observed stem biomass in Nhambita. High intensity fires lead to high top-kill rates (12%), even among large stems. Manipulating fire

intensity rather than frequency seems to be the most practical approach to limiting degradation by fire in these ecosystems.

Using a three year time series of hemispherical photographs of the tree canopy, combined with satellite data, I find that tree leaf phenology is not directly related to seasonal rainfall patterns, both in Nhambita and across Southern Africa. Pre-rain green-up is the dominant phenology, from the semi arid savannas of the south of the continent to the wet miombo of the Congo basin. Wet miombo woodlands have longer periods of green-up before rain onset (mean 60 days) compared with dry miombo (37 days). Green up-dates show little interannual variability but large spatial variability. The importance of pre-rain green-up in determining how these ecosystems will respond to changing rainfall patterns is unknown, but is an important area for future study.

I quantified carbon stocks in the Nhambita woodlands in the soil (69% of total carbon stocks of 111 tC ha^{-1}), tree stems (19%) and roots (8%) as well as other smaller pools. An allometric relationship between root and stem biomass and stem diameter was developed, and used to evaluate the uncertainties in stem carbon estimation at plot and landscape scale. We find that the uncertainty (95% confidence intervals) at plot scale can be quite large (60% of the mean) but this is reduced to around 25% at landscape scale. Strategies for effective inventories of miombo woodland are presented.

Using a chronosequence of abandoned farmland, we estimate that stem biomass recovers from clearance after around 30 years of abandonment. Changes in soil carbon stocks are less well understood and need further work.

This thesis concludes by outlining further work needed to model the carbon cycle of these woodlands, as well as discussing the implication of pre-rain green-up for satellite observations of land cover changes and biomass mapping.

This work is dedicated to Gary Goss. Without his hard work and company a lot of this would not have been possible, and it certainly would not have been as much fun.

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Acknowledgements

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1. Introduction to the thesis

This thesis describes work undertaken in a tropical savanna woodland in Mozambique. To set the context for this work, I first introduce the biogeography of savannas, and then describe in more detail the Southern African woodlands, their ecology and socio-economic situation. These woodlands are important for our understanding of the global carbon cycle and pyro-biogeochemistry and so I then describe these processes in an African context. This provides the background to the goals and motivations of this thesis and its part in the Nhambita Community Carbon Project. In Chapter 2, I describe the climate, soils and vegetation

10 of the study area. I then present the results of my studies on woodland response to fire (Chapter 3), the seasonal cycle of leaf display (Chapter 4), the response of carbon stocks to land clearance (Chapter 5), and techniques for estimating the stocks of woody biomass and quantifying uncertainty (Chapter 6a) as well as ways to efficiently minimise these uncertainties (Chapter 6b). In Chapter 7, I bring together all the data on ecosystem carbon stocks. Chapter 8 summarises the results and suggests avenues for further research.

Savannas

Savannas dominate the tropics. By one definition they cover 23% of the

20 global land surface and 50% of the tropics (Fig 1. Peel et al. 2007). The savanna climate is characterised by distinct wet and dry seasons, with little rain for 3-7 months (e.g. Frost 1996). There are many different definitions of a savanna, but the consistent theme is the coexistence of grass and trees (Walker 1987). The presence of these two competing life forms in savannas can be contrasted with other ecosystems where one life form normally dominates to the exclusion of the other (Scholes et al. 1997).

The main ecological feature of savannas - the tree-grass coexistence - has many explanations (Walker 1987). Such explanations vary: from the

spatially specific, e.g. seasonal flooding in the Llanos of Venezuela (Mistry 2000); to the functional, e.g. the rooting niche hypothesis (Walker et al. 1982) and the phenological niche (Seghieri et al. 1995; Archibald et al. 2007); and the global, e.g. fire (Bond et al. 2005; Bond et al. 2005) and grazing (Holdo 2007).
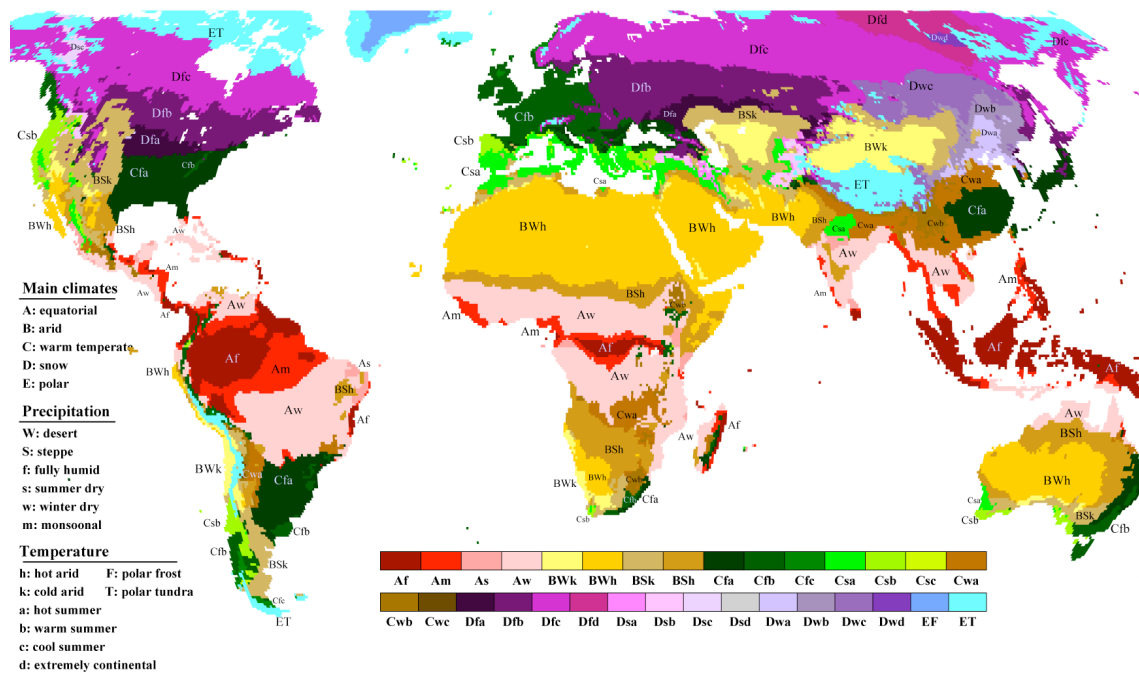
Figure 1. World Map of the Köppen-Geiger Climate classification. Savannas are found in class Aw, Cwa and BSh. Source: Kottek *et al* (2006)

Generalising on the reasons for tree-grass coexistence is almost impossible and is a fundamental stumbling block for global models of vegetation (Beerling et al. 2001). It will not detain us further, other than to state that for the purposes of this work, we use the word savanna to indicate an ecosystem that consists of both trees (not forming a closed canopy) and a continuous layer of grass. Woodland is used to describe the woody end of the spectrum, with forest being the end point. This thesis reports work from the woodlands of Mozambique, and the remainder of this introduction focuses on the savannas of Southern Africa.

The reduced tree cover of savannas allows a whole host of processes to come into play. The gaps between savanna trees, as well as possibly being

a crucible of bipedalism (Lewin et al. 1998), allow enough light down to the ground to facilitate the growth of large quantities of grass each rainy season. This grass is the fuel of the savanna's diverse mammals, and also of the widespread fires. Both of these in turn influence the woody cover and so a feedback loop is constructed (Bond et al. 1996).

Feedbacks characterise the ecology of savannas. The fuel-fire-tree cover-fuel-fire loop (Fig. 2) is explored in more detail later in this thesis (Chapter 3), but the more general idea that savannas are in dynamic equilibrium is now widespread and has replaced deterministic
10   explanations of tree-grass coexistence (Walker 1987; Scholes et al. 1997; Bond et al. 2001; Bond et al. 2005).
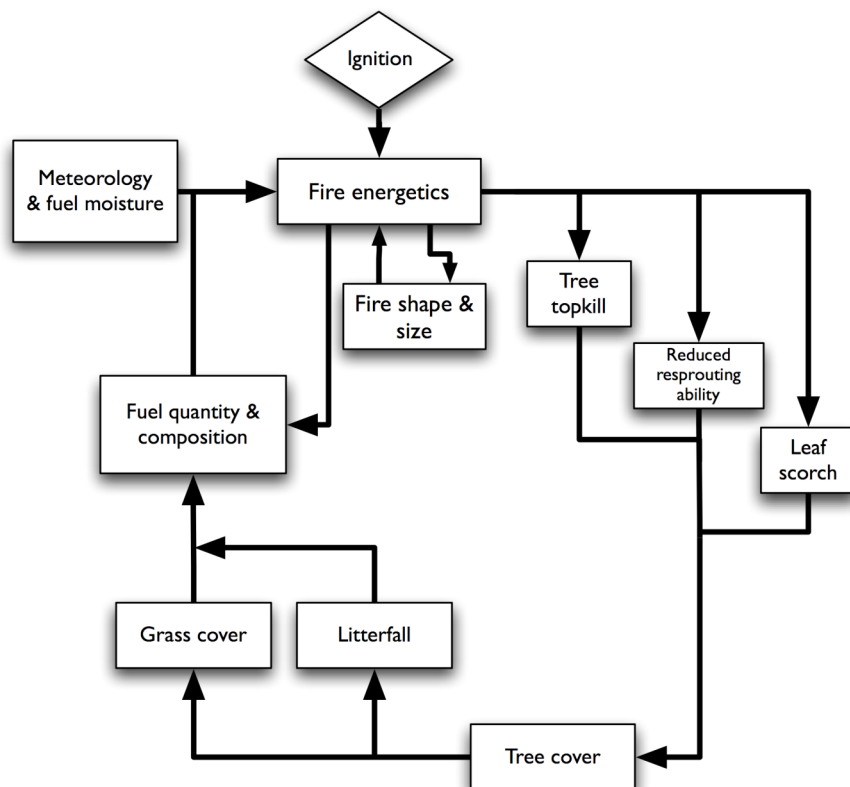
Figure 2. The fuel-fire feedback in savannas. In one variant of the feedback, tree cover is reduced by fire, allowing more grass growth and more intense fires, which further reduce tree cover. In the other variant, tree cover expands and grass growth is suppressed, leading to low intensity fires and a dominant tree layer.

Miombo woodlands
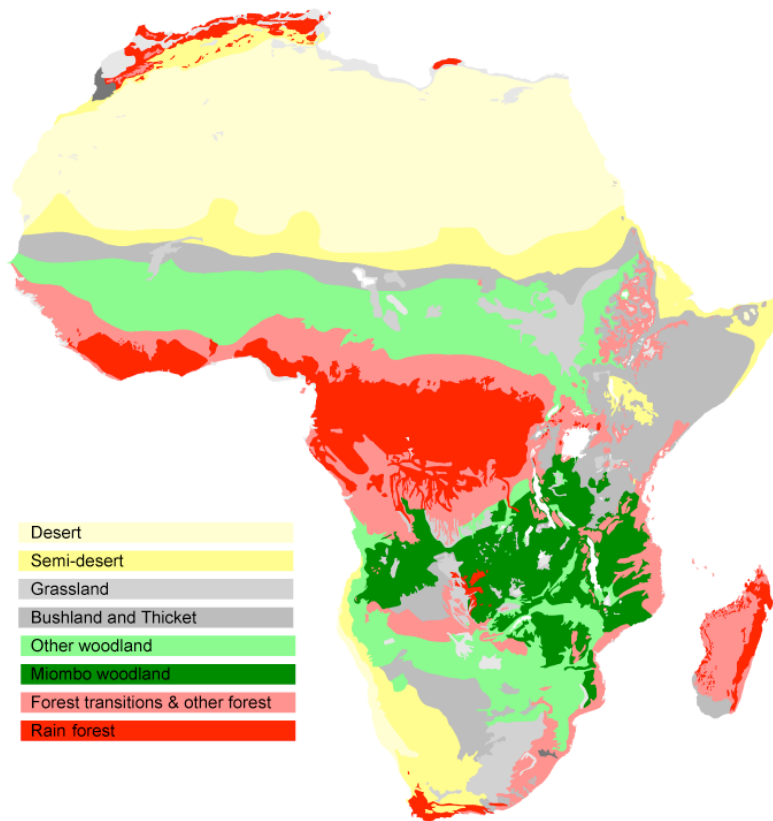
Figure 3. White's (1983) map of African vegetation. Miombo woodlands are shown in dark green.

Miombo is the vernacular (plural) name for *Brachystegia boehmii* and similar trees found across Southern Africa (Coates Palgrave *et al.* 2002). However the name miombo is widely used to describe the savanna woodlands of Southern Africa that are dominated by trees of the subfamily Caesalpinioideae of the Leguminosae, mainly of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia*. The area dominated by these trees is coincident with White's (1983) Zambezian Phytochorion, the largest of his regional centres of endemism in Africa (Chidumayo 1997). Miombo woodlands covers about 2.7 million km^2 in Southern Africa (Frost 1996).

As well as a diverse tree community, miombo is rich in other plants (Coates Palgrave et al. 2007). Common grasses include the genera *Hyparrhenia*, *Andropogon*, *Loudetia* and *Digitaria* (Frost 1996). For a

given rainfall, miombo has only around 20% of the grazer biomass expected on more fertile savanna (2.2 Mg dry matter km^{-2}) and the grazing community is dominated by elephant and buffalo, with some large antelope (including Lichtenstein's hartebeest and Sable) (Frost 1996). The nutrient-poor soils in miombo mean that the grass has very low nutrient content and this, combined with the presence of the Tstse fly in much of the region, means that miombo is not widely used for grazing cattle.

Miombo occurs on well drained soils that are derived from the African and post-African planation surfaces that form the Central African plateau (Cole 1986). They are nutrient poor and acidic (Frost 1996), with very low organic content. The dominant trees utilise ectomycorrhizae to obtain phosphorus (Hogberg 1986; Hogberg et al. 1986). Several non-dominant species have nitrogen-fixing nodules.

In the context of African savannas, miombo can be classed as a moist/distrophic savanna (van Wilgen 1997). As a moist savanna, tree cover is more limited by disturbance than by climate (Sankaran *et al.* 2005). In general, Southern African savanna structure is less determined by nutrients (Scholes 1990) than by climate and fire (Bond et al. 2003; Bond et al. 2005), and this appears true of miombo. Rooting structure of the dominant trees typically consist of a both a deep taproot and large lateral roots (Fig. 4 and (Timberlake et al. 1993), allowing deep water access and efficient nutrient uptake.
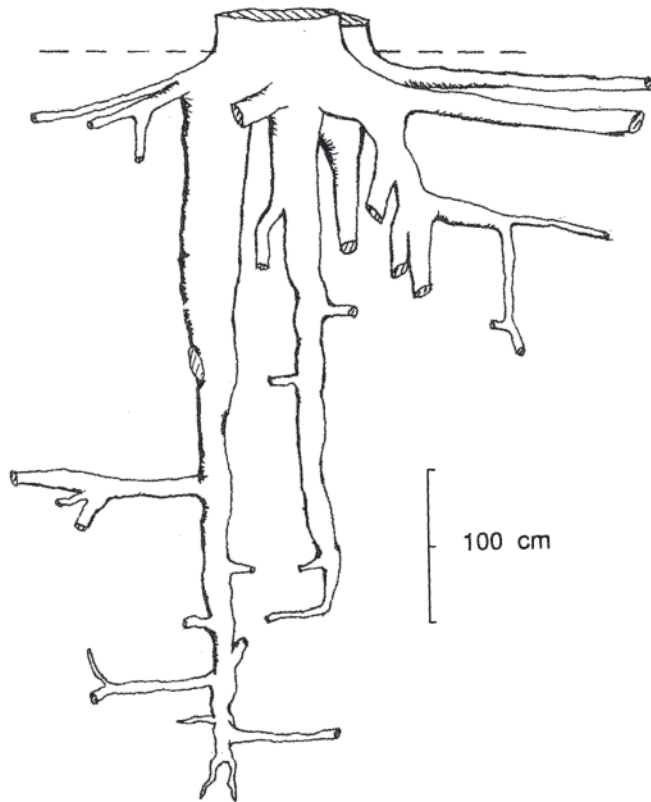
Figure 4. The root system of a typical miombo tree, *Brachystegia spiciformis* **Benth. from a site in Chati, Zimbabwe on deep sandy soils. The tree was 26 m high. Source: (Timberlake et al. 1993).**

The miombo region (along with all of Southern Africa) burns regularly, with a mean fire return interval of 2-4 years (Scholes et al. 1996; Barbosa et al. 1999; Mouillot et al. 2005). However satellite estimates of burned area are probably underestimates, as detection of small patchy burns is difficult (Laris 2005; Sa *et al.* 2007). The fires are primarily fuelled by the senesced grass layer which is flammable throughout the dry season. Nearly all fires are ignited by humans, and this has been so since at least the Iron Age (Chidumayo 1997; Eriksen 2007). Fire is used for many purposes, including hunting, clearing land, producing a new flush of grass for grazers, as well as to clear paths around houses to reduce wildlife hazards (Eriksen 2007; Stronach 2009).

The dominant trees are described as fire-tender (Trapnell 1959), although this is disputed (Chidumayo 1988). What is clear however is that fire is a

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major determinant of miombo woody biomass. Several long term fire experiments in Zimbabwe (Furley *et al.* 2008) and Zambia (Trapnell 1959) have show that fire exclusion leads to the formation of closed canopies and a succession towards forest. Annual fires have been shown to destroy all woody vegetation (Fig. 5).

Figure 5. The effect of fire in miombo at Marondera, Zimbabwe. The photo on the left shows a plot that was burned annually for 50 years. The plot on the right has been protected from fire for the same period. See Appendix 1 and Furley *et al* (2008) for further details.

Miombo trees are variously described as semi deciduous, semi evergreen, drought deciduous or simply deciduous. The seasonal cycle of leaf display is broadly in sync with the rainfall seasonality (Chidumayo 2001), but pre-rain leaf flush is often reported (Frost 1996). In many areas, the new leaves of miombo trees are coloured red, brown and yellow, due to the presence of anthocyanins (Tuohy et al. 1990; Choinski et al. 1993; Frost 1996). Evergreen trees are found in the wetter miombo areas, and along river lines (Chidumayo 1997). Other phenological strategies are also observed among co-occurring species, including the reverse phenology of *Faidherbia albida* (Barnes et al. 2003) which drops its leaves during the wet months and displays them through the dry season, making it useful in agroforestry systems.

Miombo is often divided into wet and dry miombo based on the 1000 mm isohyet. In dry miombo aboveground woody biomass averages around 55 t dry matter ha^{-1}, whilst in wet miombo 90 t dry matter ha^{-1} is typical (Frost 1996). There is a significant correlation between rainfall and

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woody biomass. These biomass values are slightly lower than dry forests under similar conditions in other continents (Frost 1996). Root biomass can comprise between 32% of total woody biomass (in Zambia, Chidumayo 1997) and 20% (in Tanzania, Malimbwi *et al*. 1994). However there are very few studies of root biomass, partly because taproots can exceed 5 m in depth (Timberlake et al. 1993). Grass biomass decreases with increasing tree biomass, but in a non-linear and complex way (Robertson 1984; Frost 1996).

A socio-ecological system

10   The savannas of Africa pre-date the evolution of *Homo sapiens* (Lewin et al. 1998; Beerling et al. 2001; Beerling et al. 2006), but have been strongly influenced by us, initially through the use of fire (Bird et al. 1998), and then through agriculture (Williams 2002).

Unlike the wetter tropical forests, miombo woodlands are heavily populated; estimates range from 50–150 million people (Campbell *et al*. 2007). Recent history has, in many ways, been cataclysmic; the Arab and European slave trades, colonialism, liberation and resource wars, economic mismanagement and misdirection, and corruption are amongst the reasons that the population of the miombo region are the poorest

20   people on the Earth (Campbell 1996; Campbell et al. 2007).

The miombo nations occupy three of the bottom five places in the global league of life expectancy with, for example, Mozambique coming fourth from last with a life expectancy of 41 years (CIA 2009). According to two studies, Mozambican average annual income in 2005 was either 280 or 150 US dollars a year (Hanlon et al. 2008): in either case, well below the poverty line. The tight link between the poor and the ecosystem they depend on has profound social, ecological and biogeochemical consequences (Steffen 2003).

In general, the rural poor of Mozambique are highly dependent on the

30   ecosystem services that the woodlands provide (Campbell 1996; Campbell

et al. 2007). The list of uses and services that subsistence farmers derive from their ecosystem is extensive. It includes building materials, fuel, food, medicine, soil fertility, fodder, and much more. But this dependence on the ecosystem has not led to its conservation; if there ever was a sustainable utilisation of the woodlands it has long gone. The pressures on the woodland ecosystem are many and various, but in Mozambique the dominant pressures are charcoal production and clearance of woodland for agriculture. These pressures are a product of poverty combined with rising population (2.0% per year in Mozambique, in 2007) and a lack of

10 rural development (World Bank 2009). These factors combine to ensure that the number of people making their livelihoods from the woodlands is rapidly increasing. Charcoal production is one symptom of this. It involves the felling of typically large, high-density woody species, and the conversion of the wood, via incomplete combustion in earth kilns, to charcoal (Falcão 2008). There is a large and growing market for this charcoal in urban centres across most of Africa (UNEP 2006), where it is a preferred cooking fuel among the affluent (Brouwer et al. 2004).

As the rural population grows and the economy fails to keep pace, the number of subsistence farmers inevitably increases, and net conversion of

20 land to agriculture takes place. In Mozambique this takes the form of what are called *machambas*, approximately 1-2 ha patches of land that are cleared of most trees and then farmed for as long as they produce good yields of crops including maize, cassava, and sorghum. They might be productive for 5-15 years, depending on soil type. In a situation of stable population this cycle of clearance and abandonment, followed by regrowth (Williams *et al.* 2008), is not a net conversion of woodland. However it is now a major driver of deforestation across the continent (Blaser et al. 2007).

Figure 6. A newly cleared machamba in Umbalaua, Nhambita.

Motivations for this work

The Nhambita Community Carbon Project

The dependence on, and destruction of, ecosystem services is the context
for the larger project of which this thesis is a part. The Nhambita
Community Carbon Project (www.miombo.org.uk) is a long-term rural
development endeavour in one of the poorest regions of Mozambique. It is
located in the Nhambita Regulado of Gorongosa district, Sofala province.
The project is run by Envirotrade, a limited company, and the local
community, and is based on monetarising the global benefit of the
region's intact carbon stocks. The project has developed a range of
agroforestry systems that are designed to intensify the local agriculture
and these, combined with other income generation activities, should
reduce the rate of woodland clearance. In addition, several woodland
management activities, including fire management and honey production,
are undertaken. More information about the project can be found in

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Appendix 2, which includes a short life history of one of the project members.

The project is one of a rapidly growing number of projects that try to finance rural development and conservation with carbon credits (De Jong *et al.* 1997; Jindal *et al.* 2008): the rationale in this case being that the project activities will reduce the emissions from woodland clearance and that polluters are willing to pay for such emissions to be avoided so as to justify emission elsewhere.

A project such as this provides a very practical and economic justification for obtaining a quantitative understanding of the carbon cycle of the surrounding ecosystem. Knowing the amount of carbon present is a prerequisite for quantifying the emissions avoided by the preservation of the woodland. Quantifying the uncertainty on carbon stock measurements is a basic need if the project activities are to have credibility. In such a poorly studied region, devising strategies for reducing such uncertainties at least cost is critical, both to the effective functioning of the carbon market, and to the quantification of the global carbon cycle.

Savanna biogeochemistry and links to Earth System Science

Our ability to quantify present stocks of carbon, although able to inform carbon management projects, needs to be supplemented by an understanding of *why* the carbon stocks are *where* they are now, to order to develop predictive ability. Such a predictive ability is needed for projections of the future of the carbon cycle and is especially important in the context of predicted changes in moisture availability (Christensen *et al.* 2007) and other global change impacts on the miombo region (Campbell et al. 2007).

This moves the theoretical questions of savanna ecology alluded to in the previous section, into a new, more applied realm, where they become part of larger issues of so called Earth system science (Walker et al. 1996;

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Desanker et al. 1997; Steffen 2003). Earth system model output is increasingly used to inform policy on many issues, including climate change (Denman *et al.* 2007), with some dramatic predictions of change in the tropics (e.g. Cox *et al.* 2000; Huntingford *et al.* 2008).

The ecological processes within such models are often constructed and parameterised with temperate process understanding and data e.g. the effects of fire (Thonicke et al. 2001; Arora et al. 2005) and ozone (Sitch *et al.* 2007). Tropical processes are typically described and validated using data from the moist tropical forests, as none of the widely used dynamic vegetation models have a savanna functional type (e.g. Woodward et al. 2004), and the data are richer in the moist tropics. Thus, there is a clear need to better understand the role of the vegetation of savanna woodlands in global biogeochemical cycles, particularly the carbon cycle. The remainder of the introduction will summarise current knowledge of two major Earth system science issues: the African carbon cycle and the role of fire.

The African carbon cycle

Africa is thought to play a major role in the global carbon cycle, particularly through fire and land use change (Fig. 7). However these fluxes are very poorly constrained (Williams *et al.* 2007).

An example of our crippling lack of knowledge is the magnitude of the decadal net carbon balance of the continent; this is estimated as being between 0.43-2.53 Pg C yr^{-1} (Bombelli *et al.* 2009), based on a variety of modeling techniques and some data. This can be contrasted with atmospheric inversions, which show no net flux when averaged over decades (Williams et al. 2007). Inversion studies do however show large inter-annual variability (from -1.8 to +1.1 PgC yr^{-1}), which is closely linked to climate.

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The African Carbon Cycle
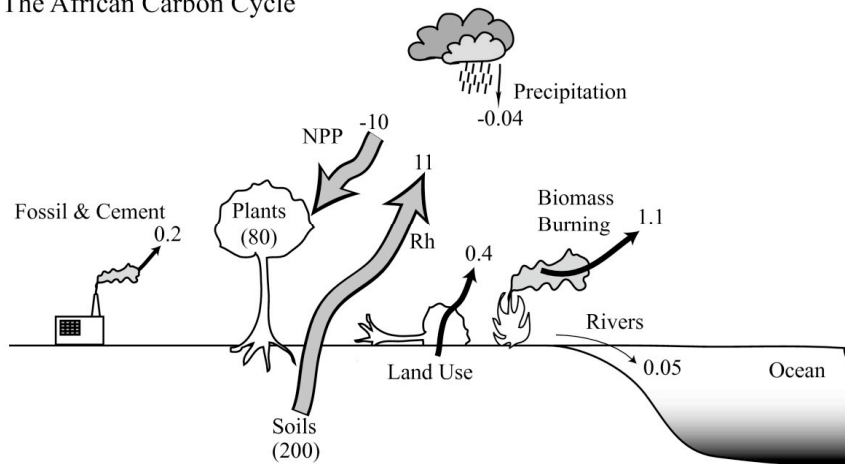
Figure 7. One estimate of the carbon cycle of Africa. Stocks are in Pg, fluxes in Pg yr^{-1}. Rh is heterotrophic respiration. Uncertainties are not shown, but are very large (see text). Source: Williams et al. (2007).

Although the atmospheric inversion studies constrain the net carbon flux over Africa to some extent, they cannot reveal the magnitude of the component fluxes, or the processes responsible. For instance a net sink in the African humid forests has been suggested at around 0.15–0.43 PgC yr^{-1} (Lewis *et al.* 2009), which must be balanced by a net source – presumably land use change – if that atmosphere is 'seeing' no net flux.

10 However estimates of land-use change (Houghton et al. 2006) do not include degradation of forest, and rely on FAO country statistics that are known to have major flaws (DeFries *et al.* 2002). Depending on assumptions made, estimates of the deforestation flux from sub-Saharan Africa range from 0.08-0.47 PgC yr^{-1} for the period 1990-99 (Houghton et al. 2006).

Thus, we cannot rule out a large vegetation sink and a large land-use source or a small sink and small source. The net balance of African woodlands and savannas has never been assessed, and systematic reinventories are very rare. Furthermore, African woodlands and

20 savannas are heavily populated and land-use has changed dramatically with conflicts and population displacements over recent history. Agricultural abandonment and subsequent reforestation is known to

influence the global carbon cycle (Vuichard *et al.* 2008) but this has not been assessed in Africa.

Quantifying the carbon balance of African vegetation is hindered by a lack of long-term carbon flux data (Friend *et al.* 2007), although some data is now becoming available as part of the CarboAfrica project (Merbold *et al.* 2008). Current estimates of net flux rely on the repeat inventory technique (Lewis et al. 2009). This approach can be subject to large uncertainties (Clark 2002; Fisher *et al.* 2008), which can only be overcome with large networks of systematic measurements (Malhi *et al.* 2002), something which is lacking in Africa.

Current best estimates of woody biomass stocks are based on a combination of satellite data and ground studies. However the problems of using optical data to infer tree biomass in mixed tree-grass ecosystems (Archibald et al. 2007) limit this approach to the closed canopy forests (Baccini *et al.* 2008; Goetz *et al.* 2009). As a result even basic stock estimates are of unknown accuracy (Roy *et al.* 2001).

Miombo in particular is very poorly studied given its size (Mistry 2000), despite a coordinated plan being produced over a decade ago (Desanker et al. 1997). A small part of SAFARI 2000 (Swap *et al.* 2003) was conducted in the miombo region (Sinha *et al.* 2004), but most of the project focused on the more arid savannas of South Africa (Swap et al. 2003). However in recent years more work has been undertaken across the miombo region, quantifying carbon stocks at various sites (Abbot et al. 1997; Luoga et al. 2002; Chidumayo et al. 2003; Chidumayo 2004; Walker et al. 2004), investigating the possibilities of using annual rings to estimate growth rates (Trouet *et al.* 2001), quantifying emissions from fires (Hoffa et al. 1999; Sinha et al. 2004), using Earth observation data to inform land cover mapping (Prins et al. 1996; Sedano et al. 2005; Ribeiro et al. 2008), and mapping vegetation complexes (Cauldwell et al. 2000; Backeus et al. 2006).

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Fire in the Earth system
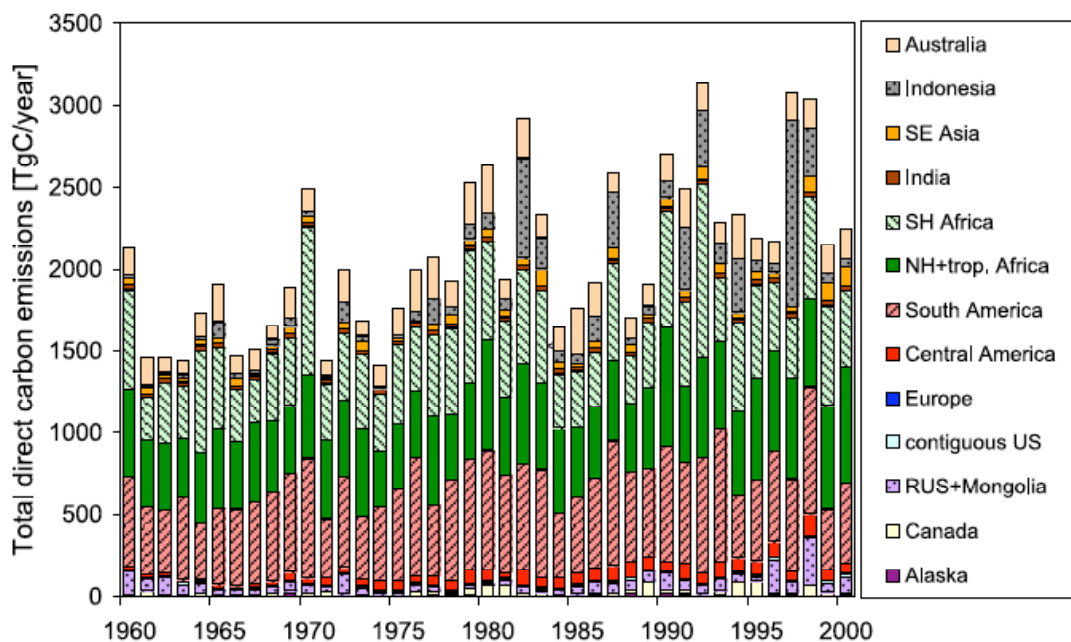
Figure 8. Modelled estimates of carbon emissions from wildfires. Note the consistency of the African emissions especially when compared with Indonesia. Source: (Schultz et al. 2008).

The role of vegetation fires in altering atmospheric composition and as a source of aerosols has received increasing attention over the last three decades (Crutzen et al. 1979). In Africa, two large field campaigns have been conducted: SAFARI 92 (van Wilgen 1997) and SAFARI 2000 (Swap et al. 2003; Shugart et al. 2004). Major findings included the quantification of pyrogenic emissions of many trace gases and estimates of the radiative forcing of fire emissions. The latter are thought to be a net negative forcing at both the top and bottom of the atmosphere, because of thick aerosol layers associated with biomass burning.

Global estimates of wildfire CO_2 emissions have converged around 1.7-2.4 Pg yr^{-1} (Schultz et al. 2008), although there is significant inter-annual variability, particularly in the El Nino-affected tropical regions (Fig. 8 and van der Werf et al. 2006). Savannas are thought to contribute around 50% of global pyrogenic CO_2 emissions (Mouillot et al. 2006; Schultz et al.

2008), and 85% of the global annually burned area (Mouillot et al. 2005), but these are mainly model results not data (Fig. 8).

Savanna fires are primarily fuelled by annual herbaceous production (Stocks *et al.* 1996; Trollope *et al.* 1996), and effectively return carbon to the atmosphere that was fixed by photosynthesis that season. As such, most savanna fires are not a net source of carbon to the atmosphere. Indeed most fires produces a small amount of charcoal or black carbon (~1% of biomass combusted, (Kuhlbusch et al. 1996), a residue of incomplete combustion of biomass. Black carbon is inert and its formation may sequester carbon on geological time scales. However little is known about its breakdown in savanna soils (Bird *et al.* 1999; Bird *et al.* 2000).

The major long-term effect of fire on the carbon cycle is to alter the structure of vegetation (Bond et al. 2005; Bond et al. 2005) and reduce standing stocks of woody vegetation. One model study suggests that global closed canopy forests would double in area in a world without fire, with most of the expansion being in African savannas (Bond *et al.* 2005). Long-term fire exclusion experiments around the world have shown that mesic savannas develop closed canopies and rapidly accrete woody biomass in the absence of fire (Furley *et al.* 2009). However representing these fire effects in global models is still in its infancy and most fire modules within global vegetation models are parameterised and tested in boreal and temperate systems (Thonicke et al. 2001; Venevsky et al. 2002; Arora et al. 2005) where fire is a stand-replacing disturbance, unlike savannas.

The scope and structure of this thesis

As a part of the Nhambita Community Carbon Project, this thesis is focused on the carbon cycle of the Nhambita area. As the preceding section makes clear, there are many uncertainties in the African carbon cycle and so I attempt to address some of these larger questions, whilst contributing to the scientific underpinning of the Project.

However, quantifying all aspects of the carbon cycle is well beyond the scope of a single thesis. Instead I have concentrated on three areas that seemed to warrant particular attention, and that I believe have the scope to inform the wider issues in tropical biogeochemistry outlined above. These areas are 1) the role of fire, particularly fire intensity in modifying vegetation structure, 2) the seasonal cycle of tree leaf display, because it is a prime constraint on productivity 3) the stocks of carbon present, and associated uncertainty in estimating them, and 4) the effects of land clearance for agriculture on soil and woody carbon stocks.

Fire

Fire is a major determinate of woody cover in African woodlands (Trapnell 1959; Trapnell et al. 1976; Yeaton 1988; Chidumayo 1989; Chidumayo 1997; Chidumayo 2004), but has been little studied in miombo (Mistry 2000). In particular, the role of fire intensity, rather than frequency, has received little attention, despite the fact that manipulation of intensity is a much more practical management objective (Parr et al. 2006) than suppression (Van Wilgen *et al.* 2004).

The fire ecology of these woodlands is addressed by two studies in this thesis. The first study is based on a set of fire experiments carried out in Nhambita in 2007. These experimental burns examined the short term effects of fire on mortality and re-sprouting rates of woody species, and the effects of fires of different intensity. These data are combined with other field surveys to parameterise a model that simulates tree populations under fire regimes of varying intensity and frequency. This study is reported in Chapter 3. The model is tested against the results of a 50-year fire experiment at Grasslands Research Station, Marondera, Zimbabwe. The data from this long term experiment have been published in Furley *et al* (2008), which I contributed to and which is presented in Appendix 1.

The seasonal cycle of tree leaf display

In deciduous ecosystems, the timing of leaf display is a major
determinant of productivity (Woodward et al. 2004; Richardson et al.
2009). However, in comparison to temperate systems, tropical phenology
is not well understood (Borchert 1994; Kikuzawa 1995; Reich 1995;
Borchert 1999; Borchert *et al.* 2002; Borchert *et al.* 2005). Many savannas
are dominated by evergreen trees (Moulin *et al.* 1997; Williams *et al.*
1997; Hoffmann *et al.* 2005), but miombo is primarily deciduous (Frost
1996; Fuller et al. 1996; Fuller 1999; Chidumayo 2001). The reasons for

10 these inter-continental differences remain unclear. In addition, many
deciduous trees in savanna ecosystems produce new leaves before the
rains, a phenomenon that has been reported globally (Myers et al. 1998;
Rivera et al. 2002; Do et al. 2005; Elliott et al. 2006; Archibald et al.
2007), but never analysed regionally in Africa. To address this, Chapter 4
reports more than 3 years of observations of leaf phenology in the
Nhambita area and uses these to inform a satellite analysis of the whole
of Southern Africa. We examine green-up dates and their relationship to
rainfall patterns for all the major vegetation types.

Carbon stocks

20 The lack of data on miombo carbon stocks is striking given the size of the
ecosystem, and this is particularly true of root and soil carbon stocks. In
the context of the increasing economic interests in biomass carbon (Gibbs
et al. 2007), and the requirements of the Nhambita project, characterising
carbon stocks is the major goal of this thesis.

Clearance for subsistence agriculture is widespread across Africa (Blaser
et al. 2007), and is the major anthropogenic influence on the African
carbon cycle (Williams 2002; Williams et al. 2007). However, the effect
that clearance has on carbon stocks is not well constrained, particularly
because the shifting pattern of cultivation creates a mosaic of secondary

30 woodland which is recovering from disturbance. We investigate this

process and look at the dynamics of stem and soil carbon recovery after clearance in Chapter 5, which has been published as Williams *et al* 2008.

Plot and landscape carbon stocks are estimated in Chapter 6 using an inventory of 12883 stems and a new allometric model of root and stem biomass. Such inventory results are frequently used for quantifying carbon stocks in the under-sampled tropics (Malhi et al. 2002; Malhi et al. 2006) and the associated errors are coming under increasing scrutiny (Condit 1998; Clark 2002; Chave *et al.* 2004). In particular, the use of allometric equations has considerable potential to introduce bias and uncertainty into such estimates (Cunia 1964; Brown *et al.* 1995; Ketterings *et al.* 2001; Chave *et al.* 2005), but this has not been examined in tropical woodlands. Thus, Chapter 6a explores the random errors and biases in carbon stock estimation and examines the implications of different allometric model forms and fitting techniques. We then go on (Chapter 6b) to examine different approaches to reducing the uncertainty of estimates of landscape mean biomass, and, based on these results, provide guidelines for efficient carbon stock estimation in miombo woodlands.

In Chapter 7 we synthesise all our data on miombo carbon stocks and fluxes, providing for the first time an overview of all the major carbon pools for one miombo site. Chapter 8 discusses the results of the thesis and suggests areas for further work.

Key findings of this thesis

The main results of this thesis in the three areas are:

Fire intensity is a crucial determinant of woody vegetation, and exceeds the influence of fire frequency. A process-based model of the short term effects of fire set against a model of photosynthesis and growth is able to predict woody vegetation structure with some skill. Annual fires in miombo remove and then suppress all woody vegetation. Low intensity

fires every 2.5 years are required to maintain observed tree biomass in the Nhambita miombo woodlands.

Tree leaf phenology is not related to seasonal rainfall patterns, both in Nhambita and across Southern Africa. Pre-rain green-up is the dominant phenological strategy, from the semi-arid savannas of the south of the continent to the wet miombo of the Congo basin. Wet miombo woodlands have longer periods of green-up before rain onset (~60 days) compared with dry miombo (37 days).

Tree carbon stocks in the Nhambita woodlands are 21.3±1.4 tC ha^{-1} aboveground and 8.6±0.46 tC ha^{-1} belowground. These woody stocks are dwarfed by the soil carbon stocks which range from 30-130 tC ha^{-1} (mean 76±10 tC ha^{-1}) and which constitute 69% of the total ecosystem carbon. Woody biomass is non-normally distributed across the landscape, with some very high aboveground woody biomass plots (>70 tC ha^{-1}) compared to the mean of 21 tC ha^{-1}. The 3% largest trees contribute 50% of the inventoried biomass. The landscape aboveground carbon stock mean (21.3 tC ha^{-1}) has a 95% confidence interval of ~30% of the mean, which could be reduced to 10% with an inventory of around 90 plots 0.25 ha in size. There is a possible bias of up to 14%, stemming from allometric model construction and fitting techniques.

Woody carbon stocks recover from clearance after 30 years of abandonment; soil carbon does not show a recovery upon abandonment, but any signal may be masked by the very high variability in soil carbon stocks across the landscape.

References

Abbot, P., J. Lowore and M. Werren (1997). "Models for the estimation of single tree volume in four Miombo woodland types." Forest Ecology and Management **97**(1): 25-37.

Archibald, S. and R. J. Scholes (2007). "Leaf green-up in a semi-arid African savanna separating tree and grass responses to environmental cues." Journal of Vegetation Science **18**: 583-594.

Arora, V. K. and G. J. Boer (2005). "Fire as an interactive component of dynamic vegetation models." Journal of Geophysical Research-Biogeosciences **110**(G2): -.

Baccini, A., N. Laporte, S. J. Goetz, M. Sun and H. Dong (2008). "A first map of tropical Africa's above-ground biomass derived from satellite imagery." Environmental Research Letters(4): 045011.

Backeus, I., B. Pettersson, L. Stromquist and C. Ruffo (2006). "Tree communities and structural dynamics in miombo (Brachystegia-Julbernardia) woodland, Tanzania." Forest Ecology and Management **230**(1-3): 171-178.

Barbosa, P. M., D. Stroppiana, J. M. Gregoire and J. M. C. Pereira (1999). "An assessment of vegetation fire in Africa (1981-1991): Burned areas, burned biomass, and atmospheric emissions." Global Biogeochemical Cycles **13**(4): 933-950.

Barnes, R. D. and C. W. Fagg (2003). Faidherbia albida : monograph and annotated bibliography. Oxford, Oxford Forestry Institute.

Beerling, D. J. and C. P. Osborne (2006). "The origin of the savanna biome." Global Change Biology **12**: 2023-2031.

Beerling, D. J. and F. I. Woodward (2001). Vegetation and the terrestrial carbon cycle : modelling the first 400 million years. Cambridge, Cambridge University Press.

Bird, M. I. and J. A. Cali (1998). "A million-year record of fire in sub-Saharan Africa." Nature **394**(6695): 767-769.

Bird, M. I., C. Moyo, E. M. Veenendaal, J. Lloyd and P. Frost (1999). "Stability of elemental carbon in a savanna soil." Global Biogeochemical Cycles **13**(4): 923-932.

Bird, M. I., E. M. Veenendaal, C. Moyo, J. Lloyd and P. Frost (2000). "Effect of fire and soil texture on soil carbon in a sub-humid savanna (Matopos, Zimbabwe)." Geoderma **94**(1): 71-90.

Blaser, J. r. and C. Robledo (2007). Initial Analysis on the Mitigation Potential in the Forestry Sector, Prepared for the UNFCCC Secretariat, available at http://unfccc.int/files/cooperation_and_support/financial_mechanism/application/pdf/blaser.pdf.

Bombelli, A., M. Henry, S. Castaldi, S. Adu-Bredu, A. Arneth, A. de Grandcourt, E. Grieco, W. L. Kutsch, V. Lehsten, A. Rasile, M. Reichstein, K. Tansey, U. Weber and R. Valentini (2009). "The Sub-Saharan Africa carbon balance, an overview." Biogeosciences Discuss. **6**(1): 2085-2123.

Bond, W. J. and J. E. Keeley (2005). "Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems " Trends in Ecology & Evolution **20**(7): 387-394.

Bond, W. J., G. F. Midgley and F. I. Woodward (2003). "What controls South African vegetation - climate or fire?" South African Journal of Botany **69**(1): 79-91.

Bond, W. J. and J. J. Midgley (2001). "Ecology of sprouting in woody plants: the persistence niche." Trends in Ecology & Evolution **16**(1): 45-51.

Bond, W. J. and B. W. van Wilgen (1996). Fire and plants. London, Chapman & Hall.

Bond, W. J., F. I. Woodward and G. F. Midgley (2005). "The global distribution of ecosystems in a world without fire." New Phytologist **165**(2): 525-537.

Borchert, R. (1994). "Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees." Ecology **75**(5): 1437-1449.

Borchert, R. (1999). "Climatic periodicity, phenology, and cambium activity in tropical dry forest trees." Iawa Journal **20**(3): 239-247.

Borchert, R., S. S. Renner, Z. Calle, D. Navarrete, A. Tye, L. Gautier, R. Spichiger and P. von Hildebrand (2005). "Photoperiodic induction of synchronous flowering near the Equator." Nature **433**(7026): 627-629.

Borchert, R., G. Rivera and W. Hagnauer (2002). "Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain." Biotropica **34**(1): 27-39.

Brouwer, R. and M. P. Falcão (2004). "Wood fuel consumption in Maputo, Mozambique." Biomass and Bioenergy **27**(3): 233-245.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira and R. A. Victoria (1995). "Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil." Forest Ecology and Management **75**(1-3): 175-189.

Campbell, B. M. (1996). The Miombo in transition : woodlands and welfare in Africa. Bogor, Indonesia, Center for International Forestry Research.

Campbell, B. M., A. Angelsen, A. Cunningham, Y. Katerere, A. Sitoe and S. Wunder (2007). Miombo woodlands – opportunities and barriers to sustainable forest management, Center for International Forestry Research.

Cauldwell, A. E. and U. Zieger (2000). "A reassessment of the fire-tolerance of some miombo woody species in the Central Province, Zambia." African Journal of Ecology **38**(2): 138-146.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera and T. Yamakura (2005). "Tree allometry and improved estimation of carbon stocks and balance in tropical forests." Oecologia **145**(1): 87-99.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao and R. Perez (2004). "Error propagation and scaling for tropical forest biomass estimates." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**(1443): 409-420.

Chidumayo, E. N. (1988). "A Re-Assessment of Effects of Fire on Miombo Regeneration in the Zambian Copperbelt." Journal of Tropical Ecology **4**(4): 361-372.

Chidumayo, E. N. (1989). "Early Post-Felling Response of Marquesia Woodland to Burning in the Zambian Copperbelt." The Journal of Ecology **77**(2): 430-438.

Chidumayo, E. N. (1997). Miombo ecology and management : an introduction. London, IT Publications in association with the Stockholm Environment Institute.

Chidumayo, E. N. (2001). "Climate and phenology of savanna vegetation in southern Africa." Journal of Vegetation Science **12**(3): 347-354.

Chidumayo, E. N. (2004). "Development of Brachystegia-Julbernardia woodland after clear-felling in central Zambia: Evidence for high resilience." Applied Vegetation Science **7**(2): 237-242.

Chidumayo, E. N. and L. Kwibisa (2003). "Effects of deforestation on grass biomass and soil nutrient status in miombo woodland, Zambia." Agriculture, Ecosystems & Environment **96**(1-3): 97-105.

Choinski, J. S. and J. M. Johnson (1993). "Changes in Photosynthesis and Water Status of Developing Leaves of Brachystegia-Spiciformis Benth." Tree Physiology **13**(1): 17-27.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. M. a. Rueda, L. Mearns, C. G. Menéndez, J. Ra isa nen, A. Rinke, A. Sarr and P. Whetton (2007). Regional Climate Projections. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manninget al. Cambridge, Cambridge University Press.

CIA. (2009). "The World Factbook." from https://www.cia.gov/library/publications/the-world-factbook/.

Clark, D. A. (2002). "Are tropical forests an important carbon sink? Reanalysis of the long-term plot data." Ecological Applications **12**(1): 3-7.

Coates Palgrave, K., R. B. Drummond, E. J. Moll and M. Coates Palgrave (2002). Trees of southern Africa. Cape Town, Struik Publishers.

Coates Palgrave, M., A. E. van Wyk, M. Jordaan, J. A. White and P. Sweet (2007). "A reconnaissance survey of the woody flora and vegetation of the Catapú logging concession, Cheringoma District, Mozambique." Bothalia **37**(1): 57-73.

Condit, R. (1998). Tropical forest census plots : methods and results from Barro Colorado Island, Panama and a comparison with other plots. Berlin ; London, Springer.

Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall and I. J. Totterdell (2000). "Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model." Nature **408**(6809): 184-187.

Crutzen, P. J., L. E. Heidt, J. P. Krasnec, W. H. Pollock and W. Seiler (1979). "Biomass burning as a source of atmospheric gases CO, H_2, N_2O, NO, CH_3Cl and COS." Nature **282**(5736): 253-256.

Cunia, T. (1964). "Weighted least squares method and construction of volume tables." Forest Science **10**(2): 180-191.

De Jong, B., R. Tipper and J. Taylor (1997). "A framework for monitoring and evaluating carbon mitigation by farm forestry projects: Example of a demonstration project in Chiapas, Mexico." Mitigation and Adaptation Strategies for Global Change **2**(2): 231-246.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole and J. Townshend (2002). "Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s." Proceedings of the National Academy of Sciences of the United States of America **99**(22): 14256-14261.

Denman, K. L., G. Brasseur, A. Chidthaisong, P. Ciais, P. Cox, R. E. Dickinson, D. Haugustaine, C. Heinze, E. Holland, D. Jacob, U. Lohmann, S. Ramachandran, P. L. d. S. Dias, S. C. Wofsy and X. Zhang (2007). Couplings Between Changes in the Climate System and Biogeochemistry. Climate Change 2007: The Physical Science Basis. S. Solomon, D. Qin, M. Manninget al. Cambridge, Cambridge University Press**:** 499-587.

Desanker, P. V., P. G. H. Frost, C. O. Frost, C. O. Justice and R. J. Scholes, Eds. (1997). The Miombo Network: Framework for a Terrestrial Transect Study of Land-Use and Land-Cover Change in the Miombo Ecosystems of Central Africa. IGBP report. Stockholm, The International Geosphere-Biosphere Programme (IGBP).

Do, F. C., V. A. Goudiaby, O. Gimenez, A. L. Diagne, M. Diouf, A. Rocheteau and L. E. Akpo (2005). "Environmental influence on canopy phenology in the dry tropics." Forest Ecology and Management **215**(1-3): 319-328.

Elliott, S., P. J. Baker and R. Borchert (2006). "Leaf flushing during the dry season: the paradox of Asian monsoon forests." Global Ecology and Biogeography **15**(3): 248-257.

Eriksen, C. (2007). "Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia." Geographical Journal **173**: 242-256.

Falcão, M. P. (2008). Charcoal production and use in Mozambique, Malawi, Tanzania, and Zambia: historical overview, present situation and outlook. The Conference on Charcoal and Communities in Africa, INBAR.

Fisher, J. I., G. C. Hurtt, R. Q. Thomas and J. Q. Chambers (2008). "Clustered disturbances lead to bias in large-scale estimates based on forest sample plots." Ecology Letters **11**(6): 554-563.

Friend, A. D., A. Arneth, N. Y. Kiang, M. L. J. Ogée, C. Rödenbeck, S. W. Running, J.-D. Santaren, S. Sitch, N. Viovy, F. I. Woodward and S. Zaehle (2007). "FLUXNET and modelling the global carbon cycle." Global Change Biology **13**(3): 610-633.

Frost, P. (1996). The ecology of Miombo woodlands. The Miombo in transition : woodlands and welfare in Africa. B. M. Campbell. Bogor, Indonesia, Center for International Forestry Research: 11-55.

Fuller, D. O. (1999). "Canopy phenology of some mopane and miombo woodlands in eastern Zambia." Global Ecology and Biogeography **8**(3-4): 199-209.

Fuller, D. O. and S. D. Prince (1996). "Rainfall and foliar dynamics in tropical southern Africa: Potential impacts of global climatic change on savanna vegetation." Climatic Change **33**(1): 69-96.

Furley, P. A., R. M. Rees, C. M. Ryan and G. Saiz (2008). "Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe." Progress in Physical Geography **32**(6): 611-634.

Furley, P. A., R. M. Rees, C. M. Ryan and G. Saiz (2009). "Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe." Progress in Physical Geography **in press**.

Gibbs, H. K., S. Brown, J. O. Niles and J. A. Foley (2007). "Monitoring and estimating tropical forest carbon stocks: making REDD a reality." Environmental Research Letters(4): 045023.

Goetz, S., A. Baccini, N. Laporte, T. Johns, W. Walker, J. Kellndorfer, R. Houghton and M. Sun (2009). "Mapping and monitoring carbon stocks with satellite observations: a comparison of methods." Carbon Balance and Management **4**(1): 2.

Hanlon, J. and T. Smart (2008). Do bicycles equal development in Mozambique?, James Curry.

Hoffa, E. A., D. E. Ward, W. M. Hao, R. A. Susott and R. H. Wakimoto (1999). "Seasonality of carbon emissions from biomass burning in a Zambian savanna." Journal of Geophysical Research-Atmospheres **104**(D11): 13841-13853.

Hoffmann, W. A., E. R. da Silva, G. C. Machado, S. J. Bucci, F. G. Scholz, G. Goldstein and F. C. Meinzer (2005). "Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna." Oecologia **145**(2): 307-316.

Hogberg, P. (1986). "Soil Nutrient Availability, Root Symbioses and Tree Species Composition in Tropical Africa: A Review." Journal of Tropical Ecology **2**(4): 359-372.

Hogberg, P. and G. D. Piearce (1986). "Mycorrhizas in Zambian Trees in Relation to Host Taxonomy, Vegetation Type and Successional Patterns." Journal of Ecology **74**(3): 775-785.

Holdo, R. M. (2007). "Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands." Ecological Applications **17**(2): 558-568.

Houghton, R. A. and J. L. Hackler (2006). "Emissions of carbon from land use change in sub-Saharan Africa." Journal of Geophysical Research - Atmospheres **111**(G02003).

Huntingford, C., R. A. Fisher, L. Mercado, B. B. B. Booth, S. Sitch, P. P. Harris, P. M. Cox, C. D. Jones, R. A. Betts, Y. Malhi, G. R. Harris, M. Collins and P. Moorcroft (2008). "Towards quantifying uncertainty in predictions of Amazon 'dieback'." Philosophical Transactions of the Royal Society B: Biological Sciences **363**(1498): 1857-1864.

Jindal, R., B. Swallow and J. Kerr (2008). "Forestry-based carbon sequestration projects in Africa: Potential benefits and challenges." Natural Resources Forum **32**: 116-130.

Ketterings, Q. M., R. Coe, M. van Noordwijk, Y. Ambagau and C. A. Palm (2001). "Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests." Forest Ecology and Management **146**(1-3): 199-209.

Kikuzawa, K. (1995). "Leaf Phenology as an Optimal Strategy for Carbon Gain in Plants." Canadian Journal of Botany-Revue Canadienne De Botanique **73**(2): 158-163.

Kottek, M., J. Grieser, rgen, C. Beck, B. Rudolf and F. Rubel (2006). "World Map of the Koppen-Geiger climate classification updated." Meteorologische Zeitschrift **15**: 259-263.

Kuhlbusch, T. A. J., M. O. Andreae, H. Cachier, J. G. Goldammer, J. P. Lacaux, R. Shea and P. J. Crutzen (1996). "Black carbon formation by savanna fires: Measurements and implications for the global carbon cycle." Journal of Geophysical Research-Atmospheres **101**(D19): 23651-23665.

Laris, P. S. (2005). "Spatiotemporal problems with detecting and mapping mosaic fire regimes with coarse-resolution satellite data in savanna environments." Remote Sensing of Environment **99**(4): 412-424.

Lewin, R. and R. H. e. Lewin (1998). Principles of human evolution : a core textbook. Malden, Mass. ; Oxford, Blackwell Science.

Lewis, S. L., G. Lopez-Gonzalez, B. Sonke, K. Affum-Baffoe, T. R. Baker, L. O. Ojo, O. L. Phillips, J. M. Reitsma, L. White, J. A. Comiskey, M.-N. D. K, C. E. N. Ewango, T. R. Feldpausch, A. C. Hamilton, M. Gloor, T. Hart, A. Hladik, J. Lloyd, J. C. Lovett, J.-R. Makana, Y. Malhi, F. M. Mbago, H. J. Ndangalasi, J. Peacock, K. S. H. Peh, D. Sheil, T. Sunderland, M. D. Swaine, J. Taplin, D. Taylor, S. C. Thomas, R. Votere and H. Woll (2009). "Increasing carbon storage in intact African tropical forests." Nature **457**(7232): 1003-1006.

Luoga, E. J., E. T. F. Witkowski and K. Balkwill (2002). "Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania." Forest Ecology and Management **164**(1-3): 15-30.

Malhi, Y., O. L. Phillips, J. Lloyd, T. Baker, J. Wright, S. Almeida, L. Arroyo, T. Frederiksen, J. Grace, N. Higuchi, T. Killeen, W. F. Laurance, C. Leaño, S. Lewis, P. Meir, A. Monteagudo, D. Neill, P. N. Vargas, S. N. Panfil, S. Patiño, N. Pitman, C. A. Quesada, A. Rudas-Ll., R. Salomão, S. Saleska, N. Silva, M. Silveira, W. G. Sombroek, R. Valencia, R. V. Martínez, I. C. G. Vieira, B. Vinceti, J. Canadell and P. S. White (2002). "An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR)." Journal of Vegetation Science **13**(3): 439-450.

Malhi, Y., D. Wood, T. R. Baker, J. Wright, O. L. Phillips, T. Cochrane, P. Meir, J. Chave, S. Almeida, L. Arroyo, N. Higuchi, T. J. Killeen, S. G. Laurance, W. F. Laurance, S. L. Lewis, A. Monteagudo, D. A. Neill, P. N. Vargas, N. C. A. Pitman, C. A. Quesada, R. Salomão, J. N. M. Silva, A. T. Lezama, J.

Terborgh, R. V. Martínez and B. Vinceti (2006). "The regional variation of aboveground live biomass in old-growth Amazonian forests." <u>Global Change Biology</u> **12**(7): 1107-1138.

Malimbwi, R. E., B. Solberg and E. Luoga (1994). "Estimation of biomass and volume in miombo woodland at Kitulangalo Forest Reserve, Tanzania." <u>Journal of Tropical Forest Science</u> **7**(2): 230-242.

Merbold, L., J. Ardö, A. Arneth, R. J. Scholes, Y. Nouvellon, A. de Grandcourt, S. Archibald, J. M. Bonnefond, N. Boulain, C. Bruemmer, N. Brueggemann, B. Cappelaere, E. Ceschia, H. A. M. El-Khidir, B. A. El-Tahir, U. Falk, J. Lloyd, L. Kergoat, V. Le Dantec, E. Mougin, M. Muchinda, M. M. Mukelabai, D. Ramier, O. Roupsard, F. Timouk, E. M. Veenendaal and W. L. Kutsch (2008). "Precipitation as driver of carbon fluxes in 11 African ecosystems." <u>Biogeosciences Discuss.</u> **5**(5): 4071-4105.

Mistry, J. (2000). <u>World savannas : ecology and human use</u>. Harlow, Prentice Hall.

Mouillot, F. and C. B. Field (2005). "Fire history and the global carbon budget: a 1° fire history reconstruction for the 20th century." <u>Global Change Biology</u> **11**(3): 398-420.

Mouillot, F., A. Narasimha, Y. Balkanski, J. F. Lamarque and C. B. Field (2006). "Global carbon emissions from biomass burning in the 20th century." <u>Geophysical Research Letters</u> **33**(1).

Moulin, S., L. Kergoat, N. Viovy and G. Dedieu (1997). "Global-Scale Assessment of Vegetation Phenology Using NOAA/AVHRR Satellite Measurements." <u>Journal of Climate</u> **10**(6): 1154-1170.

Myers, B. A., R. J. Williams, I. Fordyce, G. A. Duff and D. Eamus (1998). "Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia?" <u>Austral Ecology</u> **23**(4): 329-339.

Parr, C. L. and A. N. Andersen (2006). "Patch Mosaic Burning for Biodiversity Conservation: a Critique of the Pyrodiversity Paradigm." <u>Conservation Biology</u> **20**(6): 1610-1619.

Peel, M. C., B. L. Finlayson and T. A. McMahon (2007). "Updated world map of the Köppen-Geiger climate classification." <u>Hydrol. Earth Syst. Sci.</u> **11**(5): 1633-1644.

Prins, E. and I. S. Kikula (1996). "Deforestation and regrowth phenology in miombo woodland - Assessed by Landsat Multispectral Scanner System data." <u>Forest Ecology and Management</u> **84**(1-3): 263-266.

Reich, P. B. (1995). "Phenology of tropical forests: patterns, causes, and consequences." <u>Canadian Journal of Botany-Revue Canadienne De Botanique</u> **73**(2): 164-174.

Ribeiro, N. S., S. S. Saatchi, H. H. Shugart and R. A. Washington-Allen (2008). "Aboveground biomass and leaf area index (LAI) mapping for Niassa Reserve, northern Mozambique." <u>Journal of Geophysical Research-Biogeosciences</u> **113**.

Richardson, A. D., D. Y. Hollinger, D. B. Dail, J. T. Lee, J. W. Munger and J. O'Keefe (2009). "Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests." <u>Tree Physiol</u> **29**(3): 321-331.

Rivera, G., S. Elliott, L. S. Caldas, G. Nicolossi, V. T. R. Coradin and R. Borchert (2002). "Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain." <u>Trees-Structure and Function</u> **16**(7): 445-456.

Robertson, E. F. (1984). Regrowth of two African woodland types after shifting cultivation. Aberdeen, University of Aberdeen.

Roy, J., B. Saugier and H. A. Mooney (2001). <u>Terrestrial global productivity</u>. San Diego, Calif. ; London, Academic Press.

Sa, A. C. L., J. M. C. Pereira and R. H. Gardner (2007). "Analysis of the relationship between spatial pattern and spectral detectability of areas burned in southern Africa using satellite data." <u>International Journal of Remote Sensing</u> **29**(16): 3583-3601.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden and N. Zambatis (2005). "Determinants of woody cover in African savannas." <u>Nature</u> **438**(7069): 846-849.

Scholes, R. J. (1990). "The Influence of Soil Fertility on the Ecology of Southern African Dry Savannas." <u>Journal of Biogeography</u> **17**(4/5): 415-419.

Scholes, R. J. and S. R. Archer (1997). "Tree-grass interactions in savannas." <u>Annual Review of Ecology and Systematics</u> **28**(1): 517-544.

Scholes, R. J., J. Kendall and C. O. Justice (1996). "The quantity of biomass burned in southern Africa." <u>Journal of Geophysical Research-Atmospheres</u> **101**(D19): 23667-23676.

Schultz, M. G., A. Heil, J. J. Hoelzemann, A. Spessa, K. Thonicke, J. G. Goldammer, A. C. Held, J. M. C. Pereira and M. van het Bolscher (2008). "Global wildland fire emissions from 1960 to 2000." <u>Global Biogeochemical Cycles</u> **22**(2).

Sedano, F., P. Gong and M. Ferrao (2005). "Land cover assessment with MODIS imagery in southern African Miombo ecosystems." <u>Remote Sensing of Environment</u> **98**(4): 429-441.

Seghieri, J., C. Floret and R. Pontanier (1995). "Plant Phenology in Relation to Water Availability - Herbaceous and Woody Species in the Savannas of Northern Cameroon." <u>Journal of Tropical Ecology</u> **11**: 237-254.

Shugart, H. H., S. A. Macko, P. Lesolle, T. A. Szuba, M. M. Mukelabai, P. Dowty and R. J. Swap (2004). "The SAFARI 2000-Kalahari Transect Wet Season Campaign of year 2000." <u>Global Change Biology</u> **10**(3): 273-280.

Sinha, P., P. Hobbs, R. Yokelson, D. Blake, S. Gao and T. Kirchstetter (2004). "Emissions from miombo woodland and dambo grassland savanna fires." <u>Journal of Geophysical Research-Atmospheres</u> **109**(D11): -.

Sitch, S., P. M. Cox, W. J. Collins and C. Huntingford (2007). "Indirect radiative forcing of climate change through ozone effects on the land-carbon sink." Nature **448**(7155): 791-794.

Steffen, W. L. (2003). Global change and the earth system : a planet under pressure. Berlin ; London, Springer.

Stocks, B. J., B. W. vanWilgen, W. S. W. Trollope, D. J. McRae, J. A. Mason, F. Weirich and A. L. F. Potgieter (1996). "Fuels and fire behavior dynamics on large-scale savanna fires in Kruger National Park, South Africa." Journal of Geophysical Research-Atmospheres **101**(D19): 23541-23550.

Stronach, N. (2009). A review of the impact of fire on the carbon content, dynamics and biodiversity value of miombo woodlands A report prepared for Fauna & Flora International.

Swap, R. J., H. J. Annegarn, J. T. Suttles, M. D. King, S. Platnick, J. L. Privette and R. J. Scholes (2003). "Africa burning: A thematic analysis of the Southern African Regional Science Initiative (SAFARI 2000)." Journal Of Geophysical Research-Atmospheres **108**(D13).

Thonicke, K., S. Venevsky, S. Sitch and W. Cramer (2001). "The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model." Global Ecology and Biogeography **10**(6): 661-677.

Timberlake, J. R. and G. M. Calvert (1993). Preliminary Root Atlas for Zimbabwe and Zambia. Zimbabwe Bulletin of Forestry Research**:** 96.

Trapnell, C. G. (1959). "Ecological Results of Woodland Burning Experiments in Northern Rhodesia." Journal of Ecology **47**(1): 129.

Trapnell, C. G., M. T. Friend, G. T. Chamberlain and H. F. Birch (1976). "Effects of Fire and Termites on a Zambian Woodland Soil." Journal of Ecology **64**(2): 577-588.

Trollope, W. S. W., L. A. Trollope, A. F. L. Potgieter and N. Zambatis (1996). "SAFARI-92 characterization of biomass and fire behavior in the small experimental burns in the Kruger National Park." Journal of Geophysical Research-Atmospheres **101**(D19): 23531-23539.

Trouet, V., K. Haneca, P. Coppin and H. Beeckman (2001). "Tree ring analysis of Brachystegia spiciformis and Isoberlinia tomentosa: Evaluation of the enso-signal in the miombo woodland of eastern Africa." Iawa Journal **22**(4): 385-399.

Tuohy, J. M. and J. S. Choinski (1990). "Comparative Photosynthesis in Developing Leaves of Brachystegia-Spiciformis Benth." Journal of Experimental Botany **41**(229): 919-923.

UNEP (2006). Africa Environment Outlook 2: Our Environment, Our Wealth, Division of Early Warning and Assessment (DEWA), United Nations Environment Programme.

van der Werf, G. R., J. T. Randerson, L. Giglio, G. J. Collatz, P. S. Kasibhatla and A. F. Arellano Jr (2006). "Interannual variability in global biomass burning emissions from 1997 to 2004." Atmos. Chem. Phys. **6**(11): 3423-3441.

van Wilgen, B. W. (1997). Fire in southern African savannas : ecological and atmospheric perspectives. Johannesburg, South Africa, Witwatersrand University Press : Thorold's Africana Books [distributor].

Van Wilgen, B. W., N. Govender, H. C. Biggs, D. Ntsala and X. N. Funda (2004). "Response of Savanna Fire Regimes to Changing Fire-Management Policies in a Large African National Park." Conservation Biology **18**(6): 1533-1540.

Venevsky, S., K. Thonicke, S. Sitch and W. Cramer (2002). "Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study." Global Change Biology **8**(10): 984-998.

Vuichard, N., P. Ciais, L. Belelli, P. Smith and R. Valentini (2008). "Carbon sequestration due to the abandonment of agriculture in the former USSR since 1990." Global Biogeochem. Cycles **22**.

Walker, B. H. (1987). Determinants of tropical savannas : presentations made by savanna researchers at a workshop in Harare, Zimbabwe, 1985. Oxford, IRL Press.

Walker, B. H. and I. Noy-Meir (1982). Aspects of the stability and resilience of savanna ecosystems. Ecology of tropical savannas. B. J. Huntley and B. H. Walker. Berlin, Springer. **42:** 556-590.

Walker, B. H. and W. L. Steffen (1996). Global change and terrestrial ecosystems. Cambridge, Cambridge University Press.

Walker, S. M. and P. V. Desanker (2004). "The impact of land use on soil carbon in Miombo Woodlands of Malawi." Forest Ecology And Management **203**(1-3): 345-360.

White, F. (1983). The vegetation of Africa : a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Paris, Unesco.

Williams, C., N. Hanan, J. Neff, R. Scholes, J. Berry, A. S. Denning and D. Baker (2007). "Africa and the global carbon cycle." Carbon Balance and Management **2**(1): 3.

Williams, M., C. M. Ryan, R. M. Rees, E. Sambane, J. Fernando and J. Grace (2008). "Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique." Forest Ecology and Management **254**(2): 145-155.

Williams, M. J. (2002). Deforesting the earth : from prehistory to global crisis. Chicago, Ill. ; London, University of Chicago Press.

Williams, R. J., B. A. Myers, W. J. Muller, G. A. Duff and D. Eamus (1997). "Leaf phenology of woody species in a North Australian tropical savanna." Ecology **78**(8): 2542-2558.

Woodward, F. I. and M. R. Lomas (2004). "Simulating vegetation processes along the Kalahari transect." Global Change Biology **10**(3): 383-392.

World Bank. (2009). "Mozambique Data and Statistics." 2009, from http://go.worldbank.org/3DFXD69U00.

Yeaton, R. I. (1988). "Porcupines, Fires and the Dynamics of the Tree Layer of the Burkea Africana Savanna." The Journal of Ecology **76**(4): 1017-1029.

2. Introduction to the Nhambita area

Nearly all the fieldwork conducted for this thesis was undertaken in the Nhambita Regulado (traditional authority). The relevant site details are discussed in the introduction to each chapter, but here I set the this work in its ecological context by describing the area's geographical location, climate, soils and vegetation. Much of this Chapter is drawn from the thesis of Tinley (1977), supplemented with some of our meteorological data.

Location

The Nhambita Regulado is in the south of Gorongosa District in the Province of Sofala in central Mozambique (18.979°S, 34.176°E, Fig 1). The Regulado is partly inside the Gorongosa National Park, and occupies the western flank of the Rift Valley, the Báruè Midlands (Fig. 2). The Regulado consists of several villages, including the village of Nhambita, near which the project camp is located. The east of the Regulado is inside the Gorongosa National Park, a protected area of 40000 km^2, which, because of a unique hydrological system and extensive floodplains, is one of the most diverse areas in Mozambique (Tinley 1977). However, around 95% of the large grazer population was killed during the Independence and Civil wars (1964-75 and 1977-1992), and although the Park is now being restored, the bulk grazers that used to consume huge quantities of grass on the floodplains and supported a very large lion population, are still at very low numbers.

During the wars, the people of Nhambita moved away for several periods, and the industrial agriculture in the area (mainly cotton) was abandoned. Commercial agriculture has never been re-established and the rural population are mainly subsistence farmers, with maize as the staple crop, a pattern that was widespread across the country (Hanlon et al. 2008). A personal history of one member of the Nhambita community can be found in Appendix 2.
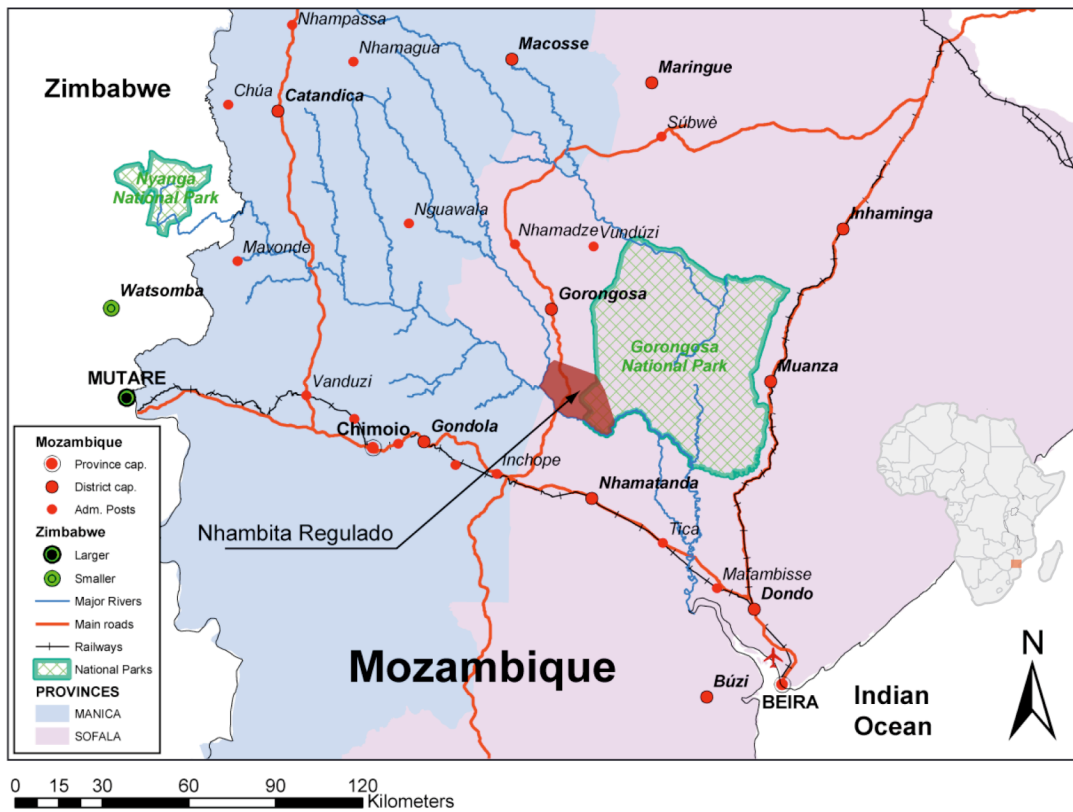
Figure 1. Location of the Nhambita Regulado in Central Mozambique. GIS data from ARA CENTRO. The red area on the insert shows the area of the larger map.
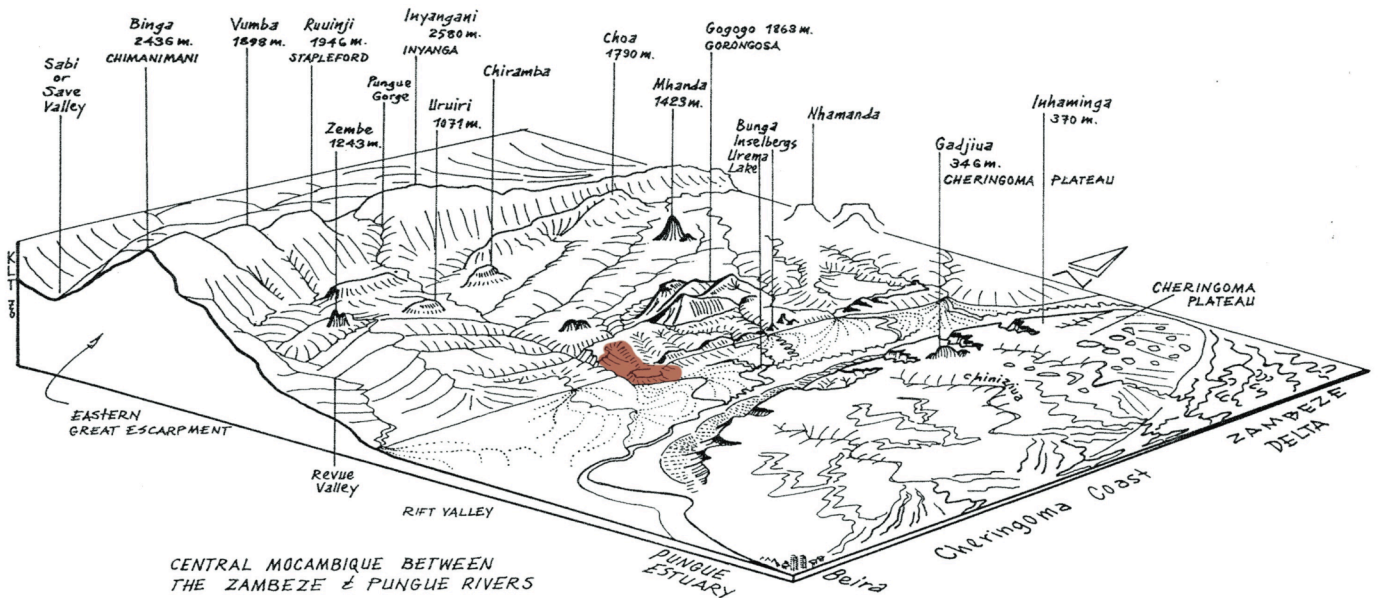

Figure 2. Salient features of the Gorongosa Ecosystem by Tinley (1977). The study area of this thesis is indicated in red.

The area is overshadowed by the Gorongosa mountain, the source of much of the area's rainfall and river flow. Rivers bound the study area – the Pungué, with its headwaters in the Eastern Highlands of Zimbabwe to the south, and the Nhandare which drains the western flank of Gorongosa mountain to the west.

Sample plot location and the scientific component of the Nhambita Community Carbon Project

In 2004 Dr Mat Williams and others established 15 permanent sample plots (PSP) in the area (Fig. 3). These supplemented a previous inventory of 30 preliminary sample plots (Mushove 2003). Data from these plots forms the basis for much of this work, along with extra plots established during the course of the PhD. The automatic weather station was installed at Chitengo in 2004 (Fig. 3). From 2004, six Masters students have conducted their dissertations in Nhambita and we use the data from two of their projects in Chapter 5. Other work has been undertaken as part of the project and is also available at www.miombo.org.uk (Table 1).

Table 1. Scientific work in Nhambita Regulado as part of The Nhambita Community Carbon Project. Source: www.miombo.org.uk.

Name	Year	Title
Alastair Herd	2007	Exploring the Socio-economic role of charcoal and the potential for sustainable charcoal production in the Chicale Regulado, Mozambique
Roberto Zolho	2005	Effect of Fire Frequency on the Regeneration of Miombo Woodland in Nhambita, Mozambique
Joao Fernando	2005	The Impact of Agriculture Activities on Soil Carbon in the Miombo Woodlands of Mozambique
Evelina Sambane	2005	Above Ground Biomass Accumulation in Fallow Fields at the Nhambita Community - Mozambique
Rohit Jindal	2004	Measuring the Socio-Economic Impact of Carbon Sequestration on Local Communities: an assessment study with specific reference to the Nhambita Pilot Project in Mozambique
Luke Spadevecchia	2004	Synthesis of Remote Sensing Products and a GIS Database to Estimate Land Usage Change an Analysis of the Nhambita Community Forest, Mozambique
Andrew Nottingham	2004	The characterisation of foliar N-concentrations and presence of N-fixers in Miombo woodland, Mozambique
Patrick Mushove	2004	Preliminary inventory of Nhambita Community Forest, Gorongosa District, Mozambique

Figure 3 (overleaf). SPOT (Satellite Pour l'Observation de la Terre) image of the Nhambita Regulado and surrounding area showing the sample plots used in this thesis and key features of the land cover. The image is from March 2007 and shows the green, red and near infra-red in the red, green and blue channels. Turquoise shows bare ground, dark red dense vegetation, pale pink and white sparse vegetation. Squares mark the 0.25 ha preliminary sample plots. Diamonds the 1 ha permanent sample plots, triangles the fire experiment plots, and circles the abandoned machambas. Stars mark other plots. An attempt to classify the landscape was not successful because of very indistinct spectral signatures of the different vegetation types, probably associated with the presence of large quantities of grass biomass.

10

EN1 to Villa Gorongosa

Fire experiment (Chapter 3)

Project camp

Fence around Park 'Sanctuary'

Urema floodplains

Machambas

Lake Urema

Tar road

Area cleared for charcoal along road

Machambas cleared along river line

Pungue village

River Pungue

Airstrip

Weather Station

Chitengo (Park camp)

EN1 to Inchope

Abandoned Machambas (Chapter 5)

Park Gate

Dirt track

Woody cover almost totally removed

Closed canopy riverine forest

Nhambita village

Kilometers

0 1.25 2.5   5   7.5   10

N

Climate

Nhambita falls into the Köppen Aw class (Tropical Savanna) with a hot wet summer and cooler dry winter. Throughout the austral summer, tropical cyclones move in from the Indian Ocean, though they are often intercepted by the island of Madagascar. In the winter, the air flow is reversed (Tinley 1977). Nhambita is on a strong orographic gradient from the floor of the Rift Valley (840 mm annual rainfall) to the slopes of the Gorongosa mountain (>2000 mm). Beira, 140 km away on the coast, receives 1430 mm (Tinley 1977)

10   The meteorological data used in this thesis comes from Chitengo, 25 km to the east of Nhambita (Fig. 3). Here, mean annual rainfall (Oct 1-Sept 30) for the years 1956-1969 and 1998-2007 was 850±269 mm (mean ±standard deviation), giving a coefficient of variation of 0.32 (Fig. 4). The rainfall is highly seasonal, with 82% falling in the 5 months between November and March (Fig. 5). May-September receive less than 20 mm month^{-1}, on average, but monthly totals vary widely between years (Fig.5).
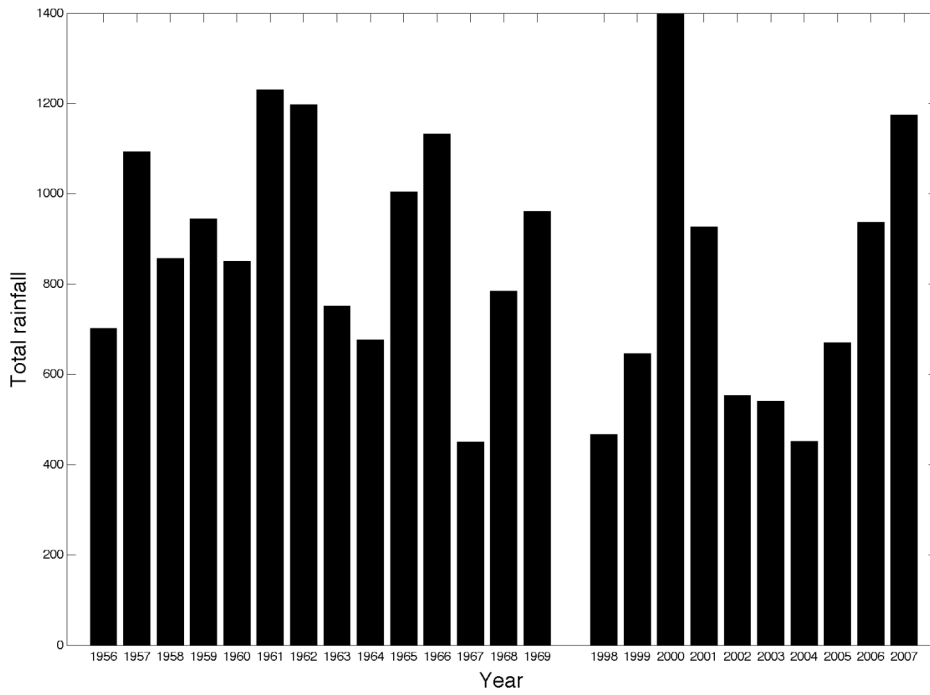
Figure 4. Annual rainfall for the period 1956-1969 and 1998-2007. Totals are for the forward year from Oct 1. Pre-2005 data from a manual rain gauge at Chitengo (kindly provided by Gorongosa National Park and ARA-Centro). Post-2005 data from the project's automated weather station, at the same location.
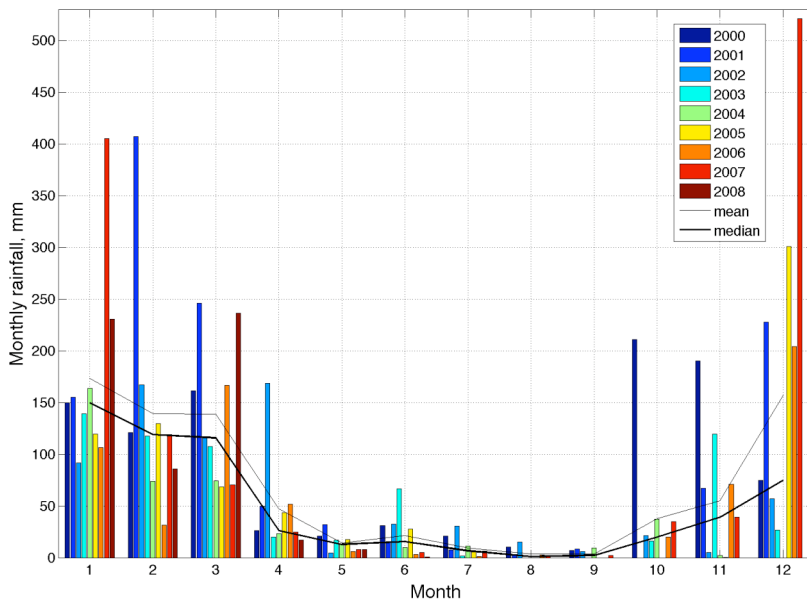

Figure 5. Monthly rainfall at Chitengo for the last 9 years. Median and mean monthly totals are also shown.

Wind speed is low (daily mean 0.5 m s^{-1}) from January-July, but rises rapidly from Aug to a peak in October (daily mean 1 m s^{-1}). The dry

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season is cooler and less humid than the wet season (Fig. 6), although very high temperatures occur year round. Frost has not been recorded.
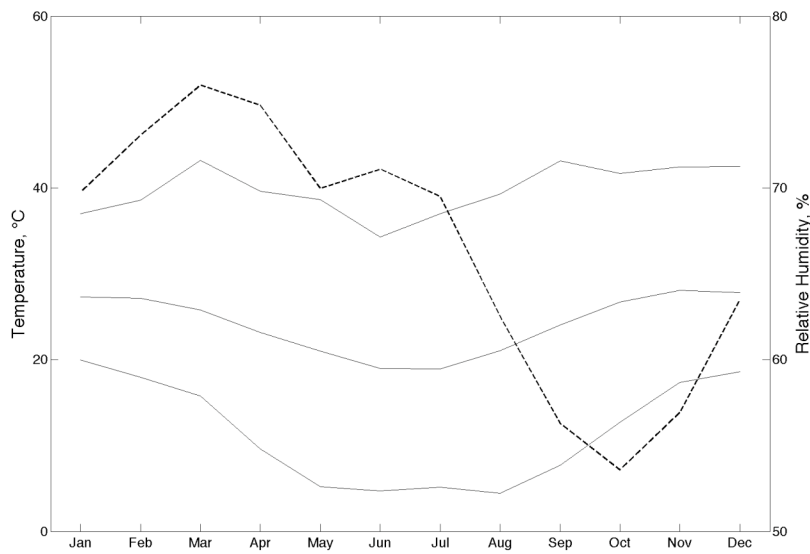
Figure 6. Seasonality of temperature and humidity at Chitengo, Gorongosa, Mozambique. Data are for the period January 2005-April 2009. Mean, maximum and minimum monthly temperatures (°C) are shown with a solid black line. Relative humidity (%) is shown with a dashed line.

Geology, Soil and Vegetation

The geology of the area is dominated by the pluton of Gorongosa Mountain and the transition from the crystalline Midlands to the depositional Rift Valley floor (Fig. 7).
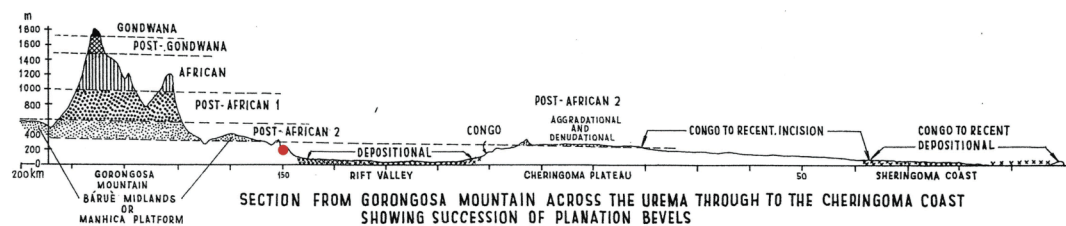
Figure 7. The surrounding geology of the Nhambita area from Tinley 1977. The Nhambita Regulado is located on the transition from the Báruè Midlands to the slopes of the Rift Valley (indicated with a red dot).

Nhambita Regulado is located on the western escarpment of the Rift Valley (Fig. 2). It ranges from uplands with well-drained soils to the bottomlands of the Valley with clay-rich, regularly flooded soils. The

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vegetation changes from miombo woodlands on the higher ground to various *Acacia* and *Combretum* savanna on the low ground, with palm woodland in the wettest areas. On more nutrient rich areas of the uplands underlain by dykes, the vegetation include thickets and other woodlands. There are also some areas of closed canopy forest, locally called *guasha* mostly associated with river lines (See map).

Most of the Nhambita Regulado is on free-draining sandy fersiallitic soils derived from metamorphic migmatitic gneiss and granite (Tinley 1977). The soils in the south and east of the Regulado are more hydromorphic in nature (Table 2). On the sandy soils, termite (*Macrotermes*) mounds provide 'islands' of loamy fertile soils and occur at a density of around 1 per hectare (Tinley 1977).

Table 2. Soils found in the Nhambita Regulado, from the soil map of (Tinley 1977). Moving from the northeast of the area to the southwest, the soils are encountered in the order listed. Most of our plots are on the first two soil types.

Geology	Soil	Vegetation types
Acid Rocks	brown granite gneiss	*Brachystegia* savanna (miombo)
Basic Rocks	red basaltic	Forest, thicket, savanna, grassland
Calcareous	grey hydromorphic	*Acacia*, Mopane, *Dalbergia*, Baobab
Detrital fan material	grey soils	*Pilostigma*, *Acacia*, *Combretum* savanna
Alluvium	Non-hydromophic alluvia	*Acacia*, *Lonchocarpus* and *Piliostigma* savanna

References

Hanlon, J. and T. Smart (2008). Do bicycles equal development in Mozambique?, James Curry.

Mushove, P. (2003). Preliminary Inventory Of Nhambita Community Forest, Gorongosa District, Mozambique ERMAL Natural Resources Consultancy, available at www.miombo.org.uk.

Tinley, K. L. (1977). Framework of the Gorongosa Ecosystem. Faculty of Science. Pretoria, University of Pretoria: 184.

3. How does fire intensity and frequency affect miombo woodland tree populations and biomass?

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10   Supplementary methods and results accompany this Chapter

Abstract

Miombo woodlands are the largest savanna in the world and dominate southern Africa. They are strongly influenced by anthropogenic fires and support the livelihoods of around 100 million people.

Managing the fire regime of such a flammable system is difficult, but crucial for sustaining biodiversity, ecosystem services and carbon stocks. Fire intensity is more easily manipulated than fire frequency as suppression is expensive and ineffective. However, there are important issues relating fire intensity to impacts on woody vegetation that need to be understood to inform management approaches. Such impacts include the links between fire intesity, top-kill, resprouting and regrowth rates.

Here we present results from a fire experiment in Mozambican miombo; the results of a 50-year fire experiment in Zimbabwean miombo; and observations of forest structure at a dry forest site in Mozambique. We synthesise these data with a process-based gap model of stem growth, regeneration and mortality, which explicitly considers the effect of different frequencies and intensities of fire. We use the model, tested against the field data, to explore the sensitivity of woodland tree population and biomass to fire intensity and frequency.

Our results show that large (>5 cm DBH) stems are vulnerable to fire with top-kill rates of up to 12% in intense fires. In contrast to idealised physical representations of tree mortality, stems > 10 cm DBH did not gain further protection from fire with increasing DBH. Resprouting was very common and not obviously linked to fire intensity.

Overall, miombo tree population and biomass are shown to be very sensitive to fire intensity, offering opportunities for effective management. At any achievable fire return interval (<5 years), low intensity fires are required to maintain observed biomass. Model

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predictions and field experiments show that no tree biomass can be sustained under annual fires.

Introduction

Fire is a global influence on vegetation structure (Bond et al. 2005; Bond et al. 2005) and carbon cycling (van Wilgen 1997). African savannas account for more than half the annual global burned area (Mouillot et al. 2005), and south of the equator miombo woodlands are the dominant vegetation cover (Frost 1996). In miombo, a deciduous savanna woodland, fire has been shown to be of critical importance in determining woody cover by several long-term fire experiments (Furley et al. 2009). These long-term plot-scale experiments have shown that under annual burning miombo woodland is converted to grassland (Furley et al. 2009), and that in the absence of fire, miombo starts to form closed canopy forest (Trapnell 1959).

However, the fixed fire return intervals used in the long-term experiments are not practical to apply as a large-scale management regime. Fire exclusion is very difficult and costly in such a flammable, populated ecosystem (Van Wilgen et al. 2004). Traditional fire management has instead focused on manipulating fire intensity, rather than frequency (Laris 2002; Laris et al. 2006). By setting fires early in the season, small, patchy burned areas are created, which act as an effective fire break later in the dry season when large destructive fires occur (Eriksen 2007). (Re)creating a fire regime of low intensity burns is now the management goal in many savanna protected areas (Van Wilgen et al. 2004; Parr et al. 2006). Implementing such a regime is not straightforward, however, and detail is needed regarding what constitutes a 'low' intensity burn and what area should be burned each year (over a large area fraction of area burned = 1/fire return interval).

Such data on fire-intensity dependent effects (Bond et al. 1996) are available in the semi-arid savannas of South Africa (Higgins et al. 2000;

Kennedy et al. 2003; Govender et al. 2006; Higgins et al. 2007), where they have informed management objectives (Van Wilgen et al. 2004). However data are lacking in the less studied miombo ecosystem (Mistry 2000), despite its large area (2.7 M km2 Frost 1996) and the importance of these woodlands and their ecosystem services to around 100 million people (Campbell et al. 2007). There is evidence that moist (>650 mm annual rainfall) "disturbance-driven savannas", which include miombo, may respond to fire disturbance very differently from arid or semi arid "climatically determined savannas" (Sankaran et al. 2005), and more

10   information is required on fire effects in moist African savanna woodlands.

The lack of information quantifying the fire-intensity dependent effects on miombo population motivates this study. Here we attempt to answer the question: *how do tree populations and biomass respond to different fire intensities and frequencies in miombo woodlands?*

Our experimental approach provides insight into the component processes that determine tree population dynamics. We use the resulting mechanistic understanding to increase our predictive skill under changed conditions and at different sites. We do this with a modelling approach,

20   explicitly representing the key process by which fire influences tree population.

There are two main ways that fire is thought to influence tree populations: by top-killing the tree, forcing it to resprout to survive; and by killing belowground organs, exterminating the organism (Bond et al. 2003; Hoffmann et al. 2003; Michaletz et al. 2007). These effects are known to vary between diameter classes and species, because, as diameter increases, the thickness of protective bark increases proportionally (Jackson et al. 1999; Sutherland et al. 2000; Johnson et al. 2001). Differing species responses occur because of different species

30   allometry and defence mechanisms (Uhl and Kauffman 1990; Gignoux et

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al. 1997; Jackson et al. 1999; Cauldwell and Zieger 2000; Sutherland and Smith 2000). Likewise the impacts on resprouting and subsequent regrowth are highly size and species dependent (Gignoux et al. 1997; Hoffmann 1999; Bond and Midgley 2001, 2003; Hoffmann and Solbrig 2003). In particular, in drier miombo woodlands, the understory dominant (*Diplorhynchus condylocarpon*) appears to be fire-resistant with thick, fissured bark and high moisture content. In contrast, the canopy dominant Caesalpinioideae species have thinner, smooth bark and lower moisture content (Chidumayo 1997). Based on these differences, species composition changes might be hypothesised under different fire regimes.

This study presents data on size- and species-specific top-kill, mortality and resprouting rates at various fire intensities in miombo woodlands. We extrapolate these rates to long-term predictions of tree population and carbon stocks, using a new model of individual stems and rootstocks. This gap phase dynamics model simulates growth based on representations of photosynthesis and carbon allocation. We test the model against data from two other sites in the miombo region with known fire regimes.

The results of this study provide a first order estimate of the woody population and carbon stock that can be expected under different fire intensity and frequency combinations. Such information is required by managers attempting to manage woody carbon stocks and biodiversity.

Key questions

1. *What are top-kill rates for stems of different diameter in different intensity fires?*

2. *How common is resprouting after top-kill and what factors affect rootstock survival and the number of resprouts?*

3. *Are some miombo species fire tender and others better protected against fire?*

4. *What is the sensitivity of tree populations to fire impacts and under what frequency and intensity of fires can miombo woodland be sustained?*

Methods

Our methods consist of data collection at three sites and the construction of a model. Questions 1-3 are addressed with data from a study of experimental burns in an area of miombo woodlands in Mozambique. Question 4 is answered with a new model of this ecosystem, parameterised using the results of the Mozambican experiment and tested against data from a 50 year fire frequency experiment in Marondera, Zimbabwe, and a dry forest in Mozambique.

Site 1. Miombo fire intensity experiment

Set up and location

The experimental burns were conducted in the dry miombo woodland (sensu, Frost 1996) of Mozambique, in the Nhambita community in the buffer zone of the Gorongosa National Park, Sofala Province (18.979°S, 34.176°E) (Williams *et al.* 2008). The climate is characterised by a six month dry period and mean annual precipitation of 850 mm (based on data from 1959-67 and 1999-2007 at Chitengo, 25 km distant). May to October has mean monthly rainfall below 30 mm and constitutes the fire season. The continuous grass layer senesces and dries out over this period and the trees shed their leaves. The soil is sandy and sandy loam. The ecology and geology of the area is described in detail in Tinley (1977; 1982).

In June 2007 we laid out eight adjacent 1.4 ha plots in a 4x2 grid in an area of woodland 6 km away from the local community. The area was selected for ease of access from the road and for its homogeneity of vegetation, as judged from the variation in NDVI (normalised difference vegetation index) from a SPOT image from April 2007. Seven of the plots were randomly assigned for burning and one was left unburned.

A 50 m fire-break was cut around the entire site and smaller traces were cleared to divide the area into the approximately 120 m square plots. We

laid out a nested (Fernandes *et al.* 2000) triangular measurement scheme designed to utilise within-plot variability in fire intensity: on each plot an 80 m equilateral triangle measurement area was set out; in each corner a 10 m triangle was marked and at each corner of these, 2 m triangles were established. Additionally, the centre of the 80 m triangle and two equidistant points along its edges were marked (see Fig. 1). Plot 5 was constrained by proximity to a fire break and had to be reduced to a 70 m equilateral triangle, but was otherwise identical to the other plots.
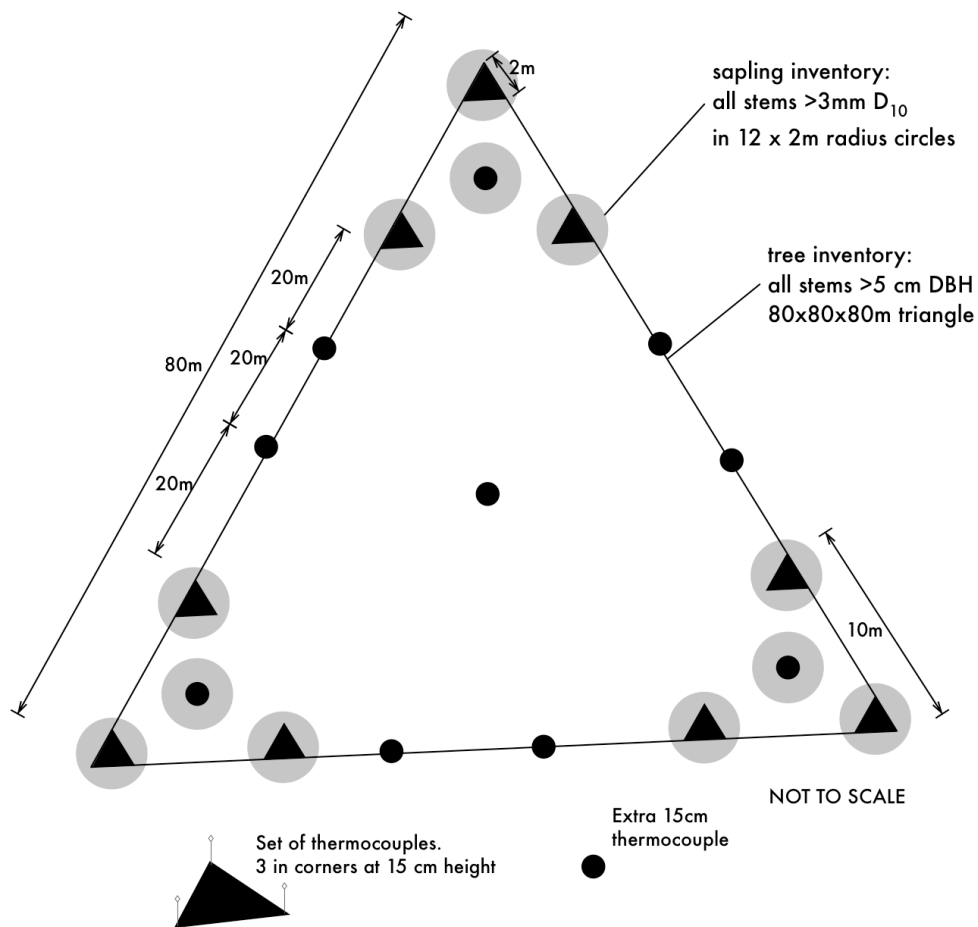
Figure 1. Thermocouple positions and sampling scheme.

10 *Pre-fire vegetation surveys*

We conducted two pre-fire surveys. The first was of trees, defined as woody species > 5 cm DBH (diameter at breast height, 1.3 m). The second

was of saplings, defined as woody species <5 cm DBH and > 0.3 cm D_{10} (diameter at 10 cm above the mineral soil), and their rootstocks.

Trees were surveyed in each 80 m triangle (area 2771 m^2) and were tagged. We recorded DBH, species and whether stems were live/dead and standing/fallen. Species identification was undertaken by local experts and follows Coates Palgrave *et al* (2002). Aboveground carbon stock was calculated as a function of DBH using our site-specific allometric, based on a destructive sample of 29 trees (Appendix Table A1).

10   At each corner and the centre of the three 10 m triangles, saplings were surveyed within a 2 m radius circle (*n*=12, total area=151 m^2 per plot). Saplings were tagged, identified by species and measured for D_{10} and height. Stems which originated from the same rootstock were recorded. Only live stems of species that become trees were included in the survey. On the single unburned plot, a larger sapling inventory was undertaken using a 10 m radius circle around the centre of the three 10 m triangles (total area 943 m^2).

Fire ignition and meteorological measurements

The seven burn plots were ignited at different times of day (08:09 - 15:34 local time) over the period 6-19 September 2007. The aim was to induce a

20   range of fire intensities, so the burns were timed to capture a wide range of meteorological conditions e.g. relative humidity 14-65%, wind speed 0.5–2 ms^{-1}, air temp 21-34 °C (all averages for the period of the burn recorded by an on-site weather station (Instromet Ltd, UK)). The nested sampling allowed us to further capture short term variations in wind speed and spatial variability in fuel loads, further expanding the range of intensities observed. Fires were ignited at 10 points along a line on the upwind edge of the square plots which encompassed the 80 m study triangles. Further ignitions were made along the flanks at the same rate of spread as the fire to prevent a 'tongue' of fire speeding through the

30   centre of the plot and the remainder being burnt in flank fires.

Fire intensity measurements

The temperature of K-type thermocouples (TC) in a 3 mm diameter mineral insulated Inconel sheath was recorded at 0.15 m above the ground as a proxy for flame temperature (Stronach et al. 1989; Smith et al. 2005). Each TC was logged at 1 second intervals by Hobo data loggers (H12 and U12, Onset Computer Corporation, MA, USA). The loggers were buried in the mineral soil and covered with a heatproof mat, through which the TC protruded vertically. TCs were placed at 0.15 m height because a preliminary experiment found that this was the height at which maximum temperature was obtained, and at which artefacts caused by the installation of the TC and mat were minimal (Fig. S6). After installation, the soil, litter and other fuel were carefully replaced. 38 loggers were deployed in each fire (Fig. 1). With the exception of one failure, all 38 temperature-time profiles from each of the seven fires were retrieved. TC data were processed using Matlab (Mathworks Inc, MA, USA) to determine a thermal anomaly (TA), °C s, which we define as the area between the temperature-time curve and the background air temperature.

The thermal anomaly data were averaged at two spatial scales. For comparison to the large tree data, (hereafter, 'plot scale') we took the plot mean of the 38 TCs, thus at plot scale $n = 7$. For comparison to the sapling and rootstock data (hereafter, 'fine scale'), we used each 2 m radius circle inventory as the unit of measurement, and compare top-kill and root stock mortality to data from the TCs within the 2 m circle. Thus all tagged saplings and rootstocks were <2 m from at least 1 TC and $n = 84$. This method allowed us to exploit the within-fire variability (Fernandes et al. 2000).

For modelling purposes, three fire intensity classes were defined (high, medium and low) based on the terciles of the observed fine-scale thermal anomalies.

Post-fire vegetation and mortality analysis

In December 2007, three months after the fires, >20 mm of rain had fallen and the surviving vegetation produced shoots and leaves which allowed top-kill to be assessed. Stems without sprouts or green leaves or buds were classed as dead. Each tagged tree was remeasured; DBH and species were recorded to check for errors in reading the tags and the stem status was recorded – alive, dead or tag lost. Rootstocks with no resprouts were recorded as dead. In addition, the number of resprouts from surviving rootstocks was recorded.

Top-kill rates are presented as the log odds of top-kill (Hoffmann 1998; Dickinson et al. 2001), defined as $Ln(p/1-p)$, where p is the top-kill rate. A variance estimate was obtained for each log odds value by bootstrapping (randomly resampling the measured sample, with replacement) n times, and recalculating p and the log odds. n is the total number of individuals sampled. The mean and ± one standard deviation of the n samples are reported.

Site 2: Dry forest site, Marrameu, Mozambique

We collected data on forest structure from a dry, closed-canopy sand forest in Marrameu district, Mozambique (18.23897 °S, 35.18608 °E). The Marrameu site is 200 km from site 1, on the Cheringoma Plateau, and has similar rainfall of ~800 mm year^{-1}, and sandy soil to >2 m depth (Tinley 1977; Tinley 1982). The area supports a mosaic of *Pterocarpus angolensis* woodland and closed-canopy sand forest and is relatively remote, being managed for hunting and timber concessions. We observed that canopy closure in the sand forest prevented grass growth, so any fires that do occur are very low intensity litter fires. In May 2008 we inventoried a circular 0.5 ha plot and recorded DBH, height and species for all stems > 10 cm DBH. In addition, we inventoried four belt transects of 1.8 m x 40 m for stems with a DBH from 5-10 cm. To estimate LAI, we took 18 photos at different locations on the 0.5 ha plot and analysed them

as described in the supplementary methods, except that LAI was assumed to equal PAI.

Site 3: Fifty-year fire frequency experiment, Marondera, Zimbabwe

We inventoried the trees on a now abandoned, 50 year fire frequency experiment at Grasslands Research Station, Marondera, Zimbabwe. Marondera receives ~880 mm rain per annum and has deep sandy soils. It supports a miombo woodland consisting almost exclusively of *Brachystegia spiciformis* and *Julbernardia globiflora*. In 1955, 22 plots were allocated a treatment of one of four fire return intervals (1, 2, 3, 4 years, and no burn) and the burns were continued until 1997 (Tsvuura 1998). Burns were all conducted at the end of the dry season. We recorded all live trees > 20 cm DBH in Oct 2007. Plot size was 0.09 ha. More details of the experiment can be found in (Furley et al. 2009).

Population modelling

To explore the long-term significance of fire-induced mortality, we constructed a gap phase dynamics model of the stems, their light environment, phenology and resultant growth, and mortality (see supplementary methods). The model is similar in conception to many other gap models (Shugart et al. 1996; Williams 1996), which have previously been used in miombo (Desanker et al. 1994; Desanker 1996) and also to simulate the effects of fire (Miller et al. 2000). Our model incorporates the observed leaf phenology and thus restricts growth to the wet season when soil moisture is plentiful. We used a gap modelling approach because of its explicit representation of population structure and variability, its ability to explore the stochastic nature of disturbance events through large modelling ensembles, and because it allowed density dependent feedbacks on growth through light competition. A full description of the model, its parameters and a sensitivity analysis is to be found in the supplementary methods. We summarise it briefly here.

The model simulates a patch with an area equivalent to the canopy of a large tree (8 m radius). The starting point is the interception of light by the leaf area of each stem at hourly time steps. Leaf area (which is a function of stem diameter) varies through the year in accordance with the observed phenology. Intercepted light is converted to carbon using a miombo-specific light response curve. The assimilated carbon is allocated to respiration, leaf and fine root construction and any remaining is used to grow the woody root and stem biomass. As trees increase in biomass their DBH, height, leaf area and canopy height increase according to site specific allometrics. After annual growth has been completed, stems are exposed to a chance of mortality which is either an intrinsic mortality or, if there is a fire that year, a fire-induced mortality that is DBH and fire intensity class specific. Mortality for the stem (top-kill) is assessed separately from root stock mortality. These fire–induced mortality rates are based on the experiment reported from Site 1, grouped into terciles of intensity (high, medium and low). Trees that are top-killed have a probability of resprouting, and resprouts have enhanced growth in their first year. Patch properties are output each model year.

Model experiment 1: comparison to dry forest site

The first model experiment evaluated model skill in predicting forest structure with little influence of fire. We parameterised the model with data from Site 1 and ran an ensemble of 50 patches all starting from bare ground, with a fire regime of Fire Return Interval (FRI) = 100 years and low intensity, and simulated 1000 years. We used the mean of the last 500 years of each simulation and compared it to observations at the dry forest site (Site 2) of basal area, leaf area index and stocking density in 11 DBH classes.

Model experiment 2: Sensitivity of woodland structure to fire regime and comparison to 50-year fire trial

The second model experiment explored the sensitivity of woodland and forest structure to fire return intervals and intensity. The model was run with FRIs varying from 1-100 years and low, medium and high fire intensities. Again, 50 patches were used and run from bare ground for 1000 years. The mean of the last 500 years is reported. As a test of the model, we compared modelled basal area to the woodland structure at the long-term fire experiment in Zimbabwe (Site 3). Using the Nhambita allometric, we also report modelled aboveground carbon stocks.

Results

Miombo fire intensity experiment

Plot-level fire, tree and sapling characteristics

The eight experimental burn plots had tree basal area of 7.4–11.3 m^2 ha^{-1}, with a mean of 8.7 m^2 ha^{-1}. Stocking density was similarly variable (303–469 stems >5 cm DBH ha^{-1}) as was tree aboveground carbon stock (16.9–30.7 tC ha^{-1}, Table 1). Floristic composition was similar on all plots, each being dominated by either *Brachystegia boehmii* or *Julbernardia globiflora*. All plots had an understory of *Diplorhynchus condylocarpon*. Other common tree species included *Erythrophleum africanum, B. spiciformis, Sclerocarya birrea, Pterocarpus rotundfolius, P. angolensis, Burkea africana* and *Xeroderris stuhlmannii*. The top five species accounted for between 76 and 92% of the basal area of each plot. The sapling layer was floristically similar, although more heavily dominated by *D. condylocarpon* and with several other species which were rare as large trees (*Combretum adenogonium, Lannea discolor, Dalbergia boehmii, Crossopteryx febrifuga, Millettia stuhlmannii*). Sapling stocking densities ranged from 6000 – 24000 stems ha^{-1}, with large variations within and between each plot. Sapling basal area ranged from 0.4–2.1 m^2 ha^{-1}.

The plots burned with a wide range of fire intensity (Table 1). Observed plot scale mean thermal anomalies ranged from 20.3 to 32.2×10^3 °C s and at the fine scale varied from 0 to 69×10^3 °C s. Plot five, ignited early in the morning, had the lowest mean TA. Plot 6, ignited on a hot windy afternoon, had the highest TA (Table 1).

Table 1. Plot level tree, sapling and fire characteristics. Data for live standing trees at the start of the experiment. Full species names are given in the text. Trees are defined as live standing woody species > 5 cm DBH. Saplings are defined as woody species <5 cm DBH and > 0.3 cm D_{10}.

Plot ID	1	2	3	4	5	6	7	8
area, ha	0.277	0.277	0.277	0.277	0.212	0.277	0.277	0.277

Large tree data

	1	2	3	4	5	6	7	8
basal area, m^2 ha^{-1}	8.5	11.3	7.7	9.8	7.4	7.5	7.5	10.7
stocking density, trees ha^{-1}	357	469	303	343	386	455	260	458
aboveground tree carbon stock, tC ha^{-1}	21.5	30.7	19.0	24.0	17.3	16.9	21.1	25.6
top 5 species by basal area. 1.	*B. boehmii*	*B. boehmii*	*B. boehmii*	*B. boehmii*	*B. boehmii*	*B. boehmii*	*B. boehmii*	*J. globiflora*
2.	*D. condylocarpon*	*D. condylocarpon*	*D. condylocarpon*	*D. condylocarpon*	*J. globiflora*	*D. condylocarpon*	*E. africanum*	*D. condylocarpon*
3.	*J. globiflora*	*E. africanum*	*E. africanum*	*J. globiflora*	*D. condylocarpon*	*S. birrea*	*B. spiciformis*	*B. boehmii*
4.	*E. africanum*	*B. spiciformis*	*S. birrea*	*P. rotundfolius*	*P. angolensis*	*P. rotundfolius*	*D. condylocarpon*	*B. spiciformis*
5.	*B. africana*	*J. globiflora*	*B. africana*	*P. angolensis*	*X. stuhlmannii*	*C. adenogonium*	*B. africana*	*P. angolensis*
top 5 spp % of total basal area	76%	90%	81%	82%	92%	85%	84%	77%

Sapling data (Standard deviations in brackets)

	1	2	3	4	5	6	7	8
inventory area, m^2	942	151	151	151	151	151	151	151
sapling basal area, m^2 ha^{-1}	0.88 (0.76)	0.68 (0.48)	0.41 (0.60)	0.76 (0.91)	2.18 (1.93)	1.12 (0.99)	1.60 (1.28)	0.81 (0.87)
stocking density, saplings ha^{-1}	6,281 (3,280)	12,401 (8,349)	6,300 (7,651)	7,228 (6,065)	24,271 (19,952)	11,075 (10,663)	16,048 (11,660)	6,499 (4,844)
top 5 species by basal area. 1.	*B. boehmii*	*B. boehmii*	*D. condylocarpon*	*D. condylocarpon*	*B. boehmii*	*D. condylocarpon*	*D. condylocarpon*	*D. condylocarpon*
2.	*D. condylocarpon*	*J. globiflora*	*Holarrena pubescens*	*C. adenogonium*	*D. condylocarpon*	*J. globiflora*	*J. globiflora*	*E. africanum*
3.	*J. globiflora*	*D. condylocarpon*	*L. discolor*	*B. boehmii*	*E. africanum*	*D. boehmii*	*B. boehmii*	*X. stuhlmannii*
4.	*C. adenogonium*	*L. discolor*	*B. boehmii*	*J. globiflora*	unidentified	*C. febrifuga*	*E. africanum*	*M. stuhlmannii*
5.	*E. africanum*	unidentified	*E. africanum*	unidentified	*M. stuhlmannii*	*B. boehmii*	*P. angolensis*	*C. adenogonium*
top 5 spp % of total basal area	86%	78%	95%	86%	92%	70%	87%	93%

Fire properties (Standard deviations in brackets)

	1	2	3	4	5	6	7	8
ignition time, GMT +1	no burn	17/9/07 14:33	15/9/07 10:21	6/9/07 15:34	19/9/07 08:09	14/9/07 15:15	12/9/07 13:31	10/9/07 14:32
thermal anomaly, °C s × 10^3		31.2 (5.1)	25.3 (2.6)	21.9 (2.1)	20.3 (5.9)	32.2 (6.5)	29.5 (5.2)	29.2 (4.3)

Vegetation Effects (sample size in brackets)

	1	2	3	4	5	6	7	8
Tree top-kill	0% (90)	5% (121)	1% (81)	1% (82)	0% (74)	13% (123)	9% (67)	4% (121)
Sapling top-kill	13% (557)	92% (153)	99% (94)	100% (93)	81% (365)	93% (166)	88% (218)	94% (98)
rootstock mortality	0.4% (255)	13.7% (73)	10.8% (37)	3.5% (57)	0% (129)	0% (68)	5.6% (108)	0% (45)

Top-kill

The tree inventory showed top-kill occurring in 38 out of the 702 live standing trees (Table 1), equal to 5.4% (or 5.9% counting as dead four trees that were not found in the resurvey) across the whole experiment. No large stems died on the unburned plot. Plot level tree top-kill ranged from 0-13%, with the log odds of top-kill well correlated (for a linear fit, r^2 = 0.82; p = 0.005) to the plot level mean thermal anomaly (Fig. 2 and Table 1).

The sapling inventory (Table 1) showed very high top-kill rates – 1116 of the 1326 stems on the burned plots were top-killed (84%). 83 tags were not located in the post-fire census, and if these lost stems are considered killed, top-kill was 90%. Burned plot-level sapling top-kill ranged from 81-100%, which contrasted with 13% (n = 591) non-fire top-kill of saplings on the unburned plot.
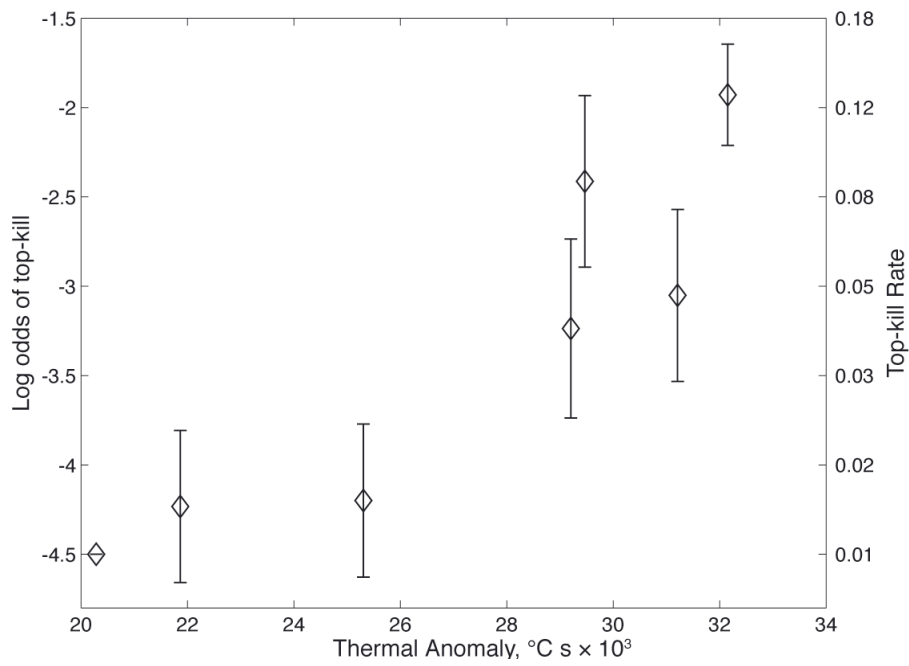
Figure 2. Mortality rate of trees >5 cm DBH on each plot against mean thermal anomaly (°C s × 10³). Probability, *p*, is transformed to the log odds (or logit, Ln(*p*/1-*p*), where Ln is the natural logarithm) on the left axis, but shown untransformed on the right. For a linear fit, $r^2 = 0.82$; p = 0.005 for log odds of top-kill vs TA. Zero mortality (–Inf log odds) is shown as -4.5 and fitted as such. See text for explanation of errorbars.
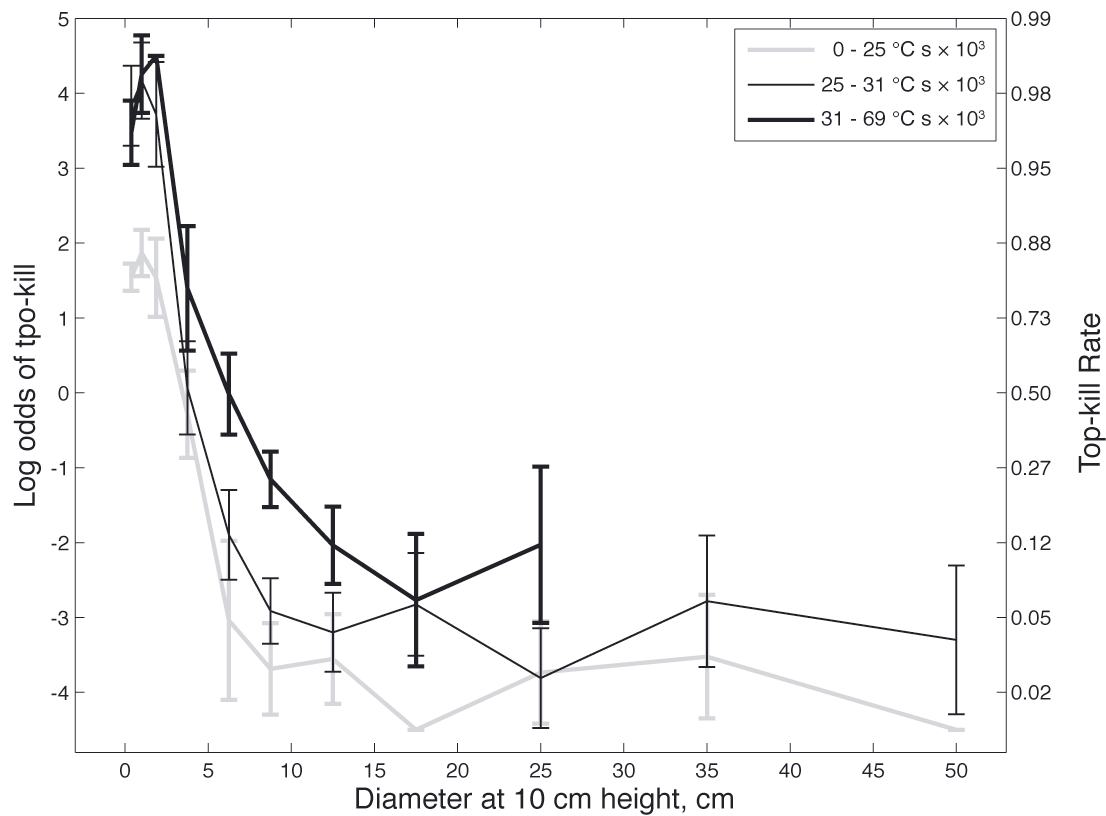
Figure 3. Top-kill rates for all stems as a function of diameter and thermal anomaly. The top-kill data are pooled into diameter bins and grouped by fire intensity class. See text for explanation of errorbars. Zero top-kill (–Inf log odds) is shown as -4.5 and no variance can be associated with it.

Stem top-kill was a function of stem diameter as well as thermal anomaly (Fig. 3). To combine the stem and sapling inventories we assumed that D_{10} = DBH + 2 cm (the mean D_{10} of a 1.3 m tall, i.e. 0 cm DBH, sapling was 2 cm) and assigned the plot scale mean TA to each tree in the large tree inventory whilst using the fine scale TA data for saplings. The results showed a clear decrease in top-kill with increasing diameter from 0-10 cm D_{10} (Fig. 3). Above 10 cm D_{10}, top-kill was unaffected by diameter. The effect of TA on top-kill, observed at plot level (Fig. 2), was also noticeable across the range of diameters. When the data were grouped into terciles of TA (the fire intensity classes), there was a clear difference in top-kill rates between fire intensity classes (Fig. 3).

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Resprouting

Of rootstocks on the burned plots, 96% survived and produced at least one new stem after the fire, with a median of 3 new stems. On the unburned plot, rootstock survival was higher at 99.6% (one death out of 259). Rootstocks which had all their stems killed by fire were more likely to produce new shoots than those with a surviving stem, 84% *vs* 24%, and also produced more new shoots, median 3 *vs* 1. Similarly to the unharmed, fire-exposed rootstocks, 24% of rootstocks on the unburned plot sent up new shoots.

Plot level rootstock mortality rates were not correlated with plot level TA. However, at the fine scale, log odds of rootstock mortality showed a non-linear relationship with the fine scale thermal anomaly data, rising until 33.5×10^3 °C s and falling thereafter (Fig. 4). The number of post-fire resprouts was not correlated with the pre-fire number or basal area of stems from the parent rootstock.
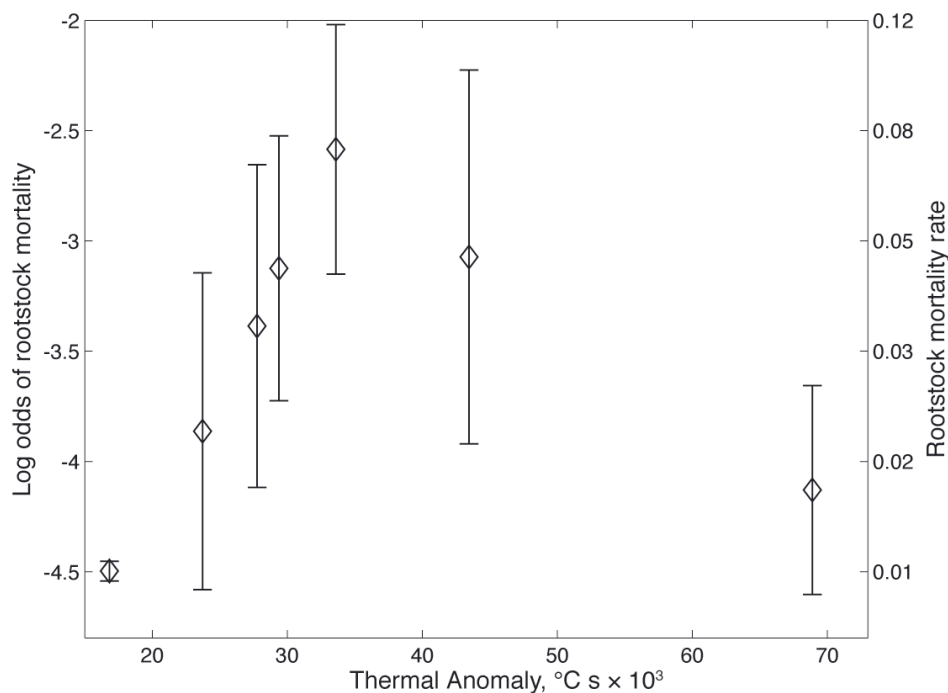

Figure 4. Rootstock mortality against fire thermal anomaly recorded by nearby thermocouples. See text for explanation of errorbars. Data are binned into TA classes to give roughly equal sample size.

Species effects

The large tree inventory showed top-kill of 5-6% among both the canopy dominants (*B. boehmii* and *J. globiflora)* and the sub-canopy dominant *D. condylocarpon. P. rotundfolius* had a higher top-kill rate (25%, but *n* = 21), *E. africanum* had no top-kill for *n* = 24. Other species had lower sample sizes and their top-kill rates are not considered further. The canopy dominants had very similar top-kill rates to the understory *D. condylocarpon,* although the canopy species seem to be slightly more vulnerable in the 4-8 cm DBH range (Fig. 5). Fitting curves to DBH *vs* log odds of top-kill resulted in no difference between the 95% confidence intervals of curve parameters for power, exponential or linear fits (for 30 > D_{10} > 0; curve fitting and parameter estimation with the Matlab curve fitting toolbox).
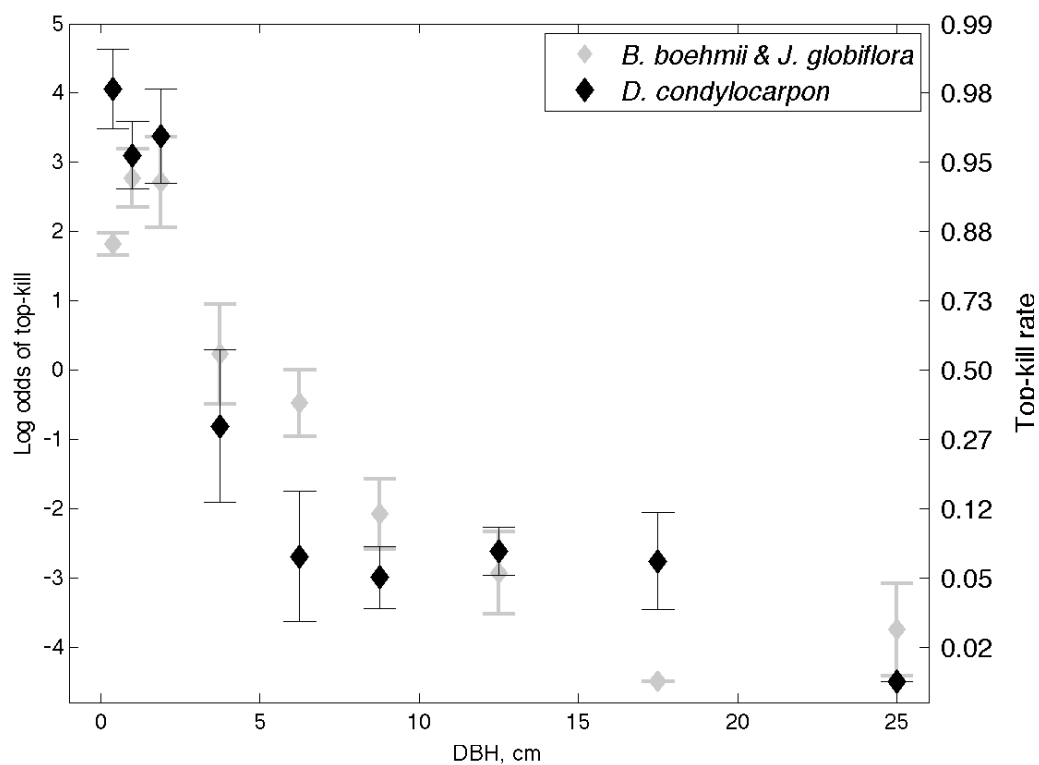

Figure 5. Comparison between size-specific top-kill rates for the dominant canopy species (*Brachystegia boehmii* and *Julbernardia globiflora, n* = 688) and dominant understory species *Diplorhynchus condylocarpon, n* = 700. See text for explanation of errorbars. Zero top-kill (–Inf log odds) is shown as -4.5 and no variance can be associated with it.

Model testing

Comparison to dry forest data

The first model experiment showed that the model had good skill in predicting forest patch properties and size distribution in the near absence of fires (FRI = 100, low intensity fires). The model output (Fig. S3), generated with parameters from Site 1 (Nhambita) and the literature, agreed well with the observed Marrameu forest attributes (Site 2). For basal area and LAI, the field data lay within one standard deviation of the 50-patch 500-year mean model prediction. For the last 500 years of model simulation, the mean predicted basal area was 22.8 ± 4.5 m^2 ha^{-1} *vs* a measured value of 22.0, and LAI was 3.9 ± 0.5 *vs* 3.3 (Fig. S3). The stocking density of stems was overestimated by the model, 1371 ± 595 *vs* 494 stems ha^{-1}, mainly in the 5-10 and 10-15 cm classes (Fig. S4). All the larger size class stocking densities were well predicted by the model.

Comparison to 50-year fire frequency experiment

The Marondera experiment showed a strong effect of fire frequency on Basal Area (BA). There was almost no large tree BA with FRI=1 (0.3 ± 0.1 m^2 ha^{-1}, $n=2$, $\pm$SD) or FRI=2 (2.7 ± 2.1 m^2 ha^{-1}, $n=4$), but significant biomass was present at FRI=3 (9.2 ± 8.4 m^2 ha^{-1}, $n=6$) and FRI=4 (15.7 ± 9.6 m^2 ha^{-1}, $n=7$). Under complete fire exclusion ($n=2$), BA averaged 30.4 ± 1.4 m^2 ha^{-1}.

The second model experiment simulated a variety of fire regimes by varying the FRI from 1-100 years for each of the three fire intensity classes. Model output was tested against the Marondera fire trial basal area data (Fig. 6). The treatment means for the BA data from Marondera fell between the predictions under the low and medium intensity fires. The predictions under all intensities were within the range of the Marondera data except on the two unburned plots, which had slightly more BA than predicted by the model.
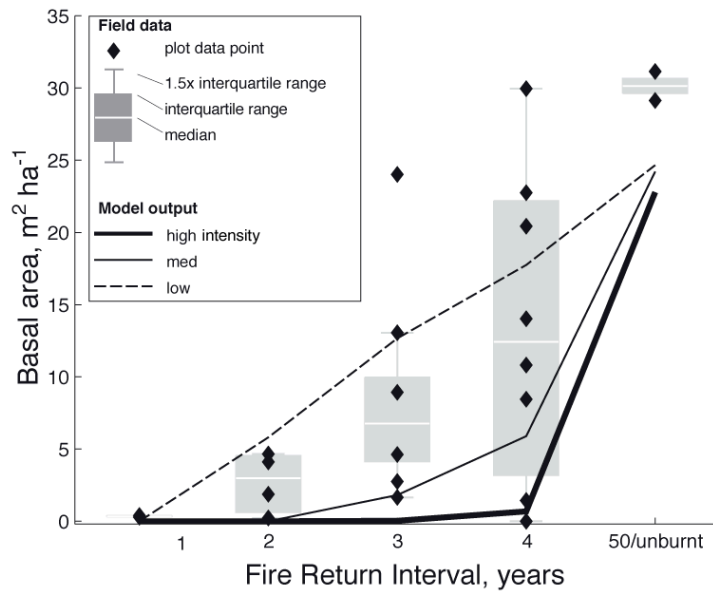
Figure 6. Modelled basal area under different fire return intervals and intensity class (black lines), compared to data from Marondera, Zimbabwe, showing the results of a 50 year burning experiment (filled diamonds and boxplots).

Predictions of C stock under different fire regimes

The model predictions of aboveground carbon stocks (Fig. 7) showed that aboveground woody biomass was very sensitive to the top-kill rates associated with different fire intensity classes, and with the frequency of fire. Annual fire (FRI=1) allowed no stems > 5 cm DBH at any intensity. With lengthening FRI, low intensity fires allowed biomass to develop at FRI=2, medium intensity fires at FRI = 3 and high intensity fires at FRI = 4. For low intensity fires, the effects of extending FRI beyond 4 were minor, as other limitations on biomass became more significant than fire. In contrast, the high large-tree top-kill rates in medium and high intensity fires influenced stand biomass even at FRI=50. The differing impact of fire intensity was greatest at FRI=4, where low intensity fires support a woodland of 65 tC ha^{-1}, compared to high intensity fires which supported 2 tC ha^{-1}.

63
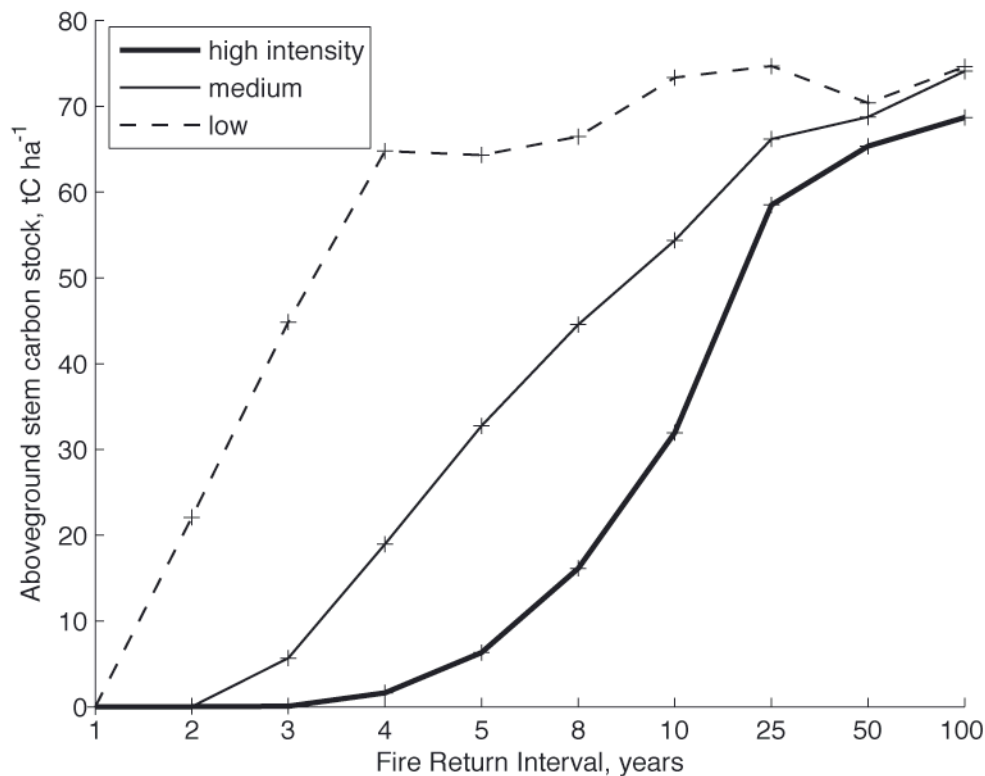
Figure 7. Modelled aboveground tree carbon stock for the three fire intensities and a range of return intervals

Discussion

We now use the experimental data and model outputs to answer our original questions.

  1. *What are top-kill rates for stems of different diameter in different intensity fires?*

At diameters < 10 cm D_{10}, top-kill was a logistic function of diameter (Fig. 3). Top-kill for stems > 10 cm D_{10} was, for a given TA, unaffected by stem diameter. These results suggest diameter is a key factor in fire protection of small trees, but that this effect is not sustained at large size classes.

As is common, stem diameter was well correlated with both stem height (r^2 =0.58, n = 80) and mean bark thickness (r^2 =0.65, n = 32), data not shown, so elucidating the mechanisms of protection is impossible with this type of observational study. This study provides some clues as to the relevant processes, however. We observed that most of the large trees that were top-killed were subject to flaming or smouldering combustion of

the bole, within the flame zone (photos in supplementary figure 2). Such trees were killed because the heat transfer from the flame was sufficient to start combustion of the tree itself, and often this was possible because the wood was exposed and rotten. Such an effect is likely to scale well with measurements of fire behaviour that are linked to time-integrated heat flux. It is also consistent with the observed levelling off of the diameter-top-kill relationship (Figure 3) as neither bark thickness nor height offer any protection from this type of fire-induced mortality. Other workers have attributed fire-induced mortality to damage from elephants (Guy 1989) and porcupines (Yeaton 1988) or previous fires (Tafangenyasha 2001; Holdo 2005). Fire-induced mortality of large trees may not, therefore, be well predicted by idealised physical representation of undamaged trees.

It is worth noting that advancing our knowledge of the response of vegetation to fires of differing intensity depends on obtaining an appropriate metric for fire "intensity". Many different metrics have been used, which mainly break down into those that are related to fire duration, flame temperature or some combination of the two (as here). However as duration and peak temperature are very often correlated and so it is difficult to establish which is the most ecologically relevant variable, particularly when the mechanism of stem death is unknown. Measures based on temperature time profiles need to be carefully compared (at an appropriate scale) to measure of heat release such as Bryam's fire line intensity to see if they are providing similar information. Also, it is not clear how different measures of fire "intensity" scale with combustion completeness and gaseous emissions. We will present data on the emissions from the fire reported here elsewhere.

2.   *How common is resprouting after top-kill and what factors affect rootstock survival and the number of resprouts?*

Sapling rootstocks were very resistant to fire - on average 96% survived the fire and produced new shoots in the next growing season (Table 1).

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This was despite high levels of aboveground mortality. It appears that top-kill stimulated resprouting, as resprouting rates were lower on the unburned plots and from fire-exposed rootstocks which were not top-killed. The number of new shoots produced by a rootstock was not correlated to any of the pre- or post-fire variables we measured (number, height, basal area of stems). We can only speculate that resprouting numbers are instead linked to the resources available to the rootstock, which will be related to its age, history and microsite conditions. Our data may be an upper bound on rootstock mortality if some rootstocks remained alive but dormant.

We found some evidence that rootstock mortality was a non-linear function of fire TA, when examined at a fine scale (Fig. 4). However, the relationship was based on only 23 rootstock deaths across the seven plots. The non-linearity is interesting and suggests that further investigation into the mechanisms of heat flux to the rootstock and the causes of mortality is warranted.

3. *Are some species-groups fire tender and others better protected against fire?*

No clear species effects were found in top-kill rates of trees and saplings, nor in resprouting rates (Fig. 5). That a difference in top-kill rates was not detected is surprising, given the large differences between the species, in terms of bark structure, thickness and moisture content (Chidumayo 1988; Chidumayo 1997). Previous reports of species fire tenderness (Trapnell 1959; Lawton 1978) may reflect relative resprouting success and growth rates, rather than fire resistance *per se,* and at a plot level, it is impossible to separate out the different mechanisms (Gignoux *et al.* 1997). Our fine-scale fire behaviour measurements and observations of individual stems failed to show significant differences in top-kill between species, which may indicate that the perceived fire tolerance of various species is due to their persistence by resprouting and superior competitive abilities in the sapling stage.

5. *What is the sensitivity of tree populations to fire impacts and under what frequency and intensity of fires can miombo woodland be sustained?*

Our modelling results suggest that no large woody vegetation can be sustained under annual burning in these dry woodlands (Fig. 10), regardless of the intensity of the fire. This is borne out at the Marondera experiment (Fig. 7), which had no woody biomass at FRI=1. Above a fire return interval of 1 year, large stems can be sustained, but this is strongly dependent on fire intensity.

10   Many experiments, in miombo and elsewhere in African savanna, have shown that early season burning allows woody biomass to develop further compared to late season burning (Ramsay et al. 1963). If we regard this effect as mainly due to the lower intensity fires resulting from wetter (grass) fuel and more benign fire weather, we can compare such early season burning with our low intensity fires (which were the product of early day burns). This assumption ignores a hypothesised (Chidumayo 1997) but unproven effect of tree growth phenology, which suggests that early burns may impact trees more severely as they are at a more vulnerable stage of growth.

20   Trapnell (1959), working in wet Zambian miombo, found mortality rates of trees > 15.2 cm DBH to be more than twice as high on annually late burned plots, compared to annually early burned plots (his Table 7 and 8). Our experiments found a similar, but much more pronounced, pattern – low intensity fires were about six times less destructive than our high intensity fires. No measures of fire behaviour were recorded by Trapnell, so it is hard to compare the experiments directly. In the Zambian experiment trees survived on the annually burned, low intensity treatment – contrary to our modelling results. This may be due to the higher rainfall (1200 mm year^{-1}) and therefore more productive site, or

30   the relatively short period of observation (23 years). A short observational period may also be why Barnes (1965, cited in Walker 1983) observed

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trees on the Marondera annually burned treatments, but Tsvuura (1998) in 1995 and then this study (in 2007) did not.

Conclusions

We have found differences in the effects of fires of different intensities on the trees of a miombo woodland. Stem top-kill was found to be a non linear function of the fire temperature–time integrals and stem diameter. We simulated the structure of the woodlands under various fire regimes and found results consistent with a long-term fire experiment in Zimbabwean miombo. Our model also showed that the structure of both miombo woodlands and a closed canopy forest can be explained by leaf-level photosynthesis growth parameters, the observed phenology, and stem allometrics, set against fire induced mortality rates. The Marondera results and the modelling strongly suggest that miombo woodlands are fire-derived. Further work is required to expand the model to simulate grass growth, and thus fuel loads, and so feed back on to the fire behaviour and consequent tree mortality.

The vegetation observed on the Nhambita plots, with ~20 tC ha^{-1}, is, according to our model, consistent with an envelope of fire regimes bounded by low intensity burns every 2 years, or high intensity burns every 9 years (Fig. 7). Such a fire regime is conspicuously absent at the moment, with high intensity fires and biennial frequency observed in the area (pers. obs.). The high top-kill rates observed in this study may thus be a consequence of a recently imposed high severity fire regime, which has predisposed many trees to fire-induced top-kill. This result calls for close monitoring and precautionary action in managing such woodlands as there is potential for rapid fire-induced degradation and loss of woody biomass.

Fire intensity is predominately controlled by fuel load and moisture, and weather conditions (Cheney *et al*. 1998). In this experiment we use the diurnal range of fuel moisture, windspeed and temperature to create

variation in fire intensity. Manipulating intensity (either through prescribed burning early in the season (Govender et al. 2006) or early in the day, or by reducing fuel loads), is a more practicable management task than reducing frequency by fire suppression (Van Wilgen et al. 2004). As an indication of the range of intensities possible, our fires had a Byram's fireline intensity of 360–3,800 kW m^{-1} as a plot mean, which can be compared to the seasonal variation of $25 - 5,300$ kW m^{-1} in Hoffa's (1999) study in Zambian miombo. However it is not clear how Byram's fire line intensity relates to the thermal anomaly measurements reported here. Our results suggest that miombo woody biomass may be preserved or enhanced by burning in low intensity conditions. Low intensity burns are likely to have been the traditional land management regime (Laris et al. 2006) and are also proposed to have biodiversity benefits (but see Parr et al. 2006).

Acknowledgements

This paper is dedicated to the memory of Paulino 'Paulito' Tique.

References

Bond, W. J. and J. E. Keeley (2005). "Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems " <u>Trends in Ecology & Evolution</u> **20**(7): 387-394.

Bond, W. J. and J. J. Midgley (2003). "The evolutionary ecology of sprouting in woody plants." <u>International Journal of Plant Sciences</u> **164**(3): S103-S114.

Bond, W. J. and B. W. van Wilgen (1996). <u>Fire and plants</u>. London, Chapman & Hall.

Bond, W. J., F. I. Woodward and G. F. Midgley (2005). "The global distribution of ecosystems in a world without fire." <u>New Phytologist</u> **165**(2): 525-537.

Campbell, B. M., A. Angelsen, A. Cunningham, Y. Katerere, A. Sitoe and S. Wunder (2007). Miombo woodlands – opportunities and barriers to sustainable forest management, Center for International Forestry Research.

Cheney, N. P., J. S. Gould and W. R. Catchpole (1998). "Prediction of Fire Spread in Grasslands." <u>International Journal of Wildland Fire</u> **8**(1): 1-13.

Chidumayo, E. N. (1988). "A Re-Assessment of Effects of Fire on Miombo Regeneration in the Zambian Copperbelt." <u>Journal of Tropical Ecology</u> **4**(4): 361-372.

Chidumayo, E. N. (1997). <u>Miombo ecology and management : an introduction</u>. London, IT Publications in association with the Stockholm Environment Institute.

Coates Palgrave, K., R. B. Drummond, E. J. Moll and M. Coates Palgrave (2002). <u>Trees of southern Africa</u>. Cape Town, Struik Publishers.

Desanker, P. V. (1996). "Development of a MIOMBO woodland dynamics model in Zambezian Africa using Malawi as a case study." <u>Climatic Change</u> **34**(2): 279-288.

Desanker, P. V. and I. C. Prentice (1994). "Miombo - a Vegetation Dynamics Model for the Miombo Woodlands of Zambezian Africa." <u>Forest Ecology and Management</u> **69**(1-3): 87-95.

Dickinson, M. B. and E. A. Johnson (2001). Fire effects on trees. <u>Forest Fires: Behavior and Ecological Effects</u>. E. A. Johnson and K. Miyanishi, Academic Press.

Eriksen, C. (2007). "Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia." <u>Geographical Journal</u> **173**: 242-256.

Fernandes, P. M., W. R. Catchpole and F. C. Rego (2000). "Shrubland fire behaviour modelling with microplot data." <u>Canadian Journal of Forest Research</u> **30**(6): 889-899.

Frost, P. (1996). The ecology of Miombo woodlands. <u>The Miombo in transition : woodlands and welfare in Africa</u>. B. M. Campbell. Bogor, Indonesia, Center for International Forestry Research: 11-55.

Furley, P. A., R. M. Rees, C. M. Ryan and G. Saiz (2009). "Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe." <u>Progress in Physical Geography</u> **in press**.

Gignoux, J., J. Clobert and J. C. Menaut (1997). "Alternative fire resistance strategies in savanna trees." <u>Oecologia</u> **110**(4): 576-583.

Govender, N., W. S. W. Trollope and B. W. Van Wilgen (2006). "The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa." <u>Journal of Applied Ecology</u> **43**(4): 748-758.

Guy, P. R. (1989). "The Influence of Elephants and Fire on a *Brachystegia-Julbernardia* Woodland in Zimbabwe." <u>Journal of Tropical Ecology</u> **5**(2): 215-226.

Higgins, S. I., W. J. Bond, E. C. February, A. Bronn, D. I. W. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. Regan, A. L. F. Potgieter, S. Scheiter, R. Sowry, L. Trollope and W. S. W. Trollope (2007). "Effects of Four Decades of Fire Manipulation on Woody Vegetation Structure in Savanna." <u>Ecology</u> **88**(5): 1119-1125.

Higgins, S. I., W. J. Bond and W. S. W. Trollope (2000). "Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna." <u>Journal of Ecology</u> **88**(2): 213-229.

Hoffa, E. A., D. E. Ward, W. M. Hao, R. A. Susott and R. H. Wakimoto (1999). "Seasonality of carbon emissions from biomass burning in a Zambian savanna." <u>Journal of Geophysical Research-Atmospheres</u> **104**(D11): 13841-13853.

Hoffmann, W. A. (1998). "Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction." <u>Journal of Applied Ecology</u> **35**(3): 422-433.

Hoffmann, W. A. and O. T. Solbrig (2003). "The role of topkill in the differential response of savanna woody species to fire." <u>Forest Ecology and Management</u> **180**(1-3): 273-286.

Holdo, R. M. (2005). "Stem Mortality Following Fire in Kalahari Sand Vegetation: Effects of Frost,Prior Damage, and Tree Neighbourhoods." <u>Plant Ecology</u> **180**(1): 77-86.

Jackson, J. F., D. C. Adams and U. B. Jackson (1999). "Allometry of Constitutive Defense: A Model and a Comparative Test with Tree Bark and Fire Regime." <u>The American Naturalist</u> **153**(6): 614-632.

Johnson, E. A. and K. Miyanishi (2001). <u>Forest fires : behavior and ecological effects</u>. San Diego, Calif. ; London, Academic.

Kennedy, A. D. and A. L. F. Potgieter (2003). "Fire season affects size and architecture of Colophospermum mopane in southern African savannas." <u>Plant Ecology</u> **167**(2): 179-192.

Laris, P. (2002). "Burning the Seasonal Mosaic: Preventative Burning Strategies in the Wooded Savanna of Southern Mali." <u>Human Ecology</u> **30**(2): 155-186.

Laris, P. and D. A. Wardell (2006). "Good, bad or 'necessary evil'? Reinterpreting the colonial burning experiments in the savanna landscapes of West Africa." <u>The Geographical Journal</u> **172**(4): 271-290.

Lawton, R. M. (1978). "Study of Dynamic Ecology of Zambian Vegetation." <u>Journal of Ecology</u> **66**(1): 175-&.

Michaletz, S. T. and E. A. Johnson (2007). "How forest fires kill trees: A review of the fundamental biophysical processes." <u>Scandinavian Journal of Forest Research</u> **22**(6): 500-515.

Miller, C. and D. L. Urban (2000). "Modeling the effects of fire management alternatives on Sierra Nevada mixed-conifer forests." Ecological Applications **10**(1): 85-94.

Mouillot, F. and C. B. Field (2005). "Fire history and the global carbon budget: a 1° fire history reconstruction for the 20th century." Global Change Biology **11**(3): 398-420.

Parr, C. L. and A. N. Andersen (2006). "Patch Mosaic Burning for Biodiversity Conservation: a Critique of the Pyrodiversity Paradigm." Conservation Biology **20**(6): 1610-1619.

Ramsay, J. and R. Rose Innes (1963). "Some quantitative observations on the effects of fire on the Guinea savanna vegetation of northern Ghana over a period of eleven years." African Soils **8**: 41-85.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden and N. Zambatis (2005). "Determinants of woody cover in African savannas." Nature **438**(7069): 846-849.

Shugart, H. H. and T. M. Smith (1996). "A review of forest patch models and their application to global change research." Climatic Change **34**(2): 131-153.

Smith, A. M. S., M. J. Wooster, N. A. Drake, F. M. Dipotso, M. J. Falkowski and A. T. Hudak (2005). "Testing the potential of multi-spectral remote sensing for retrospectively estimating fire severity in African Savannahs." Remote Sensing of Environment **97**(1): 92-115.

Stronach, N. R. H. and S. J. McNaughton (1989). "Grassland Fire Dynamics in the Serengeti Ecosystem, and a Potential Method of Retrospectively Estimating Fire Energy." Journal of Applied Ecology **26**(3): 1025-1033.

Sutherland, E. K. and K. T. Smith (2000). Resistance is not futile: The response of hardwoods to fire-caused wounding. Workshop on Fire, People, and the Central Hardwoods Landscape, Richmond, Ky, USDA Forest Service Northeastern Forest Experiment Station.

Tafangenyasha, C. (2001). "Decline of the mountain acacia, Brachystegia glaucescens in Gonarezhou National Park, southeast Zimbabwe." Journal of Environmental Management **63**(1): 37-50.

Tinley, K. L. (1977). Framework of the Gorongosa Ecosystem. Faculty of Science. Pretoria, University of Pretoria: 184.

Tinley, K. L. (1982). The influence of soil moisture balance on ecosystem patterns in Southern Africa. Ecology of tropical savannas. B. J. Huntley and B. H. Walker. Berlin, Springer: 669.

Trapnell, C. G. (1959). "Ecological Results of Woodland Burning Experiments in Northern Rhodesia." Journal of Ecology **47**(1): 129.

Tsvuura, Z. (1998). Effects of long-term burning on some vegetation and soil characteristics on a dry miombo region at Marondera, Zimbabwe. Department of Biological Sciences. Harare, University of Zimbabwe.

van Wilgen, B. W. (1997). Fire in southern African savannas : ecological and atmospheric perspectives. Johannesburg, South Africa, Witwatersrand University Press : Thorold's Africana Books [distributor].

Van Wilgen, B. W., N. Govender, H. C. Biggs, D. Ntsala and X. N. Funda (2004). "Response of Savanna Fire Regimes to Changing Fire-Management Policies in a Large African National Park." Conservation Biology **18**(6): 1533-1540.

Williams, M. (1996). "A three-dimensional model of forest development and competition." Ecological Modelling **89**(1-3): 73-98.

Williams, M., C. M. Ryan, R. M. Rees, E. Sambane, J. Fernando and J. Grace (2008). "Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique." Forest Ecology and Management **254**(2): 145-155.

Yeaton, R. I. (1988). "Porcupines, Fires and the Dynamics of the Tree Layer of the Burkea Africana Savanna." The Journal of Ecology **76**(4): 1017-1029.

Appendix

Model description
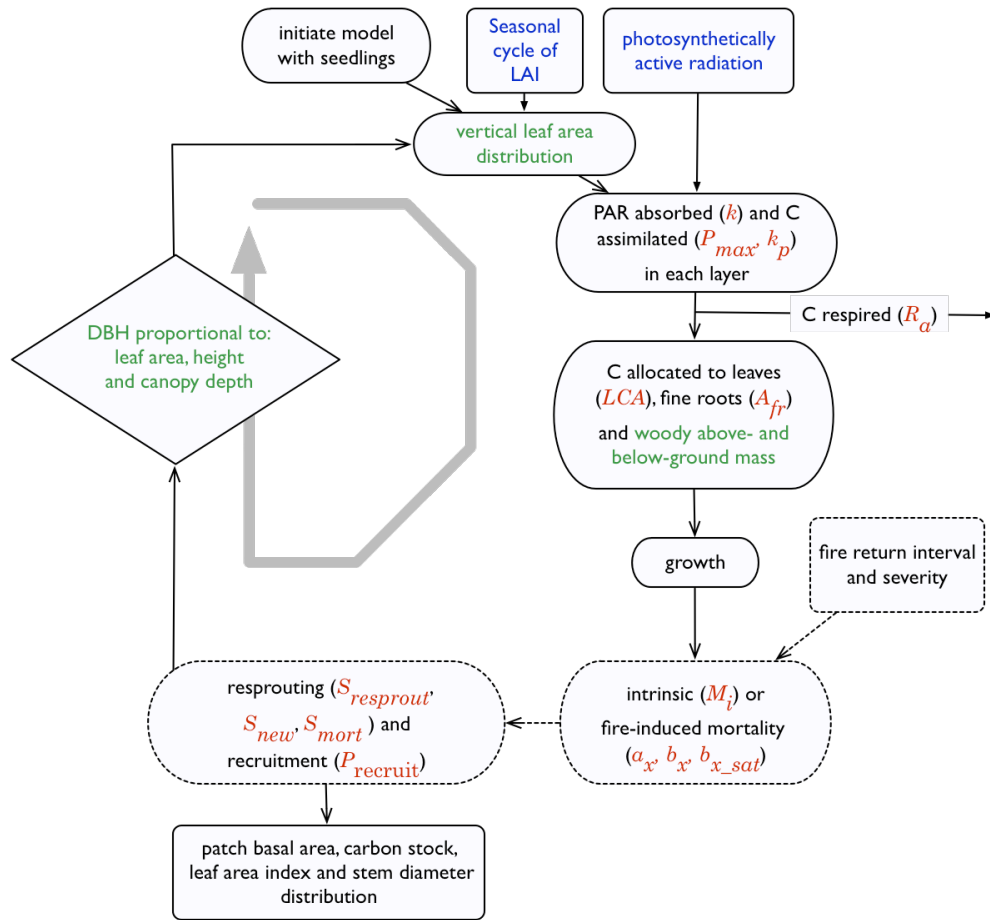
Figure A1. Gap model schematic. Parameters are shown in red (see table A2 and A3 for values, source and sensitivity of the parameters). Green shows allometric calculations based on Table A1. Model driving data is shown in blue (see Figure A1). Stochastic processes are shown with a dashed line. The model produces annual output, but the light and C assimilation functions run on hourly time steps (see text).

The model is a 1D patch model, explicitly representing each stem and its light environment, carbon assimilation, growth and mortality. Each model patch has twenty-five 1 m vertical layers and is not spatially explicit. The model is written in FORTRAN 90.

Light and seasonal and diurnal model drivers

Within each patch, the model simulates light interception by the canopy and the resulting photosynthetic assimilation. The model is driven with a

3.5 year radiation climatology from a weather station (Skye Instruments, UK) at Chitengo, 25 km from the study site. We generated a mean diurnal cycle of downwelling PAR, at hourly resolution, for each calendar month. The model is also driven with an observed monthly fraction of peak leaf area index (LAI), determined from 3.5 years of monthly hemispherical photos at two nearby permanent sample plots.
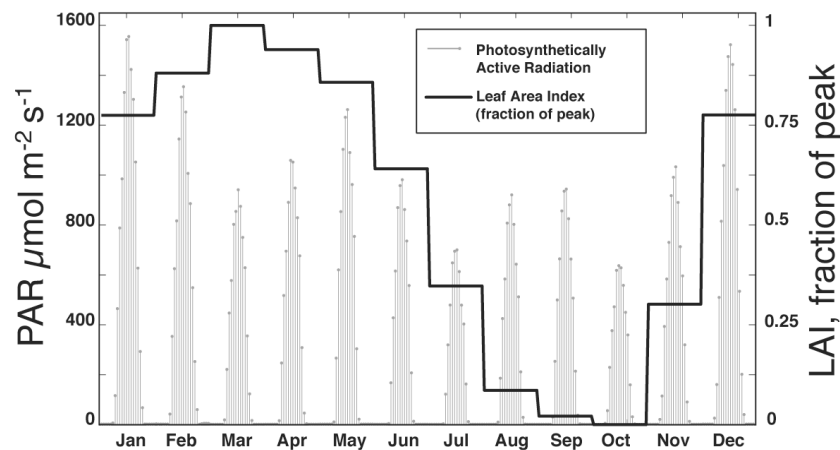
Figure A2. Data used to drive the model. A seasonal cycle of leaf area index was derived from replicated monthly hemispherical photos on two 1 ha permanent sample plots. PAR measurements are from a weather station 25 km away. 3.5 years of data were averaged by hour and month to generate a representative diurnal cycle for each month.

Plant Area Index (PAI) was estimated from hemispherical photos (Nikon Coolpix 4500 with a FC-E8 fisheye converter) collected each month at two 1 ha permanent sample plots (PSP). Nine photos were acquired on a 20 m grid on each plot, each month. The photos were thresholded to separate plant and sky pixels using the algorithm of Ridler and Calvard (1978), implemented in MATLAB to determine gap fraction, which was converted to an PAI estimate using the method of Licor (1989), with the images segmented in a similar manner to van Gardingen *et al.* (1999). As the trees are fully deciduous, PAI was converted to LAI by subtracting the lowest observed PAI from each observation point. The monthly LAI fraction represents the deciduousness of the vegetation and is an explicit representation of limits of the growing season of trees in this

environment (Fig. A2). Each year the vertical leaf area distribution is calculated based on functions which relate each stem's DBH to its total height, canopy depth and leaf area (Shinozaki *et al.* 1964) using the allometric relationships shown in Table A1. Leaves were assumed to be spread evenly throughout the canopy depth. A simple radiative transfer scheme passes light down through the canopy layers. The amount of PAR absorbed is calculated according to leaf area density using the Beer-Lambert law (Jones 1992), with an assumed spherical leaf angle distribution (*k*). All radiation was assumed diffuse and the leaves had no albedo or transmittance.

Carbon assimilation and allocation

The absorbed PAR was converted to assimilated C using photosynthetic light response curves parameterised from two studies in Zimbabwean miombo (Tuohy and Choinski 1990; Tuohy *et al.* 1991). Two parameters describe the light response curve: the maximum rate of assimilation, P_{max} and the amount of light needed to achieve half this rate, k_p. For each stem, mass of photosynthate was summed for each canopy layer, for each hour of the 12 diurnal cycles representative of each month, and scaled up to a yearly total.

Carbon allocation routines are resolved each year for each stem. We assumed that 50% of assimilate is used for respiration (Waring et al. 1998, R_a in Table A2). Of the remainder, the required amount is allocated to leaves to produce the observed phytomass of peak LAI. Leaf carbon specific area (*LCA* gC m^{-2}) is derived from field measurements (Nottingham 2004). We assumed that allocation to fine roots, A_{fr}, is equal to allocation to leaf mass. Any remaining C is allocated to woody growth, which is partitioned above and belowground according to a local DBH-specific root:shoot allometric. The increase in aboveground stem C is converted to a change in DBH using allometric equations (Table A1),

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which in turn allows the increase in height and leaf area to be calculated for the next year.

Mortality and the effect of fire

Once growth is completed, each stem is exposed to a random chance of mortality, which is either an intrinsic (non-fire) mortality or a fire-induced mortality derived from our fire experiments. These fire-induced mortality rates are DBH- and fire intensity class-specific and are based on piecewise functions of the field results (Table A3). The intrinsic mortality rate, M_i, was unknown and is very poorly constrained in this ecosystem. We used a nominal value of 2% regardless of size (similar to Desanker and Prentice 1994; Desanker 1996), and undertook sensitivity analysis (Table A2). In the model, the chance of a fire occurring was determined from a user supplied control variable, the fire return interval (FRI), and a random number generator. The chance of a fire occurring was determined as 1/FRI.

Resprouting

Because of the importance of resprouting in fire-prone ecosystems (Bond and Midgley 2001; Chidumayo 2004; Mlambo and Mapaure 2006), aboveground stem mortality (top-kill) was decoupled from belowground rootstock mortality. Stems > 2 cm DBH (parameter $S_{resprout}$) which are killed, have a probability or resprouting (1 - S_{mort}), which is based on data from the fire experiments, and we assume they achieve a 2 cm DBH in their first year. In addition, every year there is a nominal 3% chance (parameter $P_{recruit}$) of a recruitment event occurring and 200 new seedlings (parameter S_{new}) being established in the patch. We justify this low level of recruitment from studies which show that most regeneration is from sprouts and that seedling survival is low in these woodlands (Chidumayo 1992, 1997).

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Model output and initiation

After calculating mortality, the patch LAI (for stems > 1.5 m tall), basal area, aboveground C stock, and stocking density (for stems >5 cm DBH), and stem size distribution are calculated for all live stems.

The model was initiated from bare ground with 200 seedlings and tended to reach equilibrium after ~200 years. All model runs in this study used 50 patches of 0.02 ha (based on an 8 m crown radius for a typical large stem) and were 1000 years long. Output for the final 500 years is reported as the 50-patch 500-year mean with the standard deviation between the 50 patches.

Model sensitivity analysis

Method

We ran a sensitivity test of all model parameters. Each parameter was varied in turn by a factor of 0.5, 0.75, 1.5 and 2 from its nominal value (Table A2). The sensitivity, S, is defined as $S_x = ([R_{adj} - R_n]/ R_n) / ([P_{adj} - P_n]/ P_n)$, where x is the factor by which the nominal value is changed, R_{adj} is the response for the model run with the adjusted value, R_n is the response with the nominal value, and P_n and P_{adj} are the parameter values for the nominal and adjusted cases respectively. Patch basal area was used as the response variable. The parameters used in the model and their source, magnitude and sensitivity, are shown in Table A2.

Results

The model output were much more sensitive to the growth parameters compared to those controlling regeneration (Table A2). In order of sensitivity, they were: the maximum rate of photo synthesis (P_{max}); the fraction of assimilate allocated to respiration (R_a); the half-saturation rate of photosynthesis (k_p); leaf carbon per leaf area *(LCA)*; allocation to fine roots (A_{fr}); the leaf angle distribution (k); and the leaf area:basal area ratio (LA:BA). These are basic physiological parameters, which are well

constrained by local field observations (P_{max}, and k_p, by Tuohy et al. 1991; LCA and LA:BA by our data) or to a lesser degree, globally (R_a, Waring et al. 1998 and k, Norman and Campbell 1989). A_{fr} is badly constrained, particularly in savanna environments. Of the mortality and regeneration parameters, the intrinsic mortality rate (M_i) was the only one that significantly affected the final patch basal area.

Table A1. Allometric equations used in the model and derived from local field data. Equation forms are defined as follows: power, Y = aX^b; linear, Y = aX ± b. n is the number of samples of field data used to fit the function.

Dependant (Y) variable	Independent (X) variable	Form	a	b	n	r^2	min X	max X	Notes
C stock of stem, kg C	DBH, m	power	4222	2.6	29	0.93	0.05	0.72	
C stem : C root+stem	DBH, m	linear	0.32	0.6	23	0.26	0.05	0.72	
Height of top of tree, m	DBH, m	linear, with saturation	42.6		80	0.67	0.07	0.86	where DBH> 60 cm, ht = 25 m
Height of base of canopy, m	DBH, m	linear, with saturation	22.3		80	0.58	0.07	0.86	where DBH> 67 cm, canopy base = 15 m
Leaf area, m^2	Basal area, m^2	linear	1330		10	0.29	4.4	13.9	plot level data

Table A2. Parameters in the model, their source, nominal value and sensitivity, S_x, see text for symbol definitions. For the sensitivity analysis, we use the 50-patch mean basal area as the response variable. Each variable was changed in turn.

Parameter description	Parameter name	Nominal parameter value, P_n	$S_{0.5}$	$S_{0.75}$	$S_{1.5}$	S_2	Source of nominal parameter value
		Growth parameters					
fraction of GPP used for autotrophic respiration	R_a	0.5	-1.8	-1.9	-2.4	-1.0	Waring et al. 1998
extinction coefficient for Beer-Lambert law	k	0.5	0.0	-0.6	-0.2	0.1	Norman and Campbell 1989
amount of C allocated to fine roots, as a fraction of allocation to leaves	A_{fr}	1	-0.4	-0.2	-1.0	-0.6	consistent with Castellanos *et al.* (2001). Similar to Table 5 of Hendricks *et al.* (2006), which is for temperate systems.
maximum rate of photosynthesis, μmol C m^{-2} s^{-1}	P_{max}	10	2.0	2.0	2.5	2.3	Tuohy and Choinski 1990; Tuohy *et al.* 1991
PAR intensity at which 0.5 P_{max} is obtained, μmol s^{-1} m^{-2}	k_p	250	-1.7	-1.7	-1.1	-0.7	Tuohy and Choinski 1990; Tuohy *et al.* 1991
leaf carbon per leaf area, gC m^{-2}	LCA	50	-1.5	-1.1	-1.7	-0.9	Nottingham 2004; Chidumayo 1997
leaf area per unit basal area, m^2 m^{-2}	$LA{:}BA$	1330	0.0	-0.6	-0.1	-0.1	See Table A1
		Mortality and Regeneration parameters					
intrinsic mortality rate	M_i	0.02	-0.8	-1.3	-1.3	-0.5	estimated, similar to Desanker and Prentice (1994)
diameter, m, at which a seedling is considered to have developed a rootstock and the ability to resprout	$S_{resprout}$	0.02	0.0	-0.2	-0.1	0.0	estimated
number of seedlings per ha established in a recruitment year	S_{new}	100	0.0	-0.5	0.2	0.1	estimated
probability of a recruitment year occurring	$P_{recruit}$	0.03	0.1	0.1	-0.2	0.0	estimated
Probability of a root stock failing to resprout after fire	S_{mort}	0.04	-0.2	-0.3	0.1	0.0	this study

Table A3. Piecewise parameterisation of fire-induced mortality rates shown in Figure 3. These are used to calculate stem mortality in the model in years when a fire occurs.

	Fire intensity (TA tercile)		
	high	med	low
a_x	-70	-70	-60
b_x	5	4	2
b_{x_sat}	-2	-3	-3.8

Where:

DBH < 10 cm,   Log odds of top-kill $= -a_x$ DBH $+ b_x$

DBH> 10 cm,   Log odds of top-kill $= b_{x\_sat}$
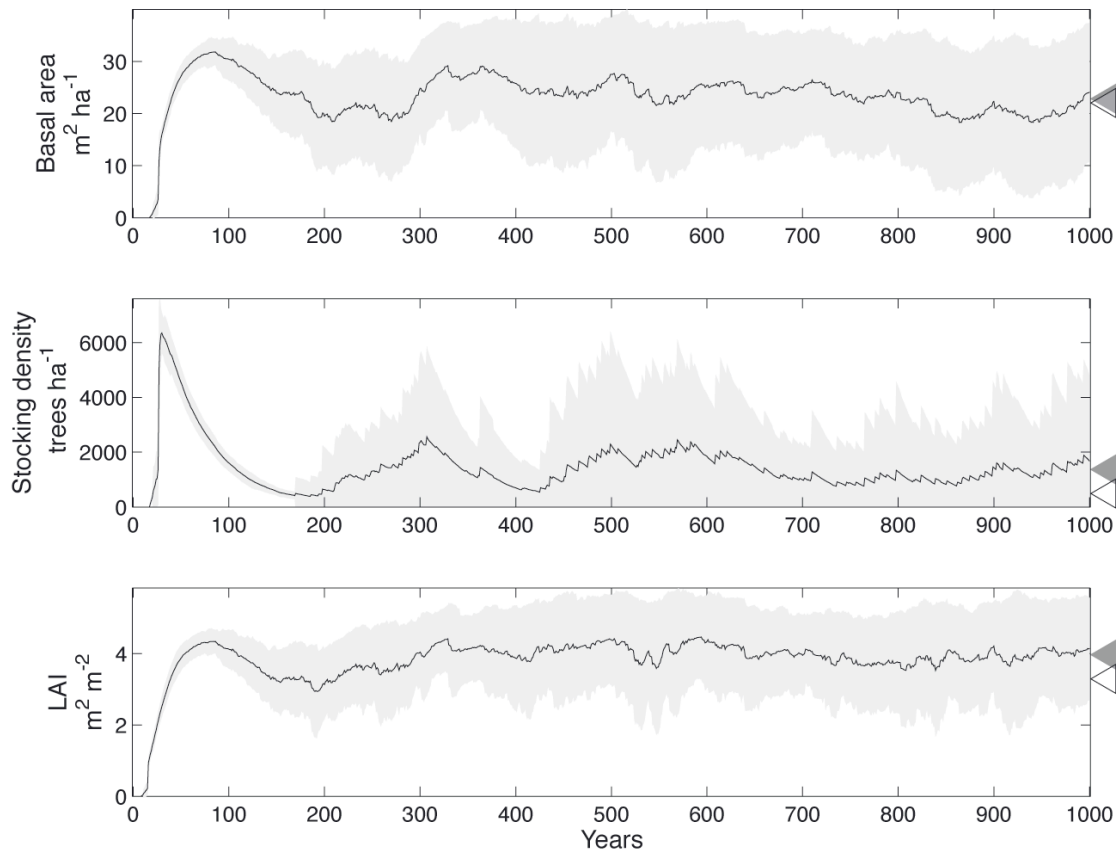
Figure A3. Model output of patch characteristics for a low fire scenario (FRI = 100, low intensity fires) from initiation with bare ground at year zero to 1000 years. The mean of the 50 patches is shown with a black line. One standard deviation of the 50 patches is shown above and below the mean with a grey shade. The white triangles on the right Y axis indicate the field data for the Marrameu forest plot (Site 2), the grey triangles indicate the 50-patch mean of the final 500 model years.
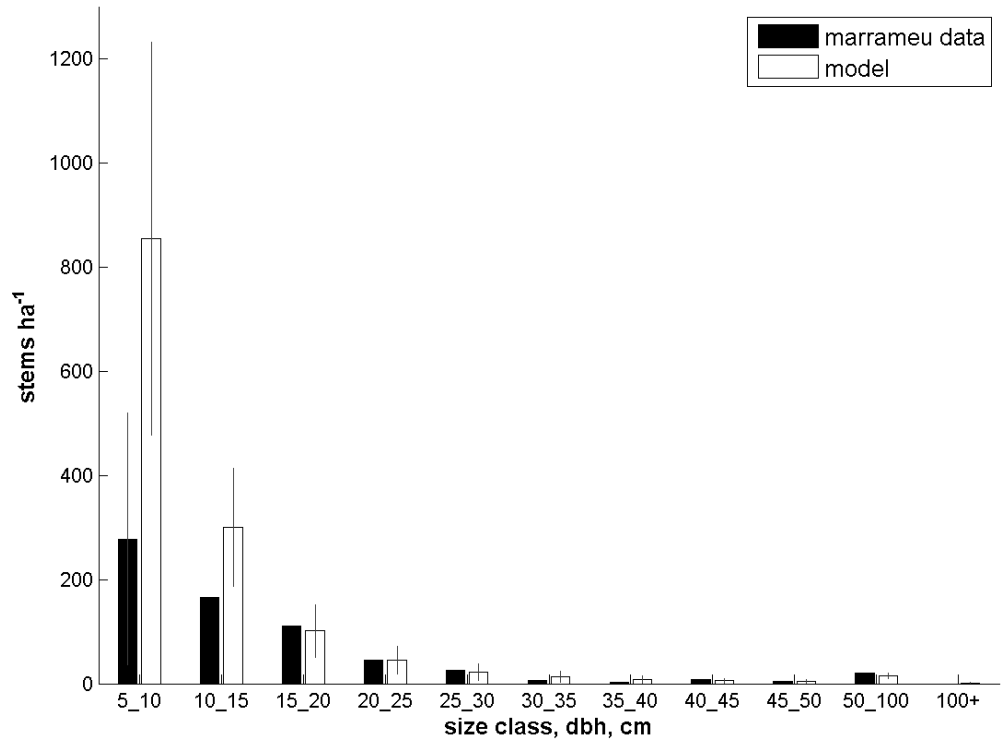
Figure A4. Comparison between the model output (open bars) for the low fire scenario (FRI = 100, low intensity fires) and a 0.5 ha inventory (filled bars) in a closed canopy dry forest (Site 2). For model results the vertical lines show the standard deviations between the 500-year 50-patch means. For the field data in the smallest size class, the standard deviation of 4 belt transects is shown. The larger size classes all come from one 0.5 ha plot with no replicates, so no standard deviation is shown.

Supplementary figures

Figure A5. a) A damaged tree bursts into flames and b) another collapses after the bole has combusted.
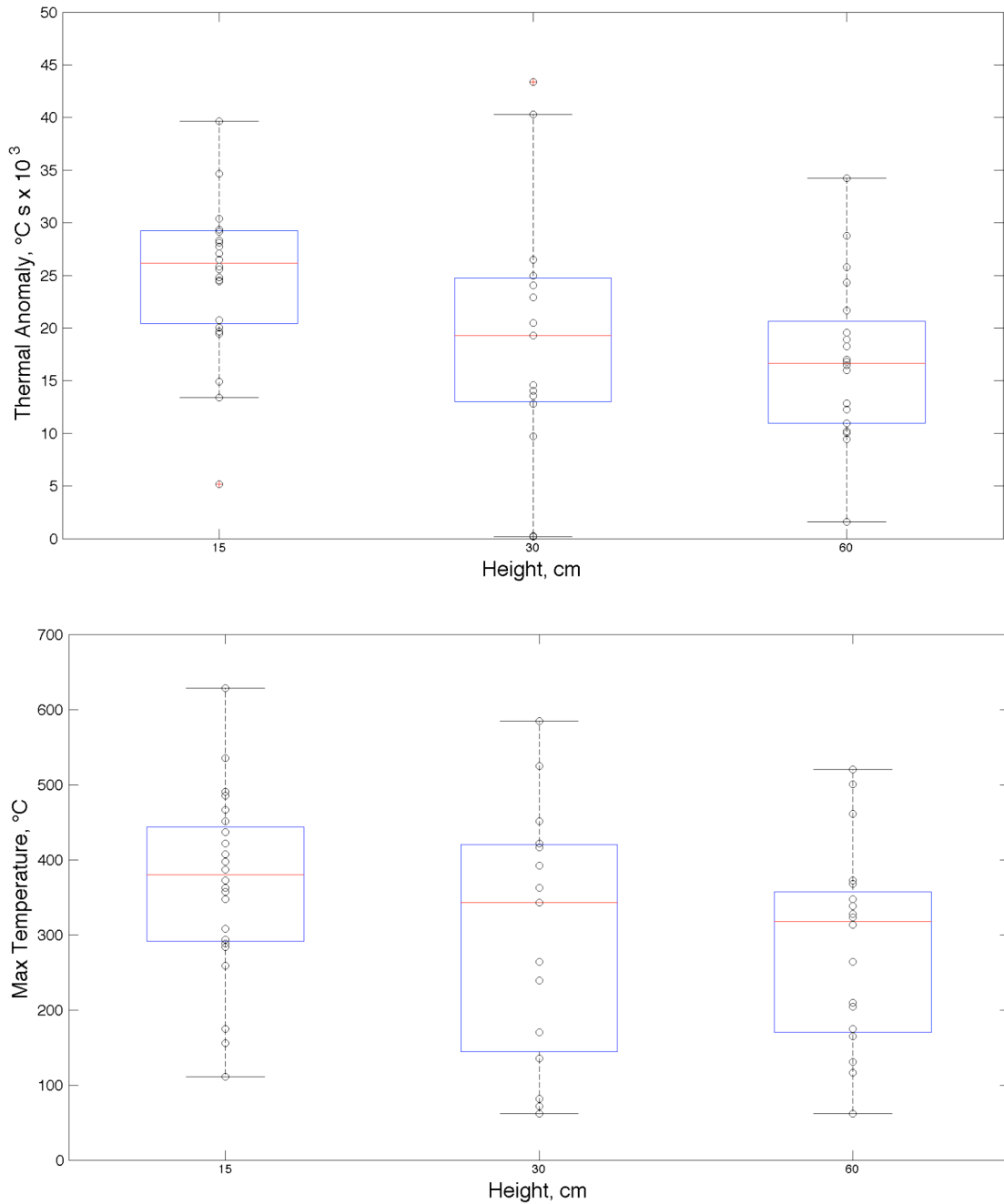
Figure A6. top) thermal anomaly and bottom b) maximum temperature recorded at various heights. Boxplots show the measurements from 68 temperature-time profiles from the 7 fires. The thermocouples were located directly above each other at the centre of each 10 m triangle. The median is shown with a red line, the boxes mark the interquartile range, and the open circles show the data.
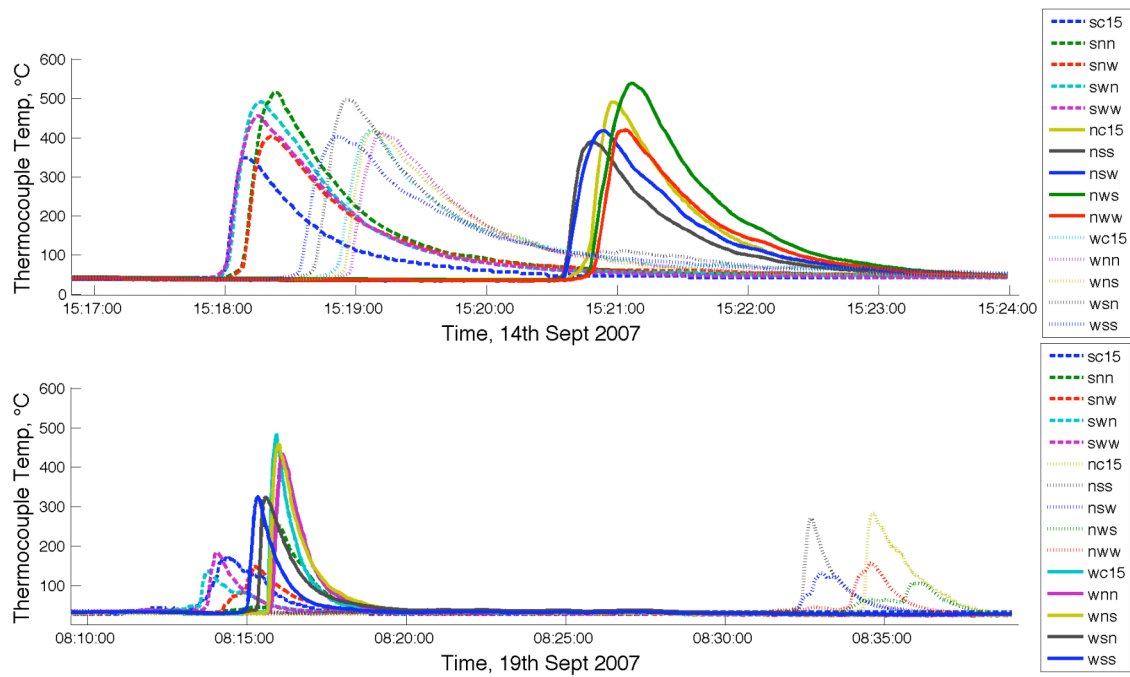
Figure A7. Examples of temperature–time profiles for a) the most intense fire (plot 6) and b) the least intense fire (plot 5), as judged by the mean of the 10 m triangle. The three 10 m triangle on each plot are indicated with solid, dashed and dotted line. The legend indicates the location of each thermocouple: the first letter indicates the cardinal location of the 10 m triangle, the second indicates which 2m triangle the TC lies in, and the third indicates which corner of the 2m triangle. Note the different X-axis time scales.

Supplementary references

Bond, W. J. and J. J. Midgley (2001). "Ecology of sprouting in woody plants: the persistence niche." Trends in Ecology & Evolution 16(1): 45-51.

Castellanos, J., V. J. Jaramillo, R. L. Sanford and J. B. Kauffman (2001). "Slash-and-burn effects on fine root biomass and productivity in a tropical dry forest ecosystem in México." Forest Ecology and Management 148(1-3): 41-50.

Chidumayo, E. N. (1992). "Seedling ecology of two miombo woodland trees." Plant Ecology 103(1): 51-58.

Chidumayo, E. N. (1997). Miombo ecology and management : an introduction. London, IT Publications in association with the Stockholm Environment Institute.

Chidumayo, E. N. (2004). "Development of *Brachystegia-Julbernardia* woodland after clear-felling in central Zambia: Evidence for high resilience." Applied Vegetation Science 7(2): 237-242.

Desanker, P. V. (1996). "Development of a MIOMBO woodland dynamics model in Zambezian Africa using Malawi as a case study." Climatic Change 34(2): 279-288.

Desanker, P. V. and I. C. Prentice (1994). "Miombo - a Vegetation Dynamics Model for the Miombo Woodlands of Zambezian Africa." Forest Ecology and Management 69(1-3): 87-95.

Hendricks, J. J., R. L. Hendrick, C. A. Wilson, R. J. Mitchell, S. D. Pecot and D. Guo (2006). "Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review." Journal of Ecology 94: 40-57.

Jones, H. G. (1992). Plants and microclimate : a quantitative approach to environmental plant physiology, Cambridge University Press.

Li-Cor (1989). LAI-2000 Plant Canopy Analyzer Operating Manual. Lincoln, NE, Li-Cor.

Mlambo, D. and I. Mapaure (2006). "Post-fire resprouting of *Colophospermum mopane* saplings in a southern African savanna." Journal of Tropical Ecology 22: 231-234.

Norman, J. and G. Campbell (1989). Canopy structure. Plant Physiological Ecology: Field Methods and Instrumentation. R. W. Pearcy, J. R. Ehleringer, H. A. Mooney and P. W. Rundel. London, Chapman & Hall: 301-325.

Nottingham, A. (2004). The characterisation of foliar N-concentrations and presence of N-fixers in Miombo woodland, Mozambique. MRes Environmental Biology, University of Dundee.

Ridler, T. W. and S. Calvard (1978). "Picture Thresholding Using an Iterative Selection Method." IEEE Transactions on Systems Man and Cybernetics 8(8): 630-632.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira (1964). "A Quantitative Analysis of Plant Form-The Pipe Model Theory: ii. Further Evidence of the Theory and its Application in Forest Ecology." Japanese Journal of Ecology 14(4): 133-139.

Tuohy, J. M. and J. S. Choinski (1990). "Comparative Photosynthesis in Developing Leaves of *Brachystegia-Spiciformis* Benth." Journal of Experimental Botany 41(229): 919-923.

Tuohy, J. M., J. A. B. Prior and G. R. Stewart (1991). "Photosynthesis in Relation to Leaf Nitrogen and Phosphorus-Content in Zimbabwean Trees." Oecologia 88(3): 378-382.

van Gardingen, P. R., G. E. Jackson, S. Hernandez-Daumas, G. Russell and L. Sharp (1999). "Leaf area index estimates obtained for clumped canopies using hemispherical photography." Agricultural and Forest Meteorology 94(3-4): 243-257.

Waring, R. H., J. J. Landsberg and M. Williams (1998). "Net primary production of forests: a constant fraction of gross primary production?" Tree Physiology 18(2): 129-134.

4. Tree green-up precedes rainfall across Southern African woodlands

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Abstract

In seasonally dry ecosystems, trees adopt a variety of phenological strategies to maximise net carbon gain in the absence of abundant water. One common strategy for woodland trees is deciduousness in phase with the seasonal rains, and deciduous trees dominate African woodlands. However, several studies have shown that these deciduous trees are in fact producing new leaves before the rains, for unknown reasons. Here both ground-based and Earth Observation data are used to show that this pre-rain green-up is the dominant strategy across all of southern tropical Africa. Green-up precedes the onset of rain by an average of 60 days (57,62, 95% confidence intervals) in wetter woodlands and 37 days (34,40) in dry miombo woodlands. These results suggest green-up is under endogenous control and that stems have a positive water status at the end of the dry season. Such endogenous control of green-up may increase vulnerability to predicted changes in rainfall patterns and raises questions about current model representations of savanna vegetations. It also highlights intercontinental differences in savanna leaf phenology strategies.

Introduction

Woodlands are the dominant vegetation type of Southern Africa and cover an area > 4.1 million km^2 (White 1983). They are found in climates with distinct wet and dry seasons, with mean annual precipitation (MAP) of 540–1700 mm and a 3-7 month dry season during which little rainfall occurs (Frost 1996). The savannas and woodlands of Africa are dominated by deciduous trees (White 1983), and this deciduousness is broadly linked to the seasonal patterns of rainfall (Moulin et al. 1997; Azzali et al. 2000; Zhang et al. 2005). However the cues and determinants of savanna

10   woodland leaf phenology are not understood and little studied. The processes controlling tropical tree leaf phenology remain obscure, even in the better studied wet tropics (Borchert 1994; Borchert 1998), but can be divided into endogenous controls, thought to be triggered by day-length (Borchert 1994; Borchert *et al.* 2002), and responses to exogenous changes in the water status of the soil-plant-atmosphere continuum (Myers *et al.* 1998; Rivera *et al.* 2002). A theory of leaf phenology has been developed (Borchert 1994; Rivera *et al.* 2002) that categorises trees as 1) evergreen/leaf exchanging species, found in locations with year-round access to soil water, 2) semi/brevi deciduous species with short periods of

20   leaflessness, which flush by some endogenous trigger before rain occurs, and need to hydrate by deep water access or from stored water reserves, or 3) true deciduous species that link their leaf display to soil-plant-atmosphere water relations and are plastic in their response to changing water availability (Myers *et al.* 1998).

There is site-specific evidence that documents tropical savanna trees flushing their leaves before the rains (Williams et al. 1997; de Bie et al. 1998; Devineau 1999; Do et al. 2005; Elliott et al. 2006; Archibald et al. 2007), but these studies are limited in temporal or spatial extent, and non-existent in the mesic woodlands of tropical Southern Africa. Despite

30   much anecdotal evidence (Frost 1996), pre-rain green-up has never been

quantified regionally across Southern African woodlands. Regional estimates are hindered by the problems of interpreting satellite data in mixed tree-grass ecosystems, but recent work (Archibald et al. 2007) provides a way forward.

An understanding of the nature of the deciduousness of southern African woodlands is vital for predicting how these woodlands will respond to, and feed-back upon, predicted changes in moisture availability (Reich 1995; Fuller et al. 1996; New et al. 2003; Christensen et al. 2007). These woodlands are inhabited by some of the poorest people on Earth
10 (Campbell *et al.* 2007), whose livelihoods are closely coupled to the ecosystems services that originate from the primary productivity of these woodlands (Frost 1996).

Here we characterise the relationship between rainfall and leaf display across Southern Africa. We report >3.5 years of ground observations of leaf display from 15 plots in the woodlands of Mozambique, and conduct a regional analysis using satellite-derived vegetation indices and rainfall data. Our aim is to characterise the phenology of southern African vegetation and analyse its relationship to rainfall in different savanna and woodlands types.

20 ## *Methods*

Our methods can be divided into two components: 1) data collection of ground-based and Earth observation (EO) time-series data relating to leaf display and rainfall at a site in Mozambique. After ensuring that the ground-based and EO data are congruent, we obtain satellite data for all of tropical southern Africa. 2) We analyse the time-series data to derive day-of-year of green-up (G_{DOY}) and the start of the rainy season (R_{DOY}). Spatial and interannual variability in these dates are then analysed by vegetation type.

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Data collection

Local observations

Site details

Fifteen 1 ha permanent samples plots (PSP) were established in a range of vegetation types in Sofala province, Mozambique in June 2004. The plots are spread through an area approximately 40 km by 40km (centred on 18.979°S, 34.176°E), adjacent to the Gorongosa National Park (Tinley 1977; Williams *et al.* 2008). The vegetation on the plots included miombo woodland that had previously been used for agriculture but is now fallow, miombo degraded by the removal of large stems for charcoal production, undisturbed miombo in the National Park, both fenced and unfenced, and *Combretum* savanna on hydromorphic soils. The plots were randomly located along the track and road network in the area, and were all > 250 m from the road.

Plant area index (PAI)

We monitored the seasonal cycle of plant area index (PAI) of trees using monthly hemispherical photography (Fuller 1999) for 46 months from June 2004 to May 2008 (inclusive) on the PSPs. On each PSP, each month, we acquired nine images on a 20 x 20 m grid. Photos were taken under diffuse light conditions – either at dawn or dusk, or during overcast condition, and from identical positions with the camera body oriented to the north and the lens rotated to the vertical. We used a Nikon Coolpix 4500 with a FC-E8 fisheye converter on a leveled tripod at 1.5 m height. The lens is fully hemispheric (Fig S3). For logistical reasons we were unable to collect photos in seven months of the 46 month period of this study.

A total of 4718 photos were acquired, coded with date and location and stored in a database (FileMaker Pro, Apple Computer Inc, CA). Each

image was visually inspected for quality control, and badly exposed or directly illuminated images were discarded.

The images were then analysed to estimate leaf area index in three stages: 1) The images were brightness-thresholded to separate sky and canopy elements. We used the algorithm of Ridler and Calvard (1978) to automatically select the threshold brightness value and used brightness in the blue channel, which is most absorbed by canopy elements. 2) Sky and non-sky pixels were counted in azimuthal and zenithal segments of the image to acquire a distribution of gap fractions. We assumed that the lens geometry was spherical (i.e. that distance from the optical centre was a linear function of zenith angle (Baret 2004)) and only used the portion of the image between a zenith angle of 0° and 60°, as beyond this the image is of low resolution and mixed pixels become common. 3) The gap fractions were converted to plant area index using the equation of (Li-Cor 1989). The three steps were undertaken using Matlab (Mathworks Inc, USA).

Enhanced Vegetation Index (EVI)

We supplemented these ground-based measurements with enhanced vegetation index (EVI) data (Huete *et al.* 2002) derived from reflectances measured by a space-borne MODIS sensor (ORNL-DAAC). We used MOD13Q1 v5 EVI data for the 250 m pixel that covers each PSP, and extracted the full time series from the Terra platform (2000-2008) using the subsetting tool of the ORNL DAAC. EVI (Huete *et al.* 2002) is calculated as follows:

$$EVI = G \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + C_1 \times \rho_{red} - C_2 \times \rho_{blue} + L}$$

where ρ are partially atmosphere corrected surface reflectances, L is the canopy background adjustment that adjusts for nonlinear, differential NIR and red radiative transfer through a canopy, and C_1 and C_2 are coefficients of the aerosol resistance term, which uses the blue band to

correct for aerosol influences in the red band. $L=1$, $C_1=6$, $C_2 = 7.5$, and $G = 2.5$ (from Huete *et al.* 2002). EVI is more robust to atmospheric composition changes than other vegetation indices. MOD13Q1 is a 16 day composite product of daily acquisitions that uses one of three compositing techniques (Huete *et al.* 2002) to minimise problems associated with clouds and off-nadir views. Our time period of interest for green-up detection was characterised by sparse cloud cover and high pixel reliability.

Precipitation

10 Rainfall data for the Nhambita area comes from three sources. 1) daily accumulations from a manual rain gauge near the Gorongosa National Park headquarters at Chitengo, 25 km from our study site (Oct 2000-Nov 2005, provided by ARA CENTRO). 2) half hourly accumulations from our automated weather station (Skye Instruments, UK), adjacent to the Park gauge (Nov 2005-present) 3) a manual gauge operated by Mr Piet van Zyl (Envirotrade Lda), at the centre of our study area. Data from 3) were used for a 4 month period (Oct 2007 - March 2008) when the automatic gauge failed. For the 5 month period when all three data sets are available, they show cumulative rainfall of 817, 821 and 803 mm,

20 respectively. As such we did not adjust the data from the different sources, and they were combined into one daily time series.

Regional observations

For the regional analysis we use MODIS EVI aggregated to a 0.05° lat/long grid (MOD and MYD 13C1.5, available from LPDAAC). These two MODIS products composite data over 16 day periods, 8 days out of sync with each other. We interleave the 16 day composites to improve the temporal resolution of the time series. There is a strong seasonal cycle to the quality (pixel reliability) of the EVI values. We address this by assigning weights based on the pixel reliability (full details are in the

30 green-up detection section).

For regional rainfall estimates we use the Global Precipitation Climatology Project (GPCP) 1° daily precipitation data set (Huffman *et al.* 2001). This product blends rainfall estimates from ground-based gauges, with satellite-borne (geostationary and low Earth orbit) infrared and microwave sensors to produce daily gridded precipitation estimates. The temporal resolution of the original data sets vary from 3 hourly to monthly.

Analysis

We use a time series ARIMA model (autoregressive integrated moving average model as implemented in SPSS for Mac (SPSS Inc. IL, USA)) to assess the correlation between the ground measurements of PAI and the MODIS measurements of EVI for our plots in Nhambita. All other processing was done in Matlab (Mathworks Inc. USA).

Green-up threshold detection (G_{DOY}*)*

Many definitions and techniques have been used to derive green-up dates from reflectance and/or EVI data (Reed et al. 1994; Kang et al. 2003; Zhang et al. 2003; Archibald et al. 2007; Bachoo et al. 2007), with no consensus as to techniques, or a precise definition of what green-up is. The challenge is to avoid classing spurious noise in the signal as green-up, whilst attempting to detect real green-up as soon as possible. We adopt an empirical method based on short and long term gradients, and conduct a sensitivity analysis to show that our conclusions are robust to reasonable definitions of what constitutes noise and signal in the time series.

Savannas and woodlands are by definition a mixed tree-grass ecosystem, and as such any satellite observation of optical spectra are a mixture of the signal from these components (Archibald et al. 2007). However, grass green-up only occurs once soil moisture is above dry season levels (Hoffmann et al. 2005; Archibald et al. 2007), and so green-up dates before the rains should represent tree green-up. The work of Archibald

and Scholes (2007) and Chidumayo (2001) support this assumption, as do our local observations (see Figure S1). As such we assume that any increase in EVI before the rains commence is a function of changes in the tree canopy and not that of the grass. We check this assumption by looking at the strength of the correlation between EVI and the PAI ground-based data in Nhambita

The calculation of day of year of green-up (G_{DOY}) is done for each pixel or PSP and for each annual (March-March) time series. First the data are smoothed with a Savatsky-Golay filter, which weights pixels with 'marginal' reliability to be half those of pixels with 'good' reliability (reliability terms are from the MODIS QA data). The smoothed data are fitted with a piecewise cubic Hermite interpolation and the year's minimum value is found. Searching forward from this point, t, G_{DOY} is indicated by the following criteria being met:

1) Instantaneous rule:

$\overline{\nabla}(EVI_{t:t+1}) > 0$, i.e. the gradient over the day must be positive

Where $\overline{\nabla}(EVI_{t:t+1})$ is the mean gradient of the smoothed EVI time series for one day.

2) Short-term rule:

$$\overline{\nabla}(EVI_{t:t+t_s}) > \frac{\Delta_S}{t_S}$$

Where $\overline{\nabla}(EVI_{t:t+t_s})$ is the mean gradient of the smoothed EVI time series for the period t to $t+t_s$. Δ_S is an EVI change threshold (default value = 0.02) that is the critical change in EVI over time period t_s (default value 30 days)

3) Long-term rule. This increase must be sustained such that:

$$\overline{\nabla}(EVI_{t:t+t_L}) > \frac{\Delta_L}{t_L}$$

Where $\overline{\nabla}(EVI_{t:t+t_L})$ is the mean gradient of the smoothed EVI time series for the period t to $t+t_L$. Δ_L is an EVI change threshold (default value = 0.2) that is the critical change in EVI over time period t_L (90 days)

The first point that matches the three rules is selected as the G_{DOY} for that year.

Δ_S was set to 0.02 EVI units to exceed the between-sensor (Aqua and Terra) noise, and because there is a 95% chance that 0.02 > the standard deviation between a smoothed line (Savatsky-Golay with 41 day window and 2 degree polynomial) and the real data. t_S was set to 30 days empirically, approximating the expected time constant for significant green-up. Δ_L was set to 0.2, to capture large seasonal changes in EVI, typical of woodlands and savannas (Zhang *et al.* 2005). t_L was set to 90 days empirically, approximating the maximum duration of a dry-wet season transition (Zhang *et al.* 2005). We conduct a sensitivity analysis on all these parameters below.

For the regional analysis we ran this procedure for each 0.05° pixel from 2°S to 23°S for the African mainland, for each March-March year (2000-2008). We excluded pixels with annual amplitude <0.1 EVI, and those with a maximum EVI < 0.3, as these likely indicate areas that are evergreen, or not wooded. For calculation of D, the number of days between green-up and rain onset, we use the 0.05° MODIS data and the 1° rainfall data, and aggregate the higher resolution data by taking the angular mean of G_{DOY}. However the histograms (Fig. 3) present the G_{DOY} data at the original 0.05° resolution.

Rain onset detection (R$_{DOY}$)

For rain onset detection we follow a similar method to the derivation of the green-up dates. For the regional analysis, we use the daily GPCP data for the same period as the MODIS observations (March 2000—2008). For each year (March-March) and for each pixel, we locate the month of minimum rainfall, and search forward from the first of that month until two criteria are met. The criteria are based on Tadross (2005) and are designed to detect rainfall that allows the start of maize cultivation. Thus they are conservative with respect to tree water

requirements, but probably match those of native grasses. The criteria are a) 10 days during which a total of 25 mm of rain fall, followed by b) 20 days with > 20 mm total rain. The same detection procedure was followed for the ground-based rainfall data.

Vegetation map

Green-up and rain onset frequencies are analysed by major vegetation types based on the map of White (1983, data from the NASA Global Change Master Directory) which we downsampled from its original resolution of 30" by taking the mode to 1° resolution for comparison to the rainfall data and to 0.05° for the EVI data (Figure S3). We excluded pixels that had more than 10% water.

Sensitivity analysis

To test the sensitivity of our regional results to the parameters used in green-up detection, we used a subsample of the EVI data (every 100th pixel) and ran the green-up detection algorithm 135 times varying the four parameters as shown in Table 1.

Table 1. Parameters used in sensitivity analysis.

Parameter	symbol	Min	Max	Default	Units
short-term time period (days)	t_s	20	40	30	Days
short-term change in EVI	Δ_s	0.01	0.03	0.02	EVI units
long-term time period (days)	t_L	60	120	90	Days
long-term change in EVI	Δ_L	0.05	0.4	0.2	EVI units

For each of the 135 runs we recalculate the mean D (days between G_{DOY} and R_{DOY}) for the wet and dry miombo regions as defined by White's map.

Results

Local observations

Mean annual rainfall in Nhambita for our study period (2000-2008) was 831±337 mm (± indicates standard deviation throughout this section), close to the long term average of 840±269 mm (Tinley 1977). Annual totals (Oct-Oct) ranged from 452-1400 mm, similar to historical extremes.

82% of the rain fell between November and March (inclusive) and May-September all average < 20 mm month^{-1} (Fig. 1 bottom panel). April and October are the transition months and have very variable rainfall (e.g. October had 211 mm in 2000 and no rain in 2001, 2005 and 2006). For the five months of May-September (inclusive) rainfall never totalled more than 90 mm, and averaged 52±33 mm. Date of rain onset according to our criteria ranged from 13 October to 2 December, mean 12 November ± 19 days (Fig. 1, blue vertical lines).

Leaf display in Nhambita had a seasonal cycle with very little interannual variability. PAI peaked in February or March and then fell to a minimum in September (Fig. 1 middle panel), with only a brief period of leaflessness. On some plots a few trees retained a small number of leaves throughout the dry season. PAI was well correlated to MODIS EVI for the Nhambita plots (p <0.001 for a AR1 model, higher order ARIMA model terms not significant).

Green-up date averaged across the Nhambita plots, based on the EVI data, was 14 September in five of the eight years and 13, 29 and 30 September for the other years (Fig. 1, green vertical lines). The precision of these dates is limited by the resolution of the smoothed time series (16 days).

The 30 days prior to green-up had 0-7 mm of total rain (mean over the eight years 2±3 mm). For the 60 preceding days this ranged from 0-40 mm (10±13 mm) and for the 90 days 0-61 mm (26±22 mm).

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The number of days between green-up and rain onset (*D*) varied from 19 to 76 (mean 55±21 days).
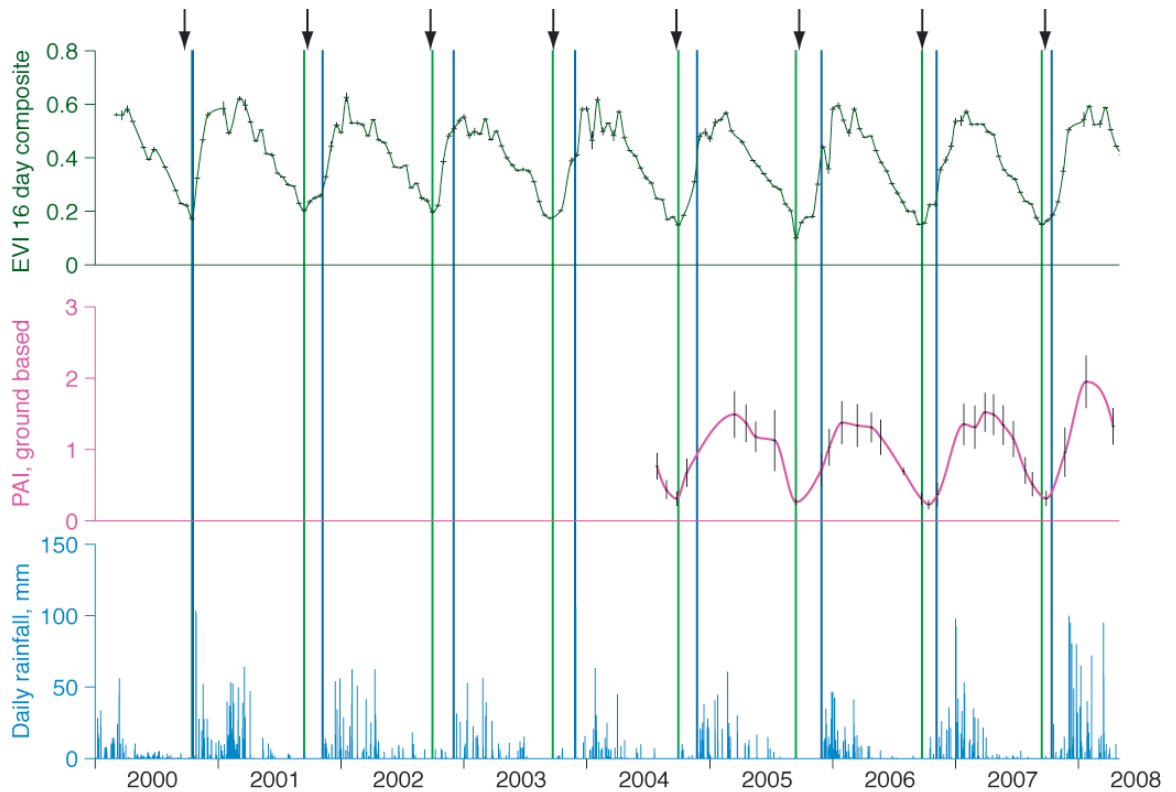
Figure 1. Time series of the MODIS Enhanced Vegetation Index (EVI, green), Plant Area Index from hemispherical photography (PAI , pink) and daily rainfall (blue) in Nhambita, Mozambique. X-axis ticks indicate 1 January. The vernal equinox (22 or 23 Sept) is shown with a black arrow (top). Vertical lines show the day of green-up (G_{DOY}, green) and the start of the rainy season (R_{DOY}, blue) as detected by our algorithms. EVI and PAI are shown as the mean of fifteen plots with ±2 s.e.m shown as a vertical black line and the time span of the measurements shown with horizontal black lines. EVI and PAI are fitted with a spline.

Regional analysis

The regional analysis revealed that pre-rain green-up is widespread across Southern Africa (Fig. 2 and 3). All major vegetation types (based on White 1983) with a strong seasonal cycle of EVI show pre-rain green-up (Figure 2, Table 2), and the number of days between green-up (G_{DOY}) and rain onset (R_{DOY}), *D* (R_{DOY}-G_{DOY} = *D*) varied from a mean of 2 to 60 days for the major vegetation types.

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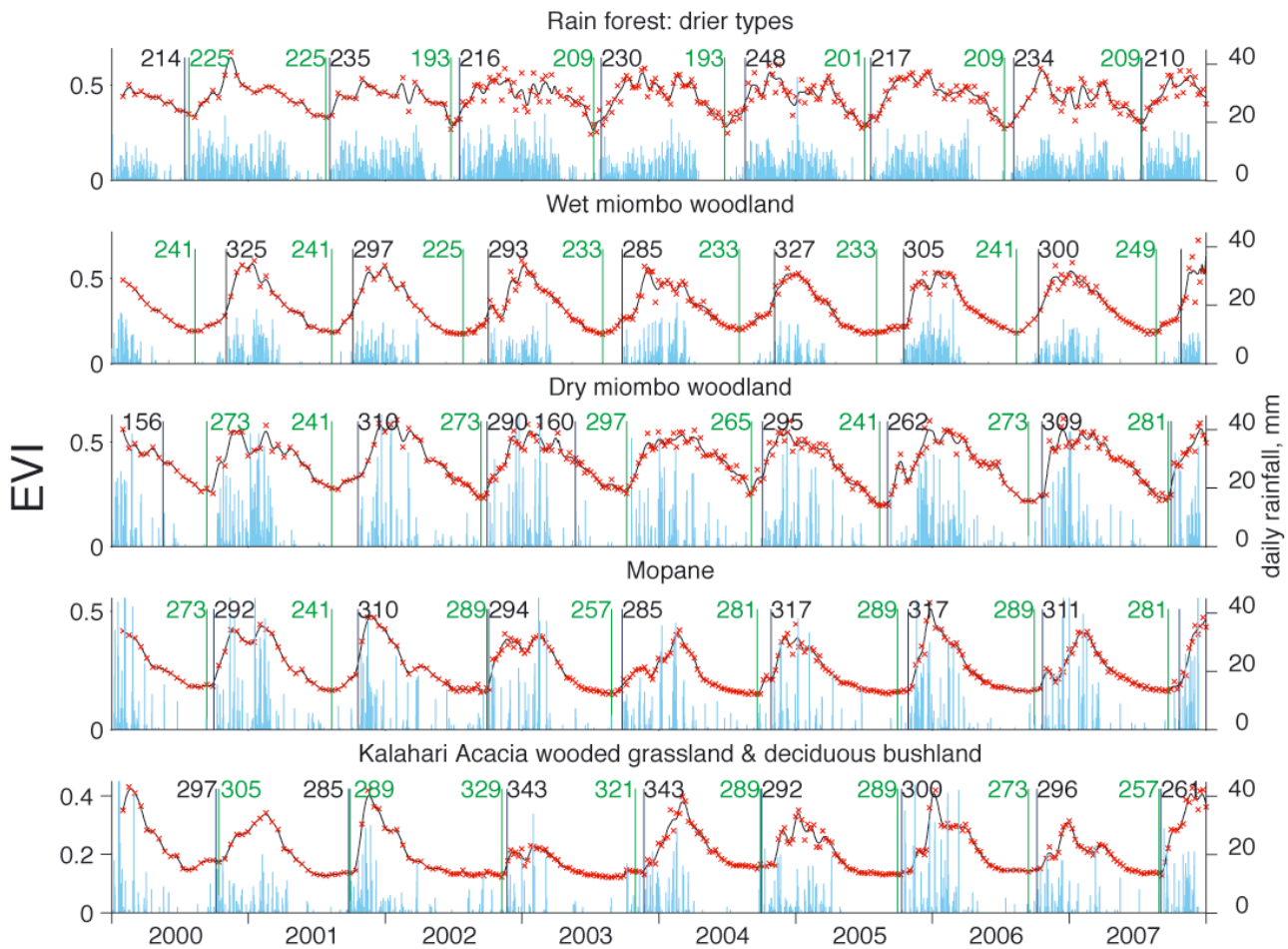
Figure 2. Examples of EVI and rainfall 8 year time series for randomly chosen locations in 5 major vegetation types in Southern Africa. EVI data points are shown with red crosses, and the smoothed fit with a black line. Green-up (G_{DOY}), as detected by our algorithm, is marked with a vertical green line with the DOY written in green. Daily rainfall (mm) is shown with blue lines and the start of the rainy season (R_{DOY}) is marked with a vertical black line and DOY. X-axis ticks mark January 1.

101
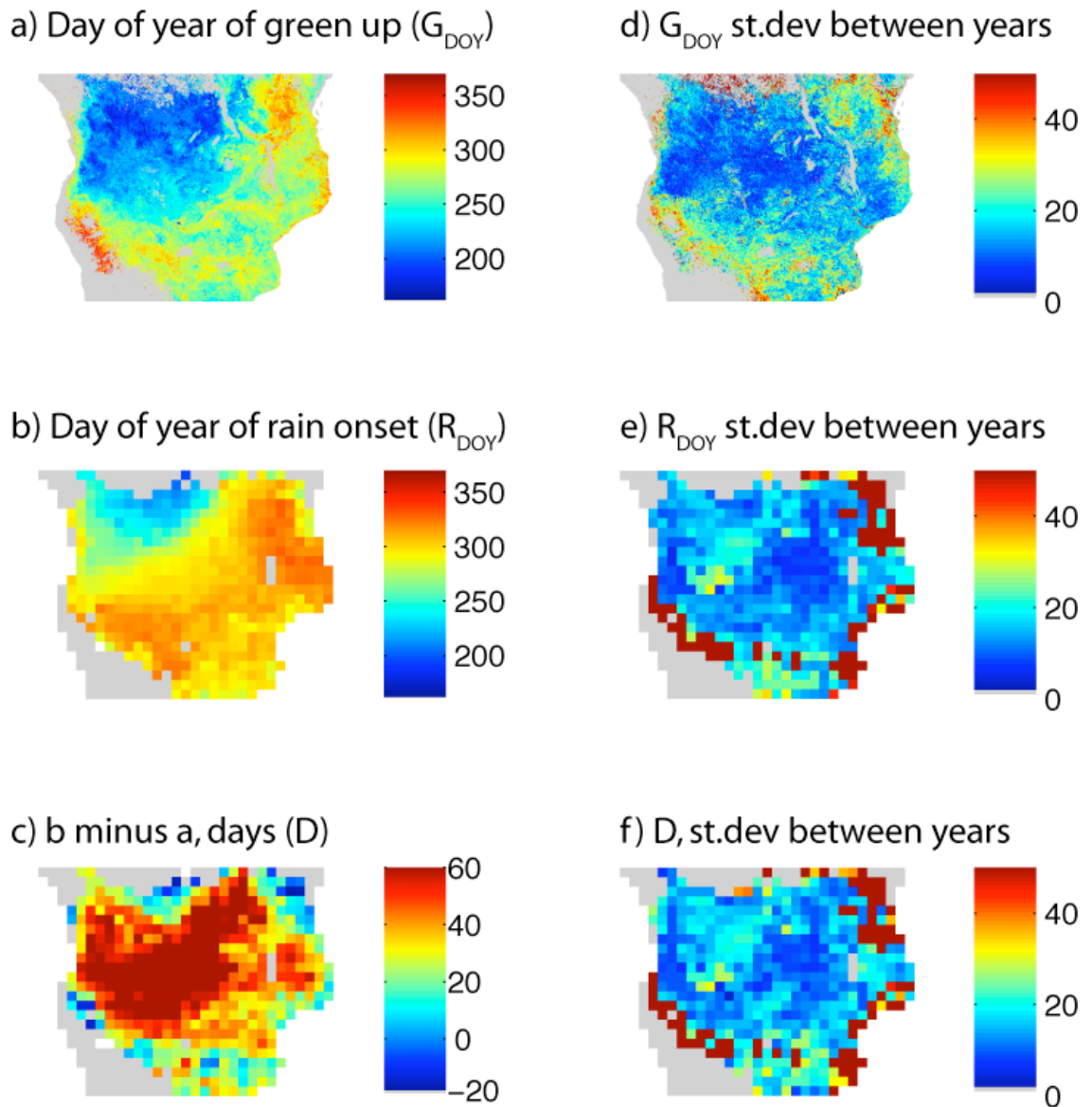
Figure 3. Maps of southern tropical Africa showing: a) mean DOY of green-up b) DOY of rain onset and c) The difference between a) and b). The right hand column of figures shows the standard deviation between the 9 years of data, 2000-8. Grey areas indicate regions which were not included in the analysis because of very sparse or evergreen vegetation, bimodal rainfall or no dry season.

Each year, the rains spread southeast from the Congo basin arriving in most of central southern Africa by DOY 280-320, and reaching the northeast and southwest of the region last, around DOY 330. Northern Angola and the Congo basin have earliest R_{DOY} from around DOY 250. Standard deviation (SD) in R_{DOY} between the 8 years was <20 days for

most of central southern Africa, but higher, i.e. more variable, in the northeast and southwest coastal regions.

Green-up DOY (G_{DOY}) followed a broadly similar, but earlier, pattern, occurring first in Angola, the Congo basin and parts of Zambia (G_{DOY} >200) and then moving south and east, reaching Zimbabwe, Botswana and Mozambique by DOY 250-280 and occurring last in Namibia and Tanzania (DOY 320). Similar to R_{DOY}, G_{DOY} was least variable in the northwest of the study area (SD ~10 days), and SD was <30 days for all the study area except the southwest shrublands and semi-deserts. Consistent with our Nhambita data, mean G_{DOY} in dry woodlands (DOY 270) closely followed the vernal equinox (DOY 266).

The number of days by which green-up preceded rain onset (D), was >15 days for 82% of the study area, > 30 days for 60% of the area, and > 60 days for 24% of area. 9% of pixels had green-up after rain onset (D<0), mostly in the wetter equatorial rainforest and arid south west.

Differences between vegetation types

We use White's vegetation map (White 1983) to analyse green-up behaviour by vegetation type. Each vegetation type had a distinctive time series of EVI, varying from the relatively aseasonal rainforest (Fig. 2a), to the highly seasonal woodlands and savannas (Fig. 2b-e). The wetter woodlands showed a clear and sustained increase in EVI months before rain onset, at which point there was a much more rapid increase in EVI (Fig. 2b). The drier (miombo, undifferentiated and mopane) woodlands had a less distinct pre-rain green-up, but EVI still increased before R_{DOY} (D = 37, 30 and 13 respectively). The *Acacia* savannas had almost synchronous (Fig. 2e) green-up and rain onset (mean D = 2, 95% confidence interval of the mean =-25, 29, Fig. 4e). The frequency distributions of G_{DOY} and R_{DOY} (Fig. 4), show that pre-rain green-up occurs in all the vegetation types analysed, but that it is rarer in both types of rainforest. In the *Acacia* savanna D is mostly > 0, but the mean

is not significantly different from zero, and D is below the resolution of the EVI time series. In the other vegetation types (the woodlands), D is always >0 and there are trends with vegetation type (Fig. 4, Table 2): Wet miombo greened-up on average 60 days before the rains, significantly different (p<1 E-22, one tailed T test), from the mean for dry miombo (37 days). This difference is part of a trend for drier woodlands and savannas to have lower values of D (Table 2). Within vegetation types, G_{DOY} was much more variable spatially than between years (shaded green area in Fig. 4), with wet miombo showing almost no interannual variability, but spatial variability in G_{DOY} from 180-300.
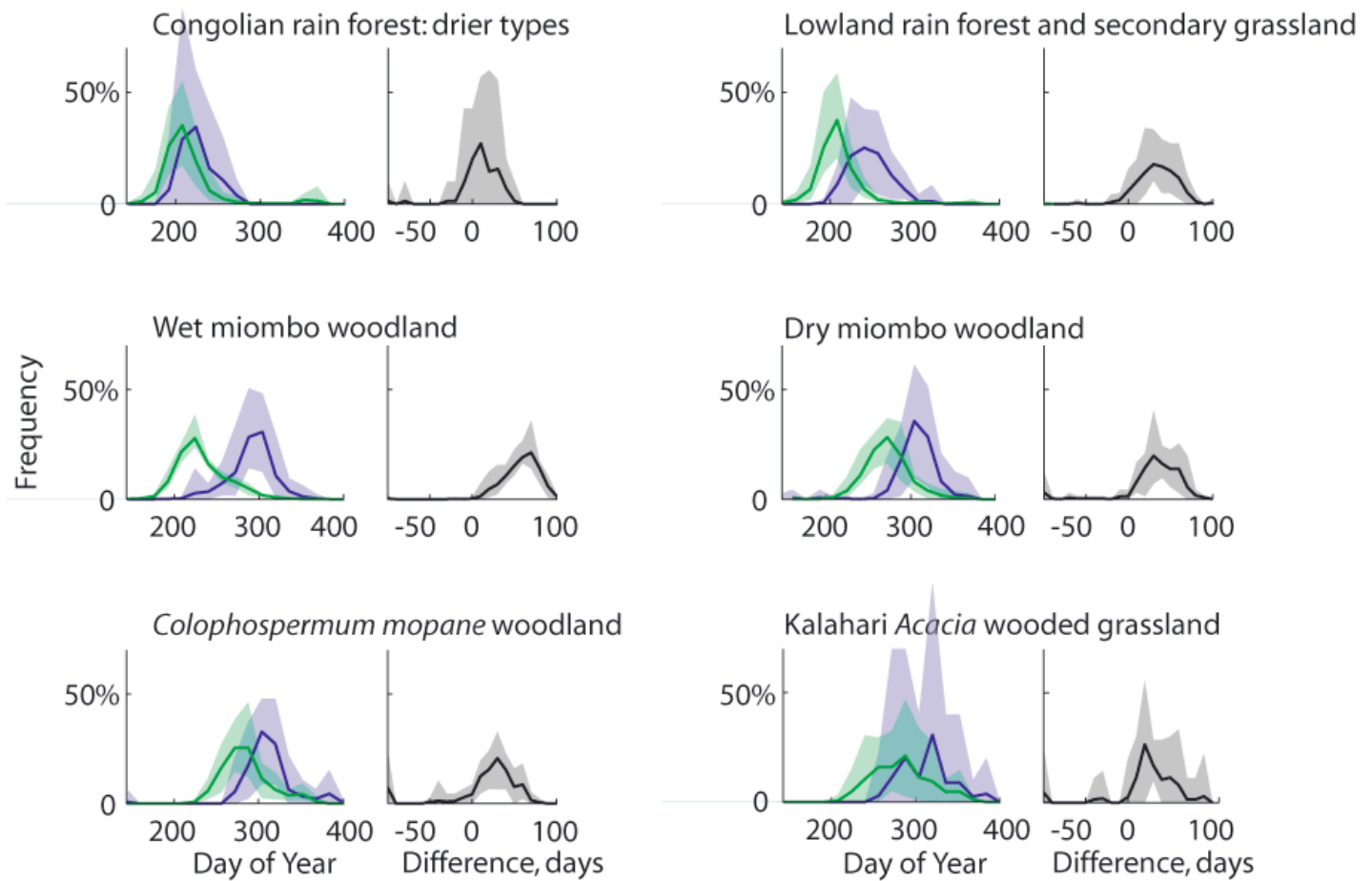
Figure 4. Frequency distributions of day of year of green-up (G_{DOY}, green) and rain onset (R_{DOY}, blue), left axes and the difference (R_{DOY}-G_{DOY}) on a per pixel basis (D, black, right axes), for the major vegetation types of Southern Africa. The pale shade shows the full interannual range of frequencies, and dark lines show the mean of the 8 years. Frequencies are calculated for 16 day bins and are for pixels at their original resolution (0.05° for G_{DOY}, 1° for R_{DOY})

We explored whether G_{DOY} varies spatially in a way that is correlated with R_{DOY}. Such a correlation would hint at site-specific adaptations to rainfall regime. We found a strong correlation in wet miombo (R^2 =0.65, p<0.001, slope=0.9 to 1.1 [95% CI], n=129), but not dry miombo (R^2 =0.02, p = 0.25, slope=-0.1 to 0.4, n=72), or other dry woodlands (Table 2). Conversely, dry miombo is much more rigid in its G_{DOY}, which is centred just after the vernal equinox.

Table 2. D, G_{DOY}, R_{DOY} and their correlation for the major vegetation types in southern tropical Africa.

Vegetation type‡	n€	D^∞	G_{DOY}	R_{DOY}	p†	$R^{2†}$	b_1†	b_2†
Wetter Zambezian miombo woodland	129	60 (57, 62)	232 (228, 236)	292 (289, 295)	**<0.001**	**0.65**	**1.02 (0.89, 1.15)**	**-65 (-103, -27)**
Mosaic of dry deciduous forest and secondary grassland	27	54 (48, 59)	259 (253, 265)	313 (310, 315)	0.129	0.09	0.6 (-0.19, 1.4)	70 (-178, 318)
Drier Zambezian miombo woodland	72	37 (34, 40)	271 (268, 273)	308 (305, 310)	0.246	0.02	0.15 (-0.11, 0.42)	223 (142, 304)
Undifferentiated woodland	32	30 (25, 35)	267 (262, 272)	297 (294, 300)	0.038	0.14	0.55 (0.03, 1.06)	105 (-48, 258)
Transition from undifferentiated woodland to Acacia deciduous bushland and wooded grassland	28	28 (22, 34)	285 (279, 290)	313 (309, 316)	0.184	0.07	0.38 (-0.19, 0.96)	165 (-14, 345)
Mosaic of lowland rain forest and secondary grassland	58	27 (20, 34)	219 (211, 228)	246 (240, 252)	**<0.001**	**0.35**	**0.84 (0.53, 1.15)**	**13 (-63, 89)**
East African coastal mosaic	24	23 (18, 28)	288 (283, 293)	311 (305, 317)	**0.001**	**0.39**	**0.5 (0.22, 0.77)**	**134 (48, 219)**
Colophospermum mopane woodland and scrub woodland	48	13 (1, 26)	286 (281, 291)	299 (290, 309)	**<0.001**	**0.32**	**-0.28 (-0.39, -0.16)**	**369 (333, 404)**
Kalahari Acacia wooded grassland and deciduous bushland	25	2 (-25, 29)	294 (286, 303)	296 (274, 319)	0.083	0.13	-0.13 (-0.28, 0.02)	334 (288, 379)

‡ Vegetation type based on White (1983)

€ The number of 1° pixels used in the analysis

∞ Mean number of days between green-up (G_{DOY}) and rain onset (R_{DOY}). 95% CI in brackets.

†. Regression where: G_{DOY} = b_1 R_{DOY} ±b_2. 95% CI for parameters shown in brackets. Correlation coefficients (R^2) and the probability of obtaining a correlation as large as the observed value by random chance (p) are given, assuming no spatial auto correlation. Significant (p<0.01) correlation coefficients are in bold.

The sensitivity analysis showed that the finding of pre-rain green-up in the wet and dry miombo regions was not affected by a wide range of parameter values in the green-up detection (Fig. 5). For all of the 135 runs mean D was significantly different from zero (one tailed T test) for both wet and dry miombo.
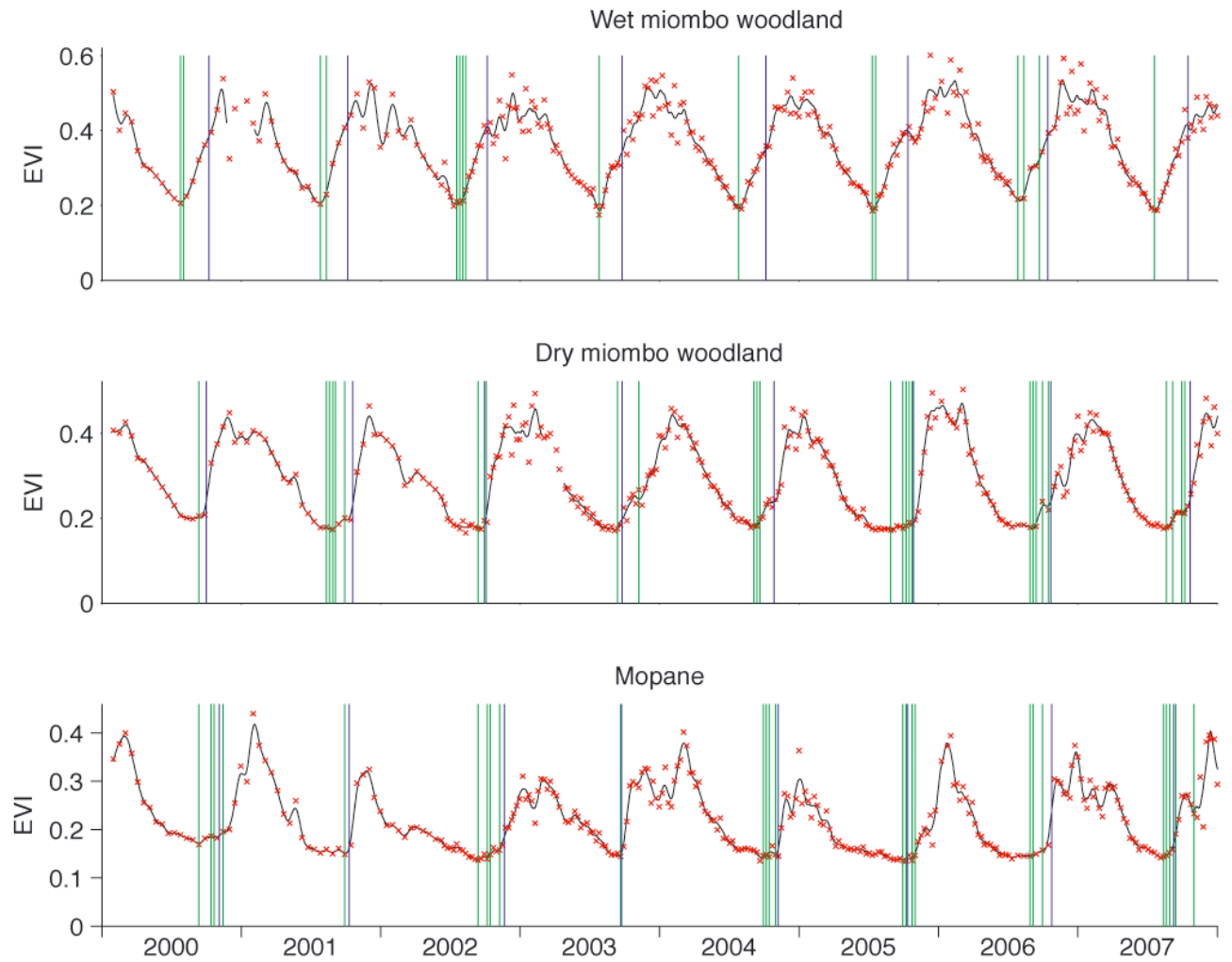

Figure 5. Sensitivity analysis of parameters of the green-up detection algorithm. Green-up dates (G_{DOY}) for the 135 different parameter combinations are shown with green lines. Blue shows the rain onset date. X-axis ticks show January 1.

Discussion

Local observations

Our local observations of leaf display show that the trees at our study site produce new leaves in mid-late September, before the start of the rainy season (Fig. 1). This conclusion appears robust – the hemispherical photographs provide a clear record of leaf phenology that is corroborated by the MODIS EVI signal. The temporal resolution of our ground data is only one month, but the EVI time resolution is 16 days and perhaps more because of the interleaved compositing period of the two MODIS data sets. This resolution is enough to confirm that green-up precedes rain onset with a mean of 55±21 days (Fig. 1). These results clearly show pre-rain green-up in these woodlands and match the description of this behaviour in other parts of the miombo region (Tuohy et al. 1990; Choinski et al. 1993; Frost 1996).

The timing of green-up was remarkably consistent, falling between 13-30 September for the eight years examined. The green-up period brackets the vernal equinox, which may indicate that the change in photoperiod is the endogenous trigger (Borchert 1996; Borchert *et al.* 2005). The consistency of green-up date was despite very variable rainfall patterns: annual totals ranged from 452-1400 mm and rain onset ranging from mid-October to December.

Green-up occurs when very little rain has fallen for the past three months (Fig. 1), the grass layer has senesced, and fires are common. Given the low rainfall and the high evaporative demand and solar radiation during the dry season, soil water content is likely very low, at least in the surface layers. Negative stem water potential is known to inhibit leaf flush (Borchert 1994), which implies that trees have either stored water reserves of water or access to ground water or wet layers of the soil.

Our method of hemispherical photography mainly records the phenological status of large trees, which dominate the leaf area and it is

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known that small trees may exhibit different phenology from large trees (Shackleton 1999).

Regional observations

Our results suggest that the phenological pattern at Nhambita is part of a much wider trend. Indeed every vegetation type with a seasonal cycle we examined across all of southern tropical Africa exhibits pre-rain green-up (Fig. 2). In many vegetation types (e.g. wet miombo, Fig. 3 and 5) the period between green-up and rain onset is in excess of one month and the results appear robust to the temporal frequency of observations and possible misidentification of green-up (Fig. 5).

The correlation between our ground data and EO data at Nhambita provides some confidence in our interpretation of the EVI signal, but the coarser spatial resolution and the reliance on EO-derived rainfall data in the regional analysis mean that smaller values of D may well have been missed. For instance (Archibald et al. 2007) show pre rain green-up in the semi arid savannas in South Africa, but our results indicate that the mean D (2 days) for this vegetation type is not significantly different from zero.

Moist vegetation types have longer periods of pre-rain green-up than more arid ones: around two months in the wet miombo; one month in the dry miombo and undifferentiated woodland; 13 days in mopane; and near zero in Kalahari wooded grassland. Rainforest and the coastal mosaic were exceptions to this trend. This trend may relate to wetter soil conditions in the more mesic environments (Shackleton 1999) or deeper rooting systems in the larger stature trees of wetter ecosystems (Eamus 1999).

The correlation between G_{DOY} and R_{DOY} for some vegetation types (Table 2), is potentially confounded by spatial auto correlation and this needs to be further explored before robust conclusions can be drawn. However our preliminary results suggest that in the wet miombo spatial variation in

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G_{DOY} co-varies with R_{DOY} to maintain a difference of around 60 days, despite spatial variation in R_{DOY} from 180-300. Thus, across their wide longitudinal range, wet miombo trees seem to green-up a similar period before the rains start, suggesting that the endogenous trigger of leaf flush varies spatially.

Maintaining positive water status during the dry season

The major question that this evidence of widespread pre-rain green-up raises is: how trees (re)hydrate their stems during the late dry season? There are two possibilities (Borchert 1994): 1) enough water is stored in the tree stem and root system to maintain a positive water status throughout the dry season; or 2) the trees are in hydraulic contact with wet soil and use soil water to maintain stem water potential.

Simple calculations show that because of the high wood density of the miombo species, water storage is only sufficient to build a leaf canopy and then transpire at realistic rates for around three days:

For a plot of 60 t woody biomass ha^{-1}, with 60% moisture in the woody tissue (data from Chapter 6 and 7), we calculate that building a leaf canopy of LAI =1 with SLA = 100g m^{-2} and leaf water content = 100%) would use about 7% of the stored water. The remaining stored water, if used up entirely over 30 days, would be sufficient to transpire 0.1 mm day^{-1}. This is an order of magnitude less than the transpiration rates measured by Choinski and Johnson (Choinski et al. 1993) of > 1.5 mmol m^{-1} s^{-1}, which convert to > 1.2 mm day^{-1}, with very conservative assumptions (assuming 12 hrs at 1.5 mmol m^{-1} s^{-1}, whereas the observed diurnal cycle peaks at 3 mmol m^{-2} s^{-1} and lasts for nearly 18 hrs). This calculation, combined with observed pre-dawn xylem water potentials of -0.8 to -1.1 MPa (Choinski et al. 1993), suggest that dry miombo trees are in contact with soil water. Do *et al.* (2005), working in the Sahel found a similar result, even in very arid areas.

Costs and benefits

The widespread pre-rain green-up of African savanna woodlands, that we demonstrate here, and which has been observed in South Africa (Archibald et al. 2007) and in the Sahel (Do *et al.* 2005), as well as on other continents (Williams *et al.* 1997; Elliott *et al.* 2006) can be analysed in terms of the costs and benefits associated with the strategy.

Hypothesised benefits include 1) the avoidance of herbivory during the vulnerable stage of leaf expansion, due to reduced insect activity in the dry season (Aide 1988); 2) avoidance of rain-induced leaching of the nutrient-rich, immature leaves (Sarmiento *et al.* 1985); and 3) as a 'be prepared' way of optimising photosynthetic gain during the short growing period (Borchert 1994). Being ready to fully exploit any rain-induced soil nutrient availability, and deprive the competing grasses of these nutrient may also be important.

Whatever the benefits are, they must exceed the considerable costs of developing a hydraulic architecture that can access deep soil or ground water (Do *et al.* 2005), and the risk of fire in the late dry season which can damage leaves (Chidumayo 1997), as such fires are typically of high intensity.

Evergreen trees pay back the costs of an embolism-resistant hydraulic system (Eamus 1999) and deep roots by being able to assimilate carbon throughout the whole year, albeit at low rates. Deciduous trees adopt the opposite strategy of low cost thin leaves, which maximises assimilation in the wet season, but are short lived (Eamus 1999). It is an open question as to why semi-deciduous trees like the ones in Nhambita develop a deep root system, but then do not use this system to access water except for a month or two before the rains. The strategy in Nhambita appears to be a blend of both evergreen and deciduous modes, but with all of the costs.

Implications and areas for further work

The questions that this paper raises could be addressed in several ways. The first would be to improve our understanding of miombo eco-physiology by measuring leaf level fluxes and sapflow throughout the periods of leaf fall and flush, expanding and replicating the previous work in Zimbabwe (Tuohy et al. 1990; Tuohy et al. 1991; Choinski et al. 1993). Irrigation (Myers *et al.* 1998) and drought experiments are needed to understand the implications of this behaviour for land-atmosphere fluxes and tree productivity under changed moisture availability.

The second approach would be to develop full cost benefit analyses of leaf phenology and hydraulic architecture. Current analyses have been limited to quantifying leaf construction costs (Eamus 1999) and photosynthetic benefits: this needs to be extended to include the costs of building and maintaining deep water access with large root systems, and even the risks of fire and herbivory. Such an analysis would allow process-based representation of trade-offs by coupling existing models of carbon assimilation (Williams *et al.* 1998) with carbon allocation models.

Representations of savannas in dynamic global vegetation models need to move beyond characterising southern African savanna as 'rain green' or 'drought deciduous' (Friend *et al.* 2007). Most such models use a soil moisture threshold (Cramer *et al.* 2001) to determine leaf phenology, but the depth at which soil moisture influences tree behaviour needs to be carefully examined, as clearly surface soil moisture is unrelated to leaf display.

Conclusions

At a site in Mozambique miombo woodlands we observed tree leaf display for 43 months and found that green-up occurs on average 55±21 days before rain onset.

A regional analysis using Earth observation data showed that pre-rain green-up is the dominant leaf phenology across Southern Africa. This

phenological strategy and the hydraulic status of these ecosystems need to be better understood if reliable predictions of vegetation productivity and land-atmosphere exchange under changed rainfall patterns are to be made.

Supplementary Figures

Figure S1. Pre-rain green-up in the Nhambita area. The image was taken at the end of the dry season, on 22/10/2006. 19.2 mm of rain had fallen in the previous 6 months, and 8 mm in the previous month, as recorded at the Chitengo weather station (see text). Note the senesced grass layer.

◼ Mosaic of *Brachystegia bakerana* thicket and edaphic grassland	◼ Transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland
◼ Kalahari *Acacia* wooded grassland & deciduous bushland	◼ Mosaic of wetter Zambezian woodland and secondary grassland
◼ *Acacia–Commiphora* deciduous bushland & thicket	◼ Undifferentiated woodland
◼ Transition from *Colophospermum mopane* scrub woodland to Karoo-Namib shrubland	◼ *Colophospermum mopane* woodland and scrub woodland
◼ Drier Zambezian miombo woodland (dominated by *Brachystegia* and *Julbernardia*)	◼ East African coastal mosaic
◼ Wetter Zambezian miombo woodland (dominated by *Brachystegia- Julbernardia* and *Isoberlinia*)	◼ Mosaic of lowland rain forest and secondary grassland
◼ Mosaic of dry deciduous forest and secondary grassland	◼ Guineo-Congolian rain forest: drier types
◼ Undifferentiated montane vegetation	◼ Lowland rain forest: wetter types
◼ Edaphic and secondary grassland on Kalahari Sand	◼ Water
◼ The Kalahari/Karoo-Namib transition	◼ Herbabeous swamp
◼ Bushy Karoo-Namib shrubland	◼ Namib desert and Other

Figure S2. White's (1983) map of African vegetation

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Plot 5. Subplot 3. Aug 2006-Aug 2007

053a060801.JPG
2006 Aug

053a070402.JPG
2007 April

053a060906.JPG
2006 Sept

053a070420.JPG
2007 April

053a061010.JPG
2006 Oct

053a070525.JPG
2007 May

053a061108.JPG
2006 Nov

053a070620.JPG
2007 June

053a070125.JPG
2007 Jan

053a070725.JPG
2007 July

053a070227.JPG
2007 Feb

053a070816.JPG
2007 Aug
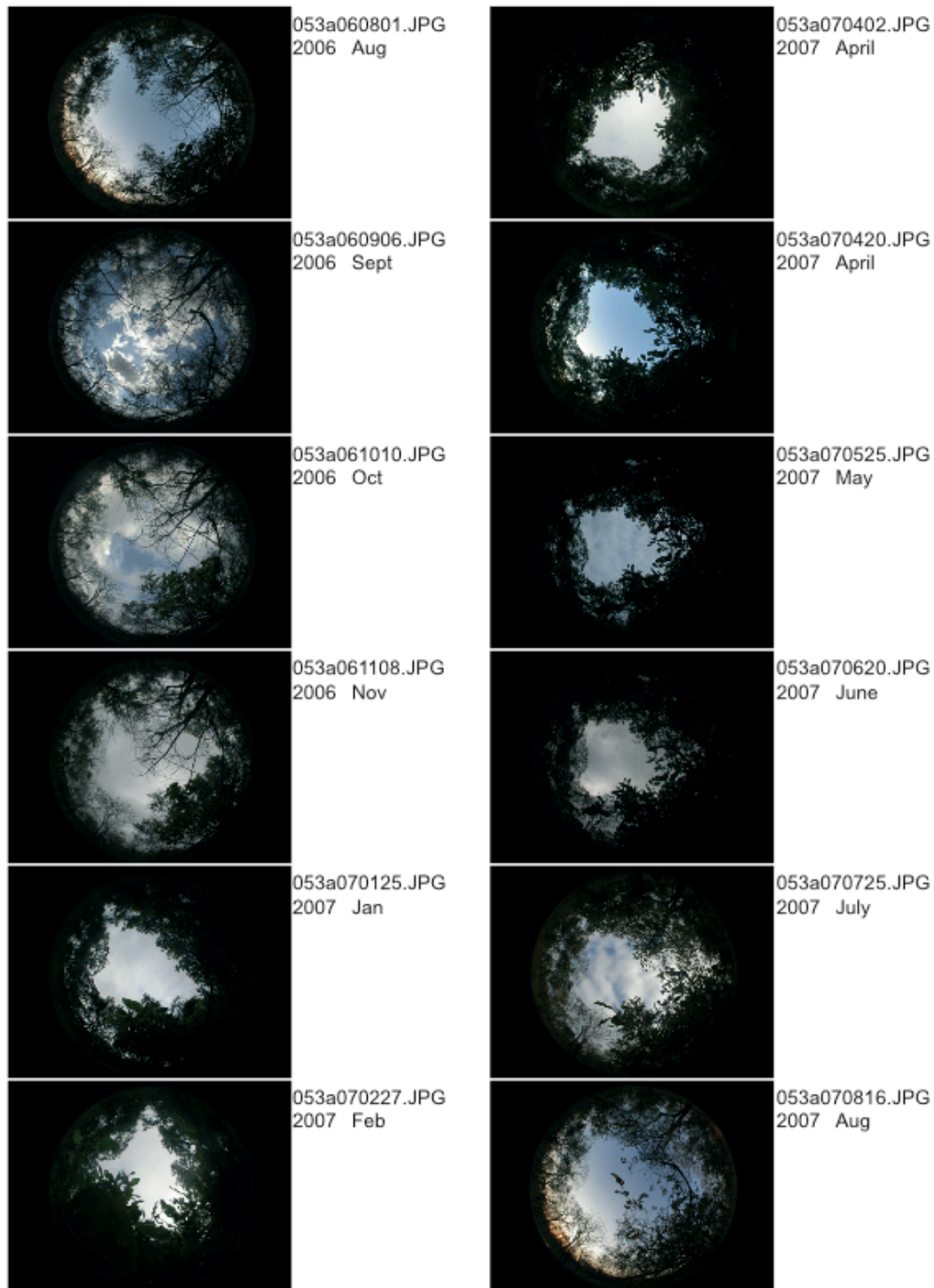
Figure S3. An example of a time series of hemispherical photos from PSP 5, subplot 3. The left column shows the period of green up and the right column show the period of leaf loss. This plot is only briefly deciduous and some trees retain a few leaves.

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Author contributions

MW and CMR designed the research. CMR and MW undertook the field analysis. CMR undertook the remote sensing analysis and led the writing. All authors contributed to the interpretation and writing.

References

Aide, T. M. (1988). "Herbivory as a selective agent on the timing of leaf production in a tropical understory community." Nature **336**(6199): 574-575.

Archibald, S. and R. J. Scholes (2007). "Leaf green-up in a semi-arid African savanna separating tree and grass responses to environmental cues." Journal of Vegetation Science **18**: 583-594.

Azzali, S. and M. Menenti (2000). "Mapping vegetation-soil-climate complexes in southern Africa using temporal Fourier analysis of NOAA-AVHRR NDVI data." International Journal of Remote Sensing **21**(5): 973-996.

Bachoo, A. and S. Archibald (2007). Influence of Using Date-Specific Values when Extracting Phenological Metrics from 8-day Composite NDVI Data. Analysis of Multi-temporal Remote Sensing Images, 2007. MultiTemp 2007. International Workshop on the.

Baret, F. (2004). A simple method to calibrate hemispherical photographs. Avignon, INRA-CSE.

Borchert, R. (1994). "Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees." Ecology **75**(5): 1437-1449.

Borchert, R. (1996). "Phenology and flowering periodicity of Neotropical dry forest species: Evidence from herbarium collections." Journal of Tropical Ecology **12**: 65-80.

Borchert, R. (1998). "Responses of tropical trees to rainfall seasonality and its long-term changes." Climatic Change **39**(2-3): 381-393.

Borchert, R., S. S. Renner, Z. Calle, D. Navarrete, A. Tye, L. Gautier, R. Spichiger and P. von Hildebrand (2005). "Photoperiodic induction of synchronous flowering near the Equator." Nature **433**(7026): 627-629.

Borchert, R., G. Rivera and W. Hagnauer (2002). "Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain." Biotropica **34**(1): 27-39.

Campbell, B. M., A. Angelsen, A. Cunningham, Y. Katerere, A. Sitoe and S. Wunder (2007). Miombo woodlands – opportunities and barriers to sustainable forest management, Center for International Forestry Research.

Chidumayo, E. N. (1997). Miombo ecology and management : an introduction. London, IT Publications in association with the Stockholm Environment Institute.

Chidumayo, E. N. (2001). "Climate and phenology of savanna vegetation in southern Africa." Journal of Vegetation Science **12**(3): 347-354.

Choinski, J. S. and J. M. Johnson (1993). "Changes in Photosynthesis and Water Status of Developing Leaves of Brachystegia-Spiciformis Benth." Tree Physiology **13**(1): 17-27.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. M. a. Rueda, L. Mearns, C. G. Menéndez, J. Ra isa nen, A. Rinke, A. Sarr and P. Whetton (2007). Regional Climate Projections. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. S. Solomon, D. Qin, M. Manninget al. Cambridge, Cambridge University Press.

Cramer, W., A. Bondeau, F. I. Woodward, I. C. Prentice, R. A. Betts, V. Brovkin, P. M. Cox, V. Fisher, J. A. Foley, A. D. Friend, C. Kucharik, M. R. Lomas, N. Ramankutty, S. Sitch, B. Smith, A. White and C. Young-Molling (2001). "Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models." Global Change Biology **7**(4): 357-373.

de Bie, S., P. Ketner, M. Paasse and C. Geerling (1998). "Woody plant phenology in the West Africa savanna." Journal of Biogeography **25**(5): 883-900.

Devineau, J. L. (1999). "Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso)." Journal of Tropical Ecology **15**: 497-513.

Do, F. C., V. A. Goudiaby, O. Gimenez, A. L. Diagne, M. Diouf, A. Rocheteau and L. E. Akpo (2005). "Environmental influence on canopy phenology in the dry tropics." Forest Ecology and Management **215**(1-3): 319-328.

Eamus, D. (1999). "Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics." Trends in Ecology & Evolution **14**(1): 11-16.

Elliott, S., P. J. Baker and R. Borchert (2006). "Leaf flushing during the dry season: the paradox of Asian monsoon forests." Global Ecology and Biogeography **15**(3): 248-257.

Friend, A. D., A. Arneth, N. Y. Kiang, M. L. J. Ogée, C. Rödenbeck, S. W. Running, J.-D. Santaren, S. Sitch, N. Viovy, F. I. Woodward and S. Zaehle (2007). "FLUXNET and modelling the global carbon cycle." Global Change Biology **13**(3): 610-633.

Frost, P. (1996). The ecology of Miombo woodlands. The Miombo in transition : woodlands and welfare in Africa. B. M. Campbell. Bogor, Indonesia, Center for International Forestry Research: 11-55.

Fuller, D. O. (1999). "Canopy phenology of some mopane and miombo woodlands in eastern Zambia." Global Ecology and Biogeography **8**(3-4): 199-209.

Fuller, D. O. and S. D. Prince (1996). "Rainfall and foliar dynamics in tropical southern Africa: Potential impacts of global climatic change on savanna vegetation." Climatic Change **33**(1): 69-96.

Hoffmann, W. A., E. R. da Silva, G. C. Machado, S. J. Bucci, F. G. Scholz, G. Goldstein and F. C. Meinzer (2005). "Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna." Oecologia **145**(2): 307-316.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao and L. G. Ferreira (2002). "Overview of the radiometric and biophysical performance of the MODIS vegetation indices." Remote Sensing of Environment **83**: 195-213.

Huffman, G. J., R. F. Adler, M. M. Morrissey, D. T. Bolvin, S. Curtis, R. Joyce, B. McGavock and J. Susskind (2001). "Global Precipitation at One-Degree Daily Resolution from Multisatellite Observations." Journal of Hydrometeorology **2**(1): 36-50.

Kang, S., S. W. Running, J. H. Lim, M. Zhao, C. R. Park and R. Loehman (2003). "A regional phenology model for detecting onset of greenness in temperate mixed forests, Korea: an application of MODIS leaf area index." Remote Sensing of Environment **86**: 232-242.

Li-Cor (1989). LAI-2000 Plant Canopy Analyzer Operating Manual. Lincoln, NE, Li-Cor.

Moulin, S., L. Kergoat, N. Viovy and G. Dedieu (1997). "Global-Scale Assessment of Vegetation Phenology Using NOAA/AVHRR Satellite Measurements." Journal of Climate **10**(6): 1154-1170.

Myers, B. A., R. J. Williams, I. Fordyce, G. A. Duff and D. Eamus (1998). "Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia?" Austral Ecology **23**(4): 329-339.

New, M., R. Washington, C. Jack and B. Hewitson (2003). "Sensitivity of southern African climate to soil moisture." CLIVAR Exchanges **8**(45-47).

ORNL-DAAC (2008). MODIS subsetted land products, Collection 5., Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

Reed, B. C., J. F. Brown, D. Vanderzee, T. R. Loveland, J. W. Merchant and D. O. Ohlen (1994). "Measuring Phenological Variability from Satellite Imagery." Journal of Vegetation Science **5**(5): 703-714.

Reich, P. B. (1995). "Phenology of tropical forests: patterns, causes, and consequences." Canadian Journal of Botany-Revue Canadienne De Botanique **73**(2): 164-174.

Ridler, T. W. and S. Calvard (1978). "Picture Thresholding Using an Iterative Selection Method." Ieee Transactions on Systems Man and Cybernetics **8**(8): 630-632.

Rivera, G., S. Elliott, L. S. Caldas, G. Nicolossi, V. T. R. Coradin and R. Borchert (2002). "Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain." Trees-Structure and Function **16**(7): 445-456.

Sarmiento, G., G. Goldstein and F. Meinzer (1985). "Adaptive Strategies of Woody Species in Neotropical Savannas." Biological Reviews **60**(3): 315-355.

Shackleton, C. M. (1999). "Rainfall and topo-edaphic influences on woody community phenology in South African savannas." Global Ecology and Biogeography **8**(2): 125-136.

Tadross, M. A., B. C. Hewitson and M. T. Usman (2005). "The Interannual Variability of the Onset of the Maize Growing Season over South Africa and Zimbabwe." Journal of Climate **18**(16): 3356-3372.

Tinley, K. L. (1977). Framework of the Gorongosa Ecosystem. Faculty of Science. Pretoria, University of Pretoria**:** 184.

Tuohy, J. M. and J. S. Choinski (1990). "Comparative Photosynthesis in Developing Leaves of Brachystegia-Spiciformis Benth." Journal of Experimental Botany **41**(229): 919-923.

Tuohy, J. M., J. A. B. Prior and G. R. Stewart (1991). "Photosynthesis in Relation to Leaf Nitrogen and Phosphorus-Content in Zimbabwean Trees." Oecologia **88**(3): 378-382.

White, F. (1983). The vegetation of Africa : a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. Paris, Unesco.

Williams, M., Y. Malhi, A. D. Nobre, E. B. Rastetter, J. Grace and M. G. P. Pereira (1998). "Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis." Plant, Cell and Environment **21**(10): 953-968.

Williams, M., C. M. Ryan, R. M. Rees, E. Sambane, J. Fernando and J. Grace (2008). "Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique." Forest Ecology and Management **254**(2): 145-155.

Williams, R. J., B. A. Myers, W. J. Muller, G. A. Duff and D. Eamus (1997). "Leaf phenology of woody species in a North Australian tropical savanna." Ecology **78**(8): 2542-2558.

Zhang, X., M. A. Friedl, C. B. Schaaf, A. H. Strahler, J. C. F. Hodges, F. Gao, B. C. Reed and A. Huete (2003). "Monitoring vegetation phenology using MODIS." Remote Sensing of Environment **84**: 471-475.

Zhang, X. Y., M. A. Friedl, C. B. Schaaf, A. H. Strahler and Z. Liu (2005). "Monitoring the response of vegetation phenology to precipitation in Africa by coupling MODIS and TRMM instruments." Journal of Geophysical Research-Atmosheres **110**(D12).

5. Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique

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I contributed to the writing of this paper, analysed all the data sets and collect the wood density data. MW led the writing and analysis, and the other data were collected by ES and JF.

Abstract

Land management in tropical woodlands is being used to sequester carbon (C), alleviate poverty and protect biodiversity, among other benefits. Our objective was to determine how slash-and-burn agriculture affected vegetation and soil C stocks and biodiversity on an area of miombo woodland in Mozambique, and how C stocks and biodiversity responded once agriculture was abandoned. We sampled twenty-eight 0.125 ha plots that had previously been cleared for subsistence agriculture and had been left to regrow for 2 to ~25 years, and fourteen 0.25 ha plots of protected woodlands, recording stem diameter distributions and species, collecting wood for density determination, and soil from 0-0.3 m for determination of %C and bulk density.

Clearance for agriculture reduced stem wood C stocks by 19.0 t C ha^{-1}. There were significant relationships between period of regrowth and basal area, stem numbers and stem biomass. During regrowth, wood C stocks accumulated at 0.7 t C ha^{-1} year^{-1}. There was no significant difference in stem C stocks on woodlands and on abandoned farmland 20-30 years old. Soil C stocks in the top 0.3 m on abandoned land had a narrower range (21-74 t C ha^{-1}) than stocks in woodland soils (18-140 t C ha^{-1}). There was no discernible increase in soil C stocks with period of regrowth, suggesting that the rate of accumulation of organic matter in these soils was very slow. The regrowing plots did not contain the defining miombo species, and total stem numbers were significantly greater than in woodland plots, but species richness and diversity were similar in older abandonments and miombo woodlands. Wood C stocks on abandoned farmland were capable of recovery within 2-3 decades, but soil C stocks did not change on this timescale.

Woodland soils were capable of storing >100 t C ha^{-1}, whereas no soil on a regrowing area exceeded 74 t C ha^{-1}, so there is a potential for C sequestration in soils on abandoned farmland. Management should focus

on identifying C-rich soils, conserving remaining woodlands to protect soil C and preserve defining miombo species, and on investigating whether fire control on recovering woodland can stimulate accumulation of soil C and greater tree biomass, and restore defining miombo species.

Introduction

The C cycle of tropical open woodlands is relatively understudied compared to other biomes. These woodlands are subject to frequent disturbance via fires and land clearance. Such woodland degradation threatens terrestrial carbon stocks (Frost 1996; Chidumayo 2002) but is little monitored or modelled. Climate change mitigation initiatives are now managing tropical woodlands to sequester carbon (Silver *et al.* 2004), including 19 current projects in sub-Saharan Africa (Jindal 2006). Alongside the potential to generate income through sales of C offsets,

10 woodland management is likely to benefit other ecosystem services and biodiversity. However, the optimal management approaches are not yet clear, due to a lack of data on vegetation and soil C stocks, as well as biodiversity indices, on the dominant land use types. Here we quantify changing C stocks and biodiversity along a chronosequence of abandoned farmland in Mozambique, and in nearby protected miombo woodlands.

Miombo is the vernacular term for the seasonally dry deciduous woodlands that are widespread across southern Africa, dominated primarily by genera *Brachystegia, Julbernadia* and/or *Isoberlinia* (Campbell 1996). These open woodlands extend across 2.7 million km² of

20 some of the world's poorest countries (Campbell 1996; Frost 1996). Low per capita income and high population growth rates in southern Africa mean that subsistence slash-and-burn farming within the miombo zone is the predominant way of life. Growing populations are increasing pressure from slash-and-burn. Loss of miombo woodland is also driven by increasing demand for fuel-wood (Abbot et al. 1999).

Our objective was to determine how slash-and-burn agriculture affected soil and vegetation C stocks on an area of miombo woodland, and how C stocks recovered once agriculture was abandoned. We hypothesised that C stocks in both soils and vegetation of abandoned slash-and-burn plots

30 would be lower than in woodland plots. Farmland is abandoned after a

few years as soil fertility declines, and we expected this fertility to recover slowly following abandonment. Thus, we hypothesised that C stocks would recover more rapidly in vegetation than in soils. We hypothesised that the species dynamics in recovering plots would indicate a return towards the dominant and defining species of local miombo woodland. We also hypothesised that this successional change in species would result in an increase in mean wood density as pioneer species were replaced with slower growing, denser miombo dominants. This study is unique in collecting and analysing data on soil and stem C (the largest stocks of C

10   in miombo), wood density and biodiversity on a range of different land use types within a small region of miombo woodland.

Study Site

This case study is located in the small community of Nhambita in Sofala Province, Mozambique, located around the operational centre of an EU-funded C sequestration pilot project at 18° 58' 44" S, 34° 10' 37" E. This is an area with little or no infrastructure, and a community still recovering from decades of war. Recent population growth means that more land is coming under the traditional slash-and-burn agricultural system. Local households clear machambas (slash-and-burn plots covering 1-3 ha) by

20   felling trees and then burning them, and then raise crops, which are planted with a stick or entrenching tool. After a few years of tillage, yields fall and the machambas are abandoned to woodland re-growth.

The Nhambita community is located on the western escarpment of the southern limit of the Rift Valley, near the Gorongosa National Park, and its ecology is comprehensively described by Tinley (1977). The area receives 850 mm mean annual precipitation (ranging from 407 – 1219 mm), 96% of which falls between October and April, based on data from 1999-2005 (Mozambique Central Water Board, ARA-Centro, 2005). Soils are highly weathered and generally freely drained sandy loams or sandy

30   silt loams. Fire is a frequent, generally annual, disturbance agent; during

June-October 2006 most natural miombo vegetation in the area was burned (personal observation). Fires are mainly lit in agricultural areas after crops have been harvested and are also set throughout the dry season for hunting and to clear areas of pests and animal hazards.

The Nhambita community lands, which covers an area of 348 km², can be divided into three zones. In the east, the community lands lie within the Gorongosa National Park, and there is no settlement, agriculture or land clearance. In the centre, the community lands lie within the Park buffer zone. There are settlements, and slash-and-burn agriculture, but land clearance is restricted legally. In the west, the community lands are outside the buffer zone, population density is greater, and land clearance is ongoing.

Methods

We surveyed tree biodiversity, above-ground woody biomass, wood density and soil C across an area of largely undisturbed primary woodlands and a series of abandoned machambas of differing ages, during 2004 and 2005. All survey plots were located in central Nhambita, within the buffer zone of Gorongosa National Park, to avoid areas with heavy disturbance.

Primary woodlands

During December 2004, surveys were undertaken of the woody vegetation in the part of the Nhambita community that lies within the buffer zone of the Gorongosa National Park. Plots were not surveyed if they showed signs of previous cultivation or charcoal burning, or if local informants knew them to have been utilised. Fourteen × 0.25 ha plots were established in pairs at seven randomly selected locations, equally spaced along the road and track network within the community buffer zone. At the seven locations, two 50 m × 50 m plots were set out at 200, 450, 700 or 950 m from the road, along a transect line perpendicular to the road. The

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distances for the paired plots were selected randomly from these four options.

All living woody specimens >0.05 m diameter at breast height (DBH) were measured, recording species local name (provided by a local informant knowledgeable in botany), species botanical name (de Koning 1993; Van Wyk 1993; Van Wyk et al. 1997; Coates Palgrave et al. 2002), and DBH (m) using diameter callipers or tape. On trees forking below 1.3 m from the ground level, each stem was measured and recorded separately. Trees forking above 1.3 m were measured at breast height. In one plot there was a single very large (2.17 m DBH) baobab tree (*Adansonia digitata*), a species with an unusual shape that does not conform to generic allometric relationships. No other baobabs were found anywhere else in the study and this single specimen was excluded from plot calculations as it heavily skewed the analyses for its plot compared to others.

Abandoned machambas

In June 2005, 28 abandoned agricultural fields were surveyed, each identified through talking with the farmers of the Nhambita community. Farmers were asked to locate machambas abandoned over past years and decades. The shortest period of regrowth was two years, and the longest exceeded 20 years. It was easier to obtain precise age estimates for more recently abandoned sites (up to 19 years). Site ages were confirmed by the secretary of the community association. Robertson (1984) used this method to obtain the fallow age of plots in Malawi and found it agreed well with estimates from aerial photographs. Several sites had been abandoned >20 years ago, but since independence in 1975, and so the ages for these sites were between 20 and 30 years. Abandoned machambas were divided into four classes, depending on fallow age: class 1, 1-5 years; class 2, 6-10 years; class 3, 11-19 years; and class 4, 20-30

years. Individual plots on age classes 1-3 have been aged precisely, but those on age class 4 have not, and may be aged between 20-30 years.

To sample the abandoned machambas, which usually extended over an area of 1-3 ha, each was divided into four approximately equal parts, and each of these parts was sampled by one 10 m radius subplot. Each subplot was randomly located, but locations were discounted that caused overlap between quadrants, or that placed subplots over the agreed boundary of the abandoned machamba. The total area of the four subplots was thus 1256 m², ~1/8 ha. Within each subplot, species and DBH for all stems >
10   0.05m DBH were recorded, a total of 1955 stems. The abandoned machambas were not randomly distributed in the area with respect to their age, but were clustered in groups of similar age.

Stem wood density

Dry bulk stem density was measured for the 21 most populous species found on the woodland and abandoned machamba plots. These species accounted for 980 of the 3166 stems enumerated, and 72% of the basal area. For the remaining, un-sampled species, each was assigned the average density, weighted by basal area, of species sampled on plots of the same age class.

20   To determine dry bulk density, during November 2005 one or more branches between 0.01-0.02 m diameter were taken from three or more trees and cut to ~0.15 m length, and the bark removed. Fresh volume was determined by displacement of water in a measuring cylinder (precision 1000 mm³) and also by calculation from three measurements of diameter and one of length (precision 0.1mm). The samples were returned to the lab and dried at 100°C to constant weight. Density was calculated from the average of the fresh volume derived from the two methods, divided by the dry weight.

This method only determines the dry bulk density of the sapwood of the
30   tree, which may differ from the density of the heartwood, which is present

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in most miombo species. However, sampling heartwood would have required the destruction of a large numbers of trees, so a sapwood-heartwood comparison was limited to five species, which were felled fortuitously. The heartwood samples were much larger than the sapwood samples, either circular cross sections of the bole at different heights (0.1-0.2 m thick) or cubes sawn from the centre of a cross section (~0.15 x 0.15 x 0.15 m). Volume was calculated both by measurement of diameter and thickness and also by measuring the weight of water displaced when placed into a full bucket. The wood samples were dried by episodic

10   heating in a microwave to constant weight.

Stem C stocks

Stem biomass was calculated using allometric relationships (Table 1) developed in the miombo woodlands of nearby countries (Frost 1996; Abbot *et al.* 1997; Chidumayo 1997) and also a generic equation for the tropics (Brown *et al.* 1989). Two of the equations relate DBH or basal area to estimate volume, and then our wood density data were used to estimate biomass. The other two equations estimated biomass directly from DBH data. Multiple approaches to biomass estimation allowed realistic uncertainties to be generated. Wood biomass was assumed to be

20   50% C (Nabuurs *et al.* 2003).

Soil properties and C stocks

At all 28 abandoned machambas soil samples were collected from four subplots. In each subplot ten soil samples were collected from the 0-0.03 m horizon and mixed to form a single composite sample for analysis. In one of the subplots soil samples from four depths were collected (0-0.03 m, 0.03-0.1 m, 0.1-0.2 m and 0.2-0.3 m). Soils data were similarly collected from nine subplots in an area of 1 ha within 500 m of the woodland plots. At five of the subplots a depth profile was sampled (0, 0.05, 0.15, 0.25 m depth) and at the remaining four, only a surface sample was taken. In the

field, all soil textures were determined by hand texturing (Rural Development Service 2006).

Soil samples were dried, sieved (2 mm sieve) and ball milled to produce a fine flour. Percentage soil C was determined on dried samples using a Carbo-Erba/400 automated CN analyser. At each soil plot, soil bulk density measurements were determined using steel rings of known volume. Before weighing, the soils samples were dried in an oven at 40° C for 24 hours. Bulk density values were calculated by dividing the mass (t) of the soil sample by volume of the cylinder (m^3). Total soil C stock was
10 determined by stepwise integration of the profile data of soil C content from 0-0.3 m.

Textural analysis on soils of abandoned machambas and woodland sites indicated that all were dominated by sand loams and sand loam silts. Single factor ANOVA revealed that there was no significant relationship between site age and bulk density (BD) on machambas, and so the data were pooled to provide a single bulk density estimate (1.26 t m^{-3}, identical to the mean woodland BD) which was applied at all sites. The pooled BD data were combined with soil %C data, and multiplied by the mass fraction of soil remaining after sieving, to generate estimates of total soil
20 C stock for each soil layer.

Biodiversity

The Shannon index (H') is a measure of biodiversity calculated from the relative abundance of species in a community:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Where $p_i = n_i/N$, n_i is the number of individuals present of species i, N is the total number of individuals, and S is the total number of species.

The Shannon index was determined for woody species >0.05 m DHB for each abandoned machamba and woodland plot.

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The Jaccard similarity coefficient (*J*) is a statistic used for comparing the similarity and diversity of sample sets. We used *J* to determine the degree of similarity of species composition of different age classes. The Jaccard coefficient is defined as the size of the intersection divided by the size of the union of the sample sets:

$$J(A,B) = |A \cap B| / |A \cup B|$$

Where *A* and *B* are binary descriptions of species presence/absence in given age classes. A value of 1 indicates complete similarity, while 0 indicates complete dissimilarity. We used a list of 161 species, comprising all those recorded in surveys within the Nhambita community on woodlands and abandoned machambas, during 2003-5.

Results

Vegetation structure and C stocks

There were clear changes in vegetation characteristics along the chronosequence of machamba abandonments. Basal area was significantly correlated ($P<0.001$) with time since abandonment (Figure 1). A linear regression was able to explain 55-68% of the observed variability (uncertainty in ages of age class 4 abandonments, which might be 20-30 years old, accounts for the range of R^2 values reported here). The slopes of the regressions indicated that basal area increment was 0.25-0.47 m^2 ha^{-1} yr^{-1} (again the uncertainty here reflects uncertainty in age of the oldest abandonments). Basal area recorded in the woodland plots varied from 2.4-13.1 m^2 ha^{-1}, reflecting the highly heterogeneous forest cover in this area. The mean value ± standard deviation, SD, for the woodland plots was 8.2 ± 3.0 m^2 ha^{-1}. However, there was no significant difference between basal area recorded in the oldest abandonments (>20 years, mean = 8.2 m^2 ha^{-1}) and the woodland plots (t-test, two sample assuming equal variances, $P>0.05$). For the woodland plots there was no

significant relationship between basal area and distance from the road (ANOVA, P = 0.59).

Stocking density (number of tree stems > 0.05 m DBH ha^{-1}) also varied along the chronosequence, initially increasing with age, peaking after 10-20 years of abandonment, and then declining (Figure 2). A third-order polynomial fit was able to explain 57% of observed variability, and revealed a highly significant relationship between stocking density and age (P<0.001). There was a significant difference between the stocking density of machambas abandoned for >20 years and the woodland plots (means are 574 and 373 trees ha^{-1} respectively, t-test, two sample assuming equal variances, P<0.01).
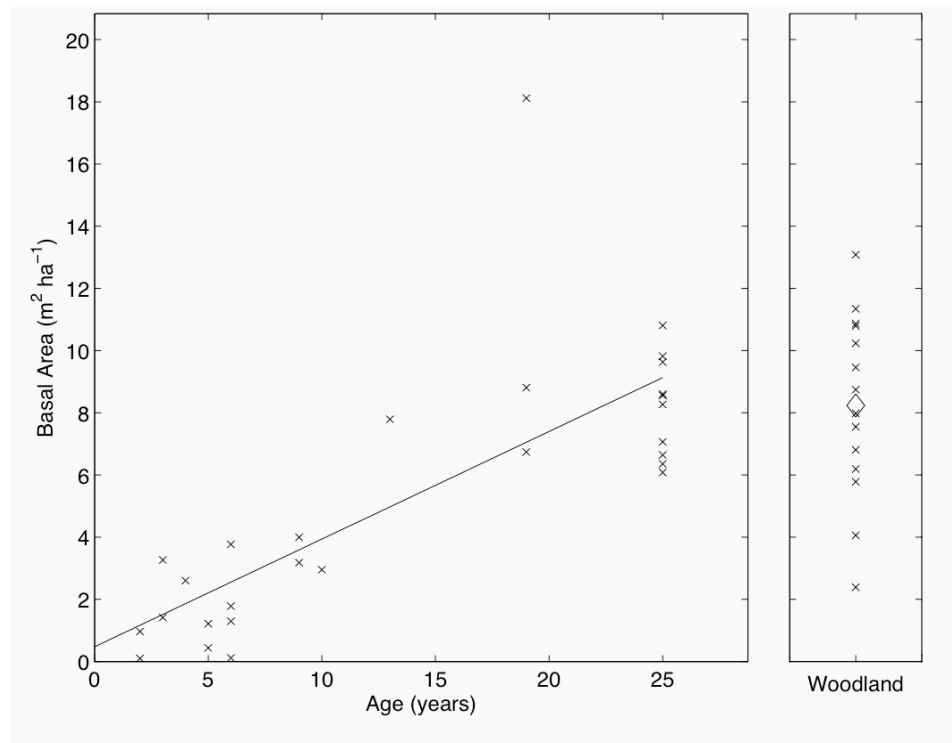
Figure 1. Measured basal area plotted against age for all abandoned machambas (left panel), and for woodland plots (right panel, diamond indicates mean), with a linear regression assuming oldest abandoned machambas, age class 4, are 25 years. The age of the oldest abandoned machambas is given as 25 years, but lies between 20 and 30 years. Regression parameters are: y=0.27x +1.13; p < 0.001; r^2 = 0.55 (age class 4 = 30 years), y=0.35x 0.48; p < 0.001; r^2 = 0.61 (age class 4 = 25 years), y=0.47x -0.41; p < 0.001; r^2 = 0.68 (age class 4 = 20 years).

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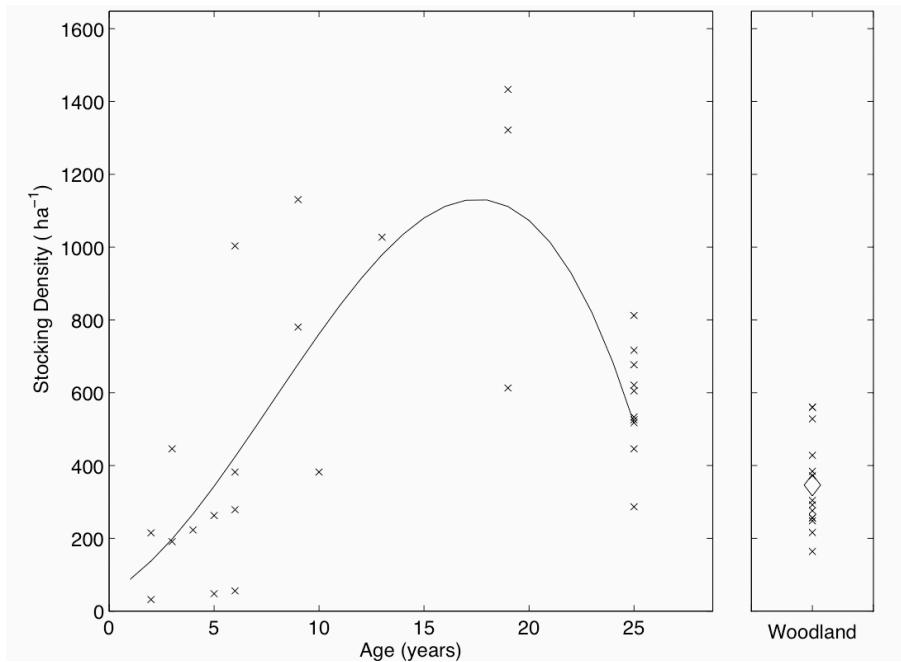
Figure 2. Measured stem stocking density (stems per ha) plotted against age (years since abandonment) for all abandoned machambas (left panel), and for woodland plots (right panel, diamond indicated mean). The age of the oldest abandoned machambas is given as 25 years, but lies between 20 and 30 years. A third-order polynomial fit to the data, SD = 49.3 + 31.2 t + 7.0 t^2 -0.30 t^3, where t is time in years.

Combining all four allometric equations, the mean ± SD estimated stem C stock estimates in the woodland plots was 19.0 ± 8.0 t C ha^{-1}. Nine of the 14 woodland plots had mean biomass estimates from 12-24 t C ha^{-1}, but plot values ranged from 4.3-33.4 t C ha^{-1}. The mean estimated stem C stock for the oldest abandoned machambas (>20 years) was 15.7 ± 3.9 t C ha^{-1}, ranging from 10.1-22.2 t C ha^{-1}. There was no significant difference (t = -1.21, P = 0.11) in the stem C stock estimates between abandoned machambas >20 years old and woodlands (t-test, two sample assuming equal variances).

Stem C stock estimates in the abandoned machambas were significantly and positively correlated with time since abandonment (P < 0.001, Figure 3). Using linear regressions for the four allometric equations, and assuming that the oldest abandonment were 25 years old, resulted in estimates of biomass accumulation rates varying from 0.43 to 0.87 t C ha^{-1} yr^{-1}, and a mean ± SD of 0.7 ± 0.19. The uncertainty in productivity

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estimates introduced by uncertainty in ages of oldest abandonments is important. Using the Brown equation (Table 1) and assuming that trees in age class 4 were 30 years old resulted in productivity estimates of 0.57 t C ha^{-1} yr^{-1}, but 0.74 t C ha^{-1} yr^{-1} if age class 4 trees were 25 years old, and 1.00 t C ha^{-1} yr^{-1} for 20 year old trees.

Table 1 Allometric equations used in this paper. B, biomass t; V, Volume m³; BA, basal area m² ha^{-1}; D, diameter in cm at 1.3 m (DBH). For the Abbot and Frost equations, wood density values determined at the site were used to calculate biomass from volume (see Table 2).

Reference	Equation(s)	Country	Notes
Abbot (1997)	$V = 10^{(-4.22 + 2.76.\log D)}$	Malawi	For canopy trees, assumed to be >4m in height for this study. Phuyu site.
	$V = (0.057 + 0.000918 D^2)^2$		Understorey species, assumed to be trees less than 4m high for our study. Phuyu site.
Frost (1996)	$V = 6.18 BA^{0.86}$	Zaire, Malawi, Zambia and Zimbabwe	Equation applied on a stand basis.
Chidumayo (1997)	$B = 3.01 D - 7.48$	Zambia	For trees <0.1 m DBH
	$B = 20.02 D - 203.37$		For trees >0.1 m DBH
Brown (1989)	$B = 34.47 - 8.067 D + 0.659 D^2$	Dry tropics	Not miombo specific, developed in "the dry tropics"
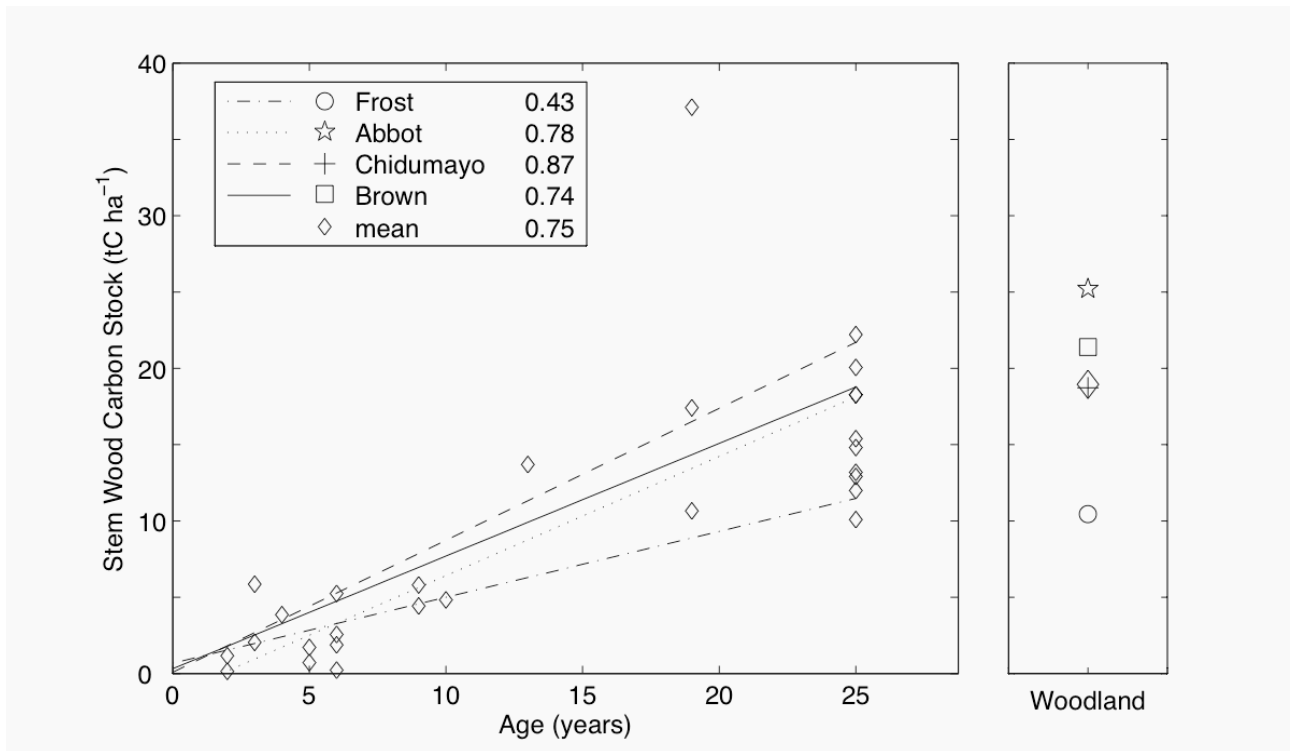
Figure 3. Estimate wood C stock plotted against age for all abandoned machambas (left panel), and for woodland plots (right panel). The age of the oldest abandoned machambas is given as 25 years, but lies between 20 and 30 years. C stock is calculated from basal area, wood density and four different allometric relationships. The data here are the mean estimates from the four different allometric equations. The linear regressions determined from each individual relationship are plotted to indicate the uncertainty in biomass estimates. The legend indicates the author of the allometric relationship and the slope of the C stock versus age relationship (i.e. annual wood C productivity, tC ha^{-1} yr^{-1}).

Wood density

Wood density for individual species ranged from 0.40 to 0.71 t m^{-3} (Table 2). The mean density ± SD was 0.56 ± 0.08 t m^{-3}. The lower bulk densities were associated with fruiting species such as marula (*Sclerocarya birrea*) and mango (*Mangifera indica*). The three defining miombo species (*Brachystegia boehmii, Brachystegia spiciformis.* and *Julbernadia globiflora*) in our sites had density values of 0.52, 0.63 and 0.63 t m^{-3}, slightly below or above the average.

The average wood density for each plot was determined from the specific measurements (Table 2), species composition and weighted by the cube of the each stem's DBH. The lowest values were found in the most recently

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abandoned machambas, while values for all abandoned machambas >7 years old were ~0.55 t m^{-3} (Figure 4), very close to the mean value from the tree samples. A non-linear curve fit using a saturation equation ($D = \chi t/(\varepsilon+t)$, where t is time since abandonment and χ and ε are parameters) was able to explain 30% of observed variation with a root-mean-square error (RMSE) of 0.006.

For the five species with both sapwood and heartwood samples, it was possible to make comparisons of wood density estimates from both types of wood (Table 3). The mean wood density was 0.57 t m^{-3} for heartwood and 0.55 t m^{-3} for sapwood. A t-test was used to determine if the heartwood and sapwood densities were significantly different. Only one species of the five had significantly different heartwood and sapwood density ($P<0.05$, t-test, two sample assuming equal variances).
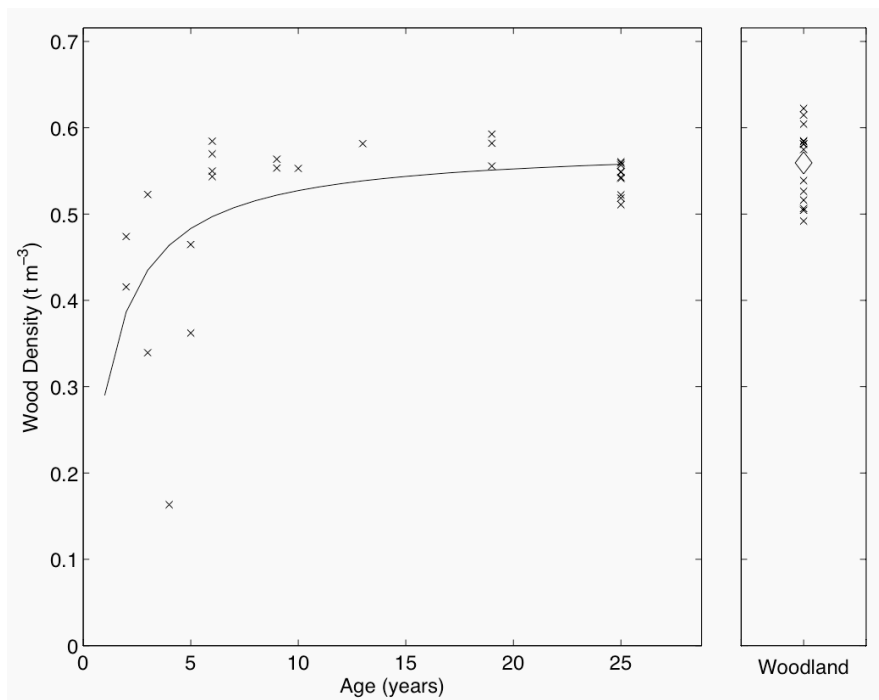
Figure 4. Wood density (D, t m^{-3}) estimates for all abandoned machambas plotted against age, and for all woodland plots. Wood density of 21 dominant species was determined and combined with species data on each plot. A non-linear curve fit for the chronosequence of abandoned machambas is shown, using a saturation equation, $D = \chi t/(\varepsilon+t)$, where t is time since abandonment (years) and χ and ε are parameters. For the best fit χ=0.58 and ε=1.00.

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Table 2 Stem sapwood dry bulk density data (mean and standard deviation) from the 21 most populous species found on the combined woodland and abandoned machamba plots. Samples were collected in Nhambita in 2006, and are sorted by increasing mean bulk wood density. *n* indicates number of sample collected per species.

Species	n	mean dry density, t m^{-3}	standard deviation, t m^{-3}
Mangifera indica	4	0.4	0.07
Khaya anthoteca	3	0.45	0.02
Acacia nigrescens	5	0.46	0.03
Commiphora mossambicensis	3	0.47	0.06
Sclerocarya birrea	12	0.47	0.12
Entada abyssinica	18	0.51	0.11
Brachystegia boehmii	6	0.52	0.09
Xeroderris stuhlmannii	3	0.52	0.02
Piliostigma thonningii	4	0.53	0.05
Combretum apiculatum	10	0.55	0.03
Philenoptera violacea	24	0.55	0.10
Albizia amara	10	0.57	0.11
Diplorhynchus condylocarpon	9	0.6	0.07
Julbernardia globiflora	8	0.63	0.07
Brachystegia spiciformis	8	0.63	0.04
Albizia lebbeck	4	0.63	0.15
Burkea africana	3	0.63	0.03
Erythrophleum africanum	3	0.64	0.15
Millettia stuhlmannii.	12	0.68	0.07
Pterocarpus rotundfolius rotundfolius	8	0.65	0.04
Cleistochlamys kirkii	3	0.71	0.11

Table 3. Heartwood and sapwood dry bulk densities for five dominant species. For each species are listed the number of branch samples measured (*n*), the mean wood density of the samples, and their standard deviation (st.dev). A t-test was used to determine if the heartwood and sapwood densities were significantly different; the t-test p values are given in the final row. There was only one significant difference (marked *) at the 5% level.

|	*Sclerocarya birrea*		*Millettia stuhlmannii*		*Philenoptera violacea*		*Albizia amara*		*Entada abyssinica*	
Wood type	heart	sap	heart	sap	heart	sap	heart	sap	heart	sap
n	4	12	5	12	3	24	2	10	5	13
Mean (t m^{-3})	0.50	0.47	0.56	0.68	0.61	0.55	0.64	0.57	0.55	0.49
St. dev.	0.03	0.12	0.05	0.07	0.04	0.10	n/a	0.11	0.03	0.12
t-test P value	0.383		0.002*		0.116		n/a		0.131	

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Soil C stocks
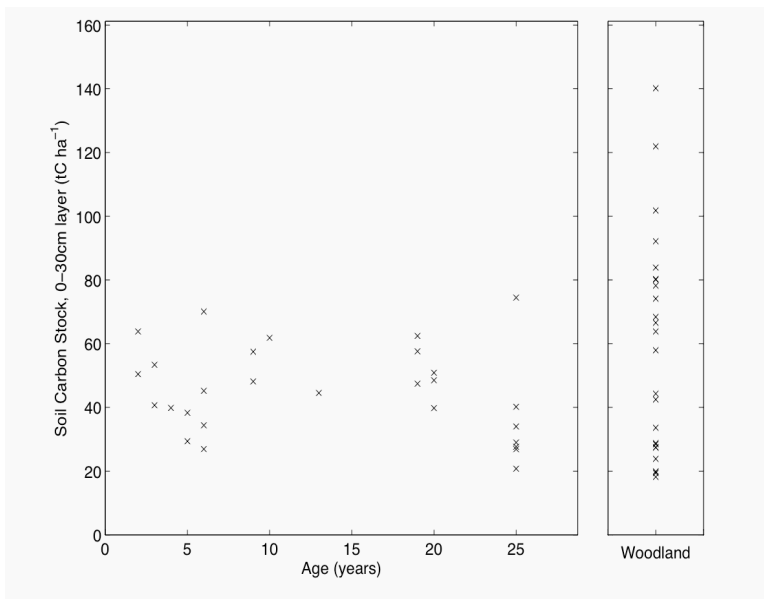
Figure 5. Total soil C content in surface 0.3 m for all sites plotted against age for all abandoned machambas (left panel) and for woodlands (right panel). The age of the oldest abandoned machambas is given as 25 years, but lies between 20 and 30 years.

There were no clear trends in soil C stocks in the top 0.3 m along the abandoned machamba chronosequence (Figure 5). The frequency distribution of soil C stocks differed between abandoned machambas and woodlands. The Shapiro-Wilks test (IMLS Stats Library) indicated that the abandoned machamba soil C stocks were normally distributed ($n = 28$, P >0.05) while the woodland plot soil C stocks were not ($n = 25$, P<0.001). The mean soil C stock (± SD) for abandoned machambas was 45.2 (± 14.1) t C ha^{-1}. The woodland plots had a clear bimodal distribution of soil C (Figure 7), with 9 of the 28 plots having values from 10-30 t C ha^{-1} and another 9 having values from 60-90 t C ha^{-1}. The median soil C stocks were 57.9 t C ha^{-1} for woodlands and 44.9 t C ha^{-1} for abandoned machambas. The highest (140 t C ha^{-1}) and lowest (18 t C ha^{-1}) soil C stocks found in all soil profiles were in woodland plots. A Wilcoxon rank sum test (IMSL Stats Library), the nonparametric equivalent of the two-

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sample t-test, indicated there was no significant difference between the woodland and abandoned machamba soil C stock estimates (P>0.05).

Biodiversity

There were 69 different woody species (DBH > 0.05 m) in the 14 woodland plots (total survey area 3.5 ha), which contained in total 1211 stems >0.05m DBH. Five species contributed 54% of the total stem count, and five species contributed 46% of the total basal area (Table 4 and 5). *Diplorhynchus condylocarpon* and *Brachystegia boehmii* were the dominant species (by stocking density and basal area respectively). The dominant species of the woodland plots are typical of those for dry miombo (Kanschik et al. 2001).

We identified 67 woody species (DBH > 0.05 m) in the 28 abandoned machamba plots (total survey area ~3.5 ha), which contained in total 1955 stems > 0.05 m DBH. The dominant species in abandoned machambas differed according to time since abandonment (Table 4 and 5), and according to whether stocking density or basal area were used as measures of dominance. The youngest plots (age class 1) were dominated by fruit trees, some exotic, such as papaya (*Carica papaya,*) marula (*Sclerocarya birrea*) and mango (*Mangifera indica*), or trees with other domestic uses, such as monkey bread (*Bauhinia thonningii*). In older abandonments (age-classes 2-4), the trees were dominated by small-to-medium sized native trees such as *Philenoptera violacea* and *Combretum apiculatum*. The dominant species in the abandoned machambas largely differed from those in the woodland plots. Comparing the oldest abandonments to the woodlands, the dominant five species by basal area had no species in common, while the dominant five by stocking density had just one in common (Table 4 and 5). The Jaccard similarity coefficient for species composition of abandoned machambas compared to woodland ranged from a minimum of 0.15 between recent abandonments and woodland plots, to a maximum of 0.31 between the oldest abandonments

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and woodland plots (Table 4). The defining miombo species found in the woodland plots (*Brachystegia boehmii, Brachystegia spiciformis, Julbernadia globiflora*) were completely absent from abandoned machambas of all ages in stems > 0.05 m DBH.

Table 4. The five most dominant species, ranked by stocking density in each age class of abandoned machamba and in woodland, are listed in order. Also shown are the percentage of total stems made up by the five dominant species, the number of plots sampled in each age class (*n*), and mean species richness. The final row shows the Jaccard similarity coefficient (*J*) for species composition of abandoned machambas of different ages (classes 1-4) compared to that of woodland.

Order	1 (1-5 yrs)	2 (6-10 years)	3 (11-20 yrs)	4 (20-30 yrs)	Woodland
1	*Sclerocarya birrea*	*Philenoptera violacea*	*Entandrophragma caudatum*	*Combretum apiculatum*	*Diplorhynchus condylocarpon*
2	*Piliostigma thonningii*	*Entandrophragma caudatum*	*Philenoptera violacea*	*Philenoptera violacea*	*Pterocarpus rotundfolius rotundfolius*
3	*Mangifera indica*	*Piliostigma thonningii*	*Piliostigma thonningii*	*Dalbergia boehmii Taub.*	*Combretum apiculatum*
4	*Acacia nigrescens*	*Albizia lebbeck*	*Combretum apiculatum*	*Commiphora mossambicensis*	*Brachystegia boehmii*
5	*Philenoptera violacea*	*Sclerocarya birrea*	*Sterculia appendiculata*	*Vitex doniana Sweet*	*Cleistochlamys kirkii*
% of total	60%	67%	57%	51%	54%
n	7	7	4	10	14
Species richness	5.2	7.4	17.5	13.8	15.1
J	0.15	0.19	0.19	0.31	N/A

Table 5 Dominant species type ranked by basal area in all abandoned machambas, and in woodland. The five most abundant species are listed in order. The final row shows the percentage of basal area made up by the five dominant species.

Rank Order	Age class 1	Age class 2	Age class 3	Age class 4	Woodland
1	*Carica papaya*	*Philenoptera violacea*	*Albizia lebbeck*	*Combretum apiculatum*	*Brachystegia boehmii*
2	*Trichilia emetica*	*Piliostigma thonningii*	*Philenoptera violacea*	*Philenoptera violacea*	*Acacia nigrescens*
3	*Mangifera indica*	*Albizia lebbeck*	*Piliostigma thonningii*	*Commiphora mossambicensis*	*Diplorhynchus condylocarpon*
4	*Acacia nigrescens*	*Entandrophragma caudatum*	*Combretum apiculatum*	*Faidherbia albida*	*Brachystegia spiciformis Benth.*
5	*Sclerocarya birrea*	*Sclerocarya birrea*	*Sclerocarya birrea*	*Albizia amara*	*Erythrophleum africanum*
% of total	69%	66%	67%	55%	46%

The lowest Shannon indices were found in the most recently abandoned machambas, and increased with time since abandonment, but then saturated at greater ages (Figure 7). A non-linear curve fit using a saturation equation ($H' = \alpha t/(\beta+t)$, where t is time since abandonment and α and β are parameters) was able to explain 62% of observed variation with a root-mean-square error (RMSE) of 0.12. Species richness also increased with time since abandonment, saturating with a similar pattern to the Shannon Index (Table 4). There were no significant differences between abandoned machambas >20 years old and the woodland plots for either Shannon indices (P = 0.15) or mean species richness (P = 0.22, t-test, two sample assuming equal variances).

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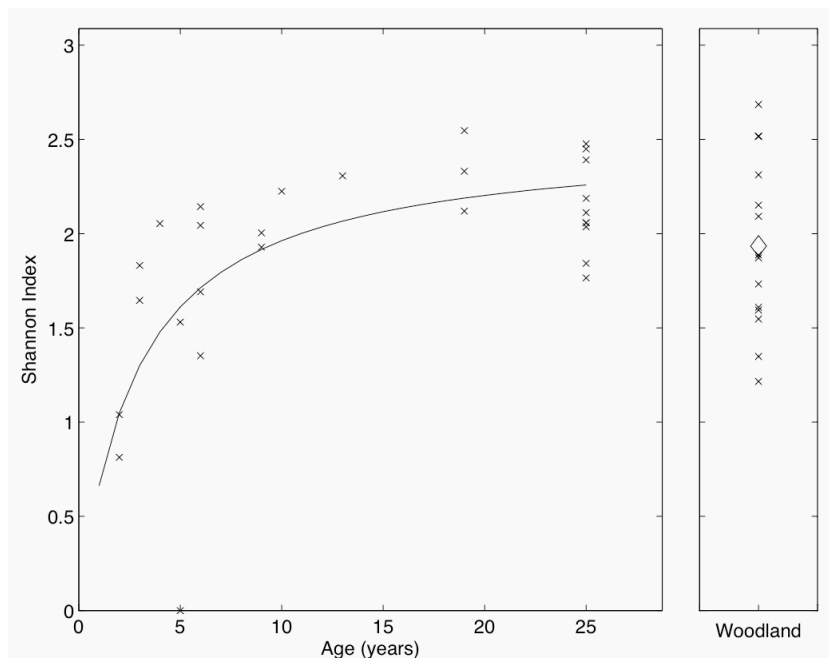
Figure 6. Shannon index (H') of species diversity plotted against age for all abandoned machambas (left panel), and for woodland plots (right panel). The age of the oldest abandoned machambas is given as 25 years, but lies between 20 and 30 years. A non-linear curve fit for the chronosequence of abandoned machambas is shown, using a saturation equation, $H' = \alpha t/(\beta+t)$, where t is time since abandonment (years) and α and β are parameters. For the best fit $\alpha=2.51$ and $\beta=2.79$.

Discussion

Because of access issues and chronosequence measurement, the sampling strategy employed was not completely randomised, and so some caution is required in interpreting the results. There was no significant effect of distance from road on woodland structure, so locating plots within easy walking distance of tracks is unlikely to have affected the results. Woodland plots were randomly located along the road/track network, but the abandoned machambas were selected on the basis of farmer interviews. The abandoned machambas were all located around the Nhambita village, and are clustered in age groups, according to the historical development of the community. Due to their proximity to human settlements, it is likely that the abandoned machambas were more disturbed than woodland plots, for example by fires, which are often started near settlements or roads, or fuel-wood harvesting. It is also possible that farmers selected woodland areas with richer soils for clearance.

Space-for-time studies have been criticised for producing artefacts because of non-random site selection (Frost 1996). If the cleared and abandoned land was never originally miombo, then the chronosequence approach is compromised. The balance of evidence suggests that these lands were most likely dry miombo. Firstly, the nearest woodland plots (three were within 2.5 km to the NW, N and SE of the cleared areas) were all dominated by the defining dry miombo species. Local seed sources were thus available, and the local climate was suitable. Secondly, there were no clear topographical or soil textural differences between these three woodland plots and the abandoned machambas lying between them. However, the lack of information concerning the natural vegetation of the machamba areas is a major, but unavoidable, cause of uncertainty.

We hypothesised that C stocks in vegetation and soils of abandoned machambas would be lower than in woodland plots, and that C stocks

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would accumulate more rapidly after abandonment in vegetation than in soils. The data for vegetation largely supported these hypotheses, but the results for soils are less clear.

C stocks in vegetation

For the abandoned machambas, there was a clear relationship between time since abandonment and increased wood C stocks (Figures 1 and 3). While the oldest abandoned machambas (>20 years) and woodland plots had similar basal area and biomass, suggesting a large degree of recovery, there were still significant differences in stocking density (Figure 2), indicating that structural differences remained. The woodland plots had a larger variation in biomass than the abandoned machambas, which we attribute to either variable natural disturbance generating a mosaic of differently structured woodland stands (Figure 1) or perhaps local variations in hydrology. However, further work is required to determine whether differences in soils or hydrology can explain these variations, and whether wood C stocks of low biomass woodlands are aggrading at the same rate as on abandoned machambas.

After abandonment, wood C stocks increased by 0.7 t C ha^{-1} yr^{-1}. The mean annual increment (MAI) of above-ground woody C was similar to other figures for dry miombo, 0.9 t C ha^{-1} yr^{-1} over 35 years in Zambia (Chidumayo 1997), 0.5 t C ha^{-1} yr^{-1} in 16 years old coppiced miombo woodland in northern Zambia (Stromgaard 1985) and 0.75 t C ha^{-1} yr^{-1} over 50 years, calculated from data in Frost (1996). There is uncertainty in the productivity estimate (± 0.2 t C ha^{-1} yr^{-1}), due to uncertainty in aging the oldest abandoned machambas, and in the allometric relationships used to generate biomass from stem diameter and wood density measurements. These two uncertainties are roughly equal – the range in productivity estimates is 0.44 t C ha^{-1} yr^{-1} due to uncertainty in allometric equations, and 0.43 t C ha^{-1} yr^{-1} due to uncertainty in time since abandonment. Thus, improvements to the productivity estimates at

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this site will require both locally determined allometric equations and a more thorough investigation of site histories and constraints on date of abandonment.

C stocks in soils

Disturbance of soils associated with cultivation generally leads to a rapid decline in soil organic C content as a consequence of enhanced microbial respiration (Schlesinger 1986; King et al. 1994). Guo and Gifford (2002) found C losses of 41% due to land use conversion to agriculture from native forest. Walker and Desanker (2004) observed C reductions of 40%

10   after conversion to agriculture from Malawian miombo woodland. In the present study, abandoned agricultural land had a median C stock 23% lower than the surrounding woodlands. There was no significant difference between the pooled abandoned machamba soil C stocks and those of woodlands, so there was no clear support for our expectation of a widespread drop in soil C stocks after slash-and-burn. However, it is possible that farmers selected areas with richer soils for clearance, in which case a real loss of C stocks may be obscured by the comparison with randomly sampled woodland. The broad range of soil C stocks in woodland suggests major variations in organic matter and probably

20   fertility (Figure 5 and 7).
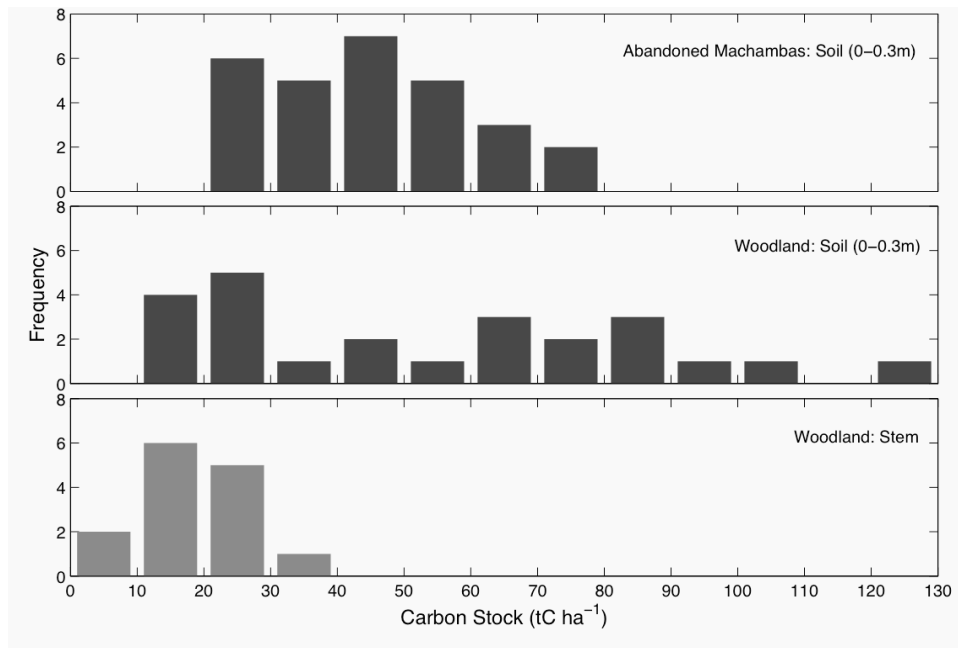
Figure 7 Frequency distributions of C stocks (t C ha⁻¹) in abandoned machamba soils (top panel), woodland soils (middle) and woodland stem C (bottom panel).

Subsequent reforestation often leads to a steady but slower accumulation of organic C as plant C inputs accumulate in the surface soil horizons (Guo et al. 2002; Jarecki et al. 2003). In a survey of regrowing tropical forests, mostly from the moist and wet tropics, Silver *et al.* (2000) found that soil C increased at 1.3 t ha⁻¹ yr⁻¹ in the first 20 years after abandonment. However, in a review of rates of C sequestration following land use change, Post and Kwon (2000) reported annual rates of C accumulation of as little as 0.03 t C ha⁻¹ yr⁻¹ in arid locations. These low rates of recovery are consistent with the lack of any identifiable change in soil C on older abandoned machambas at our dry tropical sites, and suggest very slow additions of organic matter to the soil. In a study of miombo woodlands in Malawi, Walker and Desanker (2004) also found that soil C stocks did not increase after abandonment of agriculture. This lack of accumulation is likely a result of frequent fire disturbance (Bird et al. 2000; Chidumayo et al. 2003), or perhaps termite activity (Konate *et al.* 2003) both of which remove organic material that might otherwise be added to the soil carbon pool.

The soil C stocks of the woodland plots are notable for their bimodal distribution (Figure 7). The significant departure from normality suggests a complex spatial pattern of soil C stocks, which is not easily explained given the lack of textural or bulk density differences among soil samples. Site variables such as drainage are known to influence soil organic C concentrations, but were not characterised in this study. It is possible that disturbance history, particularly frequency of fires, is a critical factor in development of soil C stocks through vegetation-fire-fuel-load feedbacks (Stromgaard 1985; Stromgaard 1986; Frost 1996). Further sampling of soils and other potentially linked environmental controls are required to test whether the bimodal distribution is widespread and to understand its cause.

The management implications are clear for sequestering C in wood. Natural regeneration will restore stem C stocks in 2-3 decades, but rates of accumulation are low and total stem C stocks in the natural vegetation are relatively small compared to soil C stocks. The potential to sequester C in soils is less clear. There is no increase in soil C stocks along the chronosequence, which indicates that inputs of organic matter to soils in regrowing miombo are very small. Woodland soil C stocks vary across almost an order of magnitude (Figure 7). If boosting the C storage of miombo soils were possible (Jarecki et al. 2003; Lal 2003), this would provide a valuable means to sequester C, with an equal or greater potential for C sequestration than restoring abandoned machambas to miombo woodland under current disturbance conditions. Whether a reduction in disturbance (i.e. fire intensity and frequency) would increase long-term wood C stocks is also a critical management issue (Trapnell 1959; Bond *et al.* 2005).

Changes in stem wood density

We hypothesised that the successional change in species would result in an increase in mean wood density as pioneer species were replaced with

slower growing miombo dominants. The evidence supports this hypothesis, but only for the very early part of the succession (<10 years) where fruit trees are dominant (Figure 4). These trees have the lowest wood density values (Table 2), but the data suggest that fruit trees are rapidly lost from regrowing woodlands. There was little difference in wood density calculated for sapwood and heartwood from a selection of common species (Table 3) suggesting that the biomass estimates derived from sapwood density data alone were reasonable. However, we were not able to sample the heartwood of larger trees, including the defining

10   miombo species, due to logistical difficulties. It is possible that using sapwood estimates of wood density for these species has resulted in an under-estimate of wood biomass and C stocks.

Species dynamics

We hypothesised that the species dynamics in recovering plots would indicate a return towards the dominant species of local miombo woodland. We reject this hypothesis. None of the defining miombo species are present in any of the abandoned machambas (Table 4 and 5) as was also found by Stromgard (1986). However, the secondary dominant species of miombo are found on abandoned machambas, and there is

20   greater similarity in species composition between older abandonments and woodlands (Table 4 and 5). Even though most species differed between abandoned machambas and woodlands (as indicated by low Jaccard similarity coefficients), the biodiversity of woody species (i.e. Shannon index and species richness) of abandoned machambas >10 years old was similar to that found in woodlands (Figure 6). Overall biodiversity has not been degraded by the slash-and-burn disturbance, but the time-scale of recovery of defining miombo species is unclear.

Miombo species are known to be able to survive the destruction of their above ground parts (Robertson 1984; Nyerges 1989; Frost 1996;

30   Chidumayo 1997). They are generally good at re-sprouting and can

reproduce from root suckers; 15 years of mattocking were required to kill *Brachystegia* spp. (Robertson 1984), and re-sprouting is a common response to destruction by fire. The defining miombo species are, however, thought to be relatively fire-tender (Trapnell et al. 1976; Cauldwell et al. 2000). We have observed that fires are commonplace in the Nhambita community, recurring every year or two. It is possible that in the open, early successional areas, the frequent fires, high grass biomass, and thus high fuels loads, mean that only fire-tolerant species can re-establish (e.g. *Philenoptera violacea, Diplorhynchus*

10 *condylocarpon, Combretum* spp.). The data show that fruit trees are replaced by fire-tolerant miombo species, but the defining miombo species do not establish over 2-3 decades.

Further work is required to study the woody biomass belowground in these sites, which is potentially significant given the prodigious sprouting behaviour from root stock of many miombo species. The bimodal distribution of soil C stocks in woodlands needs to be tested by further detailed surveys including analyses of nutrient dynamics and soil hydrology. Finally, the role of fire in miombo systems is significant and the C dynamics of these woodlands can only be fully understood and

20 predicted within the context of fire disturbance. We had hoped to use Earth Observation (EO) data to estimate the fire return interval on our plots. However the EO data did not agree with our local observations and burned area products are known to have problems detecting small patchy burns in the dry season (Laris 2005), although it is theoretically possible with high resolution imagery (Sa et al. 2007). The MODIS burned area product (Roy et al. 2005; Roy et al. 2008) which we attempted to use, is known to have particular problems in Mozambique and in the type of ecosystem in which this study was conducted (Roy et al. 2005).

Conclusions

Our objective was to determine how slash-and-burn agriculture affected soil and vegetation C stocks, and biodiversity on an area of miombo woodland, and how C stocks and species changed once agriculture was abandoned. We have shown that clearance for agriculture reduces stem wood C stocks by 19.0 t C ha^{-1} and the years following abandonment wood C stocks accumulated at 0.7 t C ha^{-1} year^{-1}. However, the regrowing areas do not contain the defining miombo species, and stem numbers are significantly greater than in woodland plots. Whether typical miombo species regain dominance is less clear, so conserving existing miombo woodlands is vital for maintaining the defining species. If fire disturbance on the abandoned machambas is heightened by proximity to human settlements (as is the case here) then more fire resistant species may dominate instead. Because woodland soil C stocks vary so much, it is not clear whether slash-and-burn reduces soil C stocks. Analysis of the abandonment chronosequence shows that there is no accumulation of soil C after 20-30 years of abandonment. This suggests that the rate of accumulation of organic matter in these soils has been very slow.

Our study emphasises the importance of measuring and monitoring *ecosystem* C stocks when assessing the potential for C sequestration. While the woodland stem C stocks are capable of recovery within a few decades, the soil stocks do not accumulate following abandonment over a few decades. Woodland soils were capable of storing >100 t C ha^{-1}, whereas no abandoned machamba soil exceeded 74 t C ha^{-1}, and no stem wood stock exceeded 33 t C ha^{-1}, so there is a potential for C sequestration in woodland soils that should be investigated as a management option, probably through experiments with fire exclusion during woodland regrowth (Chidumayo, 1997). Management for C sequestration should also focus on identifying C-rich soils and conserving remaining woodlands to protect soil C. To ensure that local communities can meet agricultural

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needs without permanent loss of woodlands, land management must provide approaches to increase crop output at low cost, e.g. agro-forestry and inter-cropping. The major challenge for C management is to understand the observed variability in vegetation and soil C stocks in woodlands, and use this understanding to manage existing forests and regrowing areas for greater C storage.

Acknowledgements

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References

Abbot, J. I. O. and K. Homewood (1999). "A history of change: causes of miombo woodland decline in a protected area in Malawi." Journal of Applied Ecology 36: 422-433.

Abbot, P., J. Lowore and M. Werren (1997). "Models for the estimation of single tree volume in four Miombo woodland types." Forest Ecology And Management 97(1): 25-37.

Bird, M. I., E. M. Veenendaal, C. Moyo, J. Lloyd and P. Frost (2000). "Effect of fire and soil texture on soil carbon in a subhumid savanna (Matopos, Zimbabwe)." Geoderma 94: 71-90.

Bond, W. J., F. I. Woodward and G. F. Midgley (2005). "The global distribution of ecosystems in a world without fire." New Phytologist 165(2): 525-538.

Brown, R. Gillespie and E. Lugo (1989). "Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data." Forest Science 35: 881-902.

Campbell, B. M. (1996). The Miombo in transition : woodlands and welfare in Africa. Bogor, Indonesia, Center for International Forestry Research.

Cauldwell, A. E. and U. Zieger (2000). "A reassessment of the fire-tolerance of some miombo woody species in the Central Province, Zambia." African Journal of Ecology 38(2): 138-146>.

Chidumayo, E. (2002). "Changes in miombo woodland structure under different land tenure and use systems in central Zambia." Journal of Biogeography 29: 1619-1626.

Chidumayo, E. N. (1997). Miombo ecology and management : an introduction. London, IT Publications in association with the Stockholm Environment Institute.

Chidumayo, E. N. and L. Kwibisa (2003). "Effects of deforestation on grass biomass and soil nutrient status in miombo woodland, Zambia." Agriculture, Ecosystems and Environment 96: 97-105.

Coates Palgrave, K., R. B. Drummond, E. J. Moll and M. Coates Palgrave (2002). Trees of southern Africa. Cape Town ; [Great Britain], Struik Publishers.

de Koning, J. (1993). Checklist of vernacular plant names in Mozambique. Wageningen, Wageningen Agricultral University.

Frost, P. (1996). The ecology of miombo woodlands. The miombo in transition: Woodlands and welfare in Africa. B. Campbell. Bogor, CIFOR.

Guo, L. B. and R. M. Gifford (2002). "Soil carbon stocks and land use change: a meta analysis." Global Change Biology 8(4): 345-360.

Jarecki, M. K. and R. Lal (2003). "Crop management for soil carbon sequestration." Critical Reviews in Plant Sciences 22(6): 471-502.

Jindal, R. (2006). Carbon Sequestration Projects in Africa: Potential Benefits and Challenges to Scaling Up. T. Damassa and S. Hanson, EarthTrends, World Resources Institute: 6.

Kanschik, W. and B. Becker (2001). "Dry miombo – ecology of its major plant species and their potential use as bio-indicators." Plant Ecology 155: 139-146.

King, J. A. and B. M. Campbell (1994). "Soil organic matter relations in five land cover types in the Miombo Region (Zimbabwe)." Forest Ecology and Management 67: 225-239.

Konate, S., X. Le Roux, B. Verdier and M. Lepage (2003). "Effect of underground fungus-growing termites on carbon dioxide emission at the point- and landscape-scales in an African savanna." Functional Ecology 17(3): 305-314.

Lal, R. (2003). "Offsetting global CO2 emissions by restoration of degraded soils and intensification of world agriculture and forestry." Land Degradation & Development 14(3): 309-322.

Laris, P. S. (2005). "Spatiotemporal problems with detecting and mapping mosaic fire regimes with coarse-resolution satellite data in savanna environments." Remote Sensing of Environment 99(4): 412-424.

Nabuurs, G.-J., N. H. Ravindranath, K. Paustian, A. Freibauer, W. Hohenstein and W. Makundi (2003). Forest Land. Good Practice Guidance for Land Use, Land-Use Change and Forestry. J. Penman, M. Gytarsky, T. Hiraishiet al. Kanagawa, Intergovernmental Panel on Climate Change, UNEP.

Nyerges, A. (1989). "Coppice swidden fallows in tropical deciduous forest: Biological, technological, and sociocultural determinants of secondary forest successions." Human Ecology 17(4): 379-400.

Post, W. M. and K. C. Kwon (2000). "Soil carbon sequestration and land-use change: processes and potential." Global Change Biology 6(3): 317-327.

Robertson, E. F. (1984). Regrowth of two African woodland types after shifting cultivation. Aberdeen, University of Aberdeen.

Roy, D. P., L. Boschetti, C. O. Justice and J. Ju (2008). "The collection 5 MODIS burned area product -- Global evaluation by comparison with the MODIS active fire product." Remote Sensing of Environment 112(9): 3690-3707.

Roy, D. P., P. G. H. Frost, C. O. Justice, T. Landmann, J. L. Le Roux, K. Gumbo, S. Makungwa, K. Dunham, R. Du Toit, K. Mhwandagara, A. Zacarias, B. Tacheba, O. P. Dube, J. M. C. Pereira, P. Mushove, J. T. Morisette, S. K. Santhana Vannan and D. Davies (2005). "The Southern Africa Fire Network (SAFNet) regional burnedarea productvalidation protocol." International Journal of Remote Sensing 26: 4265-4292.

Roy, D. P., Y. Jin, P. E. Lewis and C. O. Justice (2005). "Prototyping a global algorithm for systematic fire-affected area mapping using MODIS time series data." Remote Sensing of Environment 97(2): 137-162.

Rural Development Service (2006). Soil Texture, Technical Advice Note 52. London, Defra.

Sa, A. C. L., J. M. C. Pereira and R. H. Gardner (2007). "Analysis of the relationship between spatial pattern and spectral detectability of areas burned in southern Africa using satellite data." International Journal of Remote Sensing 29(16): 3583-3601.

Schlesinger, W. H. (1986). Changes in soil carbon storage and associated properties with disturbance and recovery. The Changing Carbon Cycle. A Global Analysis. J. R.Trabalka and D. E. Reichle. New York, Springer Verlag: 194-220.

Silver, W. L., L. M. Kueppers, A. E. Lugo, R. Ostertag and V. Matzek (2004). "Carbon sequestration and plant community dynamics following reforestation of tropical pasture." Ecological Applications 14(4): 1115-1127.

Silver, W. L., R. Ostertag and A. E. Lugo (2000). "The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands." Restoration Ecology 8(4): 394-407.

Stromgaard, P. (1985). "Biomass, growth, and burning of woodland in a shifting cultivation area of South Central Africa." Forest Ecology And Management 12(3-4): 163-178.

Stromgaard, P. (1986). "Early Secondary Succession on Abandoned Shifting Cultivator's Plots in the Miombo of South Central Africa." Biotropica 18(2): 97-106.

Tinley, K. (1977). Framework of the Gorongosa Ecosystem. Faculty of Science. Pretoria, Univeristy of Pretoria: 184.

Trapnell, C. G. (1959). "Ecological results of woodland burning experiments in Northern Rhodesia." Journal of Ecology 47(1): 129-&.

Trapnell, C. G., M. T. Friend, G. T. Chamberlain and H. F. Birch (1976). "Effects of fire and termites on a Zambian woodland soil." Journal of Ecology 64(2): 577-588.

Van Wyk, B. and P. Van Wyk (1997). Field guide to trees of Southern Africa. Cape Town, Struik Publishers.

Van Wyk, P. (1993). Southern African trees. London, New Holland.

Walker, S. and P. Desanker (2004). "The impact of land use on soil carbon in Miombo Woodlands of Malawi." Forest Ecology and Management 203: 354-360.

6a. How uncertain are carbon stock estimates at plot and landscape scales? An example from miombo woodlands

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Abstract

Quantifying vegetation carbon stocks is a crucial part of efforts to understand the global carbon cycle and its changes. Understanding the uncertainties and biases in estimates of carbon stocks at a landscape level is important for studies of the global carbon cycle. At a plot scale, knowing the uncertainty on estimates of plot carbon stocks used to 'ground truth' Earth observation data, may help calculate realistic errors in such studies.

Here we examine the uncertainty on estimates of carbon stocks at plot and landscape scale. We use a database of inventories from Sofala province, Mozambique, and a new allometric relationship of stem biomass, as well as five allometric models from the literature. We partition the uncertainty caused by measurement errors, allometric models and upscaling, and also estimate the potential biases introduced by using non-local allometric models and different assumptions in fitting such models.

Estimates of mean landscape carbon stocks vary from 17.2 to 24.6 tC ha^{-1} depending on how the allometric model deals with the heteroskedasticity of the biomass-DBH data. The form of the model introduces a level of bias that is comparable to that introduced by using non-local allometrics from the literature, and this suggests that appropriate ways to deal with heteroskedasticity in biomass data are crucial for accurate carbon stock estimation.

We find that estimates of plot biomass are very uncertain with the 95% confidence interval averaging 0.6 of the mean, even with the 'best' model. This was due to the overwhelming contribution of large stems to plot biomass: 3% of the stems in our inventory contributed 50% of the biomass. This compounds by the fact that predictions from an allometric model are very uncertain at large stem diameters. We show how the

prediction intervals from allometric models can be reduced by avoiding the logarithmic transform, and appropriately weighting the data.

In Chapter 6b we examine ways to reduce the uncertainty on estimates of landscape carbon stocks, and find that plots of around 0.25 ha are the most efficient way to sample the woodland landscape, whilst still obtaining a normally distributed sample of plot biomass estimates, a result that agrees with other studies in the wet tropics. To reduce the uncertainty in mean landscape aboveground carbon stock (95% confidence intervals) to 20% of the mean, around 100 plots would be needed. Our results show that more effort is needed to constrain uncertainties in landscape carbon stock at our site compared with studies in the wet tropics; we attribute this to the inherent variability of the savanna woodland ecosystems.

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Introduction

Quantifying vegetation carbon stocks is a crucial part of efforts to understand the global carbon cycle and its changes (Falkowski *et al.* 2000; Roy *et al.* 2001). Estimates of woody carbon stocks are normally inferred from inventories of trees on plots distributed across a landscape. This approach has a long history in temperate regions (LaBau 1990), and such inventories have also been used to estimate standing stocks of carbon in the tropics (Malhi *et al.* 2006; Nogueira *et al.* 2008). With repeat inventories over time, the method is used to quantify the temporal change in carbon stocks and infer carbon sinks and sources in large regions of the world (Malhi *et al.* 2002; Lewis *et al.* 2009; Phillips *et al.* 2009).

Such studies help address two major uncertainties in the contemporary carbon cycle: the flux from land use change in the tropics (Houghton 2007) and the net change in stocks of intact vegetation (Lewis *et al.* 2009). Indeed this inventory technique has become a critical method in understanding the role of vegetation in the Earth System. For instance, as estimates of the area of land that is deforested improve (DeFries *et al.* 2002; Achard *et al.* 2004), with advances in Earth Observation (EO) (INPE 2002), knowing the carbon stocks of the vegetation that is cleared becomes the critical uncertainty (Houghton 2005).

Typically three steps are used to produces a landscape-scale estimate of vegetation carbon stocks (Brown *et al.* 1989; LaBau 1990; Condit 1998; Chave *et al.* 2004). Firstly sample plots are established across a landscape and one or more auxiliary variables related to woody biomass are recorded for each stem e.g. diameter at breast height (D), height (H) and wood density (ρ). Secondly, a subsample of trees is destructively sampled so that an allometric model can be parameterised and the auxiliary variable(s) can be used to predict the biomass of each stem (B_i). This step is sometimes replaced with a generic allometric equation from the literature (Penman *et al.* 2003). Finally the mass of all trees on the plot is

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summed, to calculate carbon or biomass on an areal basis (B_{plot}, t ha^{-1}) and the sample of B_{plot} is used to estimate the mean and variance of the population, which in this case is the landscape carbon density ($B_{landscape}$ t ha^{-1}). A key point is that biomass of each stem, plot and the landscape is not directly determined, but is an estimate.

With the increasing effort to quantify tropical carbon stocks has come an examination of the uncertainties involved in the process (Brown et al. 1995; Clark 2002; Chave et al. 2004). Studies exploring the uncertainties in tropical vegetation stocks have been limited in several respects: firstly, they have been conducted only in the neotropical wet tropics, and have ignored the spatially dominant tropical savannas. Estimating properties of savanna woodland ecosystems may present different challenges because of sparse tree cover and different stem size distributions. Given that disturbance (by fire, grazing and humans) is a major feature of savannas (Bucini et al. 2007), the landscape may be more heterogeneous and difficult to sample.

Secondly, many such studies have typically only investigated the uncertainty in landscape level estimates of carbon density, and have not evaluated the uncertainty in measurements at a plot level. EO approaches to C stock estimation normally rely on calibrating or ground-truthing EO-derived quantities that relate to biomass/carbon stocks (e.g. radar back-scatter, optical vegetation indices such as EVI or NDVI). Such calibrations often ignore the uncertainties on the plot biomass estimates or assume that any uncertainty is normally distributed (Saatchi et al. 2007; Saatchi et al. 2007). These EO approaches are becoming more common (DeFries *et al.* 2002; Baccini *et al.* 2008; Goetz *et al.* 2009; Grainger 2009) and offer a way to overcome the limited ground data on tropical ecosystems (Fisher *et al.* 2008), but need to be informed by a realistic assessment of the limits of the so-called ground *truth* data.

Finally, several studies have looked at the uncertainty of using allometric models of biomass (Ketterings et al. 2001; Zianis et al. 2004), and advocated various model forms, the use of global allometrics (Chave *et al.* 2005), and the use of explicit modelling of heteroskedasticity in the data rather than log transformations (Brown *et al.* 1989; Parresol 1999). Other studies have evaluated the contribution to uncertainty of the choice of allometric model (Keller *et al.* 2001), but have not decomposed this into the effects of different data sets being used to fit the model, and different forms of allometric model. This is despite widely differing constructions of

10 allometric models (polynomial, linear, or piecewise approach, often using some criterion of model goodness of fit to chose between model forms (Chidumayo 1988; Grundy 1995; Abbot *et al.* 1997; Chave *et al.* 2005). Although goodness of fit may help to guide model form selection, if there is a universal functional relationship in allometry (Enquist et al. 2002; Zianis et al. 2006), using different model forms may introduce bias when allometric models are applied outside of the sample site (as they usually are). We are not aware of any studies that have explored the impact of different forms of allometric model on estimates of carbon stock or a quantification of the biases that different model treatments of

20 heteroskedasticity may introduce. In a similar way, many inventory estimates of C stocks use allometric models from the literature, rather than site-specific ones. It would be useful to know what extra uncertainty this practice introduces, to allow trade-offs between accuracy and effort to be quantified.

This paper addresses these issues, by conducting a full error analysis of woody aboveground biomass in the miombo woodlands of Mozambique. We ask:

1.   *What is the magnitude of random error in carbon stock density estimates at a) landscape and b) plot scales?*

30 2.   *What are the sources of this random error and what are their relative contributions?*

3. *What impact do different allometric model forms have on the final estimate of carbon stock density and do different model forms introduce bias?*

4. *To what extent does the use of a local allometric model reduce uncertainty in carbon stock estimates, compared to using literature (non-local) models?*

Method

We present data from an inventory of 60 plots in the woodlands of central Mozambique and combine these with a destructive harvest of 29 trees. We use these data to estimate landscape and plot carbon stocks in the manner described in the introduction. To quantify the uncertainty on these estimates we use a Monte Carlo approach to assess the importance of measurement, modelling, and upscaling uncertainties. We also use this method to quantify the contribution that each source of uncertainty makes to the total uncertainty.

We then address the potential bias created by using different forms of allometric model parameterised with our destructive data and by using non-local models from the literature. We quantify the bias that the different models produce and analyse the importance of different model forms and the treatment of heteroskedasticity in biomass data.

Inventory and destructive data

We report data from a variety of woodland inventories carried out between 2004 and 2007 in Sofala province of central Mozambique, at the southern end of the African Rift Valley (Fig. 2 in Chapter 2). The database includes 60 plots totalling 29.2 ha and 12883 stems.

The inventories included all stems > 5 cm DBH that were alive and standing. The inventories were conducted for different purposes and so the plots are of different size and shape. They ranged from 0.2 ha to 1 ha and the mean plot size was 0.46 ha. Some of the data have been reported in Chapter 3 and 5.

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The inventoried plots were contained within an area of roughly 60 km by 30 km, described in detail by Tinley (1977). This area receives annual rainfall of 850±269 mm (mean±standard deviation of 24 years of data) and is on several soil types, with sandy loams on the slopes giving way to finer hydromorphic soils on the Rift Valley floor. Rainfall is highly seasonal with 82% of rain falling between November and March. The area is subject to frequent fires in the dry season, and human use of the woodlands is extensive.

In October 2007 29 trees were destructively harvested. Target trees were chosen from the dominant five species in our inventory, with sizes that spanned the D range of each species. At five randomly located points on the road network, we located trees that matched the D and species criteria as closely as possible. These trees were felled and weighed, separating trunk and branch biomass. Thereafter, multiple subsamples were taken from the felled trees from both the trunk (cubes 10x10x10 cm) and branches (cylinders ~10 cm long). These subsamples were weighed and then dried in an oven (~80 ° C for 24 hours) to determine their dry mass fraction (DMF, defined as dry mass/wet mass). Three subsamples from 19 of the trees were returned to Edinburgh for %C analysis (Carbo-Erba/400 automated CN analyser). Biomass (B_{dest}, kgC) was calculated as the product of wet mass, DMF and %C.

Assessment of uncertainty: overview
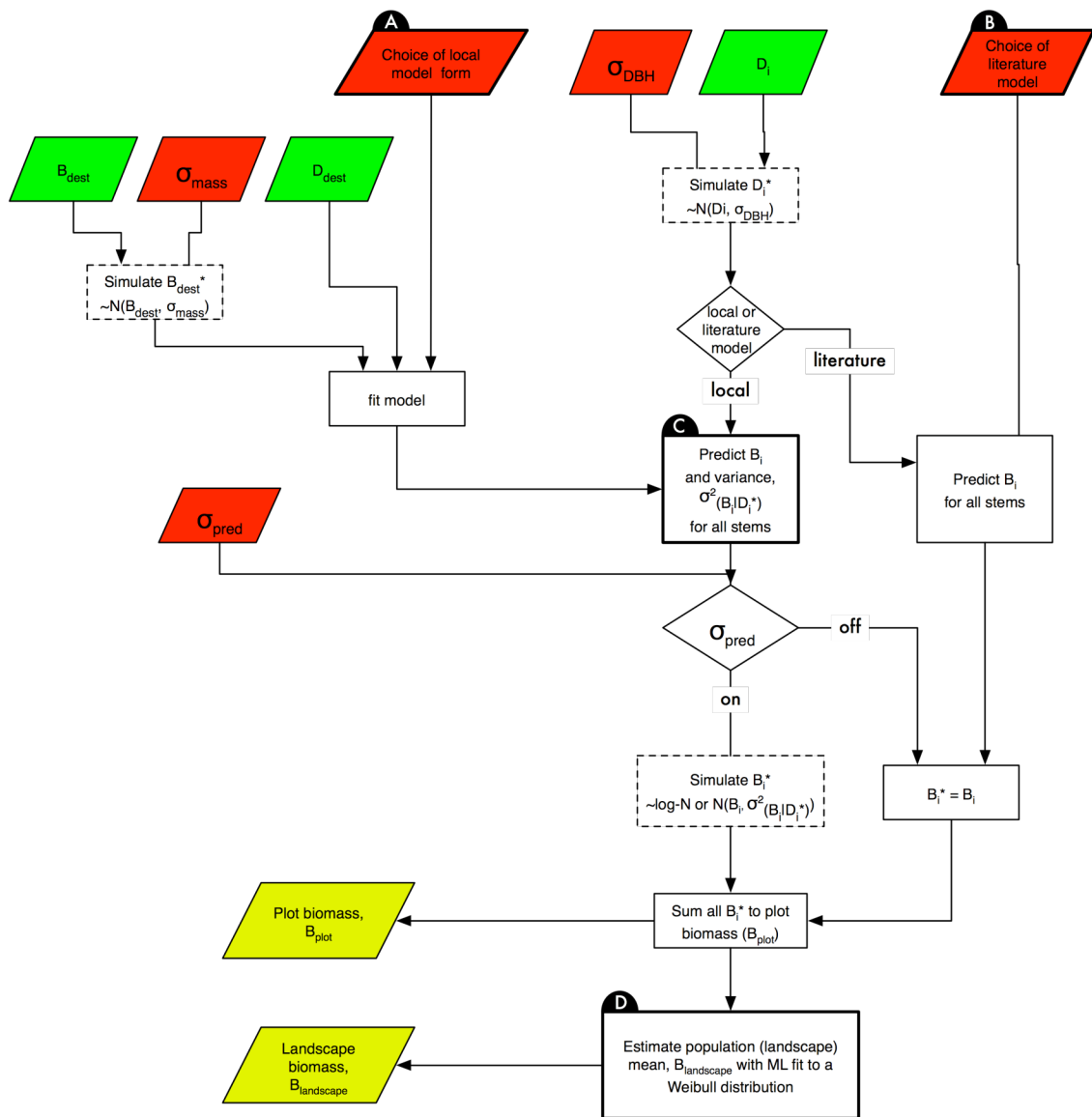
Figure 1. Overview of our method used to calculate plot and landscape biomass. Data inputs are shown in green, sources of uncertainty that we examine in red and outputs in yellow. The method is summarised in Section 3.2 and the detail of several processes, marked with a thick line and a letter in the figure, are described in sections A-D.

B = biomass carbon, D= DBH, cm. Subscripts: plot = plot carbon stock, landscape = landscape carbon stock, i= inventoried tree, dest = destructively harvested tree. * indicates variables randomly drawn from a given distribution. σ_{DBH} is the uncertainty on a DBH measurement, σ_{mass} is the uncertainty on the mass of the destructively sampled stems, σ_{pred} is the uncertainty on a new prediction from an allometric model. $\sim N(\mu,\sigma)$ indicates a normal distribution with mean μ and standard deviation σ. ML indicated maximum likelihood estimation.

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This section provides an overview of the method for determining uncertainty (Fig. 1) and further detail is given in section A-D below. Broadly, our method is based on the use of Monte Carlo (MC) simulations, calculating the output variables (B_{plot} and $B_{landscape}$ both in MgC ha^{-1}) many times, each time randomly drawing the input variables from specified distributions. To understand to what extent the outputs are influenced by uncertainties in the inputs, we adjust the variance of the distributions from which the inputs are drawn.

The main inputs to the calculation are the inventory DBH measurements (D_i) and the destructive data (D_{dest} and B_{dest}). For each of the 500 MC runs, the following procedure was followed (Fig. 1 and 2):

First, to represent random error in stem DBH measurements (D_i), realisations of possible DBH values (D_i^*) are sampled from a normal distribution with mean D_i (as measured in the inventory) and variance σ_{DBH} (specified later). D_i^* is then used to estimate B_i using an allometric model. The model (described below) is parameterised with the destructive data. These data are the DBH of the sampled stems (D_{dest}, assumed to have no errors) and the dry mass of the sampled stems (B_{dest}). To account for errors in estimating stem dry mass from the wet mass of the entire stem whilst only using subsamples to estimate DMF (see above), we draw random realisations of the mass of the destructively sampled trees (B_{dest}^*) from a normal distribution with mean B_{dest} and variance σ_{mass}, described below.

We use random sampling at a third point in each MC run (Fig. 1 and 2), to predict the biomass of each stem (B_i^*) from D_i^*. Predictions of the mass of a stem (B_i) with DBH D_i^*, using an allometric model are not deterministic, but rather each prediction is for a mean (B_i), with an associated variance ($\sigma^2_{(B_i|D_i^*)}$). Each predicted value of B_i^* is randomly sampled from a distribution with mean and variance as predicted by the

model. We term the uncertainty introduced by this process σ_{pred} (full details below).

During each run, after $B_i{}^*$ has been calculated, we sum all stems for each plot and calculate B_{plot}, (assuming the plot area measurement is exact). We then use maximum likelihood to estimate the mean and variance of the population ($B_{landscape}$) from the 60 sample plot estimates of biomass (B_{plot}). Thus the 500 Monte Carlo runs produce 500 x 60 values of B_{plot} and 500 x 1 of $B_{landscape}$. The variance of these 500 values provides an assessment of the random error (uncertainty) in the final values. For both B_{plot} and $B_{landscape}$, we summarise this error by reporting the 95% confidence interval of the 500 values, as a fraction of the mean, which we term CV_{95}.
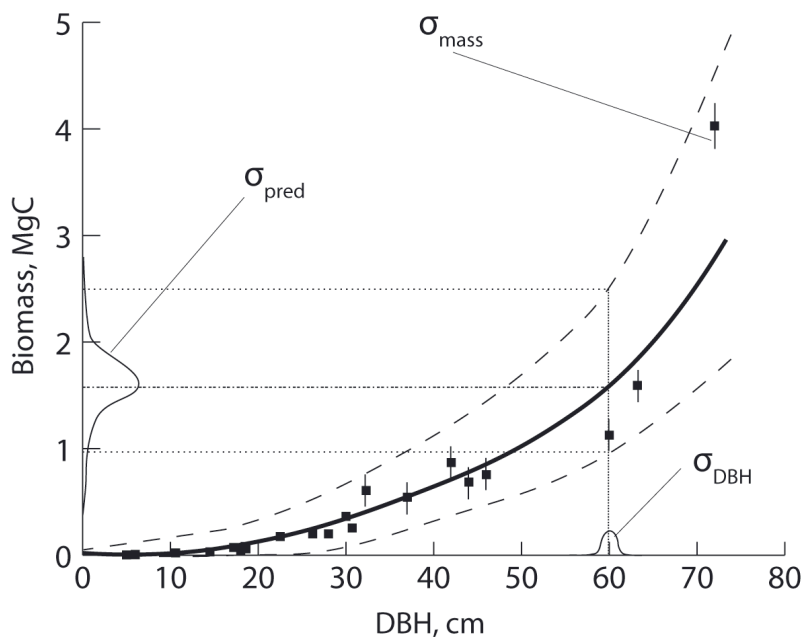
Figure 2. Schematic of the three distributions that are randomly sampled in each Monte Carlo run. σ_{DBH} represents the uncertainty on a measurement of DBH and is nominally set to a s.d. of 1 mm. σ_{mass} is the uncertainty on the mass of the destructively sampled stems, caused by uncertainties in determining the dry weight of the whole stem from subsamples. Its s.d. is nominally set to 10% of the mass. σ_{pred} is the uncertainty introduced by predicting biomass for each stem in the inventory, and is determined by the allometric model used (see text for more details). The dash-dot line shows the mean prediction of the allometric model, dotted lines the 95% prediction intervals and squares the destructive data.

A) Allometric model form

Different allometric model forms produce different variances on new predictions, depending on the method for weighting during the fitting and any log transformations of the data. We used four model forms (Table 1), some of which are commonly found in the literature (see below). Comparing outputs from the four models allows an assessment of any bias that model form may introduce. In a similar manner, we used five literature allometric models (Table 1) and compared the outputs using these models against each other and against the locally parameterised models.

The local models (M1-4) were parameterised with varying assumptions about the distribution of the error term and the method for dealing with heteroskedasticity in the destructive data. The four models were:

- M1. A non-linear least squares power fit assuming that $\varepsilon \sim N(0,\sigma)$, and

$$B = \alpha D^\beta + \varepsilon \tag{1}$$

Where: B is biomass (Mg C), D is DBH (cm), α and β are parameters to be estimated and ε is the error assumed to be normally distributed with zero mean, $N \sim (0, \sigma)$.

M1 was fitted to the data using non-linear least squares robust regression (Matlab Statistics toolbox) to estimate the weights applied to each data point. Robust regression is designed to give lower weight to points that do not fit well and is less sensitive to outliers in the data compared to ordinary least squares regression. It fits the power model of M1 using an iterative weighted non-linear least squares algorithm. The weights at each iteration are calculated as a function of the residuals from the previous iteration.

- M2. As above (using equation 1) but with non-linear least squares fitting, with no weights.

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- M3. Uses the same form as M1 and M2, but the data were log transformed before linear least squares fitting. The model that is fitted is:

$$\log(B) = \log(\alpha) + \log(D)\beta + \varepsilon \tag{2}$$

Where: log is the natural log, other terms as Eq.1.

This transformation is commonly used as a way of reducing the heteroskedasticity of the data. However the conversion back to real units is not direct, because of the implicit log-N distribution of ε, and so a range of correction factors have been suggested (Sprugel 1983). For M3,

10 We use the correction factors of Parresol (1999) for both the mean and variance estimated with this model. It is critical to note that any goodness-of-fit statistics only apply to the log-transformed model, and are not valid as a comparison with untransformed models.

- M4. Log transformed, with a simple back conversion to geometric mean and variance. Again we fit equation 2, but note that when back transformed this is equivalent to:

$$B = \alpha D^{\beta} + \varepsilon \tag{3}$$

but now:

$$\varepsilon \sim Log\text{-}N(\mu, \sigma)$$

20 No correction factors were applied to this model. The implicit log-N error structure is not adjusted with correction factors. This model predicts the geometric mean of B with the geometric variance. There are several reasons to think that there may be a log-normal error structure to our data. 1) B_i cannot be zero. 2) large data sets of B typically include a few large values (e.g. Zianis 2008, their Fig 1.)

Table 1 (overleaf). Allometric models used in this study. Models M1-4 are different model forms parameterised with our local data. M5-6 are from the dry tropics and M7-9 are from the miombo region.

	Geographic domain	Author	Form[‡]		Weights[†]	CF[Ω]	n	max D	adj r² %	RMSE	a	b	c	d
			Model summary									**parameters**		
M1	local		$B = a \cdot D^b$		Robust	n/a	29	73	98.5	0.079	1.71 E^{-5}	2.746		
M2	local	this study	$B = a \cdot D^b$		none	n/a	29	73	88.5	0.215	1.10 E^{-5}	4.533		
M3	local		$\log(B) = a+b \cdot \log(D)$		none	yes	29	73	93.1	0.518	-3.629	2.601		
M4	local		$\log(B) = a+b \cdot \log(D)$		none	none	29	73	93.1	0.518	-3.629	2.601		
M5	'Global' (Australia, India, Mexico) dry forests	Chave 2005[¶]	$\log(B) = \log(\rho) \cdot a + b \cdot \log(D) + c \cdot \log(D)^2 + d \cdot \log(D)^3$		none	yes	406	n/a	99.6	0.353	-0.667	1.784	0.207	-0.028
M6	Dry life zone	Brown 1989[∞]	$B = a - b \cdot D + c \cdot D^2$		$\varepsilon \propto D^4$	n/a	32	40	67.0	0.022	34.4703	8.0671	0.659	
M7	Miombo, Zambia	Chidumayo 1997	D<10	$B = a \cdot D - b$	none	n/a	6	25	97.0		2.23	6.44		
			D>10	$B = a \cdot D - b$	none	n/a	7		98.0		17.43	-188.8		
M8	Miombo, Malawi	Abbot 1997[§]	canopy	$\log_{10}(V) = a + b \cdot \log_{10}(D)$	none	yes	51	47	95.0	0.003	-4.22	2.76		
			understory	$sqrt(V) = a + b \cdot D_2$	none	yes	168	19	88.2	0.002	0.057	0.000918		
M9	Miombo, Zimbabwe	Grundy 1995[¶]	$\log_{10}(B) = a + b \cdot \log(D)$		none	no	280	25.8	92.7		8912.5	2.6		

[†] Weights. This describes any weights ascribed to B_{dest}, during the model parameter estimation. Robust regression is described in the text. Brown (1989) use an explicit model of the heteroskedasticity.

[Ω] Correction factor. If the destructive data are log transformed, this describes any correction factor applied to the back transformed values. If yes then the equations of Parresol (1998) were used. These are: $B_i = exp(\hat{\mu} + \hat{\sigma}^2/2)$ and $\sigma^2_{(\hat{Y}|\hat{X})} = exp(2\hat{\sigma}^2 + 2\hat{\mu}^2) - exp(\hat{\sigma}^2 + 2\hat{\mu}^2)$, where $\hat{\mu}$ and $\hat{\sigma}^2$ are the mean and variance of a new prediction as estimated by the model in log space and B_i and $\sigma^2_{(\hat{Y}|\hat{X})}$ are the mean and variance of the new prediction in arithmetic space (back transformed and corrected)

[¶] "best dry forest model" (p 93)

[∞] method based on (Cunia 1964)

[§] Only their Phyu site is used here as it is very similar to our site in terms of rainfall and floristic composition. *V* is stem volume and was converted to biomass using our site specific density data (Chapter 5).

[¶] *D* measured at 30 cm rather than 130 cm. We average the two equations for *Brachystegia spiciformis* and *Julbernardia globiflora*

[‡] Log is natural log, log 10 to the base 10

B) Allometric models from the literature

We used five allometric models from the literature (M5-9). We used three published models from the miombo region and two from the dry tropics, that related D to B (dry mass, we adapt this to carbon mass using the %C values from our model of 47%). Where the model requires ρ, we use a value of 0.56 g cm^{-3} - the mean for miombo woodland at our Nhambita site, as calculated by Williams *et al* (2008). Full details of each allometric model are in Table 1. The models are plotted in Figure 3.

C) The variance on a prediction from a regression model

Given a regression model of X on Y, for a new value of X, i.e. one that was not used to fit the model, which we denote $\tilde{X}$, the regression model generates a predicted value of Y, $\tilde{Y}$, that has a variance, $\sigma^2_{(\tilde{Y}|\tilde{X})}$ associated with it. $\sigma^2_{(\tilde{Y}|\tilde{X})}$ is calculated by:

$$\sigma^2_{(\tilde{Y}|\tilde{X})} = \hat{\sigma}^2 \left(1 + \frac{1}{n} + \frac{(\tilde{X} - \overline{X})^2}{SS_X}\right)$$

where: $\hat{\sigma}^2 = \frac{RSS}{n-2} = \frac{\sum_{i=1}^{n}\left(Y_i - \hat{Y}_i\right)^2}{n-2}$, RSS is the residual sum of squares, $\overline{X}$ is the mean value of

the Xs used in the regression, SS_x is the sum of squares of X, $= \sum_{i=1}^{n}\left(X_i - \overline{X}\right)^2$, n is the number of samples in the regression, Y_i are the observed values of Y and $\hat{Y}_i$ are the values of Y predicted by the regression (Gotelli et al. 2004).

$\sigma^2_{(\tilde{Y}|\tilde{X})}$ is distinct from (and greater than) the uncertainty associated with the estimation of model parameters $(\sigma^2_{(Y|X)})$[1]. This is because, as well as parameter uncertainty, $\sigma^2_{(\tilde{Y}|\tilde{X})}$ includes the uncertainties included in the ε term of Eqs 2 and 3. In our case, $\sigma^2_{(\tilde{Y}|\tilde{X})}$ accounts for the variation in biomass of trees of a given D.

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[1] Given by $\sigma^2_{(Y|X)} = \hat{\sigma}^2 \left(\frac{1}{n} + \frac{(X_i - \overline{X})^2}{SS_X}\right)$

Our approach to including this variance in the estimate of B_{plot} and $B_{landscape}$ is to randomly sample from a distribution with μ given by $\tilde{Y}$ from the regression equation (Eq 1 and 2) and a σ given by $\sigma^2_{(\tilde{Y}|\tilde{X})}$. If the model is fitted in log space, μ and σ are the parameters of a log-normal distribution. Alternatively, if the model is untransformed they are the parameters of a normal distribution. We call this method "σ_{pred} on" because it includes the error associated with a prediction from an allometric model. The alternative is to assume that all predictions from the regression fall exactly on the regression line and we call this approach

10   "σ_{pred} off". The models M1-M4 were chosen so as to produce a variety of different magnitudes of $\sigma^2_{(\tilde{Y}|\tilde{X})}$ (Figure 3a).

D) Estimating the mean of a population ($B_{landscape}$) from a sample (B_{plot})

The methods above generate a vector of B_{plot}, which can be used to estimate the landscape mean ($B_{landscape}$) by fitting a distribution and estimating its mean. We tested for normal, log-normal and Weibull distributions and fitted the best match as determined by the Anderson-Darling test (Trujillo-Ortiz *et al.* 2007). We used a maximum likelihood (ML) method (Matlab Statistics Toolbox) to estimate the parameters of

20   the distribution, and used these to calculate the mean. The ML method produces uncertainties on all parameters of the distribution and we combined these to estimate the mean and its confidence interval. We refer to the uncertainty on the estimate of the population mean as $\sigma_{upscale}$.

Nominal values of σ_{mass} and σ_{DBH}, and the method for assessing the contribution of each uncertainty

We define nominal values of σ_{mass} and σ_{DBH}, which are our best estimates of the appropriate values of these parameters, and use these nominal values in our 'with error' runs.

An estimate of σ_{mass} is available from the variance of the multiple subsamples used to determine the dry mass fraction of each destructively sampled tree. The fact that subsamples from a given tree have different measured moisture contents introduces uncertainty into the dry mass of the whole stem (even, assuming as we do, that we weighed all of the wet mass with high accuracy). We calculate that the uncertainty in moisture content introduces an uncertainty of about 10% of the mass to each estimate of B_{dest}. This is because the average standard error of the mean (SEM) was ~10% of the mean (SEM ranged from 7-33% of the mean).

10 For σ_{DBH}, no data were available and we used a nominal value of 1 mm, which is in the range implied by Brown *et al* (1995). We tested the robustness of our results to much higher values of σ_{DBH} (up to 1 cm) and found it did not substantially alter our conclusions.

To assess the importance of each source of uncertainty we used 'no error' values of 0% for σ_{mass} and 0 cm for σ_{DBH} and ignored the variance of the model prediction (i.e. $B_i^* = B_i$, which we term 'σ_{pred} off')

The relative importance of the different sources of error are estimated by asking the following question: 'what would the reduction in total uncertainty be if each source of error could be switched off?' Switching off
20 means using the 'no error' value defined above instead of the 'with error' value. We quantify the change in uncertainty of the output value by the percentage reduction in CV_{95}. i.e.:

$$\partial\sigma_{source} = (CV_{95,nominal} - CV_{95,\sigma_{source\_off}}) / CV_{95,nominal} \qquad (4)$$

Where: CV_{95} is the 95%CI as a fraction of the mean of either B_{plot} or $B_{landscape}$.
$\partial\sigma_{source}$ is the change in uncertainty when a given source of uncertainty is switched off.
Source can be DBH, mass or pred.
$CV_{95,nominal}$ is the uncertainty with all uncertainties set to their nominal value (see above)
$CV_{95,\sigma_{source\_off}}$ is the total uncertainty when the relevant source of uncertainty has been
30 switched off (i.e. $\sigma_{DBH} = 0$, $\sigma_{mass} = 0$, σ_{pred} "off").

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$\sigma_{upscale}$ cannot be switched off, so its influence is calculated as the remainder i.e.:

$$\partial\sigma_{upscale} = CV_{95,\sigma_{all\_off}} / CV_{95,nominal} \qquad (5)$$

Where: $CV_{95,\sigma_{all\_off}}$ is the uncertainty with all uncertainties switched off.

Relative error to quantify bias

To quantify systematic errors, or bias, introduced by different models we use relative error, defined as:

$RE_{mod} = (X_{mod}-X_0)/X_{mod}$

Where: X is the relevant quantity (B_{plot} or $B_{landscape}$) estimated with model $_{mod}$, and X_0 is the relevant quantity estimated with the reference model (defined in each case below).

Results

Destructive data

The 29 sampled trees ranged from 5-73 cm DBH. As well as the 20 target trees of the five dominant species (*Brachystegia boehmii* Taub., *Brachystegia spiciformis* Benth., *Combretum adenogonium* Steud. ex A.Rich., *Diplorhynchus condylocarpon* (Muell.Arg.) Pichon), we included nine other trees including two further species (*Crossopteryx febrifuga* (Afzel. ex G.Don) Benth. and *Pericopsis angolensi*s (Baker) Meeuwen) that had to be harvested to allow access to the target species. The sampled stems had wet mass from 8 -10,309 kg (mean 1043 kg). The subsamples had moisture content (fresh mass/dry mass) that averaged 0.65±0.01 (±sem of 29 trees) for the trunk and 0.59±0.02 for the branches. The trunk sample moisture content was significantly different from the branch samples (one tailed t test, p <0.0001), so dry mass was calculated separately from branch and trunk mass, using stem specific moisture content values. This calculation yielded dry mass estimates of 4-6954 kg dry matter (mean 674 kg). %C values were not different (2 way ANOVA p

= 0.366) between trunk and branch subsamples or between trees, so we used the mean (47%) for all conversions to C mass. Final values of B_{dest} ranged from 1.9-3268 kg C (mean 320 kg C). The 47% C value was used in combination with literature models when estimating dry C mass.

We pooled all destructive data from all species, after preliminary analysis showed no significant difference (no separation of 95% CIs) in the model parameters for a power fit of D_{dest} and B_{dest} for the different species (Curve fitting in Matlab).

Allometric data and models
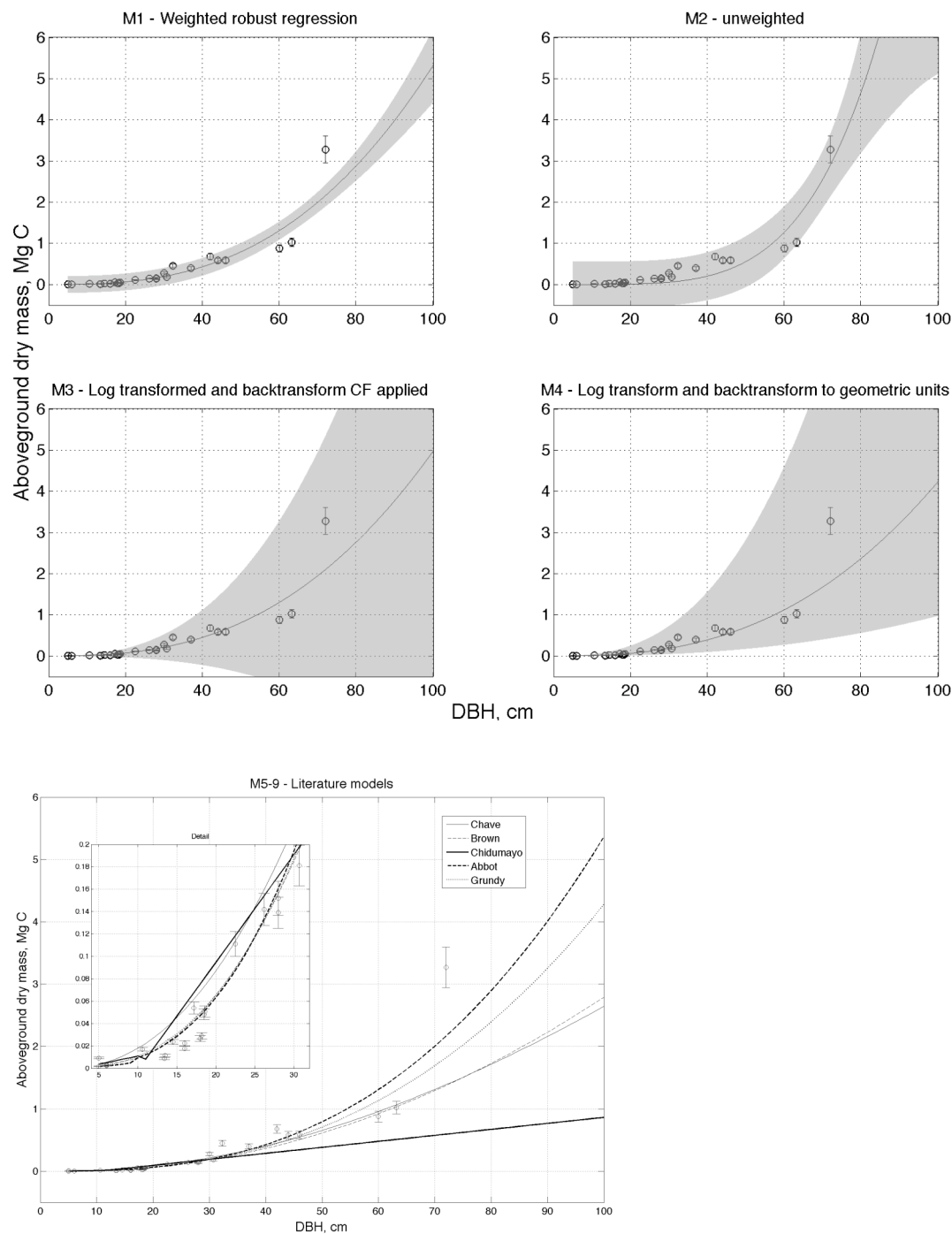
Figure 3. top) the destructively sampled data used to fit the models. The errorbars show the 10% uncertainty in the dry mass of each stem. The four local models are shown, parameterised with the destructive data. The shaded areas indicate the 95% prediction intervals. See Table 1 for explanation of models. bottom) The five allometric models from the literature, with the destructive data as in a) for reference. The inset box shows detail at low DBH.

All nine model predictions of mean B_i were very similar for D values below 40 cm, but diverged markedly above that size (Fig. 3). The prediction intervals differed markedly between the 4 local models (M1-4), depending crucially on whether a log transform was used (Fig. 3a). M2 and M3 produced physically implausible negative predictions in some cases. Prediction intervals for M1 were very tight and did not encompass several of the data points.

Field data

Applying these nine models and calculating the landscape carbon density ($B_{landscape}$) with no random uncertainty simulation, produced $B_{landscape}$ ranging from 17.2 to 24.6 tC ha^{-1}, with a mean of 21.3 tC ha^{-1} (Table 2). There were, however, very different estimates of the highest biomass plot (38.8-309.6 tC ha^{-1}) between models. This high biomass plot contained one stem of 146 cm DBH.

Table 2. Summary statistics of the plot and landscape biomass using the nine allometric models and data from 60 plots. 95% CI is the bounds of the confidence interval on the estimate of mean $B_{landscape}$. CV_{95} is the confidence interval as a fraction of the mean. Min and Max B_{plot} are the estimated C stocks for the lowest and highest biomass plots.

	Model									
	Local				'Global'		Miombo			
	M1	M2	M3	M4	M5: Chave	M6: Brown	M7: Chidu–mayo	M8: Abbot	M9: Grundy	Mean of models
$B_{landscape}$	23.0	17.2	24.6	21.3	23.7	19.5	17.8	22.7	21.5	21.3
95%CI lo	20.2	14.2	21.8	18.8	21.4	17.5	16.1	19.9	19.1	18.8
hi	26.5	21.7	28.1	24.2	26.3	21.9	19.8	26.2	24.6	24.4
CV_{95}	0.27	0.44	0.26	0.25	0.21	0.23	0.21	0.28	0.25	0.27
Min B_{plot}	1.8	0.2	2.2	1.9	3.0	1.9	2.1	1.7	2.0	1.9
Max B_{plot}	77.5	309.6	71.9	60.9	46.0	41.7	38.8	78.4	61.5	87.4
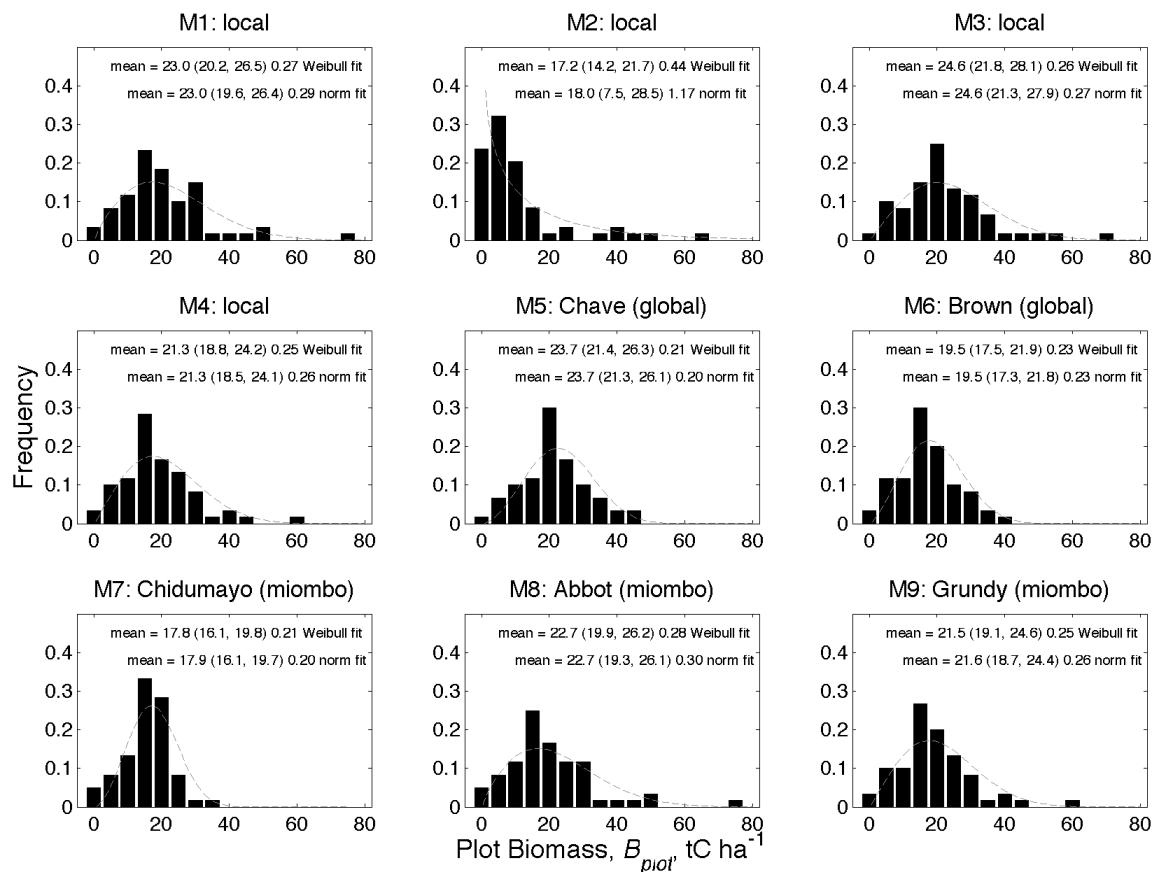
Figure 4. Distributions of plot biomass (B_{plot}) and estimates of landscape biomass using the 9 different allometric models. M1-4 are models parameterised with our destructive data, M5-6 are global dry forest models, and M7-9 are models from miombo sites. Within each panel the text shows the mean and its 95%CI in brackets, followed by the 95%CI as a fraction of the mean, assuming both a normal and Weibull distribution.

The 60 plots had B_{plot} ranging from 2.2 to 71.9 (using M3 in the simple case with no simulated uncertainties). All models, with the exception of M2, produced Weibull distributions of B_{plot} (Fig. 4). M2's B_{plot} was not normal, Weibull or log-normal, but the Weibull fitted best, so we proceed with a Weibull distribution for all models. The means calculated assuming normal or Weibull distributions were nearly always identical (to 1 decimal place), although the CIs were displaced towards higher values with Weibull fits (text in Fig. 4).

The stem size distribution of the 12883 stems was highly skewed, with only two trees >100 cm DBH and 130 trees > 50 cm DBH. These 130 stems, however, contributed 5% of the total B inventoried. Indeed, the 3%

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largest trees contributed 50% of the total inventoried biomass (Figure 5) and the top third of trees contributed 91% of the biomass.
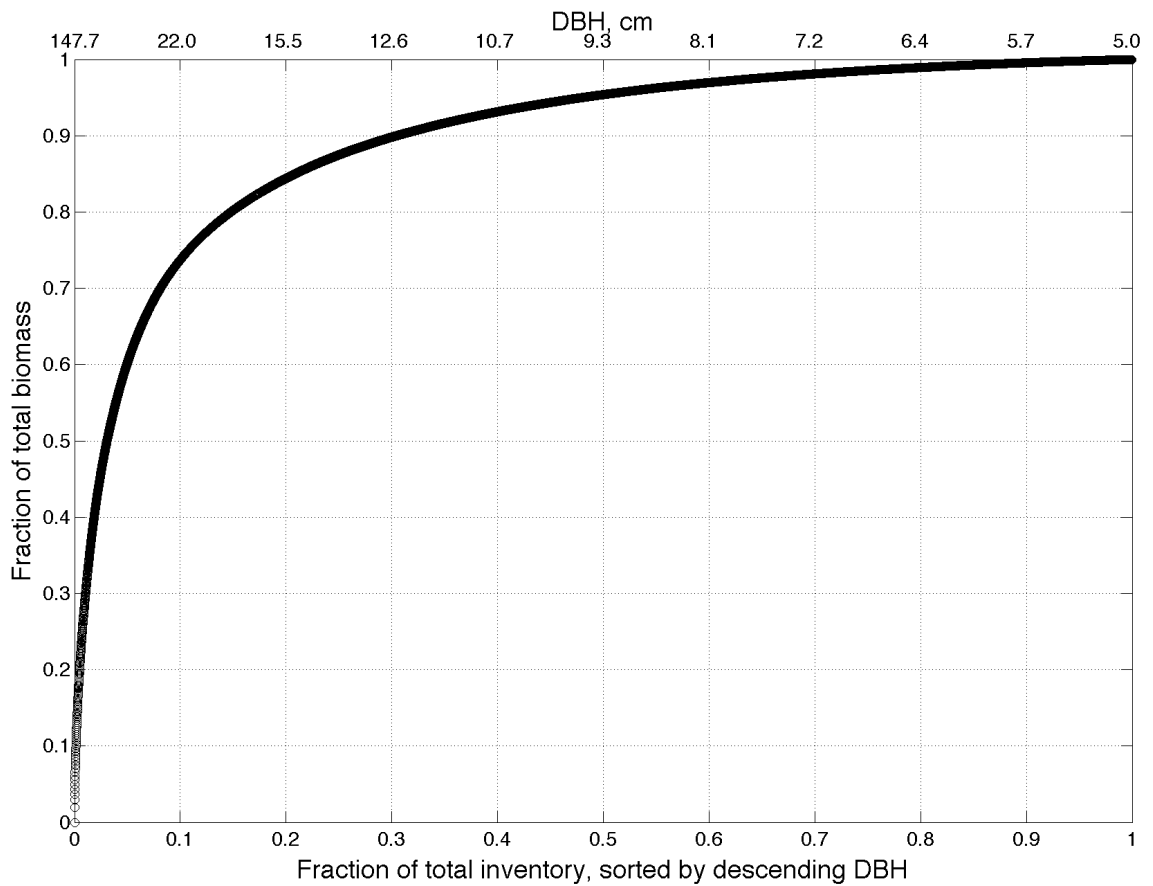
Figure 5. The contribution to total inventoried biomass of stems, sorted by DBH. The associated DBH is shown on the top X-axis.

Uncertainty at a landscape scale

Using the nominal values of our measurement uncertainties, a prediction of $B_{landscape}$ had a 95% CI as a fraction of the mean (CV_{95}) of 0.27, 0.44, 0.26 and 0.25 for model M1-4. The mean CV_{95} was 0.27 (Table 2). What caused this spread around the mean? For all models, the main contribution to the CI was $\sigma_{upscale}$, which contributed 81-99% of the total uncertainty (Table 3). The only other source of uncertainty that contributed meaningfully to uncertainty in $B_{landscape}$ was σ_{pred}, which contributed between 1 and 10%, depending on which model was used. M2 was somewhat different from the other models and, when using this

10

model, both σ_{DBH} (5%) and σ_{mass} (13%) contributed to the final uncertainty.

Table 3. The importance of each source of uncertainty to uncertainty in landscape mean biomass (CV$_{95}$ of $B_{landscape}$). Note that because the contributions interact, the percentages do not sum to 100. The contributions of each source of uncertainty were assessed by quantifying the relative change in CV$_{95}$ when each uncertainty was removed (see methods).

	$\partial\sigma_{upscale}$	$\partial\sigma_{pred}$	$\partial\sigma_{DBH}$	$\partial\sigma_{mass}$
M1	99%	1%	2%	0%
M2	81%	10%	5%	13%
M3	94%	6%	0%	0%
M4	94%	6%	0%	0%

Bias at landscape scale

Model form

Model form introduces bias to estimates of $B_{landscape}$ (Table 2). Models M1-4 gave $B_{landscape}$ means of 23.0, 17.2, 24.6, and 21.3 tC ha^{-1}. We clearly do not have an unbiased sample of possible allometric model forms, so it would be unwise to average these different means. We do note, however, that M3 is the form most often used in the literature and we would suggest the use of this model output (24.6 tC ha^{-1}) for comparisons to other studies.

We evaluated the size of the bias by calculating the relative error (RE) of the four model estimates of $B_{landscape}$ to each other. Absolute RE varied from 7 to 28%, with a mean of 17%.

Non-local allometrics

We evaluate bias caused by using non-local allometrics by comparing them to M3. All literature models (M5-9) estimated lower values of $B_{landscape}$ than M3 (Table 2). RE ranged from 3-27%. The global models (3 and 21% RE) performed no worse than the miombo region models (27, 8 and 12% RE). The mean bias introduced by the non-local models was 14% RE (underestimate).

Uncertainty at a plot scale and its causes

Using the nominal values of σ_{mass}, σ_{DBH} and with σ_{pred} on, estimates of plot biomass were very uncertain. This is shown by probability distributions of the 500 MC runs (Fig. 6). High biomass plots (40-50 tC ha^{-1}) had a 95%CI of around 20 tC ha^{-1}. For medium biomass plots (30 tC ha^{-1}) the CI was around 12 tC ha^{-1} and for low biomass plots (10 tC ha^{-1}) it was <10tC ha^{-1}).

The mean CV_{95} of B_{plot} for the 60 plots was 0.87, 9.08, 0.61 and 0.60 for the 4 local models (M1-4). M2 produced higher uncertainty than the other models, due to its extreme exponential shape. M2 also produced lower values of B_{plot}, which often stretched below zero. The log transformed models (M3-4) produced almost identical results. M1 produced larger values of CV_{95}, compared to M3-4, but this was mainly due to a lower mean, rather than a larger CI.

The dominant contribution to CV_{95} of B_{plot} was σ_{pred}, (Table 4) the uncertainty on a new prediction from an allometric model. Switching σ_{pred} off (i.e. ignoring the variance on a new prediction) lowered the uncertainty by 65% (average for all models and all plots). However, the contribution of σ_{pred} varied between models: for the untransformed models (M1 and M2), measurement errors in the destructive sample were also important ($\partial\sigma_{mass}$ = 29 and 17%), but for the log-transformed models, σ_{mass} had little influence (5 and 3%, for M3 and M4). The uncertainty in B_{plot} when using the log-transformed models was almost totally removed when σ_{pred} was switched off ($\partial\sigma_{pred}$ = 80 and 82%). σ_{DBH} was not important for any of the models when averaged over all plots, but was important for some of the plots of small area and those populated by small stems, where $\partial\sigma_{DBH}$ reached 20-40%. The sum of $\partial\sigma$ for the 3 uncertainties never summed to more than 86%, indicating that interactions between the uncertainties were responsible for 14-30% of the uncertainty.
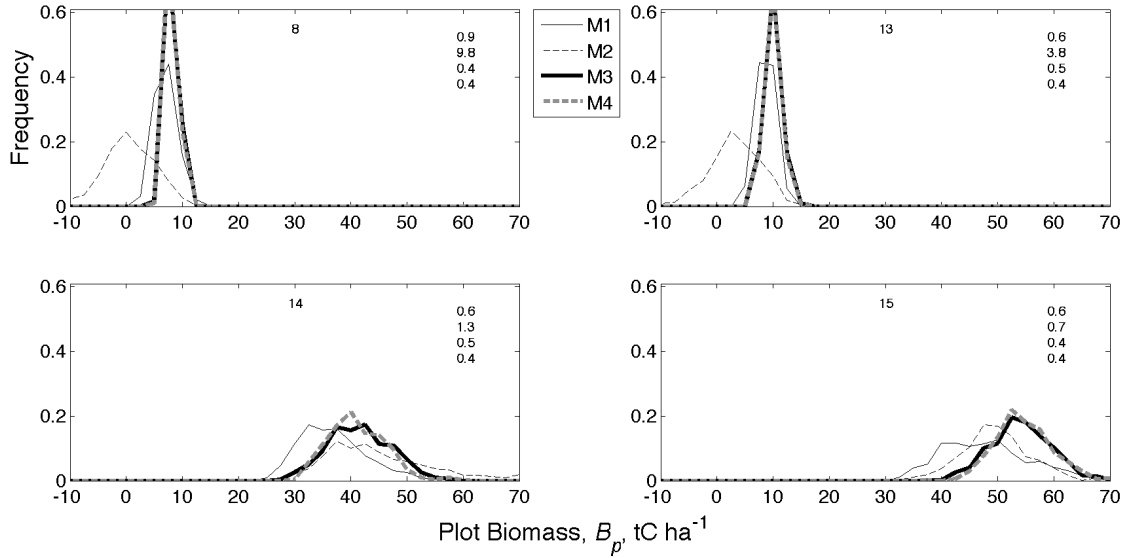
Figure 6. Probability distributions of the biomass for four example plots. The plots are all 1 ha in size. For each plot four distributions are shown, one for each model, M1-4. High biomass plots (lower panels) are contrasted with low biomass plots (top panels). Note that with M2, values of B_{plot} were often below zero. CV_{95} for the four models is shown top right in each panel, listed from M1-4 from top to bottom. The distributions are generated by binning the out put from 500 Monte Carlo runs into 5 tC ha^{-1} bins.

Table 4. Contributions to uncertainty in plot biomass. $\partial\sigma$ represents the % reduction in uncertainty achieved when removing each source of error (one by one). Where these sum to <100%, the remainder can be attributed to interactions between the uncertainties.

Data	M1	M2	M3	M4	mean of all models
CV_{95} B_{plot} (mean of all plots)	0.87	9.08	0.61	0.60	2.8
$\partial\sigma_{pred}$	41%	56%	80%	82%	65%
$\partial\sigma_{DBH}$	-1%	4%	1%	-1%	1%
$\partial\sigma_{mass}$	29%	17%	5%	3%	13%
interactions (remainder)	30%	24%	14%	16%	21%

We analysed the results by plot attribute to evaluate which features of a plot correlate to the CV_{95} of B_{plot} (Fig. 7). Correlates of CV_{95} were: the fraction of biomass in large (>40 cm DBH) trees ($B_{>40}/B_{plot}$); the number of stems on a plot; and plot area (all p>0.05). The strongest correlation was with $B_{>40}/B_{plot}$, which explained ~40% of the variation in CV_{95} B_{plot} using models M3 and M4. $B_{>40}/B_{plot}$ explained less of the variation using M1 and M2 (r^2 = 16 and 18%). Plot area was significantly and negatively correlated with CV_{95} B_{plot}, but only explained 5-17% of the variation.

Adding $n_{>40}$ (the number of stems >40 cm DBH) to a multiple regression with the above variables, increased the percentage of explained variation by 10% for M3 and M4 and had no effect on M1 and M2.
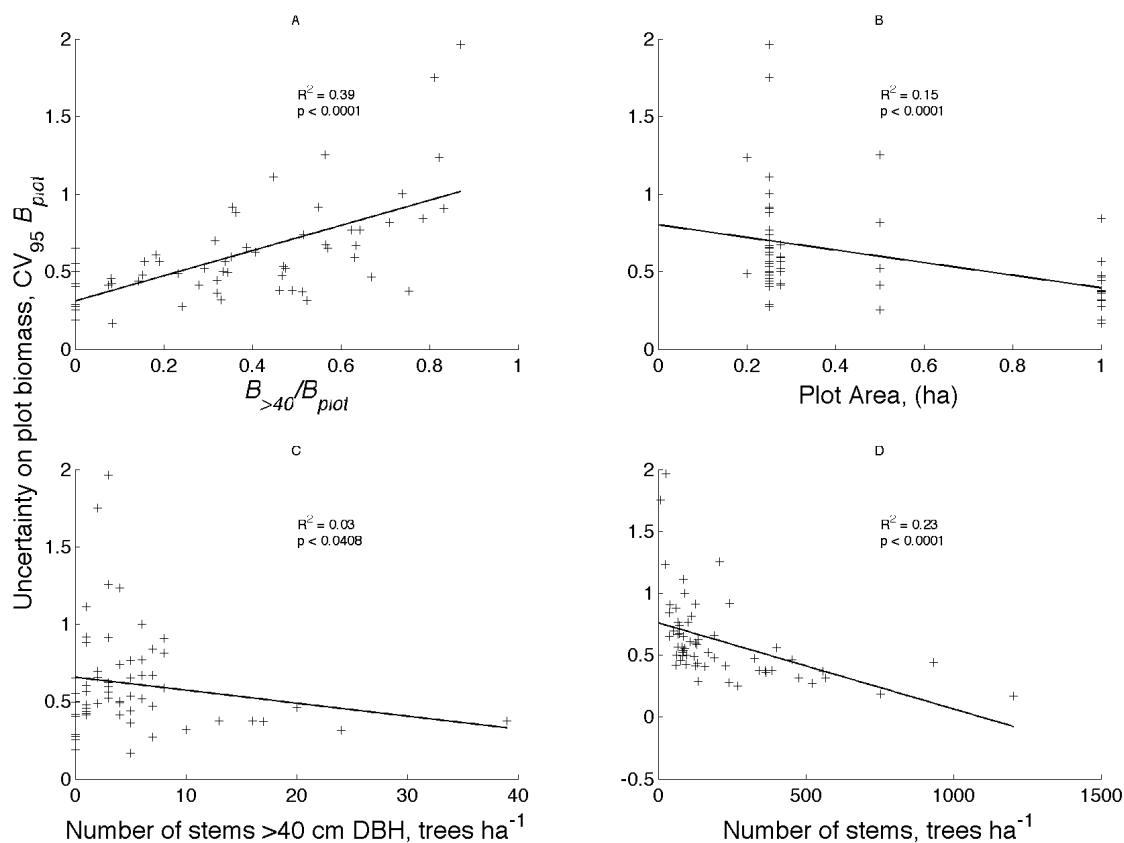

Figure 7. Correlates of plot biomass uncertainty. The strongest predictor was the fraction of large stems biomass on the plot ($B_{>40}/B_{plot}$), plot area was also (negatively) correlated to the level of uncertainty. Multiple regression (not show) showed that the number of trees on a plot was primarily a covariate of the other predictors, but that the number of large trees had some predictive power (10% increase in r^2).

Bias at a plot scale

Model form

Model form had a clear effect upon estimates of B_{plot} (Fig. 6), shifting the probability distributions as well as changing their widths. The absolute relative error (RE) on B_{plot} introduced by the different model forms (calculated by comparing each model to all others and averaged across all plots) was 28%. Most of this was due to M2, which produced very

different results to the other models – on average 47% lower than M3. M1 and M4 were on average 8 and 13% lower than M3.

Non-local allometrics

The mean absolute RE on B_{plot} introduced by non-local allometrics, averaged across all plots was 17% - slightly higher than the same bias in $B_{landscape}$. Absolute RE ranged from 0% to 272%, the median was 12%, and the mean 17%.

The non-miombo models introduced less RE (6 and 12%) than the miombo models (24, 14, 27%). M6 and M7 produced mean B_{plot} biased low (-6% and -24%), the remaining four were, on average, all biased high.

Discussion

Woody biomass in the Nhambita woodlands

The high proportion of biomass in large trees (3% of trees contain 50% of stem biomass) is striking and has important implications for carbon stock management in these woodlands. It implies that selective logging of large stems could dramatically alter woody carbon stocks, and that efforts to conserve existing carbon stocks must explicitly consider the status of large stems. We have shown that large stems may be vulnerable to fire-induced mortality (Chapter 3), and these two conclusions taken together argue for very close monitoring of the effects of fire on large trees.

We have not found any similar studies from the miombo region, but a study in Amazonia (Brown et al. 1995) found exactly the same proportion of biomass in large stems (largest 3% containing 50% of the biomass). If this phenomenon is widespread then it highlights the difficulties of monitoring degradation of carbon stocks in intact forests and woodlands.

For a discussion of the magnitude of carbon stocks in Nhambita in comparison to other studies see Chapter 7.

The causes of uncertainty at a landscape scale

Random error/uncertainty

We found that an estimate of landscape biomass typically had a 95% CI of 0.27 of the mean (Table 2). All but one model produced CV_{95} of 0.21-0.27. This uncertainty was primarily (81-99%) caused by the uncertainty in estimating the mean of the population from a sample ($\sigma_{upscale}$, Table 3). We examine in Chapter 6b how this uncertainty can be reduced. The uncertainty on a prediction from an allometric model (σ_{pred}) was the second most important source of uncertainty, but was of relatively minor importance at landscape scale (1-10%) as it averages out over the 60 plots. It is typically ignored in most studies (described as trivial in Ketterings *et al.* 2001), and this seems appropriate at the landscape scale, although it is very important at a plot scale (see below). If $\sigma_{upscale}$ could be reduced, σ_{pred} would increase in importance.

Bias

We now try to answer a simple question. What is the additional error associated with using a non-local allometric? Absolute relative error (RE) between our M3 and non-local allometrics was ~14%. This can be compared with two other studies which have estimated the bias introduced by non-local allometrics. These both found RE of 20% at Tapajos, Brazil (Keller *et al.* 2001) and BCI, Panama (Chave *et al.* 2004). Local in this context is of course subjective, but we note that the nearest literature allometric that we used comes from a site with similar (850 vs 780mm) rainfall and soils, and which is approximately 200km away; very much in the same ecological unit.

However, the literature models are not just non-local: they are also of different forms, and treat the heteroskedasticity of the data in different ways (Table 1). Thus, the figure of 14% may overestimate the impact of being non-local, because it includes potential biases from model form.

The miombo literature models were no closer to our models than the global models, which are based on dry forest data (Table 2). This result suggests that either: 1) within-miombo variability is very high, compared to dry forest *vs* miombo variation. Or, 2) the geographic origin of the data with which the model is parameterised is not the major source of difference between the models. We regard 2) as more likely; dry forest allometry is likely to be very different from miombo allometry as competition for light will drive height growth in dry forests, and there is no reason to think that miombo allometry is unusually site-specific.

10 We have shown that model form has the potential to bias estimates of $B_{landscape}$, with a mean RE between local model (M1-4) forms of 17%. Even though our models were fitted with the same data, M1-M4 produced $B_{landscape}$ estimates varying from 17.2 to 24.6 tC ha^{-1} (Table 2 and Fig. 4). Clearly, the assumptions behind the fitting of the model (i.e. the differences between M1-4) introduces a non-trivial bias; a bias of a magnitude similar to that from using non-local models. This result points to the importance of the implicit weighting of the fitted data to deal with heteroskedasticity. A similar result was found at plot scale.

Our results suggest that the model form bias subsumes the non-local
20 bias, and that the 14% (non local RE) should not be added to the 17% (model form RE) in estimates of $B_{landscape}$. Rather the 17% (model form) should be used, unless evidence is presented that the model form is in some way optimum and other reasonable model do not change the result (see below).

Thus a key conclusion of this work is that the form of the model is of crucial importance, so much so that it probably obscures smaller site-to-site differences. By form we do not just mean whether the model has a power or polynomial fit, but crucially how it deals with the heteroskedasticity of stem biomass data.

This conclusion flows from our lack of knowledge about the variance of stem biomass: we know that it is not constant across the stem diameter range, but we do not know how it scales with D. Also we typically assume that the variance is normally distributed, but this cannot be so at low D, as B cannot be negative. It is not surprising that from this lack of knowledge flows potential bias.

The causes of the uncertainty at a plot scale

Another key result is that plot biomass (B_{plot}) is highly uncertain and must be qualified with large confidence intervals (Figure 6). Plot average CV$_{95}$ was 0.87, 9.08, 0.61 and 0.60 for our four models. Even leaving aside the outlier of M2, this is a substantial uncertainty. Perhaps it should not surprise us:

".. it is very easy (and seductive) to make a point prediction from a regression line. However for most kinds of ecological data, the uncertainty associated with the prediction usually is too large to be useful" (Gotelli et al. 2004)

The uncertainty in B_{plot} was primarily caused by σ_{pred}, the uncertainty on a new prediction from a regression line. To our knowledge σ_{pred} has never been included in biomass uncertainty estimates before, despite being documented in most statistics text books. When averaged over the thousands of stems in a landscape inventory σ_{pred} becomes unimportant, but this is not the case at a plot level. Predictions of the biomass of large trees are very uncertain (Fig. 2) and with only a few large trees found on each plot (Fig. 5), plot biomass will always be an uncertain attribute. However, it is clear that measurement of D_i, does not, for a given stem, constrain B_i well. The small number of large stems on each plot means that, if an accurate value of B_{plot} is required, other auxiliary variables are likely to be required. Preliminary results predicting B_i based on a model DBH and total stem height gave no meaningful reduction in uncertainty, and further research is needed to explore which variables best constrain

B_i. Candidates would be height of bole, taper and crown diameter and height.

The importance of σ_{pred} is underlined by the finding that small plots with a high proportion of biomass in large trees can have CV_{95} of around 1 (Fig. 6). This uncertainty is exacerbated by models that have implausible prediction intervals, which leads to CV_{95} being >1 and B_i being negative in many cases.

The other significant source of uncertainty in plot biomass was the error in measuring the mass of the destructively sampled trees. However this
10   error was only important ($\partial\sigma mass$ = 29 and 17%) for models M1 and M2 (Table 4), which did not have a log-transform. It means that more attention should have been placed on very accurate determination of the dry mass of the destructively harvested stems. We estimated the 10% value for σ_{mass} based on dry mass fraction measurements on subsamples of the felled stems. This source of error could have been reduced with relatively minor effort by taking more and larger subsamples.

Bias introduced by model form and by non-local models is also important at plot scale, and is of a similar magnitude to that introduced at landscape level (see above).

20   Brown *et al* (1995) used a Monte Carlo approach to estimate uncertainty on aboveground woody biomass in a moist forest in Rondônia, Brazil and found a 95% CI of 110 t ha^{-1} for a mean of 284 t ha^{-1} (dry matter). This yields a CV_{95} of 0.4, lower than the value for our 'best' model of 0.6. However Brown's method differed substantially from ours in approach, and seems to incorporate parameter uncertainty in the regression parameters rather than prediction uncertainty. It also differs in considering tree height and wood density as well as D as auxiliary variables in predicting B_i, which may have reduced the CV_{95}. Overall however, Brown's work supports our finding of considerable uncertainty
30   in plot biomass estimation.

Model strengths and weaknesses and the merits of the log transform

"…the lognormal variable seems harmless. On the short or medium term however everything is spoilt and its behaviour looks wild. One deals with it as if it were not sulphurous, yet it is a marvellous (but dangerous) chameleon."

- Benoir B. Mandelbrot

The construction of a suitable model rests on it being an appropriate simplification of the real world. The first simplification is in the form of the *D-B* relationship (typically a power relationship), but given that homoskedasticity is rare in biomass data (Parresol 1999), this is not sufficient and the heteroskedasticity needs to be modelled too (Cunia 1964).

An allometric model that explicitly considers the heteroskedasticity of stem biomass data would have to directly model the error structure of the biomass data used in constructing the model. Such an approach is detailed in Parresol (1999) and used by Brown (1989) who assumed that variance scales with D^4, and that it is normally distributed. Such a model of heteroskedasticity needs to be tested against a large data set (such as that of Chave *et al.* 2005) to be validated. A model of heteroskedasticity based on data would be a significant step forward, and would eliminate the need for heuristic weighted regression or log transformations. This seems like a low cost way of improving plot biomass estimates.

Other ways to reduce the prediction uncertainty can be inferred from the equation for the variance of a new prediction:

$$\sigma^2_{(\tilde{Y}|\tilde{X})} = \hat{\sigma}^2\left(1 + \frac{1}{n} + \frac{(\tilde{X} - \overline{X})^2}{SS_X}\right)$$

where: $\hat{\sigma}^2 = \frac{RSS}{n-2} = \frac{\sum_{i=1}^{n}\left(Y_i - \hat{Y}_i\right)^2}{n-2}$, RSS is the residual sum of squares, $\overline{X}$ is the mean value of

the *X*s used in the regression, SS_x is the sum of squares of $X, = \sum_{i=1}^{n}\left(X_i - \overline{X}\right)^2$, *n* is the number

of samples in the regression, Y_i are the observed values of Y and $\hat{Y}_i$ are the values of Y predicted by the regression (Gotelli et al. 2004).

One way to reduce prediction uncertainty is to increase the number of destructively sampled trees (n). However in our study $1/n$ was a relatively small contribution to $\sigma^2_{(\hat{Y}|\tilde{X})}$ and experiments with pseudo data showed no meaningful improvement in prediction intervals even with an order of magnitude more destructive data. This is similar to the result of Grundy (1995), who looked at the effect of destructively sampling different numbers of trees, and concluded that no improvement to model accuracy was achieved above n=20.

The size of the prediction interval also depends on the distance of $\tilde{X}$ (the D of a new prediction) from the mean D of the destructively sampled trees ($\overline{X}$). Thus, sampling more large trees so that the mean is nearer the magnitude of large stems will reduce the impact of σ_{pred}. This suggests that destructive samples should focus more on the size of the harvested stems rather than n.

Key Conclusions

1) At both a plot and landscape scale, significant bias (17%) is introduced by different model forms (M1-4). This bias is slightly higher than that introduced by using non-local (literature) allometric models (14%).

2) $\sigma_{upscale}$, the uncertainty in estimating the mean of a sample of plots, is the dominant (81-99%) uncertainty in $B_{landscape}$. Depending on the model used, uncertainty (95%CI) in $B_{landscape}$ ranged from 0.21-0.44 of the mean.

3) Plot biomass (B_{plot}) estimates have an uncertainty (95% CI) of between 0.6 and 0.87 of the mean, but this depends strongly on the type of model used, and the plot attributes. Small plots with a few large trees have the most uncertain biomass.

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4) Uncertainty in B_{plot} is mainly caused by the uncertainty in a prediction from an allometric model. This is exacerbated by the rarity of large stems and the use of log transformed models.

5) Developing a model of the heteroskedasticity of biomass data would allow allometric models with smaller prediction intervals to be developed. This requires a large data set of destructively sampled stems.

6b. Reducing uncertainty in estimates of landscape biomass

Chapter 6a identifies the key sources of uncertainty in estimating landscape ($B_{landscape}$) and plot biomass (B_{plot}). For $B_{landscape}$ the uncertainty is primarily caused by the error in estimating the mean of a population from a sample ($\sigma_{upscale}$). Other studies also report that this is the dominant source of uncertainty (Chave *et al*. 2004). This section addresses ways in which this uncertainty can be reduced.

$\sigma_{upscale}$ is the same as the standard error of the mean (although we use ML methods to estimate it), which is given by:

$$\mathbf{sem} = s / \sqrt{n}$$

Where s is the variance of the sample and n is the sample number

Thus it can be reduced in two ways: 1) sample more plots (increase n), 2) sample less variable plots (reduce s).

A less variable sample can be achieved in two ways: 1) by stratifying the landscape into land cover classes, and sampling these separately, and 2) sampling very large plots. Stratifying however, has the potential to introduce other uncertainties relating to the classification method and area estimation. For instance, the long tail of our B_{plot} distribution (Fig. 3) is caused by high biomass, typically riverine areas. Such areas can often be less than 10 m, or two trees, wide and because of their dendritic shape are very time-consuming to demarcate. Determinations of riverine area are thus likely to have high associated uncertainty. Savannas are by definition a mosaic of vegetation and attempts to stratify such a mosaic need very high resolution spatial data.

A more feasible method to reduce $\sigma_{upscale}$ is to sample more plots. This Chapter uses a subsampling method to understand the relationship

between plot number (n_p) and plot area (A_p), and $\sigma_{upscale}$, and makes recommendations about the size of inventories in miombo woodlands.

Method

We conduct two simulation experiments. In Experiment 1, we subsample our data and estimate the marginal reduction in $\sigma_{upscale}$ obtained by adding another plot or another unit of area to the inventory. In Experiment 2, we examine the trade off between plot size (A_p) and plot number (n_p). All data and symbols are those used in Chapter 6a.

Experiment 1: $\sigma_{upscale}$ as a function of plot size and area

We subsample our data set of 60 plots randomly, picking n_i plots from our data base and calculating the CV_{95} of $B_{landscape}$ (with σ_{mass} and σ_{DBH} set to zero, and σ_{pred} off). For each value of n_i, we repeat this process 100 times, and report the 100 CV_{95} as boxplots. We vary n_i from 5 to 60 and also report the total area inventoried (A_{inv}). We then extrapolate the CV_{95} values to higher numbers of plots than actually sampled (60), by fitting a rational (ratio of polynomials) model to the observed 'data' and predicting new values of CV_{95} for n_i up to 1000. We report the 95% CI for new predictions of the model.

Experiment 2: the trade off between area and quantity of plots

Here we utilise only the plots for which we have XY coordinate data for each stem location. Such data exist for the fifteen 1 ha permanent sample plots in Nhambita. We exclude one deforested plot (PSP 12) from our data set, so n_p=14.

We create pseudo plots of varying size (A_p) and number (n_p), by subsampling square plots smaller than that actually inventoried. We varied the sample from 14 x 1 ha to 1400 x 0.1 ha plots in nine increments and examined how the normality of the sample, the estimated mean (B_{plot}) and its CV_{95} changed. We use the Anderson-Darling test for

goodness-of-fit to a normal distribution, and if the distribution is not normal tested for a log normal and Weibull distributions (Trujillo-Ortiz *et al.* 2007). We also report summary statistics for each sample.

We conduct a further examination of the importance of plot size. For the 14 plots with stem coordinate data, we explore the effects of reducing the plot size (whilst not increasing n_p as above). For each plot we sample a randomly located circular pseudoplot of area A_p. giving 14 A_p sized plots. We use the 14 B_{plot} values to estimate $B_{landscape}$ as before and report the CV_{95} of $B_{landscape}$. We repeat this process 50 times for 10 sizes of A_p (0.003 − 1ha) and report the results as boxplots of the 50 values.

Results

Experiment 1

The uncertainty in $B_{landscape}$, expressed as the 95%CI as fraction of the mean, (CV_{95}) fell from an average of 0.72 with 5 plots to 0.43 with 20 and the became asymptotic, only reducing to 0.30 with 40 plots (Figure 8). By 60 plots it was 0.25, but, extrapolating beyond our sample, progress beyond this was very slow: CV_{95} only fell below 0.2 with 90 plots and 0.1 with 250, although the uncertainties become overwhelming beyond n_p=100.
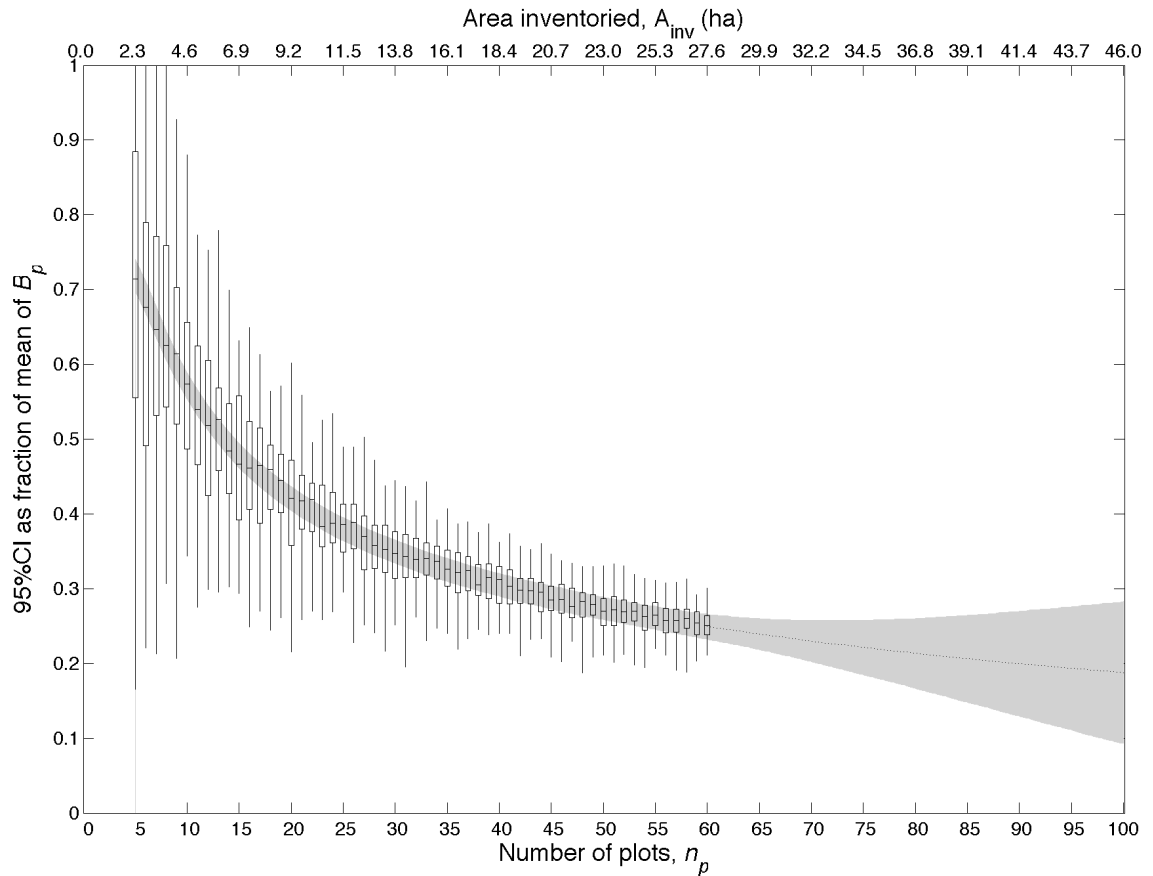
Figure 8. Uncertainty in $B_{landscape}$, expressed as the 95%CI as fraction of the mean, (CV$_{95}$) for different numbers of plots. Boxplots show the subsampled data: the horizontal bar is the median of the 100 random samples, the boxes show the interquartile range, and the whiskers show the full extent of the data. The shaded area is the 95% CI of the predictions from a rational (5:5) fit to the data and the dashed line is the mean predication.

Experiment 2

Pseudo plots smaller than 0.2 ha produced biomass distributions that had high levels of skew and kurtosis (Figure 9), and did not fit a normal, log normal or Weibull Distribution (Table 5). A_p >0.2 ha produced normal distributions, with low skew and kurtosis. Small plot sizes produced smaller standard error of the mean, but these are, of course, not valid given the non-normality.

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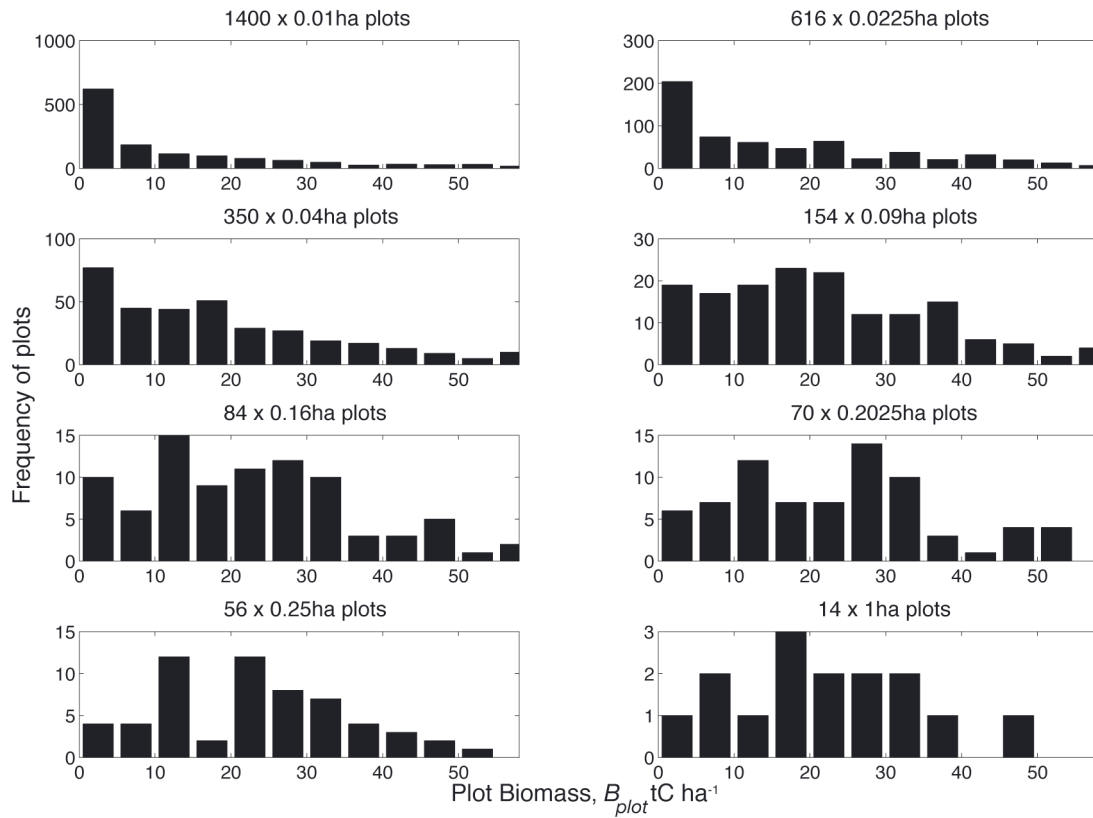
Figure 9. Frequency distributions of plot biomass (B_{plot}), with different sampling strategies. Data were randomly sampled (with replacement) from the stems and spatial structure of 14 permanent sample plots.

A_p (ha)	n_p	H	p	S.D tC ha⁻¹	Skew	Kurtosis	$B_{landscape}$ mean tC ha⁻¹	S.E.M tC ha⁻¹	CV₉₅
0.010	1400	1	<0.001	42.8	4.6	29.8	21.9	1.14	0.20
0.023	616	1	<0.001	27.9	2.6	13.3	22.8	1.13	0.19
0.040	350	1	<0.001	22.2	1.7	7.0	22.9	1.19	0.20
0.063	224	1	<0.001	19.2	1.4	5.2	22.4	1.28	0.22
0.090	154	1	<0.001	20.1	1.6	6.7	24.0	1.62	0.26
0.123	112	1	<0.001	16.0	0.9	4.4	22.8	1.51	0.26
0.160	84	1	<0.001	15.5	1.3	5.6	22.8	1.69	0.29
0.203	70	0	0.4	14.5	0.3	2.5	24.7	1.73	0.28
0.250	56	0	0.2	14.1	0.6	3.1	23.7	1.88	0.31
1.000	14	0	0.9	12.5	0.2	2.7	22.4	3.34	0.59

Table 5 Descriptive statistics of the different sampling strategies in Figure 9. H is a test for normality: 1 means we can reject the hypothesis of normality with p probability, in this case the mean and sem are in grey. 0 mean that the hypothesis of normality cannot be rejected.

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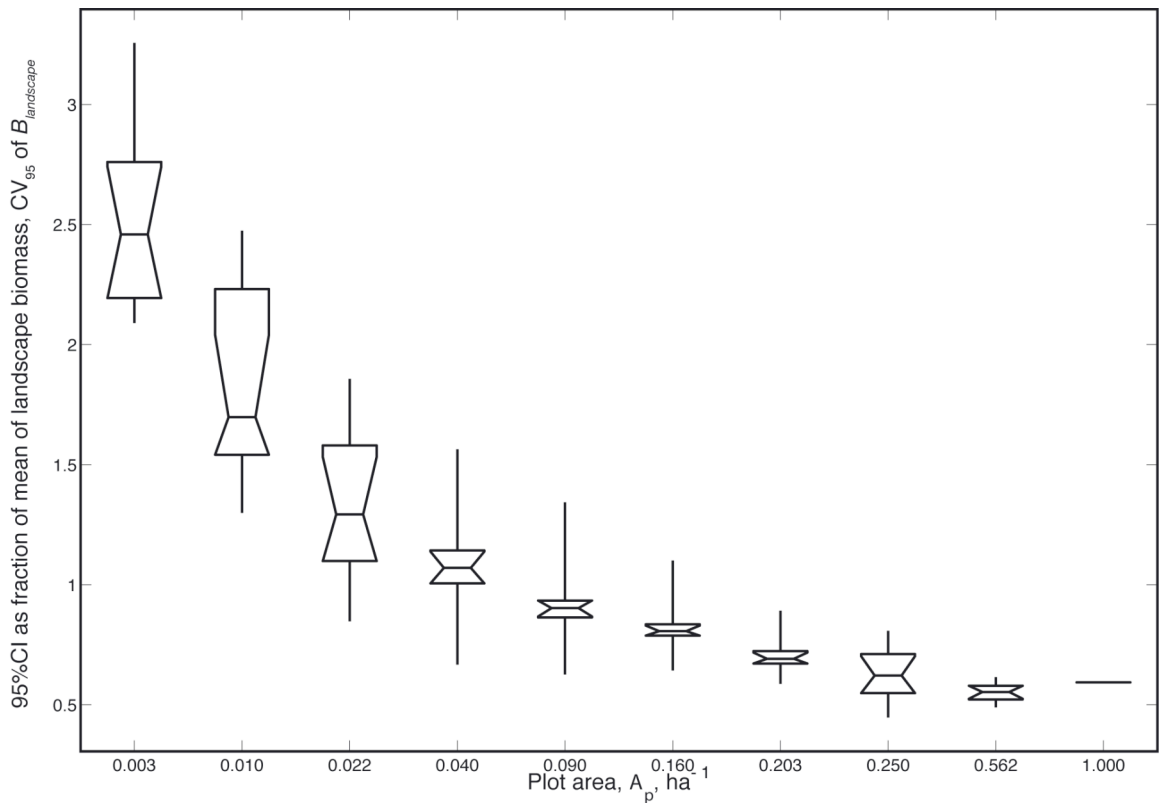
Figure 10. Effect of subsampling the 14 PSPs and simulating inventories with smaller plots. This asks the question: what effect would smaller plots have had on the observed CV_{95} of $B_{landscape}$? Boxplots show the results of 50 random samples of pseudo plots of various sizes, and the 95%CI of the resulting sample as a fraction of the mean.

Uncertainty on $B_{landscape}$ was asymptotically related to the area of the 14 plots (A_p) (Figure 10). Increasing plot size rapidly reduced uncertainty on landscape biomass until A_p >0.2 ha. The CV_{95} of $B_{landscape}$ with plots of 0.2, 0.25 and 0.5 ha was not significantly different, although then means did decrease with increasing A_p.

Discussion and conclusion

Experiment 1 showed that the uncertainty on an estimate of landscape biomass can be reduced by increasing the number of sampled plots, but that this is subject to the law of diminishing returns. Around 90 plots may be needed to reduce the 95% CI to 20% of the mean, and 250 plots should reduce CV_{95} to 0.1. These estimates are based on a mean plot area of 0.46 ha.

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Experiment 2 suggests that large plots are not necessary: plot size above 0.2 ha gives normal distributions of B_{plot} (Fig. 9 and Table 5), and increasing plot size beyond this seems to contribute little extra information (Fig. 10). A similar result was found by Chave *et al.* (Chave et al. 2004) who showed that only plots above 0.25 ha produced normally distributed samples of B_{plot}.

These results imply that the time and cost of landscape inventories can be minimised and the accuracy of the result maximised, with a large sample of 0.2-0.25 ha plots. This inference only applies to the domain of our data, and further work is required to validate its generality in the miombo region.

Keller *et al* (2001) obtained a similar result in Tapajos National Forest, Brazil, based on an inventory of 4 x 100 ha plots and a Monte Carlo subsampling analysis which showed that smaller plots (0.09-0.25 ha) were most efficient in terms of total area inventoried in constraining the CV_{95} of $B_{landscape}$ to 0.2, although they did not consider the normality of their data. They also found a CV_{95} of 0.15 for $B_{landscape}$, despite inventorying 400 ha, emphasising the importance of plot number rather than area.

It may be that the high variability of miombo, particularly at our study site, makes accurate determination of $B_{landscape}$ exorbitant in terms of the area inventoried, at least in comparison to the better studied moist forests. Chave (2004) found that to reduce the SEM of $B_{landscape}$ to 10% of the mean (roughly equivalent to a CV_{95} of 0.2) required a 5 ha inventory at BCI. This is markedly different from our results which showed that such a level of accuracy would have required around 90 plots with a minimum size 0.25 ha (A_{inv}= 22.5 ha).

Key conclusions and recommendations from Chapter 6a and 6b

Inventories seeking to minimise the uncertainty on $B_{landscape}$ need to sample around 100 plots. After this number of plots the marginal increase in certainty is likely to be very small. These plots however need not be large – 0.2 ha may well suffice.

Such inventories will be subject to bias, likely to be in the order of ±17%. This results from uncertainty in the form of the allometric model. Using a literature allometric model rather than a local allometric does not seem to increase this bias, beyond that introduced by model form, and so can be recommended, at least until a consolidated miombo-specific allometric model has been produced. Producing such a miombo model could be achieved by pooling the existing data sets, if they are archived and available. With such a large data set (n=535 for the papers considered in Table 2), it should be possible to model the heteroskedasticity appropriately.

To reduce the uncertainty of $B_{landscape}$ below CV$_{95}$=0.1 looks to be very difficult (Fig. 8), although this is based on an extrapolation. Either a very large sample size is required (n_p>250), or some form of stratification is needed. Such a stratification will require EO data to be effective. Optical EO data has some severe challenges in mixed tree-grass ecosystems such as this, and effective classification at a suitable spatial scale requires detailed ground work and multi-temporal imagery (Sedano *et al.* 2005). Radar data offers a promising approach (Ribeiro *et al.* 2008).

Designing an inventory for establishing calibration sites for EO data has very different requirements. Obviously plot area needs to relate to the spatial resolution and accuracy of the EO sensor, but furthermore the requirement is for well constrained estimates of B_{plot}. Such estimates are likely to be achieved on plots that are large enough to contain many large stems (>1 ha). Even then, the ability of simple DBH-Biomass allometrics

to accurately predict B_{plot} is very limited, and probably can only be improved by incorporating auxiliary variables that describe stem shape in some detail. The uncertainty on B_{plot} seems to be approximately normal (Fig. 6) so large numbers of calibration plots may overcome this problem to some extent.

Acknowledgements

10

References in Chapters 6a and b

Abbot, P., J. Lowore and M. Werren (1997). "Models for the estimation of single tree volume in four Miombo woodland types." Forest Ecology and Management **97**(1): 25-37.

Achard, F., H. D. Eva, P. Mayaux, H. J. Stibig and A. Belward (2004). "Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s." Global Biogeochemical Cycles **18**(2).

Baccini, A., N. Laporte, S. J. Goetz, M. Sun and H. Dong (2008). "A first map of tropical Africa's above-ground biomass derived from satellite imagery." Environmental Research Letters(4): 045011.

Brown, R. Gillespie and E. Lugo (1989). "Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data." Forest Science **35**: 881-902.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira and R. A. Victoria (1995). "Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil." Forest Ecology and Management **75**(1-3): 175-189.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. Cid Ferreira and R. A. Victoria (1995). "Uncertainty in the biomass of Amazonian forests: An example from RondÙnia, Brazil." Forest Ecology and Management **75**(1-3): 175-189.

Bucini, G. and N. P. Hanan (2007). "A continental-scale analysis of tree cover in African savannas." Global Ecology and Biogeography **16**(5): 593-605.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Folster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riera and T. Yamakura (2005). "Tree allometry and improved estimation of carbon stocks and balance in tropical forests." Oecologia **145**(1): 87-99.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao and R. Perez (2004). "Error propagation and scaling for tropical forest biomass estimates." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **359**(1443): 409-420.

Chidumayo, E. N. (1988). "Estimating Fuelwood Production and Yield in Regrowth Dry Miombo Woodland in Zambia." Forest Ecology and Management **24**(1): 59-66.

Clark, D. A. (2002). "Are tropical forests an important carbon sink? Reanalysis of the long-term plot data." Ecological Applications **12**(1): 3-7.

Condit, R. (1998). Tropical forest census plots : methods and results from Barro Colorado Island, Panama and a comparison with other plots. Berlin ; London, Springer.

Cunia, T. (1964). "Weighted least squares method and construction of volume tables." Forest Science **10**(2): 180-191.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole and J. Townshend (2002). "Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s." Proceedings of the National Academy of Sciences of the United States of America **99**(22): 14256-14261.

Enquist, B. J. and K. J. Niklas (2002). "Global Allocation Rules for Patterns of Biomass Partitioning in Seed Plants." Science **295**(5559): 1517-1520.

Falkowski, P., R. J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N. Gruber, K. Hibbard, P. Hogberg, S. Linder, F. T. Mackenzie, B. Moore, III, T. Pedersen, Y. Rosenthal, S. Seitzinger, V. Smetacek and W. Steffen (2000). "The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System." Science **290**(5490): 291-296.

Fisher, J. I., G. C. Hurtt, R. Q. Thomas and J. Q. Chambers (2008). "Clustered disturbances lead to bias in large-scale estimates based on forest sample plots." Ecology Letters **11**(6): 554-563.

Goetz, S., A. Baccini, N. Laporte, T. Johns, W. Walker, J. Kellndorfer, R. Houghton and M. Sun (2009). "Mapping and monitoring carbon stocks with satellite observations: a comparison of methods." Carbon Balance and Management **4**(1): 2.

Gotelli, N. J. and A. M. Ellison (2004). A primer of ecological statistics, Sunderland.

Grainger, A. (2009). "Towards a New Global Forest Science." International Forestry Review **11**(1): 126-133.

Grundy, I. M. (1995). "Wood biomass estimation in dry miombo woodland in Zimbabwe." Forest Ecology and Management **72**(2-3): 109-117.

Houghton, R. A. (2005). "Aboveground forest biomass and the global carbon balance." Global Change Biology **11**(6): 945-958.

Houghton, R. A. (2007). "Balancing the global carbon budget." Annual Review of Earth and Planetary Sciences **35**: 313-347.

INPE (2002). Projeto PRODES: Monitoramento da floresta Amazônica Brasileira por satélite.

Keller, M., M. Palace and G. Hurtt (2001). "Biomass estimation in the Tapajos National Forest, Brazil: Examination of sampling and allometric uncertainties." Forest Ecology and Management **154**(3): 371-382.

Ketterings, Q. M., R. Coe, M. van Noordwijk, Y. Ambagau and C. A. Palm (2001). "Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests." Forest Ecology and Management **146**(1-3): 199-209.

LaBau, V. J. C., Tiberius (1990). State-of-the-art methodology of forest inventory: a symposium proceedings. Gen. Tech. Rep. Portland, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 635.

Lewis, S. L., G. Lopez-Gonzalez, B. Sonke, K. Affum-Baffoe, T. R. Baker, L. O. Ojo, O. L. Phillips, J. M. Reitsma, L. White, J. A. Comiskey, M.-N. D. K, C. E. N. Ewango, T. R. Feldpausch, A. C. Hamilton, M. Gloor, T. Hart, A. Hladik, J. Lloyd, J. C. Lovett, J.-R. Makana, Y. Malhi, F. M. Mbago, H. J.

Ndangalasi, J. Peacock, K. S. H. Peh, D. Sheil, T. Sunderland, M. D. Swaine, J. Taplin, D. Taylor, S. C. Thomas, R. Votere and H. Woll (2009). "Increasing carbon storage in intact African tropical forests." Nature **457**(7232): 1003-1006.

Malhi, Y., O. L. Phillips, J. Lloyd, T. Baker, J. Wright, S. Almeida, L. Arroyo, T. Frederiksen, J. Grace, N. Higuchi, T. Killeen, W. F. Laurance, C. Leaño, S. Lewis, P. Meir, A. Monteagudo, D. Neill, P. N. Vargas, S. N. Panfil, S. Patiño, N. Pitman, C. A. Quesada, A. Rudas-Ll., R. Salomão, S. Saleska, N. Silva, M. Silveira, W. G. Sombroek, R. Valencia, R. V. Martínez, I. C. G. Vieira, B. Vinceti, J. Canadell and P. S. White (2002). "An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR)." Journal of Vegetation Science **13**(3): 439-450.

Malhi, Y., D. Wood, T. R. Baker, J. Wright, O. L. Phillips, T. Cochrane, P. Meir, J. Chave, S. Almeida, L. Arroyo, N. Higuchi, T. J. Killeen, S. G. Laurance, W. F. Laurance, S. L. Lewis, A. Monteagudo, D. A. Neill, P. N. Vargas, N. C. A. Pitman, C. A. Quesada, R. Salomão, J. N. M. Silva, A. T. Lezama, J. Terborgh, R. V. Martínez and B. Vinceti (2006). "The regional variation of aboveground live biomass in old-growth Amazonian forests." Global Change Biology **12**(7): 1107-1138.

Nogueira, E. M., P. M. Fearnside, B. W. Nelson, R. I. Barbosa and E. W. H. Keizer (2008). "Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories." Forest Ecology and Management **256**(11): 1853-1867.

Parresol, B. R. (1999). "Assessing Tree and Stand Biomass: A Review with Examples and Critical Comparisons." Forest Science **45**: 573-593.

Penman, J., M. Gytarsky, T. Hiraishi, T. Krug, D. Kruger, R. Pipatti, L. Buendia, K. Miwa, T. Ngara, K. Tanabe and F. Wagner (2003). Good Practice Guidance for Land Use, Land-Use Change and Forestry and Definitions and Methodological Options to Inventory Emissions from Direct Human-induced Degradation of Forests and Devegetation of Other Vegetation Types, Institute for Global Environmental Strategies (IGES) for the Intergovernmental Panel on Climate Change.

Phillips, O. L., L. E. O. C. Aragao, S. L. Lewis, J. B. Fisher, J. Lloyd, G. Lopez-Gonzalez, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Banki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jimenez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patino, M. C. Penuela, A. Prieto, F. Ramirez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. t. Steege, J. Stropp, R. Vasquez, P. Zelazowski, E. A. Davila, S. Andelman, A. Andrade, K.-J. Chao, T. Erwin, A. Di Fiore, E. H. C, H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramirez-Angulo, A. Rudas, R. Salamao, N. Silva, J. Terborgh and A. Torres-Lezama (2009). "Drought Sensitivity of the Amazon Rainforest." Science **323**(5919): 1344-1347.

Ribeiro, N. S., S. S. Saatchi, H. H. Shugart and R. A. Washington-Allen (2008). "Aboveground biomass and leaf area index (LAI) mapping for Niassa Reserve, northern Mozambique." J. Geophys. Res. **113**.

Roy, J., B. Saugier and H. A. Mooney (2001). Terrestrial global productivity. San Diego, Calif. ; London, Academic Press.

Saatchi, S., K. Halligan, D. G. Despain and R. L. Crabtree (2007). "Estimation of Forest Fuel Load From Radar Remote Sensing." Geoscience and Remote Sensing, IEEE Transactions on **45**(6): 1726-1740.

Saatchi, S. S., R. A. Houghton, A. Dos Santos, R. C., J. V. Soares and Y. Yu (2007). "Distribution of aboveground live biomass in the Amazon basin." Global Change Biology **13**: 816-837.

Sedano, F., P. Gong and M. Ferrao (2005). "Land cover assessment with MODIS imagery in southern African Miombo ecosystems." Remote Sensing of Environment **98**(4): 429-441.

Sprugel, D. G. (1983). "Correcting for Bias in Log-Transformed Allometric Equations." Ecology **64**(1): 209-210.

Tinley, K. L. (1977). Framework of the Gorongosa Ecosystem. Faculty of Science. Pretoria, University of Pretoria**:** 184.

Trujillo-Ortiz, A., R. Hernandez-Walls, K. Barba-Rojo and A. Castro-Perez (2007). AnDartest:Anderson-Darling test for assessing normality of a sample data. A MATLAB file.

Williams, M., C. M. Ryan, R. M. Rees, E. Sambane, J. Fernando and J. Grace (2008). "Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique." Forest Ecology and Management **254**(2): 145-155.

Zianis, D. (2008). "Predicting mean aboveground forest biomass and its associated variance." Forest Ecology and Management **256**(6): 1400-1407.

Zianis, D. and M. Mencuccini (2004). "On simplifying allometric analyses of forest biomass." Forest Ecology and Management **187**(2-3): 311-332.

Zianis, D. and K. Radoglou (2006). "Comparison between empirical and theoretical biomass allometric models and statistical implications for stem volume predictions." Forestry **79**(4): 477-487.

7. Summary of carbon stocks in the Nhambita woodlands

This Chapter gives a brief overview of the carbon stocks of the Nhambita woodlands. It synthesises data from the preceding chapters into a full description of the ecosystem carbon stocks. It also includes some data sets not presented elsewhere. The key question I set out to answer is: *What is the magnitude of the different carbon pools in the Nhambita woodlands?*

I do this by collating data on carbon stocks in the following pools: tree leaves, stems and roots, sapling stems and roots, grass (aboveground only) and soil carbon from the surface to 0.5 m depth. I do not fully explore the errors associated with each measurement (see Chapter 6 for an example of this), but instead only report standard errors of the estimate of the means.

Methods

Leaf biomass

Leaf biomass is estimated by converting our Leaf Area Index (LAI) measurements in Nhambita (Chapter 2) into biomass using the specific leaf area (SLA) measurements of Nottingham (2004). We use a single average value of SLA, which Nottingham based on the dominant species on our permanent sample plots. As we include a measure of leaf biomass when it is present on the trees, to avoid double counting, we do not assess leaf biomass in the litter layer.

Tree stem and root biomass

Stem and root biomass are calculated based on the inventory of 60 plots and a new allometric model that relates diameter to stem and root biomass. We use the same inventory data set as in Chapter 6a, and our model for stem biomass is model M4 from that chapter. For both stem and root biomass, this is a simple power relationship, fitted to log

transformed variables, and then back transformed with no correction factors.

The root biomass allometric model is parameterised with destructively harvested root biomass data collected from 23 of the trees that were sampled in Chapter 6. For each sampled stem, we excavated the area under the canopy to approximately 1 m depth using a mechanical digger. The excavated soil was sifted by hand and large root (>2cm diameter) biomass was collected, weighed and then subsampled for moisture content and % C using the same method as for the aboveground parts (See Chapter 6). Any large roots that extended deeper than 1 m were excavated individually, although it was often impossible to follow them to their end; we excavated beyond 2 m in most cases, and until the roots had diameter less than 5 cm.

Sapling stem and root biomass

Saplings, defined as stems <5 cm DBH but greater than 0.3 cm at 10 cm above ground level (D_{10}), were inventoried on the fire experiment plots (Chapter 3) in 2007. We use an allometric model based on a destructive sample of the above and below ground parts of 45 saplings. The saplings were located in the area that had to be cleared to excavate the large trees (above). We fit 2nd order polynomials to the data, to relate D_{10} to wet biomass. Ten of the saplings were dried (~80°C for 24 hrs) and reweighed to determine dry mass fraction. We measured %C on seven saplings that were sampled as part of the fire experiments.

Grass aboveground biomass

Grass biomass was assessed as part of the fire experiments (Chapter 3) using a disc pasture meter (DPM) (Trollope *et al.* 1996; Dorgeloh 2002; Zambatis *et al.* 2006). We constructed a DPM (disc area=0.72 m^2) and calibrated it with 67 destructive harvests of the grass beneath the disc. The destructive samples were dried in an oven (~80°C for 24 hrs) and weighed. Seven grass subsamples were returned to Edinburgh for C:N

analysis. As well as estimating grass loads on the eight fire plots, we also used the DPM to assess grass biomass on 6 PSPs in May 2008, which we estimate is the time of peak grass biomass. We assume peak biomass occurs in May because thereafter the soil starts to dry out and little rain falls (see Introduction for monthly rainfall figures).

Soil carbon

Using the method described in Chapter 5, we sampled soil at depths of 5, 10, 20 and 50 cm on 13 PSPs. We sampled depth profiles at 5 locations on each plot and also sampled surface soil at 9 locations. We use the same method as Chapter 5 to integrate the C stocks to 0.5 m depth. Three replicate bulk density measurements were made at 2.5 cm and 30 cm depth, at the centre of each PSP.

Statistical tests

We test distributions of plot level carbon stocks for normality using the Jarque-Bera (J-B) test for goodness-of-fit to a normal distribution, rejecting the hypothesis of normality if the test is significant at the 5% level (i.e. $p < 0.05$). If we reject the hypothesis of a normal distribution, we then test for a log normal distribution by transforming the data and repeating the J-B test. If that is not accepted, we test for the Weilbull distribution using the Anderson-Darling test, again rejecting the hypothesis of a Weibull distribution at the 95% confidence level. Having established a distribution that the sample is drawn from, we report the mean and standard error of the mean (±SEM).

Terminology

Throughout this chapter we use B to denote tree biomass, SB for sapling biomass, GB for grass biomass, $R{:}S$ for the root stem ratio. Subscript s for stem, r for root, $_{total}$ for $_{s+r}$, $_{plot}$ for plot level biomass. DBH in cm is D, D_{10} is diameter at 10 cm above the ground in mm. All stocks in tC ha^{-1} are on a dry weight basis.

Results

Tree leaf biomass

For the 3 complete years of LAI images, max LAI, averaged across all the PSPs, was 1.50±0.14 in 2005, 1.41±0.17 in 2006, and 1.42±0.14 in 2007.

Nottingham collected 2615 leaves from 228 trees from 11 of the PSPs, and found leaf carbon content of 47%C. SLA ranged from 32-257gC m^{-2}, with 2 outliers above 300 gC m^{-2} and was log-normally distributed (J-B test p = 0.6). The mean and SD of the log-normal distribution were 52±27 gC m^{-2}, and the SEM, using n=228 (trees, rather than leaves to avoid pseudo replication) was 1.8 gC m^{-2}.

Converting the LAI values to C stocks yields a mean peak leaf carbon stock of 0.75±0.13 tC ha^{-1}, combining the standard errors in quadrature.

Tree stem and root biomass

Log-transformed allometric models of diameter vs stem, root and total woody biomass fitted well (Fig. 1, upper panel) and gave the following equations:

$$log(B_s) = 2.601\ log(D)\text{-}3.629$$

adj r^2 = 0.93, RMSE = 0.52, n = 29

$$log(B_r) = 2.262\ log(D)\text{-}3.370$$

adj r^2 = 0.94, RMSE = 0.43, n= 23

$$log(B_t) = 2.545\ log(D)\ \text{-}3.018$$

adj r^2 = 0.96, RMSE = 0.30, n = 23

Where B_t is total tree biomass, B_s is stem (aboveground) biomass, and B_r is root biomass, all in kgC. D is diameter at breast height in cm.

The stem and root allometric models show that root:stem decreases with stem size (Fig. 1, lower panel), and that:

$$R{:}S = 2.3\ D^{-0.512}$$

adj r^2 = 0.36, RMSE = 0.27, n = 23

Where $R{:}S$ is the root stem ratio and D is diameter at breast height in cm.
Root mass for the destructively harvested stems varied from 1.3-760 kgC, with a mean of 123 kgC. D of the sampled stems ranged from 5-72 cm. Carbon content averaged 47±0.23% (±SEM of the 23 stems). Dry mass fraction averaged 0.59±0.01. Stem mass data are presented in Chapter 6a.

Applying the model to the inventory data yielded $B_{total,plot}$ varying from 3–77 tC ha^{-1}, mean 30.0±1.8 (±SEM). Mean $B_{s,plot}$ was 21.3±1.4, mean $B_{r,plot}$ was 8.6±0.46. Root:stem varied from 0.28–0.58, mean 0.42±0.01 and was weakly but significantly correlated with $B_{total,plot}$ ($R{:}S$ = -0.00261 $B_{total,plot}$ + 0.4997, adj r^2 = 0.42, p<1E-8).

10
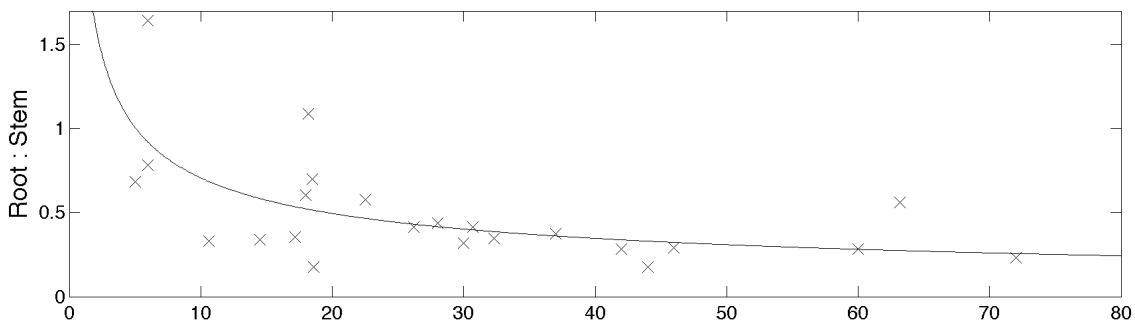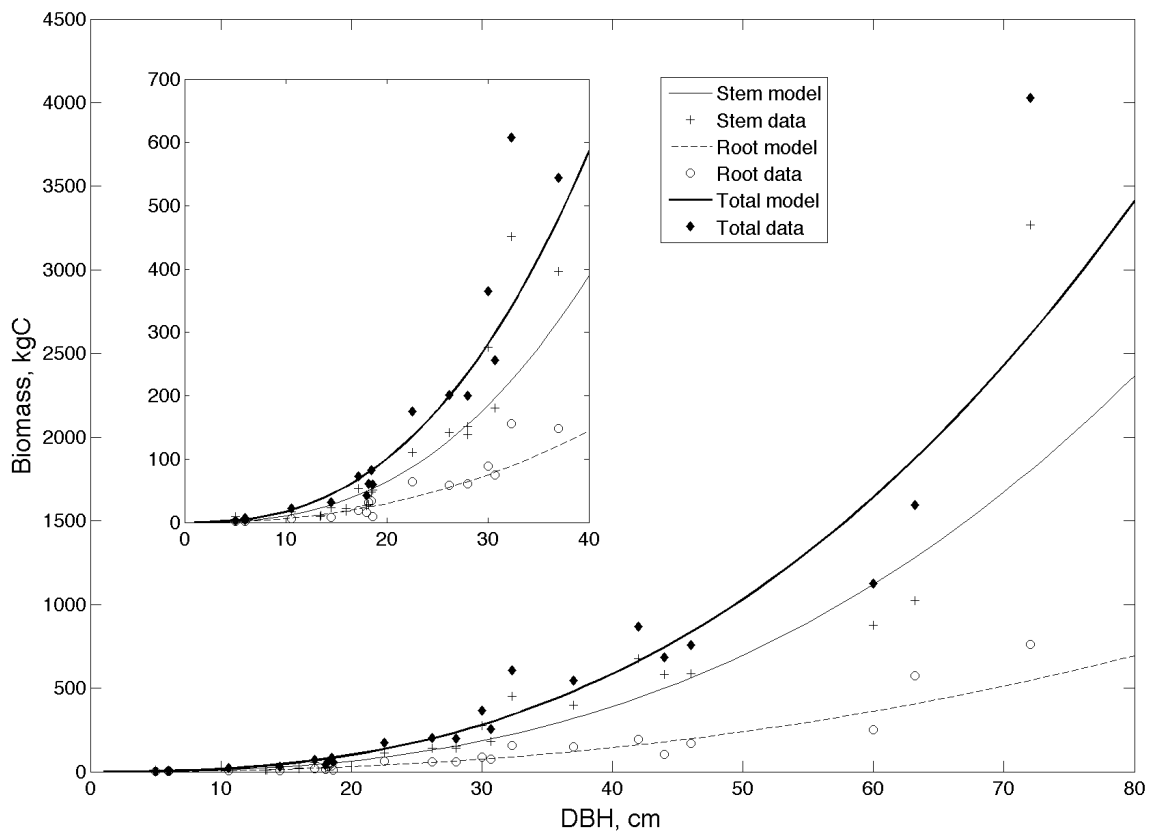
Figure 1. Top panel shows the allometric models of stem, root and total biomass and the destructive harvested data. The models are fitted to the log of *D* and *B*, but are shown back transformed. Bottom panel shows the allometry of the root stem ratio and DBH.
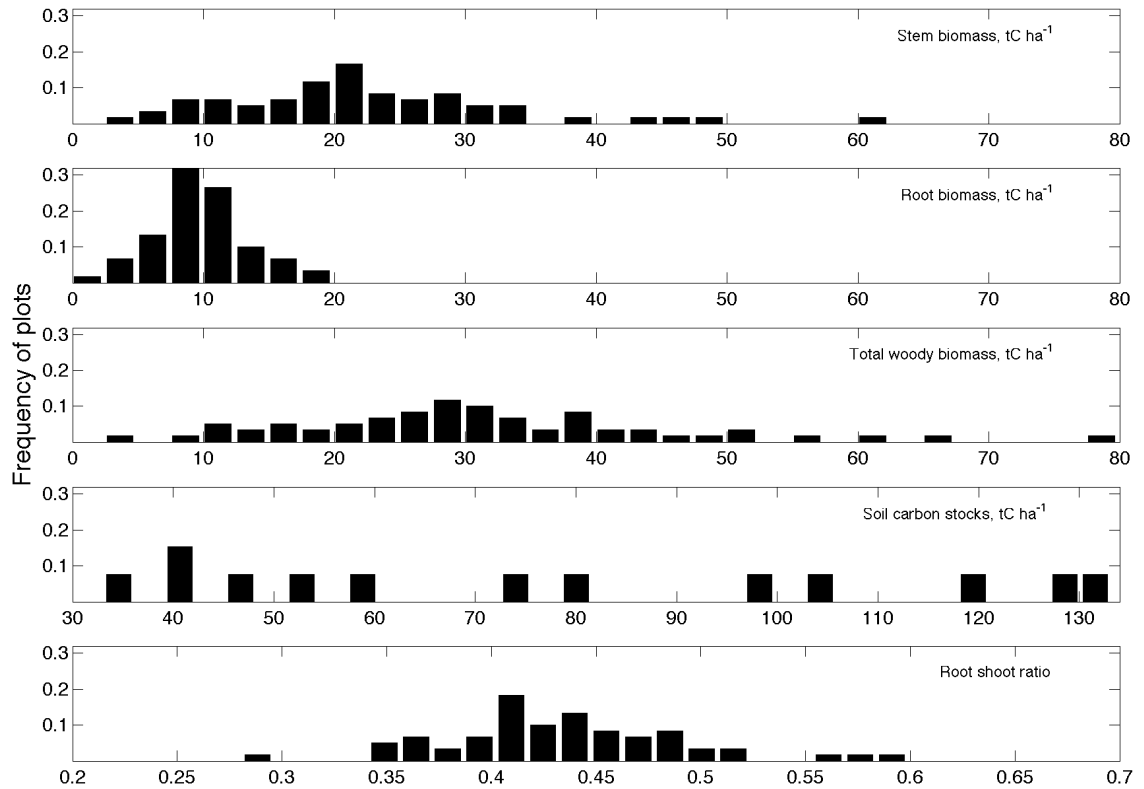
Figure 2. Histograms of stem, root and total woody biomass carbon stocks on the 60 plots, and soil carbon stocks (to 50 cm depth) on 13 plots, as well as root:stem on the 60 plots. Note change in X-axis values for soil carbon stocks. Stem biomass has a Weibull distribution, p = 0.24, mean = 21.3±1.4 tC ha^{-1}. Root biomass is normally distributed, p = 0.27, mean = 8.6±0.5 tC ha^{-1}. Total woody biomass is normally distributed, p = 0.086, mean 29.9±1.9 tC ha^{-1}. We cannot reject the hypothesis of soil carbon stocks being normally distributed (p = 0.6, but *n* is only 13), mean = 76±10 tC ha^{-1}. Root:stem was normally distributed, p = 0.17, mean = 0.42±0.01.

Sapling biomass

The allometric equations for sapling stem and root biomass, were fitted to a 2° polynomial:

$$SB_r = 0.1761 \; D_{10}^2 + 0.0153 \; D_{10} + 0.1488 \qquad\qquad r^2 = 0.73$$

$$SB_s = 0.0717 \; D_{10}^2 + 0.0784 \; D_{10} \qquad\qquad r^2 = 0.67$$

Where: SB is wet shrub biomass in kg, D_{10} is diameter at 10 cm above ground in mm.

$n = 45$

Dry mass fraction was 0.61, based on moisture measurements of the 10 saplings that were dried. %C was 44.6±0.3, based on 7 subsamples.

Using these allometric equations, and the dry mass and %C data to calculate standing stock of sapling biomass, yielded the following plot level data: $SB_{r,plot}$ ranged from 0.5-4.7 tC ha^{-1}, with a mean of 2.2±0.6 tC ha^{-1}. $SB_{s,plot}$ ranged from 0.2-1.7 tC ha^{-1}, with a mean of 0.9±0.2 tC ha^{-1}. Root:stem averaged 2.37±0.01.

Grass biomass

The 67 destructive grass samples used to calibrate the DPM ranged from 41-1147 g dry mass m^{-2}. A liner fit of the grass biomass to the DPM height gave the following equation:

$$GB = 4.68\ h\ +\ 31.6$$

Where GB is dry grass biomass in g m^{-2}, and h is the height of the disc of the DPM in cm. n = 67, r^2 = 0.48.

The seven grass subsamples had a %C of 41.1-43.5%, mean 42.3±0.01. Using these values, calculated grass biomass on the 6 PSPs and 8 fire plots varied from 0.57 to 2.1 tC ha^{-1}. The mean and SEM were 1.15±0.18 tC ha^{-1}.

Soil carbon

Across the 13 PSPs with soil data, soil carbon stocks averaged 8.0±0.4 tC ha^{-1} from 0-2.5 cm, 17.7±2.0 from 2.5-10 cm, and 16.0±2.4 from 10-20 cm and 34.5±5.4 tC ha^{-1} from 20-50 cm (±SEM). Summing the 0-50 cm profile, soil C stocks averaged 76.3±9.9 tC ha^{-1}. However, the distribution of the 13 plot-level soil C stock values was almost uniform, meaning that estimating the population mean is problematic. The mean bulk density at 0 cm was 1.2±0.03 t m^{-3}, and 1.5±0.04 t m^{-3} at 30 cm.

Overview of carbon pools

Soil carbon dominated the carbon pools, with on average 76 of the 111 tC ha^{-1} being found in the soil. Soil and tree biomass accounted for 95% of the carbon stocks (Figure 3 and 4). 22% of the carbon was aboveground (stems and grass).
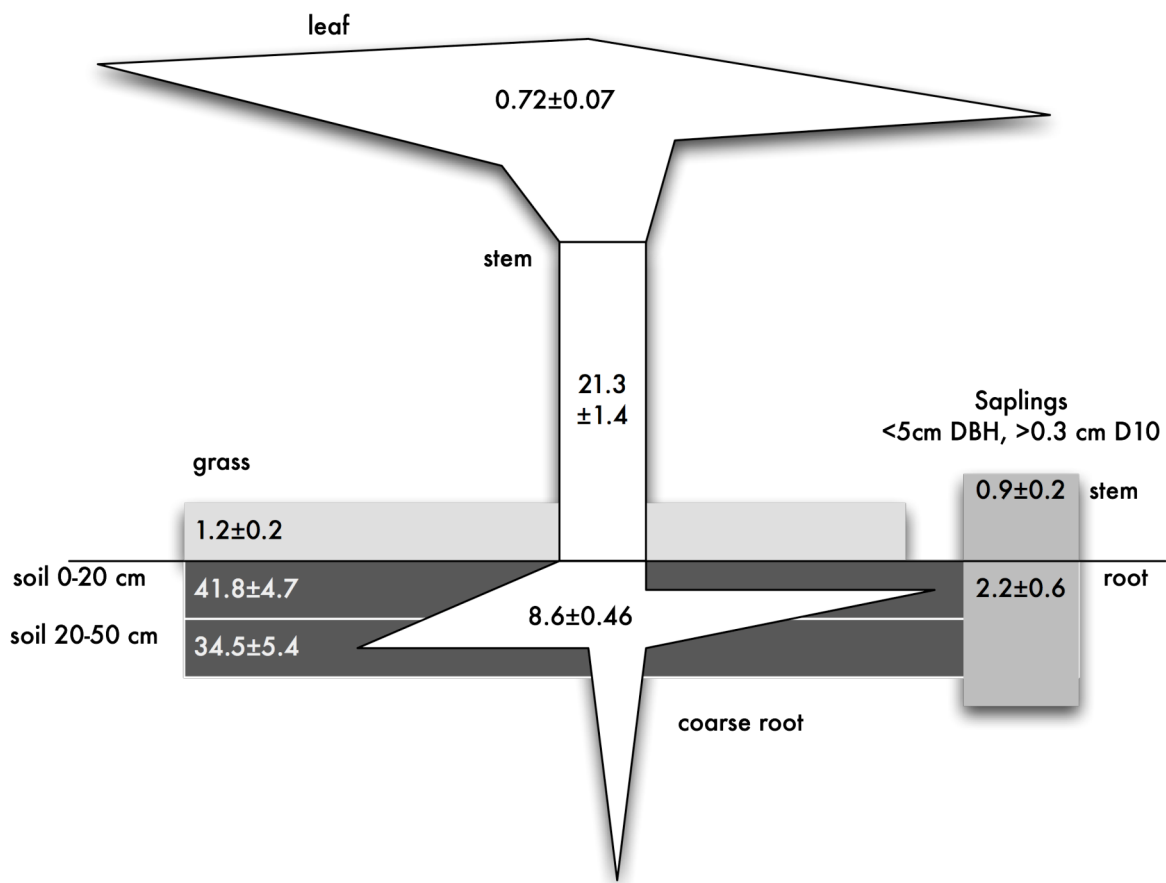
Figure 3. Measured carbon stocks in the Nhambita woodlands. Trees are defined as >5 cm DBH, saplings as < 5 cm DBH, but > 0.3 mm D at 10 cm above the ground. Stocks are for annual maxima of grass and leaf biomass. All stocks are in tC ha^{-1}.
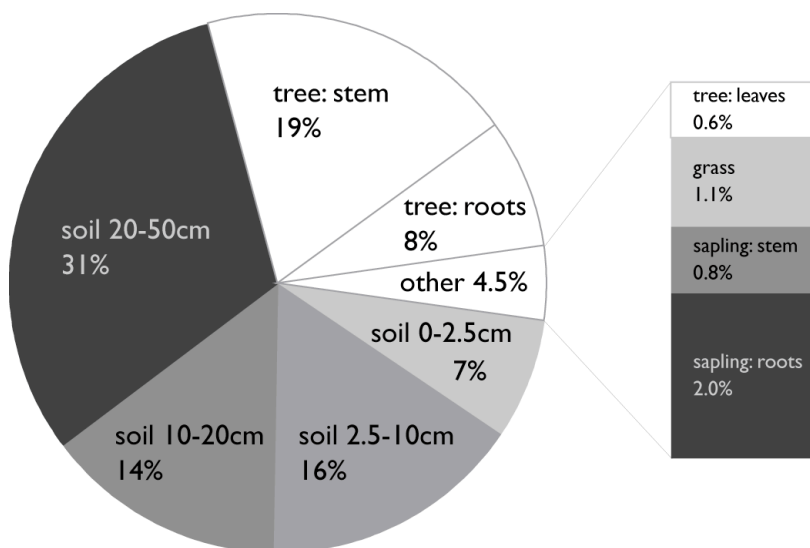
Figure 4. Measured carbon stocks in the Nhambita woodlands area as a percentage of the total.

Discussion and Conclusion

Aboveground biomass in Nhambita (21.3 ± 1.4 tC ha^{-1}) can be compared to Frost's (1996) "average for dry miombo in Zimbabwe and Zambia" of 26 tC ha^{-1} (we convert dry mass to C mass assuming 47%C throughout this discussion). Frost developed a relationship between annual rainfall and woody biomass: using a value of 850 mm yr^{-1}, and Frost's equation ($Y = 0.14 X - 56.21$, Y is Mg dry matter ha^{-1}, X is rainfall in mm), our biomass data (21.4 tC ha^{-1}) are lower that the equation's prediction (29.5 tC ha^{-1}).

10   We found plot level root:stem ratios from 0.28 – 0.58, with a mean of 0.42. To compare our data with other tropical woodlands and savannas, we conducted a literature search. Root biomass estimates in miombo are rare, but our average of root:stem (0.42) can be compared to Chidumayo's (1997) values of 0.53 and 0.47 for two wet miombo sites in Zambia (calculated in Frost 1996).

Outside of the miombo region, we found data on $B_{s, plot}$ and $R{:}S$ for 18 sites in 11 countries in Latin America and Africa (Sarmiento and Vera 1979; Murphy and Lugo 1986; Castellanos *et al.* 1991; Woomer 1993; Malimbwi *et al.* 1994; Frost 1996; De Castro and Kauffman 1998; Tiessen

20   *et al.* 1998; Lilienfein *et al.* 2001; Jaramillo *et al.* 2003).

This summary showed that $R{:}S$ falls rapidly as $B_{s, plot}$ increases, up until around 20 tC ha^{-1} (Fig. 3) where after it levels off at $R{:}S \sim = 0.3$. It can be modelled by the following equation (Fig. 3):

$$R{:}S = a \cdot exp(b \cdot B_{s,plot}) + c \cdot exp(d \cdot B_{s,plot})$$

Where $R{:}S$ is the root:stem ratio, $B_{s,plot}$ is aboveground biomass (tC ha^{-1}). Fitted parameters (with 95% confidence intervals) are: a = 3.19 (1.53, 4.85), b = -0.14 (-0.34, 0.06) c = 0.26 (-1.33, 1.85), d = 0.004 (-0.13, 0.13). n= 17, adj r^2 = 0.61, RMSE = 0.66. For our data, the model is:

$$R{:}S = a \cdot B_{s,plot} + b$$

Coefficients (with 95% confidence bounds) are a = -0.00359 (-0.0046, -0.0026) and b =0.498 (0.474, 0.522), n = 60, adj r^2 = 0.46, RMSE = 0.041.

The mean result from this study fitted into the literature pattern at $B_{s,\,plot}$ = 21.3, $R{:}S$ = 0.42. However, our plot-level data showed a different pattern: plots with low $B_{s,\,plot}$ had much lower $R{:}S$ than comparable sites in the literature (Fig. 3). This suggests a functional difference, probably in stem size distributions, between low biomass miombo plots, and other savannas with low biomass.

10   The $B_{s,\,plot}$ vs $R{:}S$ relationship can be compared to the IPCC LULCF good practice guidelines (Penman *et al*. 2003) default figure for 'Woodland/savanna' of 0.48±0.19 SD, which is based on Australian and Indian data, and would seem to drastically underestimate root biomass for low biomass savannas in the neotropics and West Africa, but is similar to values from this study.
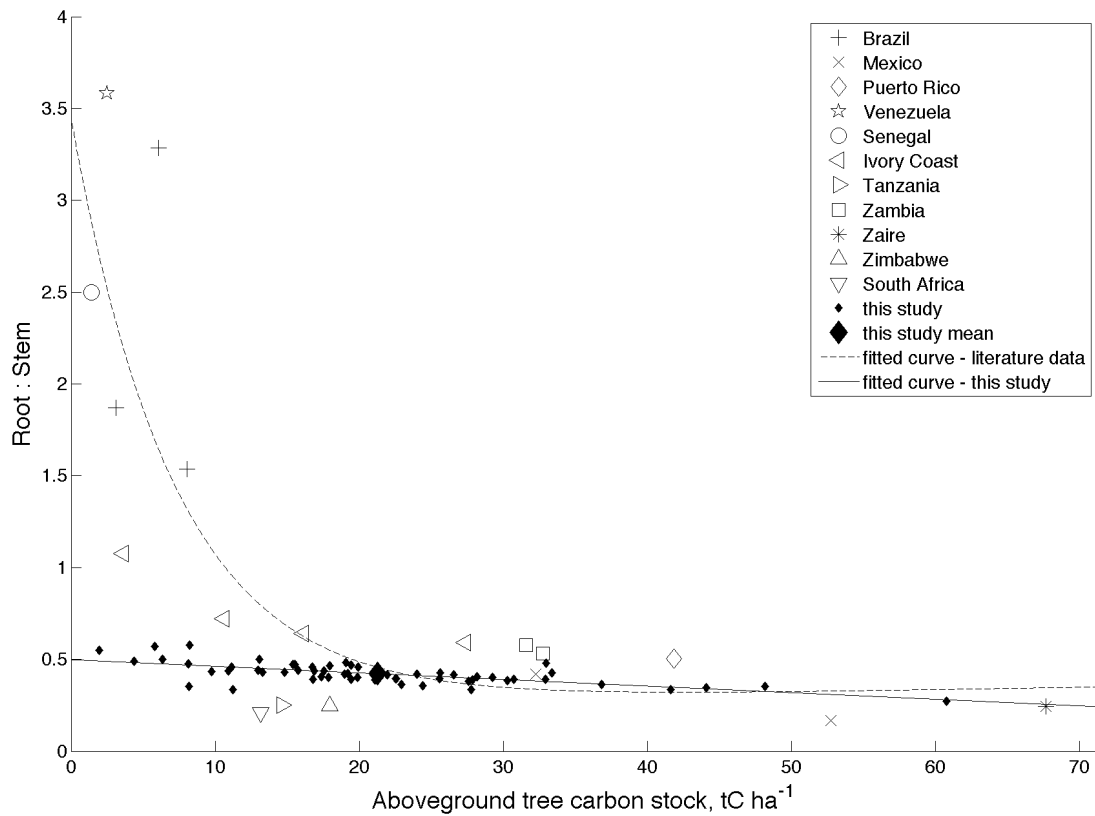
Figure 3. Root:stem ratios as a function of aboveground biomass, across the seasonally dry tropics. Definitions of stem and root biomass vary according to the source, but are 'coarse' roots (often >2 cm diameter) and trees (mainly >5 cm DBH).

Comparing this study to that of Ribeiro *et al* (2008) in Niassa Reserve in miombo woodland in Northern Mozambique (annual rainfall 900-1200 mm), our woodlands falls into their 'Medium density woodland' class (for which $B_{landscape}$ = 19.5 tC ha^{-1}). However they found corresponding LAI values of 0.76±0.4, half of the value found in this study. The practical and theoretical difficulties of using optical methods to estimate LAI in such discontinuous canopies (with the Licor LAI 2000 in Ribeiro *et al* and hemispherical photography in this study), mean that absolute values of LAI are potentially biased.

Overall the carbon stocks in these woodlands are dominated by soil carbon, which comprises 76 of the total stocks of 111 tC ha^{-1} (69%, Figure 4). This figure is similar to the 60% reported in Walker and Desanker

(2004) in Malawian miombo, who found soil C stocks of 58 tC ha^{-1} to 60 cm depth (adapted from their Table 2).

Walker and Desanker (2004) report that upon conversion to agricultural land, miombo woodland lose around 47% of its soil C (to 1.5 m depth). For our site this implies a loss of 36 tC ha^{-1} upon conversion to agriculture, slightly higher than that if all the tree biomass was lost (31 tC ha^{-1}).

Several caveats to the results presented here must be mentioned. Firstly our plots are located on a transition from miombo woodland to the plains of the Rift valley (see Introduction), where a change in soil type and

10   seasonal flooding produce a more diverse and complex woodland formation. Secondly, our plots are not evenly or randomly distributed across the landscape, but instead follow the road network and are clumped together. However preliminary examination of the semi variogram of B_{plot} showed no spatial dependence. Finally, we did not measure several pools that contribute to the ecosystem carbon stocks. The major missing pool is likely to be grass root biomass, which is typically larger than grass aboveground biomass, but is difficult to measure on large scales. We hope to develop an allometric relationship between aboveground grass biomass and root biomass in the future. We also do

20   not present data on coarse woody debris in this study, but hope to do so as part of a future investigation into fuel loads in miombo.

Conclusions

Miombo carbon stocks are dominated by soil carbon: 76 of the 111 tC ha^{-1} are in the soil. However soil carbon is very variable across the landscape, and has an almost uniform distribution rather than converging around a mean. This requires further investigation at various spatial scales if estimates of carbon stocks in this ecosystem are to be better constrained.

Woody tree carbon averages 21.3±1.4 tC ha^{-1} aboveground and 8.6±0.5 tC ha^{-1} belowground, based on allometric relationships. Chapter 4 has shown

that these types of allometric models can introduce important biases, and these estimates are bound to be subject to such biases.

Acknowledgements

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References

Castellanos, J., M. Maass and J. Kummerow (1991). "Root biomass of a dry deciduous tropical forest in Mexico." Plant and Soil V131(2): 225-228.

Chidumayo, E. N. (1997). Miombo ecology and management : an introduction. London, IT Publications in association with the Stockholm Environment Institute.

De Castro, E. A. and J. B. Kauffman (1998). "Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire." Journal of Tropical Ecology 14: 263-283.

Dorgeloh, W. G. (2002). "Calibrating a disc pasture meter to estimate above-ground standing biomass in Mixed Bushveld, South Africa." African Journal of Ecology 40(1): 100-102.

Frost, P. (1996). The ecology of Miombo woodlands. The Miombo in transition : woodlands and welfare in Africa. B. M. Campbell. Bogor, Indonesia, Center for International Forestry Research: 11-55.

Jaramillo, V. J., J. B. Kauffman, L. Rentería-Rodríguez, D. L. Cummings and L. J. Ellingson (2003). "Biomass, Carbon, and Nitrogen Pools in Mexican Tropical Dry Forest Landscapes." Ecosystems V6(7): 609-629.

Lilienfein, J., W. Wilcke, R. Zimmermann, P. Gerstberger, G. M. Araújo, et al. (2001). "Nutrient storage in soil and biomass of native Brazilian Cerrado." Journal of Plant Nutrition and Soil Science 164(5): 487-495.

Malimbwi, R. E., B. Solberg and E. Luoga (1994). "Estimation of biomass and volume in miombo woodland at Kitulangalo Forest Reserve, Tanzania." Journal of Tropical Forest Science 7(2): 230-242.

Murphy, P. G. and A. E. Lugo (1986). "Structure and Biomass of a Subtropical Dry Forest in Puerto-Rico." Biotropica 18(2): 89-96.

Penman, J., M. Gytarsky, T. Hiraishi, T. Krug, D. Kruger, et al. (2003). Good Practice Guidance for Land Use, Land-Use Change and Forestry and Definitions and Methodological Options to Inventory Emissions from Direct Human-induced Degradation of Forests and Devegetation of Other Vegetation Types, Institute for Global Environmental Strategies (IGES) for the Intergovernmental Panel on Climate Change.

Ribeiro, N. S., S. S. Saatchi, H. H. Shugart and R. A. Washington-Allen (2008). "Aboveground biomass and leaf area index (LAI) mapping for Niassa Reserve, northern Mozambique." Journal of Geophysical Research-Biogeosciences 113.

Sarmiento, G. and M. Vera (1979). "Composición, estructura, biomasa y producción de diferentes sabanas en los Llanos de Venezuela." Boletín de la Sociedad Venezolana de Ciencias Naturales 136: 5-41.

Tiessen, H., C. Feller, E. V. S. B. Sampaio and P. Garin (1998). "Carbon Sequestration and Turnover in Semiarid Savannas and Dry Forest." Climatic Change 40(1): 105-117.

Trollope, W. S. W., L. A. Trollope, A. F. L. Potgieter and N. Zambatis (1996). "SAFARI-92 characterization of biomass and fire behavior in the small experimental burns in the Kruger National Park." Journal of Geophysical Research-Atmospheres 101(D19): 23531-23539.

Walker, S. M. and P. V. Desanker (2004). "The impact of land use on soil carbon in Miombo Woodlands of Malawi." Forest Ecology And Management 203(1-3): 345-360.

Woomer, P. L. (1993). "The impact of cultivation on carbon fluxes in woody savannas of Southern Africa." Water, Air, & Soil Pollution 70(1): 403-412.

Zambatis, N., P. Zacharias and C. Morris (2006). "Re-evaluation of the disc pasture meter calibration for the Kruger National Park, South Africa." African Journal of Range and Forage Science 23(2): 85-97.

8. Discussion

This thesis has quantified the ecosystem carbon stocks of the Nhambita area, and provided some quantitative understanding of the role of fire, and clearance for agriculture, in modifying these stocks. I have also quantified the seasonal cycle of leaf display. I now review the key findings of this thesis and discuss some of the implications for 1) modelling the carbon cycle of miombo woodlands and 2) approaches to detecting deforestation and mapping biomass. I also 3) summarise some of the key issues relating to fire management in these woodlands.

10 ## *Towards a model of miombo carbon cycling*

One long term goal of my work and that of others involved in this project is to produce a process-based model of carbon cycling in miombo woodlands. Such a model could be built upon an existing infrastructure (e.g. SPA and DALEC (Williams et al. 1998; Williams et al. 2005), but these biogeochemical approaches will need much more work to capture the effects of disturbance, and to represent constraints on the growing season. A model of these woodlands needs to avoid heuristic representations of key processes so that it is able to predict future changes in ecosystem functioning under global change drivers. This is

20 particularly important, and difficult, due to the dynamic equilibrium of savannas (Walker 1987) and the key role of disturbance (Bucini et al. 2007), as well as the more easily modelled effects of rainfall (Sankaran *et al.* 2005) and nutrients (Scholes 1990). Dynamic Global Vegetation Models struggle to represent these processes (TROBIT 2009) and to characterise the important role of the savanna biome in the global carbon cycle (Grace *et al.* 2006). Developing a miombo carbon cycle model would provide a bottom up approach to resolving these problems, but will require a fusion between biogeochemical modelling of stocks and fluxes, and population models (like that in Chapter 3), which can represent

30 effects at the level of individual stems (Moorcroft *et al.* 2001).

This thesis has contributed to the development of a miombo carbon cycle model, but the final goal is still some way off. Here we review the findings of this thesis, examine some of its limitations and describe some of the key challenges and areas for further work.

Fire and the carbon cycle

Chapter 3 provides a rough outline of a carbon cycle model of miombo woodlands, but it can only be considered a first draft.

Key results were:

1. Stem mortality in fires is a logistic function of stem size below 10 cm DBH and increases linearly with fire intensity. However stems do not gain increasing protection from fire as stem diameter increases beyond 10 cm DBH. The effects of accumulated damage to large stems may be important for understanding fire-induced mortality, and undermine idealised physical models of heat flux to the stem.

2. Resprouting is very common in miombo, as has been shown in many other studies. Fire intensity, as measured in our study, is only weakly related to the death of below ground organs, or rates of resprouting.

3. Tree species seem to be affected by fire in broadly similar ways, at least for the dominants considered in this study. No significant difference was found between the response to fire of the canopy miombo species and the understory trees.

4. Fires of different intensity produce large differences in ecosystem structure over the long term. High intensity burns are very destructive to woody biomass: aboveground carbon stocks can only be maintained under high intensity fires with improbably long fire return intervals (> 4 years). Low intensity burns allow woody

biomass to develop to the levels observed in Nhambita, given biennial fires.

The long term predictions from Chapter 3 are very dependent on assumptions about tree growth and resprouting rates. Data to constrain such rates are, to my knowledge, unavailable in the miombo region, and so the model uses a process-based carbon assimilation scheme to predict growth rates. However the lack of data available to constrain several parameters of the model mean that predictions must be considered preliminary.

10 ### *Implications for modelling the carbon cycle*

The key results of Chapter 3 show that a model of fire/carbon interactions needs to represent impacts in a way that is stem size- and fire intensity-specific, as mortality rates varied widely in different intensity fires. However the non-linear relationship between stem size and mortality needs further quantification, particularly to understand what aspects of fire behaviour best scale with impacts. This is particularly true of belowground effects which are less well studied and harder to quantify.

If a model can be constructed that explicitly represents fire intensity-determined effects, it will need to be driven by spatial and temporal fire 20 intensity data. Such data could come from two sources. Firstly, knowing the seasonality and time of day of the burn may allow fire intensity to be modelled as these are the main determinant of fire line intensity in savanna fires (Cheney *et al.* 1998). Combining meteorological measurements (Govender *et al.* 2006) with EO data on fire occurrence may also provide the required drives. A second method is to use observations of fire radiative power from space (Smith et al. 2005; Roberts et al. 2008). Although such data are currently at a spatial resolution that is difficult to relate to ecological studies, they offer a direct quantification of one measure of fire intensity.

One issue that arises is how to define and then measure fire intensity. The term fire intensity is used to describe many different physical aspects of a fire, and often is used interchangeable with fireline intensity. Whether the measure used in Chapter 3 (Thermal anomaly, °C s) or Byram's fire line intensity is the most relevant measure of fire intensity is an area for further study. Other metrics that scale better with the flux of heat to the stem might be better properties to measure and model: these could include the depth of penetration of a critical temperature into the bole (Dickinson et al. 2001; Michaletz et al. 2007), the residence time above some critical temperature, or direct measurements of heat flux.

A model of fuel moisture and grass senescence would be needed to capture the fuel-fire feedback. This could be modelled by parameterising the relationship between tree cover and grass load. Such data already exist (Frost 1996), and are available for our site (Chapter 7), but mechanistic understanding of this relationship has been difficult to generalise (Scholes et al. 1997). Grass growth is influenced by many factors (such as grazing, nutrients, fire and disturbance), and these may be difficult to represent in a process-based way. For example the effects of the previous year's dead grass, if not burned, suppressing new growth appears to be important, but would be challenging to model.

Phenology

Chapter 4 quantified the seasonal cycle of leaf display in Nhambita and across Southern Africa. Key findings were:

1. In Nhambita tree green-up occurred between September 13-30 over the last eight years, despite large differences in the date of rain onset. The trees displayed leaves for 55±21 days before the rains.

2. At a regional scale, in both wet and dry miombo, interannual variability in leaf flush dates is very low for the period 2000-2008, despite large variation in the date of rain onset. Spatial variability is much larger.

3. Across Southern Africa, leaf green-up precedes the onset of the rains by 37 days in dry miombo woodlands and by ~60 days is wetter woodlands.

These results are based on a combination of ground based photos from Nhambita and EO data from MODIS and various sensors that detect rainfall. The conclusions based on ground-based data appear robust. It should be noted however, that the relative temporal changes in leaf area index are much better constrained than absolute values. Absolute estimates of LAI are sensitive to the image processing techniques used (Weiss *et al.* 2004), and to the model used to convert gap fraction to LAI.

The regional analysis is only as reliable as the interpretation of the EO data that it is based on. Remote quantification of rainfall is difficult, and potentially confounded by the large convective storms that precede the onset of the rainy season, but which do not precipitate to ground level. The green-up detection method used is simple and very empirical: we tested a broad range of parameters and found that our conclusions were robust, but more accurate detection of green-up could be achieved by using daily EVI data, and could be validated with data from other sensors.

Implications for modelling the carbon cycle

A process based model of carbon cycling would need to be able to mechanistically represent the constraints on the growing season of grass and trees. For grass this is relatively well understood (Archibald et al. 2007), as it appears directly linked to rainfall events, and there is a large literature on the economically important links between grass productivity and rainfall in South Africa (Scholes et al. 2004). However in the miombo region, more data on grass rooting depths would be needed to understand the links between soil moisture and grass senescence.

For trees, modelling leaf the phenology is a key challenge given that leaf display seems to be endogenously controlled (Chapter 4). There must however be some set of necessary external conditions, that allow the endogenous trigger. The spatial and floristic variations shown in Fig. 3 of Chapter 4 might inform this (for example the topographic trends (Shackleton 1999), and the possible functional difference between wet and dry miombo), but require much more exploration. Initial approaches could include evaluating the importance of soil type and depth, temperature and humidity on the timing of leaf flush. As the time series of quality EO measurements extends across more extreme and unusual events, we may be able to interpret them in ways that reveal process understanding (Borchert *et al.* 2002).

Current models of savanna phenology use empirical relationships between leaf display and rainfall (Woodward et al. 2004), LAI and soil moisture (Jolly et al. 2004), or leaf flush and day length (Archibald et al. 2007). Although these all seem to adequately describe the current behaviour of the ecosystems for which they were calibrated, the use of the models for predictions under changing climate and water availability (New *et al.* 2003; Christensen *et al.* 2007) must be questioned. Further mechanistic understanding of tropical tree leaf phenology and associated eco-physiology appears to be a prerequisite for robust predictions of the effects of climate change upon vegetation structure and function (Reich 1995).

In the meantime, in the absence of a mechanistic basis for modelling tree leaf phenology, assimilation of EO data seems to be the best way to model current conditions. The strong relationship between the seasonal cycles of MODIS EVI and our ground based LAI estimates is encouraging in this respect. There are clearly two seasonal cycles that need to be decomposed from such EVI time series, that of grass and trees, and this could be done,

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based on our ground based tree LAI data, with rainfall data constraining the grass behaviour.

Carbon stocks

This thesis quantified the carbon stocks in the Nhambita area and quantified the recovery of vegetation stocks after disturbance. I also examined the uncertainty on C stock estimates at plot and landscape scales. Key findings were:

1. Woody biomass is non-normally distributed across the landscape, with some very high aboveground woody biomass (>70 tC ha^{-1}) plots compared to a mean of around 21 tC ha^{-1}.

2. A few large trees (the 3% largest) contribute 50% of the sampled biomass.

3. Root biomass is significant and the root stem ratio is > 1 for small trees. Plot-level root:stem can be as high as 0.55 on plots dominated by small trees. Root:stem is lower for large trees (0.3 for a 73 cm DBH tree). Averaged across our inventoried plots, the root:stem was 0.42.

4. Soil carbon is the major carbon pool (69% of total stock), is not obviously related to woody carbon stocks (26%), and varies widely from 30-130 tC ha^{-1} (to 50 cm depth) across the landscape.

5. Aboveground biomass recovers to pre-disturbance levels after around 30 years of the land being abandoned, although pre-disturbance is hard to define.

6. Landscape estimates of biomass can be significantly biased by the choice of allometric model, by up to 17% relative error: this relates to both the way the model is constructed, if using a site specific allometric, and also to the use of literature allometrics.

7. Plot level estimates of biomass are badly constrained by the use of simple DBH-Biomass allometric models, even with a locally parameterised model. 95% confidence intervals may be as high as 0.9-0.6 of the mean biomass for typical miombo plots. Measurements of stem characteristics other than diameter may be needed to constrain plot biomass estimates. These might include bole height, taper and rottenness.

8. Inventories of landscape biomass in miombo can optimise the effort uncertainty ratio by reducing plot size to around 0.2 ha, and inventorying many plots. Sample sizes of around 100 plots may be needed to constrain the 95% CI of the mean landscape biomass to <0.2 of the mean.

9. Site specific allometrics are not warranted unless progress can be made on characterising and modelling the heteroskedasticity of the biomass-DBH relationship.

Implications for modelling the carbon cycle

Soil C does not seem to be a function of observed aboveground biomass (Chapter 5). This relationship needs to be understood if soil carbon is to be included (and valued) in management approaches as measurements of soil carbon are costly and impractical. A particular problem is the almost uniform distribution of soil carbon stock measurements (Chapter 7), this makes it very hard to make inferences about mean landscape carbon stocks, and significantly more work is warranted in this area, given that soil is the major ecosystem carbon pool. Approaches to address this problem might start with examining the link between hydrology, topography, soil texture and carbon stocks. Also, more work is needed to understand the role of fire and termites in limiting inputs to the soil carbon pool.

Stocks of stem carbon are non-normal and have a long 'tail' of high biomass plots. These high biomass areas (40-80 tC ha^{-1}, stem biomass) are possibly more fertile and/or moist, and seem to be targets for conversion to agriculture (See map in Introduction). This suggests that the loss of carbon from the landscape as a result of clearance may be more than double that which would be estimated if the mean value (~20 tC ha^{-1}) was used. A similar issues may apply to soil carbon stocks.

Using phenological information to detect land cover change and map C stocks

10 The detection of land cover change is difficult in tree-grass ecosystems, but of key importance for modelling the carbon cycle (DeFries et al. 2002; Houghton et al. 2006). Recent work has shown the power of using the phenological signal of different cover types to assess the conversion from forest (Morton *et al*. 2006). The results of Chapter 4 suggest that when miombo is cleared, there should be change in green-up date from one that pre-empts the start of the rains to one that follows it. The interannual variability in green-up dates of grass/crops should also be much higher than that of woodland.

The separation of woodland and grassland EVI signals is illustrated in
20 Fig. 1. The strength of the deforestation signal will be proportional to the area in red – this depends on the length of the pre-rain leaf display period, and also the magnitude of LAI during this period. It will therefore be easier to detect in years when the rains start late. The wet miombo time series (Fig. 2), shows the signal in a very pronounced way, and the approach might be most useful in this region, compared to others with a smaller period between green-up and rain onset. Using daily EVI data would be an obvious way of improving the power of this approach, particularly with a kernel smoothing approach to modelling the EVI signal (Quaife et al. 2009).

Rains start   Rains end

rain-induced grass green-up
early tree green-up
grass senescence
later tree senescence

grass

+

tree

=

EVI signal

difference between deforested
and intact woodland pre-rain signal
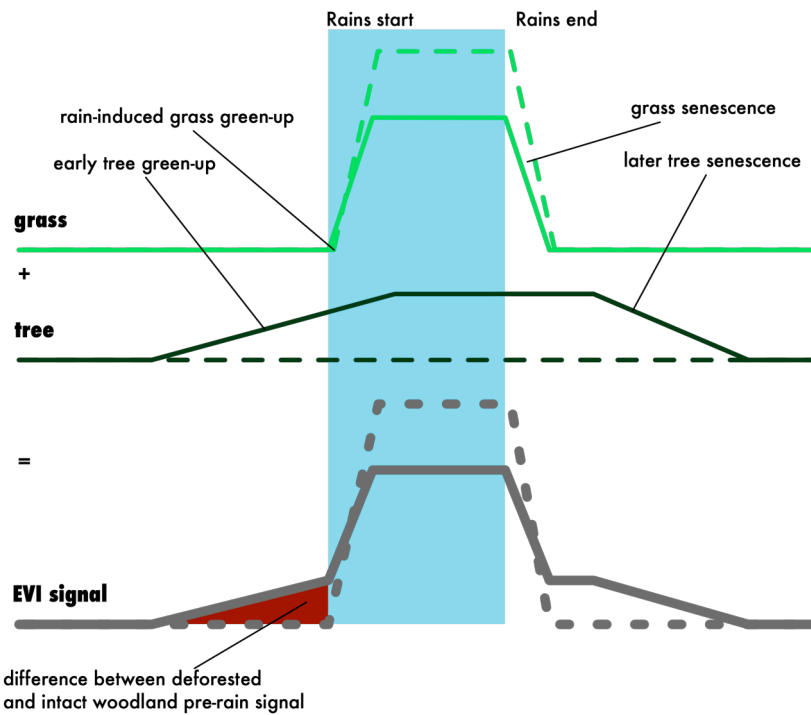
Figure 1. Schematic of the tree and grass EVI signal and the change upon deforestation. Solid lines show the EVI time series with trees present and dashed lines show the signal after deforestation. The red area represents the size of the signal upon deforestation. One annual cycle is shown.
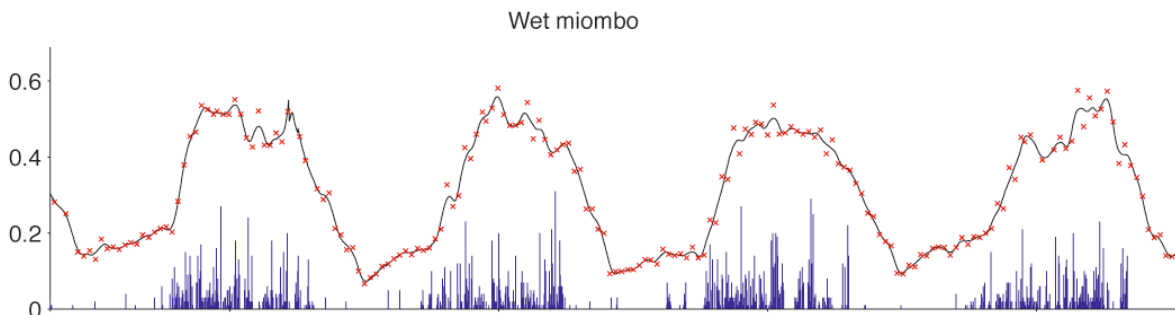
Wet miombo

Figure 2. Four years of EVI data for a randomly selected wet miombo pixel. EVI data is from MODIS at 0.05° resolution (red crosses), the black line shows the smoothed time series and the blue bars depict daily rainfall from GPCP. The pre-rain tree green-up can be seen each year, as can the effect of rain-induced grass growth later in the season.

10   The relationship between tree biomass and optical vegetation indices such as NDVI and EVI is mediated by LAI. This relationship is potentially a useful way to estimate biomass in savannas, as the tree-leaf layer is not optically thick and so the EVI signal should not saturate. However, separating the grass LAI from the tree LAI is a vital

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precondition for this approach to be valid in savannas (Archibald et al. 2007). Pre-rain green-up makes this possible as the spring flush of tree leaves occurs with no grass layer. The strength of the biomass-LAI relationship seems to be at its highest during the period of pre-rain green-up (Fig. 3), and this could be exploited for biomass mapping.
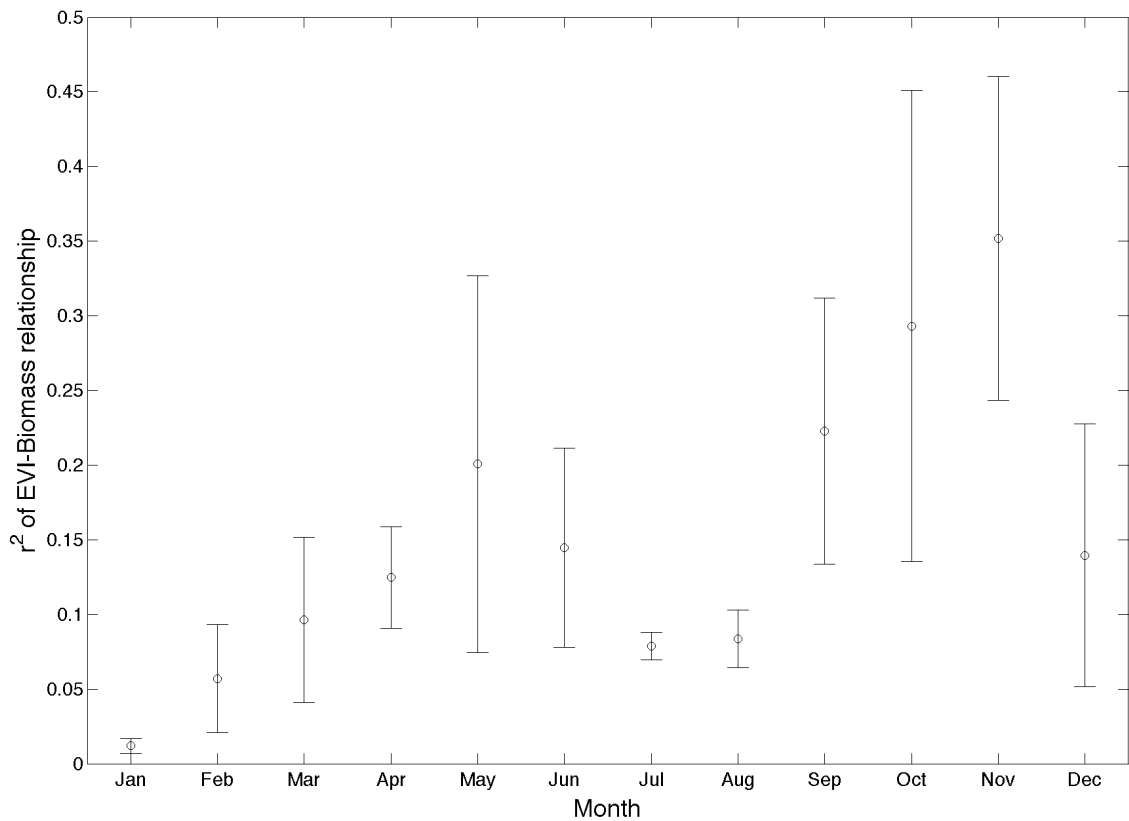
Figure 3. The seasonal evolution of the strength of the EVI-Biomass relationship. Each month (from June 2004–May 2008), EVI from MODIS (250 m pixel) is regressed against the stem carbon stock for the 15 PSPs. Standard error of the mean of the 4 years is shown with error bars. Only the regressions in October and November had a slope coefficient significantly different (p<0.1) from zero.

Patch mosaic burning as a strategy for managing fire in miombo?

Our results (Chapter 3) and those of the long term fire experiments (Appendix 1) show that miombo cannot be sustained under annual fires. We also show that even relatively infrequent high intensity fires cannot sustain tree populations. Estimates put the fire return interval in the

region at between 2-4 years (Scholes et al. 1996; Barbosa et al. 1999; Mouillot et al. 2005), and EO data show that most fires in the region occur at the height of the dry season (Roberts *et al.* 2009) and in the afternoon (Roberts *et al.* 2005) when intensity can be expected to be very high (Chapter 3). Over the four years of this study, we observed that more than half of the PSPs burned each year, always in the hot dry season. This intense fire regime is hard to reconcile with the observed woody biomass given the data in Chapter 3 and Appendix 1.

One answer may be found in the traditional patterns of burning in the miombo region (Eriksen 2007) and similar ecosystems across Africa (Laris 2002; Laris et al. 2006) and around the world (Pyne 1997). There seems to be a common thread through these accounts of burning being initiated early in the season, as soon as the grass will carry a fire:

"In the Spring . . . the old squaws began to look for the little dry spots of headland or sunny valley, and as fast as dry spots appeared they would be burned. In this way fire was always the servant, never the master . . . By this means, the Indians always kept their forest open, pure and fruitful, and conflagrations were unknown".

(Miller, 1887, cited in Laris 2002)

Such fire management results in a radically different fire regime than if burning is not managed and is allowed to occur at the height of the dry season. For instance, contrast the early burning regime on the left of Fig. 4, to that on the right. The burned area is almost the same, but the ecological effects, based on what we know about the effects of different fire intensities, must be radically different.
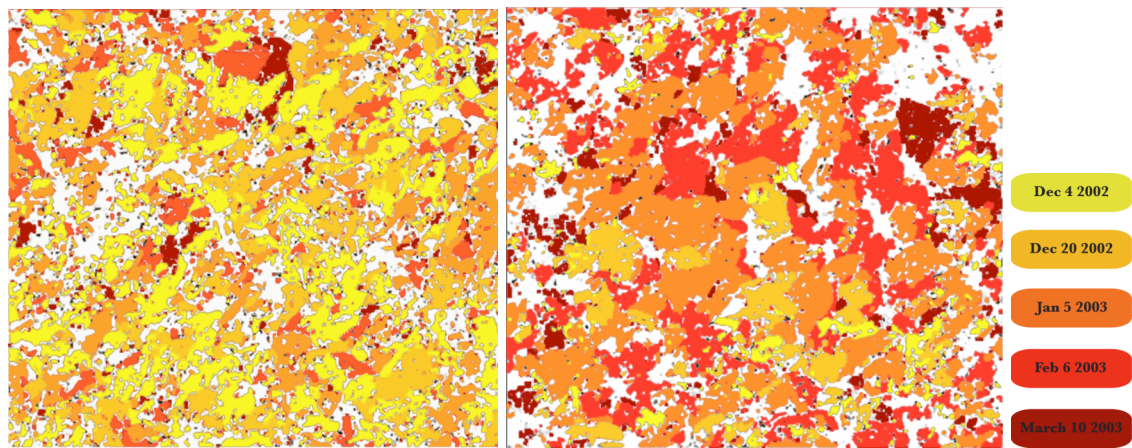
Figure 4. Two areas of Mali with very different fire regimes. Left, an area actively managed by the local community with many small burns early in the season. Right a nearby area with no active management characterised by late season large burns. Each image is 50 km across, and burned areas were mapped from a time series of Landsat ETM images. Source: redrawn from Laris (2002).

Did a fire regime such as the one on the left ever exist in the miombo woodlands? It is certainly not present in Nhambita now, but one interpretation of the model results in Chapter 3 is that the woodlands we now observe are a product of a much milder fire regime than is present now. This possibility calls for close monitoring of the effects of fire in these woodlands, as the intense fire regime may be degrading them rapidly. Several protected areas in savanna regions now try to implement a pattern of mosaic burning, partly because of hypothesised biodiversity benefits (Parr et al. 2006), but no large scale experiment has been conducted to test the effectiveness of this as a management tool. Current efforts to implement early burning in Nhambita should therefore be carefully monitored to assess impacts on tree mortality. The discussion above also suggests that palaeo reconstructions of the fire regime might be a useful aide to understanding the present, if they are able to tease apart the signal from fire frequency, burned area and intensity.

References

Archibald, S. and R. J. Scholes (2007). "Leaf green-up in a semi-arid African savanna separating tree and grass responses to environmental cues." <u>Journal of Vegetation Science</u> **18**: 583-594.

Barbosa, P. M., D. Stroppiana, J. M. Gregoire and J. M. C. Pereira (1999). "An assessment of vegetation fire in Africa (1981-1991): Burned areas, burned biomass, and atmospheric emissions." <u>Global Biogeochemical Cycles</u> **13**(4): 933-950.

Borchert, R., G. Rivera and W. Hagnauer (2002). "Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain." <u>Biotropica</u> **34**(1): 27-39.

Bucini, G. and N. P. Hanan (2007). "A continental-scale analysis of tree cover in African savannas." <u>Global Ecology and Biogeography</u> **16**(5): 593-605.

Cheney, N. P., J. S. Gould and W. R. Catchpole (1998). "Prediction of Fire Spread in Grasslands." <u>International Journal of Wildland Fire</u> **8**(1): 1-13.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. M. a. Rueda, L. Mearns, C. G. Menéndez, J. Ra isa nen, A. Rinke, A. Sarr and P. Whetton (2007). Regional Climate Projections. <u>Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change</u>. S. Solomon, D. Qin, M. Manning et al. Cambridge, Cambridge University Press.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole and J. Townshend (2002). "Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s." <u>Proceedings of the National Academy of Sciences of the United States of America</u> **99**(22): 14256-14261.

Dickinson, M. B. and E. A. Johnson (2001). Fire effects on trees. <u>Forest Fires: Behavior and Ecological Effects</u>. E. A. Johnson and K. Miyanishi, Academic Press.

Eriksen, C. (2007). "Why do they burn the 'bush'? Fire, rural livelihoods, and conservation in Zambia." <u>Geographical Journal</u> **173**: 242-256.

Frost, P. (1996). The ecology of Miombo woodlands. <u>The Miombo in transition : woodlands and welfare in Africa</u>. B. M. Campbell. Bogor, Indonesia, Center for International Forestry Research**:** 11-55.

Govender, N., W. S. W. Trollope and B. W. Van Wilgen (2006). "The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa." <u>Journal of Applied Ecology</u> **43**(4): 748-758.

Grace, J., J. S. José, P. Meir, H. S. Miranda and R. A. Montes (2006). "Productivity and carbon fluxes of tropical savannas." <u>Journal of Biogeography</u> **33**(3): 387-400.

Houghton, R. A. and J. L. Hackler (2006). "Emissions of carbon from land use change in sub-Saharan Africa." <u>Journal of Geophysical Research - Atmospheres</u> **111**(G02003).

Jolly, W. M. and S. W. Running (2004). "Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari." <u>Global Change Biology</u> **10**(3): 303-308.

Laris, P. (2002). "Burning the Seasonal Mosaic: Preventative Burning Strategies in the Wooded Savanna of Southern Mali." <u>Human Ecology</u> **30**(2): 155-186.

Laris, P. and D. A. Wardell (2006). "Good, bad or 'necessary evil'? Reinterpreting the colonial burning experiments in the savanna landscapes of West Africa." <u>The Geographical Journal</u> **172**(4): 271-290.

Michaletz, S. T. and E. A. Johnson (2007). "How forest fires kill trees: A review of the fundamental biophysical processes." <u>Scandinavian Journal of Forest Research</u> **22**(6): 500-515.

Moorcroft, P. R., G. C. Hurtt and S. W. Pacala (2001). "A method for scaling vegetation dynamics: the ecosystem demography model (ED)." <u>Ecological Monographs</u> **71**(4): 557-586.

Morton, D. C., R. S. DeFries, Y. E. Shimabukuro, L. O. Anderson, E. Arai, F. del Bon Espirito-Santo, R. Freitas and J. Morisette (2006). "Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon." <u>Proceedings of the National Academy of Sciences</u> **103**(39): 14637-14641.

Mouillot, F. and C. B. Field (2005). "Fire history and the global carbon budget: a 1° fire history reconstruction for the 20th century." <u>Global Change Biology</u> **11**(3): 398-420.

New, M., R. Washington, C. Jack and B. Hewitson (2003). "Sensitivity of southern African climate to soil moisture." <u>CLIVAR Exchanges</u> **8**(45-47).

Parr, C. L. and A. N. Andersen (2006). "Patch Mosaic Burning for Biodiversity Conservation: a Critique of the Pyrodiversity Paradigm." <u>Conservation Biology</u> **20**(6): 1610-1619.

Pyne, S. J. (1997). <u>World fire : the culture of fire on earth</u>. Seattle, University of Washington Press.

Quaife, T. and P. Lewis (2009). "Temporal constraints on linear BRF model parameters." <u>IEEE Transactions on Geoscience and Remote Sensing</u> **accepted**.

Reich, P. B. (1995). "Phenology of tropical forests: patterns, causes, and consequences." <u>Canadian Journal of Botany-Revue Canadienne De Botanique</u> **73**(2): 164-174.

Roberts, G., M. J. Wooster and E. Lagoudakis (2009). "Annual and diurnal african biomass burning temporal dynamics." <u>Biogeosciences</u> **6**(5): 849-866.

Roberts, G., M. J. Wooster, G. L. W. Perry, N. Drake, L. M. Rebelo and F. Dipotso (2005). "Retrieval of biomass combustion rates and totals from fire radiative power observations: Application to southern Africa using geostationary SEVIRI imagery." <u>J. Geophys. Res.</u> **110**.

Roberts, G. J. and M. J. Wooster (2008). "Fire detection and fire characterization over Africa using Meteosat SEVIRI." <u>Ieee Transactions on Geoscience and Remote Sensing</u> **46**(4): 1200-1218.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger,

H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden and N. Zambatis (2005). "Determinants of woody cover in African savannas." Nature **438**(7069): 846-849.

Scholes, R. J. (1990). "The Influence of Soil Fertility on the Ecology of Southern African Dry Savannas." Journal of Biogeography **17**(4/5): 415-419.

Scholes, R. J. and S. R. Archer (1997). "Tree-grass interactions in savannas." Annual Review of Ecology and Systematics **28**(1): 517-544.

Scholes, R. J., J. Kendall and C. O. Justice (1996). "The quantity of biomass burned in southern Africa." Journal of Geophysical Research-Atmospheres **101**(D19): 23667-23676.

Scholes, R. J. and B. H. Walker (2004). An African savanna : synthesis of the Nylsvley study. Cambridge, UK, Cambridge University Press.

Shackleton, C. M. (1999). "Rainfall and topo-edaphic influences on woody community phenology in South African savannas." Global Ecology and Biogeography **8**(2): 125-136.

Smith, A. M. S. and M. J. Wooster (2005). "Remote classification of head and backfire types from MODIS fire radiative power and smoke plume observations." International Journal of Wildland Fire **14**(3): 249-254.

TROBIT (2009). Diversity of Tropical Biome Structure and Function

Walker, B. H. (1987). Determinants of tropical savannas : presentations made by savanna researchers at a workshop in Harare, Zimbabwe, 1985. Oxford, IRL Press.

Weiss, M., F. Baret, G. J. Smith, I. Jonckheere and P. Coppin (2004). "Review of methods for in situ leaf area index (LAI) determination: Part II. Estimation of LAI, errors and sampling." Agricultural and Forest Meteorology **121**(1-2): 37-53.

Williams, M., Y. Malhi, A. D. Nobre, E. B. Rastetter, J. Grace and M. G. P. Pereira (1998). "Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis." Plant, Cell and Environment **21**(10): 953-968.

Williams, M., P. A. Schwarz, B. E. Law, J. Irvine and M. R. Kurpius (2005). "An improved analysis of forest carbon dynamics using data assimilation." Global Change Biology **11**: 89-105.

Woodward, F. I. and M. R. Lomas (2004). "Simulating vegetation processes along the Kalahari transect." Global Change Biology **10**(3): 383-392.

9. Key Conclusions

Fire intensity is a crucial determinant of woody vegetation in miombo, and exceeds the influence of fire frequency. A process-based model of the short term effects of fire set against a model of photosynthesis and growth is able to predict woody vegetation structure with some skill. Annual fires in miombo remove and then suppress all woody vegetation. Low intensity fires every 2.5 years are required to maintain observed tree biomass in Nhambita.

Tree feaf phenology is not related to seasonal rainfall patterns, both in Nhambita and across Southern Africa. Pre-rain green-up is the dominant phenological strategy, from the *Acacia* savannas of the south of the continent to the wet miombo of the Congo basin. Wet miombo woodlands have longer periods of green-up before rain onset (~60 days) compared with dry miombo (37 days). Much more work is needed to understand the seasonal constraints on productivity in these woodlands.

Tree carbon stocks in the Nhambita woodlands are 21.3±1.4 tC ha^{-1} aboveground and 8.6±0.46 tC ha^{-1} belowground. These woody stocks are dwarfed by the soil carbon stocks which range from 30-130 tC ha^{-1} (mean 76±10 tC ha^{-1}). Woody biomass is non-normally distributed across the landscape, with some very high aboveground woody biomass plots (>70 tC ha^{-1}) compared to the mean of 21 tC ha^{-1}. The 3% largest trees contribute 50% of the inventoried biomass. The landscape aboveground carbon stock mean (21.3 tC ha^{-1}) has a 95% confidence interval of ~30% of the mean, which could be reduced to 10% with an inventory of around 90 plots 0.25 ha in size. There is a possible bias of up to 14%, stemming from allometric model construction and fitting techniques.

Woody carbon stocks recover from clearance after 30 years of abandonment; soil carbon does not show a recovery upon abandonment,

but any signal may be masked by the very high variability across the landscape.

"Take what you have gathered from coincidence"
    Bob Dylan

Appendices

1. Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe

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2. Fire and finance in rural Mozambique

10 A non-technical introduction to the project and fire management in the area, with a short life history of one member of the Nhambita community written by Casey Ryan for submission to *The Ecologist*.

3. Plot-level inventory data
4. Destructively harvested tree data

Appendix 1. Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe

Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe

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Abstract: Long-term fire experiments in savannnas are rare, given the difficulties and demands of operation. Controlled fire experiments date from colonial times in West Africa, although the largest and best-known is located in the Kruger National Park, South Africa. The achievements of these experiments are assessed from examples in Africa, South America and Australia. A less well-known experiment in Zimbabwe was sited at the Marondera Grassland Research Station and ran from 1953 to 1991. Some of the preliminary results on the impact of fire on vegetation are analysed and compared with further vegetation surveys in 2007. Studies on tree growth in this *miombo* savanna woodland indicate that the plots burned at three- and four-year intervals recovered to greater mean heights than the unburned control plots. There was no significant variation between treatments, suggesting that the few trees that did survive in the frequently burned plots were large specimens. *Brachystegia* and *Julbernadia* dominated the plots throughout and after the experiment. Basal area and stocking density were highest in the four-yearly burned plots but there was a high variability throughout the experiment, suggesting that many trees may have attained heights and bark thicknesses sufficient to protect from fire damage. Fire also affected the composition of the herbaceous plant community, but not the number of species. By the end of the experiment some grass and sedge species had flourished while others revealed greater susceptibility to fire, and fire-tolerant species predominated in the most frequently burned areas. The experimental design appeared to cope well with the variability between plots and indicated the soundness of the initial design and its implementation.

Key words: fire experiments, Marondera, *miombo*, savanna woodlands, Zimbabwe.

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I Introduction

Tropical savannas are characterized by a co-dominance of trees, shrubs and herbaceous plants, whose proportions are determined by environmental, ecological and human parameters and fashioned by fire. Savanna vegetation is typically fire-adapted and re-silient. Nevertheless, the frequency and intensity of fires affect vegetation structure and many of its constituent and associated characteristics, presenting major problems for ecosystem assessment and resource management (Frost and Robertson, 1987; Lonsdale and Braithwaite, 1991; Bond and van Wilgen, 1996; Braithwaite, 1996; Bond *et al.*, 2005; Bond and Keeley, 2005; Bowman and Franklin, 2005; van Langevelde *et al.*, 2003). Recent developments in spatial data acquisition from remote sensing, and handl-ing within GIS, have provided more accurate information on the incidence, frequency and impact of fires (eg, Palacios-Orueta *et al.*, 2004*;* 2005; Schroeder *et al.*, 2005; 2008; Lentile *et al.*, 2006; Chongo *et al.*, 2007; Verbesselt *et al.*, 2007). The ability to ob-serve fires from airborne and satellite sensors has been a catalyst in stimulating interest in the role of biomass burning particularly in the tropics. Satellite images, linked to models, reveal that in Africa over 2.6 million km^2 of savanna burn every year, contributing 48% of global pyrogenic CO_2 emissions, albeit with a high estimated error (Schultz *et al.*, 2008).

Numerous experiments and models of savanna burning have been developed in order to understand the nature and impact of fires, although relatively few have been maintained for a long period or have been suffi-ciently replicated to give a consistent picture (Bond and van Wilgen, 2005). In any case it has proved difficult to include all possible variables in field experiments that might influence burning, and therefore all controlled experiments are to some degree distant from the reality of highly varied wildfire events.

Field experiments manipulating burning episodes vary greatly in rigour but have been assayed for well over half a century. Four main groups of objectives can be extracted from the literature: (1) many of the early experi-ments were carried out in savanna woodlands or tropical forests with the aim of assessing the effects of slash-and-burn agriculture or clearance on the environment; (2) field experiments were established to analyse the effects of burning or various forms of management for grazing; (3) several long-term experiments were set up by colonial regimes to test the impact of fire frequencies or timing on vegetation, mostly to improve management; (4) wider environmental con-cerns have more recently been addressed, such as biomass change, carbon emissions and sequestration, as well as particulate and other gas fluxes.

The present objective is to assess the in-formation from global fire experiments with particular reference to the impact of long-term fire trials on vegetation, and to illustrate the inherent concepts in a long-term fire ex-periment in Zimbabwe.

II Savanna fire experiments: a global perspective

Observations of the effects of fire on veget-ation have been published since early colonial experiments in Africa (see Aubreville, 1947). The experiments then established form some of the longest-running ecological experiments in the tropics. However, with some excep-tions in richer countries, they have been little reported in the scientific literature and their results have rarely been synthesized. This is despite an upsurge of interest in the biogeo-chemistry of biomass burning and in the role of fire in the earth system – such as the NASA/ University of Maryland Fire Information for Resource Management System (FIRMS), the Australian SENTINEL system for mapping fires, SAFARI (Southern Africa Fire Atmo-sphere Research Initiative) and SavFIRE (Savanna Fire Ignition Research Experiment). However, there are numerous difficulties in designing and operating such experiments, particularly when continued over decades where the aims may change over time, where

there are funding difficulties, and where there are problems in carrying through the experiments consistently with sufficient replication (Vogl, 1974). There have been several other serious criticisms of some burning trials, relating to the lack of an initial sound protocol and the inevitability of a rigid design. The experimental plots have often been relatively small in relation to the area represented (to permit adequate control), contrived (since wildfires are frequently spontaneous and irregular), and artificial (in the sense that they try to simplify conditions whereas the reality is a heterogeneous ecosystem). The experimental conditions may also be considered untypical of the areas outside the fire trials. Sometimes the documentation of the pre-fire conditions has been shown to be inadequate and there is frequently a lack of supporting environmental and ecological information (such as soils and drainage, rainfall and seasonality, phenology, herbivory or the ecological context beyond the experimental boundaries; see Sankaran *et al*., 2008). Despite these criticisms, a great deal of valuable information has been derived from past experiments, especially from an ecological and biogeographical perspective, providing a test bed for ideas as well as fundamental data on the effects of burning (van Wilgen *et al*., 2007; Higgins *et al*., 2007).

Not only have fire trials have been conducted for diverse reasons, but the original objectives have often been added to or modified over time. For example, some experiments designed to test the effects of burning on bush encroachment for pasture research have later been utilized to study changing vegetation structure and plant composition. The development of concepts on savanna heterogeneity (such as non-equilibrium theory, patch mosaics and theories on the dynamics of tree-grass co-existence) has frequently drawn on the data from existing field experiments. Early controlled experiments were carried out in West Africa and were established by colonial regimes in many countries in East and Southern Africa,

with the largest and best-documented study located in the Kruger National Park. Other well-documented studies have been published in Australia (notably in the Kakadu National Park), in the Brazilian *cerrados* (Projeto Fogo, administered by the environment agency, IBAMA, and earlier studies) and in the Venezuelan/Colombian *llanos*.

When controlled field experiments were first initiated, fires were generally perceived as detrimental leading to land degradation (see the summary of ideas in Laris and Wardell, 2006). They have long been seen as instrumental in influencing forest-savanna boundaries (Furley *et al*., 1992; Hoffman *et al*., 2003; Fensham *et al*., 2003; Müller *et al*., 2007). Aubreville's pioneer experiments in West Africa in the 1930s influenced a succession of later African studies – such as Charter and Keay (1960), Hopkins (1965) and Rose-Innes (1971) at Olokomeji, Nigeria; Ramsay and Rose-Innes (1963), Brookman-Amissah *et al*. (1980), Swaine (1992) and Swaine *et al*. (1992) in Ghana; Trapnell (1959) and Lawton (1978) in what was then Northern Rhodesia, and later the work of Chidumayo and his associates (Chidumayo, 1988; 1997; Chidumayo *et al*., 1996); Nangendo *et al*. (2005) in the Murchison Falls National Park; Eldroma (1984) in the Queen Elizabeth National Park, Uganda; Ferguson (1998) and van de Vijver *et al*. (1999) in Tanzania. The results, also confirmed in other parts of the world, tended to show that over time fires (especially late dry season), created a landscape with fewer trees and larger expanses of grassland, while fire suppression promoted a reverse trend, later substantiated by work such as Menault and Cesar (1982) and Louppe *et al*. (1995) in Ivory Coast. Research since the 1960s has indicated a growing awareness and understanding of the complexity and dynamics of the savanna biome, and has included a multitude of environmental and human variables in process models. For example, savanna woodland diversity and structure has been shown to reflect combinations of factors such as

prescribed fire along with grazing and termite activity (eg, Traore *et al.*, 2008, in Burkina Faso), and seed germination (Gashaw and Michelsen, 2002, in Ethiopia), or numerous publications on fire and elephant interactions (eg, Lock, 1977). More detailed ecological parameters have included different timing of burns, different fire intensities and irregular fire behaviour patterns. While the early research concentrated on the impact of fires on the environment, more recent studies have also concentrated on managing fire regimes for grazing (eg, Savadogo *et al.*, 2007), for wildlife and conservation, and on designing improved fire policy (Dyer *et al.*, 2001; Dyer and Smith, 2003; Bond and Archibald, 2003; Whitehead *et al.*, 2005).

1 Fire experimentation in northern Australia
Australian savannas occur at the drier end of the savanna spectrum with frequent fires and woody plants characterized by eucalyptus. The emphasis of research into fire impact and management has been predominantly in northern Australia (Bradstock *et al.*, 2002). An overview of fire experiments in the 2m km^{-2} of tropical savanna is given in R.J. Williams *et al.* (2003), and there are numerous research sites and studies reflected in published literature and in reports from the research stations. Controlled experiments of international significance have been sited at Munmarlarly, Kidman Springs and the well-known Kapalga sites in the Kakadu National Park. Munmarlarly ran from 1973 to 1996 in a eucalypt-dominated savanna woodland, with four replicated 1 ha plots designed to investigate the interactions between fire, landscape and biodiversity. Lonsdale and Braithwaite (1991), in a statistical analysis of earlier studies, concluded that the different fire regimes resulted in negligible changes in the vegetation, suggesting long-term stability. In a later detailed assessment, Russell-Smith *et al.* (2003a) explored relationships between fire regimes and savanna responses, and detailed the variations between the types of woodland savanna, different timings for

burning and associated effects on some soil properties. Frequent burns at low or moderate intensities produced a structurally stable system, though the authors suggest that, no matter how rigorous the fire plot design, the results are limited for fire-management purposes in view of the idiosyncratic nature of natural fire regimes over multiple temporal and spatial scales. The Kidman Springs experiment examined the productivity and composition of the herbaceous layer in an effort to better inform pasture management. The Kapalga experiment in the Kakadu National Park ran from 1989 to 1995 with a range of fire treatments similar to those at Munmarlarly but with very large plots of 10–20 km^2 in subcatchments and can claim to be the world's largest fire experiment. There have been numerous published studies from Kapalga and the wider National Park, covering a gamut of ecological and environmental issues (see, for instance, Liedloff *et al.*, 2001, who modelled fire and grazing interactions; Edwards *et al.*, 2003, looking at fire regimes and biodiversity; Price *et al.*, 2005, studying fire heterogeneity; Prior *et al.*, 2006, examining the biotic and abiotic factors influencing tree growth rates). The well-documented results from Kapalga are summarized in the book by Andersen *et al.* (2003) and subsequent articles (eg, Andersen *et al.*, 2005). The main results showed that, with the exception of riparian vegetation and associated streams and also small mammal populations, much of the savanna biota showed little or no response to burning, even with the most extreme fire regimes, and is therefore extremely resilient to fire. Where fire did have a marked effect it was felt between burned and unburned areas rather than high- versus low-intensity fires and this emphasized the importance of analysing fire frequencies.

Less well-known Australian studies were sited in the Bowling Green Bay National Park near Townsville, Queensland (P.R. Williams *et al.*, 2003a), where three fire regimes were studied between 1997 and 2001 over an area

of 10 ha. The abundance of most species was stable irrespective of the fire regime, although several subshrubs, ephemeral and perennial forbs and grasses did increase in abundance particularly following late-season fires. The density of trees increased markedly in the absence of fire for four years. Fire patterns and frequencies were compared over a four-year period by satellite imagery for two areas in northern Queensland by Felderhof and Gillieson (2006), where the Mount Isa area in semi-arid conditions showed patterns and frequencies similar to those reported elsewhere in arid parts of Australia, whereas the Cape York Peninsula more closely resembled more mesic savannas. At the Bradshaw research station (Northern Territory), Gill *et al*. (2003) also examined fire and patchiness. Other studies have looked at the depth of fire penetration into the ground (P.R. Williams *et al*., 2004), fire effects on seedbanks and seedlings (Radford *et al*., 2001); burning and the breaking of seed dormancy (P.R. Williams *et al*., 2003a; 2003b); alien grass invasions (a major topic elsewhere as in Brazil) (Rossiter *et al*., 2003); important contributions to the debates on fire and productivity (eg, Bennet *et al*., 2003; Beringer *et al*., 2007); or the long history of fires in Australia and the role of the aboriginal activities (Preece, 2002; Russell-Smith *et al*., 2003b; Bowman *et al*., 2004; Bowman and Prior, 2004). There are also valuable accounts of fire impacts on wildlife which cannot be covered in this assessment but are summarized in publications such as Whitehead *et al*. (2005) or Woinarski *et al*. (2004).

2 Fire experimentation in southern Africa
Fire has always been to the forefront in consideration of African savannas (eg, Booyson and Tainton, 1984). In southern Africa, the research carried out in the Kruger National Park stands out in terms of its large scale, high level of replication, long-term studies and the extensive range of associated botanical, wildlife and environmental concerns (over 70 publications on different aspects of the

research). As Higgins *et al*. (2007) have commented, few long-term data sets are available anywhere to document the extent to which fire can structure savannas. The Kruger research provides invaluable information on fire impacts and also offers a yardstick of comparison for the neighbouring Zimbabwe experiments described later. The National Park at Kruger was established in 1926 and the long-term, plot-based fire experiment started in 1954 in order to provide a scientific basis for fire management. The large area covers a range of rainfall from 350 mm in the north to 750 mm in the south with extended wet and dry periods significantly affecting fire occurrence, principally through the combustible fuel load (van Wilgen *et al*., 2003). Four representative woody savannas are dominated by *Acacia nigrescens* and *Colophosperum mopane* over basaltic soils, *Terminalia sericea* and *Combretum* spp. on granite soils. Natural fires typically break out in the late dry season with a mean fire return interval (1941–96) of 4.5 years. The fire experiments comprised burns at varying return intervals and seasons in a series of 7 ha plots in the four types of savanna vegetation. The plots have been open to wildlife grazing and it has been suggested that this may have influenced some of the results. A valuable overview is presented in du Toit *et al*. (2003) and useful evaluative commentaries are given in Woods *et al*. (2002) and Higgins *et al*. (2007). Van Wilgen *et al*. (2007) give a helpful summary table of fire effects on vegetation, wildlife and a number of environmental properties. As far as the effects of fire on woody plants is concerned, the key findings were that fire frequency, fire season and complete exclusion from burning did not affect the size of tree populations and that there was no decrease in tree density with increasing fire frequency. This apparently unlikely result was attributed to the ability of the woody (and other species) to resprout from the base and immediate subsurface. Resprouting increased with fire intensity, which scorched

aerial parts of the trees (Trollope, 1982; 1984; Trollope *et al*., 1995; Bond and Midgely, 2001; Kennedy and Potgieter, 2003; Nefabas and Gambiza, 2007). While constant fires lowered the size of individual species, they rarely killed them. Nevertheless fire had significant effects on the size, structure and biomass of the tree populations, and studies on fire intensity reveal the interaction of numerous controlling factors, particularly seasonality (influencing fuel moisture) and past fire frequency (Govender *et al*., 2006). Enslin *et al*. (2000) and Shackleton and Scholes (2000) showed that, while there had been no significant changes in woody species from 1954 to 1998, density decreased on biennial but increased on triennial treatments. Control plots where fire was excluded often had dominant larger trees, whereas the fire-affected plots possessed numerous stunted individuals. The influence of fire exclusion was more obvious in areas of higher rainfall, resulting in higher biomass figures. The timing of the fire season was also significant (Govender *et al*., 2006) with intensities being lower in summer and highest in the winter fires, though intensities did not vary between annual, biennial, triennial and quadrennial intervals.

As far as the impact of fires on the herbaceous components is concerned, current research appears to indicate that fires in the dormant season have little effect on community composition, but wet-season fire and fire exclusion does have a significant effect (van Wilgen *et al*., 2007). Fire is known to be important in influencing herbaceous plant communities in savanna woodlands, particularly where there are effects on the seasonal availability of water (Chidumayo, 1997). Post-fire succession in the Okavango, Botswana, was shown to be a reflection of the plant species characteristics, the seedbank and plant mobility in early successional stages and of competition and niche differentiation at later stages (Heinl *et al*., 2007). After 50 years of burning, grass species richness at Kruger was greatest where fire was excluded or burned

during the wet growing season – again more marked in areas of higher rainfall (van Wilgen *et al*., 2007). These findings suggest that in the Kruger experiment the manipulation of fire regimes is not critical for the maintenance of diversity in the herbaceous component. In a similar vein, Hudak *et al*. (2004) concluded that increased fire occurrence promoted landscape heterogeneity while fire exclusion did not. Mycorrhizae and root architecture are believed to be strongly affected by fire (Hartnett *et al*. 2004) and the extensive mycorrhizal network underpinning savanna vegetation, particularly in low-nutrient conditions, represents a valuable strategy for maximizing resources under stress and disturbance.

3 Fire experimentation in South America
South and Central American savannas are among the most humid of global savannas and tend to occur over highly weathered, infertile soils. Work on long-term fire experiments in savannas of South America has been mostly conducted in Brazil and to a lesser extent in Venezuela (San José and Fariñas, 1991; San José and Montes, 1997; Mistry, 1988; Miranda *et al*., 2002). One of the best-known long-standing fire experiments is located at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) and in the adjacent University Agua Limpa Reserve near Brasilia. The IBGE Reserve has sections that have been protected from fire since 1972, and contains an array of study plots established on different *cerrado* physiognomies that are subjected to different fire regimes (Santos *et al*., 2003). There are even older fire experiments set up in Brazilian Cerrados (Coutinho, 1982; 1990), although they do not present rigorous information on the initial environmental conditions before the trials commenced (Moreira, 2000). More recently, work has been conducted both on the changes in structure and composition on a fire-protected *cerrado sensu stricto* in NE Brazil (Roitman *et al*., 2008), and on the interaction between soil and

vegetation under different fire frequencies in study sites located in the Emas National Park (da Silva and Batalha, 2008). Research on the impact of exclusion of fires on savanna vegetation in Venezuela has been conducted since 1960 at the Llanos Biological Station in the central part of the country and has been the subject of long-term monitoring as shown in successive studies published by San José and Fariñas (1983; 1991). Research in this region was subsequently extended with a view of studying the impact of various regimes of land use and fire frequency on the ecosystem (Silva *et al*., 2001).

A common pattern observed in all the studies mentioned above is that of the increases in the woody component of *cerrado* sites protected from fire. Moreira (2000) conducted research at the IBGE Ecological Reserve comparing five different savanna physiognomies that were burned every two years to another five savanna counterparts that were excluded from fire for over 18 years. The study shows that fire exclusion favoured fire-sensitive species and led to an increase in woody elements in all physiognomies studied, although the effect of fire was shown to have a stronger effect on open savannas than on intermediate physiognomies. This work, along with previous studies in the *cerrados*, concluded that if sites were to be protected for long periods of time it would encourage the more wooded (*cerradão)* physiognomies (Eiten, 1972; Coutinho, 1990; Ratter, 1992; Furley, 1999; Oliveira-Filho and Ratter, 2002; Hoffman and Moreira, 2002). Roitman *et al*. (2008) also showed that the structure and composition of a fire-protected savanna underwent significant changes (see also Hoffman, 2002; Hoffman and Solbrig, 2003; Hoffman *et al*., 2003). Studies carried out in the Venezuelan *llanos* also showed a highly significant increment of the woody component and a change in floristic composition of the herbaceous layer after exclusion of fire and cattle grazing (San José and Fariñas, 1983; 1991); Silva

et al., 2001). An increased occurrence of fires in the *cerrado* formations has also been evaluated with the aid of matrix model projections (Hoffmann, 1999), showing reductions in the density and size of woody plants as a result of increases in the number of fire events. The persistence of woody shrub elements in the more open *cerrado* reflects their ability to resist burning, through the development of resistant underground ligno-tubers (Medeiros and Miranda, 2008).

Several studies have suggested that burning is the main determinant factor explaining the differences in vegetation between fire-protected and unprotected sites given a lack of other significant factors, such as differences in soil properties (Moreira, 2000; Roitman *et al*., 2008). While some of the work carried out in *cerrados* has reflected this absence of relationship between soil properties and the different *cerrado* formations, this may result from the flux of vegetation over the landscape with time, and other studies have indicated stronger links between soil fertility and a gradient of *cerrado* physiognomies (Goodland and Pollard, 1973; Lopes and Cox, 1977a; 1977b; Furley, 1996). This is likely to relate to the increased organic matter found in the more wooded formations and in part to local differences in parent material. Uptake of soil water was also shown to be greater for protected areas than for burned areas (Quesada *et al*., 2008).

Numerous studies illustrate how the spectrum of *cerrado* physiognomies reacts to and is resilient to fire, and Felfili *et al*. (2000) and Roitman *et al*. (2008) show how fire acts as an intermediate disturbance factor impeding the ability of the *cerrado* formations to reach 'carrying capacity'. Overall, there seems to be a common view shared by all long-term fire-exclusion studies, in South American studies and elsewhere, that an extremely complex interaction exists between fire and the dynamics of woody cover in savanna communities and that burning results in constant disequilibrium.

III Achievements of long-term experimentation on savanna vegetation

The results from global long-term experiments afford many valuable insights into the effects of burning (Miao *et al*., 2009). Early ideas considered fire to be entirely harmful, leading to land degradation with woodland or forest retreat and savanna advance. The role of fire has subsequently been explored in much greater detail and precision, and has shown that regular low-intensity fires at critical seasons can reduce fuel load, lower pest infestations, return nutrients to the ground and encourage plant diversity. The influence of fire behaviour, intensity and frequency, the timing of burns, and the overall impacts on vegetation structure, species composition and species resilience in varying conditions of rainfall, soil fertility, herbivory and human interaction have been shown to be intricately interwoven and to some extent site-specific.

The degree to which fire influences savanna vegetation is still controversial (see Scholes *et al*., 2003; van Wilgen *et al*., 2003) but plant species have indisputably evolved fire-tolerant and fire-persistent traits (Allen, 2008). A number of general observations stand out as a result of prolonged burning:

(1) Vegetation structure is strongly affected, lowering the proportions of trees to shrubs and herbaceous plants and reducing ground cover; irregular fire behaviour leads to patchiness; ground layer plants change from perennials to a dominance of annuals.
(2) Tree height decreases inversely with fire frequency; total above-ground biomass is severely reduced.
(3) Tree and woody shrub density remains fairly constant through seedling recruitment and resprouting, though numbers of individual species numbers may be affected.
(4) Overall plant composition is little affected, although there may be feedback behaviour between fire and biodiversity.
(5) Once trees reach a certain height (~3 m plus), they are less susceptible to burns.
(6) Burning has relatively little impact on subsurface rooting structures and, except with extraordinary intensities, does not penetrate far below the ground surface; however, surface soil organic matter (0–5 cm) can respond rapidly to changes in fire regime (Bird *et al*., 2000; M. Williams *et al*., 2008).
(7) Burning has significant effects on soil nutrient dynamics (which in turn can influence plant growth) and greenhouse gas exchange (Rees *et al*., 2006).

Further characteristic features include:

(8) Fire has a more marked effect on the structure of woody vegetation when it occurs in higher rainfall areas (over *c*. 600 mm y^{-1}).
(9) The burn season and timing affects its impact on the vegetation, mediated by factors such as fuel moisture, fire weather and whether the vegetation has senesced.
(10) Fire intensity and thus severity varies with fuel load, moisture content and meteorological conditions.
(11) Characteristic plants found over the spectrum of savanna formations may be fire-sensitive or fire-tolerant and the proportions vary with fire frequency, intensity and behaviour.
(12) Micro-environmental variations (such as soils or moisture availability) can have a distinct impact on burning and recovery.
(13) The fire return interval in savannas is typically ~3 years but can in places be annual.

Overall, however, the ability of the vegetation to recover from severe fires relates to favourable climate and local factors such as bark thickness, coppicing, suckering and resprouting from basal stems or rootstocks

and the supporting role of mycorrhizae (Högberg, 1992; Hartnett *et al*., 2004). Taller woody plants tend to survive many of the fires by growing higher than the flame zone (Gignoux *et al*., 1997; Caldwell and Zieger, 2000). The role of key environmental and ecological pressures, among which are soils and drainage, and patterns of herbivory, have also been added into dynamic models of savanna response to fire.

The present objective is to assess the information from global fire experiments with particular reference to the impact of long-term fire trials on vegetation, and to illustrate the inherent concepts in a long-term fire experiment in Zimbabwe.

IV Fire trials in Zimbabwe

As in many parts of Africa, there is evidence of sustained use of fire throughout the country for thousands of years and for a multitude of purposes, and natural fires have occurred since long before man appeared. In what is now Zimbabwe, extensive fires caused by human activity over prolonged periods have resulted in a manmade landscape over most if not all of the country, and it has been suggested that the savanna woodlands as well as the grasslands are the end result of human disturbance (Austen, 1972; West, 1972), the fire climax of Trapnell (1959) and Lawton (1978). Stem mortality is especially noticeable in the more semi-arid districts, such as the savannas on Kalahari sands in the west of the country (Holdo, 2005), where late dry-season fires can severely damage woody plants (Gambiza *et al*., 2005). The savanna woodlands are crucial to the livelihoods of many rural people and a simulation of woodland dynamics under different management systems is assessed by Gambiza *et al*. (2000).

The two best-known and most detailed studies are located at the Grassland Research Station at Marondera in dry woodland savanna (*miombo*) to the west of the country, and at Matapos research station in the southwest with a tree-bush vegetation cover. At Matapos, early small plot experiments were started in 1947 to study different management strategies, and the results of the trials were later reported by Kennan (1972). Two typical areas of *thornveld* (*Acacia*-dominated tree-bush savanna on moderately fertile red or black soils derived from epidiorite and schist), and *sandveld* (*Terminalia-Burkea* tree-bush cover on relatively infertile gneiss and granite) were studied. The plots on the *sandveld* (started in 1947) measured 100×90 ft (30.48×27.43 m) and those on the *thornveld* (90×75 ft (27.43×22.86 m) but otherwise all the plot experiments were identical (12 randomized treatments, replicated three times). While grazing by domestic animals was excluded, the sites were open to wildlife and therefore grazed. Despite considerable care, the results have been difficult to interpret, though the point quadrat and tree count data yielded useful information. Basal cover was affected by fire frequency, which also reflected a succession of stages from more open to more woody conditions. There were also interesting comments made on the susceptibility or resilience to fire by different grass, shrub and tree species and on the effects of burning at different times of the year, with the *sandveld* vegetation being on the whole much more resistant to burning than the *thornveld*. Additional trials were also carried out at Nyamandhlova Station (hotter and drier) with similar results to the *thornveld* over a 17-year period of analysis, and at Tuli (low veld with very high temperatures and low rainfall) but the latter was abandoned because of the extreme irregularity of rainfall (Kennan, 1972).

The other major long-term experiment was situated at Marondera, and the remainder of this paper will outline and analyse the preliminary results from this set of fire trials.

V The Marondera fire trials from 1953 onwards

A long-term burning experiment was set up in 1953 at the Marondera Grassland Research Station southeast of Harare. The station is situated within one of the largest blocks of *miombo* vegetation in southern Africa and lies at an altitude of 1610 m. There are two distinct seasons – hot and rainy from November to April and then a cool and dry season. Some rain occurs in every month, with a maximum in December and February. The driest months of the year are July and August. The mean annual rainfall is around 900 mm, but there are wide variations between years. There have been a number of very dry years (linked to El Niño events), with < 500 mm total annual rainfall, including 1990/1 and 1991/2 towards the end of the fire experiments. Above-average rainfall was received in several years, including 1953 when most of the treatments began. Over the period 1941–97, the maximum total annual rainfall recorded was 1700 mm in 1980/1. Mean monthly temperatures range from 11°C in June to 19°C in November. Temperatures appear to have been slightly higher than average from 1993 to 1997. Occasional night frosts in the winter period over elevated ground restrict the growth of plants.

The *miombo* is a mesic to dystrophic savanna woodland (Campbell *et al.*, 1995; 1998; Chidumayo, 1997). It is a diverse formation with an estimated 8500 species of higher plants, of which 334 are trees (Frost, 1996). It is dominated by *Brachystegia*, *Julbernadia* and *Isoberlinia* (Fabaceae, subfamily Caesalpinioideae). In the central plateau of Zimbabwe, which incorporates the study area, the natural vegetation is described as deciduous *miombo* woodland with *B. spiciformis* and *J. globiflora* as dominants. Other common associated plants are *Albizia antunesiana*, *Combretum molle*, *Faurea speciosa*, *Strychnos cocculoides* and *Vangueria infausta*. There is considerable variation in the composition and biomass of the herbaceous layer, and this includes the grasses *Hyparrhenia*, *Andropogon*, *Loudetia*, *Digitaria*, *Eragrostis* (Frost, 1996), and also *Brachiaria brizantha*, *Craspedorhachis rhodesiana* and *Rhynchelytrum nyassanum*. The shrubs typically comprise the genera *Dolichos*, *Eriosema* and *Indigofera*.

The soils in the Marondera region are mostly Ultisols, but over the experimental plots are Alfisols (orthoferrallitic group, Thompson and Purves, 1978; Nyamapfene, 1991). They are generally coarse-grained sandy soils derived from granite, characterized by a kaolinitic clay fraction and free sesquioxides. Less than 5% consists of weatherable material and the soils are heavily leached. They are acidic and nutrient–poor, with low levels of exchangeable bases, nitrogen and extractable phosphorus. The weak cation exchange capacity results from low levels of organic matter and the low-activity clay fraction.

The objective of the original study was to investigate the effectiveness of fire in controlling coppice regrowth of the woody vegetation (Barnes, 1965; Strang, 1974). Originally the area was covered by dense woodland and, before the beginning of the experiment, the vegetation was cleared manually (in 1948) by cutting the woody component at ground level. However, there were no measurements made of either the vegetation or the soils prior to the application of the burning regime. At the start of the experiment, the dense coppice that had grown since 1948 (1.8–4.6 m high with a few large trees) was cut to ground level and the first of the fire treatments started in 1953 (Barnes, 1965).

The fire experiment consisted of a 5 × 2-split plot design plus control plots with replicates in two randomized blocks. Each plot (36 × 60 m) was subdivided into two equal parts of 18 × 60 m. One part was cleared by mattock and both parts were included in the fire frequency trials. The implications of the mattock plus burn treatments are not considered here. The fire treatments

established five burn frequencies. These were burning annually, burning every second year, every third year, every fourth year, and no burn (control plots). Replications were assigned to the longer intervals between fires so that at each frequency there was a plot burned each year. Fires were started late in the dry season, before the spring rain, to achieve as high a burn temperature as possible. The plots were surrounded by a 3 m wide firebreak and grazing was excluded from the area.

The treatments are described and numbered as follows:

- burned annually, started in 1953 (F1)
- burned biennially, started in 1953 (F2)
- burned biennially, started in 1954 (F2)
- triennial burn, started in 1953 (F3)
- triennial burn, started in 1954 (F3)
- triennial burn, started in 1955 (F3)
- four-year burn, started in 1953 (F4)
- four-year burn, started in 1954 (F4)
- four-year burn started in 1956 (F4)
- control, complete protection from fire (F0)

These plots were laid out in two parallel blocks, as illustrated in Figure 1, and lie on a north-facing, gentle slope (*c*. 3 degrees). The fire treatments continued until 1963 when they were temporarily abandoned because of severe damage from cockchafer grubs (Strang, 1974). The fire experiment was finally concluded in 1991 and species abundance was analysed for data collected in 1987, 1988 and 1990. Further measures of basal area and tree height were undertaken later in 2007, 16 years after the last fire treatments.

1 The effect of burning on tree growth
After nine years (1953–62), the growth of trees and regrowth coppice was slight and there was little difference evident between the burn frequencies (Table 1, left). Even with a four-year burn interval there was little sign of a growth in height. The plots that had complete protection from fire showed

the greatest tree growth, height and canopy development by 1962. Clearly burning has had a dramatic impact, though it should be remembered that half of each plot was cleared of woody vegetation before the start of the fire treatments and therefore there was less buffering effect. As previously reported (Campbell *et al*., 1995), fire is the principal agent in preventing regeneration and crippling young stems. Grundy (1992) and Grundy *et al*. (1994) observed that *Brachystegia* and *Julbernadia* increased rapidly after cutting and thereafter more slowly, but there is little evidence from our data that there was much growth during the early years of the experiment. However, later studies (Campbell *et al*., 1995) and our observations from 2007 (Table 1, right), indicate that the three and four-year burn plots had recovered with greater mean heights (14.8–15.6 m) than were present in the control plots (9.5 m) (p < 0.05). These canopies had a similar species composition to the protected plots but a less evolved structure. The height data show no significant variation between treatments. This indicates that the few trees that did survive on the frequently burned plots were large specimens similar in stature to those on the unburned plots.

Brachystegia and *Julbernardia* dominated the plots in 2007. The number of large stems of these two species, as a fraction of the total number of large stems, was 0.89 ± 0.16 for F3, 0.83 ± 0.05 for F4 and 0.98 ± 0.03 for F0. F1 had no large trees (all data refer to live trees >20 cm dbh (diameter at breast height)). There was no significant treatment effect (one-way ANOVA p = 0.89). From the historic notes it appears that this dominance was sustained throughout the experiment. Trees were almost completely absent from annually burned plots even after 16 years (without fire) from the end of the experiment, but were somewhat more abundant in two-yearly and three-yearly burned plots, where they tended to occur as suppressed saplings. *Brachystegia* and *Julbernardia* tend to be fire-sensitive when
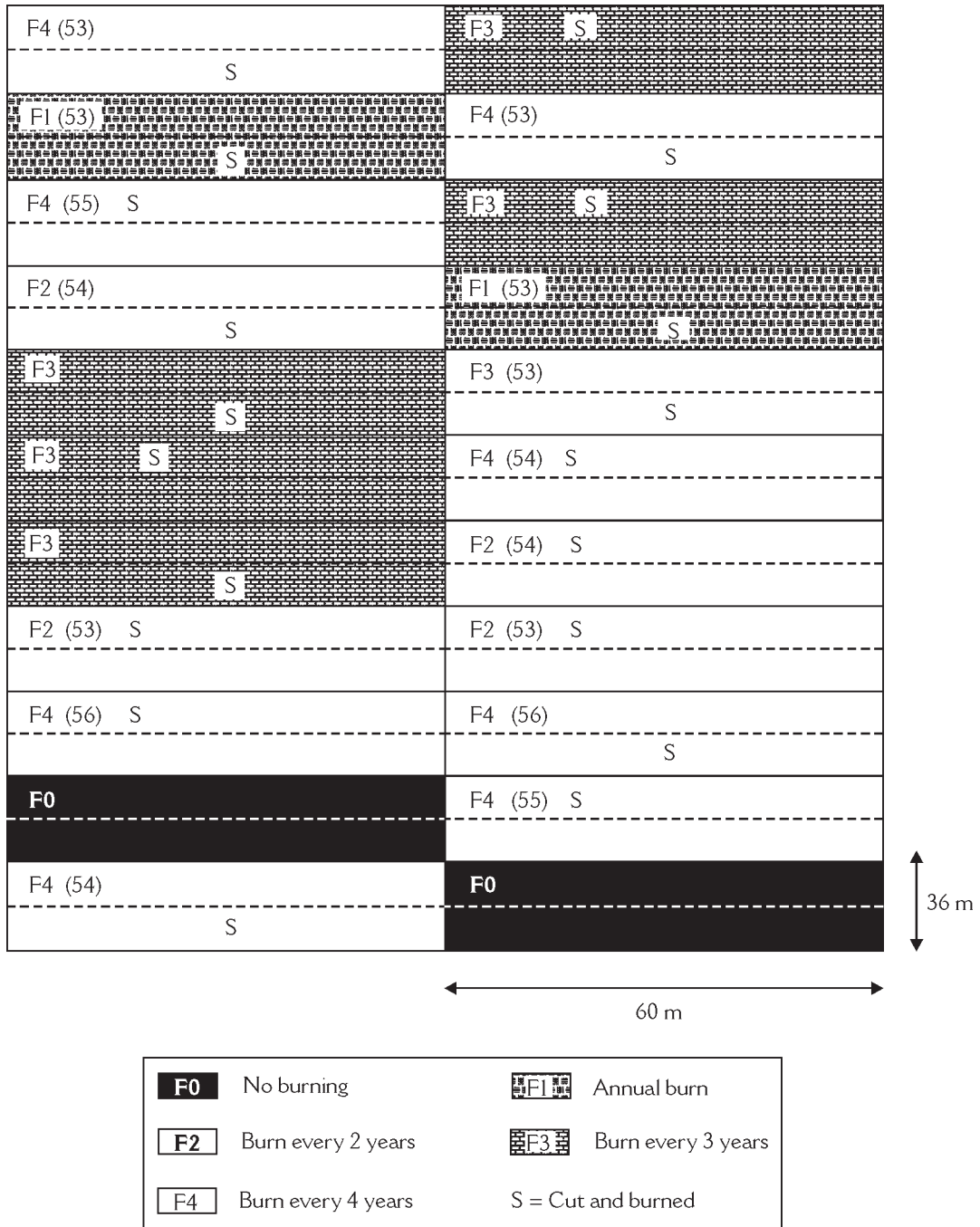
Figure 1 Marondera site plan. The plot numbering begins at the top left (no.1) down the left-hand side to no.11, and continues from the top right down to no.22 in the bottom right-hand corner

Table 1 Effect of frequency of burning on tree height in 1962 and 2007

Fire treatment	Average tree height (m)	
	1962	2007
F0 (protected)	2.83	15.0
F1 (annual burn)	0.18	6.7
F2 (biennial burn)	0.46	11.3
F3 (triennial burn)	0.88	11.2
F4 (quadriennial burn)	0.27	10.6
Significance	$P < 0.01$	$P = 0.46$

young and increasingly tolerant when they grow up to greater canopy height.

The basal area of trees measured in 2007 and stocking density was highest in the quadrennial burn treatment, but due to the high variability within plots, these differences were only significant at $p < 0.1$ (Figure 2). The long intervals between fire (triennial and quadrennial burns) allowed many trees to attain heights and bark thicknesses where they were less susceptible to fire damage, and such observations are consistent with previous studies (eg, Higgins *et al.*, 2007; van Wilgen *et al.*, 2007). The relatively larger trees and biomass in the four-year burn compared with the complete protection treatment may have reflected the response of trees to the release of nutrients resulting from the burning treatments. The small plots, coupled with the intrinsic variability of woodland vegetation structure, means that the replication is critical for detecting differences between treatments. The ANOVA table (both parametric and non-parametric) for plot basal area shows that the variation within treatments, although large, was smaller than between treatments. The 17 replicates were enough to control for this heterogeneity and credit must be given to those who designed this experiment for achieving sufficient replication. This is in contrast to many other long-term experiments in Africa, which were unreplicated.

The floristic composition of the plots was not affected by the burning treatments, with 80–100% of the trees being of the two dominant species. This is in contrast to other long-term fire experiments (eg, Zambia; Trapnell, 1959), where the protected plots in wetter *miombo* conditions were invaded by forest and evergreen species. This may be due to a lack of nearby forest as a source of seeds at Marondera.

2 Effects of fire on herbaceous plants

The composition of herbaceous plant communities was influenced by treatments during the course of the experiment with both increases and decreases in individual species. Some of the grass species flourished after burning, while others decreased. For example, in relative terms, *Hyparrhenia filipendula*, *Heteropogon contortus* and *Eriosema affin* showed significantly higher numbers in burned plots than in protected plots ($p < 0.001$, $p < 0.01$ and $p < 0.01$, respectively). There was no significant difference between the annual burn and the quadrennial burn (Figure 3a). On the other hand, burning significantly reduced the numbers of some grass species such as *Rhynchelytrum nyassanum*, *Digitaria gazensis* and *Eragostis racemosa* ($p < 0.05$) (Figure 3b). At the same time the numbers of other species increased significantly following burning – *Crasspedhorachis qfricana*, *Andropogon* spp. and *Trachypogon spicatus* – but there was no apparent trend (Table 2). This matches some of the observations in Strang (1974), although the trends were not statistically significant. The numbers of sedges and further grass species (such as *Rhytichelytrum repens* and *Nidorela uricrata*) were not significantly affected by the fire treatments. However, while there is evidence that the sedges were reduced by fire, no apparent trend could be discerned for *R. repens* or *N. uricrata* (Table 3). These results parallel conclusions elsewhere illustrating
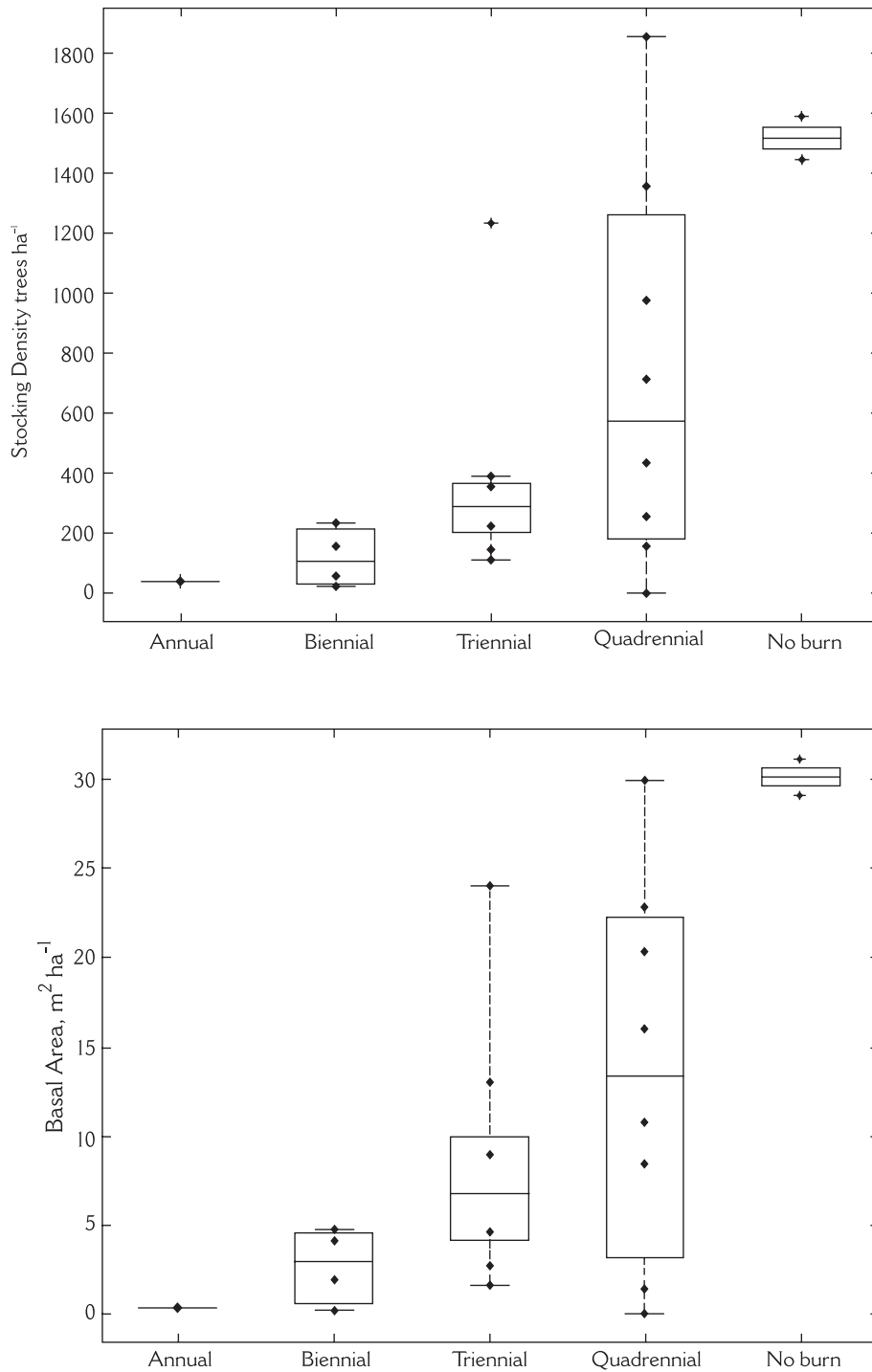
Figure 2   Basal area and stocking density in 2007 for live trees >20 cm dbh
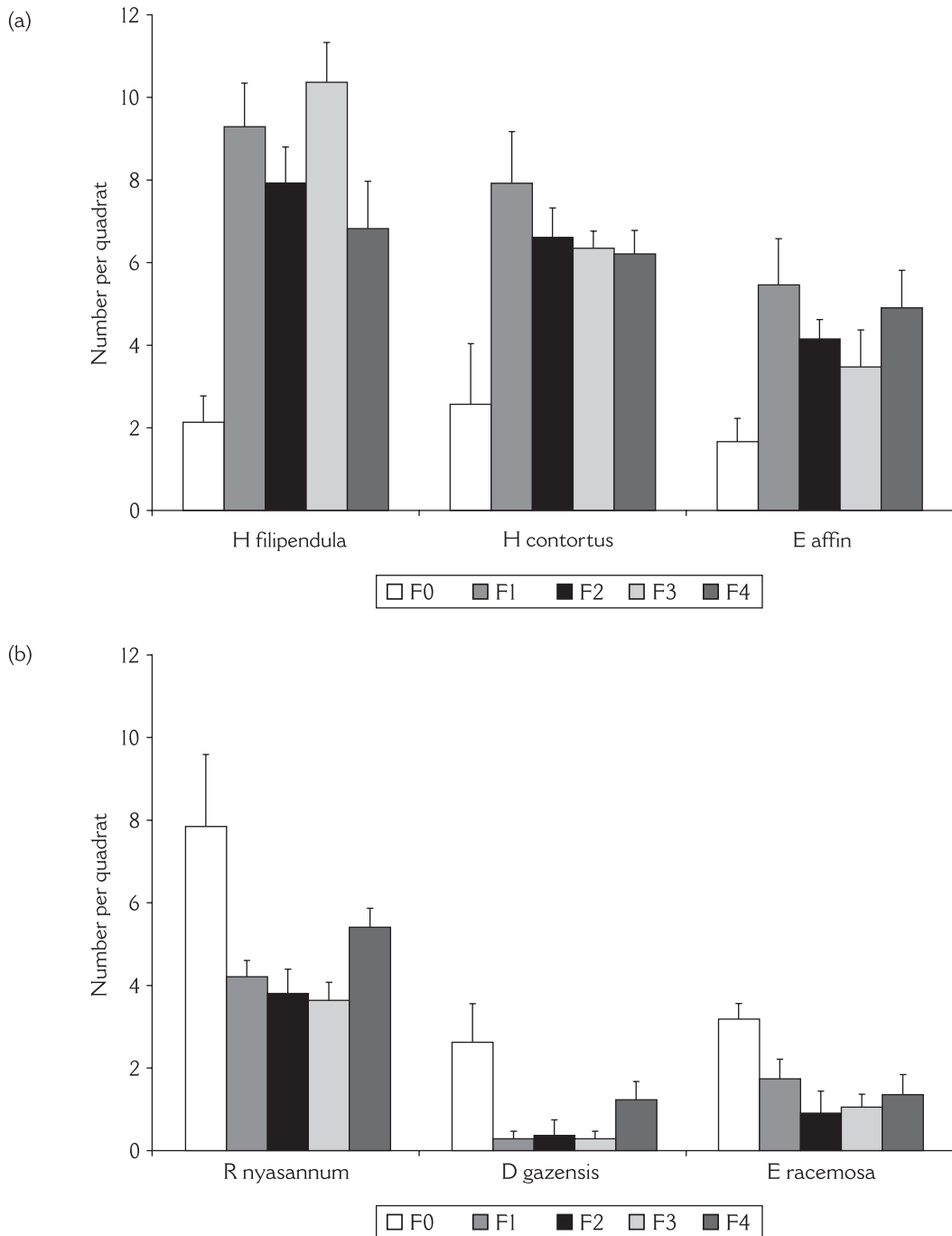
Figure 3   Numbers per quadrat of: (a) *Hyparrhenia filipendula*, *Heteropogon contortus* and *Eriosema affin*; (b) *Rhynchelytrum nyassanum*, *Digitaria gazensis* and *Eragostis racemosa*

Table 2   Effect of frequency of burning on numbers of three grass species

Fire treatment	*Trachypogon spicatus*	*Andropogon* spp.	*Crasspedhorachis africana*
FO	1.13	1.01	2.56
FI	2.24	2.85	3.57
F2	1.02	1.60	7.96
F3	0.33	0.20	5.29
F4	1.93	4.82	3.74
Significance	*	*	*
SED	0.63	0.91	1.34
LSD	1.34	1.96	2.87

*Significant at $p < 0.05$.

Table 3   Effect of frequency of burning on numbers of three selected species

Fire treatment	Sedges	*Rhytichelytrum repens*	*Nidorela uricrata*
FO	3.64	1.89	3.95
FI	0.69	1.93	1.87
F2	1.53	1.59	2.99
F3	1.12	2.74	4.75
F4	1.71	1.76	3.49
Significance	NS	NS	NS

how fires influence the demography of the herbaceous strata (such as Garnier and Dajoz, 2001).

Overall, the preliminary evidence from this long-term experiment indicates that frequent burning (annual, biennial and to a large extent triennial fires) severely inhibits woody plant growth and has a mixed impact on the herbaceous cover (Figure 4). Interestingly, the tree growth in the triennial and quadrennial fire frequencies ends up by being greater than that for the control plots. The results suggest that regeneration following fire is slow and patchy, but that once woody plants have reached a stage where they are relatively resistant to fire *miombo* woodland can develop rapidly. Frost (1996) suggests that this is likely to occur when trees reach 2 m or more. Other research suggests figures of 3 m plus, and other unpublished results in nearby Mozambique suggest that there is a step change in survivorship at 12 cm dbh. The present research indicates that this occurs

after 10 years. The patchiness may reflect the nature and distribution of the pre-fire trial vegetation and its subsequent resprouting, and may indicate small-scale vegetation patterns and nutrient cycling related to factors such as past disturbances or termite mounds (Campbell *et al.*, 1988; 1995; Gill *et al.*, 2003; Traore *et al.*, 2008). This variability in the burning impact is also likely to be the result of increasing bark resistance, lower levels of combustible material and gradual reduction in grass cover (potential comestible load) and therefore less severe fires. Conversely, as the woody cover is removed, so the herbaceous layer is likely to increase (increased light and moisture) leading to a greater fuel load and risk of burning (Gambiza *et al.*, 2000).

While the herbaceous cover predominates under frequent fires, the species composition varies, with a number of characteristic grass species flourishing following fires while others are severely reduced. Similar changes in species composition have been reported
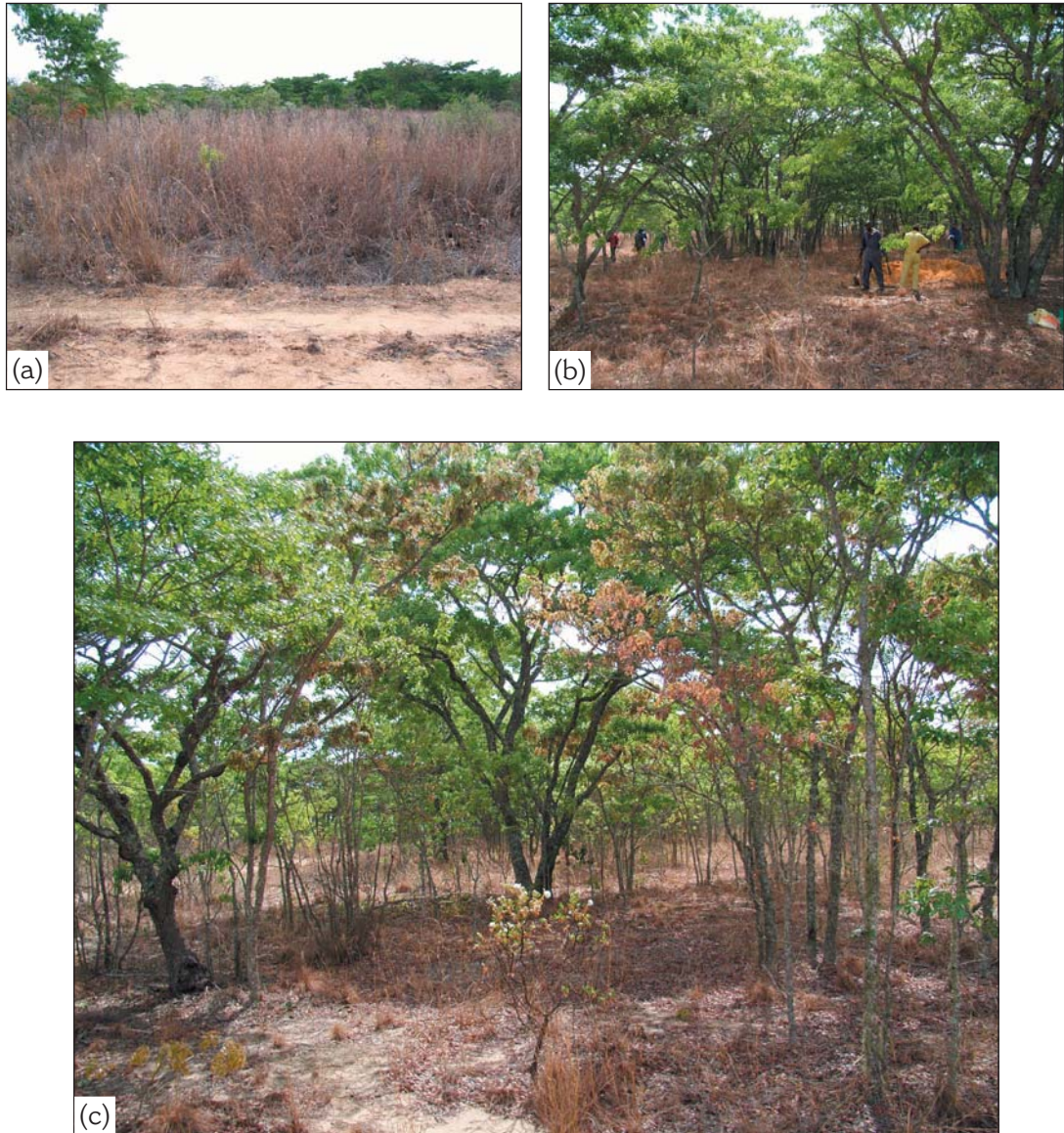
Figure 4 (a) Plot 2 (see Figure 1) of the fire experiment at Marondera after 50 years of annual burning, showing the predominance of grasses and other herbaceous plants with a sparse cover of shrubs. (b) Plot 10 (see Figure 1) of the fire experiment at Marondera after 50 years of complete protection. This is an unburned control plot, showing the plant growth without fire since 1948. (c) Plot 11 (see Figure 1) of the fire experiment at Marondera after 50 years of four-yearly burning, showing the large trees that survived the burns and new cohort of saplings that have grown since the experiment ceased. Note the low grass biomass

Source: All three photographs were taken in 2007 by C.M. Ryan after the close of the experiment and with no further fires from 1997 to 2007.

elsewhere (eg, Hoffman and Moreira, 2002). The economic significance of this, for instance with regard to palatability for livestock (Lowry, 1995; Hassan *et al*., 2008), would be worth further investigation.

VI Conclusions

The value of long-term studies in environmental and ecological research is controversial but the general consensus is that there is much useful information to be derived from well-founded and rigorously controlled fire experiments (Brown *et al*., 2001). While there are many examples of field studies over years or even a few decades, the number of longer fire trials is very low. Marondera represents one of the few studies that have been soundly established and systematically carried out over nearly four decades (1953–91) and in the face of numerous difficulties. The plots have remained intact since the cessation of the fire trails and continue to provide valuable information on regrowth.

The preliminary results for this dry *miombo* savanna woodland are in general accord with other reported work with a few significant additions. Frequent fires (especially annual and biennial) have had a marked impact on the vegetation structure and tree density, reducing the plots to fire-resistant grasses with a scattering of shrubs. A distinct recovery was observable with fire return intervals longer than two years and reseeding, resprouting and coppicing were evident, resulting in a large number of individuals in any of the woody species populations following a number of years without fire. With repeated burning at short return intervals, plant composition changed in that fire-tolerant species became more dominant. Extreme burning over a prolonged period had a persistent effect for long after the fire experiment had ceased. However, since seedlings are generally fire-resistant and regeneration is so effective, it is probable that a fire-free period will enable the species composition to mirror that reported elsewhere and remain relatively constant. This is being investigated at present with resurveys following the termination of the fire trials. The control plots illustrate the likely form of the vegetation structure and plant composition with fire elimination although the greatest growth was reported in the less frequently burned plots.

References

Allen, H.D. 2008: Fire: plant functional types and patch mosaic burning in fire-prone ecosystems. *Progress in Physical Geography* 32, 421–37.

Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J. and **Woinarski, J.C.Z.** 2005: Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga experiment. *Austral Ecology* 30, 155–67.

Andersen, A.N., Cook, G.D. and **Williams, R.J.,** editors 2003: *Fire in tropical savannas: the Kapalga Experiment*. New York: Springer.

Aubreville, A. 1947: *The disappearance of tropical forests of Africa*. Rome: Food and Agriculture Organization of the United Nations (FAO).

Austen, B. 1972: The history of veld burning in the Wankie National Park, Rhodesia. In *Proceedings of the Annual Tall Timbers Fire Ecology Conference* 11, 277–96.

Barnes, D.I. 1965: The effect of frequency of burning and mattocking on the control of coppice in the marandellas sandveld. *Rhodesia Journal of Agricultural Research* 3, 55–56b.

Bennett, L.J., Judd, T.S. and **Adams, M.A.** 2003: Growth and nutrient content of perennial grasslands following burning in semi-arid, sub-tropical Australia. *Plant Ecology* 164, 185–99.

Beringer, J., Hutley, L.B., Tapper, N.G. and **Cernusak, L.A.** 2007: Savanna fires and their impact on net ecosystem productivity in North Australia. *Global Change Biology* 13, 990–1004.

Bird, M.I., Veenendaal, E.M., Moyo, C., Lloyd, J. and **Frost, P.** 2000: Effect of fire and soil texture on soil carbon in a sub-humid savanna (Matapos, Zimbabwe). *Geoderma* 94, 71–90.

Bond, W.J. and **Archibald, S.** 2003: Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire* 12, 381–89.

Bond, W.J. and **Keeley, J.E.** 2005: Fire as a global herbivore: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20, 387–94.

Bond, W.J. and **Midgely, J.J.** 2001: Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16, 45–51.

Bond, W.J. and **van Wilgen, B.W.** 1996: *Fire and plants*. London: Chapman and Hall.

— 2005: The global distribution of ecosystems in a world without fire. *New Phytologist* 165, 525–38.

Bond, W.J., Woodward, F.I. and **Midgley, G.F.** 2005: The global distribution of ecosystems in a world without fire. *New Phytologist* 165, 525–38.

Booyson, P. de V. and **Tainton, N.M.** 1984: *Ecological effects of fire in South African ecosystems*. New York: Springer.

Bowman, D.M.J.S. and **Franklin, D.C.** 2005**:** Fire ecology. *Progress in Physical Geography* 29, 248–55.

Bowman, D.M.J.S. and **Prior, L.D.** 2004: Impact of Aboriginal landscape burning on woody vegetation in *Eucalyptus tetrodonta* savanna in Arnhem Land, northern Australia. *Journal of Biogeography* 31, 807–17.

Bowman, D.M.J.S., Walsh, A. and **Prior, L.D.** 2004: Landscape analysis of Aboriginal fire management in Central Arnhem Land, north Australia. *Journal of Biogeography* 31, 207–23.

Bradstock, R.A., Williams, J.E. and **Gill, A.M.**, editors 2002: *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge: Cambridge University Press.

Braithwaite, R. 1996: Biodiversity and fire in the savanna landscape. In Solbrig, O.T., Medina, E. And Silva, J.A., editors, *Biodiversity and savanna ecosystem processes,* New York: Springer, 121–42.

Brookman-Amissah, J., Hall, J.B., Swaine, M.D. and **Attakorah, J.Y.** 1980: A re-assessment of a fire protection experiment in northeastern Ghana savanna. *Journal of Applied Ecology* 17, 85–99.

Brown, J.H., Whitham, T.G., Ernest, S. and **Gehring, C.** 2001: Complex species interactions and dynamics of ecological systems: long term experiments; ecology through time. *Science* 293, 643–49.

Caldwell, A.E. and **Zieger, U**. 2000: A reassessment of the fire tolerance of some miombo species in Central province, Zambia. *African Journal of Ecology* 38, 138–46.

Campbell, B.M., Cunliffe, R.N. and **Gambiza, J**. 1995: Vegetation structure and small-scale pattern in miombo woodland, Marondera, Zimbabwe. *Bothalia* 25, 121–26.

Campbell, B.M., Frost, P., King, J.A., Mawanza, M. and **Mhlanga, L.** 1994: The influence of trees on soil fertility on 2 contrasting semiarid soil types at Matapos, Zimbabwe. *Agroforestry Systems* 28, 159–72.

Campbell, B.M., Swift, M.J., Frost, P.G.H. and **Kirchmann, H**. 1998: Comparative ecosystem characteristics of a miombo woodland and an adjacent agricultural field. In Bergstrom, L. and Kirchmann, H, editors, *Carbon and nutrient dynamics in natural and agricultural tropical ecosystems,* Wallingford: CAB International, 201–26.

Campbell, B.M., Swift, M.J., Hatton, J.C. and **Frost, P.G.H.** 1988: Small-scale vegetation pattern and nutrient cycling in miombo woodland. In Verhoeven, J.T.A., Heil, G.W and Werger, M.J.A., editors, *Vegetation structure in relation to carbon and nutrient economy,* The Hague: SPB Academic Publishing, 69–85.

Charter, J.R. and **Keay, R.W.J.** 1960: Assessment of the Olokomeji fire control experiment 28 years after institution. *Nigerian Forestry Information Bulletin* 3, 1–32.

Chidumayo, E.N. 1988: A re-assessment of the effects of fire on miombo regeneration in the Zambian copperbelt. *Journal of Tropical Ecology* 7, 430–38.

— 1997: *Miombo ecology and management*. Stockholm: Stockholm Environment Institute.

Chidumayo, E.N., Gambiza, J. and **Grundy, I.** 1996: Managing miombo woodlands. In Campbell, B.M. editor, *The miombo in transition: woodlands and welfare in Africa,* Bogor, Indonesia: Center for International Forestry Research (CIFOR), 175–93.

Chongo, D., Nagasawa, R. and **Ahmed, A.O.C.** 2007: Fire monitoring in savanna ecosystems using MODIS data: a case study of Kruger national park, South Africa. *Landscape and Ecological Engineering* 3, 79–88.

Coutinho, L.M. 1982: Ecological effects of fire in Brazilian cerrados. In Huntley, B.J. and Walker, B.H., editors, *Ecology of tropical savanna,* Berlin: Springer, 273–91.

— 1990: Fire in the ecology of the Brazilian cerrados. In Goldammer, J.G., editor, *Fire in the tropical biota: ecosystem processes and global challenges,* Berlin: Springer, 82–105.

da Silva, D.M. and **Batalha, M.** 2008: Soil-vegetation relationships in cerrados under different fire frequencies. *Plant and Soil* 311, 87–96.

du Toit, J., Rogers, K.H. and **Biggs, H.C.**, editors 2003: *The Kruger experience: ecology and management of savanna heterogeneity*. New York: Island Press.

Dyer, R. and **Smith, M.S.** 2003: Ecological and economic assessment of prescribed burning impacts in semi-arid pastoral lands of northern Australia. *International Journal of Wildland Fire* 12, 403–13.

Dyer, R., Jacklyn, P., Partridge, I., Russell-Smith, J. and **Williams, D.,** editors 2001: *Savanna burning: understanding and using fire in northern Australia*. Darwin: Tropical Savannas CRC.

Edwards, A., Kennett, R., Price, O., Russell-Smith, J., Spiers, G. and **Woinarski, J.** 2003: Monitoring the impacts of fire regimes on vegetation in northern Australia: an example from Kakadu National Park. *International Journal of Wildland Fire* 12, 427–40.

Eiten, G. 1972: The cerrado vegetation of Brazil. *Botany Review* 38, 201–341.

Eldroma, E.L. 1984**:** Effects of burning and grazing on the productivity and number of plants in the Queen Elizabeth National Park, Uganda. *African Journal of Ecology* 22, 165–74.

Enslin, B.W., Potgieter, A.L.F., Biggs, H.C. and **Biggs, R.** 2000: Long term effects of fire frequency and season on the woody vegetation dynamics of the *Sclerocarya birrea/Acacia nigrescens* savanna of the Kruger National Park. *Koedoe* 43, 27–37.

Felderhof, L. and **Gillieson, D.** 2006: Comparison of fire patterns and fire frequency in two tropical savanna bioregions. *Austral Ecology* 31, 736–46.

Felfily, J.M., Rezende, A.V. and **Silva Junior, M.C**. 2000: Changes in floristic composition of cerrados sensu stricto in Brazil over a 9-year period. *Journal of Tropical Ecology* 16, 576–90.

Fensham, R.J., Fairfax, R.J., Butler, D.W. and **Bowman, D.M.J.S**. 2003: Effects of fire and drought in a tropical eucalypt savanna colonized by rain forest. *Journal of Biogeography* 30, 1405–14.

Ferguson, K. 1998: The effects of fire on shrub survival in Mkomazi. In Coe, M., McWilliam, N., Stone, G. and Packer, M., editors, *Mkomazi: the ecology, biodiversity and conservation of a Tanzananian savanna*. London: Royal Geographical Society, 159–70.

Frost, P.G.H. 1996: The ecology of miombo woodlands. In Campbell, B.M., editor, *The miombo in transition: woodlands and welfare in Africa*, Bogor, Indonesia: Center for International Forestry Research (CIFOR), 11–57.

Frost, P.G.H. and **Robertson, F.** 1987: The ecological effects of fire in savannas. In Walker, B.H., editor, *Determinants of savannas*, Oxford: IRL Press.

Furley, P.A. 1996: The influence of slope on the nature and distribution of soils and plant communities in the central Brazilian cerrado. In Anderson, M.G. and Brooks, S.M., editors, *Advances in hillslope processes*, volume 1, Chichester: Wiley, 327–46.

— 1999: The nature and diversity of neotropical savanna vegetation with particular reference to the Brazilian cerrados. *Global Ecology and Biogeography* 8, 223–41.

Furley, P.A., Proctor, J. and **Ratter, J.A.** 1992: *Nature and dynamics of forest-savanna boundaries*. London: Chapman and Hall.

Gambiza, J., Bond, W., Frost, P.G.H. and **Higgins, S.** 2000: A simulation model of miombo woodland dynamics under different management regimes. *Ecological Economics* 33, 353–68.

Gambiza, J., Campbell, B.M., Moe, S.R. and **Frost, P.G.H**. 2005: Fire behaviour in a semi-arid *Baikiaea plurijuga* savanna woodland on Kalahari sands in western Zimbabwe. *South African Journal of Science* 101, 239–44.

Garnier, L.K.M. and **Dajoz, I**. 2001: The influence of fire on the demography of a dominant grass species of West African savannas, *Hyparrhenia diplandra, Journal of Ecology* 89, 200–208.

Gashaw, M. and **Michelsen, A**. 2002: Influence of heat shock on seed germination from regularly burnt savanna woodlands and grasslands in Ethiopia. *Plant Ecology* 159, 83–93.

Gignoux, J., Clobert, J. and **Menault, J.-C.** 1997: Alternative fire resistance strategies in savanna trees. *Oecologia* 110, 576–83.

Gill, A.M., Allan, G. and **Yates, C.** 2003: Fire-created patchiness in Australian savannas. *International Journal of Wildland Fire* 12, 323–31.

Goodland, R. and **Pollard, R.** 1973: The Brazilian cerrado vegetation: a fertility gradient. *Journal of Ecology* 61, 219–24.

Govender, N., Trollope, W.S.W. and **van Wilgen, B.W.** 2006: The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43, 748–58.

Grundy, I.M. 1992: Regeneration of *Brachystegia spiciformis* and *Julbernardia globiflora* in Zimbabwean miombo woodland. In Piearce, G.D. and Gumbo, D.J. editors, *The ecology and management of indigenous forests in southern Africa,* Symposium Proceedings, Victoria Falls, Harare: Zimbabwe Forestry Commission and SAREC, 191–96.

Grundy, I.M., Campbell, B.M. and **Frost, P.G.H.** 1994: Spatial pattern, regeneration and growth-rates of *Brachystegia spiciformis* and *Julbernardia globiflora*. *Vegetatio* 115, 101–107.

Hartnett, D.C., Potgieter, A.L.F. and **Wilson, G.W.T.** 2004: Fire effects on mycorrhizal symbiosis and root systems architecture in southern African savanna grasses. *African Journal of Ecology* 42, 328–37.

Hassan, S.N., Rusch, G.M., Hytteborn, H., Skarpe, C. and **Kikula, I.** 2008: Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *African Journal of Ecology* 46, 174–85.

Heinl, M., Sliva, J., Murray-Hudson, M. and **Tacheba, B.** 2007: Post-fire succession on savanna habitats in the Okavango delta wetland, Botswana. *Journal of Tropical Ecology* 23, 705–13.

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. and **Trollope, W.S.W.** 2007: Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88, 1119–25.

Hoffman, W.A. 1999: Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80, 1354–69.

— 2002: Direct and indirect of fire on radial growth of cerrados savanna trees. *Journal of Tropical Ecology* 18, 137–42.

Hoffman, W.A. and **Moreira, A.G.** 2002: The role of fire in population dynamics of woody plants. In Oliveira, P.S. and Oliveira, R.J., editors, *The cerrados of Brazil*, New York: Columbia University Press, 159–77.

Hoffman, W.A. and **Solbrig, O.T**. 2003: The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180, 273–86.

Hoffman, W.A., Orthen, B. and **do Nascimento, P.K.V**. 2003: Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology* 17, 720–26.

Högberg, P. 1992: Root symbiosis of trees in African dry tropical forests. *Journal of Vegetation Science* 3, 393–400.

Holdo, R.M. 2005: Stem mortality following fire in Kalaharis and vegetation: effects of frost, prior damage and tree neighbourhoods. *Plant Ecology* 180, 77–86.

Hopkins, B. 1965: Observations on savanna burning in the Olokemeji Forest Reserve, Nigeria. *Journal of Applied Ecology* 2, 367–81.

Hudak, A.T., Fairbanks, D.H.K. and **Brockett, B.H**. 2004: Trends in fire patterns in a southern African savanna under alternative land use practices. *Agriculture Ecosystems and Environment* 101, 307–25.

Kennan, T.C.D. 1972: The effects of fire on two vegetation types at Matopos, Rhodesia. In *Proceedings of the Annual Tall Timbers Fire Ecology Conference* 11, 53–98.

Kennedy, A.D. and **Potgieter, A.L.F.** 2003: Fire season affects size and architecture of *Colophospermum mopane* in southern African savannas. *Plant Ecology* 167, 179–92.

Laris, P. and **Wardell, D.A.** 2006: Good, bad or 'necessary' evil? Re-interpreting the colonial burning experiments in the savanna landscapes of West Africa. *The Geographical Journal* 172, 271–90.

Lawton, R.M. 1978: A study of the dynamic ecology of Zambian vegetation. *Journal of Ecology* 66, 175–98.

Lentile, L.B., Holden, Z.A., Smith, A.M.S., Falkowski, M.J., Hudak, A.T., Morgan, P., Lewis, S.A., Gessler, P.E. and **Benson, N.C.** 2006: Remote sensing techniques to assess active fire characteristics and post-fire effects. International *Journal of Wildland Fire* 15, 319–45.

Liedloff, A.C., Coughenour, M.B., Ludwig, J.A. and **Dyer, R.** 2001: Modelling the trade-off between fire and grazing in a tropical savanna landscape, northern Australia. *Environment International* 27, 173–80.

Lock, J.M. 1977: Preliminary results from fire and elephant exclusion plots in Kabalega National Park, Uganda. *East African Wildlife Journal* 15, 229–32.

Lonsdale, W.M. and **Braithwaite, R.W.** 1991: Assessing the effects of fire in tropical savannas. *Austral Ecology* 16, 363–74.

Lopes, A.S. and **Cox, E.R.** 1977a: A survey of the fertility status of surface soils under cerrados vegetation in Brazil. *Soil Science Society of America Journal* 41, 742–47.

— 1977b: Cerrado vegetation in Brazil: an edaphic gradient. *Agronomy Journal* 69, 828–31.

Louppe, D., Oattara, N. and **Coulibaly, A.** 1995: The effects of brush fires on vegetation: the Aubreville fire plots after 60 years. *Commonwealth Forestry Review* 74, 288–92.

Lowry, J.B. 1995: Deciduous trees: a dry season feed resource in Australian tropical woodlands? *Tropical Grasslands* 29, 13–17.

Medeiros, M.B. and **Miranda, H.S.** 2008: Post-fire resprouting and mortality in cerrados woody plant species over a three-year period. *Edinburgh Journal of Botany* 65, 53–68.

Menault, J.C. and **Cesar, J.** 1982: The structure and dynamics of a West African Savanna. In Huntley, B.J. and Walker, B.H., editors, *Ecology of tropical savannas,* New York: Springer, 80–100.

Miao, S., Carstenn, S. and **Nungesser, M.**, editors 2009: *Real world ecology: large-scale and long-term case studies and methods*. Berlin: Springer, in press.

Miranda, H.S., Bustamente, M.M.C. and **Miranda, A.C.** 2002: The fire factor. In Oliveira, P.S. and Oliveira, R.J., editors, *The cerrados of Brazil*, New York: Columbia University Press, 51–68.

Mistry, J. 1988: Fire in the cerrados (savannas) of Brazil: an ecological review. *Progress in Physical Geography* 22, 425–48.

Moreira, A.G. 2000: Effects of fire protection on savanna structure in Central Brazil. *Journal of Biogeography* 27, 1021–29.

Müller, S.C., Overbeck, G.E., Pfadenhauer, J. and **Pillar, V.D.** 2007: Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* 189, 1–14.

Nangendo, G., Stein, A., ter Steege, H. and **Bongers, F.** 2005: Changes in woody plant composition of three vegetation types exposed to a similar fire regime for over 46 years. *Forest Ecology and Management* 217, 351–64.

Nefabas, L.L. and **Gambiza, J.** 2007: Fire tolerance mechanisms of common woody plant species in a semi-arid savanna in south-western Zimbabwe. *African Journal of Ecology* 45, 550–56.

Nyamapfene, K. 1991: *Soils of Zimbabwe*. Harare: Nehanda Publishers.

Oliveira-Filho, A.T. and **Ratter, J.A.** 2002: Vegetation physiognomies and woody flora of the cerrado biome. In Oliveira, P.S. and Marquis, R.J., editors, *The cerrados of Brazil*, New York: Columbia University Press, 91–120.

Palacios-Orueta, A., Chuvieco, E., Parra, A. and **Carmona-Moreno, C.** 2004: Remote sensing and geographic information systems methods for global spatiotemporal modelling of biomass burning emissions: assessment in the African continent. *Journal of Geophysical Research – Atmospheres* 109, D14SO9.

— 2005: Biomass burning emissions: a review of models using remote-sensing data. *Environmental Monitoring and Assessment* 104, 189–209.

Preece, N. 2002: Aboriginal fires in monsoonal Australia from historical accounts. *Journal of Biogeography* 29, 321–36.

Price, O., Edwards, A., Connors, G., Woinarski, J., Ryan, G., Turner, A., and **Russell-Smith, J.** 2005: Fire heterogeneity in Kakadu national park, 1980–2000. *Wildlife Research* 32, 425–33.

Prior, L.D., Brook, B.W., Williams, R.J., Werner, P.A., Bradshaw, C.J.A. and **Bowman, D.M.J.S.** 2006: Environmental and allometric drivers of tree growth rates in a north Australian savanna. *Forest Ecology and Management* 234, 164–80.

Quesada, C.A., Hodnett, M.G., Breyer, L.M., Santos, A.J.B., Andrade, S., Miranda, H.S., Miranda, A.C. and **Lloyd, J.** 2008: Seasonal variations in soil water in two woodland savannas of central Brazil with different fire history. *Tree Physiology* 28, 405–15.

Radford, I.J, Nicholas, D.M. and **Brown, J.R.** 2001: Impact of prescribed burning on *Acacia nilotica* seed banks and seedlings in northern Australia. *Journal of Arid Environments* 49, 795–807.

Ramsay, J.M. and **Rose Innes, R.** 1963: Some quantitative observations on the effects of fire on the Guinea savanna vegetation of northern Ghana over a period of eleven years. *African Soils* 8, 41–85.

Ratter, J.A. 1992: Transitions between cerrado and forest vegetation in Brazil. In Furley P.A., Proctor J. and Ratter, J.A., editors, *Nature and dynamics of forest-savanna boundaries*, London: Chapman and Hall, 417–29.

Rees, R.M., Wuta, M. and **Furley, P.A.** 2006: Nitrous oxide fluxes from savanna (miombo) woodlands in Zimbabwe. *Journal of Biogeography* 33, 424–37.

Roitman, I., Felfili, J.M. and **Rezende, A.V.** 2008: Tree dynamics of a fire-protected cerrados sensu stricto surrounded by forest plantations, over a 13-year period (1991–2004) in Bahia, Brazil. *Plant Ecology* 197, 255–67.

Rose Innes, R. 1971: Fire in West African vegetation. In *Proceedings of the Annual Tall Timbers Fire Ecology Conference* 11, 147–73.

Rossiter, N.A., Setterfield, S.A., Douglas, M.M. and **Hutley, L.B.** 2003: Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* 9, 169–76.

Russell-Smith, J., Whitehead, P.J., Cook, G.D. and **Hoare, J.L.** 2003a: Response of eucalyptus-dominated savanna to frequent fires: lessons from Munmarlary 1973–1996. *Ecological Monographs* 73, 349–75.

Russell-Smith, J., Yates, C., Edwards, A., Cook, G.D., Cooke, P., Craig, R., Heath, B. and **Smith, R.** 2003b: Contemporary fire regimes of northern Australia, 1997–2001: change since Aboriginal occupancy, challenges for sustainable development. *International Journal of Wildland Fire* 12, 283–97.

San José, J.J. and **Fariñas, M.R.** 1983: Changes in tree density and species composition in a protected *Trachypogon* savanna protected for 25 years. *Acta Oecologica* 12, 237–47.

— 1991: Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years. *Acta Oecologica* 12, 237–48.

San José, J.J. and **Montes, R.A.** 1997: Fire effect on the coexistence of trees and grasses in savannas and the resulting outcome on organic matter budget. *Interciencia* 22, 289–98.

Sankaran, M., Ratnam, J. and **Hanan, N**. 2008: Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17, 236–45.

Santos, A.J.B., Silva, G.T.D.A., Miranda, H.S., Miranda, A.C. and **Lloyd, J.** 2003: Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in Central Brazil. *Functional Ecology* 17, 711–19.

Savadogo, P., Zida, D., Sawadogo, L., Tiveau, D., Tigabu, M. and **Oden, P.C.** 2007: Fuel and fire characteristics in a savanna-woodland of West Africa in relation to grazing and dominant grass type. *International Journal of Wildland Fire* 16, 531–39.

Scholes, R.J., Bond, W.J. and **Eckhardt, H.C.** 2003: Vegetation dynamics in the Kruger ecosystem. In Du Toit, J., Rogers, K.H. and Biggs, H.C., editors, *The Kruger experience: ecology and management of*

savanna heterogeneity, New York: Island Press, 242–62.

Schroeder, W., Morisette, J.T., Csiszar, I., Giglio, L., Morton, D. and **Justice, C.** 2005: Characterizing vegetation fire dynamics in Brazil through multisatellite data: common trends and practical issues. *Earth Interactions* 9(13), 1–26.

Schroeder, W., Prins, E., Giglio, L., Csiszar, I., Schmidt, C., Moritte, J. and **Morton, D.** 2008: Validation of GOES and MODIS active fire detection products using ASTER and ETM-plus data. *Remote Sensing of the Environment* 112, 2711–26.

Schultz, M.G., Heil, A., Hoelzemann, J.J., Spessa, A., Thonicke, K., Goldammer, J.G., Held, A.C., Pereira, J.M.C. and **van het Bolscher, M.** 2008: Global wildland fire emissions from 1960 to 2000. *Global Biogeochemical Cycles* 22, GB2002, DOI: 10.1029/2007GB003031.

Shackleton, C.M. and **Scholes, R.J.** 2000: Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. *Koedoe* 43, 75–81.

Silva, J.F., Zambrano, A. and **Fariñas, M.R.** 2001: Increase in the woody component of seasonal savannas under different fire regimes in Calabozo, Venezuela. *Journal of Biogeography* 28, 977–83.

Strang, R.M. 1974: Some man-made changes in successional trends on the Rhodesian highveld. *Journal of Applied Ecology*, 11, 249–63.

Swaine, M.D. 1992: Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* 3, 365–74.

Swaine, M.D., Hawthorne, W.D. and **Orgle, T.K.** 1992: The effects of fire exclusion on savanna vegetation at Kpong, Ghana. *Biotropica* 24, 166–72.

Thompson, J.G. and **Purves, W.D.** 1978: *A guide to the soils of Rhodesia*. Rhodesia Agricultural Journal Technical Handbook 3, Salisbury.

Traore, S., Nygard, R., Guinko, S. and **Lepage, M.** 2008: Impact of *Macrotermes termitaria* as a source of heterogeneity on tree diversity and structure in a Sudanian savannah under controlled grazing and annual prescribed fire (Burkina Faso). *Forest Ecology and Management* 255, 2337–46.

Trapnell, C.G. 1959: Ecological results of woodland burning in Northern Rhodesia. *Journal of Ecology* 47, 129–68.

Trollope, W.S.W. 1984: Fire in savanna. In Booysen, P. de V. and Tainton, B.M. editors, *Ecological effects of fire in South African ecosystems*, Berlin: Springer, 149–75.

— 1982: Ecological effects of fire in South African savannas. In Huntley, B.J. and Walker, B.H., editors, *Ecology of tropical savannas*, Berlin: Springer, 292–306.

Trollope, W.S.W., Potgieter, A.L.F. and **Zambatis, N.** 1995: Effect of fire intensity on the mortality and topkill of bush in the Kruger National Park in South Africa. *Bulletin of the Grassland Society of Southern Africa* 6, 66.

van de Vijver, C.A.D.M., Foley, C.A. and **Olff, H.** 1999: Changes in the woody component of an East African savanna during 25 years. *Journal of Tropical Ecology* 15, 545–64.

van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., van de Koppel, J., de Ridder, N., van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. and **Rietkerk, M.** 2003: Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84, 337–50.

van Wilgen, B.W., Govender, N. and **Biggs, H.C**. 2007: The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *International Journal of Wildland Fire* 16, 519–30.

van Wilgen, B.W., Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F. and **Brockett, B.H.** 2003: Fire as a driver of ecosystem variability. In Du Toit, J., Rogers, K.H. and Biggs, H.C., editors, *The Kruger experience: ecology and management of savanna heterogeneity*, New York: Island Press, 149–70.

Verbesselt, J., Somers, B., Lhermitte, S., Jonckheere, I., van Aardt, J. and **Coppin, P.** 2007: Monitoring herbaceous fuel moisture content with SPOT VEGETATION time series for fire risk prediction in savanna. *Remote Sensing of Environment* 108, 357–68.

Vogl, R.J. 1974: Effects of fire on grasslands. In Kozlowski, T.T.T. and Ahlgren, C.E., editors, *Fire and ecosystems,* New York: Academic Press, 7–45.

West, O. 1972: Fire, man and wildlife as interacting factors limiting the development of climax vegetation in Rhodesia. *Proceedings of the Tall Timbers Fire Ecology Conference* 11, 121–46.

Whitehead, P.J., Russell-Smith, J. and **Woinarski, J.C.Z.** 2005: Fire, landscape heterogeneity and wildlife management in Australia's tropical savannas: introduction and overview. *Wildlife Research* 32, 369–75.

Williams, M., Ryan, C.M., Rees, R.M., Sarnbane, E., Fernando, J. and **Grace, J.** 2008: Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique. *Forest Ecology and Management* 254, 145–55.

Williams, P.R., Congdon, R.A., Grice, A.C. and **Clarke, P.J.** 2003a: Fire related cues break seed dormancy of six legumes of tropical eucalyptus savannas in north-east Australia. *Austral Ecology* 28, 507–14.

— 2003b: Effect of fire regime on plant abundance in a tropical eucalypt savanna of north-eastern Australia. *Austral Ecology* 28, 327–38.

— 2004: Soil temperature and depth of legume germination during early and late dry season fires in a tropical eucalypt savanna of north-eastern Australia. *Austral Ecology* 29, 258–63.

Williams, R.J., Woinarski, C.J.Z. and **Andersen, A.N.** 2003: Fire experiments in northern Australia: contributions to ecological understanding and biodiversity conservation in tropical savannas. *International Journal of Wildland Fire* 12, 391–402.

Woinarski, J.C.Z., Risler, J. and **Kean, L.** 2004: Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical *Eucalyptus* open forest, Northern territory, Australia. *Austral Ecology* 29, 156–76.

Woods, D., Potgieter, A., Landmann, T. and **Govender, N.** 2002: Fire policy. Experiments and experience in the Kruger National Park, South Africa. Southern African fire network (SAFNet). Gaborone, Botswana. *South African Journal of Science* 96, 167–78.

Appendix 2. Fire and finance in rural Mozambique

By Casey Ryan

Sabado Joaquim and his team of 10 friends and family get paid 8 000 Mts (£160) to do a straightforward job. They cut two parallel meter-wide strips of grass and then burn the vegetation between them. In doing so, they create a fire break about 50 meters wide, one that should, with a bit of luck, stop the woodlands in which they live from burning this year. The fire break encircles the woodlands and village of N'hambita, in central Mozambique, where an combination of subsistence farmers, high finance, ecology and fire is being fused into a rural development project with a difference.

The project is pioneering a new commercial opportunity opened up by the commodification of our increasingly warm atmosphere – or carbon finance – and is using this to fund rural development in the world's eighth poorest country. In return for protecting their woodlands and planting trees, the people of N'hambita are being paid by carbon emitters in London and California. Sabado's work is part of that, and his salary a small part of the rapidly growing voluntary carbon offset market.

Sabado's life has followed most of Mozambique's calamitous recent past. Born in 1944, his family lived by growing maize and millet in two hectare fields. As the Portuguese tried to jump start the economy of their increasingly unwilling colony, he got a job in 1964 as a tractor driver at a commercial farm 100 km away. But the wheels soon came off the Portuguese empire, and, forced by a combination of a guerrilla independence war and unrest at home, the Portuguese left Mozambique in a hurry, pausing only to pour concrete down the drains of their houses and dismantle any infrastructure they could.

Sabado and most of the farm workers stayed on at the farm, but switched from industrial cotton production to subsistence farming with a hoe.

Mozambique's birth as an independent nation was a difficult one – opposition to the socialist liberation movement, eagerly supported and armed by the *apartheid* regime in South Africa and the cold warriors in Washington DC, spiralled into civil war. Sabado returned home and started a family, continuing to subsist on what they grew and selling any surplus to buy soap and salt. As the civil war intensified, both sides marrauded through N'hambita fighting for control of the nearby larder and national park as well as the supply route to Rhodesia. "When we had food we gave them food, and when we had money we gave them money"

10   said Sabado, but he and all his friends had family executed by the guerrillas. The final straw came in 1987, when, with the war still raging, the crops failed. Normally way above head height, with only a quarter of the normal rainfall the maize and millet grew less than half a meter. Sabado and his family, along with most of the population of N'hambita, left the area for a internal refugee camp near the remains of the farm where Sabado had learnt to drive a tractor.

Mozambique has no oil or diamonds that might have fuelled the conflict, and with the collapse of the Soviet Union and the end of the *apartheid* regime, the civil war spluttered out, allowing the start of a successful

20   reconciliation process and relatively fair elections in 1994. The people of N'hambita reassembled back in their village and resumed farming on their land.

Conserving forests and woodlands has never been so high up the political agenda and blending this aim with the rehabilitation of N'hambita became the challenge of a project linking ecologists at the University of Edinburgh with a new company called Envirotrade. From the G8 to the IPCC, and even some of the royal family, stemming deforestation is seen as one of the easier ways to reduce our greenhouse emissions. This is the origin of Sabado's new-found employment and it is an 'efficient'

30   economist's dream come true. To reduce emissions where it costs least,

companies buy carbon emission offsets from projects such as the one in N'hambita, and continue their emissions. The net effect is no extra greenhouse gas emissions; the concentration of greenhouse gases in the atmosphere isn't reduced, but it stops rising so fast. Stabilising concentrations requires rapid reductions in emissions, but offsetting is seen by some as a useful stop gap while we learn to decarbonise our economy.

The N'hambita project tries to use the flow of money from North to South to do more than offset emissions. The carbon finance is used as a catalyst for rural development and community management of natural resources. It is from the businesses of London and California that money flows into the project and ultimately, to Sabado and his crew to cut the fire breaks. The idea behind avoided deforestation projects such as these is straightforward – if you preserve a forest that was threatened with destruction then you have stopped the emission of the carbon in the wood to the atmosphere. Dry wood is 50% carbon and the world's woodlands and forest and their soils contain much more carbon than the atmosphere. This means that the atmospheric concentration is very sensitive to changes in the amount stored in the biosphere.

It all adds up to a scientific case for protecting woodlands to slow climate change: in areas with rampant degradation and loss of woodlands, establishing projects that conserve woodlands is a way of earning emissions offsets that can be traded. Using carbon finance to fund community development is a idea that is taking hold. There are now projects all over Africa and South America that are based on voluntary carbon offsets, and international NGOs are moving towards the idea.

So the N'hambita project set out to protect the woodlands and bring new opportunities into the community. Creating jobs is the primary way of protecting the trees – a salaried worker doesn't need to grow crops to survive and so doesn't clear any new land. In addition, the project runs a

tree nursery that provides seedling to farmers. The species chosen all have uses that make them attractive to farmers – mangos and cashews provide fruit and cash income, others fix nitrogen from the air and help fertilise the soil, leading to better crop yields. To bridge the gap until the trees are large enough to bear fruit, the farmers are paid for the anticipated carbon that will be sequestered as the trees grow. In return they have to ensure that the trees are growing well and their lands are not burned. To provide further income for the community, the project is also claiming avoided deforestation carbon credits for some areas of the community's land. This means curbing the deforestation by charcoal producers and creating fire breaks.

So why fire breaks? Tropical deforestation conjures up images of desolate charred wastelands on the edge of the Amazon – forest razed to the ground for soya or cattle production. But although this is a real enough process, there is another story of deforestation that is quieter and more insidious.

The woodlands and savannas that span the gap between the tropical forests and the deserts of the southern hemisphere are an ecological paradox. Trees and grass are competing life forms and normally one excludes the other. A forest floor is too shaded for grass to grow, and a grassland is too dense or dry for tree seedlings to establish. But savannas hold the dominance of both in check, and, with wildly varying and dynamic results, they support a continuous grass layer and a scattering of trees. The tree layer can be dense or very sparse, with rainfall, soil, nutrients, human use and luck all affecting the final composition. Savannas are dry places – most receive rainfall for only part of the year – but what resources they have are readily available to animals and humans. The grass provides grazing for an enormous diversity and abundance of large wildlife that tropical forests, with their fruit and seeds 30m above ground, cannot rival. The ability to follow the herds of

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antelope, wildebeest and buffalo, and their carcasses, may have been what drove the evolution of the early bipeds.

For a long time, ecologists explained the coexistence of trees and grass by the different rooting depths - trees exploited the water deeper down whilst grass utilised the surface water. But recently a new explanation has emerged for the ecological oddity of savannas – fire.

To anyone who lives in a savanna or woodland, fire is a regular occurrence. It is an important part of the seasonal cycle of rains followed by a long dry season during which the trees shed their leaves and the tall grass dies back, leaving a crisp dry bed of fuel ready to burn. Humans have been using this opportunity for land management for millions of years and very few fires are the result of lightning or other natural sources. Savannas are burnt for many reasons: to produce a flush of new grass growth that is highly nutritious and attracts animals to be hunted; to drive animals into smaller areas where they are easy to hunt; to clear land that might harbour predators and snakes, and by accident, when field preparation gets out of hand, or smoking bees out of their hives ends in chaos.

Fire has been a part of savanna ecology for long enough that the whole system is evolved and adapted to its effects. The perennial grasses die back before the fire season, and survive to regrow from dense fire-resistant bases that stash resources below ground. Savanna trees have thick tough bark and also put a lot of resources below ground. The challenge for trees is to grow from seedling to a sapling thick and tall enough to survive fire. To help with this, most trees are very good at resprouting – if their above ground parts are killed by fire, or cut, they harness all their large root system to send up new shoots that grow fast and can escape the competing grass. These young trees are held in a cycle of growing fast each year, accumulating resources below ground, only to be 'topkilled' in a fire and having to resprout the following wet season.

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These trees, called 'Gullivers' by the more literary ecologists, await a year or two without fire and then grow rapidly to a point where they can survive a fire.

This means that a gap between fires is critical for maintaining the tree cover on savannas and it is this relief from burning that the Nhambita project is trying to create with its programme of fire breaks. By allowing a few years without fire, the woodland should produce a new generation of saplings to replace the large trees that are now covered in burn scars and queuing up for the crematorium.

10   The advent of satellites able to detect fires and measure the area burned has allowed ecologists to grasp the continental scale effects of the livelihoods of the rural population of Africa. In many areas, the rural population is fast expanding and this is leading to a increase in the number of fires being set. This seems to be combining with a breakdown in traditional land use that used to allow some areas to be burned to create fire breaks ensuring that other areas escaped fire for a few years The N'hambita project is trying to recreate this traditional land management. Every year small areas of the woodland are burned, creating a mosaic of burned and unburned patches. These act as natural

20   fire breaks and also provide edges between different types of vegetation – something that should encourage grazing animals and other biodiversity.

The vision is for a community with diverse sources of income, no longer needing to over-exploit its woodland resources. And in fact, with new skills and relief from the toil of subsistence farming, it becomes possible to fully exploit the products of the woodlands, but in a way that keeps their structure and function intact. Bee keeping is taking off in the community and a local sawmill and carpentry - based solely on logs recovered from the woodland floor - is producing furniture for the nearby national park. The local farming is becoming more intensive, market

30   gardens are springing up, and the rate of land clearance should decrease

in future. The carbon finance is providing an opportunity to switch from a aid-dependent subsistence economy to one that should be resilient to the future changes in global climate and economics.

As for Sabado, he is sanguine about the future "I was born with difficulty and have always lived with difficulty" he says. "No doubt I'll die with difficulty too. But since the project arrived the sick have been treated and the dead have had coffins". Progress of a kind.

Appendix 3. Plot-level inventory data

This appendix lists all plots inventoried as part of this thesis, along with other work kindly supported by Envirotrade. It contains the following columns:

PID	plot ID, see codes below
My plot ID	further detail relevant to particular sites
SD	Stocking Density (trees ha^{-1})
BA	Basal Area (m^2 ha^{-1})
Chidumayo	Biomass according to allometric model of Chidumayo 1997, Mg dry matter ha^{-1}
Brown	Biomass according to Brown 1989, Mg dry matter ha^{-1}
Ryan allometric.	Aboveground C stock (Mg C ha^{-1}) according to he following
	M = (0.0267*dbh$^{2.5996}$). Where M is in KgC and dbh is diameter at 1.3 m in cm. Dry matter is assumed 0.46 carbon.
Frost	Biomass according to Frost 1996, Mg dry matter ha^{-1}
DBH max	largest stem on plot, cm
DBH med	as before, median
Area	area of plot, ha
Shannon	H', calculated as:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where: $p_i = n_i/N$, n_i is the number of individuals in species I, N is the total number of all individuals and S is the number of species

Lat (South)	decimal degrees of plot centre, all in southern hemisphere
Long	decimal degrees of plot centre
Alt	m above sea level

All data are for live standing trees > 5 cm DBH except, for PID 4xxx which only included trees >10 cm DBH.

Plot ID	type	location	Rainfall	Rain Notes	Year of inventory	Notes
3000	fire exp	Nhambita	840		2007	See Chapter 3
4000	one off	Marrameu	762	1999-2007	2008	near Envirotrade camp, in Marrameu and Cheringoma District
5000	one off	Marrameu	762	1999-2007	2007	for Envirotrade survey
6000	one off	Quirimbas National Park	750	interp	2007	for Envirotrade survey
7000	preliminary sample plots	Nhambita	840		2004	Mushove's report (See intro)
8000	one off	Nhambita, managed area			2007	
9000	PSP	Nhambita			2006	

PID	my plot ID	SD	BA	Chidumayo	Brown	Ryan	Frost	DBH max	DBH med	Area	Shannon	Lat (South)	Long	Alt	Dominant species by basal area
9001	1	424	5.0	22	22	11	11	74.3	8	1	2.91	18.863540	34.100084	330	*Acacia nigrescens*
9002	2	352	8.6	39	46	24	41	65	9	1	3.26	18.900833	34.120600	206 142	*Bombax rhodognaphalon*
9003	3	503	9.2	44	45	23	46	65	8.3	1	1.94	18.941803	34.135132		*Diplorhynchus condylocarpon*
9004	4	538	7.8	38	36	18	34	56	8.2	1	2.84	18.975585	34.101789	110	*Julbernardia globiflora*
9005	5	582	12.1	55	64	33	70	65	7.75	1	2.68	18.935137	34.141296	138	*Pterocarpus rotundfolius rotundfolius*
9006	6	394	10.0	45	53	28	52	77.9	10.3	1	2.12	18.964046	34.167480	103	*Brachystegia boehmii*
9007	7	568	12.2	53	63	34	71	100	9.7	1	2.18	18.995633	34.200617		*Brachystegia boehmii*
9008	8	370	5.8	21	29	19	18	143.2	9.4	1	0.53	19.006820	34.236368	72	*Combretum adenogonium*
9009	9	1207	18.0	83	74	37	118	80.5	10.5	1	1.13	19.005783	34.281283		*Combretum adenogonium*
9010	10	960	9.8	41	39	20	51	87.4	8.5	1	2.65	18.880308	34.093433	309	*Brachystegia boehmii*
9011	11	763	10.5	51	44	21	56	59	9.4	1	2.97	18.914162	34.083244	269	*Brachystegia boehmii*
9012	12	38	2.4	10	15	8	-10	70	14.05	1	2.07	18.913611	34.107186	225	*Diplorhynchus condylocarpon*
9013	13	329	5.0	20	24	13	11	90.5	8.4	1	1.90	19.015111	34.220147	90	*Combretum adenogonium*
9014	14	463	13.1	52	73	42	78	99	10	1	2.68	19.053233	34.224651	56	*Sclerocarya birrea*
9015	15	347	14.7	60	87	49	91	98	10	1	1.57	18.952286	34.184165	126	*Erythrophleum africanum*
5001	1	983	21.2	82	117	70	145	86	8.5	0.06		17.998096	35.257639	209	
5002	2	250	15.5	57	99	60	97	88	8.65	0.12		18.401034	35.146624	211	
5003	3	469	14.6	73	77	39	90	58	13.5	0.16		18.426060	35.118183	242	
5004	4	473	20.3	77	125	75	137	86	8.8	0.11		18.419915	35.089789		
5005	5	231	11.6	55	66	34	65	65	16.5	0.16		17.999833	35.286865	54	
5006	6	130	7.6	30	48	28	32	80.3	9.05	0.2		17.956232	35.301622	34	
5007	7	620	8.8	42	37	18	43	41.9	9.45	0.2		17.989910	35.261426	43	
5008	8	433	11.0	49	59	30	61	57	9.5	0.12		17.989841	35.261066	47	
6001	Melucox1	1500	11.7	46	37	18	66	29.5	8.5	0.16		12.629419	39.425090	350	
6002	Melucox2	306	8.9	42	46	24	43	66	14	0.16		12.574912	39.472633	345	
6003	Melucox3	450	7.0	33	29	14	27	39.3	10.55	0.16		12.573495	39.474968	346	
6005	Macomiay2	956	14.8	71	66	32	91	55.2	9	0.16		12.104611	40.272600	59	
6006	Macomiay3	438	18.1	84	103	54	119	67	12.6	0.16		12.116706	40.243329	167	

PID	my plot ID	SD	BA	Chidu mayo	Brown	Ryan	Frost	DBH max	DBH med	Area	Shann on	Lat (South)	Long	Alt	Dominant species by basal area
7011	1a	360	3.6	16	13	6	-1	38	8	0.25	2.96	18.863900	34.099833	332	*Faidherbia albida*
7012	1b	316	7.0	32	38	19	28	52	7	0.25	2.27	18.862533	34.101500	330	*Brachystegia boehmii*
7023	2c	372	8.4	38	44	23	39	50.5	8.3	0.25	2.60	18.899600	34.116100	212	*Pterocarpus rotundfolius rotundfolius*
7024	2d	540	14.0	73	67	33	85	61.4	14	0.25	1.34	18.899283	34.114100	235	*Pterocarpus rotundfolius rotundfolius*
7032	3B	372	6.2	27	32	17	21	73.2	7.4	0.25	2.52	18.941167	34.136767	164	*Brachystegia spiciformis*
7033	3C	292	7.6	37	39	20	32	60.8	11	0.25	2.69	18.940667	34.139183	131	*Commiphora mossambicensis*
7043	4C	344	8.8	44	42	21	42	47	12.65	0.25	2.08	18.970833	34.099333	127	*Brachystegia boehmii*
7044	4D	360	10.7	54	57	28	58	50.3	11.35	0.25	1.48	18.969700	34.097033	154	*Brachystegia boehmii*
7053	5C	428	10.8	48	57	30	59	68.4	10.3	0.25	1.73	18.932100	34.145567	130	*Brachystegia boehmii*
7054	5D	248	8.7	49	44	21	42	37.4	19.5	0.25	1.35	18.930433	34.147333	138	*Brachystegia boehmii*
7061	6A	304	8.0	42	40	19	36	40.1	12.1	0.25	2.15	18.963417	34.167717	120	*Julbernardia globiflora*
7062	6B	256	5.8	30	27	13	17	37	11.15	0.25	1.89	18.963900	34.165383	105	*Brachystegia boehmii*
7071	7A	164	11.3	44	72	42	63	85.9	11.1	0.25	1.87	18.995367	34.200550	154	*Acacia nigrescens*
7072	7B	528	10.2	44	51	28	54	76.4	9.1	0.25	2.09	18.994000	34.202400	151	*Acacia nigrescens*
7082	8B	156	1.3	4	4	2	-20	25	9	0.25	0.44	19.008533	34.235450	71	*Combretum apiculatum*
7083	8C	32	3.1	13	19	11	-5	73.2	23.7	0.25	1.21	19.010700	34.234767	75	*Commiphora mossambicensis*
7091	9A	788	9.8	43	40	19	51	51.2	10	0.25	1.60	19.006250	34.280433	36	*Combretum apiculatum*
7092	9B	452	5.4	26	23	11	14	44.3	8	0.25	1.41	19.004633	34.278617	40	*Philenoptera violacea*
7101	10A	1004	8.1	30	31	16	37	65	8	0.25	2.35	18.879800	34.093233	306	*Brachystegia boehmii*
7102	10B	784	8.2	33	33	17	37	54	8.2	0.25	2.18	18.881783	34.094283	292	*Brachystegia boehmii*
7112	11B	1020	5.9	23	19	8	19	22	7.2	0.25	1.86	18.915283	34.081483	251	*Brachystegia boehmii*
7113	11C	680	7.8	38	33	15	34	38.2	8	0.25	2.60	18.916350	34.079683	257	*Brachystegia boehmii*
7122	12B	268	6.3	32	30	15	22	50.2	12	0.25	2.21	18.911833	34.107333	234	*Diplorhynchus condylocarpon*
7123	12C	104	11.7	34	80	61	67	147.7	17.55	0.25	2.09	18.909917	34.106700	231	*Khaya anthoteca*
7132	13B	560	4.1	15	12	6	3	18	8.2	0.25	1.22	19.015267	34.221867	82	*Combretum apiculatum*
7133	13C	256	2.4	9	9	4	-11	40.3	8.25	0.25	1.59	19.014733	34.224250	98	*Acacia nigrescens*
7141	14a	560	10.9	50	52	27	59	65	10.35	0.25	2.31	19.053817	34.225250	60	*Cleistochlamys kirkii*

PID	my plot ID	SD	BA	Chidumayo	Brown	Ryan	Frost	DBH max	DBH med	Area	Shannon	Lat (South)	Long	Alt	Dominant species by basal area
7142	14b	388	13.1	52	75	44	78	95.8	11.3	0.25	2.55	19.054350	34.222933	60	*Adansonia digitata*
7153	15c	216	6.8	32	35	18	26	50.4	12.05	0.25	1.61	18.955333	34.187000	121	*Burkea africana*
7154	15d	276	9.5	44	54	28	48	57.3	8.1	0.25	1.55	18.956983	34.188467	130	*Brachystegia spiciformis*
8001	w12	412	7.6	32	39	23	33	111.41	8.4	0.5	2.83	18.972820	34.148540	97	
8002	w22	225	7.5	31	43	24	32	94	10.1	0.5	2.25	18.954793	34.151653	115	
8003	w125	464	7.1	34	32	16	28	48.9	9	0.5		18.973560	34.151630	109	
8004	520	549	7.2	35	27	13	29	34.9	10.35	0.5	2.52	18.970542	34.149815	129	
8005	w24	338	6.8	31	34	17	25	60	8.7	0.5	2.07	18.956226	34.152707	114	
4001	woodland	126	15.0	62	95	53	94	78	31.3	0.5		18.242140	35.186620	227	*Pterocarpus angolensis*
4002	forest	494	22.0	95	123	71	151	118.4	16	0.5				227	
3001	NhamEx1	357	8.5	41	43	40	21	46	10	0.277	1.67	18.957531	34.168897	114	*B. boehmii*
3002	NhamEx2	469	11.3	50	59	63	31	60.7	9.75	0.277	1.56	18.956287	34.168918	114	*B. boehmii*
3003	NhamEx3	303	7.7	38	38	33	19	48.7	11.5	0.277	1.68	18.955321	34.168317	114	*B. boehmii*
3004	NhamEx4	332	9.7	48	48	49	24	45.7	11.95	0.277	1.84	18.954227	34.168167	114	*B. boehmii*
3005	NhamEx5	387	7.4	37	36	22	17	46.5	9.3	0.212	1.85	18.957896	34.167566	114	*B. boehmii*
3006	NhamEx6	451	7.5	35	34	31	17	49.2	10	0.277	2.07	18.956802	34.167395	114	*B. boehmii*
3007	NhamEx7	260	7.5	34	41	32	21	55.5	8.9	0.277	1.87	18.955493	34.167094	114	*B. boehmii*
3008	NhamEx8	458	10.7	54	53	58	26	45.1	10.8	0.277	1.66	18.955493	34.167094	114	*J. globiflora*

Appendix 4. Destructively harvested tree data

The collection of these data is described in Chapters 6 and 7.

The local (Senna) names of the trees were converted to the botanical names using Meg Coates-Palgrave's Nhambita vernacular dictionary.

DMF Dry mass fraction i.e wet mass/dry mass

%C   % carbon determined on a sawdust sample with a CarboErba 400 C N analyzer.

tree ID	Senna name	Botanical name	dbh (cm)	total ht (m)	stem trunk wet mass (Kg)	stem branch wet mass (Kg)	stem total wet mass (Kg)	root 'trunk' wet mass (Kg)	root 'branch' wet mass (Kg)	root total wet mass (Kg)	stem trunk DMF	stem branch DMF	root 'trunk' DMF	root 'branch' DMF	stem dry mass (Kg)	root dry mass (Kg)	%C	stem C mass (Kg)	root C mass (Kg)	root:stem	total C mass (Kg)
1	M'fiti	*Combretum adenogonium* Steud. ex A.Rich.	28.0	12.0	459.25		459.25	198.4		198.4	0.64	0.52	0.65	0.59	296	129	0.47	139	61	0.436	200
2	Chuanga	*Pericopsis angolensis* (Baker) Meeuwen	13.5	5.0	40.4		40.4				0.61				25		0.47	12			12
3	Nhantomole	*Diplorhynchus condylocarpon* (Muell.Arg.) Pichon	18.5	5.0	5.4	159.3	164.7	55.6	71.0	126.6	0.62	0.62	0.54	0.59	103	72	0.47	48	34	0.701	82
4	Mefuti	*Brachystegia boehmii* Taub	46.0	16.0	1399.2	588.4	1987.6	240.3	417.0	657.3	0.63	0.62	0.57	0.55	1246	363	0.47	585	171	0.292	756
5	Nhantomole	*D. condylocarpon*	26.2	6.0	188.5	360.3	548.8	161.4	78.5	239.9	0.61	0.52	0.55	0.47	302	125	0.47	142	59	0.415	201
6	Nhantomole	*D. condylocarpon*	18.2	7.8	100.8		100.8	43.0	93.0	136.0	0.61	0.52	0.55	0.47	62	67	0.47	29	32	1.091	61
7	Mefuti	*B. boehmii*	30.7	10.0	56.0	620.7	676.7	131.0	141.2	272.2	0.65	0.56	0.64	0.53	385	159	0.47	181	75	0.413	256
8	Messasa	*Brachystegia spiciformis* Benth.	60.0	18.3	1427.0	1422.8	2849.8	443.3	388.8	832.1	0.65	0.66	0.62	0.66	1864	531	0.47	876	250	0.285	1126
9	Nhantomole	*D. condylocarpon*	13.4	6.0	31.0		31.0				0.60				19		0.47	9			9
10	Nhantomole	*D. condylocarpon*	16.0	7.0	79.1		79.1				0.60		0.66		48		0.47	22			22
11	Messasa	*B. spiciformis.*	44.0	17.0	1021.9	991.7	2013.6	203.8	168.2	372.0	0.65	0.58	0.59	0.58	1240	218	0.47	583	103	0.176	686
12	Nhantomole	*D. condylocarpon*	18.0	7.9	92.0		92.0	37.5	22.9	60.4	0.61	0.39	0.64	0.44	57	34	0.47	27	16	0.607	43
13	Muhimbe	*J. globiflora* (Benth.) Troupin	17.2	11.5	59.0	121.5	180.5	43.4	17.1	60.5	0.69	0.61	0.69	0.61	115	41	0.47	54	19	0.354	73
14	Muhimbe	*J. globiflora*	30.0	14.0	454.0	386.0	840.0	172.8	103.7	276.5	0.74	0.66	0.69	0.66	589	188	0.47	277	89	0.320	365
15	Muhimbe	*J. globiflora*	37.0	13.0	752.1	532.0	1284.1	252.0	273.7	525.7	0.66	0.65	0.55	0.64	844	315	0.47	396	148	0.373	544

tree ID	Senna name	Botanical name	dbh (cm)	total ht (m)	stem trunk wet mass (Kg)	stem branch wet mass (Kg)	stem total wet mass (Kg)	root 'trunk' wet mass (Kg)	root 'branch' wet mass (Kg)	root total wet mass (Kg)	stem trunk DMF	stem branch DMF	root 'trunk' DMF	root 'branch' DMF	stem dry mass (Kg)	root dry mass (Kg)	%C	stem C mass (Kg)	root C mass (Kg)	root:stem	total C mass (Kg)
16	M'fiti	*C. adenogonium*	14.5	6.0	28.5	56.7	85.2	19.5	11.8	31.3	0.63	0.58	0.55	0.54	50	17	0.47	24	8	0.339	32
17	Mucombago	*Crossopteryx febrifuga* (Afzel. ex G.Don) Benth.	18.6	7.8	123.0	53.5	176.5	20.4	15.0	35.4	0.63	0.58	0.61	0.44	108	19	0.47	51	9	0.177	60
18	Mefuti	*B. boehmii*	63.2	20.0	2343.0	1391.9	3734.9	966.9	1021.0	1987.9	0.63	0.50	0.69	0.54	2174	1217	0.47	1022	572	0.560	1594
19	Nhantomole	*D. condylocarpon*	6.0	4.7	6.9	1.1	8.0	3.2	6.2	9.4	0.63	0.50	0.59	0.32	5	4	0.47	2	2	0.786	4
20	M'fiti	*C. adenogonium*	5.0	5.2	1.3	6.7	8.0	2.3	3.5	5.8	0.61	0.50	0.59	0.41	4	3	0.47	2	1	0.665	3
21	M'fiti	*C. adenogonium*	6.0	5.2	2.2	8.6	10.8	11.0	8.0	19.0	0.58	0.54	0.54	0.47	6	10	0.47	3	5	1.628	7
22	Mefuti	*B. boehmii*	22.5	12.2	196.8	193.7	390.5	119.0	112.6	231.6	0.66	0.54	0.62	0.55	236	136	0.47	111	64	0.575	175
23	Muhimbe	*J. globiflora*	42.0	17.5	1203.0	902.4	2105.4	39.5	648.9	688.4	0.73	0.63	0.63	0.59	1441	409	0.47	677	192	0.284	869
24	Messasa	*B. spiciformis.*	32.3	17.4	750.8	712.5	1463.3	380.1	185.7	565.8	0.71	0.60	0.60	0.57	961	332	0.47	452	156	0.345	608
25	Messasa	*B. spiciformis.*	72.0	23.0	6629.2	3680.2	10309.4	1778.7	1068.2	2846.9	0.70	0.63	0.53	0.63	6954	1618	0.47	3268	760	0.233	4029
26	Nhantomole	*D. condylocarpon*	10.6	5.5	34.4	19.3	53.6	5.9	13.3	19.2	0.70	0.63	0.65	0.60	36	12	0.47	17	6	0.327	23
27	Nhantomole	*D. condylocarpon*	16.0	7.0	25.0	27.5	52.5				0.72	0.71	0.65	0.71	38		0.47	18			18
28	mefuti	*B. boehmii*	28.0	12.0	246.5	214.0	460.5				0.72	0.68	0.65	0.68	323		0.47	152			152
29	miomba	*Pterocarpus rotundifolius* (Sond.) Druce *subsp. polyanthus* Mendonça & E.P.Sousa	5.0	5.0	16.0	10.0	26.0				0.73	0.78	0.65	0.78	20		0.47	9			9