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

CASEY M. RYAN[1] AND MATHEW WILLIAMS

School of GeoSciences, Crew Building, King's Buildings, University of Edinburgh, Edinburgh, EH9 3JN United Kingdom

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 over 100 million people. Managing the fire regime of these flammable systems is difficult, but crucial for sustaining biodiversity, ecosystem services, and carbon stocks. Fire intensity is more easily manipulated than fire frequency, because 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 intensity, tree 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 synthesize these data with a process-based gap model of stem growth, regeneration, and mortality; this model 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 populations and biomass to fire intensity and frequency.

The fire experiments 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 idealized physical representations of tree mortality, stems of $>$10 cm dbh did not gain further protection from fire with increasing dbh. Resprouting was very common and not obviously linked to fire intensity. The modeling showed that miombo tree populations and biomass are very sensitive to fire intensity, offering opportunities for effective management. At any achievable fire return interval ($<$5 years), low-intensity fires are required to maintain observed biomass. Model predictions and field experiments show that no tree biomass can be sustained under annual fires.

Key words: burn management; carbon stocks; fire-induced mortality; fire intensity; gap model; miombo woodland; Mozambique; resprouting; savanna; stem mortality; top-kill; Zimbabwe.

INTRODUCTION

Fire is a global biogeochemical agent (Bowman et al. 2009), influencing vegetation structure (Bond and Keeley 2005, Bond et al. 2005) and carbon cycling (van Wilgen 1997). African savannas account for more than half of the annual global burned area (Mouillot and Field 2005). Miombo woodlands, a type of savanna, are the dominant vegetation cover in southern Africa (Frost 1996). In these woodlands, several long-term fire experiments have shown fire to be of critical importance in determining woody cover (Furley et al. 2008). These long-term plot-scale experiments have shown that, under annual burning, miombo woodland is converted to grassland (Furley et al. 2008) 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 (Russell-Smith et al. 2003, van Wilgen et al. 2004). Traditional fire management has instead focused on manipulating fire intensity, rather than frequency (Laris 2002, Laris and Wardell 2006). By setting fires early in the season, small, patchy, burned areas are created and 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 and Andersen 2006), with biodiversity and cultural/historic criteria being used to justify this approach. However, implementing such a regime is not straightforward, and detail is needed regarding what constitutes a low-intensity burn and what area should be burned each year.

Data on fire-intensity-dependent effects (Bond and van Wilgen 1996) are available for the semiarid savannas of South Africa (Higgins et al. 2000, 2007, Kennedy and Potgieter 2003, Govender et al. 2006), where they have, to some extent, informed management objectives (van Wilgen et al. 2004) and allowed identification of "thresholds of potential concern" (Bond and Archibald 2003) and the promotion of

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[1] E-mail: casey.ryan@ed.ac.uk

policies that result in variable fire intensity and sizes (van Wilgen et al. 2004). However, data are lacking in the less-studied miombo ecosystem (Mistry 2000), despite its large area (2.7 million km^2; Frost 1996) and the importance of these woodlands and their ecosystem services to roughly 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 semiarid "climatically determined savannas" (Sankaran et al. 2005).

The lack of information quantifying the fire-intensity-dependent effects on miombo tree populations 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? We acknowledge that there are important issues regarding the response of other parts of the ecological system to fire, but here we focus exclusively on trees.

There are two main ways in which 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 and Midgley 2003, Hoffmann and Solbrig 2003, Michaletz and Johnson 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 and Smith 2000, Johnson and Miyanishi 2001). Differing species responses occur because of different allometry and defense mechanisms (Uhl and Kauffman 1990, Gignoux et al. 1997, Jackson et al. 1999, Cauldwell and Zieger 2000, Sutherland and Smith 2000). Likewise the impacts on resprouting and subsequent regrowth are highly dependent on size and species (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 wood moisture content. In contrast, the canopy dominant species (family Caesalpinioideae) have thinner, smooth bark and lower moisture content (Chidumayo 1997). Based on these differences, species composition changes might be hypothesized 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 dynamic model of individual stems and rootstocks. This gap phase dynamics model simulates growth based on representations of photosynthesis and carbon allocation and local allometric data. 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 populations 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 addressed in this study are as follows. (1) What are top-kill rates for stems of different diameter in fires of different intensity? (2) What is the frequency of resprouting after top-kill and what factors affect rootstock survival and the number of resprouts? (3) How do miombo species vary in their susceptibility to 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, parameterized 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

Setup 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 characterized by a six-month dry period and mean annual precipitation of 850 mm (based on data from 1959–1967 and 1999–2007 at Chitengo, 25 km distant). The period 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 are described in detail in Tinley (1977, 1982).

In June 2007 we laid out eight adjacent 1.4-ha plots in a 4 × 2 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 (normalized difference vegetation index) from a SPOT (Satellite Pour l'Observation de la Terre) image from April 2007. Seven of the plots were randomly assigned for burning and one was left unburned.

A 50-m firebreak was cut around the entire site and smaller breaks were cleared to divide the area into approximately 120 × 120 m square plots. We laid out a nested (Fernandes et al. 2000) triangular measurement scheme designed to utilize 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 10-m triangles, 2-m triangles were established. Additionally, the center of the 80-m triangle and two equidistant

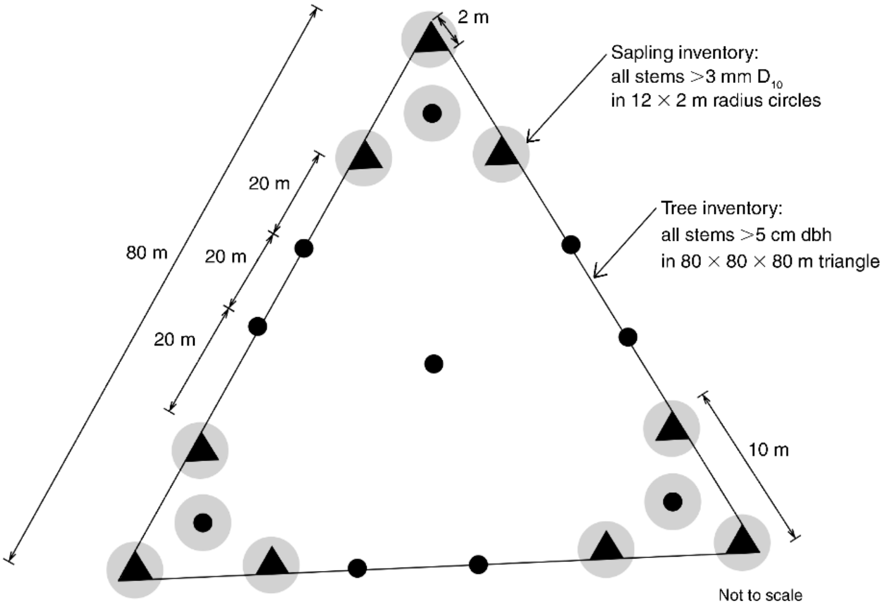

FIG. 1. Thermocouple positions and vegetation sampling scheme for the fire experiment plots in Nhambita, Mozambique. A nested triangular sampling scheme was used to position the thermocouples: each black circle is a thermocouple at 15 cm height; in each black triangle there are three thermocouples at 15 cm height (one in each corner). Trees were sampled in the full 80-m triangle (black line), and saplings were sampled in the gray circles (12 × 2 m radius). D_{10} is stem diameter at 10 cm above the mineral soil.

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.

Prefire vegetation surveys.—We conducted two prefire surveys. The first was of trees, defined as woody species of >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).

At each corner and the center 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 that 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 center 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 hours local time) over the period 6–19 September 2007. The aim was to induce a range of fire intensities, so the burns were timed to capture a wide range of meteorological conditions: relative humidity ranged from 15% to 55%, wind speed 0.9–2.4 m/s, and air temperature 25–33°C (all averages for the period of the burn recorded by an on-site weather station [Instromet, North Walsham, UK]; see Appendix: Table A4 for more details). September represents the late dry season at the site, with severe fire weather. However, early-morning conditions still result in mild, controllable burns. The nested sampling and monitoring design allowed us to capture short-term variations in wind speed during the burn 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 that 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 center of the plot and the remainder being burned 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. Each TC was logged at 1-s intervals by Hobo data loggers (H12 and U12, Onset Computer Corporation, Bourne, Massachusetts, USA). The loggers were buried in the mineral soil and covered with a heat-proof 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 (data not shown). After installation, the soil, litter, and other fuel were carefully replaced. We deployed 37 loggers in each fire (Fig. 1). With the exception of one failure, all 37 temperature–time profiles from each of the seven fires were retrieved. TC data were processed using MATLAB (MathWorks, Natick, Massachusetts, 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 37 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 compared top-kill and rootstock 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 modeling purposes, three fire intensity classes were defined (high, medium, and low) based on the terciles of the observed fine-scale thermal anomalies.

Postfire 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 and Johnson 2001), defined as $\ln(p/1 - p)$, where p is the top-kill rate (number of stems that died during the fire divided by total number of live stems at start of the experiment). 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, where n is the total number of individuals sampled. All values are reported as the mean ±SD of the n samples.

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 rainfall similar to Site 1 (~800 mm/yr), and sandy soil to >2 m depth (Tinley 1977, 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 × 40 m for stems with a dbh of 5–10 cm. To estimate leaf area index (LAI), we took 18 photos at different locations on the 0.5-ha plot and analyzed them as described in the Appendix.

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, twenty-two 0.09-ha plots were allocated to 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), when the experiment was stopped. All burns were conducted at the end of the dry season. We recorded all live trees of >20 cm dbh in Oct 2007. More details of the experiment can be found in Furley et al. (2008).

Population modeling

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 Appendix). The model is similar in conception to many other gap models (Shugart and Smith 1996, Williams 1996) that have been used previously in miombo (Desanker and Prentice 1994, Desanker 1996) and also to simulate the effects of fire (Miller and Urban 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-modeling approach because of its explicit representation of population structure and variability, its ability to explore the stochastic nature of disturbance events through large modeling 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 may be found in the Appendix. We summarize 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 and leaf and fine-root construction; any

TABLE 1. Plot-level tree, sapling, and fire characteristics in eight experimental burn plots in the dry miombo woodland of Nhambita, Mozambique.

	Large-tree data			Sapling data‡		Fire properties§			Vegetation effects (%)¶		
Plot no.†	BA (m^2/ha)	Stocking (no./ha)	Carbon (Mg C/ha)	BA (m^2/ha)	Stocking (no./ha)	Date	Time	TA (°C·s; $\times 10^{-3}$)	Tree top-kill	Sapling top-kill	Rootstock mortality
1	8.5	357	21.5	0.88 (0.76)	6281 (3280)	no burn			0% (90)	13% (557)	0.4% (255)
2	11.3	469	30.7	0.68 (0.48)	12 401 (8349)	17	14:33	31.2 (5.1)	5% (121)	92% (153)	13.7% (73)
3	7.7	303	19.0	0.41 (0.60)	6300 (7651)	15	10:21	25.3 (2.6)	1% (81)	99% (94)	10.8% (37)
4	9.8	343	24.0	0.76 (0.91)	7228 (6065)	6	15:34	21.9 (2.1)	1% (82)	100% (93)	3.5% (57)
5	7.4	386	17.3	2.18 (1.93)	24 271 (19 952)	19	08:09	20.3 (5.9)	0% (74)	81% (365)	0% (129)
6	7.5	455	16.9	1.12 (0.99)	11 075 (10 663)	14	15:15	32.2 (6.5)	13% (123)	93% (166)	0% (68)
7	7.5	260	21.1	1.60 (1.28)	16 048 (11 660)	12	13:31	29.5 (5.2)	9% (67)	88% (218)	5.6% (108)
8	10.7	458	25.6	0.81 (0.87)	6499 (4844)	10	14:32	29.2 (4.3)	4% (121)	94% (98)	0% (45)

Notes: Data are for live standing trees at the start of the experiment. Trees are defined as live standing woody species of >5 cm dbh. Saplings are defined as woody species <5 cm dbh and >0.3 cm D_{10} (diameter at 10 cm above the mineral soil). BA is basal area; stocking refers to stocking density (the number of large trees or of saplings/ha); carbon is given as the aboveground tree stock; TA is thermal anomaly (values in the table should be multiplied by 10^3 to obtain true values). See Appendix: Table A4 for further metrological data and Appendix: Table A6 for detailed species composition of the plots.

† All plots are 0.277 ha except for plot 5, which is 0.212 ha in area.

‡ The total inventory area for all sapling plots is 151 m^2 per plot except for plot 1, which is 942 m^2. Values in parentheses are SD.

§ Experimental burns were in September 2007: day and time of ignition are given. Values in parentheses are SD.

¶ The percentage of all trees, saplings, and rootstocks showing mortality. Values in parentheses are sample sizes.

remaining is used to grow the coarse-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 specific to dbh and fire intensity. Mortality for the stem (top-kill) is assessed separately from rootstock 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 determined from our observations, 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 parameterized 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 we 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 to 100 years and low, medium, and high fire intensities. Again, 50 patches were used and were run from bare ground for 1000 years. The mean of the last 500 years is reported. As a test of the model, we compared modeled basal area to the woodland structure at the long-term fire experiment in Zimbabwe (Site 3). Using the Nhambita allometric equation, we also report modeled 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, with a mean of 8.7 m^2/ha. Stocking density was similarly variable (303–469 stems/ha of >5 cm dbh), as was tree aboveground carbon stock (16.9–30.7 Mg C/ha; Table 1). Floristic composition (Appendix: Table A5) 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 (Appendix: Table A5), although more heavily dominated by *D. condylocarpon* and with several other species that were rare as large trees (*Combretum adenogonium*, *Lannea schimperi*, *Dalbergia boehmii*, *Crossopteryx febrifuga*, *Millettia stuhlmannii*). Sapling stocking densities ranged from 6000 to 24 000 stems/ha, with large variations within and between each plot. Sapling basal area ranged from 0.4 to 2.1 m^2/ha.

The plots burned with a wide range of fire intensity (Table 1). Observed plot-scale mean thermal anomalies ranged from 20.3 °C·s 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,

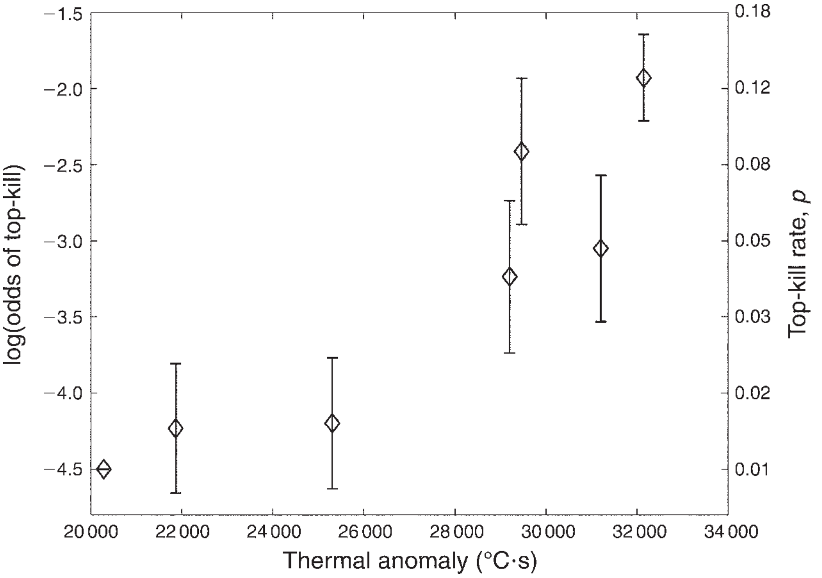

FIG. 2. Mortality rate of trees >5 cm dbh on each plot vs. mean thermal anomaly (°C·s). Probability, p, is transformed to the log odds (or logit, $\ln(p/1-p)$, where ln is the natural logarithm) on the left axis, but is shown untransformed on the right. For a linear fit, $r^2 = 0.82$; $P = 0.005$ for log odds of top-kill vs. thermal anomaly. Zero mortality (–infinity log odds) is shown as –4.5 and is fitted as such. Error bars show ±SD, estimated by bootstrapping.

ignited on a hot, windy afternoon, had the highest TA (Table 1).

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% to 13%, with the log odds of top-kill well correlated (for a linear fit, $r^2 = 0.82$, $P = 0.005$) with the plot-level mean thermal anomaly (Fig. 2, 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%). Eighty-three tags were not located in the postfire census, and if these lost stems are considered killed, top-kill was 90%. Burned plot-

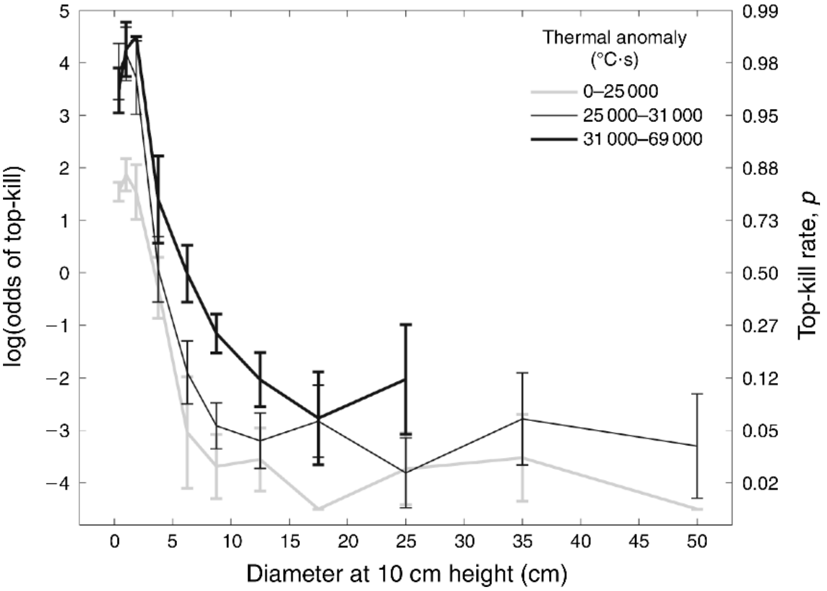

FIG. 3. Top-kill rates for all stems as a function of diameter and thermal anomaly. The top-kill data are pooled into diameter bins and grouped by fire intensity class. Error bars show ±SD, estimated by bootstrapping. Zero top-kill (–infinity log odds) is shown as –4.5, and no variance can be associated with it.

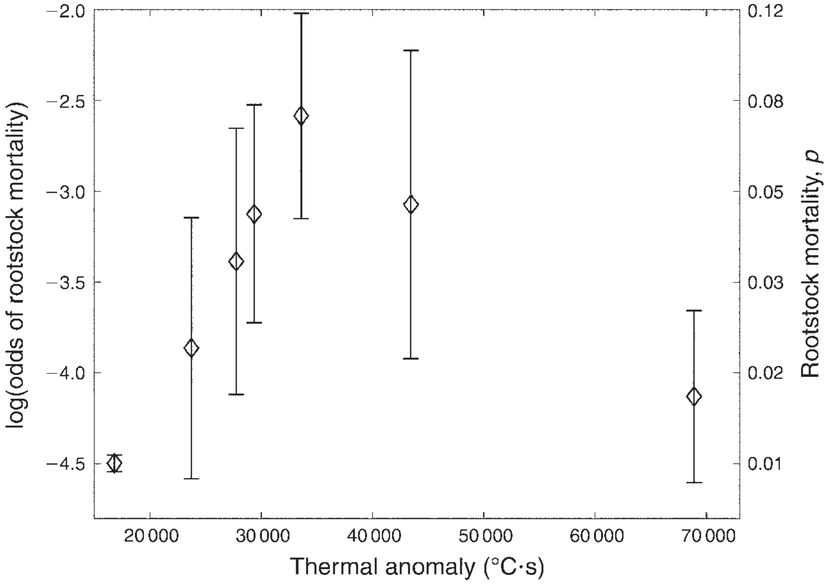

FIG. 4. Rootstock mortality vs. fire thermal anomaly (TA) recorded by nearby thermocouples. Error bars show ±SD, estimated by bootstrapping. Data are binned into TA classes to give roughly equal sample size.

level sapling top-kill ranged from 81% to 100%, which contrasted with 13% (n = 591) non-fire top-kill of saplings on the unburned plot.

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 sapling; i.e., 0 cm dbh, sapling was 2 cm) and assigned the plot-scale mean TA to each tree in the large tree inventory while using the fine-scale TA data for saplings. The results showed a clear decrease in top-kill with increasing diameter from 0 to 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, with higher mortality in classes of higher fire intensity (Fig. 3).

Resprouting.—Of rootstocks on the burned plots, 96% survived and produced at least one new stem after the fire, with a median of three new stems. On the unburned plot, rootstock survival was higher at 99.6% (one death out of 259). Rootstocks that had all their stems killed by fire were more likely to produce new shoots than those with a surviving stem (84% vs. 24%, respectively), and also produced more new shoots (median 3 vs. 1, respectively). 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 nonlinear relationship with the fine-scale thermal anomaly data, rising until 33.5×10^3 °C and falling thereafter (Fig. 4). The number of postfire resprouts was not correlated with the prefire number or basal area of stems from the parent rootstock.

Species effects.—The large-tree inventory showed top-kill of 5–6% among both the canopy dominants (*B. boehmii* and *J. globiflora*) and the subcanopy 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 top-kill rates very similar to those of 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).

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 years, low-intensity fires). The model output (Appendix: Fig. A3), 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

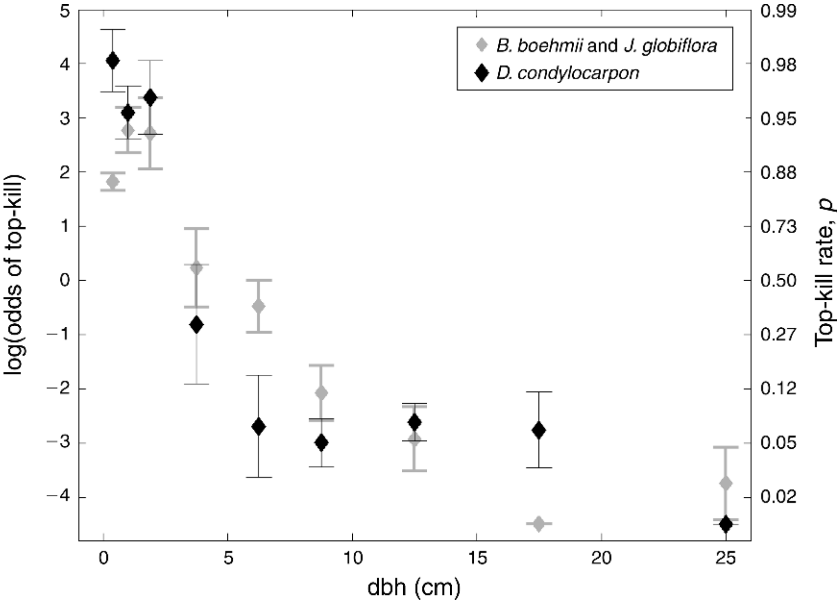

FIG. 5. Comparison between size-specific top-kill rates for the dominant canopy species (*Brachystegia boehmii* and *Julbernardia globiflora*, $n = 688$) and dominant understory species *Diplorhynchus condylocarpon*, $n = 700$. Error bars show ±SD, estimated by bootstrapping. Zero top-kill (−infinity log odds) is shown as −4.5, and no variance can be associated with it.

was 22.8 ± 4.5 m^2/ha vs. a measured value of 22.0 m^2/ha, and LAI was 3.9 ± 0.5 vs. 3.3 (Appendix: Fig. A3). The stocking density of stems was overestimated by the model, 1371 ± 595 vs. 494 stems/ha, mainly in the 5–10 and 10–15 cm dbh classes (Fig. 6). All of 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 year (0.3 ± 0.1 m^2/ha, $n = 2$) or FRI = 2 years (2.7 ± 2.1 m^2/ha, $n = 4$), but significant biomass was present at FRI = 3 years (9.2 ± 8.4 m^2/ha,

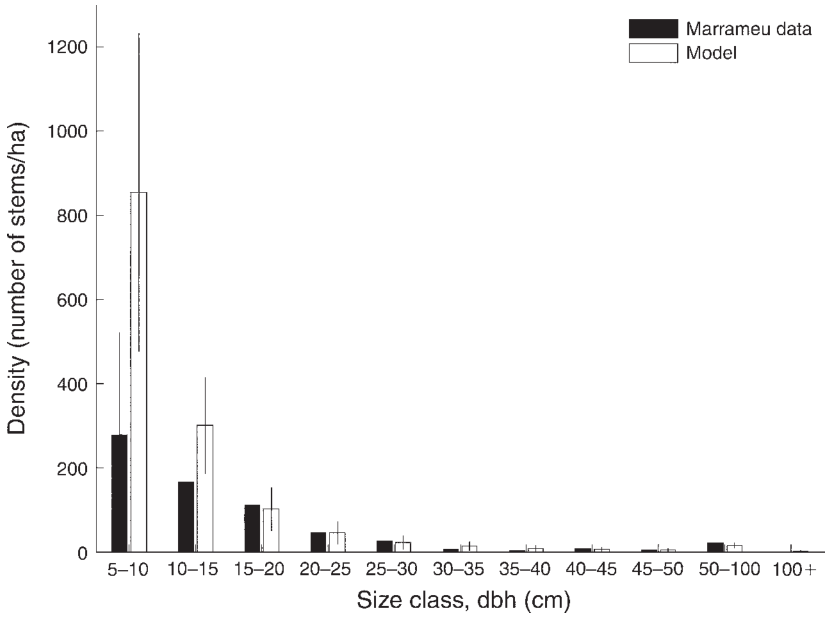

FIG. 6. Comparison between the model output (open bars) for the low fire scenario (fire return interval, FRI = 100 years, with low-intensity fires) and a 0.5-ha inventory (solid bars) in a closed-canopy dry forest at Marrameu, Mozambique (Site 2). For model results the vertical lines show the standard deviations between the 500-year 50-patch means. For the field data in the smallest size class, the standard deviation of four 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.

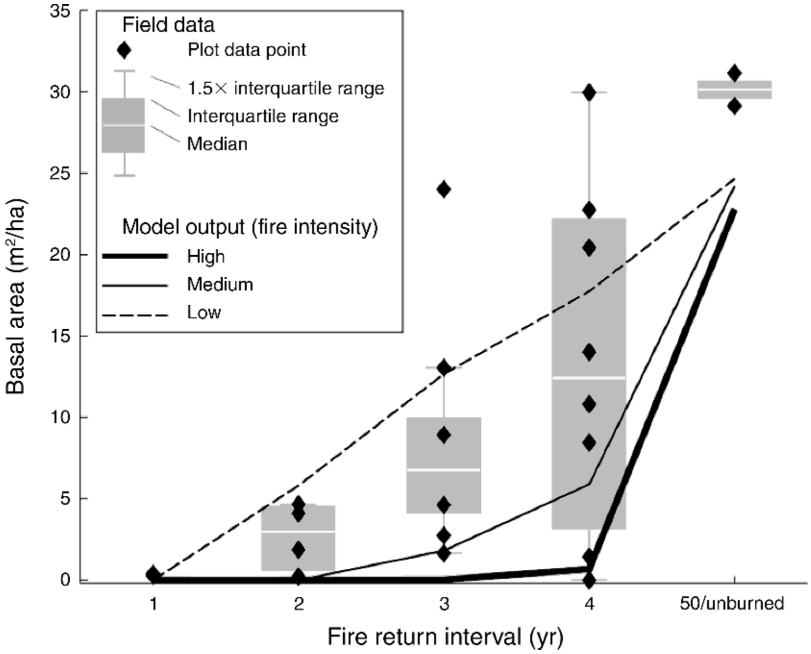

FIG. 7. Modeled basal area under different fire return intervals and intensity classes (three line types), compared to field data from Marondera, Zimbabwe, showing the results of a 50-year burning experiment (solid diamonds and boxplots).

$n = 6$) and FRI = 4 years (15.7 ± 9.6 m^2/ha, $n = 7$). Under complete fire exclusion ($n = 2$), BA averaged 30.4 ± 1.4 m^2/ha.

The second model experiment simulated a variety of fire regimes by varying the FRI from 1 to 100 years for each of the three fire intensity classes. Model output was tested against the Marondera fire trial basal area data (Fig. 7). 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.

Predictions of C stock under different fire regimes

The model predictions of aboveground carbon stocks (Fig. 8) 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 of >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 years were minor, as other limitations on biomass became more significant than fire. In contrast, the high top-kill rates for large trees in medium- and high-intensity fires influenced stand biomass even at FRI = 50 years. The differing impact of fire intensity was greatest at FRI = 4, where low-intensity fires supported a woodland aboveground carbon stock of 65 Mg C/ha, compared to high-intensity fires, which supported 2 Mg C/ha.

DISCUSSION

The experimental data and model outputs can be used to answer our original four questions.

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

Overall, stem top-kill rates varied from near >95% for small stems to 5–13% for large trees, depending on fire intensity. Top-kill of 50% occurred around 5–8 cm dbh,

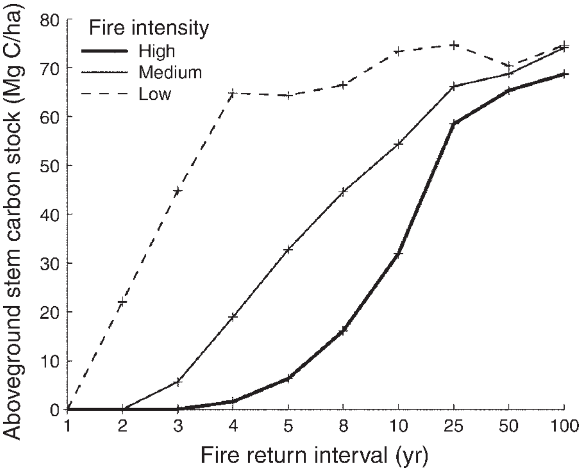

FIG. 8. Modeled aboveground tree carbon stock for the three fire intensity classes and a range of return intervals.

similar to the findings of Hoffman et al. (2009) and Holdo (2005). At diameters <10 cm D_{10}, top-kill rates decreased as diameter increased (Fig. 3), but top-kill rates for stems >10 cm D_{10} were unaffected by stem diameter. These results suggest that 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 fire 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 smoldering combustion of the bole, within the flame zone (see Plate 1 and color photos in the Appendix: Fig. A2). 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 behavior that are linked to time-integrated heat flux. It is also consistent with the observed leveling off of the diameter–top-kill relationship (Fig. 3), because neither bark thickness nor height offers 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 idealized physical representation of undamaged trees.

What is the frequency of 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). 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 that were not top-killed. The number of new shoots produced by a rootstock was not correlated with any of the pre- or postfire variables that 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 soil conditions (Hoffmann et al. 2009). 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 nonlinear 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 nonlinearity is interesting and suggests that further investigation into the mechanisms of heat flux to the rootstock and the causes of mortality is warranted.

How do miombo species vary in their susceptibility to fire?

No clear species effects were found in top-kill rates of trees and saplings, or 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, 1997). Previous reports of fire sensitivity differences among species (Trapnell 1959, Lawton 1978) may reflect relative resprouting success and growth rates, rather than fire resistance per se. At a plot level, it is impossible to separate out these different mechanisms (Gignoux et al. 1997). Our fine-scale fire behavior measurements and observations of individual stems failed to show significant differences in top-kill between species, which may indicate that the reported fire tolerance of various species (Trapnell 1959, Lawton 1978) is due to their persistence by resprouting and superior competitive abilities in the sapling stage.

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

Our modeling results suggest that no large woody vegetation can be sustained under annual burning in these dry woodlands (Fig. 8), 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 year. Above a fire return interval of 1 year, large stems can be sustained, but this is strongly dependent on fire intensity.

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 and Rose Innes 1963). If we regard this effect as mainly due to the low-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 in the late season). Trapnell (1959: Tables 7 and 8), working in wet Zambian miombo, found mortality rates of trees of >15.2 cm dbh to be more than twice as high on annually late-burned plots, compared to annually early-burned plots. 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 behavior were recorded by Trapnell, so it is hard to compare the experiments directly. However, in the Zambian experiment, trees survived on the annually burned, low-intensity treatment, contrary to our modeling results. Similarly, in northern Australia, large trees persisted on annually burned plots (Russell-Smith et al. 2003). This may be due to the higher rainfall (>1000 mm/yr) and therefore more productive sites. The length of the treatment and observation may also be important: for instance Barnes (1965, cited in Walker and Noy-Meir

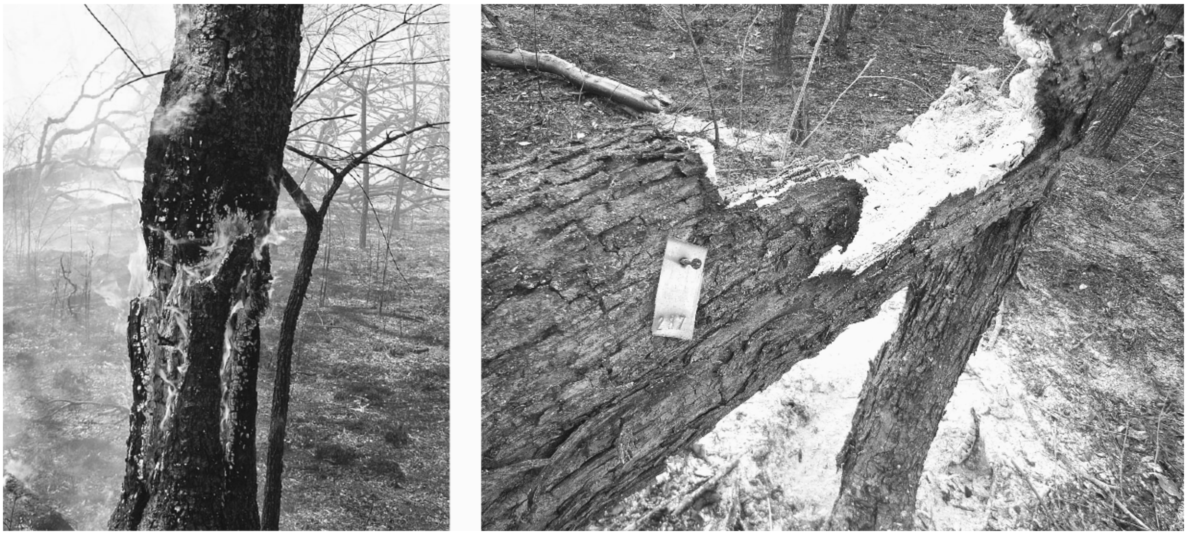

PLATE 1. Fire damage in miombo. (Left) A damaged tree bursts into flames, and (right) another collapses after the bole has combusted. A color version of each photograph is available in the Appendix. Photo credit: C. M. Ryan.

1982) observed trees on the Marondera annually burned treatments, but Tsvuura (1998) in 1995 and then this study (in 2007) did not.

Limitations

A key limitation of this study is that the limited plot size and invariant fire return intervals of experiments such as those at Marondera mean that they are not simulations of real heterogeneous landscapes (Chidumayo 1988, 1997). A comparison between a landscape-scale fire experiment and a plot-based one in northern Australia showed that the fire regime was much milder on the plot-based experiment (Russell-Smith et al. 2003), and this may well be the case in comparing Marondera to the landscape fires that affect miombo. In particular, the small plot size may have led to important edge effects in both fire behavior and tree growth, and limited replication (especially for the unburned treatment) precludes robust statistical comparisons with our model results. It is important to note that the gap model does not explicitly consider moisture limitations, although it does utilize the observed phenology to constrain growth primarily to the wet season. Thus if wet-season competition for water is an important limitation, the gap model may be overestimating tree growth rates. Also, the use of miombo species parameters for simulation of dry-forest rates of resprouting may introduce errors and could explain why small stem densities are overestimated at the Marrameu site (Fig. 6).

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 nonlinear 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 modeling 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 onto the fire behavior and consequent tree mortality.

The vegetation observed on the Nhambita plots, with aboveground carbon stocks of ~20 Mg C/ha, is, according to our model, consistent with an envelope of fire regimes bounded by low-intensity burns every two years, or high-intensity burns every nine years (Fig. 8). Such a fire regime is conspicuously absent at the moment, with high-intensity fires and biennial frequency observed in the area (C. M. Ryan and M. Williams, *personal observation*). 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. Such action may be a precondition for meaningful participation in global efforts to reduce greenhouse gas emissions from deforestation and forest degradation.

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, wind speed, 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 (Russell-Smith et al. 2003, van Wilgen et al. 2004). As an indication of the range of intensities possible, our fires had a Byram's fireline intensity of 360–3800 kW/m as a plot mean, which can be compared to the seasonal variation of 25–5300 kW/m in Zambian miombo (Hoffa et al. 1999). Our results suggest that miombo woody biomass may be preserved or enhanced by burning in low-intensity conditions. Low-intensity early, patchy, burns are likely to have been the traditional land management regime (Laris and Wardell 2006) and are also proposed to have biodiversity benefits (but see Parr and Andersen 2006).

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

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APPENDIX

Model description and color photographs depicting fire in miombo woodlands (*Ecological Archives* A021-003-A1).