Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna–forest boundaries

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Abstract   The higher flammability of tropical savanna, compared with forest, plays a critical role in mediating vegetation-environment feedbacks, alternate stable states, and ultimately, the distribution of these two biomes. Multiple factors contribute to this difference in flammability, including microclimate, fuel amount and fuel type. To understand this transition in flammability, we studied fuel characteristics and microclimate across eight savanna–forest boundaries in south-central Brazil. At each boundary, the environment was monitored for one week with automated measurements of near-surface wind speed, air temperature, relative humidity and presence of dew. Manual measurements were performed to quantify fuel amounts and fuel moisture. These data were used to parameterize the fire behaviour model BehavePlus5 in order to simulate fire behaviour over the savanna–forest boundary. There were strong gradients across the boundary in all variables with the exception of total fuel load. During the day, savannas had higher wind speed and air temperature, and lower relative humidity and fuel moisture than forests. Although fuel loads were similar in savanna and forest, savanna was characterized by lower fuel bulk density, largely because of the presence of grasses. Based on these measurements, the fire behaviour model predicted savanna fires to be faster, more intense, and with greater flame lengths, relative to forest. A sensitivity analysis indicated that the primary cause of these differences was the low fuel bulk density characteristic of grassy fuels, with lesser contributions from wind speed, fuel moisture and total fuel load. These results indicate that the dominance of grassy fuels is the primary cause of the high flammability of savanna.

Key words: C4 grass, Cerrado, fire behaviour, fire intensity, positive feedback.

INTRODUCTION

Fire has long been recognized to play an important role in governing the balance between mesic tropical savanna and forest (Bowman & Fensham 1991; Hopkins 1992). Savannas are highly flammable and therefore typically subjected to frequent fire. In contrast, tropical forests are not nearly as flammable as savanna, so savanna fires are commonly extinguished as they reach a forest edge (Biddulph & Kellman 1998; Hennenberg et al. 2006). This transition in flammability plays an important role in mediating a positive feedback between vegetation and fire. Frequent burning in savanna reduces tree dominance (Higgins et al. 2000; Furley et al. 2008) and thereby maintains an open, highly flammable vegetation. In contrast, the

low flammability of forest allows it to maintain a closed canopy despite frequent burning in the adjacent savanna. As fire can maintain open savanna conditions where climate and soils are otherwise able to support forest, these fire-vegetation feedbacks permit the existence of alternate stable states (Wilson & Agnew 1992; Beckage et al. 2009; Warman & Moles 2009).

The presence of grasses has often been regarded as the primary factor responsible for the high flammability of savanna ecosystems (Stott 2000; Hennenberg et al. 2006; Bond 2008). Grasses form a loosely packed fuel bed with high surface : volume ratio that strongly enhances flammability. Literature from tropical forest ecosystems, however, has typically emphasized the role of microclimate in determining flammability, primarily because of the effects of solar radiation, air temperature and relative humidity on fuel moisture (Uhl & Kauffman 1990; Cochrane et al. 1999; Ray et al. 2005, 2010). This is a serious concern in tropical forests that have been degraded by selective logging or other disturbances that reduce canopy cover and generate a drier microclimate, allowing pasture fires to spread into forest (Uhl & Buschbacher 1985). In these

disturbed forests, grasses are commonly absent (but see Veldman *et al*. 2009), making it straightforward to attribute flammability to the altered microclimate.

At the savanna–forest boundary, however, it is more difficult to assess the relative effects of microclimate and grasses, as these factors are confounded by the strong dependence of savanna grasses on high-light environments. Most grasses of tropical savannas possess the C_4 photosynthetic pathway, which permits high net primary productivity, but predisposes them to be intolerant of shade (Sage *et al*. 1999). As a result, C_4 grasses produce abundant fuel in the savanna where the microclimate is favourable to burning, but are absent in forest, where the microclimate is more humid.

Microclimate and grasses undoubtedly both contribute to the greater flammability of savanna, but to our knowledge, no study has quantified the relative roles of these two factors. Thus, the objective of this study was to quantify the relative importance of fuel characteristics and microclimate in determining changes in fire behaviour across savanna–forest boundaries. We measured fuels and microclimate at eight savanna–forest boundaries, and used these data to parameterize a model of fire behaviour. Sensitivity analysis was used to quantify the contribution of fuels and microclimate to differences in fire behaviour between savanna and forest.

METHODS

Study site

The study was performed at the IBGE Ecological Reserve, near Brasília, DF, Brazil, at an elevation of approximately 1100 m. Mean annual temperature on the reserve was 22.5°C for 1993–2002, and mean annual rainfall was 1426 mm with a distinct dry season from May to September. Precipitation was slightly above average (1596 mm) for the 2007–2008 rainy season which preceded this study. During the 6 weeks (29 April to 8 June) before the start of this study, <2 mm of precipitation was recorded, while no precipitation was recorded during the study (9 June to 5 August, 2008).

We performed measurements along eight transects located at savanna–forest boundaries within the IBGE Ecological Reserve. At each boundary, a 70 m transect was centred at the forest edge and positioned perpendicularly to it. The location of the forest edge was defined as the furthermost extent of savanna grasses along the transect. Transects were organized in pairs, with at least 50 m between transects within a pair, and at least 1 km between pairs of transects. All transects were at gallery (riparian) forest edges, but locations were chosen to include only sites on well-drained soils occurring far upslope from streams.

Microclimatic measurements

Meteorological sensors were placed at 20 m intervals along the transects at positions located 30 m and 10 m into the forest and 10 m and 30 m into the savanna. At each station, sensors were installed to measure wind speed, relative humidity, air temperature and presence of dew. Wind speed was measured with a cup anemometer (Inspeed, Sudbury, MA, USA) installed at a height of 1.3 m. Relative humidity and air temperature were measured with a EHT relative humidity/temperature sensor (Decagon Devices, Pullman, WA, USA) enclosed within a radiation gill, installed 1 m above the ground. Presence of dew was determined with a LWS leaf wetness sensor (Decagon Devices, Pullman, WA, USA) installed at 1 m. At a single location within each vegetation type, we measured photon flux density and shortwave radiation with a LI-190 quantum sensor (LI-COR, Lincoln, NE, USA) and a PSP pyranometer (Eppley Laboratory, Newport, RI, USA), both installed at 1.3 m from the ground and 20 m from the forest boundary.

Sensor measurements were performed at 15 s intervals and means were recorded at 5 min intervals using CR1000 data loggers (Campbell Scientific, Logan, UT, USA). Sensors remained in place for one week before being moved to the next site. To avoid biases caused by effects of individual sensors, the positions of the four sets of sensors were randomized each time they were moved to a new site. Furthermore, the wind sensors were each calibrated in the field against a newly purchased (and recently calibrated) 014A anemometer (Met One Instruments, Grants Pass, OR, USA). The first measurements were performed on 9 June 2008 and the last measurements were performed on 5 August 2008.

Fuel characteristics

Fuels were characterized at 10 m intervals along five of the transects. Fuels were collected within a 0.5 m^2 quadrat, and sorted into several fuel classes, including live dicot leaves, dead dicot leaves, live dicot stems, dead dicot stems, total grass and woody fuels of standard diameter classes: 0–6.4 mm (1-h time lag), 6.5–25.4 mm (10-h time lag) and 25.5–76.0 mm (100-h time lag). Each class was oven-dried at 60°C for at least 5 days and weighed. Subsamples of these fuels were collected to determine surface area: volume ratio. Depth of the fuel bed was determined as the average depth of the grass layer, where this was present, or the depth of the leaf litter where grasses were absent. Fuel bulk density (fuel mass per volume of fuel bed) was calculated as fuel load (fuel mass per area) divided by depth of the fuel bed.

For each transect, midday fuel moisture was determined for live and dead dicot leaves, live and dead grass leaves and duff. Midday fuel moisture was determined on three dates, at 2-week intervals at the beginning, middle and end of July. The samples were collected at 10-m intervals along each transect. Samples were weighed in the field upon collection using a battery-operated digital balance. The samples were then dried at 60°C and reweighed.

Birch wood dowels of various diameters were used to characterize moisture of standard fuel classes. Dowels with diameters of 3.2, 12.5 and 31.8 mm were used to represent 1-h, 10-h and 100-h timelag fuels, respectively. These dowels were cut to lengths of 15 cm, and were dried to constant mass at 60°C. Each dowel was weighed, individually labelled and soaked overnight in water before deploying in the field.

Supports were constructed with galvanized wire to hold the fuel rods parallel to the soil at a height of 30 cm. The 1-h fuel rods were placed at 10 m intervals along each transect, while the 10-h fuels were placed at 20 intervals, and the 100-h fuels were placed only at 30 m into the forest and 30 m into the savanna. One week after deploying in the field, and at 1-week intervals thereafter, the weight of each fuel rod was determined between 13:00 and 15:00 with a field-portable digital balance. Fuel moisture was calculated as a percentage of dry fuel mass, as is typical for characterization of fuels.

To examine the relationship between tree density and fuel loads, we utilized data on tree basal area and fuel loads from two other sources (Castro & Kauffman 1998; Ottmar *et al.* 2001). We did not measure basal area at our sites, but one of our transects coincided with a separate study for which we had basal area data along the transect (E.L. Geiger 2008, unpubl. data), so we combined these data with those from the literature.

Analysis

For microclimatic variables and fuel moisture, which were measured on more than a single date at each site, data for a site were averaged over all collection dates, yielding a single value for a particular position along the transect. We then used single-factor analysis of variance (ANOVA) and regression to test for differences in fuel and microclimate characteristics across the savanna–forest boundary, utilizing data from all sites.

Modelling

We used the BehavePlus5 model (Andrews *et al.* 2008) to simulate fire behaviour over the savanna–forest boundary. This model is based on Rothermel's (1972) fire spread equations, and predicts fire behaviour for a user-defined set of fuel and environmental conditions. We parameterized the model for four points along the savanna–forest boundary corresponding to 30 and 10 m into the forest and 10 and 30 m into the savanna. For each point, these parameters were calculated from mean values of fuel loads, fuel moisture and microclimatic variables from all transects. Fire was simulated for each of these points to predict fire behaviour across the savanna–forest boundary. The model parameters used for each simulation are presented in supplemental information (Appendix S1).

The model simulations required information on fuel loads of living and dead grass, but we had only measured total grass loads, so we relied on data from previous work at the same study site to estimate these fractions. Hoffmann *et al.* (2005) measured changes in living and dead leaf area at five locations over four dates over the dry season of 2003. These were converted into percentages, which were interpolated to our study dates. These percentages were then multiplied by our measured grass fuel loads to obtain live and dead grass loads. The rate of grass senescence may have differed quantitatively between 2003 and 2008, because of higher rainfall in 2003 at the beginning of the dry season. In 2003 total precipitation for April and May was 195 mm, compared with 83 mm in 2008. However, no rainfall was recorded in either year for the sampling period (June to early August), so in both years the grass layer exhibited the typical pattern of gradual curing over the dry season.

A sensitivity analysis was performed to quantify the contributions of fuels and microclimate to the simulated differences in fire behaviour between savanna and forest. As a baseline for this analysis, we used a reference scenario with mean parameter values from all savanna and forest sites. Based on this parameter set, we then modified individual parameters or groups of related parameters to quantify the effect of various factors on fire behaviour. For example, to quantify the contribution of wind speed, we performed one run using the observed mean midday wind speed of forest sites and another run using the mean midday wind speed of savanna sites. All other parameters were identical to the reference scenario. The contribution of wind speed to fire behaviour was then calculated from the difference in simulated fire behaviour between these two scenarios. Similarly, pairs of simulations were performed to quantify the contribution of fuel characteristics, including load, moisture, bulk density and distribution of fuel classes. To quantify the role of fuel moisture, all fuel moisture parameters were modified collectively to reflect either savanna or forest conditions. To quantify the role of fuel bulk density, which is calculated as the fuel load divided by depth of fuel bed, we modified only the depth of fuel bed to generate bulk densities characteristic of savanna or forest. To quantify the role of fuel load, we modified the fuel amounts without changing bulk density or the relative proportions of the various fuel classes. To prevent changes in bulk density resulting from the changes in fuel load, the depth of the fuel bed was changed to maintain a bulk density equal to the reference scenario. To quantify the effect of fuel class distribution, the relative amount of each fuel class (1-h, 10-h, live herbaceous, live woody) was changed, while the total fuel load was kept constant. The ratio of surface area to volume of each fuel class was also changed, as this is an associated characteristic of fuel class.

RESULTS

Microclimate

There were significant gradients across the savanna–forest boundary for almost every environmental variable measured (Fig. 1). At midday, savanna had higher air temperature and lower relative humidity than forest (Fig. 1). At night, however, this pattern was reversed, with savanna having lower air temperature and higher relative humidity than forest. As a result, dew was present on the leaf wetness sensors for a mean duration of 5.6 h per night in savanna, but dew was never detected in any forest site. In savanna, dew was present most nights, but tended to become less frequent as the dry season progressed (not shown).

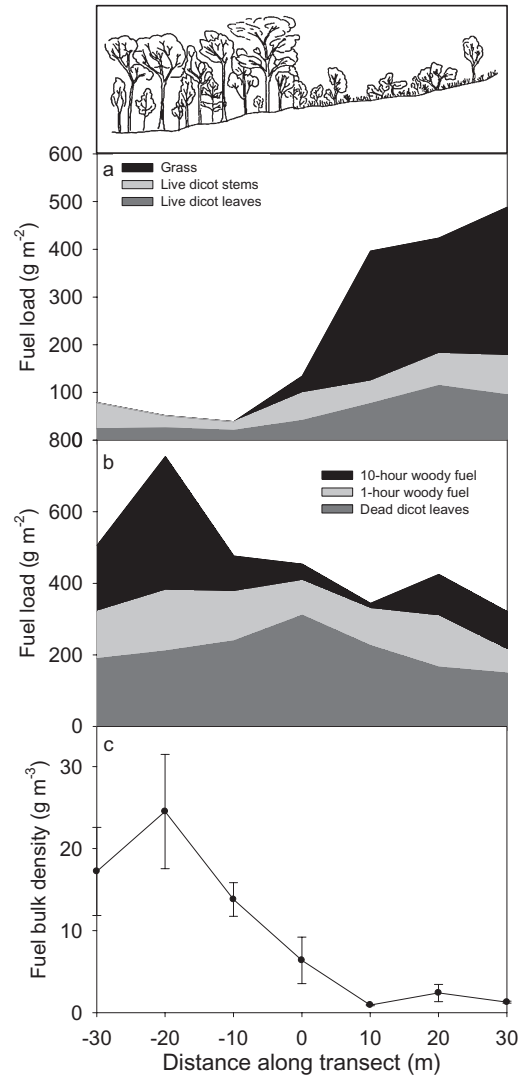Midday wind speeds were greater in savanna than in forest, but there was little wind in either environment
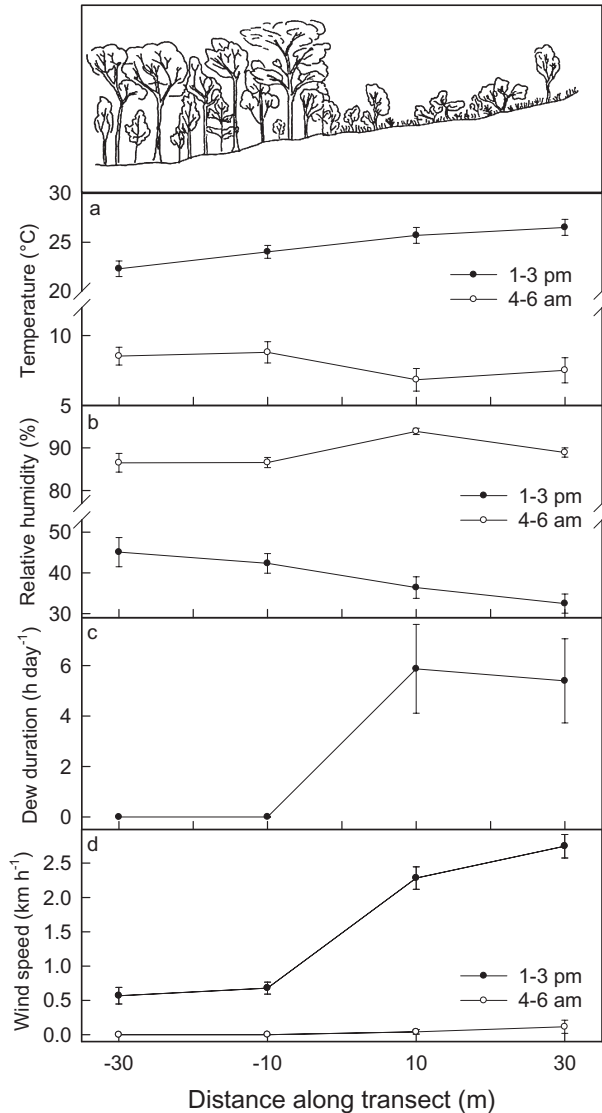
Fig. 1. Gradients of microclimate across the savanna–forest boundary. Means are based on eight transects, each of which was measured for one week. Error bars represent one standard error, calculated from the variation among transects.

Fig. 2. Gradients of fuel load (fuel mass per ground area) and bulk density (fuel mass per volume of fuel bed) across the savanna–forest boundary. Values correspond to mean values for five transects. The 1-h and 10-h fuels correspond to dead branches with diameters of <6.5 and 6.5–25.4 mm, respectively. In (a) and (b) the shaded areas are stacked.

at night. In the forest, solar radiation at 1.3 m was only 14.3% of values measured in savanna (19.6 *vs.* 137.2 $Wm^{-2} s^{-1}$), while photosynthetic photon flux density was only 10.4% of that in savanna (24.7 *vs.* 238.1 $\mu mol \, m^{-2} \, s^{-1}$). These values represent 24-h means.

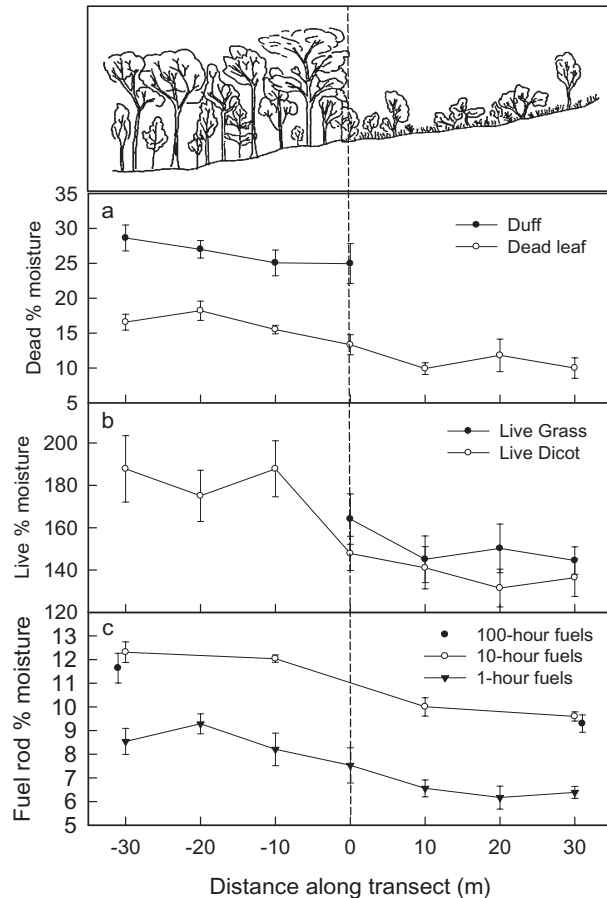## Fuels

Total fuel loads were higher, but not significantly so, in savanna than forest (0.76 *vs.* 0.57 kg m^{-2}, $F_{1,28} = 3.85$, $P = 0.06$). The composition of these fuels differed substantially, however. Most notably, grasses were absent from forest but accounted for 34% of the fuel loads in savanna (Fig. 2a). Live dicot fuels increased along the gradient, including leaves ($r^2 = 0.46$, $P < 0.0001$) and stems ($r^2 = 0.14$, $P = 0.03$, Fig. 2a). Dead woody fuels declined significantly along the gradient from forest to savanna for both the 1-h size-class ($r^2 = 0.13$, $P = 0.04$) and the 10-h size-class ($r^2 = 0.14$, $P = 0.02$, Fig. 2b). Dicot leaf litter did not vary significantly along the gradient ($r^2 = 0.044$, $P = 0.23$, Fig. 2b). Total dead fine fuels (dead grass, dead dicot leaves and 1-h woody) increased significantly along the gradient ($r^2 = 0.31$, $P = 0.01$, data not shown), with average loads of 0.35 kg m^{-2} in forest and 0.51 kg m^{-2} in savanna.

Fig. 3. Patterns of fuel moisture across the savanna–forest boundary. Moisture content is expressed as a percentage of dry fuel mass. In (a) and (b) the values were obtained from naturally occurring fuels, and in (c) the values were from wooden dowels placed in the field.

Midday moisture of dead leaves, 1-h woody fuels, 10-h fuels and 100-h fuels declined along the transect from forest to savanna ($r^2 > 0.20$; $P < 0.0001$, Fig. 3). Midday moisture of live dicot leaves also declined along the transect ($r^2 = 0.25$, $P < 0.001$).

Fuel bulk density was strongly influenced by the presence of grasses, being highest in sites with no grass biomass and dropping sharply with the presence of even a small amount of grass biomass (Fig. 4a). Biomass of grass fuels was negatively correlated with tree basal area in the dataset compiled from our work and the literature. Grasses were absent or scarce where basal areas exceed 20 m² ha⁻¹ (Fig. 4b). This decline in grass fuel loads is partially offset by an increasing load of dicot leaf litter (Fig. 4c).
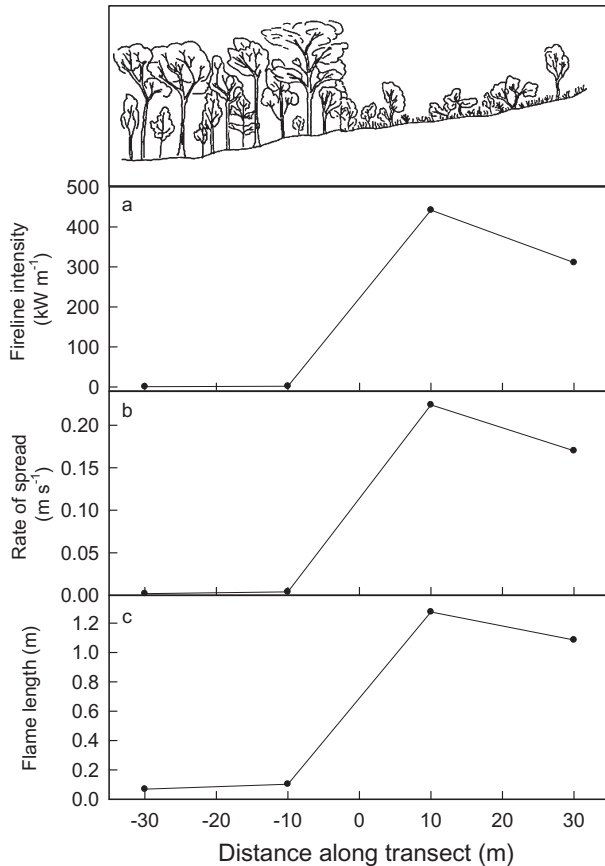
Predicted fire behaviour

Fire behaviour, as predicted by Behave5Plus, varied strongly across the savanna–forest boundary. Relative
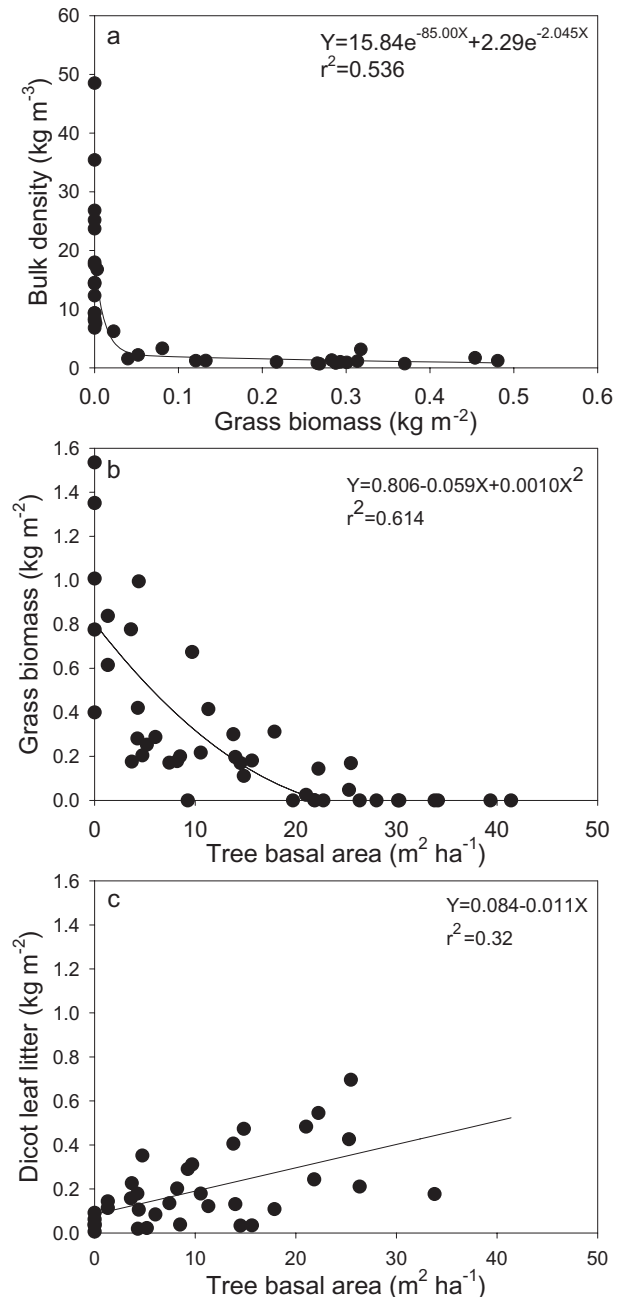
Fig. 4. Structural determinants of fuel characteristics. (a) Relationship between grass biomass and fuel bulk density. Effect of tree basal area on (b) grass biomass and (c) dicot litter. Data were compiled from Castro and Kauffman (1998), Ottmar *et al.* (2001) and the present study.

to forest, fire in savanna was predicted to have much higher flame length (1.18 *vs.* 0.09 m), intensity (376 *vs.* 1.3 W m⁻¹) and rate of spread (0.197 *vs.* 0.003 m s⁻¹ Fig. 5). The low rates of spread in forest are below thresholds for sustaining burning (0.0033–0.0042 m s⁻¹) observed in experimental studies in a variety of fuel types (Marsden-Smedley *et al.* 2001; Fernandes *et al.* 2008).
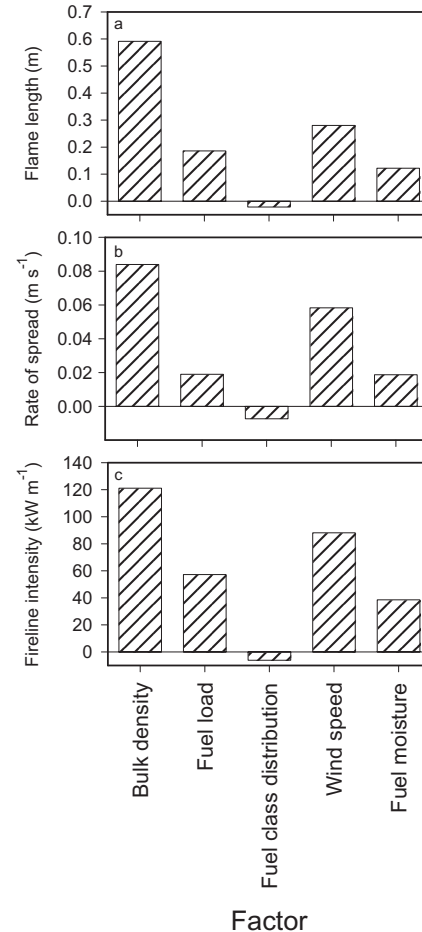
Fig. 5. Predicted patterns of fire behaviour across the savanna–forest boundary. The results were simulated by the fire behaviour model, BehavePlus 5, using inputs derived from measurements of fuel characteristics, fuel loads and wind speed shown in Figures 1–3.

Fig. 6. Contribution of several factors to the greater flame length (a), rate of spread (b) and intensity (c) in savanna relative to forest. Each value represents the first-order estimate of the effect resulting from changing a single factor in the fire behaviour model.

The sensitivity analysis revealed that fuel bulk density was the factor that most strongly contributed to the differences in fire behaviour between forest and savanna (Fig. 6). Wind speed, fuel load and fuel moisture also made substantial contributions to the difference in fire behaviour, in declining order of importance. The combined effect of fuel bulk density, fuel load and fuel class distribution (three factors determined by the amount and type of fuels present) accounted for an estimated 66% of the increase in flame length in savanna, relative to forest (Fig. 6). Similarly, these three factors accounted for 57% and 58% of the increased rate of spread and fireline intensity, respectively.

DISCUSSION

Our results reveal that the higher flammability of savanna, relative to forest, can be attributed largely to the presence of grasses, rather than to the hotter,

drier and windier microclimate. Grasses had this effect because they produce a fuel bed with low bulk density (Fig. 4a), which, in turn, was the parameter that most strongly contributed to the faster and more intense fires in savanna (Fig. 6). Although the importance of fuel bulk density at the savanna–forest boundary was inferred from model output in the present study, experimental work has repeatedly shown that low fuel bulk density enhances flammability (Scarff & Westoby 2006; Plucinski & Anderson 2008; Ganteaume *et al.* 2009). Low bulk density enhances availability of oxygen during combustion and allows thermal radiation from the flame to extend further ahead of the fire front (Rothermel 1972). This extends the distance over which the fire pre-heats the fuels, thereby increasing the rate of fire spread by bringing a greater area of unburned fuels close to the temperature of combustion.

Grasses create fuel beds with low bulk density because of their upright architecture, combined with

leaves that do not abscise when they senesce. In forest, where grasses are absent, tree leaf litter forms a more densely packed fuel bed which is not conducive to intense, rapid fires. This dense fuel packing is prevented in the savanna because the scaffold created by grasses entraps much of the fallen leaf litter. Tree and shrub litter contribute an increasing fraction of the dead fine fuel load as tree density increases (Fig. 4c), replacing the declining load of grass fuel (Fig. 4b). As tree density increases, therefore, the structure provided by grasses may be of greater consequence than their contribution to fuel loads, because grass biomass need not be high to create a fuel bed with low bulk density (Fig. 4a). As tree density reaches a level where grass biomass is greatly reduced, flammability is probably much more strongly determined by the continuity of the grass layer than by its biomass.

It has been suggested that mesic savanna trees may promote burning by generating highly flammable litter, compared with forest trees (Bowman 2000; Beckage *et al*. 2009). Although flammable resins do not appear prevalent in trees of the Cerrado, their litter may enhance flammability somewhat because they tend to produce large leaves, which can reduce bulk density by reducing fuel packing (Scarff & Westoby 2006; Plucinski & Anderson 2008) and by increasing the tendency for leaves to be entrapped by grasses. More importantly, however, savanna trees indirectly promote ecosystem flammability because of a low capacity to suppress grasses, owing to their lower leaf area index relative to forest species (Hoffmann *et al*. 2005; Gotsch *et al*. 2010) and more open, irregular architecture that allows high light availability near the ground.

In this study, we interpreted the lower fuel moisture in savanna to be an effect of microclimate. However, low bulk density and high surface area : volume ratio of savanna fuels may also enhance the rate of fuel drying independently of microclimate effects. Biddulph and Kellman (1998) concluded that savanna fuels dry more rapidly than forest fuels after rainfall largely because of their physical characteristics, rather than microclimate. It is not clear whether this effect would persist for long after rainfall events, such as in the present study which was initiated after a 6-week period with cumulative rainfall of <2 mm. If so, we may have underestimated the contribution of grasses to the flammability of savanna.

Despite the dominant role of grasses in determining flammability of savanna, the role of microclimate should not be disregarded. The higher wind speed in savanna, in particular, contributed substantially to flammability in our simulations (Fig. 6), which is consistent with observations for savanna fires (Savadogo *et al*. 2007). In simulations for Cerrado savanna,

Mistry and Berardi (2005) found that an increase in wind speed from 5 to 15 km h^{-1} resulted in fivefold increases in rate of spread and fireline intensity, as well as a doubling of flame height. Those wind speeds, however, are substantially greater than the mean midday value (2.5 km h^{-1}) we observed in savanna at a height of 1.3 m. The values we observed, however, may be uncharacteristically low for most of the savanna landscape in the Cerrado, owing to the low topographic position and proximity to tall forest. If we had compared our forest sites to more exposed savanna sites with greater wind speed, wind speed would have made an even greater contribution to the flammability of savanna.

Our simulations, which correspond to conditions in the middle of the dry season, predicted rates of fire spread in forest (0.003 m s^{-1}) that are too low to sustain fires, based on minimum thresholds observed for experimental burns (0.0033–0.0042 m s^{-1}) (Marsden-Smedley *et al*. 2001; Fernandes *et al*. 2008). Consistent with this, savanna fires commonly fail to propagate into tropical forest (Hennenberg *et al*. 2006), though forests in the Cerrado region do sometimes burn late in the dry season (Hoffmann *et al*. 2009). Tropical forests can also become flammable following selective logging (Uhl *et al*. 1988; Cochrane *et al*. 1999; Nepstad *et al*. 2001), largely because of changes in microclimate which accelerate fuel drying (Uhl & Kauffman 1990; Ray *et al*. 2005, 2010). Thus where grasses are absent, microclimate can be particularly important in governing the transition to a more flammable state.

Understanding the drivers of flammability is inherently complicated by non-linear effects and strong interactions among factors. For example there is a strong interaction between the effects of fuel moisture and bulk density, such that fuels with low bulk density can sustain burning at higher moisture contents than is possible in dense fuels (Ganteaume *et al*. 2009). Also, rate of spread is particularly insensitive to changes in fuel moisture over a range of 10–20%, corresponding to our measured values for forest litter, but as fuel moisture drops below 10%, rate of spread increases dramatically (Rothermel 1972). Such complications could cause a shift in the relative importance of grasses *versus* microclimate towards the end of the dry season as fuels continue to dry. It is not likely, however, that this could have resulted in frequent burning of forest under natural fire regimes in the Cerrado, as most lightning-caused fires originate in the wet season (Ramos-Neto & Pivello 2000) when fuel moisture is high and forests are not susceptible to burning. But with the arrival of indigenous peoples, who utilize fire throughout the dry season (Mistry *et al*. 2005), microclimatic influence over forest flammability should have become increasingly important, as is also the case under current land-use practices.

The difference in flammability between savanna and forests has important consequences for vegetation dynamics. In areas of humid tropical forest where the biota has had relatively little exposure to fire, burning can have devastating effects, often causing more than 40% mortality to trees (Woods 1989; Kauffman 1991; Holdsworth & Uhl 1997; Cochrane & Schulze 1999; Barlow & Peres 2008). In transitional forests, where historical exposure to fire has probably been much higher, these fires may cause little tree mortality because most species can resprout (Fensham *et al.* 2003; Balch *et al.* 2008; Hoffmann *et al.* 2009). Nevertheless, the frequent burning in savanna prevents forest expansion because seedlings of forest species tend to be vulnerable to burning (Hoffmann 2000; Gignoux *et al.* 2009), and thin-barked forest species are particularly susceptible to a demographic bottleneck, which prevents saplings from reaching maturity because of repeated top-kill (Hoffmann *et al.* 2009). Frequent burning in savanna therefore maintains the open canopy which, in turn, favours the grasses that promote burning. The abrupt decline in flammability at the forest edge therefore helps sharpen the boundary by preventing the spread of most savanna fires into the forest. While these feedbacks between fire and vegetation have been widely recognized (Wilson & Agnew 1992; Bowman 2000; Beckage & Ellingwood 2008), we believe that ours is the first study to demonstrate that the feedback is mediated primarily by the structure of grasses, rather than the microclimatic consequences of tree cover.

This result emphasizes the significance of the worldwide expansion of C_4 grasses <10 million years ago (Cerling *et al.* 1997). Before this, vegetation–fire feedbacks were probably much weaker in the tropics and subtropics than they are today, and fire was probably not frequent in areas now dominated by tropical savanna. The feedback between grasses and fire which currently maintains mesic savannas may also have been instrumental in the expansion of C_4 grasses in the Miocene (Bond *et al.* 2003; Keeley & Rundel 2005; Osborne 2008). Curiously, however, the Cerrado region is unique among tropical savannas because a C_3 grass (*Echinolaena inflexa*) makes up a large fraction of the grass biomass in some sites. If this species was widespread in the Cerrado before the expansion of C_4 grasses, it appears not to have generated a strong fire cycle, as evidenced by the recent origin (<10 mya) of fire-adapted woody plants in the Cerrado (Simon *et al.* 2009). An absence of such a feedback could be explained by lower flammability, lower productivity and higher rates of decomposition of C_3 compared with C_4 grasses (Bond 2008; Ripley *et al.* 2010).

Currently, areas of the Cerrado and other savannas are subject to an exacerbated grass-fire feedback resulting from invasive exotic grasses that produce higher fuel loads than native grasses (Hoffmann *et al.* 2004; Setterfield *et al.* 2010; Martins *et al.* 2011) and much more intense fires (Berardi 1994; Setterfield *et al.* 2010). At our study site, the African grass *Melinis minutiflora* is locally abundant in high-nutrient soils near gallery forests (Hoffmann *et al.* 2004), while the native fern, *Pteridium aquilinum*, has recently become invasive at many wet gallery forest edges (W.A. Hoffmann 1992–2010, pers. obs.). The latter is similar to C_4 grasses in that it generates high loads of fine fuels that remain upright following senescence, in addition to being favoured by fire (Alonso-Amelot & Rodulfo-Baechler 1996; Silva Matos *et al.* 2002). It is important to understand these and other changes to vegetation–fire interactions that have the potential to change the structure and distribution of tropical savannas and forests in the future.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parameter values used to simulate fire behaviour across the savanna–forest boundary.