CSIRO PUBLISHING

International Journal of Wildland Fire **2014**, *23*, 410–416
http://dx.doi.org/10.1071/WF13119

Research Note

Effect of patches of woody vegetation on the role of fire in tropical grasslands and savannas

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Abstract. In tropical grasslands and savannas, fire is used to reduce woody vegetation expansion. Woody vegetation in these biomes is often patchily distributed, and micro-climatic conditions can largely vary locally with unknown consequences for fire effects. We hypothesised that (1) fire has higher temperature and maintains high temperatures for a longer period at the windward side than at the leeward side of wooded patches, (2) this difference increases with patch size, (3) fire has a larger effect on woody vegetation at the windward side than at the leeward side of wooded patches and (4) this effect increases with patch size. We planted tree seedlings around wooded patches in a grassland and burnt these plots. We found that fire had a lower temperature and had an elevated temperature for a shorter time period at the leeward side of wooded patches than at the windward side. Also, we found smaller effect of fire on the seedlings at the leeward side. We conclude that patches of woody vegetation can have a large effect on the role of fire in tropical grasslands and savannas. This effect suggests a 'safe zone' for seedlings at the leeward side, which consequently promotes woody vegetation expansion. This paper contributes to understanding of the effect of patchiness of woody vegetation on the role of fire in tropical grasslands and savannas in reducing woody vegetation expansion.

Additional keywords: bush encroachment, fire temperature, micro-climatic variation, seedling growth, spatial heterogeneity.

Received 24 July 2013, accepted 12 November 2013, published online 31 March 2014

Introduction

In tropical grasslands and savannas, fire is a major determinant of vegetation structure (Heisler *et al.* 2003; Bond *et al.* 2005). In these systems, grass biomass is the major fuel for fire, determining fire intensity and hence the effect of fire on woody vegetation (Van Langevelde *et al.* 2003), whereas dense woody vegetation without herbaceous understorey limits fire spread (Hennenberg *et al.* 2006). Fire can limit woody cover by preventing the establishment and release from seedlings and saplings to adult trees rather than by killing existing adult trees (Hoffmann 1996, 1999; Bond 2008). Besides grass biomass as fuel load, fire spread and intensity is determined by weather and micro-climatic conditions, of which relative humidity, ambient temperature and wind speed are the most important (Higgins *et al.* 2000; Govender *et al.* 2006).

The effect of fire on trees is well studied: for example, on the woody cover in savannas (Lehmann *et al.* 2008; Sankaran *et al.* 2008), on the growth of individual trees (Murphy *et al.* 2010), in relation to the spatial distribution of trees (Groen *et al.* 2008; Holdo *et al.* 2009), on the stability of wooded patches in a grassland (Mourik *et al.* 2007), and in relation to the co-existence of trees and grasses in savannas (Staver *et al.* 2009). Woody vegetation in these biomes is often patchily distributed. However, the effect of the patches of woody vegetation on grass fire is still unknown, although we may expect that micro-climatic conditions vary locally in spatially heterogeneous vegetation (Breshears *et al.* 1998; Vanwalleghem and Meentemeyer 2009; Villegas *et al.* 2010). For example, it is well known from studies on wind erosion that vegetation can have dramatic effects on wind speed (e.g. Stockton and Gillette 1990).

Differences in wind speed may cause differences in micro-climatic conditions between the leeward (direction downwind) and windward (direction upwind) side of a patch of woody vegetation due to its wind-blocking capacity (Leenders *et al.* 2007; Al-Amin *et al.* 2010). These differences between the leeward and windward side potentially increase when the diameter and density of these patches increase

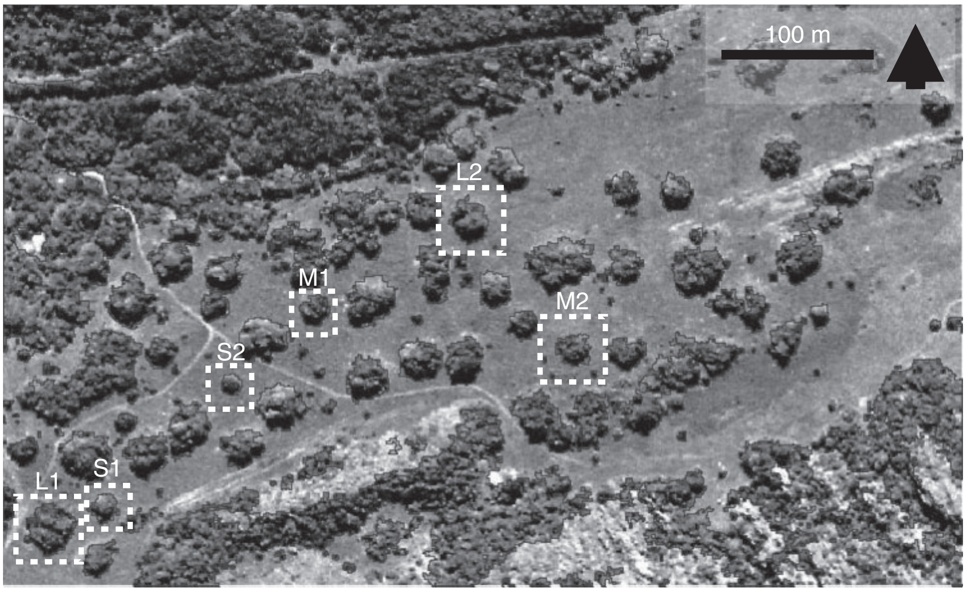

Fig. 1. Wooded patches at Lajuma Research Centre used for the burning experiment. The area of the small patches was S1 = 280 m^2, S2 = 180 m^2; the medium-sized patches, M1 = 355 m^2, M2 = 430 m^2; and the large patches, L1 = 1110 m^2, L2 = 620 m^2. The contours of the patches were S1 = 50.5 m, S2 = 45.3 m, M1 = 71 m, M2 = 69.3 m, L1 = 98.8 m, and L2 = 88.1 m.

(Mohammed *et al.* 1996; Bird 1998). We expected that these differences in micro-climatic conditions due to differences in wind speed would cause variation in fire characteristics in heterogeneous vegetation, because fire intensity and temperature are a function of wind speed (Byram 1959; Trollope 1984). High wind speeds result in more intense fire because more oxygen is available, allowing better combustion. We use temperature as proxy for the intensity of fire (energy release rate) (Keeley 2009). We hypothesise that (1) fire has higher temperature and maintains high temperatures for a longer period at the windward side than at the leeward side of wooded patches and (2) this difference increases with increasing patch size, that is, an interaction between patch side and patch size can be expected. The windward side of a wooded patch is the side where the fire front arrives first, and the leeward side is the opposite side of the patch relative to the fire front. If fire indeed releases energy at a higher rate at the windward side than at the leeward side of wooded patches, we can also expect differences in the effect of fire, particularly on young trees, at these sides. We thus hypothesise that (3) at the windward side, fire has a larger effect on young trees than at the leeward side of wooded patches and (4) this effect increases with patch size, that is, an interaction between patch side and patch size can be expected. To test these hypotheses, we plant tree seedlings around established wooded patches of various sizes in a grassland and burn these plots. We measure several characteristics of the young trees to examine the effect of fire on their performance: height of the plants, stem diameter at the base, total leaf area and biomass of the seedlings. We can expect that the differences in the characteristics of the young trees planted at these different sides will increase after the fire as recovery depends on fire characteristics (cf. Williams *et al.* 1999).

Methods

Site description

The experiment was conducted at the Lajuma Research Centre (29°26′E and 23°01′S, ~1420 m above sea level), located in the Soutpansberg Conservancy in the north-east of South Africa. The area has an average annual rainfall of 730 mm $year^{-1}$. The summer period accounts for most of the rainfall as 92% of the total precipitation falls between October and April. The vegetation varies from mountainous grassland (Soutpansberg Summit Sourveld), consisting of generally unpalatable grass species, to savanna (Soutpansberg Mountain Bushveld) and forest (Northern Mistbelt Forest). Part of the upper reaches is characterised by patches of semi-deciduous forest in a grass matrix. These wooded patches are variable in size, ranging from 150 to 1200 m^2 and ~500 m^2 on average (Mourik *et al.* 2007). The boundaries of these wooded patches are characterised by a sharp transition from trees and shrubs to grassland. The grass matrix consists of short acidophilic, unpalatable grass species and is dominated by *Loudetia simplex*. The wooded patches and surrounding grassland had not burnt over the previous 10 years until we conducted our experiment, but at unknown intervals before then.

Effect of size and side of wooded patches on fire characteristics

To test the differences in fire characteristics between the different sides of wooded patches relative to the fire front, we performed experimental burns around six wooded patches of different sizes: small, medium and large (Fig. 1). The burnings happened as head fire at the end of the dry season under low wind speed conditions for safety reasons (the burnings started between 1000 and 1130 hours on 7 and 8 October 2008).

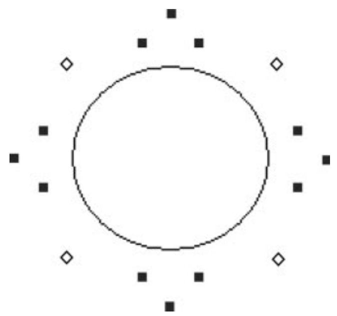

Fig. 2. Location of the thermocouples (black squares) and grass samples (white diamonds) around a wooded patch. The thermocouples situated closest to the patch were placed 2 m away from the edge with 1 m in between the thermocouples. The grass samples were harvested to measure moisture content of the grass.

Fire characteristics were measured at point locations around these six wooded patches using thermocouples connected to HOBO Type K Thermocouple Family loggers that recorded temperatures every half second. Three thermocouples were placed in a triangle at four sides of each patch (Fig. 2).

We measured the following variables that affect fire characteristics: grass biomass near the thermocouples, average moisture content of the grass, ambient temperature, wind speed and relative humidity during the fire. To avoid destructive harvesting of the grass at the locations of the thermocouples, we measured grass biomass and sward height, using a disc pasture meter (DPM) (Zambatis *et al.* 2006), in 30 plots of 25×25 cm at different locations in the grassland surrounding the wooded patches to determine the relationship between dry grass biomass and sward height. We found the following relationship:

$$\text{Biomass} = 131.5 + 10.7 \times \text{Grass height}$$

where Biomass is measured grams per square metre and Grass height in centimetres (ordinary least square regression, $n = 30$, $R^2 = 0.76$, for the coefficient for grass height: $t = 9.552$, $P < 0.001$). Using this relationship, we could estimate grass biomass on the days when the burning took place by taking DPM measurements around the patch near the thermocouples that were furthest away from the wooded patch (Fig. 2). To determine average moisture content of the grass, we clipped the grass at four different locations around each patch (Fig. 2), and dried the samples in an oven at 80°C for 48 h. Ambient temperature, wind speed and relative humidity at the moment of burning were obtained from a weather station ~2 km from the burning site.

We measured two fire characteristics: maximum temperature (°C) and the duration of the period that the temperature of the fire was above 40°C (s). We tested the effects of the size of the wooded patches and the side relative to the fire front, and the interaction between size and side, on these fire characteristics using a linear mixed model (LLM). We nested the data from the loggers within each patch. We transformed the dependent variables to meet the assumptions of the test. We included the climate and grass variables as covariates. Given our *a priori* expectations, we used the least squared differences (l.s.d.) test for pair wise comparisons between the different sizes and sides of the patches.

Effect of fire on tree seedlings for different sizes and sides of wooded patches

To test the effect of fire on young woody vegetation, we planted six 2-year old seedlings of locally available *Rhus lancea* in 40×60-cm blocks in the grassland before the burning experiment, on all four sides of the six wooded patches. We placed the thermocouples to measure the fire characteristics around these locations. We used *R. lancea* because it is abundant in the wooded patches and its seedlings were in large supply. It is an evergreen tree and it is considered to be fire resistant. Seedlings were also planted in the same way around two large wooded patches that were not burnt (similar in size to the burnt large patches). All seedlings were protected from browsing. Each block contained six seedlings, amounting to 192 in total. The seedlings were given 6 L of water per block at the moment of planting and once a week thereafter until the start of the wet season (in total three times). To determine the characteristics of the seedlings, we measured six times the height of the seedlings (cm), the stem diameter at the base (mm) and the total leaf area of the plant (mm^2): once before the fire (30 September 2008) and five times after the fire (14 October, 28 October, 11 November, 25 November and 9 December 2008). During the five sample dates after the fire, we also measured the height of new shoots (cm) that occurred after fire and the stem diameter at the base of these new shoots (in mm). To determine the total leaf area, pictures were taken of the seedlings with squared paper held under four representative leaves of that plant. Total leaf area was calculated as the average leaf area × the total number of leaves. Biomass of each seedling was measured at the end of the experiment after harvesting and drying the plants (oven drying at 80°C for 48 h).

First, we compared the seedling characteristics between the patches with and without fire using *t*-tests. We used repeated-measure Anova to test for differences in the seedling characteristics, measured on the five sample dates after the fire, between the different patch sizes and the sides of the wooded patches where the seedlings were planted relative to the fire front. We also included the interaction between patch size and patch side. For the seedling biomass, we used Anova to test for differences between patch sizes and sides, and added also the interaction between patch size and patch side. We included maximum fire temperature and fire duration as covariates in each model. For the Anova tests, we applied the commonly used Type III sum-of-squares method.

Results

Effect of size and side of wooded patches on fire characteristics

We found a significantly higher maximum temperature and longer fire duration at the windward side than at the leeward side of the large wooded patches, whereas there was no significant difference between the windward and leeward side of the small and medium-sized wooded patches (Fig. 3). When relative humidity was added as a covariate for explaining maximum temperature, and ambient temperature for fire duration, both had

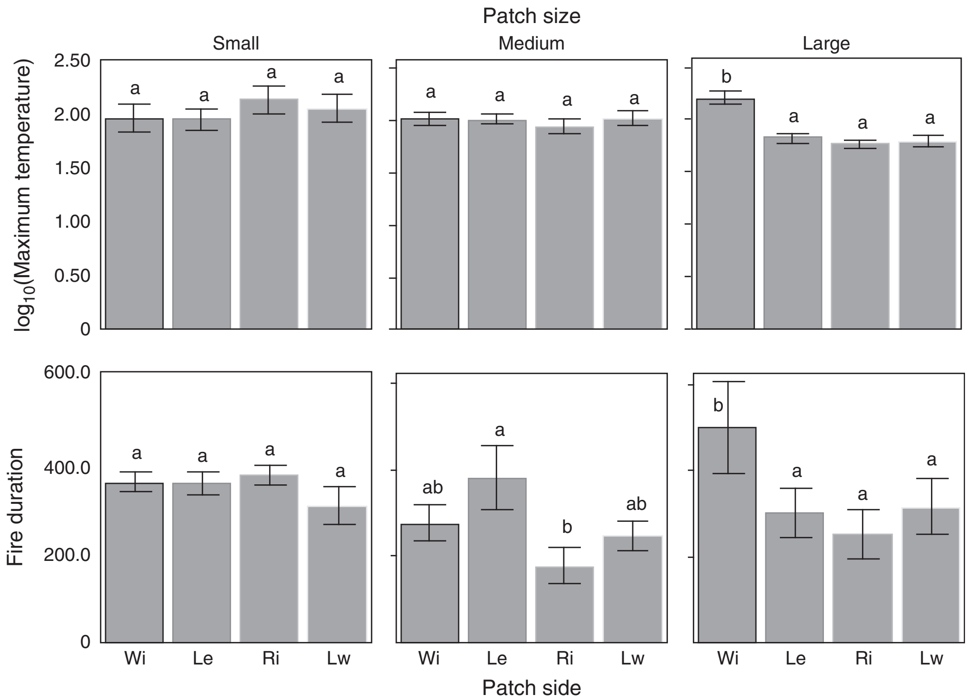

Fig. 3. Effect of the size of the wooded patches (small, medium and large) and the side of the wooded patches relative to the fire front (Wi, windward; Le, left side; Ri, right side; Lw, leeward side) on two fire characteristics, namely the maximum temperature (log_{10}-transformed) and the fire duration. The statistics are given in Table 1. The error bars show one standard error. Letters indicate significant differences within a panel.

Table 1. Results of the linear mixed models with two fire characteristics, namely maximum temperature (log_{10}-transformed) and the fire duration, explained by the size of the wooded patches, the side of these patches relative to the fire front (windward, left and right side and leeward side), and the interaction between patch size and side

We also added climate and grass variables to the models, but we could only significantly retain relative humidity and ambient temperature (both had a negative effect) in some models. The *F*- and *P*-values are given

	Maximum temperature		Duration	
	F	*P*	*F*	*P*
Patch size	5.25	0.008	1.02	0.340
Patch side	1.53	0.219	3.27	0.029
Patch size × patch side	2.66	0.026	2.42	0.040
Relative humidity	4.31	0.043	–	–
Ambient temperature	–	–	13.35	0.001

a negative effect (Table 1). The mean relative humidity was 49.0% ± 11.1 standard deviation (s.d.), and the mean ambient temperature was 21.7°C ± 2.2. Grass biomass (467 g m^{-2} ± 121) and wind speed (1.4 m s^{-1} ± 0.6) did not significantly influence the measured fire characteristics.

Effect of fire on tree seedlings for different sizes and sides of wooded patches

We found significantly smaller seedlings around the burnt large wooded patches than around the large patches that were not burnt (*t*-test, d.f. = 14, *t* = 4.20, *P* = 0.001: 24.2 cm ± 0.76 standard error (s.e.) *v.* 28.8 cm ± 0.78), whereas there were no differences in stem diameter (*t*-test, d.f. = 14, *t* = 0.74, *P* = 0.470: 3.73 mm ± 0.13 *v.* 3.89 mm ± 0.16). When testing for the effect of the size and the side of the burnt patches on the plant characteristics, we found that the seedlings were not significantly taller around the medium-sized patches (26.1 cm ± 0.21) than around the large patches (24.2 cm ± 0.76), and seedlings around the medium-sized patches were significantly taller than around the small patches (23.1 cm ± 0.69) (repeated-measure Anova: $F_{2,12} = 6.15$, $P = 0.014$). There were no differences in seedling height at the different sides of the wooded patches ($F_{3,12} = 0.74$, $P = 0.550$, Fig. 4), and also the interaction between size and side was not significant ($F_{6,12} = 1.04$, $P = 0.445$).

For the height and diameter of new shoots after the fire, we did not find a difference between the sides of the wooded patch or the size of the patches (Fig. 4; repeated-measure Anova for height of the new shoots: patch size $F_{2,12} = 0.60$, $P = 0.565$, patch side $F_{3,12} = 1.61$, $P = 0.239$, patch size × patch side $F_{6,12} = 0.47$, $P = 0.818$; repeated-measure Anova for diameter of the new shoots: patch size $F_{2,12} = 0.95$, $P = 0.413$, patch side $F_{3,12} = 0.656$, $P = 0.595$, patch size × patch side $F_{6,12} = 0.28$, $P = 0.936$).

For total leaf area, we found an effect of patch side (repeated-measure Anova: $F_{3,18} = 3.49$, $P = 0.037$). The total leaf area was higher at the leeward side of the wooded patches (Fig. 4). For the large patches, we observed a larger difference in total leaf area between the leeward and windward side than for the small

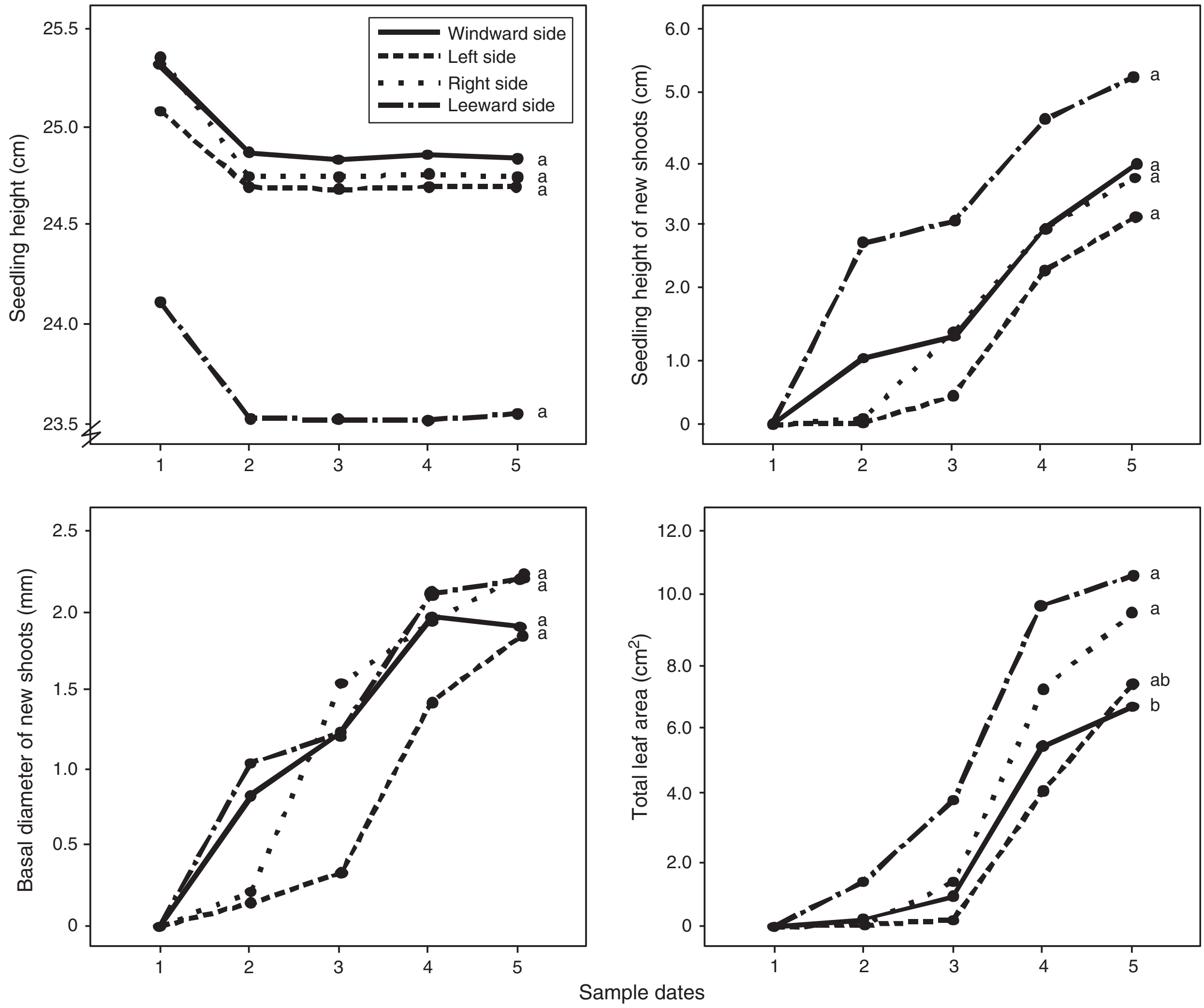

Fig. 4. Change in seedling characteristics, height (cm), height of new shoots after the fire (cm), basal diameter of new shoots (mm), and total leaf area of a plant (cm^2) for the four different sides of the wooded patches (windward, left side, right side and leeward side), measured during the five sample dates after the fire (14 October, 28 October, 11 November, 25 November and 9 December 2008). Letters indicate significant differences between the sides of the wooded patches. Note the range of the *y*-axis in the panel illustrating the height of the seedlings.

patches: total leaf area was 24.9% ± 0.2 s.e. lower at the windward side than at the leeward side of the small patches, and this was 18.4% ± 37.2 for the medium-sized patches and 54.7% ± 8.8 for the large patches. However, the effect of patch size on total leaf area was not significant ($F_{2,18} = 1.75$, $P = 0.202$), and also the interaction between patch side and size was not significant ($F_{6,12} = 0.33$, $P = 0.906$). We did not find a difference in seedling mass between the different patch sizes or sides (Anova, patch size: $F_{2,12} = 0.04$, $P = 0.966$, patch side: $F_{3,12} = 0.123$, $P = 0.945$, interaction between size and side: $F_{6,12} = 0.49$, $P = 0.807$). Mean dry weight of the seedlings was 16.5 g ± 1.6 s.d.

Discussion

In this paper, we show that patches of woody vegetation affect the role of grass fire. We found that fire had a lower temperature and had an elevated temperature for a shorter time period at the leeward side of wooded patches than at the windward side, as predicted. Also as expected, the differences in these fire characteristics were not significantly different between the windward and leeward side of the smaller patches, whereas they were higher at the windward side of the larger patches than at the leeward side. Considering the lower temperature and shorter duration, fire at the leeward side of the wooded patches did not change into a so-called backfire (fire against the wind direction, Trollope *et al.* 2002) as might happen due to turbulence behind wind-blocking elements (Wang *et al.* 2001). Backfire has a lower speed and consequently would have a longer duration (Shea *et al.* 1996), and is known to have a large effect on the vegetation due to higher temperatures (Trollope *et al.* 2002), especially close to the ground.

Besides patchiness of woody vegetation, other causes for spatial variation in fire characteristics may be due to patchy grass production (Chidumayo 1997), patchy herbivory (Coughenour 1991), the effects of tree neighbourhoods on grass production (Mordelet and Menaut 1995) and different grass moisture content (Vetaas 1992). However, we did not find an effect of grass biomass or grass moisture content on the measured fire characteristics, so the differences in fire characteristics can be explained by the location relative to the fire front. The lack of effects of these variables could be due to the small range of values we measured in this experiment. We also measured fire temperature and duration at the left and right side of the wooded patches. We found that they were not different from the leeward side of the wooded patches. A possible explanation for the difference between the windward side and the left and right side is that, at the latter positions, the fire front is only approximately half the size compared with the fire front at the windward side so that the release of heat energy to ignite the grass might be lower (Byram 1959).

Spatial variation in fire characteristics might result in spatial variation in seedling establishment and tree release. We found that fire had a larger effect on seedling height compared with seedlings that were not subjected to the burning. Between the different sides around the wooded patches, there was no difference in height and diameter of existing and new shoots of the seedlings over time after the fire, despite a higher fire temperature and longer duration of high temperature at the windward side of the large patches. The absence of an effect on the stem and twigs might be related to the fire resistance of the tree species we used. The total leaf area at the front side was significantly lower than the total leaf area at the leeward side. This lower total leaf area for the seedlings may have reduced the re-sprouting capacity of the plants (Givnish *et al.* 1986; Waters *et al.* 2010). Although we observed a larger difference in total leaf area between the leeward and windward side of the large patches than of the small patches, the effect of patch size on total leaf area was not significant, perhaps due to low sample size. Due to regulations governing controlled burning of vegetation in the area, we burnt under mild weather conditions that did not allow a very intense fire. These conditions prevented high fire temperatures and consequently mortality of our seedlings. We expect that more intense fire would increase the differences between the leeward and windward sides of the patches with larger effects on the seedlings at the windward sides.

This paper contributes to understanding of the effect of woody vegetation patches on the role of fire in tropical grasslands and savannas in reducing woody vegetation expansion. It has been shown that fire can enhance tree aggregation by burning seedlings and saplings that are isolated from wooded patches, whereas seedlings in the proximity of adult trees might be protected against fire (Hochberg *et al.* 1994; Groen *et al.* 2008). Although these isolated saplings are not necessarily killed by the fire, they are trapped in the flame zone (Bond and Van Wilgen 1996). Our results suggest that the effect of fire on patches of woody vegetation is localised, namely at the windward side of these patches, whereas the leeward side, especially of large wooded patches, might experience a smaller effect of fire. These wooded patches could create a 'safe zone' at the leeward side where seedlings can establish and saplings can grow above the flame height. This suggests that large patches could facilitate tree release at the leeward side of these patches in frequently burnt areas, given the prevailing wind direction. Yet, tree species vary greatly in seedling tolerance to burning (Hodgkinson 1991). Seedlings of some woody species, especially in frequently burnt areas, can acquire the ability to re-sprout within their first growing season without being killed (Hoffmann 1999; Bond and Midgley 2003). Other seedlings are less tolerant to fire and can be killed by fire years after establishment (Bond 2008). Seedlings of these species especially can benefit from the localised reduced effect of fire in spatially heterogeneous vegetation.

Acknowledgements

We thank Winston Trollope and Oldrich van Schalkwijk for technical and practical advice and Femke Koopmans and Jana Lindenborn for field assistance.

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