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Research Article

Ecological Implications of Fine-Scale Fire Patchiness and Severity in Tropical Savannas of Northern Australia

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ABSTRACT

Understanding fine-scale fire patchiness has significant implications for ecological processes and biodiversity conservation. It can affect local extinction of and recolonisation by relatively immobile fauna and poorly seed-dispersed flora in fire-affected areas. This study assesses fine-scale fire patchiness and severity, and associated implications for biodiversity, in north Australian tropical savanna systems. We used line transects to sample burning patterns of ground layer vegetation in different seasons and vegetation structure types, within the perimeter of 35 fires that occurred between 2009 and 2011. We evaluated two main fire characteristics: patchiness (patch density and mean patch length) and severity (inferred from char and scorch heights, and char and ash proportions). The mean burned area of

RESUMEN

El estudio del impacto del fuego en pequeños parches de vegetación tiene muchas implicancias para los procesos ecológicos y la conservación de la biodiversidad. Este impacto puede provocar extinciones locales o recolonizaciones por fauna relativamente inmóvil o semillas poco dispersadas en parches afectados por el fuego. Este estudio evaluó el impacto del fuego y su severidad a pequeña escala en parches de vegetación, además de sus implicancias para la biodiversidad, en ecosistemas de sabanas tropicales del norte de Australia. Utilizamos transectas lineales para muestrear patrones de quema de la vegetación a ras del suelo en temporadas y estructuras vegetales diferentes dentro del perímetro dibujado por 35 incendios ocurridos entre el 2009 y el 2011. Evaluamos dos características de los incendios: los parches de vegetación quemados (su densidad y longitud media) y la severidad (inferida por las marcas de carbón, la altura de quemado del tronco y las ground vegetation was 83% in the early dry season (EDS: May to July) and 93% in the late dry season (LDS: August to November). LDS fires were less patchy (smaller and fewer unburned patches), and had higher fire severity (higher mean char and scorch heights, and twice the proportion of ash) than EDS fires. Fire patchiness varied among vegetation types, declining under more open canopy structure. The relationship between burned area and fire severity depended on season, being strongly correlated in the EDS and uncorrelated in the LDS. Simulations performed to understand the implications of patchiness on the population dynamics of fire-interval sensitive plant species showed that small amounts of patchiness substantially enhance survival. Our results indicate that the ecological impacts of high frequency fires on fire-sensitive regional biodiversity elements are likely to be lower than has been predicted from remotely sensed studies that are based on assumptions of homogeneous burning.

proporciones de carbón y ceniza). La media de vegetación quemada a ras de suelo fue del 83% al comienzo de la estación seca (EDS: mayo a julio) y del 93% al final de la misma (LDS: agosto a noviembre). Los incendios LDS fueron menos irregulares (parches más pequeños y con menos áreas sin quemar), y experimentaron mayor severidad (media más alta de altura de quemado y el doble de proporción de ceniza) que los incendios EDS. Los parches quemados variaron entre especies vegetales, disminuyendo en bosques con doseles más abiertos. La relación entre superficie quemada y severidad dependió de la estación, correlacionándose altamente en los EDS y sin correlación en los LDS. Las simulaciones efectuadas para evaluar las implicancias de los parches en la dinámica poblacional de especies vegetales sensibles al intervalo de incendios demostraron que una pequeña cantidad de parches aumentan considerablemente la supervivencia de estas especies. Nuestros resultados indican que los impactos ecológicos resultantes de incendios de alta frecuencia sobre especies vegetales sensibles al fuego son menores que los predichos por estudios realizados con imágenes satelitales basados en la premisa de quemas homogéneas.

Keywords: biodiversity, fire patchiness, fire patterns, fire-sensitive plants, fire severity, northern Australia savannas, season, unburned patch, vegetation communities

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INTRODUCTION

North Australian tropical savannas cover 1.9 M km^2 and are among the most fire-prone ecosystems in the world. Over that vast region, annual fire frequencies range from over 50% in higher rainfall regions to <5% in heavily grazed semi-arid savanna regions, with an overall mean frequency of 19%, over the period from 1997 to 2005 (Russell-Smith *et al.* 2007). In these ecosystems, fire is a natural ecological process required for maintaining biological diversity (Russell-Smith *et al.* 2002*a,* Bowman *et al.* 2003). Fire patchiness is an important ecological component of savanna fire regimes because unburned patches can influence a variety of processes, including local extinction of and recolonisation by relative immobile fauna and poorly seed-dispersed flora (Prada 2001, Russell-Smith *et* *al.* 2002*b,* Gill *et al.* 2003, Parr and Chown 2003, Price *et al.* 2003). Understanding fire patchiness has significant implications for biodiversity conservation and ecologically sustainable fire management in fire-prone systems (Bradstock *et al.* 1998, Ooi *et al.* 2006, Parr and Andersen 2006, Driscoll *et al.* 2010).

In general, a patch can be defined as a set of contiguous, adjacent observations of the same attribute (Turner 1990) and is therefore dependent on the scale of observations. This study focused on the distribution of burned and unburned ground layer patches contained within fire perimeters; that is, within the entire outer edge or boundary of a fire. The distribution of unburned patches within a burned area can be deterministic, attributed to a landscape condition (e.g., heterogeneity of fuel type, topography, drainage lines), fire behaviour, or weather; or it may be stochastic, regarded as being caused by chance, if their place of occurrence in successive fires is unpredictable (Gill *et al.* 2003). These unburned patches provide refuge for relatively immobile animals and fire-sensitive plants, becoming an important source for the propagation of seeds, especially when an area is burned so frequently that local extinction of obligate-seeder plant species can occur (Bradstock *et al.* 1998, Edwards *et al.* 2001*,* Burrows and Wardell-Johnson 2003, Panzer 2003). Fire patchiness also has implications for watershed hydrology and soil stability, and may be applied strategically to reduce the risk of hazardous wildfires (Bradstock *et al.* 1998).

Prior to European colonisation, indigenous (Aboriginal) people managed north Australian savanna landscapes with fire, commencing burning in the early part of the dry season, (EDS; May to July) and producing highly patchy fires (Russell-Smith 1995, Yibarbuk *et al.* 2001, Garde *et al.* 2009). Traditional burning was progressively abandoned throughout most of northern Australia as a consequence of European colonisation. Contemporary fire regimes are characterised by frequent, extensive and homogeneous, anthropogenic fires occurring mostly in the late dry season (LDS; August to November), under severe fire-climate conditions (Gill *et al.* 1996). Such fire regimes are also the source of significant emissions of accountable greenhouse gases, and annually represent 2% to 4% of Australia's National Greenhouse Gas Inventory (AGO 2013). In northern Australia, contemporary fire regimes and associated reduction in fire patchiness are implicated in population declines of a range of obligate-seeder taxa, including the native cypress *Callitris intratropica* L. (Bowman and Panton 1993) and the endemic myrtaceous shrub *Petraeomyrtus punicea* L. (Russell-Smith *et al.* 2002*a*), granivorous birds (Franklin 1999) and small mammals (Braithwaite 1995, Woinarski *et al.* 2001, Price *et al.* 2005).

Various studies have been undertaken to better understand fire patchiness, for a variety of ecological and associated land management purposes, in the USA (Turner *et al.* 1994, Slocum *et al.* 2003), southern Africa (Hudak *et al.* 2004), Spain (Román-Cuesta *et al.* 2009), and Australia (Russell-Smith *et al.* 1997, Allan 2001, Russell-Smith *et al.* 2002*b,* Russell-Smith and Edwards 2006). Russell-Smith and Edwards (2006) reported that EDS fires have 80% probability of being of low severity and would therefore be expected to have greater internal patchiness than LDS fires. In semi-arid savannas, Allan (2001) reported that EDS fires had more internal area unburned (14.8%) compared with LDS fires (8.5%). Price *et al.* (2003) assessed fine-scale patchiness through field measurements in northern Australia and stated that a key issue with the above studies is that the scale of most remotely sensed imagery used, predominantly from the MODIS and Landsat sensors, cannot detect fine-scale patches (≈1 m scale). Although the importance of fire patchiness has been widely questioned and recognised, evidence regarding its ecological significance is largely anecdotal

(Bradstock *et al.* 1996, Ooi *et al.* 2006, Parr and Andersen 2006).

The aim of this study was to describe fine-scale fire patchiness and severity in northern Australia savannas, by season and savanna vegetation type, and also to describe how patchiness is likely to affect the demography of fire-interval sensitive (obligate seeder) plants. The following hypotheses were tested: 1) burned area and fire severity are highest, and patchiness lowest, in the LDS; 2) patchiness and burned area differ by vegetation structure type; 3) percentage area burned is a scale-dependent function of fire severity; and 4) plant survival increases with fire patchiness.

DATA AND METHODS

Data Collection and Study Areas

We used line transects to assess fire patchiness along recently burned areas, covering five different vegetation structure types that correspond broadly to the types defined in Edwards and Russell-Smith (2009):

- open forests (OF) dominated by tall *Eucalyptus* spp. (8 m to 20 m) with foliage projected cover (FPC) >30 %, developed on well drained deeper sands, over a range of shrubs and slender perennial and annual grasses;
- woodlands (WD), typically dominated by *Eucalyptus tetrodonta* L. and *Eucalyptus miniata* L., with ≤30 % FPC, over an understory of perennial and annual grasses;
- open woodlands (OW), also dominated by *E. tetrodonta* and *E. miniata,* with ≤10 % FPC;
- sandstone woodlands (SW), with FPC <30 %, dominated by *Eucalyptus* spp. with well-developed shrub layers and a mixture of native perennial and annual tussock and hummock (*Triodia*) grasses, occurring on shallow to rocky soils also derived from sandstone;
- and sandstone heaths (SH), with FPC ranging from 10 % to 30 %, typically comprising a diverse range of shrubs and occasional small trees over a diverse herbaceous ground layer dominated by perennial hummock (*Triodia*) grasses, and occupying rugged, dissected substrates derived from sandstone.

The surveyed burned areas are all located in the Northern Territory, Australia, where the climate is defined by wet and dry seasons with 90 % of the annual rainfall occurring in the wet season months of December to April, and an average annual rainfall between 2000 mm and 500 mm along a north-south gradient (Australian Bureau of Meteorology 2013). All the areas sampled burned between 2009 and 2011, either in the EDS or in the LDS (Appendix 1). The distribution of 68 study locations is given in Figure 1.

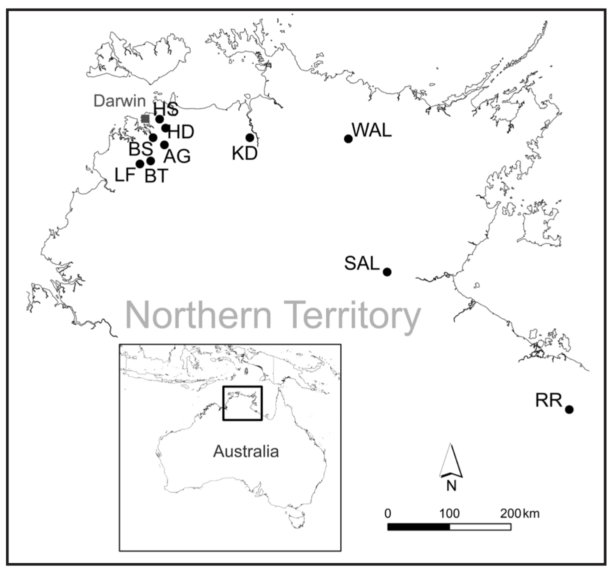

Figure 1. Location of the study areas in the Northern Territory, Australia.

The starting point and direction of each transect was haphazardly selected within the boundary of the fire, and a footfall method was used: the observer walks along the selected bearing and, for every footfall (at ≈1 m intervals), records whether the ground immediately in front of the toe of the shoe is burned or unburned. For burned sample points, it was recorded whether the surface was covered with char, ash, vegetation (photosynthetic or non-photosynthetic vegetation—i.e., green vegetative material or dry grass, dead leaves, stems, and twigs), bare soil, or rock. If the sample point was unburned, the presence of vegetation and bare soil or rock was recorded (Table 1). Typically, a burned point contained burned vegetation, ash, or bare soil or rock, while an unburned point comprised a live plant or unburned litter. Every 50 steps (≈50 m), we recorded average char and scorch heights (to the nearest hundredth meter) by visual estimation, over the entire 50 m. Char height was recorded as the height above ground of blackened (burned) fire-affected material. Scorch height was recorded as the height above ground of heat-affected (scorched) foliage. We used the field database CyberTracker (www.cybertracker.org), installed on a handheld computer, to record observations and an associated GPS location for each sample point (accuracy of 2 m to 5 m). These were plotted in ArcGIS to determine transect length, and to calculate the mean footfall distance (1.062 m), which was assumed to be the constant inter-point distance in subsequent analyses.

Our sampling design is factorial and unbalanced. Representative fragments of recently burned areas in the Northern Territory in May to July and August to November for the years 2009 to 2011 form our population. Experimental units are the fragments that were intersected by our 68 transects of haphazard starting points and directions. Two treatments were "applied" to each fragment: the season, which was determined by the moment when the fire occurred; and the vegetation type, which was determined by the existent vegetation type prior to fire. Since transects are sufficiently separated in time and space, we consider that those treatments were independently applied to each fragment. The number of replicates is not constant for all combinations of season and vegetation type, so the sampling design is unbalanced. Observational units are either footfall recordings (burned or unburned, surface cover) or 50-step recordings (char and scorch heights). For each variable, those repeated measures were averaged for each fragment, to obtain the corresponding experimental unit value.

Data Analysis

Each transect was described by season, vegetation type, number of sampled footfall points, field measurements, and additional variables derived from the field data (percentage burned, unburned patch density, and mean unburned patch length) (Table 1).

Table 1. Field data collected along transects and derived variables.

Measurement frequency	Fire class	Field measurements and derived variables
≈1 m	Burned	Char (yes or no)
		Ash (yes or no)
		Vegetation (yes or no)
		Rock or bare soil (yes or no)
	Unburned	Vegetation (yes or no)
		Rock or bare soil (yes or no)
≈50 m		Char height (m)
		Scorch height (m)
Transect		Unburned patch density (km^{-1})
		Mean unburned patch length (m)

Percentage burned was calculated by dividing the number of burned points by the total number of points on a transect. Unburned patch density (km^{-1}), was obtained by counting the number of unburned patches (contiguous unburned footfall points) on a transect, and dividing this by the total length of the transect. Mean unburned patch length was obtained by averaging the length of unburned patches. Unburned patch density and mean unburned patch length were used for assessments of fire patchiness; char height, scorch height, and mean percentage of char and ash were used for assessments of fire severity.

Data were analyzed both by season and vegetation type. To assess the data by season, we used the transect as the unit of measurement (n = 68). To assess the data by vegetation structure type and season, each transect containing more than one vegetation type was segmented by vegetation type, and only its longest segment was kept. This ensured that all resulting 68 transects remained independent. Field measurements and derived variables were compared for seasonal and vegetation type differences using analysis of variance (ANOVA). Before performing ANOVA, the normality and homogeneity of variances of the data were tested using the Shapiro-Wilk and the Bartlett tests, respectively.

Regression analysis of fire severity metrics. Regression analysis was used to assess the existence of a relationship between fire severity and percentage area burned. Char and scorch heights were used as indicators of fire severity, because they are strongly related to fire intensity in northern Australia (Williams *et al.* 2003), and with fire severity (Keeley 2009, Edwards *et al.* 2013). Specifically, regression analyses were performed for char height vs. scorch height, char height vs. percentage burned, and scorch height vs. percentage burned. The initial char and scorch height data, collected every 50 m, were aggregated at different levels (100 m, 150 m, and 200 m) to assess the effects of spatial scale. The highest level of aggregation was kept at 200 m in order to not eliminate data, since several transect units were around 200 m in length.

Simulation of plant population dynamics. Implications of patchiness on the population viability of fire-interval sensitive (obligate seeder) plants was investigated via a simulation analysis whereby a population of plants that is killed by fire but can establish from seed after fire was subjected to a fire regime with different fixed levels of patchiness. For modeling purposes, we assumed that reproductive maturity of our hypothethical species could be attained after seven years based on observations for *Callitris intratropica,* a common coniferous tree in regional savannas (Bowman and Panton 1993), and *Petraeomyrtus punicea,* a regionally endemic myrtaceous shrub (Russell-Smith 2006). At the start of the simulation, there were 1000 locations each occupied by a plant. Each plant was considered independently. The chance that it burned in each year was the product of the probability of a fire occurring (set at 0.3 for all simulations to reflect typical savanna fire return intervals under higher rainfall conditions; e.g., Russell-Smith *et al.* 2007) and the percentage burned by the fire, which was set as one of four levels (50 %, 83 %, 93 %, or 100 %). The 83 % and 93 % values reflect levels of the burned area in EDS and LDS fires found in this study, and the bounding 50 % and 100 % values are used for comparisons. A random number drawn from a lognormal distribution (as described in Oliveira *et al.* 2013) was used to determine whether a location burned in any one year. A burned location could be re-populated (probability R) if there were no fires for seven subsequent years (to reflect the life cycle of our hypothetical obligate seeder taxa), determined by a random number proportional to the overall population size (R = $N \times 0.02$ if $N < 500$ and R = 1 if $N \geq 500$). The simulation was run for 100 years.

RESULTS

Field Transects

The number and length of surveyed line transects is presented in Table 2, grouped according to season and vegetation structure type. Thirty four transects were surveyed separately in both the EDS and LDS. There were fewer sandstone heath and sandstone woodland transects due to accessibility limitations. The profiles of unburned points for each transect are shown in Figure 2.

Comparison of burned transects by season. The mean percentage burned within fire perimeters was higher in the LDS (93%; SE = 1.5) compared to the EDS (83%; SE = 1.7) (Figure 3a). At least 54% of the ground vegetation was burned in all transects. In the EDS, only one transect was burned completely, while in the LDS, 10 transects were completely burned. The percentage of exposed rock and bare soil was higher in transects sampled in the LDS (Figure 3b). Relative proportions of char and ash were dependent on season: mean percentage ash was twice as high in the LDS (12%) than in the EDS (6%), and mean percentage char was lower in the LDS (59%) compared to the EDS (65%). Ash indicates near-complete combustion of the fuel while char indicates incomplete combustion, which corroborates the higher fire severity pattern in the LDS than in the EDS. Both char height and scorch height were higher in the LDS (Figure 3c). The mean char and scorch heights were higher (1.4 m and 7.2 m, respectively) for transects that burned completely in the LDS than the mean values for all LDS transects. This observation reinforces the idea that there is a quantitative relationship between char and scorch heights and burned area. Unburned patch density and mean unburned patch length were higher in the EDS than in the LDS (Figure 3d, 3e). The majority of unburned patches (51%) corresponded to a single observation (≈1 m). Small patches (1 m) were considerably more common in the EDS (Figure 4) and large patches (≥20 m) were also more abundant in the EDS. A large percentage of patches (87% in the EDS and 89% in the LDS) were ≤5 m and only a small percentage of patches were ≥20 m (3% in the EDS and 2% in the LDS).

Table 2. Summary of seasonality and vegetation structure characteristics of surveyed transects. (EDS = early dry season, LDS = late dry season, OF = open forests, WD = woodlands, OW = open woodlands, SW = sandstone woodlands, SH = sandstone heaths).

Season	Vegetation	Transects (*n*)	Total transects (*n*)	Length (m)	Total length (m)
EDS		34	68	23 710	38 160
LDS		34		14 450	
EDS	OF	12	79	4 951	
	WD	18		13 092	
	OW	9		2 889	
	SW	2		757	
	SH	6		2 020	
LDS	OF	15		3 676	
	WD	7		4 469	
	OW	6		4 799	
	SW	2		455	
	SH	2		1 051	

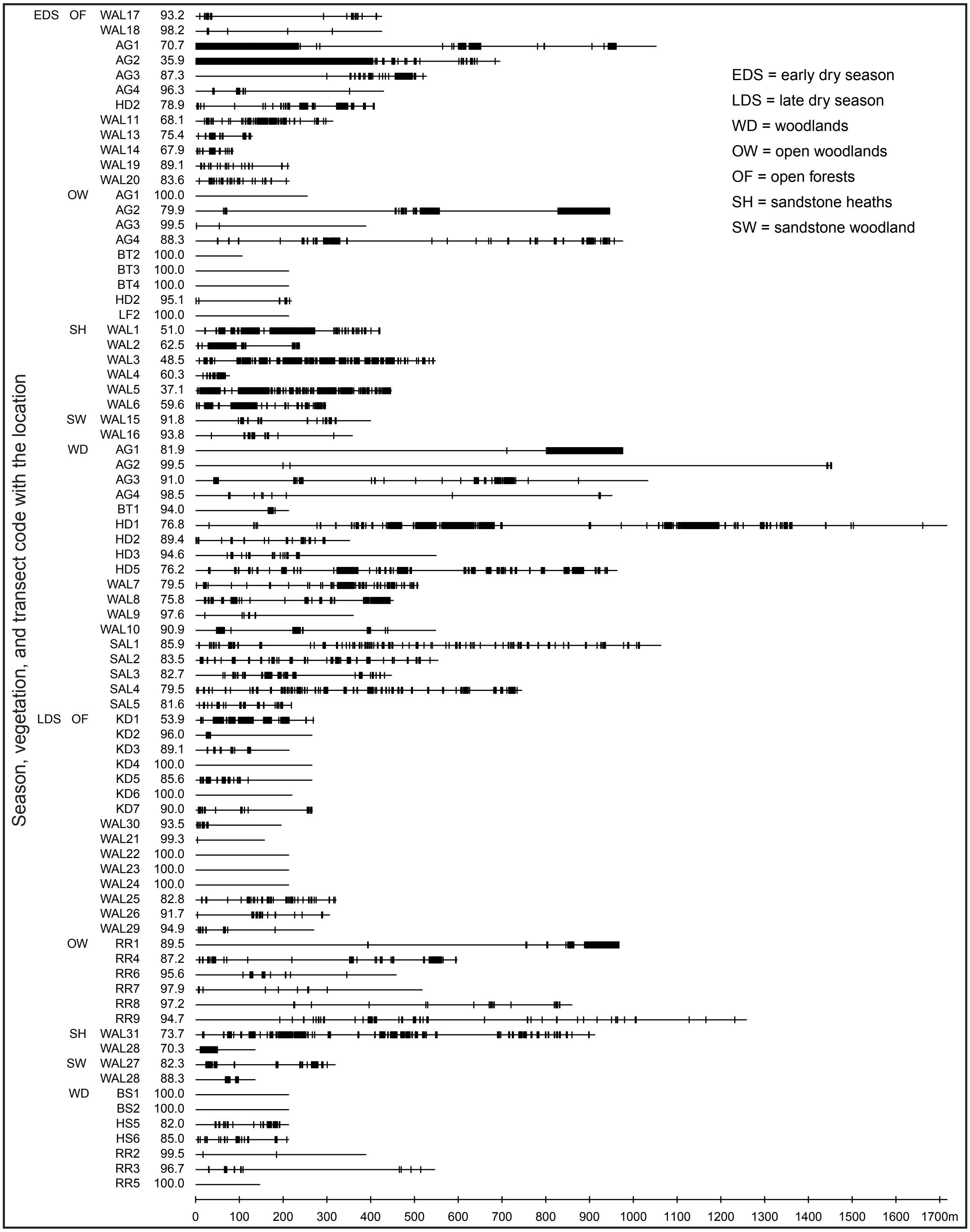

Figure 2. Transect profiles of unburned points (black vertical lines) grouped by season and vegetation type. Each transect containing more than one vegetation type was segmented by vegetation type, and for two-way ANOVA only its longest segment was kept. Next to each transect is the percentage of the transect that burned.

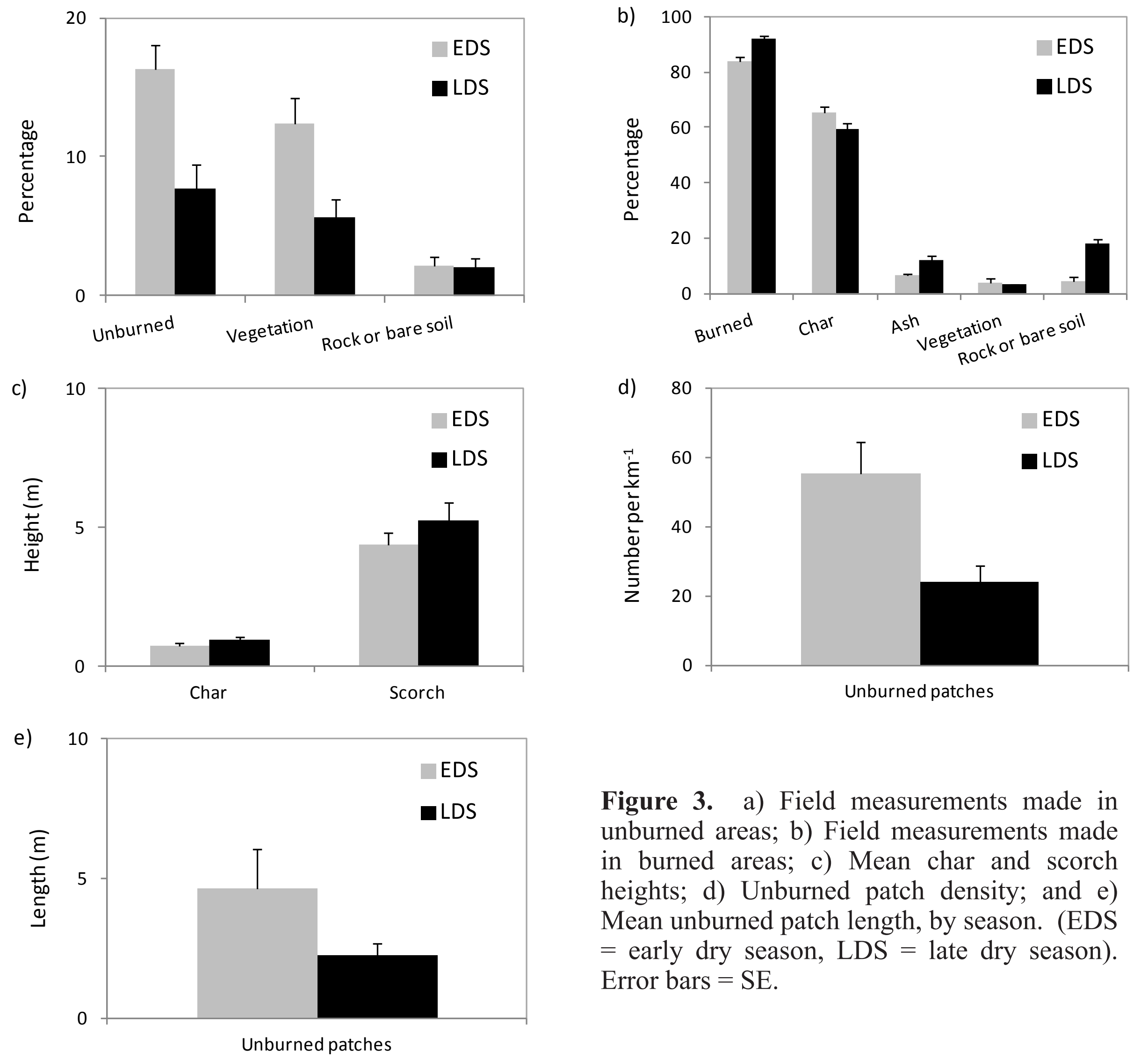

Figure 3. a) Field measurements made in unburned areas; b) Field measurements made in burned areas; c) Mean char and scorch heights; d) Unburned patch density; and e) Mean unburned patch length, by season. (EDS = early dry season, LDS = late dry season). Error bars = SE.

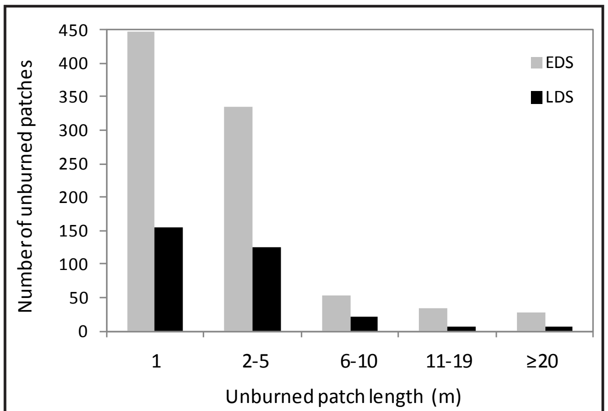

Figure 4. Frequency distribution of unburned patch size for the early dry season (EDS) and late dry season (LDS).

Comparison of burned transects by season and vegetation structure type. When considering the partitioned transects by vegetation type, the same overall seasonal trends described for fire transects by season were observed (Appendix 2). Burned area was also lowest in the EDS, and unburned patch density and mean unburned patch length were highest in the EDS, for almost all vegetation types. Open woodlands were the most extensively burned vegetation type and sandstone woodlands the least. Mean char and scorch heights were highest in open woodlands in the EDS, and in woodlands in the LDS. Unburned patch density was highest in sandstone heaths and lowest in open woodlands. Mean unburned patch length was almost five times higher in open forests when compared to the lowest value, observed in open woodlands.

Statistical Comparison by Season and Vegetation Structure Type

There was no evidence to reject the assumption of normality of the data and the homogeneity of variances. The *P*-values of the two-way ANOVA tests are displayed in Table 3. The results suggest that percentage burned, percentage char, percentage ash, and unburned patch density differed by season; percentage char percentage ash, unburned patch density, and patch length differed by vegetation type; and significant interaction effects between season and vegetation type were observed for percentage char, percentage ash, and unburned patch length.

Regression Analysis of Fire Severity Measures

The level of data aggregation that produced the strongest correlation between char and scorch heights was 200 m (Figure 5). There was a weak positive correlation between these two variables in the EDS ($R^2 = 0.30$) and a stronger correlation in the LDS ($R^2 = 0.66$); the regressions were significant at the 0.01 % level ($P = 0.000$ for both). The correlations with data aggregated at 50 m, 100 m, and 150 m were $R^2 = 0.28$, 0.29, and 0.34, respectively, in the EDS, and $R^2 = 0.43$, 0.51, and 0.49, respectively, in the LDS; all regressions were significant at the 0.001 level.

When assessing the relationship between scorch height and percentage burned area, the best results were also obtained when aggregating data at 200 m. The relationship between the two variables was approximately logarithmic (Figure 6). Seventy percent of the EDS burned area variability is explained by mean scorch height (Figure 6a) but no relationship was found for the LDS (Figure 6b). The correlations with data aggregated at 50 m, 100 m, and 150 m were approximately $R^2 = 0.23$, 0.39, and 0.59 in the EDS, respectively, and $R^2 = 0$ in the LDS. The relationship between char height and burned area (Figure 6c, 6d) is also more pronounced for the EDS. The correlations with data aggregated at 50 m, 100 m, and 150 m were approximately $R^2 = 0$ in the LDS, and $R^2 = 0.19$, 0.23, and 0.40 in the EDS, respectively. Figure 6 shows that, for the EDS, completely burned transects have higher values for char and scorch heights than partially burned transects.

Simulation of Plant Population Dynamics

Plant population simulation results suggested that the higher the patchiness, the greater the number of surviving obligate

Table 3. Significant *P*-values for the ANOVA.

	P-values		
	Season	**Vegetation**	**Season *x* vegetation**
Percentage burned	<0.001		
Percentage char	0.0619	<0.001	0.0651
Percentage ash	0.0178	0.0176	0.0557
Scorch height			
Char height			
Unburned patch density	<0.001	0.0798	
Unburned patch length		0.0011	<0.001

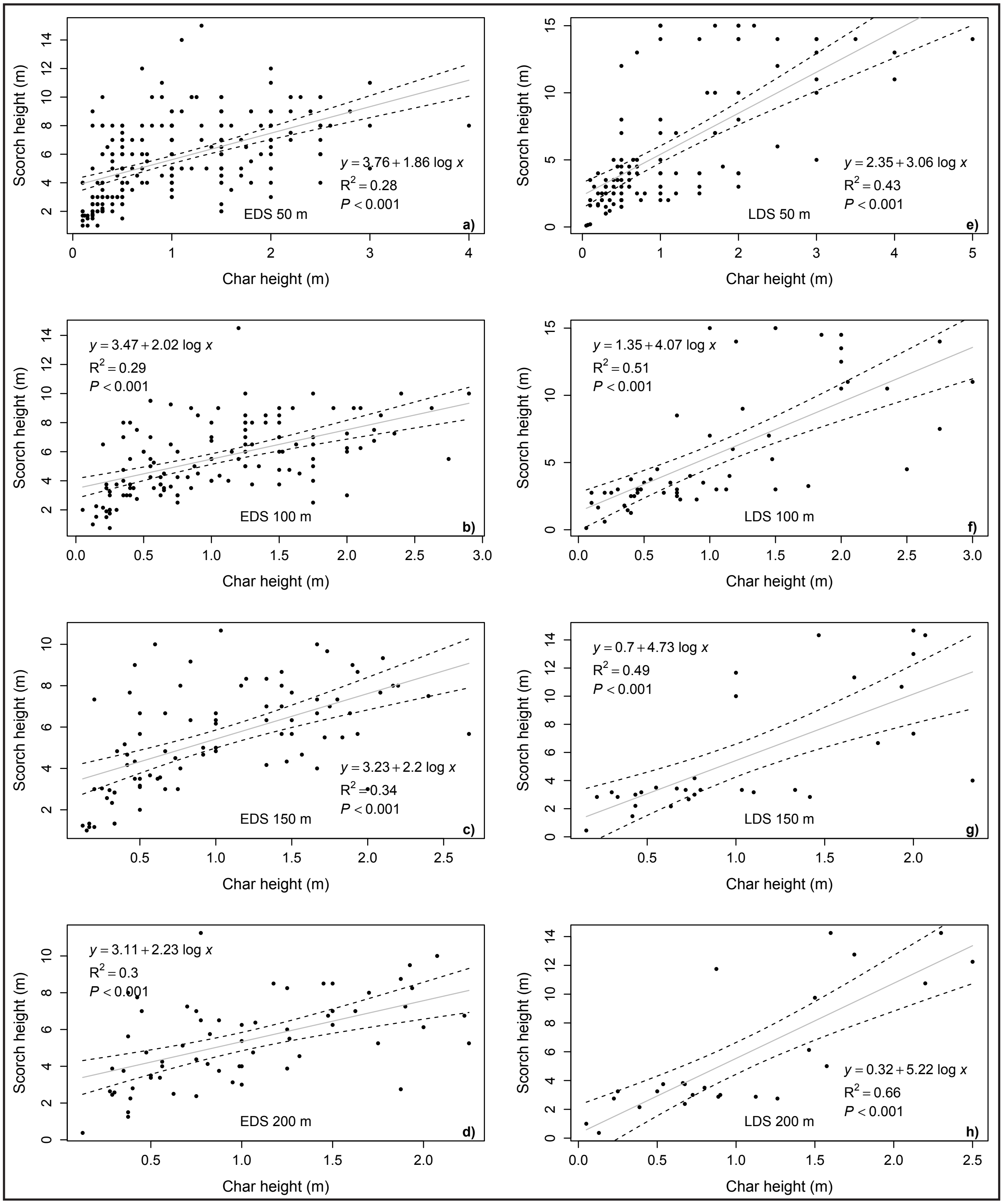

Figure 5. Regression analysis between char and scorch heights in the early dry season (EDS) for data aggregated at a) 50 m, b) 100 m, c) 150 m, and d) 200 m, and in the late dry season (LDS) for data aggregated at e) 50 m, f) 100 m, g) 150 m, and h) 200 m. Dashed lines correspond to a 95% confidence band around the regression line.

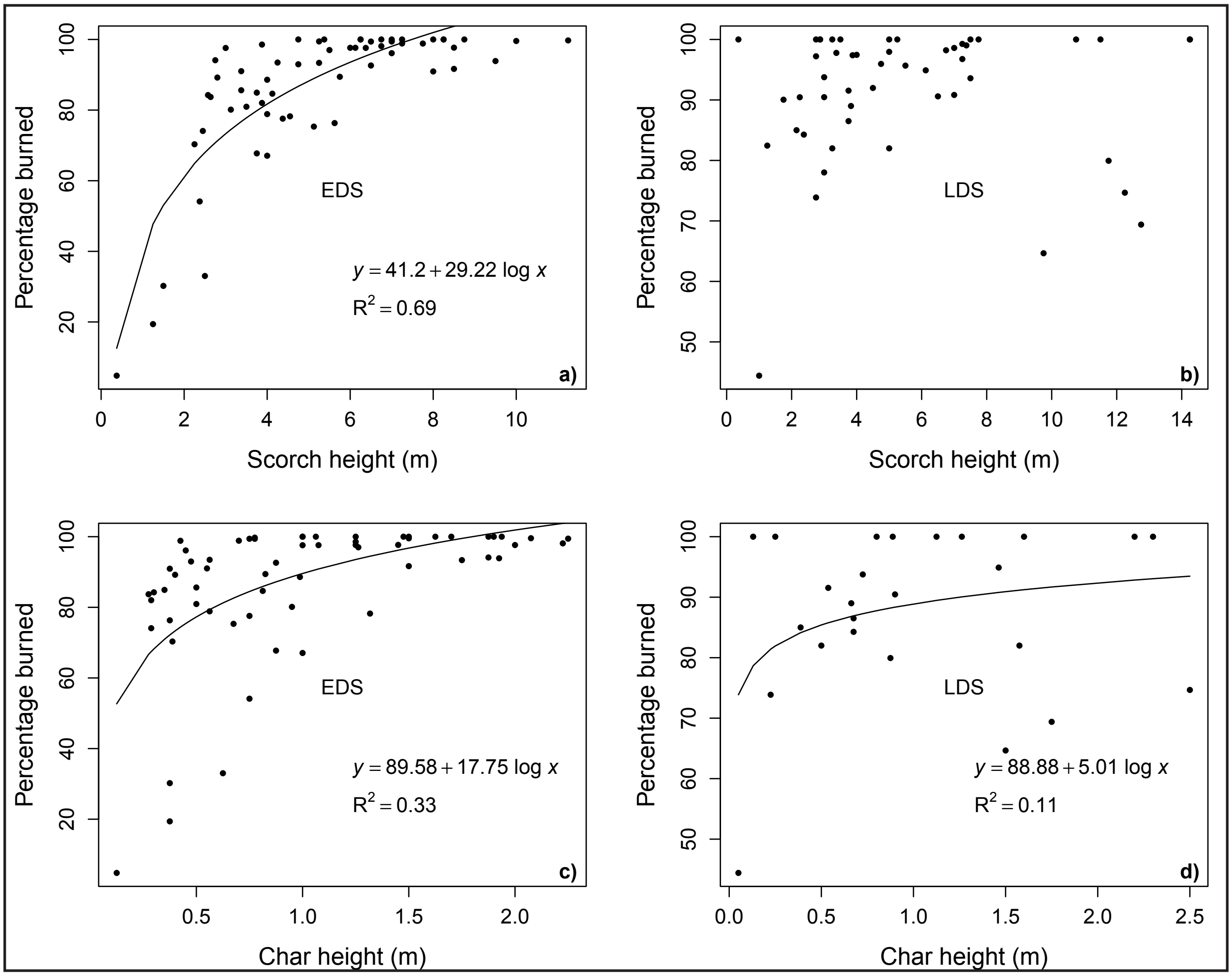

Figure 6. Scatter plots of the percentage burned and scorch height (m) in the a) early dry season (EDS), and b) late dry season (LDS); scatter plots of the percentage burned and char height (m) in the c) early dry season (EDS), and d) late dry season (LDS), for data aggregated at 200 m. The solid line is the best logarithmic curve fitted to the data. Since the logarithm of scorch height and percentage burned for LDS were uncorrelated ($R^2 \approx 0$), the curve is omitted.

seeding plants. The plants became extinct after 22 years when there was no patchiness, or after 40 years with 93 % burned (mean burned area of LDS transects) (Figure 7). The population persisted for at least 100 years with higher levels of patchiness, with a mean remnant population of 19 plants with 83 % burned (mean burned area of EDS transects) and 284 with 50 % burned. When the simulations were repeated without the ability to repopulate, extinction occurred in all scenarios, but the time taken to extinction increased with patchiness.

DISCUSSION

This study extends the findings of previous work on fire patchiness in tropical savannas of northern Australia (e.g., Price *et al.* 2003, Russell-Smith *et al.* 2003, Williams *et al.* 2003). Table 3 shows that the percentage of burned area is only significantly affected by seasonality. Moreover, of the two patchiness metrics, patch density and patch length, the first is more sensitive to season while the second depends mostly on vegetation type and on the interaction between both factors.

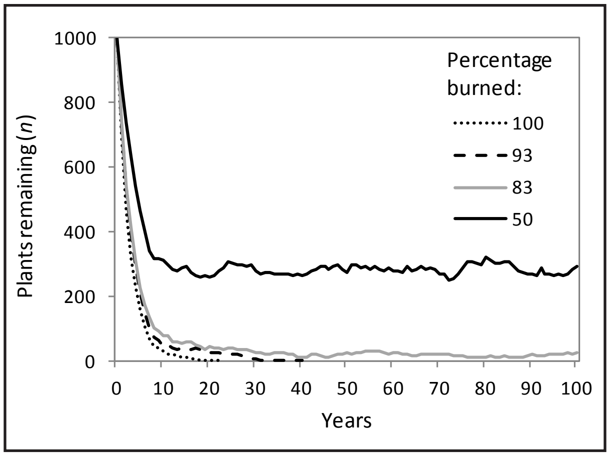

Figure 7. Plant survival according to different percentage burned (100%, 93%, 83% and 50%) with ability to recolonise after seven years without fire.

Concerning fire severity, the two-way ANOVA suggests that only variables related to the abundance of combustion products (percentage char and percentage ash) differ significantly with both season and vegetation type. This indicates that scorch height and char height are not sensitive to those two factors.

Late dry season fires tend to burn over more area and, in this study, were found to be more severe and less patchy (shorter and fewer unburned patches) than EDS fires, which is congruent with other Australian and worldwide studies (e.g., Allan 2001, Slocum *et al.* 2003, Russell-Smith and Edwards 2006). Grasses, the dominant component of the combustible fuel in these savannas, progressively cure and collapse with the onset of the dry season (Russell-Smith and Yates 2007, Cheney and Sullivan 2008). In addition, relative humidity and soil moisture decrease whereas temperature and wind speed increase (Gill *et al.* 1996), creating ideal conditions for fire spread. The internal unburned percentage recorded in this study (17% for the EDS and 7% for the LDS) was very similar to the results obtained by Allan (2001) for a semi-arid savanna in northern Australia (15% for the EDS and 8.5% for the LDS). Our LDS values are also similar to those given in Russell-Smith *et al.* (2003). However, compared to the study of Price *et al.* (2003), the fires studied here had lower patchiness and the unburned patches were generally much smaller.

Much of the patchiness described in Price *et al.* (2003) was due to rockiness, and most of their transects (including all of the LDS fires) were in rocky areas. In this study, the mean percentage of rock was 2% and, accounting for bare soil, the percentage increased to 16%, a value much lower than the 39% reported by Price *et al.* (2003) for mean rockiness. Another reason for the disparity in results may be the fact that Price *et al.* (2003) included some fires or parts of fires, from both seasons, for which intensity was very low. Likewise, for prescribed burns in southern Australian eucalypt forests, Penman *et al.* (2007) reported greater patchiness than observed here, with burned area values ranging from 10% to 100%, with a mean of 65%. By contrast, in this study, open forest burned area ranged from 77% in the EDS to 93% in the LDS. There are several likely reasons for this: prescribed burns are typically of low intensity, fire intensities of fuel reduction burns are higher in northern Australia compared to southern Australia (Williams *et al.* 1998), and differences in fuel type and architecture influence fire behaviour.

Unburned patch density and mean unburned patch length were lowest in open woodlands, which was also the vegetation structure type with the highest percentage burned (in agreement with Russell-Smith *et al.* 2003). According to Cheney and Sullivan (2008), fuel continuity, the extent to which the surface of the ground is covered by fuel, is the main characteristic influencing fire spread. Open woodlands are dominated by flammable tall annual *Sorghum* spp. and perennial grasses, supplemented by scattered leaf litter that can fill bare patches in the grass sward, making for a more continuous fuel bed. On the other hand, percent burned was lowest in sandstone types and unburned patch frequency was highest, due to decreased fuel continuity caused by a large proportion of exposed rock surfaces. Rocky surfaces and bare soil act as barriers to fire spread and discontinuous grasslands will not carry a fire until the wind speed exceeds a particular threshold (Cheney and Sullivan 2008).

Open forests exhibited the longest mean unburned patches, possibly due to greater fuel moisture content, associated with the highest percentage canopy cover of all vegetation types. Moisture content has a major effect on fire spread; fires typically will not spread when grasslands are ≤50 % cured, and only reach their full fire spread potential when they are >95 % cured (Cheney and Sullivan 2008).

There was a strong relationship between char and scorch heights in the LDS, mostly because of the influence of very high values of scorch height and because there is much less charred material to assess in the lower severity char heights in the EDS. Burned area and severity were strongly correlated in the EDS, with 70 % of burned area explained by mean scorch height. In the LDS, the percentage burned was very high (close to 100 %) across a wide range of scorch height values, which explains the weak relationship between the two variables. There is an improvement in the relationship between these variables with spatial aggregation, given that variance is reduced by data smoothing. By aggregating the data (initially collected every 50 m) up to 200 m, disparate observations are diluted, confirming the scale dependence of this relationship.

In this study, scorch height was found to be a better surrogate of fire severity than char height, being better related to percentage area burned than char height. Some authors recommend that measurements of fire severity should be restricted to measures of organic matter loss, such as canopy scorch or ash deposition (e.g., Keeley 2009), which is potentially what one is measuring with scorch height in tropical savanna habitats dominated with ground fires, given little or no canopy fire spread. Char height may not always be closely correlated with flame length (and thus, fire severity), given localized variation in wind and variation in the size and moisture content of leaves (Williams *et al.* 2003), but also due to the paucity of vegetation between ground and upper strata. White ash is also an important indicator of fire severity (Edwards *et al.* 2013). It has been positively correlated with fire intensity and represents near-complete combustion of the available fuel, offering little protection to the soil from rainfall and, therefore, erosion (Roy *et al.* 2010). The increased percentage of ash in the LDS (twice as high) confirms the greater severity of the LDS fires. Charred vegetation is typically conspicuous in the EDS, associated with variable, low severity fires.

Plants respond in different ways to fire, depending on variables such as post-fire climate conditions, the life history attributes of the species, and the productivity of the sites. Some species survive fire and then resprout, but even these species may not resprout when fires are too severe. Other species are killed by fire, but germinate from fire-resistant seeds. If fire severity is high or fire patchiness is low or both, the seed bank could be at risk (Bowman and Panton 1993, Russell-Smith 2006). An important observation of this study is that obligate seeder survival simulations are sensitive to small differences in fire patchiness, such as the 10 % difference observed between the EDS and the LDS. *Petraeomyrtus punicea* seed fall is limited to the near vicinity of mature canopies, with secondary transport downslope (Russell-Smith 2006), so small unburned patches (<5 m), like the ones observed in this study, are very important for plant reproduction. *Callitris intratropica* seedlings can survive a fire if only partially scorched or, in cases of low severity fires, even if totally scorched (Russell-Smith 2006).

Thus, even though most unburned patches were <5 m wide, they provided an important refuge for fire-sensitive plants.

Fire impacts on fauna vary markedly, and are harder to assess than impacts on flora. Some animals show a preference for no or little burning, others for more frequent burning, and others have more complex responses that depend on fire patchiness and landscape context (Andersen *et al.* 2005). Examples of regionally vulnerable fauna that rely on unburned patches include rock rats (*Zyzomys* sp.; Trainor *et al*. 2000); the Leichhardt's grasshopper, *Petasida ephippigera* White (Lowe 1995); the white-throated grass-wren, *Amytornis woodwardi* Hartert (Noske 1992); and the partridge pigeon, *Geophaps smithii* Jardine & Selby (Fraser *et al.* 2003). The latter is particularly vulnerable to fire patchiness because it requires unburned areas for nesting, and open burned areas, preferably from patchy EDS fires, for grass-seed feeding habitat (Fraser *et al.* 2003).

The ideal unburned patch size for maintaining local populations is hard to define because different fauna have different home ranges, varying from square meters for invertebrates and small lizards to 0.1 km^2 for small mammals and birds, to tens of square kilometers for some macropods and granivorous birds. Undoubtedly, the most vulnerable species are the small and relatively immobile fauna that are restricted to small isolated habitats such as rocky outcrops and monsoon forests (Woinarski *et al.* 2005, Yates *et al.* 2008). It follows that these animals can find refuge in the small unburned patches reported in this study (<5 m), whether in holes, crevices, under rocks, or in above-ground shrub foliage and tree hollows.

These findings support arguments advanced by many authors concerning the regional biodiversity benefits of smaller, patchier EDS savanna fires (e.g., Edwards *et al.* 2001; Russell-Smith *et al.* 2002*b,* 2003; Andersen *et al.* 2005; Yates *et al.* 2008). Many studies have also argued that implementing a prescribed EDS burning program has substantial benefits in restricting the spread of extensive LDS wildfires (e.g., Russell-Smith *et al.* 1997, 2003; Yates *et al.* 2008; Price *et al.* 2012). For example, by imposing prescribed EDS burning over 24 000 km^2 in western Arnhem Land, between 2005 and 2009, Price *et al.* (2012) showed that mean fire extent in the LDS period was reduced by 16.5 % by comparison with the mean annual extent for the prior 15 years, yielding a mean overall reduction of 6 %. Reduction in the extent and severity of LDS fires is known to have significant benefits both for obligate seeders and resprouting species (Williams *et al.* 1998, 1999; Russell-Smith *et al.* 2002*b,* 2012).

A considerable challenge for biodiversity management is to better understand and deliver spatio-temporal fire patchiness, especially in relation to rapid accumulation of grassy fuels. Another approach for biodiversity management should be increasing both the spatial heterogeneity and non-randomness of EDS burning through strategic application of prescribed burning (e.g., using streams and tracks as fire breaks), so that patches of long-unburned vegetation are more effectively compartmentalised, reducing the potential for large, severe fires (Turner *et al.* 1994, Andersen *et al.* 2005).

CONCLUSION

Current freely available, systematically acquired remote sensing data are inadequate to study fire patterns at a spatial scale relevant to individuals and populations of plants, and lack the spatial resolution to account for the fine-scale patchiness that is associated with fire scars, especially in more patchy EDS fires. High resolution commercial satellites are available (e.g., WorldView3, GeoEye-1, and IKONOS, with a resolution of 1.24 m, 1.6 m, and 3.2 m for the multispectral imagery, respectively) but image acquisition is expensive for extensive areas. For these reasons, *in situ* transects were used in this study to detect and describe fire patterns at a finer spatial scale (≈1 m) than in previous studies.

We found that seasonal timing of fires affected burned area, vegetation structural type influenced fire patchiness, and the interaction between season and vegetation type affected fire severity. All initial hypotheses were supported: 1) burned area and fire severity were higher in the LDS and patchiness lower (shorter and less frequent unburned patches) than in the EDS; 2) patchiness differed by vegetation structure type, with sandstone heaths having the highest patch frequency (low fuel continuity due to larger proportion of exposed rock surfaces), open woodlands the lowest (associated with greater continuity of grassy fuels), open forests had the longest mean unburned patches (associated with highest canopy cover and possibly greater fuel moisture content); 3) fire severity and percentage area burned were strongly related in the EDS, with 70% of EDS burned area being explained by mean scorch height with the relationship between these two variables increasing with spatial aggregation of the data, and, most importantly from a biodiversity conservation perspective, 4) even small increases in fire patchiness were shown to substantially enhance the survival of fire-sensitive (obligate seeder) species.

The risk of localized extinction of fire-sensitive obligate seeders may be reduced with the use of prescribed burning undertaken in the EDS through increased fire patchiness and reduced severity. In this study, almost all fires surveyed contained unburned patches, although most of these were very small (<5 m). These results suggest that the ecological impacts of high frequency fires are likely to be lower than has been predicted based on assumptions of homogeneous burning derived from remotely sensed studies; there was almost always some chance that fire-sensitive species could survive a fire, and this chance increased in rockier habitats that contain the greater proportion of regional endemics.

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Appendix 1. List of transects surveyed in the field.

Place	Transect	Date (mm/yyyy)	Length (m)
Acacia Gap (AG)	AG1	06/2010	2281
	AG2	06/2010	3091
	AG3	06/2010	1948
	AG4	06/2010	2354
Batchelor (BT)	BT1	06/2009	212
	BT2	06/2009	106
	BT3	08/2009	212
	BT4	08/2009	212
Berry Springs (BS)	BS1	09/2009	212
	BS2	09/2009	212
Humpty Doo (HD)	HD1	05/2010	1715
	HD2	05/2010	978
	HD3	05/2010	549
	HD4	05/2010	962
Howard Springs (HS)	HS5	10/2009	212
	HS6	10/2009	212
Kakadu National Park (KD)	KD1	11/2009	270
	KD2	11/2009	266
	KD3	11/2009	213
	KD4	11/2009	266
	KD5	11/2009	266
	KD6	11/2009	220
	KD7	11/2009	267
Litchfield National Park (LF)	LF1 LF1	08/2009	212
Robinson River (RR)	RR1	09/2011	900
	RR2	09/2011	389
	RR3	09/2011	546
	RR4	09/2011	597
	RR5	09/2011	147
	RR6	09/2011	516
	RR7	09/2011	458
	RR8	09/2011	859
	RR9	09/2011	1257
South Arnhem Land (SAL)	SAL1	05/2010	1062
	SAL2	05/2010	553
	SAL3	05/2010	447
	SAL4	05/2010	744
	SAL5	05/2010	218
West Arnhem Land (WAL)	WAL1	07/2009	417
	WAL2	07/2009	238
	WAL3	07/2009	547
	WAL4	07/2009	78
	WAL5	07/2009	447
	WAL6	07/2009	297
	WAL7	07/2009	509
	WAL8	07/2009	451
	WAL9	07/2009	360
	WAL10	07/2009	548
	WAL11	07/2009	313
	WAL13	07/2009	130
	WAL14	07/2009	86
	WAL15	07/2009	399
	WAL16	07/2009	358
	WAL17	07/2009	425
	WAL18	07/2009	425
	WAL19	07/2009	213
	WAL20	07/2009	213
	WAL21	09/2009	157
	WAL22	09/2009	212
	WAL23	09/2009	212
	WAL24	09/2009	212
	WAL25	09/2009	321
	WAL26	09/2009	306
	WAL27	09/2009	319
	WAL28	09/2009	272
	WAL29	09/2009	270
	WAL30	09/2009	195
	WAL31	10/2009	915

Appendix 2. Field measurements made in a) unburned areas, b) burned areas, c) mean char height, d) mean scorch height, e) unburned patch density, and f) mean unburned patch length, by vegetation type and season. (EDS = early dry season, LDS = late dry season, WD = woodlands, OW = open woodlands, OF = open forests, SH = sandstone heaths, SW = sandstone woodlands). Char and scorch heights were not assessed in EDS transects. Error bars = SE.