Trees (2016) 30:329–335
DOI 10.1007/s00468-015-1285-1

SHORT COMMUNICATION

Mineral nutrition and specific leaf area of plants under contrasting long-term fire frequencies: a case study in a mesic savanna in Australia

Marcelo Claro de Souza[1,2] · Davi Rodrigo Rossatto[3] · Garry David Cook[4] · Ryosuke Fujinuma[5] · Neal William Menzies[5] · Leonor Patricia Cerdeira Morellato[6] · Gustavo Habermann[6]

Received: 24 January 2015 / Revised: 26 August 2015 / Accepted: 28 August 2015 / Published online: 12 September 2015

Abstract

Key message **The association between frequent long-term fires and soil fertility may control the nutritional status and leaf scleromorphism of Australian savanna species.**

Abstract Fire frequency is considered to be a controlling factor for the structure of savanna vegetation, also affecting functional aspects of plants, yet studies contrasting long-term burnt and unburnt sites within the same area are rare. At fire-protected sites, one may expect to find woody vegetation with non-sclerophyllous leaves exhibiting a high nutrient concentration and growing on soils of high fertility. Using a burnt (14 times within the last 20 years) and an unburnt site (over the same period) within the same area of a mesic Australian savanna, we compared the soil fertility, specific leaf area (SLA) and leaf macronutrient concentration of the exclusive (species that occur at a single site), common (species that occur at both sites) and total (exclusive and common species combined) sampled tree species from the two sites. The exclusive, common and total sampled tree species had a lower SLA when growing at the burnt site than at the unburnt site. Soil from the burnt site was less fertile than the soil from the unburnt site, and the plants from the burnt site exhibited lower leaf nutrient concentrations when compared with those from the unburnt site. The association between fire and soil fertility was consistent with the differences in leaf scleromorphism between the sites under contrasting fire frequencies.

Keywords Fire management · Leaf scleromorphism · Native plant nutrition · Soil fertility

Communicated by A. Franco.

✉ Marcelo Claro de Souza
marcelo.claro.souza@gmail.com

1 Departamento de Botânica, Instituto de Biociências, Programa de Pós Graduação em Biologia Vegetal, Univ Estadual Paulista, Unesp, Av. 24-A, 1515, Rio Claro, SP 13506-900, Brazil

2 Present Address: Departamento de Ciências Farmacêuticas, Faculdade de Ciências Farmacêuticas de Ribeirão Preto, Universidade de São Paulo, USP, Av. do Café s/n, Ribeirão Preto, SP 14040-903, Brazil

3 Departamento de Biologia, Faculdade de Ciências Agrárias e Veterinárias, Univ Estadual Paulista, Unesp, Via de Acesso Paulo Donato Castellani s/n, Jaboticabal, SP 14884-900, Brazil

4 CSIRO Land and Water Flagship, Darwin, NT, Australia

5 School of Agriculture and Food Sciences, University of Queensland, Brisbane, Australia

6 Departamento de Botânica, Instituto de Biociências, Univ Estadual Paulista, Unesp, Av. 24-A, 1515, Rio Claro, SP 13506-900, Brazil

Introduction

The species composition and individual species characteristics of savanna vegetation are shaped by fire (Williams and Cook 2001; Bond et al. 2005; Hoffmann et al. 2012), soil water availability (Cook et al. 2002; Scholes et al. 2004; Scott et al. 2009; Rossatto et al. 2012; Murphy et al. 2015), soil nutrient stocks and climate (Pinheiro and Monteiro 2010; Lehmann et al. 2011, 2014). Savannas around the world are frequently burnt by natural or anthropogenic means, and up to 75 % of some savanna areas burn annually (Hao et al. 1990), which affects plant recruitment (Rossiter-Rachor et al. 2008) and development (Beringer et al. 2015) and their phenological and functional events (Hoffmann 1998; Pausas et al. 2004; Alvarado et al.

2014). Despite the intense wet season from December to May, Australian savannas are the most frequently burnt vegetation in the world (Andersen et al. 2005; Chuvieco et al. 2008; Beringer et al. 2015). Across Australian savannas, half of the vegetation burns annually (Edwards et al. 2001; Andersen et al. 2005; Beringer et al. 2015) and in the Kakadu National Park (Northern Territory, Australia) few areas remain unburnt for more than 2–3 years (KBMPA 1999; Cook 2001).

Soils from savannas often have limited nutrient availability, affecting the leaf nutrient concentrations (mainly N and P) and leading to changes in the specific leaf area (SLA, ratio of leaf area per unit leaf dry mass) of some Australian species (Wright et al. 2001; Prior et al. 2003, 2005). Frequent incidence of fire over a long time frame may limit the available pool of soil nutrients, and fire may also diminish the soil organic matter concentration and accumulation (Andersson et al. 2004; Silva and Batalha 2008) when litter is incinerated (Oesterheld et al. 1999). In addition, frequent fires can result in savanna physiognomies with a conspicuous dominance of grasses, whereas trees and shrubs are more evident in savannas with lower fire incidence (Sankaran et al. 2005). Conversely, savanna vegetation protected from fire for long periods (>10 years) becomes less flammable as the density of trees increases over time, resulting in low sunlight interception and less vegetative biomass at the ground level, due to denser tree crowns, when compared to frequently burnt areas (Andersen et al. 2005; Beringer et al. 2015). Therefore, sunlight availability may also influence SLA in such a manner that

Table 1 List of plant species from the burnt and unburnt Australian savanna sites, Northern Territory, 2013

Family	Species	Burnt	Unburnt
Anacardinaceae	*Buchanania obovata* Engl.	×	×
Combretaceae	*Terminalia ferdinandiana* Exell	×	×
Lecythidaceae	*Planchonia careya* (F.Muell) R.Knuth	×	×
Leguminosae	*Acacia dimidiata* Benth.	×	
Leguminosae	*Acacia lamprocarpa* O.Schwarz	×	
Leguminosae	*Erythrophleum chlorostachys* (F.Muell.) Baillon	×	
Leguminosae	*Acacia auriculiformis* Benth.		×
Leguminosae	*Exocarpus latifolius* Baker		×
Malvaceae	*Brachychiton megaphyllus* Guymer	×	×
Myrtaceae	*Eucalyptus miniata* A.Cunn	×	×
Myrtaceae	*Eucalyptus tetrodonta* F.Muell	×	×
Myrtaceae	*Syzygium suborbiculare* (Benth.) T.G.Hartley & L.M.Perry		×
Picrodendraceae	*Petalostigma quadriloculare* F.Muell	×	×
Proteaceae	*Persoonia falcata* R.Br.	×	×
Proteaceae	*Grevillea decurrens* Ewart	×	
Rhamnaceae	*Alphitonia excelsa* (Fenzl) Reissek ex Benth.		×
Rubiaceae	*Gardenia megasperma* F.Muell	×	
Rubiaceae	*Pogonolobus reticulatus* F.Muell	×	

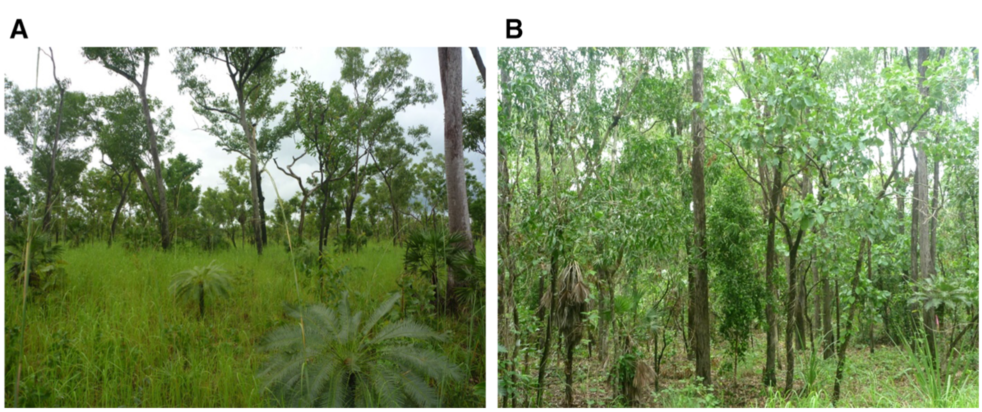

Fig. 1 Mesic Australian savanna, Darwin, Northern Territory, 22 February 2013. **a** Burnt site (14 fire events in 20 years), and **b** unburnt site (>20 years without any fire events)

in savannas high sunlight availability is associated with low SLA (Prior et al. 2003; Franco et al. 2005), while in low light environments, such as forests, high SLA is predominant (Givnish 1988; Prior et al. 2003; Habermann and Bressan 2011).

In this study, we examined the concentration of nutrients in leaves, the SLA and the soil fertility of two sites in a mesic savanna at the Territory Wildlife Park in the Northern Territory, Australia. One site has been protected from fire for the past 20 years, referred to here as the 'unburnt site', while the other site ('burnt site') has burnt 14 times during this same period. We screened and identified tree species unique to each site as well as those species common to both the burnt and unburnt sites. Due to the scarcity of sites protected from fire for more than 5 years within Australian savanna areas (KBMPA 1999; Cook 2001) we were unable to identify additional unburnt sites for this study. Thus, a single pair of burnt and unburnt sites ca. 30 km apart were assessed to understand the relationships between plant nutrition, soil nutrient stocks and SLA of mesic savanna vegetation under contrasting fire regimes. Plants within the unburnt site were expected to exhibit higher foliar nutrient concentrations and greater SLA compared to vegetation from the burnt site. This should contribute to the understanding of how fire and soil fertility affects the mineral nutrition and leaf scleromorphism of Australian savanna species.

Materials and methods

Leaf nutrient concentrations and SLA of the most representative species in two mesic savanna sites in the Northern Territory, Australia, were examined (Table 1). A savanna site in the Territory Wildlife Park (S12° 36′ 56.0″ E131° 00′ 45.3″), which has burnt 14 times during the last 20 years, was selected to represent the burnt savanna. Within the same region, a savanna remnant in Berrimah, a suburb of Darwin (S12° 24′ 43.7″ E130° 55′ 08.3″) that has been protected from fire for more than 20 years was selected as a representative unburnt savanna site (BOM 2013) (Fig. 1). The two sites are approximately 30 km apart; both sites are ~30 m above sea level and receive approximately 1700 mm annual rainfall (Prior et al. 2003; BOM 2013).

Plant species were identified and classified as being unique to each site (exclusive) or common to both sites (common). This procedure was used to avoid differences between nutritionally distinct groups of plants (e.g., leguminous species) and those species that may be influenced by fire frequency or soil fertility (Araújo and Haridasan 1988). The tree species that were found in both sites included eight common species; four species were exclusively found at the unburnt site and six were unique to the burnt site (Table 1). We recognize that this scenario (eight common species, four species from the unburnt site, and six species from the burnt site) may limit conclusions to a local plant community structure. However, studies examining the effects of fire on plant communities growing close to each other and with the same physiognomy are extremely rare (see Alvarado et al. 2014). In addition, this is a study of frequent long-term fire and fire protection effects on savanna vegetation, which is also uncommon (Cook 2001; KBMPA 1999; Edwards et al. 2001). Moreover, the dominant woody species in Australia are principally eucalypts (*Eucalyptus* and *Corymbia* spp.) (Burrows 2013), and this might be due to their fire resistance capacity, especially during the juvenile plant phase. Other woody species occurring in Australia belong to *Acacia*, *Terminalia*, *Erythrophelum*, *Syzygium* and *Xanthostemon* genera (Bond et al. 2012), and these genera were considered in the present study. Therefore, the plant communities from the two sites can be considered as representative tree species occurring in the region.

To determine the SLA and leaf nutrient concentration, we used four adult trees per species and sampled five fully expanded undamaged leaves per tree (therefore, 20 leaves/species) at the end of February 2013. In both sites, a mix of leaves was sampled under and outside the canopy. Due to the higher density of trees, we were not able to only sample sunlight leaves on the unburnt site. Ten leaf disks (6 mm in diameter) not including the midrib were obtained per leaf and oven-dried at 60 °C to constant mass. The SLA was calculated as the ratio between the leaf disk area (cm^2) and its dry mass (g) (Habermann and Bressan 2011). The same leaf samples used for measuring SLA were washed in deionized water, oven-dried for 72 h at 60 °C, ground and digested in a 5:1 nitric:perchloric acid solution (Ratnam et al. 2008). After digestion, the P, K, Ca and Mg

Table 2 Chemical properties of the soils collected from the burnt and unburnt sites of a mesic Australian savanna, Northern Territory, 2013

Soil properties	Burnt	Unburnt	*p* values
pH (in $CaCl_2$)	5.26 ± 0.02	5.41 ± 0.02	<0.01
N (%)	0.06 ± 0.01	0.16 ± 0.01	<0.01
OM (g dm^{-3})	2.48 ± 0.00	5.90 ± 0.01	<0.01
P (mg dm^{-3})	8.05 ± 0.34	12.06 ± 0.30	<0.01
Ca ($mmol_c$ dm^{-3})	1.19 ± 0.11	6.01 ± 0.21	<0.01
K ($mmol_c$ dm^{-3})	1.31 ± 0.07	2.41 ± 0.10	<0.01
Mg ($mmol_c$ dm^{-3})	1.76 ± 0.17	9.00 ± 0.34	<0.01
Al ($mmol_c$ dm^{-3})	3.29 ± 0.67	7.46 ± 0.18	<0.01
CEC ($mmol_c$ dm^{-3})	7.55 ± 0.54	24.9 ± 2.91	<0.01
Al saturation (m%)[a]	43.28 ± 4.07	30.00 ± 0.74	<0.01

[a] Al saturation (m%) = [Al/(Al + Ca + K + Mg)]×100

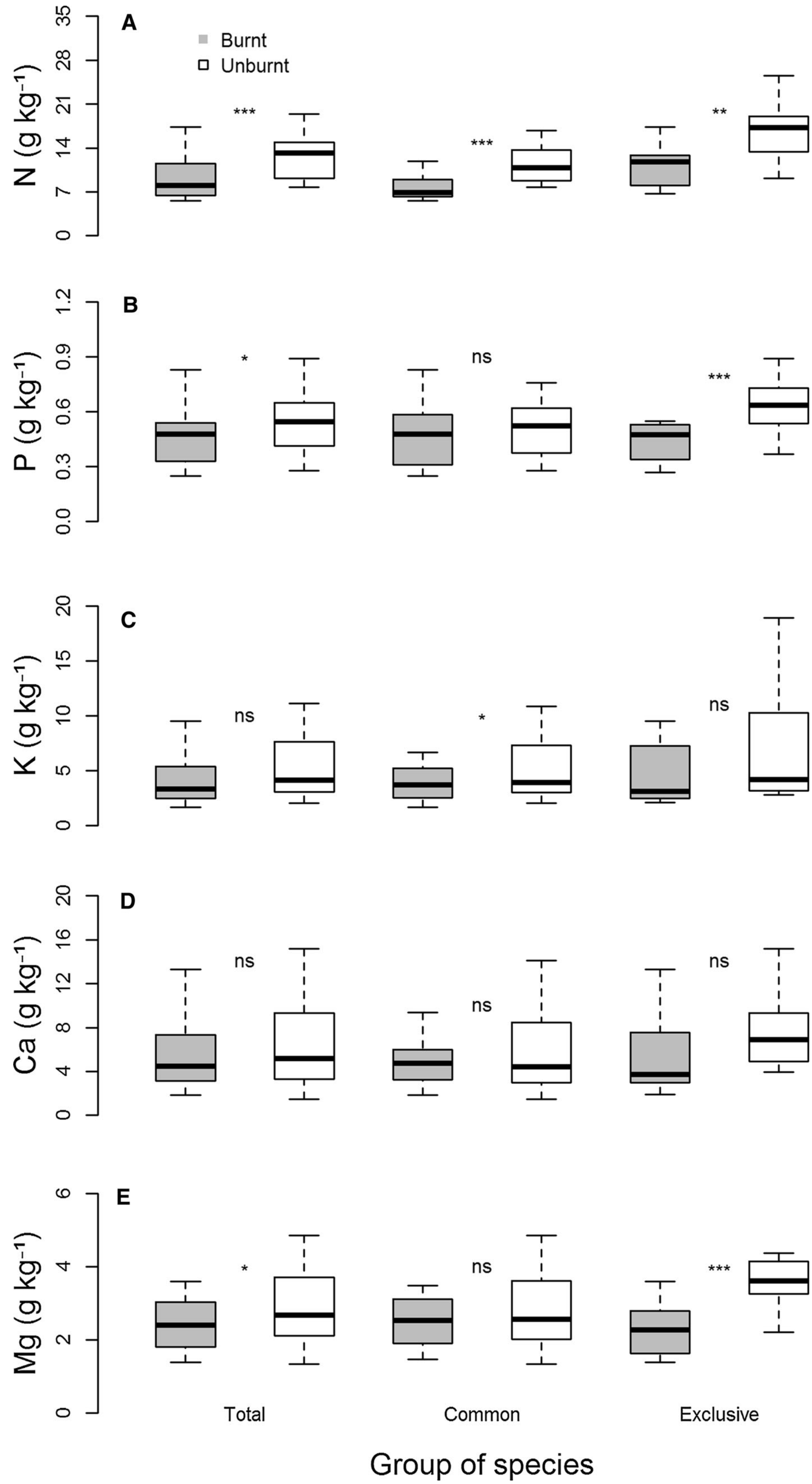

Fig. 2 Leaf macronutrient concentrations of the total (common + exclusive), common and exclusive species from the burnt and unburnt sites of a mesic Australian savanna. The *box* extends from the 25th to 75th percentiles, the *continuous line within the box* shows the median, and *error bars* represent 5th and 95th percentiles ($n = 4$ individuals per species). (*ns* not significant, *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$ using ANOVA)

concentrations were assessed using inductively coupled plasma (ICP) spectrometry (Leman Labs, Hudson, MA, USA). Nitrogen (N) was determined by combustion, using a LECO CHN analyzer (LECO Corp., St Joseph, MI, USA).

At each site, four soil samples were collected at a depth of 10–20 cm, where the roots of most native plants are able to absorb nutrients (Wigley et al. 2013). These samples were analyzed to assess fertility parameters. Soil pH (in $CaCl_2$), base (K, Ca and Mg) concentrations, cation exchange capacity (CEC), organic matter (OM), N, P and Al concentrations, as well as Al saturation (m %), were determined according to the international standard procedure for soil analysis (Robertson et al. 1999).

Plant species were grouped into exclusive, common and total (exclusive + common) species for statistical analysis. We used the Kolmogorov–Smirnov test to check the normality of data. A one fixed factor multivariate analysis of variance (MANOVA) was used to detect variations in leaf traits (N, P, K, Ca, Mg and SLA) of exclusive, common and total species between the burnt and unburnt sites. If MANOVA was significant, individual univariate ANOVAs were performed as post hoc test ($\alpha = 0.05$) to determine which response variable differed between sites (Zar 2010). The variations on soil fertility between burnt and unburnt sites were determined using a Student t test (Zar 2010). The statistical procedures were performed using R (R Development Core Team 2012).

Results and discussion

Fire disrupts the nutrient cycle in savannas because it incinerates the biomass, volatilizes nutrients from plants and litter, and moves ash due to convection during the fire (Oesterheld et al. 1999). In Australian savannas, a single fire event promotes the loss of up 94 % N, 54 % P and 82 % K from plant biomass (Cook 1994). Consistent with previous studies (Cook 1994), the concentrations of N, P, K, Ca and Mg in the soil from the burnt and unburnt sites differed significantly ($p < 0.05$), being 63, 33, 46, 80 and 80 % lower, respectively, in the burnt than in the unburnt site. In addition, soil from the burnt site contained 42 % less organic matter when compared to soil from the unburnt site, possibly indicating a reduction in litter accumulation as a result of frequent fire, as also observed by Mills and Fey (2004). The soil fertility was lower at the frequently burnt than at the unburnt site (Table 2), which was reflected in the lower leaf nutrient concentrations observed in plants from the burnt site when compared to those in plants from the unburnt site (Fig. 2).

Leaf nutrient concentration and SLA significantly differed between the burnt and unburnt sites (MANOVA: Wilks' $\lambda = 0.23039$; $F = 10.5$). Across all plant species (common + exclusive), plants from the burnt site exhibited lower N, P and Mg leaf concentrations as compared to leaves of plants from the unburnt site. Common species growing at the burnt site had lower leaf concentrations of N and K, and species exclusive to the burnt site contained less N, P, and Mg (Fig. 2). The exclusive, common and total (common + exclusive) species from the unburnt site exhibited greater SLA than those from the burnt site (Fig. 3). A long period (>10 years) of fire exclusion may result in vegetative systems with high tree density (Andersen et al. 2005; Durigan and Ratter 2006). Thus, the higher tree density on the unburnt site may have resulted in lower irradiances (high SLA), because we were not able to only sample sunlit leaves.

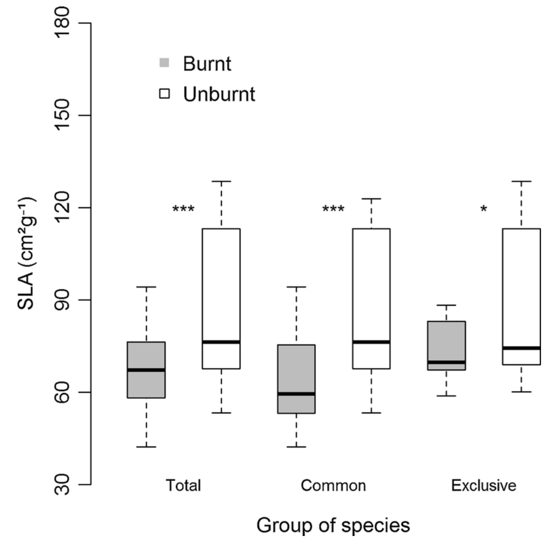

Fig. 3 Specific leaf area (SLA) of the total (common + exclusive), common and exclusive species from the burnt and unburnt sites of a mesic Australian savanna. The *box* extends from the 25th to 75th percentiles, the *continuous line within the box* shows the median, and *error bars* represent 5th and 95th percentiles ($n = 4$ individuals per species). (*ns* not significant, *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$ using ANOVA)

Related studies (Wright et al. 2001; Prior et al. 2005; Delgado et al. 2013) have demonstrated that sclerophyllous leaves (low SLA) of savanna species exhibit low leaf nutrient concentration and this response is influenced by the low soil fertility observed in savanna areas. Scleromorphism could also be influenced by the seasonal dry conditions of savanna areas, as longer dry seasons can be associated with low SLA in the Brazilian savanna (Souza et al. 2015). However, in the present study, both burnt and unburnt sites were located within the same region (30 km apart). Therefore, the rainfall and/or the length of dry seasons are unlikely to explain the differences in SLA observed between these sites.

In this study, we provide evidence that greater SLA and higher leaf nutrient concentrations seem to be favored in fire-protected savanna ecosystems, whereas frequent long-term fires seem to be associated with low soil fertility and with plants with sclerophyllous leaves and low nutrient concentrations.

Author contribution statement Conceived and designed experiments: MCS, GDC, GH, DRR. Performed experiments: MCS, GDC. Analyzed data: MCS, DRR, GH, RF, GDC. Contributed reagents/materials/analytical tools: MCS, GDC, NWM, RF, DRR, LPCM, GH. Wrote manuscript: MCS, DRR, GDC, RF, NWM, LPCM, GH.

Acknowledgments MCS acknowledges the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) and the São Paulo Research Foundation (FAPESP) for PhD fellowships (Grants #2010/07809-1 and BEPE-FAPESP #2012/13762-3). GH (Grant #308902/2014-9) and LPCM (Grant #306119/2011-0 and #306243/2010-5) acknowledge the National Council for Scientific and Technological Development (CNPq) for research productivity fellowships. The authors also thank Jon Schatz (CSIRO) for assistance in the field, and Laura Wendling for editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Alvarado ST, Buisson E, Rabarison H, Rajeriarison C, Birkinshaw C, Lowry PP, Morellato LPC (2014) Fire and the reproductive phenology of endangered Madagascar sclerophyllous tapia woodlands. S Afr J Bot 94:79–87. doi:10.1016/j.sajb.2014.06.001

Andersen AN, Cook GD, Corbett LK, Douglas MM, Eager RW, Russell-Smith J, Setterfield SA, Williams RJ, Woinarski JCZ (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. Aust Ecol 30:155–167. doi:10.1111/j.1442-9993.2005.01441.x

Andersson M, Michelsen A, Jensen M, Kjøller A (2004) Tropical savannah woodland: effects of experimental fire on soil microorganisms and soil emissions of carbon dioxide. Soil Biol Biochem 36:849–858. doi:10.1016/j.soilbio.2004.01.015

Araújo GM, Haridasan M (1988) A comparison of the nutritional status of two forest communities on mesotrophic and dystrophic soils in Central Brazil. Comun Soil Sci Plant Anal 19:1075–1089. doi:10.1080/00103628809367996

Beringer J, Hutley LB, Abramson D et al (2015) Fire in Australian savannas: from leaf to landscape. Glob Change Biol 21:62–81. doi:10.1111/gcb.12686

BOM-Bureau of Meteorology, Australian Government (2013) [Cited 8 October 2013]. http://www.bom.gov.au. Accessed 9 Sept 2015

Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. New Phytol 165:525–537. doi:10.1111/j.1469-8137.2004.01252.x

Bond WJ, Cook GD, Williams RJ (2012) Which trees dominate in savannas? The escape hypothesis and eucalypts in northern Australia. Aust Ecol 37:678–685. doi:10.1111/j.1442-9993.2011.02343.x

Burrows GE (2013) Buds, bushfire and resprouting in eucalypts. Aust J Bot 61:331–349. doi:10.1071/BT13072

Chuvieco E, Giglio L, Justice C (2008) Global characterization of fire activity: toward defining fire regimes from Earth observation data. Glob Change Biol 14:1488–1502. doi:10.1111/j.1365-2486.2008.01585.x

Cook GD (1994) The fate of nutrients during fires in a tropical savanna. Aust J Ecol 19:359–365. doi:10.1111/j.1442-9993.1994.tb00501.x

Cook GD (2001) Effects of frequent fires and grazing on stable nitrogen isotopes ratios of vegetation in northern Australia. Aust Ecol 26:630–636. doi:10.1046/j.1442-9993.2001.01150.x

Cook GD, Williams RJ, Hutley LB, O'Grady AP, Liedloff AC (2002) Variation in vegetative water use in the savannas of the North Australian Tropical Transect. J Veg Sci 13:413–418. doi:10.1111/j.1654-1103.2002.tb02065.x

Delgado MN, Gomes MRA, Báo SN, Rossatto DR (2013) Fertilization residues alter leaf scleromorphy in an evergreen savannah shrub (*Maprounea brasiliensis*, Euphorbiaceae). Aust J Bot 61:266–273. doi:10.1071/BT12231

Durigan G, Ratter JA (2006) Successional changes in cerrado and cerrado/forest ecotonal vegetation in western São Paulo state, Brazil, 1962-2000. Edinb J Bot 63:119–130. doi:10.1017/S0960428606000357

Edwards A, Hauser P, Anderson M, McCartney J, Armstrong M, Thackway R, Allan G, Hempel C, Russell-Smith J (2001) A tale of two parks: contemporary fire regimes of Litchfield and Nitmiluk National Parks, monsoonal northern Australia. Int J Wildl Fire 10:79–89. doi:10.1071/WF01002

Franco AC, Bustamante M, Caldas LS, Goldstein G, Meinzer FC, Kozovitz AR, Rundel P, Coradin VTR (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. Trees 19:326–335. doi:10.1007/s00468-004-0394-z

Givnish TJ (1988) Adaptation to sun and shade: a whole plant perspective. Aust J Plant Physiol 15:63–92. doi:10.1071/PP9880063

Habermann G, Bressan ACG (2011) Root, shoot and leaf traits of the congeneric *Styrax* species may explain their distribution patterns in the cerrado sensu lato areas in Brazil. Funct Plant Biol 38:209–218. doi:10.1071/FP10182

Hao WM, Liu M-H, Crutzen PJ (1990) Estimates of annual and regional releases of CO_2, and other trace gases to the atmosphere from fires in the tropics, based on FAO statistics for the period 1975–1980. In: Goldammer JG (ed) Fire in the tropical biota, ecological studies 84. Springer-Verlag, New York, pp 440–462

Hoffmann WA (1998) Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. J Appl Ecol 35:422–433. doi:10.1046/j.1365-2664.1998.00321.x

Hoffmann W, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol Lett 15:759–768. doi:10.1111/j.1461-0248.2012.01789.x

KBMPA–Kakadu Board of Management and Parks Australia (1999) Kakadu national park plan of management. Kakadu board of management and parks Australia, Jabiru

Lehmann CER, Archibald S, Hoffmann WA, Bond WJ (2011) Deciphering the distribution of the savanna biome. New Phytol 19:197–209. doi:10.1111/j.1469-8137.2011.03689.x

Lehmann CER, Anderson M, Sankaran M et al (2014) Savanna vegetation-fire-climate relationships differ among continents. Science 343:548–552. doi:10.1126/science.1247355

Mills AJ, Fey MV (2004) Frequent fires intensity soil crusting: physiochemical feedback in the pedoderm of long-term burn experiments in South Africa. Geoderma 121:45–64. doi:10.1016/j.geoderma.2003.10.004

Murphy BP, Liedloff AC, Cook GD (2015) Does fire limit tree biomass in Australian savannas? Int J Wildland Fire 24:1–13. doi:10.1071/WF14092

Oesterheld M, Loreti J, Semmartin M, Paruelo JM (1999) Grazing, fire, and climate effects on primary productivity of grasslands and savannas. In: Walker LR (ed) Ecosystems of disturbed ground. Elsevier, Amsterdam, pp 287–306

Pausas JG, Bradstock RA, Keith DA, Keeley JE (2004) Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85:1085–1100. doi:10.1890/02-4094

Pinheiro MHO, Monteiro R (2010) Contributions to the discussions on the origin of the cerrado biome: Brazilian savanna. Braz J Biol 70:95–102. doi:10.1590/S1519-69842010000100013

Prior LD, Eamus D, Bowman DMJS (2003) Leaf attributes in the seasonally dry tropics: a comparison of four habitats in northern Australia. Funct Ecol 17:504–515. doi:10.1046/j.1365-2435.2003.00761.x

Prior LD, Bowman DMJS, Eamus D (2005) Intra-specific variation in leaf attributes of four savanna tree species across a rainfall gradient in tropical Australia. Aust J Bot 53:323–335. doi:10.1071/BT04080

Ratnam J, Sankaran M, Hanan NP, Grant RC, Zambatis N (2008) Nutrient resorption patterns of plant functional groups in a tropical savanna: variation and functional significance. Oecologia 157:141–151. doi:10.1007/s00442-008-1047-5

Robertson GP, Bledsoe CS, Coleman DC, Sollins P (1999) Standard soil methods for long-term ecological research. Oxford University Press, New York

Rossatto DR, Silva LCR, Villalobos-Vega R, Sternberg LSL, Franco AC (2012) Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. Environ Exp Bot 77:259–266. doi:10.1016/j.envexpbot.2011.11.025

Rossiter-Rachor NA, Setterfield SA, Douglas MM, Hutley LB, Cook GD (2008) *Andropogon gayanus* (Gamba Grass) invasion increases fire-mediated nitrogen losses in the tropical savannas of northern Australia. Ecosystems 11:77–88. doi:10.1007/s10021-007-9108-x

Sankaran M, Hanan NP, Scholes RJ et al (2005) Determinants of woody cover in African savannas. Nature 438:846–849. doi:10.1038/nature04070

Scholes RJ, Frost PGH, Tian Y (2004) Canopy structure in savannas along a moisture gradient on Kalahari sands. Glob Change Biol 10:292–302. doi:10.1046/j.1529-8817.2003.00703.x

Scott KA, Setterfield SA, Andersen AN, Douglas MM (2009) Correlates of grass-species composition in a savanna woodland in northern Australia. Aust J Bot 57:10–17. doi:10.1071/BT08120

Silva DM, Batalha MA (2008) Soil–vegetation relationships in cerrados under different fire frequencies. Plant Soil 311:87–96. doi:10.1007/s11104-008-9660-y

Souza MC, Franco AC, Haridasan M, Rossatto DR, Araújo J, Morellato LPC, Habermann G (2015) The length of the dry season may be associated with leaf scleromorphism in cerrado plants. An Acad Bras Cienc. doi:10.1590/0001-376520150381 **(in press)**

R Development Core Team (2012) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. http://www.r-project.org. Accessed 9 Sept 2015

Wigley BJ, Coetsee C, Hartshorn AS, Bond WJ (2013) What do ecologists miss by not digging deep enough? Insights and methodological guidelines for assessing soil fertility status in ecological studies. Acta Oecol 51:17–27. doi:10.1016/j.actao.2013.05.007

Williams D, Cook GD (2001) Savanna landscapes. In: Dyer R, Jacklyn P, Partridge I, Russell-Smith J, Williams D (eds) Savanna burning. Understanding and using fire in northern Australia. Tropical Savannas Co-operative Research Centre, Darwin, pp 5–14

Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high-and-low-rainfall and high and low-nutrient habitats. Funct Ecol 15:423–434. doi:10.1046/j.0269-8463.2001.00542.x

Zar JH (2010) Biostatistical analysis, 5th edn. Prentice Hall, Upper Saddle River