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Ants, fire and bark traits affect how African savanna trees recover following damage

Benjamin J. Wigley[1, 2*], Corli Coetsee[3, 2], Laurence M. Kruger[4,5], Jayashree Ratnam[1], & Mahesh Sankaran[1, 6]

[1]National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK, Bellary Road, Bangalore, 560 065, India

[2]School of Natural Resource Management, Nelson Mandela University, George Campus, Madiba Drive, Private Bag X6531, George 6530, South Africa

[3]Scientific Services, Kruger National Park, Private Bag X402, Skukuza, 1350, South Africa

[4]Organisation for Tropical Studies, Skukuza, South Africa

[5]Biology Department, University of Cape Town, Rondebosch, 7700, South Africa

[6]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK

[*]Correspondence author. E-mail: benwigley@gmail.com, telephone: +27 (0) 834818829

Other authors:

CC: corli.wigley-coetsee@sanpark.org
LMK: laurence.kruger@gmail.com
JR: j.ratnam.bangalore@gmail.com
MS: mahesh@ncbs.res.in

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ABSTRACT

Bark damage resulting from elephant feeding is common in African savanna trees with subsequent interactions with fire, insects and other pathogens often resulting in tree mortality. Yet, surprisingly little is known about how savanna trees respond to bark damage. We addressed this by investigating how the inner bark of marula (*Sclerocarya birrea*), a widespread tree species favoured by elephants, recovers after bark damage. We used a long-term fire experiment in the Kruger National Park to measure bark recovery with and without fire. At 24 months post-damage, mean wound closure was 98, 92, and 72% respectively in annual and biennial burns and fire exclusion treatments. Fire exclusion resulted in higher rates of ant colonisation of bark wounds, and such ant colonisation resulted in significantly lower bark recovery. We also investigated how ten common savanna tree species respond to bark damage and tested for relationships between bark damage, bark recovery and bark traits while accounting for phylogeny. We found phylogenetic signal in bark dry matter content, bark N and bark P, but not in bark thickness. Bark recovery and damage was highest in species which had thick moist inner bark and low wood densities (Anacardiaceae), intermediate in species which had moderate inner bark thickness and wood densities (Fabaceae) and lowest in species which had thin inner bark and high wood densities (Combretaceae). Elephants prefer species with thick, moist inner bark, traits that also appear to result in faster recovery rates.

KEY-WORDS: bark damage, bark traits, elephants, interactions, Kruger National Park, long-term fire experiment

ELEPHANTS HAVE A RANGE OF EFFECTS IN SAVANNA ECOSYSTEMS RANGING FROM POSITIVE, (e.g., dispersal of seeds, facilitation of feeding by other herbivores, Rutina *et al.* 2005, Young *et al.* 2005, Pringle 2008, Nasseri *et al.* 2011) to negative, e.g., limiting tree survival and recruitment and decreasing woody densities, as well as simplification of vegetation structure, which decreases habitat for other fauna (Dublin *et al.* 1990, Cumming *et al.* 1997, McCauley *et al.* 2006, Landman & Kerley 2014, McCleery *et al.* 2018). Elephants can cause significant tree mortality through different mechanisms including ringbarking and pollarding (Coetzee *et al.* 1979; Gadd 2012; Helm *et al.* 2009, 2011; Midgley *et al.* 2010; Moncrieff *et al.* 2008;

O'Connor *et al.* 2007; Shannon *et al.* 2011; Vanak *et al.* 2012). Elephants have been observed to disproportionately damage some species (e.g. marula, *Sclerocarya birrea*) leading to increased mortality of these species and their eventual replacement by others (Coetzee *et al.* 1979, Helm *et al.* 2009, 2011, Shannon *et al.* 2011, Gadd 2012, Vanak *et al.* 2012). Although ringbarking by elephants – the stripping of bark around the entire circumference of the trunk or stem – is a major cause of tree mortality, there is no clear consensus on why elephants prefer the bark of certain species (Anderson & Walker 1974, Croze 1974, Bash 2002, O'Connor *et al.* 2007, Boundja & Midgley 2010).

Previous studies have related the degree of bark damage by elephants to several factors which include calcium and water content (Anderson & Walker 1974, Croze 1974, Bash 2002), ease of debarking (O'Connor *et al.* 2007) and the structure of the main stem (Anderson & Walker 1974, O'Connor *et al.* 2007, Boundja & Midgley 2010). However these are not necessarily mutually exclusive (e.g., thick easy to peel bark is also often high in water and sugar content, O'Connor *et al.* 2007, Rosell *et al.* 2014). Ultimately, the net effect of elephants on savanna vegetation depends not only on which species they utilise, but also on how well different species respond to, and recover from, damage from both elephants and fires, which commonly occur in savannas. Bark removal, even if relatively limited, has been shown to negatively affect post-fire recovery of savanna trees (Yeaton 1988, Moncrieff *et al.* 2008, Midgley *et al.* 2010). In fact, the synergistic effects of fire and elephants appear to be more important for tree mortality than either disturbance alone, with previous studies showing that bark damage when combined with fire can result in increased rates of tree mortality in African savannas (Laws 1970, Moncrieff *et al.* 2008, Shannon *et al.* 2011, Owen-Smith & Chafota 2012, Vanak *et al.* 2012, Pringle *et al.* 2015).

This study attempts to improve our understanding of bark recovery in savanna trees by addressing the following main objectives: 1) To determine rates of bark recovery and examine the interaction between bark recovery and fire in marula (*Sclerocarya birrea)*; a widespread species that is heavily utilized by elephants in Southern African savannas. We hypothesize that the interaction between fire and bark damage should result in slower bark recovery rates. 2) To measure rates of inner bark recovery in ten widespread savanna tree species and determine how recovery is related to bark and stem traits, and the extent to which these species are damaged by elephants. We hypothesize that trees with thicker inner bark will have lower bark dry matter content (i.e. higher moisture) and recover faster from damage

than species with thin inner bark. We also expect elephants to preferentially select for species with thicker inner bark and higher moisture content.

METHODS

STUDY SITES — The study took place in the 20 000 km^2 Kruger National Park (KNP) situated in the north-eastern corner of South Africa, bordering Zimbabwe to the north and Mozambique to the east. A long-term fire experiment, established in 1954 (called the experimental burn plots or EBPs), presented the ideal opportunity to study the effects of different fire regimes on bark recovery of trees. The experiment has 12 different burning treatments that manipulate burning season (i.e. August, December, October, February, April) and frequency of burn (i.e. annual, biennial and triennial), including one fire-exclusion treatment and is replicated in four of the six major vegetation types of KNP (see Biggs *et al.* (2003), Higgins *et al.* (2007) for a more comprehensive background). In each of the four vegetation types, there are four replicate blocks, called strings, each consisting of the 12 burning treatments applied over plots of ~7 ha. We explored the interaction between fire and bark recovery in marula (*Sclerocarya birrea* (A. Rich) Hochst. subsp. *caffra*), in the EBPs established in the Sourveld vegetation type around Pretoriuskop. The soils of the Pretoriuskop region are derived from the underlying Nelspruit granite suite consisting of migmatite, gneiss and granite (Barton *et al.* 1986) and the mean annual rainfall for the area is approximately 750 mm. Our study was restricted to three of the 12 burning treatments at the site: annual August burn (moderate fire intensity in dry season), biennial August burn (higher fire intensity in dry season because of an additional season of fuel accumulation), and fire-exclusion. We used all four replicate strings, referred to as Shabeni (25.117133° S, 31.237050° E), Fayi (25.193144° S, 31.283546° E), Numbi (25.133364° S, 31.210246° E) and Kambeni (25.15540° S, 31.264882° E), for our study.

The second part of our study, which considered bark recovery of ten common savanna tree species, took place at five sites in the central and southern parts of Kruger National Park (Table 1). Soils at the five study sites are derived from granite, gabbro and basalt, and mean annual rainfall ranges from ~500 to 700 mm (Table1). Rain falls mainly between October and April and consists predominantly of convective thunderstorms from the north and northeast or tropical cyclones off the Indian Ocean. Mean monthly temperatures are between 26.3 °C and 17.5 °C. Species nomenclature is based on Coates-Palgrave (2002).

Sampling Methodology

Bark recovery rates in marula trees and interactions with fire — In each of the three fire treatments (annual August burn, biennial August burn, and fire exclusion) we selected five fully grown healthy adult marula trees in each of the four replicate strings (i.e. N = 20 per treatment). We removed a circular section of bark of 50 mm diameter (~20 cm^2) from each tree in July 2016 using a hammer and sharpened soil corer. The bark of marula trees is predominantly composed of living inner bark with a thin layer of flaky dead outer bark (see Fig. 1a). For the purposes of this study, we were interested in the recovery of the living inner bark as defined by Romero (2006) and Baldauf and Dos Santos (2014), and therefore removed the thin layer of outer bark (i.e. periderm/cork) using a wood chisel and then removed the entire layer of inner bark (i.e. secondary phloem), while ensuring not to damage the underlying wood. The bark cores were removed at a height of 0.5 m above ground level to ensure that they were within the flame zone of subsequent fires. For each of the selected trees, we measured stem diameter at the height at which the cores were removed. Each tree was then tagged and a GPS location recorded. Both of the fire treatments were burnt in August 2016 and the annual August burn was burnt again in August 2017 and 2018. All trees were resurveyed in June 2017, September 2017 and again in July 2018. As recovery only took place from the outer edges of the removed bark sections (i.e. all inner bark was removed), the diameter of the recovered proportions of inner bark was measured on both the vertical and horizontal planes and then converted to percentage recovered, and a photograph taken. During our surveys, we noticed a number of ant nests in the bark wounds, and to determine if ant presence influenced bark recovery, we made a note of the presence/absence of ant nests in the wounds to include as a co-variate in our analyses.

Bark recovery in ten common savanna tree species and relationships with bark damage, bark traits and wood density — Bark cores were removed from five healthy (i.e. undamaged) adult individuals for each of ten dominant species (see Table 1) in October 2015. For this part of the study we were again only interested in the recovery of living inner bark and therefore removed the outer phellogen (if present) before sampling. All trees were resurveyed in January 2016, June 2016 and September 2017. The removal of bark and measures of recovery were performed using the same methodology as described above. After removal from the tree, bark cores were kept on ice and wet weights and inner bark thickness

measured once back at the laboratory. Bark dry matter content (BDMC) is the oven-dry mass (mg) of a bark core divided by wet weight (g) expressed as mg g^{-1}. Inner bark thickness was measured on two sides of the core using vernier calipers. Relative bark thickness was calculated as the ratio of total (i.e. inner and outer) bark thickness (measured on the trees during sampling) to stem radius (Hoffmann *et al.* 2012). The inner bark cores were oven dried at 65 °C, weighed and then finely ground for the analysis of bark total nitrogen (N) and phosphorus (P). Bark N concentrations were determined using a Leco TruSpec CN Analyser (LECO Corporation, St. Joseph, MI). Bark P was analysed using inductively coupled plasma-optical emission spectrometry (ICP-OES, Varian Vista MPX, Palo Alto, CA, USA). Wood density (mg mm^{-3}) was measured on five different individuals of the same species at each site using the volume displacement method outlined in Cornelissen *et al.* (2003).

MEASURES OF BARK DAMAGE — Data from two different sources were combined and averaged to provide a measure of elephant bark damage for the ten species. The first dataset was collected by sampling ten adult individuals for each of the species selected at each of the five sites (Table 1). For each tree the stem diameter, height, number of stems and the presence of bark damage on the main stem/stems were noted. The percentage bark damage for both the circumference and height of the trunk was then visually estimated and recorded. The second dataset was collected as part of a broader study, which aimed to assess both the susceptibility to elephant stripping and recovery response of the dominant tree species in southern KNP. This dataset was collected by walking widespread transects in the southern KNP between 2014 and 2017. For each individual tree of the ten dominant species we encountered along these transects; species identity, height (m) and diameter (cm) were recorded. We then estimated and recorded how much of the total circumference of bark on the stem had been damaged and to what height. This allowed us to calculate the total percentage of bark damage for each tree stem.

STATISTICAL ANALYSES — All analyses were performed using R version 3.4.2 (R Development Core Team 2016). To test for differences in rates of bark recovery among treatments (annual burn, biennial burn and no burn) and for trees with and without ant nests, we used the function 'glm' in the *stats* package in R. To model bark recovery, we ran Generalized Linear Models (GLM) using a quasibinomial distribution (bark recovery data were measured as continuous proportions) with a logit link function. A model which included both treatment and sampling month (i.e. 10, 14 and 24 months) showed no significant interaction, we therefore tested if bark recovery differed between treatments at 24

months only. We then ran a model which included both treatment and presence of ant nests which showed no significant interaction, we therefore tested if bark recovery differed between trees with ant nests *vs.* trees with no ant nests present. We used the chi-square test to check if the occurrence of ant nests was equally likely across the three treatments.

For our second objective, the phylogenetic tree (81 species; (Wigley *et al.* 2016)) was trimmed to include only the ten species sampled for bark traits using the function 'drop.tip' in the *ape* package for R (version 3.5, Paradis *et al.* 2004). To test for relationships between bark damage, bark recovery and the measured bark and stem traits, we performed phylogenetic generalised least squares (PGLS) regression on species means to account for phylogenetic dependence (Duncan *et al.* 2007), using the *caper* package (version 0.5.2; Orme *et al.* 2013) in R. For the PGLS analyses, λ (the extent to which covariance in traits depends on phylogenetic branch length) was estimated using the Brownian Motion model of evolution (Pagel 1999). Ordinary least squares (OLS) models, ignoring phylogenetic relatedness, and PGLS models were fitted for each comparison. We then tested for the most appropriate model using the Akaike Information Criterion (AIC). We also explored the influence of phylogenetic relatedness on recovery and bark and stem traits by plotting trait values onto the phylogenetic tree for the 10 species in this study and then tested for significant phylogenetic signal (Blomberg's K, Blomberg *et al.* 2003) in the traits using the function 'multiPhylosignal' as implemented in the R package *picante* (Version 1.7, Kembel *et al.* 2010).

RESULTS

BARK RECOVERY RATES IN MARULA TREES AND INTERACTIONS WITH FIRE — Bark recovery was significantly lower in unburned plots than in either the annual and biennial burn treatments ($F = 4.73$, $df = 57$, $p = 0.03$). Trees in all treatments had recovered at least 72% of bark within 24 months (98%, 92% and 72%, for annual burn, biennial burn and no burn, respectively). Although bark recovery continued to increase over time, rates of increase were mostly low after 10 months (Fig. 2) for all three treatments. Thus, in the studied marula trees, the majority of bark recovery appears to occur within the first year after damage. The presence of ant nests in bark wounds resulted in lower net bark recovery across all treatments ($F = 32.1$, $df = 58$, $p = <0.0001$, Fig. 3a). However, bark recovery in trees without ant nests present did not differ between annual burn, biennial burn and no burn treatments (Fig 3a). Overall, the proportion of trees with ant nests present was significantly higher in unburned

plots compared to annual ($\chi^2 = 18.5$, $p < 0.001$) and biennial burn treatments ($\chi^2 = 8.3$, $p = 0.004$, Fig 3b).

BARK RECOVERY IN TEN COMMON SAVANNA SPECIES AND PHYLOGENETIC RELATIONSHIPS WITH BARK DAMAGE, BARK TRAITS AND WOOD DENSITY — Bark recovery in the ten common tree species found in southern KNP was highly variable (Table 2). The two species in the Anarcardiaceae family had the highest bark recovery rates (47 – 100%) compared to the four species in the Fabaceae (22 – 46%, Fig. 5, Table 2). Bark recovery in the Combretaceae was the lowest (3 – 13%, Table 2). Bark damage and bark thickness were both highest in the Anacardiaceae, followed by the Fabaceae and lowest in the Combretaceae (Table 2, Fig. 4).

Bark dry matter content showed the strongest phylogenetic signal (Blomberg's K = 0.3, $p = 0.007$), followed by bark [N] ($p = 0.04$), while wood density also showed some evidence for phylogenetic signal ($p < 0.10$, Table 3). Bark damage was positively correlated with bark recovery, i.e. species that were more utilized recovered faster ($F = 6.40$, $\lambda = 0.34$, $p = 0.04$, Table 3). Bark damage was also positively related to bark thickness ($F = 6.93$, $\lambda = 0$, $p = 0.03$) and marginally related to wood density ($F = 3.91$, $\lambda = 0$, $p = 0.08$). Bark recovery was positively correlated with bark thickness ($F = 34.4$, $\lambda = 0$, $p < 0.001$), negatively related to BDMC ($F = 7.83$, $\lambda = 0$, $p = 0.02$) and marginally correlated with wood density ($F = 3.80$, $\lambda = 0$, $p = 0.09$), however none of these relationships were influenced by phylogeny (i.e. $\lambda = 0$). Bark recovery was not significantly correlated with bark [N] or bark [P] ($p > 0.5$, Table 3).

DISCUSSION

Contrary to our prediction, we found that bark recovery rates were higher in plots that burned compared to unburnt plots. Slower bark recovery rates were associated with the presence of ant nests in the wounds, the frequency of which was higher in unburned compared to burned plots (i.e. recovery did not differ between the three treatments when ant nests were not present). We also found significant variability across tree species and families in bark recovery rates following damage. Recovery rates were most strongly related with bark thickness and moisture content and were highest in the Anacardiaceae and slowest in the Combretaceae. As expected, species with thicker bark were also preferentially utilised by elephants and recovered bark relatively rapidly following damage compared to less-preferred species.

Previous studies have shown that debarked savanna trees that are subsequently exposed to fire have much higher rates of mortality than those that recover without exposure to fire (Moncrieff *et al.* 2008, Helm *et al.* 2011, Owen-Smith & Chafota 2012). Surprisingly, our results show that fire itself did not impede bark recovery in marula; to the contrary, trees in burnt treatments recovered bark more rapidly (96% recovery in trees uncolonized by ants in annual burn over 24 months) than uncolonized trees in unburned treatments (86%, Fig. 2a). Such high recovery rates are likely related to the high relative bark thickness in marula; an important plant functional trait that has been shown elsewhere to be positively related with higher survival rates after disturbance in savanna species (Hoffmann *et al.* 2003, 2012, Midgley *et al.* 2010, Lawes *et al.* 2011, 2013). Thick bark, with high water content, is advantageous during fires as a high proportion of the heat may be absorbed by warming and vaporising water in the bark (Poorter *et al.* 2014) and species with thick bark can recover rapidly following fire (Pinard & Huffman 1997, Schoonenberg *et al.* 2003). However, we predict that the interactive effects of bark damage and fire would depend on the size of the area initially damaged; larger wounds would probably be more susceptible to damage from subsequent fires than the relatively small areas damaged in this study.

Our findings suggest that if the damaged area is not colonised by ants, bark recovery in marula trees can be rapid, even if the trees are subsequently exposed to fires (see Fig. 1b). However, the colonization of bark wounds by ants – which we found to be negatively related to fire frequency – significantly impaired bark recovery (e.g. Fig. 1c). Fire seldom has direct long-term negative effects on ants, although it has been shown to decrease ant colonisation in the short term (Kimuyu *et al.* 2014) and drive changes in ant species composition by altering vegetation structure and associated micro-climate (Andersen 1991, Sensenig *et al.* 2017). Parr *et al.* (2004) working on the same long-term fire experiment found significant differences in the composition of ant assemblages between burn and no burn treatments, as has been shown elsewhere (Andersen 1991, Andersen *et al.* 2006, Frizzo *et al.* 2012). Furthermore, Frizzo *et al.* (2012) suggested that fire can destroy the nests of arboreal species. Our results suggest that fire exclusion can benefit arboreal nesting ants such as *Crematogaster castanea;* the main nest-building ant species in the removed bark cores on the fire experiment plots. This genus is known to build nests in the large galls of some Acacia species, e.g. *A. depanolobium* and *A. seyal* (Young *et al*. 1996, Palmer *et al.* 2008), as well as in rotten wood and under bark (Slingsby 2017). *Crematogaster* spp. are often forest-

associated species and have also been shown to increase with fire exclusion in Australian savannas (Andersen *et al.* 2006).

Several previous studies have reported that insect (and fungal) damage, particularly by species that burrow into dry wood such as beetles and borers, can slow bark recovery, especially in tree species with slow recovery rates (Geldenhuys *et al.* 2006, Delvaux *et al.* 2009, Vermeulen *et al.* 2012). On the other hand, the presence of termite tunnels in *Warburgia salutaris* and several other woodland species has also been shown to benefit wound recovery by keeping wounds from drying out (Geldenhuys *et al.* 2006). At present, we are unaware of any literature that documents how species that live or make nests on the surface (e.g., ants) influence bark recovery, and the mechanisms by which ants impede bark recovery remain unclear.

Bark recovery was highly variable among the ten common savanna tree species at the study sites and was not phylogenetically determined (see Table 3). The lack of phylogenetic signal in bark recovery was surprising as recovery was highest amongst species belonging to the Anacardiaceae (thick moist bark), lowest in the Combretaceae (thin bark with low moisture), and intermediate in the Fabaceae (intermediate bark thickness and moisture content). Bark recovery was most strongly related to bark thickness with no phylogenetic dependence ($\lambda = 0$); species with thicker inner bark had higher rates of recovery following damage. Faster rates of recovery in thick barked species compared to species with thin bark has been reported from other systems such as the Bolivian Amazon (Romero & Bolker 2008, Baldauf & dos Santos 2014).

As predicted, the species with thicker moist bark were preferentially utilized by elephants. Our results show that bark damage was not related to bark N or P which is in contrast to patterns previously reported (Anderson & Walker 1974, Croze 1974, Thomson 1975, Field & Ross 1976, O'Connor *et al.* 2007). Although we don't rule out that elephants may prefer thick barked species because of compounds not measured in our study (e.g., sugars and other compounds), they appear to preferentially select for trees with high bark moisture content. Species with thick, moist bark also recovered more rapidly from bark damage, which would prevent further damage from fire and boring insects. Similarly, Romero & Bolker (2008) found that species with thick bark (and exudates and trunk thorns) had the fastest recovery rates in Amazonian forest trees. Delvaux *et al.* (2013) also showed that the thickness of the conducting phloem was an important factor explaining bark recovery

rates. On the other hand, species with thin inner bark, high bark dry matter content, high wood densities (which may combine with low growth rates such as in Combretaceae) had slow or limited bark recovery (see Fig. 1d) and these species were not preferred by elephants and tended to suffer little bark damage. However, if these species are damaged it is likely that compartmentalisation of wound damage occurs quickly and stem decay is limited (Romero & Bolker 2008, Ngubeni *et al.* 2017).

To conclude, the removal of fire resulted in changes in ant communities (either directly or indirectly), such that arboreal ant species nested more frequently in damaged bark, resulting in lower bark recovery. These findings remind us of the importance of the often-overlooked indirect effects of fires in savanna ecosystems. We highlight the need for further studies that examine the interactions between invertebrates, fire, elephants and tree mortality. Our second major finding was that certain bark and stem traits were influenced by the phylogenetic relatedness of the ten species in this study, which in turn determined the degree of utilisation or damage by elephants. Tree species with moist (and thicker) inner bark were favoured by elephants but at the same time, better able to recover after damage. Our results also suggest that bark recovery is largely limited to the first year since damage for many of the studied species. Phylogenetic constraints on bark traits may thus act as a filter on tree species assembly in fire-prone and herbivore-rich habitats.

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DATA AVAILABILITY

The data used in this study will be archived at the Dryad Digital Repository

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TABLES

Table 1. Dominant tree species, underlying geology, mean annual rainfall (MAP), latitude and longitude for the five sites in the southern Kruger National Park, South Africa.

Site name	Species	Geology	MAP (mm)	CO-ORD E	CO-ORD S
Nhlangwini	*Sclerocarya birrea*				
	Terminalia sericea	Granite	678	31.293	-25.199
Ship Mountain	*Acacia nigrescens*				
	Combretum apiculatum	Gabbro	676	31.373	-25.213
Makhohlolo	*Acacia gerrardii*				
	Albizia harveyi	Basalt	550	31.914	-25.262
Satara Basalt	*Acacia tortilis*				
	Combretum imberbe	Basalt	525	31.815	-24.277
Satara Granite	*Combretum zeyheri*				
	Lannea schweinfurthii	Granite	576	31.643	-24.526

Table 2. Mean ± se for bark damage (% circumference damaged), bark recovery (% core recovered), bark thickness (BT, mm), relative bark thickness (RBT, %), wood density (WD, mg mm^{-3}), bark dry matter content (BDMC, mg g^{-1}), bark nitrogen (N, %) and bark phosphorus (P, %) for the species in each of the three families. No se is shown for N and P as they were measured using pooled bark samples from five individuals.

Species	Family	Damage	Recovery	BT	RBT	WD	BDMC	N	P
Lannea schweinfurthii	Anacardiaceae	17.5 ± 3.8	47.0 ± 9.70	9.80 ± 1.50	8.70 ± 1.50	0.54 ± 0.02	514 ± 18.1	0.06	0.024
Sclerocarya birrea	Anacardiaceae	37.5 ± 5.6	100 ± 0.00	21.8± 0.70	4.70 ± 0.70	0.63 ± 0.04	537 ± 12.5	0.08	0.017
Combretum apiculatum	Combretaceae	14.2 ± 3.1	12.7 ± 6.90	4.00 ± 0.50	2.10 ± 0.50	0.79 ± 0.02	895 ± 15.3	0.27	0.014
Combretum imberbe	Combretaceae	0.0 ± 0.0	11.5 ± 8.80	3.90 ± 0.30	2.90 ± 0.50	0.90 ± 0.01	665 ± 20.9	0.13	0.019
Combretum zeyheri	Combretaceae	7.50 ± 3.8	3.30 ± 5.70	5.20 ± 0.30	5.60 ± 0.30	0.66 ± 0.03	775 ± 18.0	0.27	0.028
Terminalia sericea	Combretaceae	16.3 ± 4.2	12.5 ± 8.30	8.90 ± 0.70	3.00 ± 0.70	0.70 ± 0.05	758 ± 29.3	0.11	0.001
Acacia gerrardii	Fabacea	15.0 ± 7.6	45.6 ± 20.3	7.40 ± 0.50	11.5 ± 0.50	0.75 ± 0.03	719 ± 46.1	1.04	0.011
Acacia nigrescens	Fabacea	25.9 ± 4.6	29.4 ± 6.50	10.9 ± 0.40	3.70 ± 0.40	0.79 ± 0.02	659 ± 18.8	1.14	0.024
Acacia tortilis	Fabacea	20.0 ± 6.2	27.7 ± 13.6	6.20 ± 0.90	6.50 ± 0.90	0.81 ± 0.02	679 ± 17.4	0.70	0.037
Albizia harveyi	Fabacea	3.80 ± 2.0	21.6 ± 6.50	5.50 ± 0.40	6.60 ± 0.40	0.72 ± 0.02	700 ± 15.9	0.50	0.009

Table 3 Tests for phylogenetic signal in the measured bark traits (Blomberg's K) and results from the phylogenetic generalised least squares (PGLS) models showing R^2, λ, F and p values for correlations between bark damage, bark recovery, inner bark thickness, bark dry matter content (BDMC), wood density, bark nitrogen and bark phosphorus concentrations.

Trait	Blombergs K	bark damage				bark recovery			
		R^2	λ	F	p	R^2	λ	F	p
bark recovery	0.14 (p = 0.14)	0.37	0.34	6.34	0.04				
bark thickness	0.11 (p = 0.28)	0.40	0	6.93	0.03	0.79	0	34.4	<0.001
BDMC	0.30 (p = 0.007)	0.15	0.95	2.53	0.15	-0.43	0	7.83	0.02
wood density	0.14 (p = 0.09)	0.24	0	3.91	0.08	0.24	0	3.8	0.09
bark [N]	0.22 (p = 0.04)	-0.06	0	0.47	0.51	-0.1	0.68	0.04	0.85
bark [P]	0.03 (p = 0.93)	-0.11	0.25	0.10	0.76	-0.1	0.73	0.45	0.52

FIGURE LEGENDS

Figure 1. a) A fresh wound caused by removing a bark core from a marula (*Sclerocarya birrea)* tree. b) A fully recovered bark wound 24 months after removing a bark core from a marula tree in the annual burn treatment of the long-term fire experiment. c) An ant (*Crematogaster castanea*) nest in the wound area from which a bark core was removed from a marula tree growing in the no burn treatment of the long-term fire experiment. The ant nest resulted in zero bark recovery in this marula tree. d) A photo of the wound where a bark core was removed from a *Combretum apiculatum* tree after 21 months, note the lack of recovery and thin bark found in this species.

Figure 2. Mean ± se bark recovery, measured as the percentage of the original removed core that recovered after ten, fourteen and twenty-four months in the annual, biennial and no burn fire treatments in the Pretoriuskop strings of the Kruger National Park long-term fire experiment. N = 20 for each treatment.

Figure 3. a) Mean ± se bark recovery after twenty-four months in trees with and without ant nests present in damaged areas from which bark cores were removed in annual, biennial, no burn and across all treatments. b) Percentages of trees with ant nests present in the no burn, annual and biennial fire treatments. Total n for each treatment = 20, for number of trees with ants present n = 3 for annual burn, n = 5 for biennial burn and n = 10 for no burn.

Figure 4. Phylogenetic relationships among the ten species included in this study and associated relative trait values, squares of similar size and colour indicate similar trait values.

FIGURES

Figure 1

Figure 2

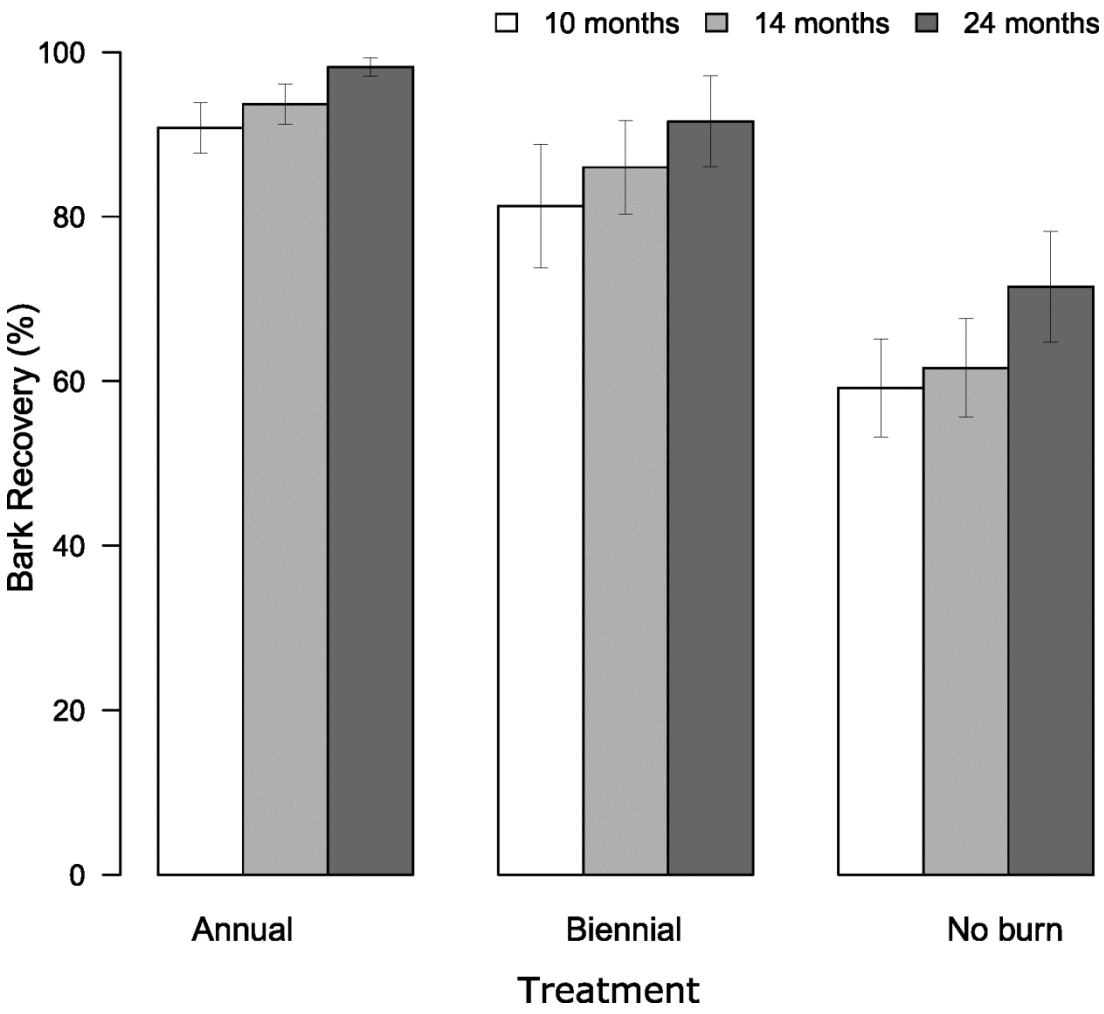

10 months
14 months
24 months
100
80
60
40
20
0
Bark Recovery (%)
Annual
Biennial
No burn
Treatment

Figure 3

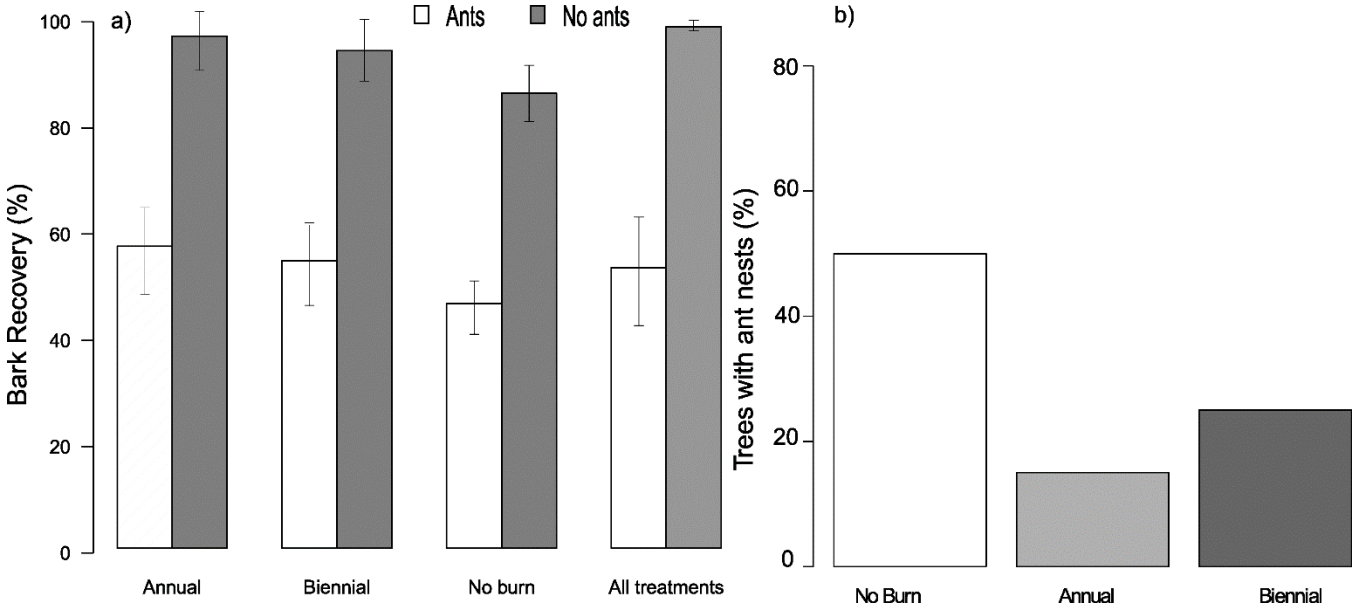
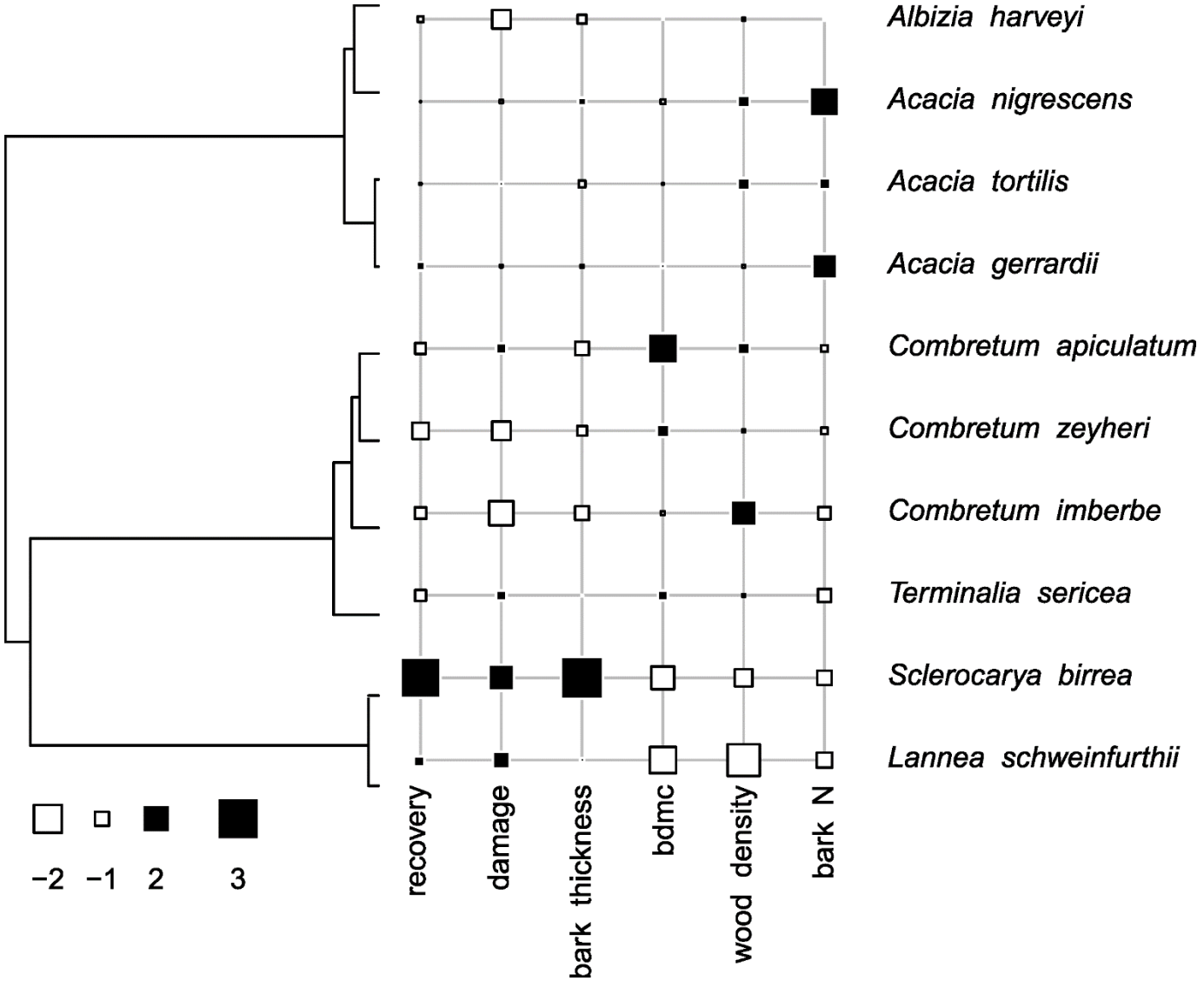

a)
Ants
No ants
Bark Recovery (%)
100
80
60
40
20
0
Annual
Biennial
No burn
All treatments
b)
Trees with ant nests (%)
80
60
40
20
0
No Burn
Annual
Biennial

Figure 4


Albizia harveyi
Acacia nigrescens
Acacia tortilis
Acacia gerrardii
Combretum apiculatum
Combretum zeyheri
Combretum imberbe
Terminalia sericea
Sclerocarya birrea
Lannea schweinfurthii
recovery
damage
bark thickness
bdmc
wood density
bark N
−2
−1
2
3