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Bark traits, decomposition and flammability of Australian forest trees

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Abstract. Bark shedding is a remarkable feature of Australian trees, yet relatively little is known about interspecific differences in bark decomposability and flammability, or what chemical or physical traits drive variation in these properties. We measured the decomposition rate and flammability (ignitibility, sustainability and combustibility) of bark from 10 common forest tree species, and quantified correlations with potentially important traits. We compared our findings to those for leaf litter, asking whether the same traits drive flammability and decomposition in different tissues, and whether process rates are correlated across tissue types. Considerable variation in bark decomposability and flammability was found both within and across species. Bark decomposed more slowly than leaves, but in both tissues lignin concentration was a key driver. Bark took longer to ignite than leaves, and had longer mass-specific flame durations. Variation in flammability parameters was driven by different traits in the different tissues. Decomposability and flammability were each unrelated, when comparing between the different tissue types. For example, species with fast-decomposing leaves did not necessarily have fast-decomposing bark. For the first time, we show how patterns of variation in decomposability and flammability of bark diverge across multiple species. By taking species-specific bark traits into consideration there is potential to make better estimates of wildfire risks and carbon loss dynamics. This can lead to better informed management decisions for Australian forests, and eucalypt plantations, worldwide.

Additional keywords: decay, *Eucalyptus*, litter, wildfire.

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Introduction

Bark is unequivocally a special feature in Australian forests. With a great variety of types (e.g. smooth bark, stringybark, ironbark; Table 1, Fig. 1), it is often used in floral keys as the first step for identifying *Eucalyptus* species (Millett 1969; Brooker and Kleinig 1990; Robinson 2003). Many species of *Eucalyptus* and other genera in the Myrtaceae family shed their bark annually, which leads to a spectacular accumulation of bark on the forest floor and long ribbons hanging down from the trunk and branches. This gives eucalypt forests, which cover 92 million ha of land surface in Australia (ABARES 2016), and 20 million ha of plantations around the world (Booth 2013), their unique appearance.

Bark shedding, especially of 'smooth bark' species, happens mainly in the Australian summer, often around December (Lamb 1985; Crockford and Richardson 1998). The 'how and why' of this bark shedding is still poorly understood, but is likely to depend on endogenous factors (e.g. tree size, growth, vigour) and on environmental factors, especially weather conditions (Crockford and Richardson 1998). The potential adaptive value of bark shedding in smooth bark species is thought to include promoting photosynthesis by the living tissues of the trunk (Aschan and Pfanz 2003; Cernusak and Hutley 2011), and eliminating pathogens and sap-feeding herbivores (Paine *et al*. 2010). It may also be a simple physical consequence of lateral stem growth, especially of thick-walled smooth bark (Jacobs 1955; Crockford and Richardson 1998). Some authors speculate that the loose hanging bark could promote fire spread from the surface layer up to the canopy by acting as 'ladder fuels' (Gould *et al*. 2011), thereby potentially benefitting pyrophytic tree species to promote their own competitive position by having a hot flammable burning strategy (the 'kill thy neighbour' effect, Bond and Midgley 1995).

Although we know relatively little about the causes of bark shedding, we know even less about the ecological effects. Bark contributes greatly to the litter layer on the forest floor. Depending on the age and composition of the tree species, bark can easily account for up to ~20–45% of the litter layer in *Eucalyptus* forests (McColl 1966; Woods and Raison 1983; Lamb 1985); the other chief components being leaves, twigs and fruits. This

Table 1. Species list and additional bark information for the 10 species used in this study

Species	Location[A]	Bark type[D] and shedding (in red)	Field observations
Angophora costata	West Head[B,C]	Smooth bark 	Bark comes off in large patches, leaving the entire tree (trunk + branches) orange/salmon coloured
Angophora hispida	West Head[B]	Full bark 	Shrub-tree up to 4 m high. Bark is curly, more fibrous than smooth bark. Comes off from the younger branches
Corymbia gummifera	West Head	Full bark 	Bark is shed from the upper limbs or younger stems, not from the main trunk. The bark comes off in thin flakes, partly curled
Corymbia maculata	Blackwall Mountain	Smooth bark 	Bark comes off in patches similar to *Angophora costata*. The old bark is grey/purple, while the new bark (underneath the old layer) is green
Eucalyptus eugenioides	Bobbin Head	Stringy bark 	Typical stringy bark with long fibres. Bark comes occasionally off in strips but we had to pull it off
Eucalyptus haemastoma	West Head[B]	Smooth bark 	Bark comes off in (large) strips and patches. Leaving the entire tree grey/yellow coloured. The bark displays recognisable scribbles made by moth larvae
Eucalyptus pilularis	Blackwall Mountain	Part bark 	Bark comes off in long strips (ribbons). The bark is a substantial component of the litter layer. Trunk is white once the bark is shed except from the trunk-base which remains grey and fibrous
Eucalyptus piperita	Bobbin Head	Part bark 	Grey fibrous trunk, upper limbs are white/yellow. Bark comes off from the upper limbs in long ribbons, partly curled
Eucalyptus punctata	Bobbin Head	Smooth bark 	Trunk looks dirty grey. Big piles of thick bark can be found under the tree. Bark comes off in large thick slabs, shedding from the entire tree
Syncarpia glomulifera	West Head[B]	Stringy bark 	Typical stringy bark with long fibres. Bark comes occasionally off in strips but we had to pull it off

[A] West Head and Bobbin Head are both part of Ku-ring-gai Chase National Park.
[B] Also abundant at Bobbin Head.
[C] Also abundant at Blackwall Mountain.
[D] Bark types following Robinson (2003); the ‘full bark’ and ‘part bark’ classification says something about the distribution of the bark on the trunk, not about the material properties as such.

Fig. 1. Examples of the variability in bark morphology among different tree species. (*a*) *Eucalyptus punctata*, note the vast accumulation of thick bark-slabs near the trunk; (*b*) the 'flaky' shedding of bark from a *Angophora costata* stem; (*c*) *Syncarpia glomulifera*, a typical stringybark. Photographs by S. Grootemaat.

contribution of bark to the litter layer can have strong effects on upper soil properties and dynamics, like nutrient availability (Lamb 1985; Johnson *et al*. 2014) and microclimate (moisture retention and temperature regulation; Facelli and Pickett 1991). At the same time, the bark fraction affects the fuel availability and flammability of the litter layer in case of surface fires (Hines *et al*. 2010). Once the bark has dropped on the forest floor, several processes can potentially affect bark litter, namely: (i) leaching of water-soluble nutrients, (ii) breakdown of the woody material by UV light or fragmentation, (iii) decomposition by (micro-) organisms, or (iv) combustion in a fire (Cornwell *et al*. 2009). In this study we focussed on the latter two processes, as they are the dominant pathways for carbon loss from organic matter.

For leaves, which are another important component of the litter layer, decomposition and flammability are reasonably well understood. Leaf litter decomposition rates are a function of environmental conditions (air temperature, litter moisture content, UV radiation) as well as chemical composition of the leaf material (Adair *et al*. 2008; Cornwell *et al*. 2008; Makkonen *et al*. 2012). Higher initial concentrations of nitrogen (N) and phosphorus (P) lead to higher decomposition rates in the early stage of decomposition (Woods and Raison 1983; Berg and McClaugherty 2003), whereas recalcitrant structural compounds like lignin slow the decomposition process, especially in the later stages (Melillo *et al*. 1982; Berg and McClaugherty 2003). Under controlled conditions, leaf ignitibility (a measure of ease of ignition) is strongly driven by variation in specific leaf area (Murray *et al*. 2013; Grootemaat *et al*. 2015), whereas mass-standardised flame and smoulder durations are mainly determined by leaf chemistry (Grootemaat *et al*. 2015).

The growing understanding of leaf decomposition and flammability, and the underlying role of traits therein, contrasts with a lack of understanding of the trait-drivers of bark decomposition and flammability. Comparative studies on bark from multiple species are rare. The only study that we are aware of that explicitly included bark decomposition (Johnson *et al*. 2014) suggests substantial interspecific differences in bark decomposability amongst three tree species of the northern hemisphere. Previous work on bark flammability showed considerable differences among species (Gill and Ashton 1968, three species; Frejaville *et al*. 2013, eight species). However, these studies only looked at a limited set of bark traits.

The aim of this study was to lay a foundation for predicting surface litter (fuel) accumulation and flammability in Australian forests that are dominated by species of the Myrtaceae family. We investigated the relative decomposability and flammability (as described by ignitibility, fire sustainability and combustibility; Anderson 1970) of a range of tree species, while paying special attention to the bark. We examined the following specific questions and expectations:

(i) How variable is bark decomposability among species, and how does bark decomposability compare to that of leaves? Specifically, although we expect substantial interspecific variation in bark decomposability based on their great visual differences in morphology, we also expect that bark will generally decompose more slowly than leaves because it contains more structural compounds such as lignin and cellulose (O'Connell 1997) and lower amounts of N and P (Lamb 1985).

(ii) How variable is bark flammability among species, and how does bark flammability compare to that of leaves? Based on field observations (S. Grootemaat, personal obs.) we expect 'stringybarks' to ignite more easily than smooth barks. When comparing mass-standardised combustion of bark and leaves, we expect longer flame and smoulder durations for bark, because bark is richer in structural compounds, which take more time to combust.

(iii) Is bark flammability correlated with bark decomposition rate? Based on previous work on leaves (Grootemaat *et al.* 2015) we hypothesise that decomposability and flammability are not correlated across species, starting from the premise that different traits underpin decomposability versus flammability (and its various parameters, i.e. ignitibility, fire sustainability and combustibility).

Materials and methods

Site description and species selection

Ten tree species with characteristic bark features were selected in the dry sclerophyll forests of Ku-ring-gai Chase National Park (33°37′25″S, 151°14′39″E) and Blackwall Mountain Reserve (33°30′26″S, 151°20′0″E), north of Sydney (New South Wales, Australia). The soils at these sites are predominantly sandy (derived from Hawkesbury Sandstone) and very low in P (30–80 mg kg^{-1}; Leishman and Thomson 2005). Mean annual temperature was 17°C and mean annual rainfall 1332 mm for these sites over the past 50 years or more (http://www.bom.gov.au/climate/data/, accessed on 8 October 2015).

Tree species, all belonging to the Myrtaceae family, were selected based on their bark characteristics, abundance and their contribution of bark to the litter layer (a full list of species is provided in Table 1). We deliberately chose species with visually different bark types, including ‘smooth barks’ and ‘stringybarks’ (Fig. 1). Although the stringybark species (*Eucalyptus eugenioides* Sieber ex Spreng. and *Syncarpia glomulifera* Sm. Nied.) do not shed their bark like the other species, they were included for comparison and because of their importance in fire spread (see further discussion below).

Material collection and trait measurements

Bark

Bark from nine individual trees per species was collected in December 2012 and stored in paper bags under ambient laboratory conditions (21°C). Depending on the species, the bark came off in different sizes and shapes (flakes, slabs and ribbons). For comparison we roughly standardised the bark samples by splitting them into pieces of ~13 cm^2 (one sided surface area). This size was practical to work with, both for the decomposition experiments (limited by the size of the litterbags) and for the experimental burns (limited by the size of the muffle furnace).

Leaves

Freshly senesced leaves of the same species were collected from the forest floor after windy days; these were easily distinguished from older (partially decomposed) senesced leaves by their yellow colour. Unlike the samples of bark, which were true replicates of nine individual trees, the leaf samples were taken from a bulk-sample from ~10–40 individual trees per species. The samples were stored in paper bags under ambient laboratory conditions (21°C).

Trait measurements

Subsamples of bark and leaves were kept aside for trait measurements (Table S1, available as Supplementary Material to this paper). Length and width were measured with a ruler. Thickness (mean of three measurements for bark) was measured with a thickness gauge. Dry mass was determined after oven drying at 60°C (when equilibrium was reached). One-sided surface area was estimated with a LI-3100C area meter (Li-Cor, Lincoln, NE, USA). Bark particle volume was estimated by using the gravimetric (water replacement) method. For leaf volume, leaf area was multiplied by mean leaf thickness. Tissue density was calculated as dry mass per volume. Bark tensile strength was measured by means of a 3 mm punch-test, using an Instron machine, model 5542 (Instron, Norwood, MA, USA). Fuel moisture contents were measured on air-dried subsamples just before the experimental burns. These samples were remeasured after 24 h of oven-drying at 105°C. Fuel moisture content was then expressed as a percentage of oven-dry weight. Energy content (MJ kg^{-1}) of ground bark or leaf material was measured with a Parr 6400 calorimeter (Parr Instrument Co., Moline, IL, USA). Detailed extraction methods for analysing bark and leaf chemistry can be found in the Supplementary Material (Text S1). In short, carbon (C) and N were measured with a CHN combustion analyser (Rayment and Lyons 2011). Calcium (Ca), copper (Cu), potassium (K), magnesium (Mg) and P concentrations were quantified by acid digestion followed by spectrometry (Martinie and Schilt 1976). Tannins were quantified following Dalzell and Kerven (1998), and lignin, cellulose and ash concentrations were measured with an ADF extraction method (Rowland and Roberts 1994).

Decomposition experiment

Fibreglass litterbags (20 × 15 cm; 1.5–2 mm mesh) were filled with bark particles of ~13 cm^2 each, or 1.0 g of intact senesced leaves, and placed in a common garden at Macquarie University Fauna Park, North Ryde (33°46′9″S, 151°6′46″E) in January 2013. This site consists mainly of *S. glomulifera* forest – a characteristic vegetation type of this region (Martyn 2010). Long-term climate data indicate a mean annual rainfall of 1397 mm (Turramurra weather station) and mean annual temperature of 17.3°C (Riverview Observatory; Australian Bureau of Meteorology), i.e. similar to the climate of the collection sites. An overview of the seasonal pattern of rainfall and temperature during our study period is shown in Fig. S1, available as Supplementary Material to this paper.

Litterbags were distributed at random on the cleared forest floor and staked down with 10 cm long nails. Large trees surrounding our plots (semi-)shaded the litterbags for most of the time. We deliberately left the samples uncovered, so natural processes like revegetation and litterfall could continue as per normal. We started the decomposition experiment with 270 bark litterbags (10 species × nine replicates × three retrieval times) and 180 leaf litter bags (10 species × six replicates × three retrieval times). After 3 months one replicate of each species (both for bark and leaf samples) was harvested to obtain a preliminary estimate of the decomposition rate. Based on the latter, we decided to harvest the first batch of leaves after 3.5 months. Since bark decomposition was slower, we left the bark for a later harvest. The two other harvest moments were after 12 and 24 months (bark and leaves). After harvesting, samples were dried at 60°C for $\geq$10 days until equilibrium mass. After brushing off any dirt, the remaining sample mass was weighed.

Experimental burns

Leaves were burned as described by Grootemaat *et al*. (2015). Samples were horizontally inserted into an open-doored muffle furnace (Charles Moloney, Sydney, NSW, Australia) set at 400°C. The leaves were held by tongs on the petiole, in a parallel direction to the furnace door. A high frequency electrical spark gun was held ~8 mm above the centre of each sample to provide a source of ignition (Gill and Moore 1996). Three thermocouples (type K, chromel-alumel) were attached to a stainless steel grill perpendicular to the opening of the furnace. When the average temperature value of the three thermocouples was ~400°C (± 10°C) leaf samples were inserted.

A similar set-up was used for the experimental burns of bark, with a few adjustments: the bark samples were inserted by tongs and then left on the grill. The remaining ash was collected in a stainless steel dish (99 × 99 × 18 mm) underneath the grill. However, the mass of the remaining ash was undetectable on a scale with three digits and therefore we considered the burns as complete combustions.

The combustion process was filmed and subsequently analysed by using the digital video editor 'VideoPad' (NCH Software, Canberra, ACT, Australia). This allowed us to measure time-to-ignition (TTI) as a proxy for ignitibility, while sustainability was registered both by flame duration (FD) and smoulder duration (SD) (Grootemaat *et al*. 2015). Combustibility was expressed as initial sample mass (corresponding approximately with total mass burnt) divided by total burning time (sum of FD and SD).

Statistical analyses

We chose to report the percentage mass lost at a given (standard) point in time rather than a *k*-value (Olson 1963), because (i) there was no exponential trend in our data, which forms the basis of such decomposition models; and (ii) the decomposition constant *k* averages the decomposition rate over the different stages (months) and is strongly dependent on variations in temperature and moisture content (Woods and Raison 1983). Several other decomposition models have been proposed for leaves and coarse woody debris (Harmon *et al*. 2004; Adair *et al*. 2008; Cornwell and Weedon 2014) but they cannot always account for the complexity of the litter, nor for the complex heterotrophic interactions (Facelli and Pickett 1991).

Variance component analyses were used to partition the total variance in decomposability and flammability into within-species and among-species components. Since the variation in bark FD and SD was strongly driven by sample mass (88 and 97% respectively), we standardised by dry mass, and then used these new variables, i.e. 'FD/mass' and 'SD/mass', in subsequent analyses. For comparison, we also mass-standardised the leaves.

Next, measurements were averaged per species and the flammability parameters and trait measurements were $\log_{10}$-transformed to satisfy the assumptions of normality and homogeneity of variance. Linear regressions were used to compare (i) decomposability (as % mass loss) of leaves and bark, (ii) flammability (as ignitibility, sustainability and combustibility) of leaves and bark, and (iii) decomposability and flammability for a given material. To test for correlations with bark SD/mass we used non-parametric Spearman's *rho* because bark SD/mass was not normally distributed. One-way ANOVAs were used to compare the ignitibility and sustainability of the non-shedding stringybarks with the other (smooth) bark types.

Bivariate regressions were used to quantify trait effects on decomposition and flammability of bark and leaves. Wherever appropriate, ANCOVAs were used to test if the slopes from the bivariate regressions differed for bark and leaves. Stepwise multiple linear regressions were used to determine whether the measured traits together could account for the variation in bark and leaf decomposability and flammability. Because of the likelihood of collinearity between certain traits, the variance inflation factor (VIF) was calculated. Results with VIF $\geq$4 are highlighted in the results section.

All statistical analyses were carried out using SPSS Statistics ver. 22.0 (IBM Corp., Armonk, NY, USA).

Results

Bark versus leaf decomposition

In the first year bark material decomposed much slower than leaves. After 12 months 7–28% of the initial bark mass was lost (species means) compared with 22–60% for leaves (Fig. 2). In the second year the rate of bark decomposition approached that of leaves, which (depending on species) led to 27–72% mass loss for bark and 56–92% mass loss for leaves after 24 months (Fig. 2). Percentage mass loss after 12 and 24 months were strongly correlated ($r^2 = 0.77$ for bark; $r^2 = 0.92$ for leaves). Still, for completeness, we report decomposability as percentage mass loss at both harvest times throughout this paper. After 12 months, there was a weak tendency for leaf decomposition to be correlated with bark decomposition ($r^2 = 0.34$, $P = 0.075$; Fig. 3), implying that species with easily decomposable leaves also have easily decomposable bark. However, after 24 months there was no relationship at all ($P = 0.411$).

Bark versus leaf flammability

The most widely recognised trait influencing fuel flammability is moisture content. Because all leaf and bark samples were air-dried before the experimental burns, they varied little in moisture content (species means ranging from 11.8 to 14.4% for bark and 7.3 to 10.0% for leaves). Apart from a significant correlation with bark TTI ($r^2 = 0.40$, $P = 0.049$; Table S2), interspecific variation in fuel moisture content had no strong effects on the measured flammability parameters (all $P \geq 0.05$; Table S2; data not shown for leaves). Because all samples were stored under similar conditions, we consider it fair to make the comparison between bark and leaf flammability.

There was considerable variation in bark and leaf flammability, both within and among species (Fig. 4). Overall, bark took longer to ignite than leaves (species means: 2.6–14.0 s versus 1.9–4.2 s, respectively, Fig. 4*a*). Bark flamed and smouldered for longer than leaves, even after standardisation by mass (Fig. 4*b*, c) and consequently, bark was less combustible

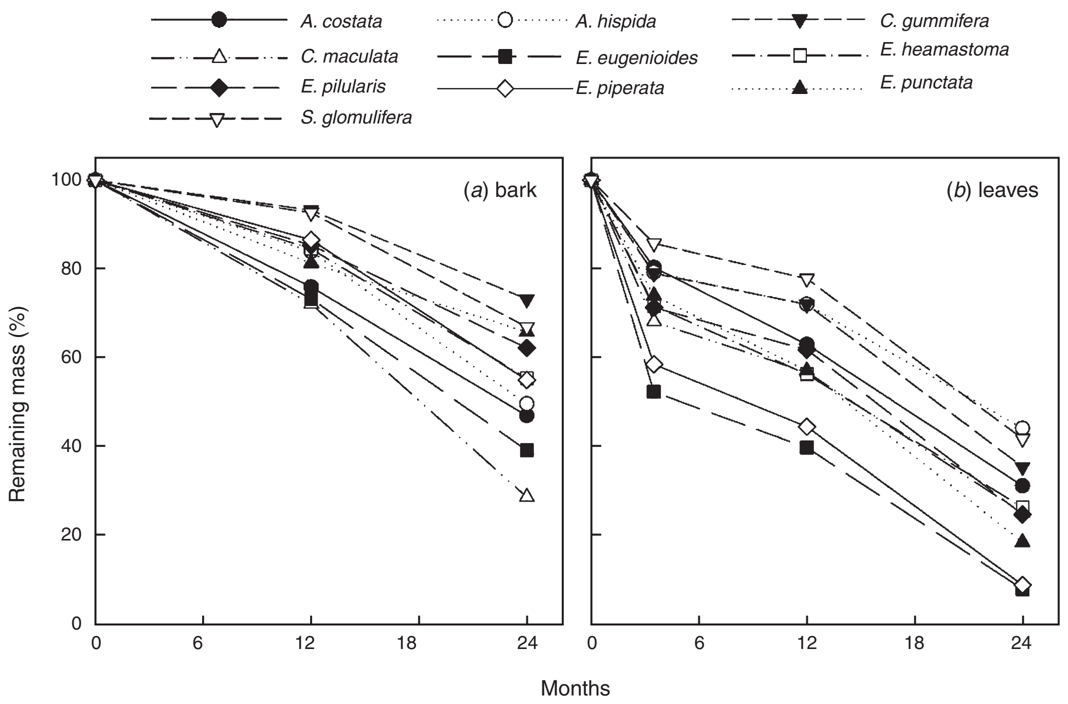

Fig. 2. Decomposition of (*a*) bark and (*b*) leaves over a period of 24 months, starting in January 2013 (summer in the southern hemisphere). Decomposition is presented as the percentage remaining mass of the initial litter samples (species means).

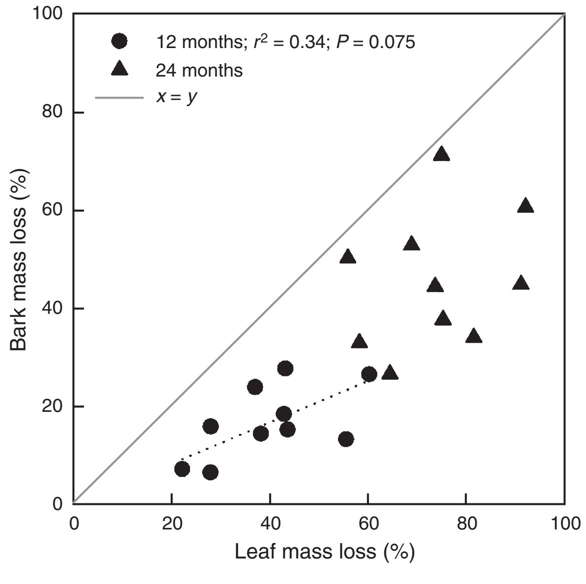

Fig. 3. Decomposability of leaves (% mass loss) versus decomposability of bark (% mass loss) from 10 woody species. Each dot represents a species mean.

(4.9–7.5 mg s^{-1}) than leaves (9.8–18.3 mg s^{-1}) (Fig. 4*d*). Bark from the stringybark species (*E. eugenioides* and *S. glomulifera*) had shorter ignition times than the bark from the other species ($P < 0.001$), but the two species-groups did not differ in FD/mass, SD/mass or combustibility (all $P \geq 0.392$). Bark from *Eucalyptus punctata*, which is characterised by very thick slabs, had the longest time-to-ignition and highest SD/mass. This means that although *E. punctata* bark does not ignite easily, it can still play an important role in wildfires (and their effects) due to its prolonged smouldering. Bark and leaf flammability were unrelated for all four flammability parameters (all $P \geq 0.322$). For example, species whose leaves ignited easily and quickly did not necessarily have easily ignitable bark.

Decomposition and flammability explained by different drivers

The rate of bark decomposition (after either 12 or 24 months) was unrelated to any measure of bark flammability, and the same was true for leaf decomposition and flammability (all $P \geq 0.180$; Table S3). The relevant traits, associated with the two turnover processes, will be discussed below.

Lignin concentration drives decomposition

After both 12 and 24 months, initial lignin concentration was the strongest predictor of bark decomposition ($r^2 = 0.66$ and 0.64, respectively, Fig. 5*a*), followed by cellulose concentration ($r^2 = 0.57$ and 0.43; Table S2). Lignin and tannins are recalcitrant compounds which impede decomposition. Higher values of cellulose, instead, make the plant material more decomposable. After 12 months, the energy content and tissue carbon concentration also accounted for a substantial portion of the variation in bark decomposition ($r^2 = 0.55$ and 0.56; both negatively); but after 24 months these trends were no longer significant. Stepwise multiple regressions showed that tannin concentration accounted for 21% (12 months) and 18% (24 months) of the variation in bark decomposability in addition to the 66 and 64% already accounted for by lignin

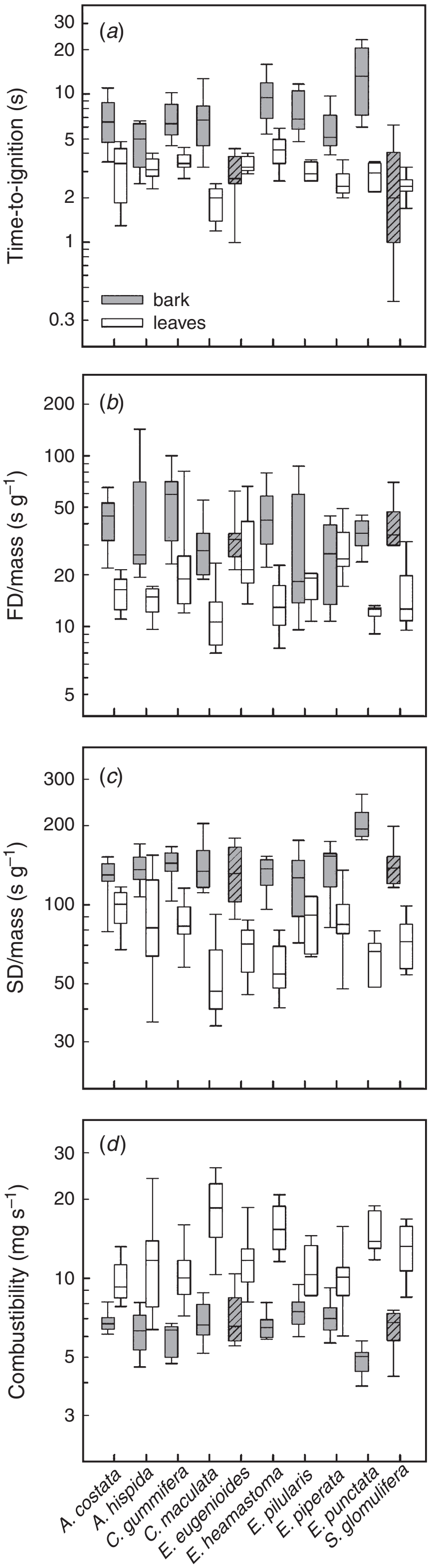

Fig. 4. Flammability of bark (grey) and leaves (white) as described by (*a*) time-to-ignition, (*b*) mass-standardised flame duration, i.e. FD/mass, (*c*) mass-standardised smoulder duration, i.e. SD/mass, and (*d*) combustibility. $n = 9$ per species. The hatched boxes characterise the stringybarks; *y*-axes are on a log-scale.

(Table S4). The high VIF of 11.9 between initial lignin and cellulose concentrations, reflecting that these compounds constitute the main components of woody material, suggests that the relationship between decomposition and lignin also indirectly includes the effects of cellulose on mass loss. However, lignin had a stronger relationship with decomposition than cellulose (both after 12 and 24 months), and was therefore chosen by the stepwise regression.

As for bark, initial lignin concentration was also the most important (negative) driver for leaf decomposition ($r^2 = 0.64$ and 0.55; Fig. 5*a*) with an additional 27% accounted for by leaf thickness (negative correlation) after 24 months (i.e. total $r^2 = 0.82$; Table S4; lignin concentration and leaf thickness were not correlated). Even though the decomposability of both bark and leaves was driven by initial lignin concentration, the slopes were different (e.g. after 12 months, ANCOVA interaction term $P = 0.023$; Fig. 5*a*). Therefore, we conclude that there is no common decomposability-lignin function *across* tissue types.

Bark flammability is driven by bark area per mass and chemical composition

Several traits were important for the ignitibility, sustainability and combustibility of bark. Bark area per mass (BAM; cm^2 g^{-1}), analogous to specific leaf area (SLA; cm^2 g^{-1}), did not affect ignitibility when all species were included (Fig. 5*b*, $r^2 = 0.10$, $P = 0.385$). However, as already noted, the two stringybark species (*E. eugenioides* and *S. glomulifera*) are quite different from the other species in their morphology and ignitibility, and are not classified as bark shedding species. Once these were excluded, BAM showed a strong negative relationship with time-to-ignition of the smooth bark species ($r^2 = 0.89$, $P < 0.001$). Taking all 10 species into account, [N] was the most important driver of bark ignitibility (Fig. 5*c*, $r^2 = 0.69$, $P = 0.003$). At higher N concentrations, bark samples took less time to ignite. Calcium concentration added another 27% (negative correlation) to the explained variance of bark ignitibility (Table S4). Since [Ca] was positively correlated with [Mg] (VIF = 6.651), these results indirectly also include effects of [Mg]. In fact, a similar model built with [N] and [Mg] gave similar but slightly weaker results (total $r^2 = 0.93$, $P = 0.001$) and the retarding effects of [Ca] and [Mg] on ignitibility can be considered as similar. Higher fuel moisture contents delayed the bark ignition ($r^2 = 0.40$, Table S2), but this moisture effect was not strong enough, or sufficiently independent of the [N] and [Ca] effects to influence the multiple regression model results.

Bark sample mass accounted for 88 and 97% of the variation in flame and smoulder durations respectively. When we standardised FD and SD by dry mass, within-species variance accounted for a far larger proportion than among-species variance (88 and 71% within species, 12 and 29% among species; Table S5). Also, bark combustibility was more variable within than among species (73% vs 27%; Table S5). Thus, despite the clear morphological and chemical differences of the bark from different species, once the samples were alight, the combustibility, flame and smoulder durations varied relatively

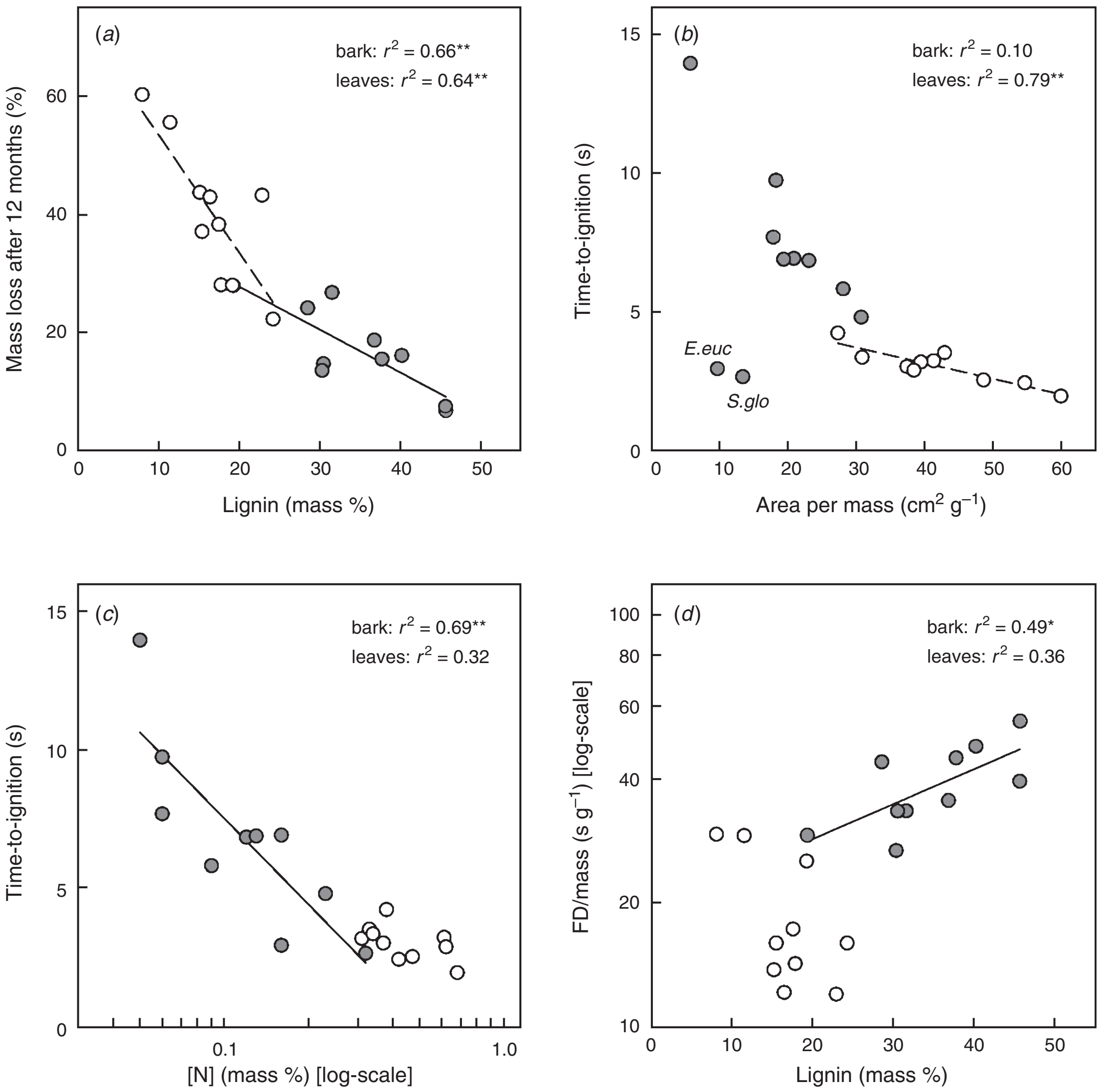

Fig. 5. Relationships for interspecific variation in (*a*) decomposability, (*b*, *c*) ignitibility, (*d*) mass-standardised flame duration, and some relevant traits (i.e. initial lignin concentration, area per mass, initial nitrogen- and lignin concentration, respectively) for bark (grey) and leaves (white). Each dot represents a species mean; significant ($P \leq 0.05$) relationships are represented with a regression line. In (*b*) *E.euc* = *Eucalyptus eugenioides*, *S.glo* = *Syncarpia glomulifera* (both stringybarks); when the stringybarks were excluded from the analysis, bark time-to-ignition was strongly driven by bark area per mass (BAM; $r^2 = 0.89$***). Significant differences are indicated: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

little among species (at least, compared with variation within any given species).

Variation among species in bark FD/mass was most strongly positively associated with both copper concentration ($r^2 = 0.54$) and lignin concentration ($r^2 = 0.49$; Table S2, Fig. 5*d*). Phosphorus concentration accounted for 26% on top of the explained variance by [Cu] (Table S4); at a given [Cu], bark samples with higher [P] had shorter flame durations per gram material. Through a correlation with [Cu], i.e. VIF = 5.078, lignin effects on FD/mass are implicitly included through the effects of [Cu].

Calcium concentration and cellulose together accounted for 79% of the variation in combustibility among species (Table S4). Higher [Ca] lowered the combustibility. However, as seen before, the significant effects of [Ca] also include indirect effects of [Mg] since [Ca] and [Mg] are quite strongly correlated.

Drivers of leaf flammability

Specific leaf area was the most important correlate of leaf TTI. Species with higher SLA ignited more quickly ($r^2 = 0.79$, $P = 0.001$; Table S4; Fig. 5*b*). Similarly but less markedly than was the case for bark, more variation in leaf FD/mass, SD/mass and combustibility was found within species than among species (Table S5). Leaf FD/mass was negatively correlated with potassium concentration ($r^2 = 0.44$; Table S4). None of the measured leaf traits were correlated with SD/mass or with combustibility. This suggests that standardising by mass explains most variation in leaf SD and combustibility. The more material there is to start with, the longer the smouldering phase will take, and the slower the combustibility.

Discussion

Slow decomposition of bark

Higher lignin concentrations slowed the decomposition of both leaf material (see also Melillo *et al*. 1982; Adair *et al.* 2008; Freschet *et al*. 2012) and bark. The higher initial lignin concentrations in bark compared with leaves might explain the slower decomposition rates of the former, especially in the first year. Other reasons for the lag-phase of bark decomposition could be local nutrient limitation (since bark had lower [N] than leaves; Table S1) and/or priority effects among decomposers (i.e. the decomposers prefer leaves over bark).

The lower decomposability of bark may cause a long-term slow release of nutrients to the forest soil (Lamb 1985; O'Connell 1997; Johnson *et al*. 2014) and accumulation of fuel for potential fires (Hines *et al*. 2010). In contrast, the rapid initial decomposition in leaves, likely associated with leaching of water-soluble compounds (Woods and Raison 1983; Berg and McClaugherty 2003) and higher initial concentrations of N and P (Cornwell *et al*. 2008), releases nutrients relatively quickly. The different rates of bark and leaf decomposition thus provide important information for estimating the carbon and nutrient balance of the forest.

Ignitibility of bark is lower than that of leaves, but bark burns for longer

Previous studies of bark flammability have typically focussed on bark that is still attached to the tree, e.g. quantifying the ability of bark to protect the vascular cambium (Uhl and Kauffman 1990; Pinard and Huffman 1997; Lawes *et al*. 2011), but our study compared the flammability of bark chunks as components of the litter layer. Bark flammability varied 1.5- to 5.4-fold among the 10 tree species examined in this study. In general, bark took longer to ignite than leaves, and burned more slowly. The sustainability of fire in bark (and leaves) was strongly mass dependent; the more mass available, the longer the flame and smoulder duration, and therefore the lower the combustibility. Thus, the species-specific contribution of bark to the litter layer can be very important for the duration of a surface fire. When high temperatures (≥70°C) prevail, this can lead to extensive thermal damage to the local flora and soil fauna (Neary *et al*. 1999; Gagnon *et al*. 2010).

FD/mass and SD/mass varied mostly within species, prompting two observations: (i) despite huge variety in bark morphology and chemistry, once ignited, the flame and smoulder durations among species hardly varied; and (ii) even after standardising by mass, the bark samples still flamed and smouldered longer than the leaf samples. The latter is explained by bark being richer in structural compounds (e.g. lignin; Fig. 5*d*), which have higher thermal stability and therefore require more time, or higher temperatures, for combustion (Philpot 1970; Di Blasi 2008). In addition, the greater thickness of bark compared with leaves may also have contributed to the lower combustibility by constraining heat supply to the inner parts of bark chunks by means of conduction (Lawes *et al*. 2011).

Drivers of flammability

The strongest driver of interspecific bark ignitibility in our dataset was N concentration; bark samples with a higher N concentration ignited more quickly. This was contrary to expectation because N, at least in ammonium phosphates, has fire retardant properties (Duquesne *et al*. 2003). However, we have little understanding of the relationship between [N] and ignitibility when it is part of other chemical compounds.

Leaf ignitibility was strongly correlated with SLA (leaf area per mass) (Murray *et al*. 2013; Grootemaat *et al*. 2015). Similarly, at least when the stringybarks were excluded from the analysis, a strong relationship was found between the SLA-analogue BAM (bark area per mass) and ignitibility. This predictive power of surface area per mass could improve fire prediction models that take plant traits into account (e.g. Zylstra *et al*. 2016).

The remaining interspecific variation in bark FD/mass was mostly correlated with [Cu] and secondly with [P]. Although P has known flame retardant properties (Green 1992; Scarff *et al.* 2012), we only have an indirect explanation for the apparent flame-prolonging effects of [Cu]. A possible explanation may lie in the correlation of [Cu] with lignin, and lignin has more complex carbohydrate chains which take longer to disintegrate during the depolymerisation phase (pyrolysis) than, for example, cellulose or volatiles (Sullivan and Ball 2012). The lower combustibility of bark at higher concentrations of Ca or Mg agrees with the common perception that the presence of cations, or higher nutrient concentrations in general, promotes the formation of chars during the pyrolysis, at the expense of volatile tar formation. This makes the fuel less flammable (King and Vines 1969; Mak 1982).

Despite the large variation in bark morphological and chemical traits (Paine *et al*. 2010; Poorter *et al*. 2014; Rosell *et al*. 2014), relatively little is known about how this variation affects the ecological functions of bark. Pausas (2015) suggested that fire regimes can explain a large portion of the variance in bark thickness (e.g. thicker bark in ecosystems with frequent low intensity fires), although thin and thick barked plants can co-exist under a given fire regime (Rosell 2016; present study). Most likely, different plant strategies (such as serotiny and resprouting) have evolved as fire survival traits, and thicker bark is only one of them (Pausas 2017).

Bark flammability and spotting

Ignitibility is of special importance for wildfires, since material with shorter ignition times is likely to start or propagate a wildfire more easily, and fire spread can be seen as an accumulation of ignition steps (Rothermel 1972; Grootemaat *et al*. 2017). Bark ignitibility plays a particularly important role in Australian ecosystems because loose bark may form firebrands (large embers) which can travel through the air and start new fires in unburnt forests far ahead of the actual fire front (so-called 'spotting') (Hines *et al*. 2010; Ellis 2011; Cruz *et al*. 2012). Stringybarks are known for short to medium distance spotting (up to 4 km) and the shorter ignition times of *E. eugenioides* and *S. glomulifera* found in this study could be relevant information for estimating spotting potential. Also, the morphology of ‘ribbon bark’, especially the longitudinal curvature, is a key factor in determining the spotting distance due to the burnout time (FD + SD) of the bark (Hall *et al*. 2015). Firebrands of ribbon bark have been found to travel tens of kilometres (Cruz *et al*. 2012). Two of our smooth bark species, *E. pilularis* and *E. piperata*, could be classified as ribbon barks. In our study, however, we did not examine the longitudinal curvature, and used samples with different levels of curvature - although we tried to avoid cylinders with multiple rotations of bark. This may explain the larger variation in FD and SD found for these species.

Turnover processes were unrelated, comparing across tissue types

The decomposition rate of bark was unrelated to that of leaves. Similarly, the various flammability properties were unrelated across tissue type. Can we explain this lack of correlation by a lack of functional coordination between plant tissues? For example, there is a general tendency for species with leaf traits promoting fast growth to also have stem and root traits that promote fast growth (Freschet *et al*. 2010; Reich 2014). Further, Freschet *et al*. (2012, 2013) found that, as an ‘afterlife’ consequence, the decomposability of leaves, stems and roots were positively correlated. This has given rise to the idea of a ‘fast-slow’ plant economics spectrum (Reich 2014). The present study suggests that this same pattern does not extend to bark versus leaves. Presumably this reflects the very different functions these tissues fulfil. The main function of leaves is carbon acquisition by means of photosynthesis. By contrast, although some species have weakly photosynthetic bark (Aschan and Pfanz 2003; Cernusak and Hutley 2011), the main functions of bark, besides photosynthate transport, are protection from pests and fire, water storage, and biomechanical support (Niklas 1999; Rosell *et al*. 2014) – functions that are not directly related to growth rate.

Turnover processes were unrelated, within each tissue type

For any given material (i.e. for bark or for leaves), decomposability and flammability were unrelated across our 10 study species. This is a confirmation of our previous findings, for leaves only, for a different set of 32 species (Grootemaat *et al*. 2015). The results here suggest a similar ‘decoupling’ for bark: at a given bark decomposition rate, a full range of bark ignitibility, fire sustainability and combustibility values is possible. Presumably this lack of correlation reflects the fact that variation in decomposition and flammability are driven by different traits, as quantified in this study.

Concluding remarks

This study examined (mostly) bark shedding species, because of the substantial contribution of bark to the litter layer and fuel load in Australian forests. In most forests there will be a mix of relatively fast and slow decomposing species, and species with high and low flammability characteristics. This leads to variation in litter turnover rates and litter accumulation, both for bark and for leaves. The contribution of bark of some species to the litter layer in dry sclerophyll forests can be substantial (up to ~45%; McColl 1966; Lamb 1985). Combined with differences in decomposability and flammability, our findings suggest that it is important to consider the species composition of the litter, and relative contribution of leaf and bark tissues, when estimating carbon and nutrient loss rates, fuel loads and fire risks.

Conflicts of interest

The authors have no conflicts of interest to declare.

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