Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species

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Summary

1. In fireprone ecosystems, two important alternative fates for leaves are burning in a wildfire (when alive or as litter) or they get consumed (as litter) by decomposers. The influence of leaf traits on litter decomposition rate is reasonably well understood. In contrast, less is known about the influence of leaf traits on leaf and litter flammability. The aim of this study was two-fold: (i) to determine which morphological and chemical leaf traits drive flammability and (ii) to determine whether different (combinations of) morphological and chemical leaf traits drive interspecific variation in decomposition and litter flammability and, in turn, help us understand the relationship between decomposability and flammability.

2. To explore the relationships between leaf traits and flammability of individual leaves, we used 32 evergreen perennial plant species from eastern Australia in standardized experimental burns on three types of leaf material (i.e. fresh, dried and senesced). Next, we compared these trait–flammability relationships to trait–decomposability relationships as obtained from a previous decomposition experiment (focusing on senesced leaves only).

3. Within the three parameters of leaf flammability that we measured, interspecific variation in time to ignition was mainly explained by specific leaf area and moisture content. Flame duration and smoulder duration were mostly explained by leaf dry mass and to a lesser degree by leaf chemistry, namely, nitrogen, phosphorus and tannin concentrations.

4. The variation in the decomposition constant across species was unrelated to our measures of flammability. Moreover, different combinations of morphological and chemical leaf properties underpinned the interspecific variation in decomposability and flammability. In contrast to litter flammability, decomposability was driven by lignin and phosphorus concentrations.

5. The decoupling of flammability and decomposability leads to three possible scenarios for species' influence on litter fates: (i) fast-decomposing species for which flammability is irrelevant because there will not be enough litter to support a fire; (ii) species with slow-decomposing leaves and a high flammability; and (iii) species with slow-decomposing leaves and a low flammability. We see potential for making use of the decoupled trait–decomposition–flammability relationships when modelling carbon and nutrient fluxes. Including information on leaf traits in models can improve the prediction of fire behaviour. We note that herbivory is another key fate for leaves, but this study was focused on fire and decomposition.

Key-words: carbon cycling, decay, fire, functional traits, litter fates

Introduction

Large amounts of carbon and nutrients are stored in woody perennial plants (Chapin, Schulze & Mooney 1990;

Bonan 2008). More specifically, live biomass is estimated to store 42% of the current global terrestrial carbon stock, and another 8% and 5% are stored in dead wood and fine litter (Pan *et al.* 2011). This carbon can be released by herbivores (Cebrian 1999), through combustion during a bush fire, or by micro-organisms as part of the decomposition

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process (Cornwell *et al.* 2009). This study is focused on fire and decomposition. A fundamental difference between these two fates is that fire is a very rapid process with a quick release of carbon and nutrients, while decomposition is a relatively slow, semi-continuous process. Both turnover processes are highly dependent on weather conditions and on the morphological and chemical properties ('quality') of the fuel/litter. For example, decomposition is more rapid in warmer and wetter conditions but, in addition, interspecific variation in leaf litter quality determines variation in decomposition rates within a given climatic region (Coûteaux, Bottner & Berg 1995; Gholz *et al.* 2000; Cornwell *et al.* 2008; Makkonen *et al.* 2012). All else being equal, leaves with higher lignin contents, lower specific leaf area (SLA; ratio of leaf area to dry mass) and lower nutrient concentrations show lower decomposition rates as litter (through the so-called trait afterlife effects; Cornelissen 1996; Pérez-Harguindeguy *et al.* 2000; Cornwell *et al.* 2008). These relationships connect species' variation in litter decomposability with the so-called leaf economic spectrum (Wright *et al.* 2004; Santiago 2007; Freschet, Aerts & Cornelissen 2012), which describes differences among species in several intercorrelated traits important to leaf-level carbon gain strategy. Through these afterlife effects, and also through differences in species' abundance, leaf traits can strongly influence biogeochemical cycles (Brovkin *et al.* 2012).

Likewise, even though any organic matter will burn during a high-intensity wildfire, at the start of a fire or under mild conditions (low temperatures, humid conditions), material of some species ignites, while that of others does not (Plucinski & Anderson 2008; Gill & Moore 1996; S. Grootemaat, personal observation). While the influence of leaf traits on litter decomposition is well documented, relationships between leaf traits and leaf or litter flammability parameters (as measurements of flammability components, see below) are relatively less well understood and only rarely quantified.

For understanding trait–flammability relationships, it is essential to make a distinction between the different components of flammability. Following Anderson (1970) (and further discussed by Gill & Zylstra 2005), flammability can be said to include ignitibility (how well the fuel ignites), combustibility (how well it burns) and sustainability (how long it burns). These components of flammability are not necessarily all positively correlated (Montgomery & Cheo 1971). For example, a eucalypt leaf may be hard to ignite due to its thick waxy cuticle, but once it is ignited, it will burn fiercely because of the volatile oils. In other words, some caution is needed when commenting on 'the flammability' of species. Since these flammability components follow different mechanisms in the combustion process, and assuming that leaf traits affect flammability, we expect that leaf traits fulfil different functions in the specified components of flammability.

In litterbeds, leaf size is a dominant driver of different flammability parameters by influencing the packing (Scarff

& Westoby 2006; van Altena *et al.* 2012; Engber & Varner 2012; de Magalhães & Schwilk 2012), while leaf traits such as thickness, moisture content, phosphorus content and secondary chemistry (lignin, terpenoids) are deemed to play important roles as well (Montgomery & Cheo 1971; Ormeño *et al.* 2009; Plucinski *et al.* 2010; Scarff, Gray & Westoby 2012). However, the role of interspecific variation in leaf traits in the different phases of a fire deserves more attention (Schwilk & Caprio 2011; de Magalhães & Schwilk 2012).

Leaf traits identified as important drivers of flammability overlap only partly with those identified for litter decomposition. For instance, leaves with higher surface area-to-volume ratios (SA : V) decompose faster (Swift, Heal & Anderson 1979) and ignite more quickly (Gill & Moore 1996) due to a relative larger contact area for decomposition or pyrolysis to take place. But leaf litter moisture content, which is a function of litter type, air temperature and humidity (Anderson 1990; Sullivan *et al.* 2012), has contradicting effects on decomposition and flammability. Higher litter moisture concentrations will speed up decomposition rates (Meentemeyer 1978; Gholz *et al.* 2000) but will lower the ignitibility by requiring more energy for water evaporation and preheating of the fuel (Byram 1959; Sullivan *et al.* 2012). How rapid the changes in litter moisture occur depends strongly on the size and shape of the leaves (Swift, Heal & Anderson 1979; Anderson 1990). As a result, in spite of some overlap in explanatory power of individual traits for both fire and decomposition, we hypothesize that leaf litter decomposability and intrinsic flammability are unrelated (i.e. 'decoupled') across species when considering a whole suite of leaf traits. Here, we test this hypothesis by investigating (i) how interspecific differences in intrinsic flammability can be predicted from variation in leaf traits (for fresh, dried and senesced leaves, respectively) and (ii) whether these trait–flammability relationships for senesced leaves are decoupled from trait–decomposability relationships.

By using 32 evergreen shrub and tree species from eastern Australia, we quantified relationships between morphological and chemical leaf traits and litter decomposability (which was measured as part of a previous study). Next, we quantified relationships between leaf traits and three parameters of flammability measured during experimental burns: time to ignition (TTI[a] a proxy for ignitibility), flame duration (FD[a]) and smoulder duration (SD[a]; both proxies for fire sustainability). Finally, we asked which combinations of traits defined decomposability and flammability of leaf litter and how decomposition and flammability were themselves related. Understanding the relationships of fire and decomposition with leaf traits is important to give us a better insight into the carbon and

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[a]An overview of the abbreviations used in this manuscript can be found in the Table S1, Supporting information.

nutrient fluxes and could potentially improve the modelling of ecosystem processes.

Materials and methods

SITE AND SPECIES SELECTION

The leaves for this study were collected from four sites in New South Wales, Australia. The leaf traits related to species' carbon and nutrient economies are well documented for these sites (Wright, Reich & Westoby 2001; Wright & Westoby 2002, 2003), and a detailed description of the sites can be found in Wright, Reich & Westoby (2001). In summary, two vegetation types on nutrient-rich and nutrient-poor soils were sampled, in each of two rainfall zones. The wetter sites were located in Kuring-Gai Chase National Park, Sydney, with an average annual rainfall of 1220 mm. The drier sites were located in Round Hill Nature Reserve, some 580 km inland, with an average annual rainfall of 387 mm. The use of these four different sites expanded our range of plant traits without actually focussing on the patterns due to rainfall or site nutrient concentrations. The same sites were used for the litter collection for a common garden decomposition experiment by Cornwell (2006). By using the same sites and leaves for a subset of 32 species from the 51 species used in that experiment, we had the unique opportunity to investigate interactions between leaf traits, decomposability and flammability.

For our experimental burns, we chose the more abundant species that also had a minimum leaf size of 1·0 cm^2, which is about the minimum size to obtain meaningful flammability data when leaves are burned individually (see below). These 32 species (Table S2, Supporting information) were all evergreen perennials, representing 14 different families of distant lineages. The set consisted of species with a variety of growth forms (trees, shrubs, one cycad and one grass), leaf sizes (1–45 cm^2) and morphologies (e.g. both broad- and needle-leaved species).

Individual leaves

We determined the flammability of individual leaves under carefully controlled conditions (here called 'intrinsic' flammability) in order to test whether differences among species in flammability did or did not relate to differences in key leaf traits and to decomposition rates. We used individual leaves (following Gill & Moore 1996; Zylstra 2011) to distinguish measured differences in intrinsic flammability rather than differences in flammability due to variation in the fuel bed packing density (which is strongly related to leaf size) and therefore oxygen limitation (Scarff & Westoby 2006; van Altena *et al.* 2012; de Magalhães & Schwilk 2012). We expect that traits other than leaf size play a role when oxygen is not limiting.

MATERIAL TYPES

During a bush fire, leaves can burn while still green and attached to the plant, or as litter ('senesced' leaves) on the forest floor. The moisture contents of green leaves will vary between very low ('dried' leaves, representing the state they may be at when the likelihood of wildfire is highest) and saturated ('fresh' leaves), and here, we chose these two extremes to represent the maximum range of environmental moisture. Therefore, three material types were included in our analyses: fresh green leaves ('fresh'), dried green leaves ('dried') and dried senesced leaves ('senesced'). Representative fully expanded outer canopy leaves were picked fresh and stored with a moist paper towel in a plastic zip-locked bag (>12 h) until the time of the burning

experiments. These experiments were run within 72 h after picking. By using the zip-locked bags, we aimed to minimize the moisture loss of the freshly picked leaves (Pérez-Harguindeguy *et al.* 2013). Dried leaves were collected in the same way as the fresh leaves but stored in paper bags at 37 °C for over 72 h until they reached a constant weight (mean moisture content = 6·3%; range = 4·5–9·7%). Senesced leaves were collected while still attached to twigs. Only leaves that were easily detached were collected, with the ease of detachment indicating the presence of an abscission layer and completion of any nutrient resorption (Killingbeck 1996). For species for which we could not collect sufficient material this way, we supplemented this material with recently fallen leaf litter, identified on the basis of colour and lack of any signs of decomposition. Senesced leaves will usually be dry in periods of high fire likelihood; therefore, they were also air-dried at 37 °C for over 72 h until they reached an equilibrium (mean moisture content = 8·5%; range = 2·1–15·0%). Leaves were collected from more than 15 individuals per plant species. Ten replicates per species, per material type, were used in the experimental burns.

LEAF TRAIT MEASUREMENTS

Standard protocols were followed for measuring leaf length (mm), effective leaf width (mm), thickness (mm) and mass (g) (Pérez-Harguindeguy *et al.* 2013). Surface area (SA, in cm^2) was estimated with a LI-3100C area meter (LI-COR, Lincoln, NE, USA). For terete leaves (e.g. *Allocasuarina* spp., *Hakea teretifolia* and *Acacia havilandiorum*), one-sided leaf area was calculated as projected area * π/2. The volume of the terete leaves was calculated as π(diameter/2)^2 * length. For broad-leaved species, leaf volume (cm^3) was calculated as one-sided leaf area multiplied by leaf thickness. Specific leaf area was calculated as the one-sided leaf area divided by mass, on the state of the materials as they would be burned (i.e. fresh area/fresh mass, dried area/dried mass, senesced area/senesced mass). As a general rule, SLA is calculated as the one-sided surface area of a fresh leaf divided by its oven-dry mass (Pérez-Harguindeguy *et al.* 2013), but for the purpose of this study, we did not oven-dry the samples because we were particularly interested in the flammability across the three material types in the actual condition they were in (i.e. fresh, dried and senesced). We therefore named this variable, based on the actual weight, 'SLA*'. Subsamples for fuel moisture content (FMC) were held apart; leaves were measured at their actual weight and remeasured after 24 h of drying at 105 °C, when equilibrium was reached (Matthews 2010). Fuel moisture content, as a percentage of oven dried weight, was then defined as follows:

$$FMC = \frac{\text{Actual weight - dry weight}}{\text{Dry weight}} * 100\%. \qquad \text{eqn 1}$$

Data on chemical leaf traits were taken from Cornwell's decomposition experiment (2006). In brief, litter N and P were quantified by Kjeldahl digestions and colorimetric assays (OI Analytical, Wilsonville, OR, USA). Lignin was calculated as the difference between the sum of non-polar, water-soluble and acid-soluble fractions from the total sample. Soluble polyphenols (tannins) were determined using the Folin–Denis method (Allen *et al.* 1974).

DECOMPOSITION EXPERIMENT

Cornwell (2006) quantified interspecific variation in leaf litter decomposability across 51 native woody Australian species in a common litterbed experiment. Recently senesced leaves were collected as described above, air-dried and staked to the ground in 1-mm mesh litterbags (six replicates per species). The litterbed

was located in a woodland at Macquarie University campus (33°46′S, 151°7′E) with a mean annual temperature of 18 °C and a long-term rainfall of 1200 mm year^{-1}. The litterbed was shaded by trees overhead (estimated projected canopy cover 80%). During the course of this experiment, the rainfall was well below the long-term average, namely 837 mm year^{-1}. The litterbags were harvested after 11 and 22 months. The partly decomposed leaves were dried and cleaned of dirt before the percentage weight lost was measured. Decomposition constants were calculated for each species as described in 'Calculations and statistical analysis'.

BURNING EXPERIMENTS

Individual leaf specimens were exposed to a temperature of 400 °C in a muffle furnace with a chamber size of 15 × 10 × 23 cm (Charles Moloney, Sydney; experimental conditions following Gill & Moore 1996; Zylstra 2011). The furnace door was kept open during the measurements to assure there was an abundant oxygen supply and to provide the opportunity to film the processes within. The furnace was used in a well-ventilated room without strong drafts. As a result of the open door, there was a temperature gradient inside the furnace. Three thermocouples (type K, chromel-alumel) were adjusted to a gauze steel cradle perpendicular to the opening of the furnace. The thermocouples were connected to a computer via a CR10WP data logger (Campbell Scientific, Logan, UT, USA). When the average temperature value of the three thermocouples was *c.* 400 °C (±10 °C), leaf samples were inserted.

After running a series of pilot experiments at a variety of temperatures, a set temperature of 400 °C was chosen to be sure that most of the samples would ignite while at the same time, this temperature left enough opportunity for detecting differences in flammability across species. Besides, the volatiles of plant-based material tend to ignite at temperatures between 300 and 600 °C (DeBano, Neary & Ffolliott 1998) and during fires in dry sclerophyll forests, the temperatures range roughly from 100 to 1100 °C (Wotton *et al.* 2012). We consider the set temperature of 400 °C therefore as a reasonable representation of field conditions.

Leaf samples were horizontally placed in the middle of the oven, with their direction parallel to the furnace door. They were held just above the cradle surface, *c.* 3·5 cm above the furnace floor. Samples were held by tongs on the petiole. For some samples (e.g. *Macrozamia communis* and *Eucalyptus haemostoma*), it was necessary to cut off a part of the leaf tip so the sample would fit in the furnace. To provide a source of ignition, a high-frequency electrical spark gun was held *c.* 8 mm above the centre of each specimen (Gill & Moore 1996). This spark gun was inserted simultaneously with the leaf sample and removed as soon as the sample ignited. Filter paper was used as a control, to satisfy ourselves that the method used was reproducible. The entire combustion process was videotaped and subsequently analysed by using the digital video editor 'VideoPad' (NCH Software, Canberra, ACT, Australia).

This experimental set-up allowed us to measure TTI as a proxy for ignitibility, while sustainability was represented by both FD and SD. TTI was defined as the time from insertion into the furnace (and sparking) till the first visible flame. FD was defined as the time from the first visible flame until no more flames could be seen. SD was defined as the time from when no more flames could be seen, until the glowing phase died out. All these measurements were made in seconds, with an accuracy of one-tenth of a second (decimals). Although this set-up worked well for measuring ignitibility and sustainability, combustibility could not be measured because (i) the temperature in the furnace was set (so flame temperature or heat release could not be measured) and (ii) the

samples were too small, and almost completely consumed, for estimating mass loss.

CALCULATIONS AND STATISTICAL ANALYSIS

To satisfy the assumptions of normality and homogeneity of variance, all three fire parameters were log-transformed. For most of the leaf traits, a log transformation was also appropriate. Per material type, variance component analyses were used to differentiate total variance into within-species and among-species components. Next, we quantified the predictive power of species-mean leaf traits, for explaining interspecific variation in TTI, FD and SD, using both bivariate and multiple regressions. For this purpose, individual flammability measurements and leaf trait measurements were averaged for each species per material type. The bivariate regressions were run for all possible combinations of traits, material types and flammability parameters. The strong collinearity (Graham 2003) of some leaf trait measurements, especially the traits related to leaf dimensions (e.g. leaf length, width, surface area, volume and dry mass), gave complications for multiple regressions. Therefore, we took a subset of traits to be included in the stepwise forward regressions, namely SLA*, dry mass, FMC, N, P, lignin and tannin concentration.

The comparison between the three flammability parameters and decomposability was made on the senesced material only, since decomposition had been measured exclusively on senesced material. Decomposition is commonly described by a negative exponential function (Olson 1963):

$$M_t = M_0 e^{-kt}, \qquad \text{eqn 2}$$

where M_t is the mass of litter at a given time; M_0 is the initial mass of litter; k is the decomposition constant; and t is the time passed since the initial measurement. Higher k-values correspond to faster decomposition rates and vice versa. The decomposition constant used here was calculated after 1 year (therefore called k_1), before the decomposition limit was reached (Berg *et al.* 1996). Bivariate regressions were used to compare decomposability (represented by k_1) with TTI, FD and SD, respectively. To evaluate how the leaf traits, decomposability and flammability parameters were associated, we ran a PCA with species means as data points. The same subset of trait variables was used as for the multiple regressions, except that FMC was excluded because this analysis had been performed on air-dried material only. All statistical analyses were carried out using SPSS Statistics V21.0 (IBM, Armonk, NY, USA).

Results

LEAF TRAITS AS DRIVERS OF DECOMPOSITION

After 316 days, 10–71% of the litter had been decomposed (species means), which corresponds to decomposition constants (k_1 in year^{-1}) of 0·11 (*M. communis*) to 1·24 (*Geijera parviflora*). Many traits were collinear, like leaf dimensional measurements or litter nutrient concentrations. The best predictors of litter decomposition rate for our 32 species were lignin ($R^2 = 0.35$, $P < 0.001$) and litter P concentrations ($R^2 = 0.22$, $P = 0.008$; Table S3, Supporting information). Leaves with higher nutrient concentration and lower lignin concentration showed faster decomposition rates. SLA* was unrelated to litter decomposition rate in this data set ($P = 0.495$).

DIFFERENCES IN FLAMMABILITY AMONG SPECIES

All three parameters of leaf flammability (TTI, FD and SD) differed significantly among the 32 species ($P < 0.001$, Table 1). Variance components analysis indicated that each of these parameters could be considered as a 'species-level' property, with among-species variance (all > 70%) being far greater than within-species variance (all < 30%; Table S4, Supporting information). Depending on the material type (fresh, dried or senesced), TTI varied 6·7- to 10·5-fold among species. For example, species-mean TTI for senesced material ranged from 1·6 s (*Brachychiton populneus*) to 17·2 s (*Santalum acuminatum*) (Fig. 1a; Table S4). Flame duration varied 7·5- to 13·3-fold among species (depending on the material), whereas SD varied 15·9- to 21·8-fold (Fig. 1b,c; Table S4). These results are all in line with our assumption that plant species differ strongly in their intrinsic leaf flammability (i.e. flammability of individual leaves under controlled conditions).

As expected, fresh material of a given species took longer to ignite than dried or senesced material, while dried (green) leaves ignited slightly faster than (dried) senesced ones (Fig. 1a). The differences in flame and SDs between the three material types were far less obvious (Fig. 1b,c), although statistically significant (Table 1, $P < 0.001$). Compared to the variation in FD and SD explained by material types, the species effect was much stronger (effect size species > material, Table 1).

CORRELATIONS BETWEEN FLAMMABILITY PARAMETERS

The ranking of species was not consistent across the three flammability parameters: TTI was unrelated to either FD or SD (Fig. 2a,b; all $P > 0.126$; $R^2 \leq 0.08$). In other words, species which ignite easily do not necessarily have a shorter (or longer) flame or smoulder duration. However, FD and SD were positively related, and quite tightly so (Fig. 2c, $R^2 = 0.59$–0.75, all $P < 0.001$), meaning that leaves that flamed longer, smouldered for a longer period of time as well. Based on fuel dynamics, we actually expected a negative relationship (i.e. when FD is shorter, SD takes longer; Sullivan & Ball 2012), but apparently the total fuel mass, related to leaf dimensions, was more

important here (Fig. 3e,h). We checked this by dividing each of FD and SD by dry leaf mass (Fig. 2d). A similar relationship was found: mass-normalized FD and SD were tightly correlated, and positively so.

LEAF TRAITS AS DRIVERS OF FLAMMABILITY

Time to ignition

Variation among species in TTI was driven by morphological traits (i.e. SLA*, SA, leaf thickness or density) rather than by chemical traits (N, P, lignin and tannin concentrations all $P > 0.259$, Table S5, Supporting information). For all three material types, the strongest predictor of TTI turned out to be SLA* ($R^2 = 0.59$, 0·70 and 0·68 for fresh, dried and senesced leaves, respectively, all $P < 0.001$) (Fig. 3a). Species with a higher SLA* ignited more quickly than species with lower SLA*. As expected, FMC played a role in the ignition phase for the fresh material ($R^2 = 0.12$, $P = 0.051$), but not for the dried or senesced material (Fig. 3c). SA : V was negatively correlated with TTI ($R^2 = 0.13$, $P = 0.044$ for fresh material; Table S5), but far more weakly than SLA*.

Multiple stepwise regressions were used to quantify how the morphological and chemical traits together explained the variation in the flammability parameters (Table S6). For the fresh material, an additional 16% was explained by FMC on top of the 61% variance explained by SLA*. For the dried and senesced material, leaf dry mass came in as the second explanatory variable, adding another 7%, respectively. Lignin concentration turned out to affect the ignitibility for dried leaves, providing an additional 3% explanatory power. The total explained variation in TTI was 79%, 89% and 83% for the fresh, dried and senesced material types, respectively.

Flame duration

As expected, larger (and heavier) leaves had longer FDs than smaller leaves. Leaf dry mass was the most important driver of FD, explaining 59–88% of variation among species (Fig. 3e) ($R^2 = 0.88$, 0·67 and 0·59 for fresh, dried and senesced leaves, respectively, all $P < 0.001$). Interestingly, SLA* hardly showed any relation with FD (all $P > 0.084$;

Table 1. Variance components (ANOVA) for the three flammability parameters (time to ignition TTI, flame duration FD, smoulder duration SD), with species and material (fresh, dried and senesced leaves) treated as fixed factors. Effect size was calculated as the partial eta-squared

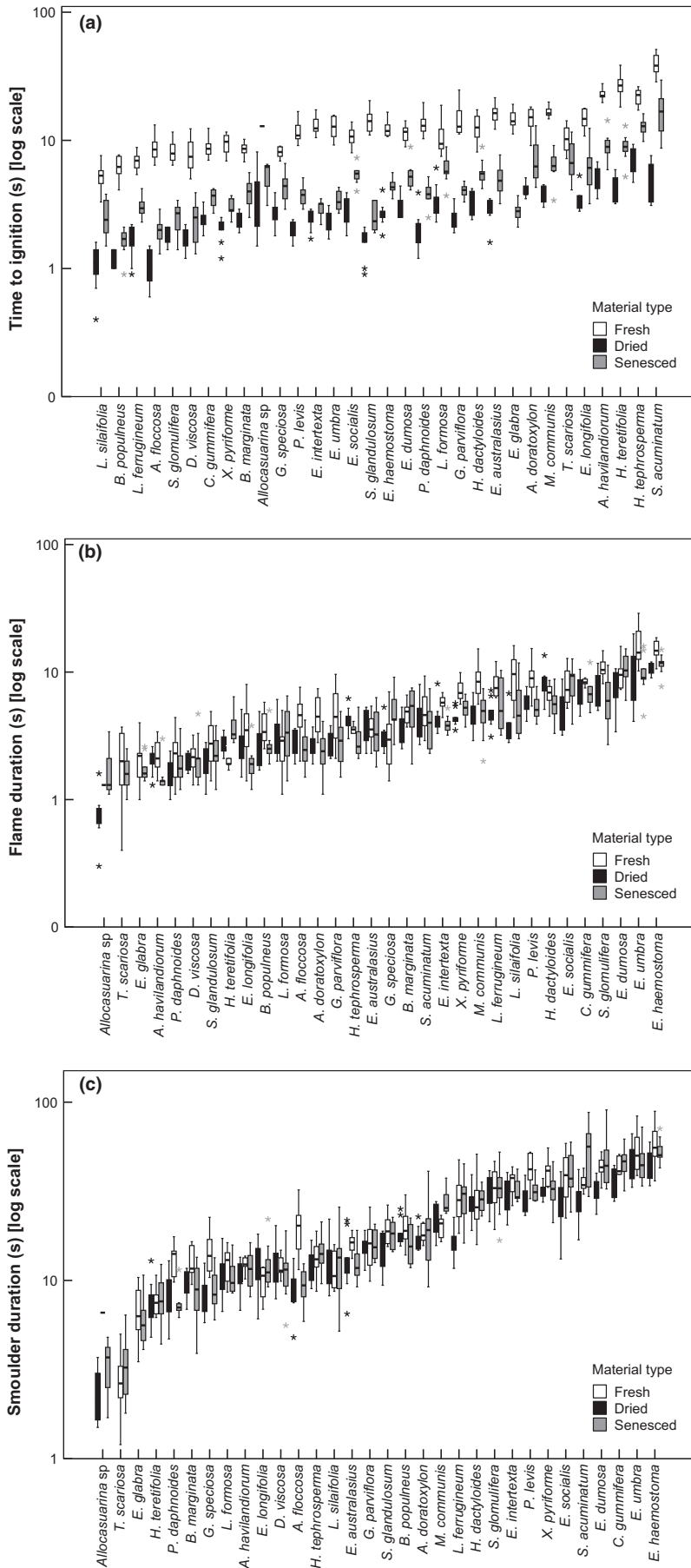| Flammability parameter	Source	Degrees of freedom	*F*-value	Sig (*P*)	Effect size
Log TTI	Species	31	92·5	<0·001	0·78
	Material	2	2711·7	<0·001	0·87
	Species*material	60	6·5	<0·001	0·33
Log FD	Species	31	74·0	<0·001	0·74
	Material	2	48·6	<0·001	0·11
	Species*material	60	3·5	<0·001	0·21
Log SD	Species	31	175·8	<0·001	0·87
	Material	2	46·9	<0·001	0·11
	Species*material	60	3·2	<0·001	0·20

Fig. 1. Variance in flammability response across the species; (a) time to ignition, (b) flame duration and (c) smoulder duration (all in seconds, log-scale). See supporting information for the complete species list (Table S1). Species are ordered from lowest to highest values; $N = 10$ per box (with some exceptions).
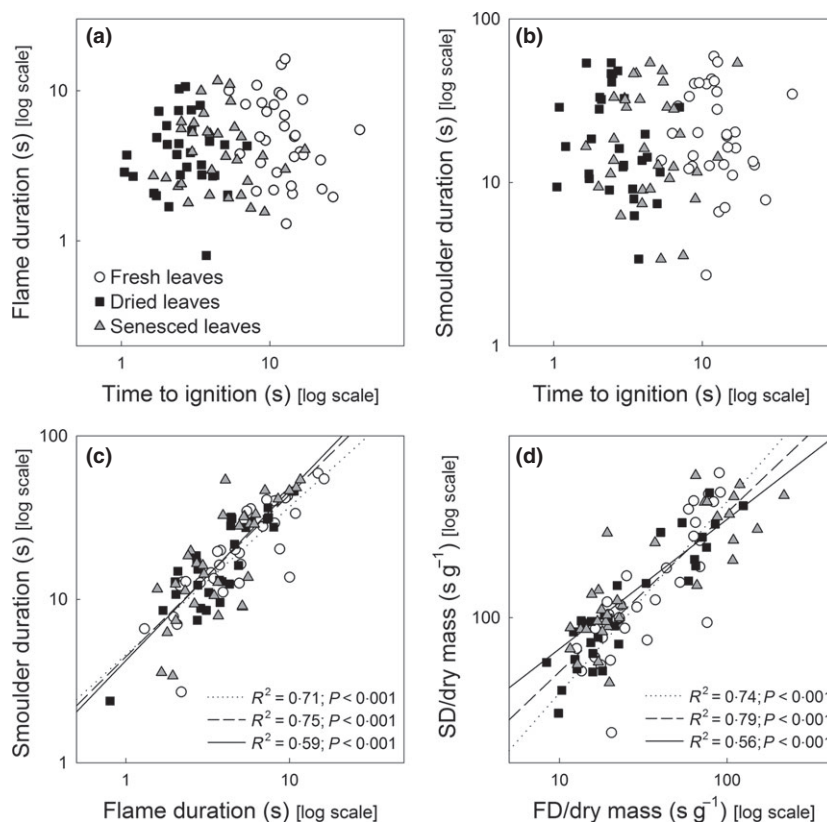
Fig. 2. Pairwise relationships of the three flammability parameters (a) TTI-FD, (b) TTI-SD, (c) FD-SD and (d) FD/dry mass-SD/dry mass. Significant relationships are represented with lines and their corresponding R^2- and P-values. Dotted lines represent fresh leaves, dashed lines represent dried leaves, and solid lines represent senesced leaves.

$R^2 \leq 0.10$) (Fig. 3d, Table S5). Secondly, leaf chemistry turned out to have an influence on FD. Leaves with higher nitrogen concentrations flamed for a shorter period of time (Fig. 3f) ($R^2 = 0.26$, $P = 0.005$ for dried material; $R^2 = 0.33$, $P = 0.001$ for senesced material). Also, phosphorus concentration was related to a decrease in FD ($R^2 = 0.15$, $P = 0.041$ for dried material; $R^2 = 0.15$; $P = 0.037$ for senesced material; Table S5).

In combination, leaf dry mass and either N or P explained 69–78% of the variation in FD in the dried and senesced material. N and P explained substantial variation in FD (up to 17%) after dry mass was first accounted for (Table S6, Supporting information). Note that N and P are strongly correlated and the effect of either N or P was non-significant once the other nutrient was added to the model. SLA* added another 6% to the explained variance in the dried material (Table S6).

Smoulder duration

Similar to FD, heavier leaves smouldered for a longer period of time than smaller leaves (R^2 ranging from 0.74–0.81; Fig. 3h). A significant positive effect of tannins was also noted (Fig. 3i) ($R^2 = 0.27$, 0.18 and 0.24 for fresh, dried and senesced leaves, respectively; P-values vary between 0.002 and 0.020); the higher the amount of tannins, the longer the SD.

In the multiple regressions, leaf dry mass was clearly the main driver of SD, explaining >76% of the variation. The effect of leaf tannin concentration showed up for all mate-

rial types, adding 5–9% to the explained variation (Table S6). For dried and senesced leaves, SLA* and lignin were selected by the model, adding small but significant amounts to the additional explained variation (≤8%; Table S6). Altogether, 84%, 92% and 93% of the total variation in SD were explained by the leaf traits for the three material types (Table S6).

DECOMPOSITION AND FLAMMABILITY

All three flammability parameters showed a clear lack of relationship with the litter decomposition constant k_1 (Fig. 4). TTI was unrelated to k_1 across all species (Fig. 4a; $R^2 = 0.06$, $P = 0.194$), meaning that species that decompose quickly do not necessarily ignite quickly as well. Similar to TTI, FD was overall unrelated to k_1. However, we noted that there were no species in the upper-right corner of the graph (Fig. 4b), meaning that there were no rapidly decomposing species with long FDs. Smoulder duration did not show any relationship with the decomposition constant k_1 (Fig. 4c).

When the species mean values for leaf traits, flammability parameters and decomposition rates were combined in a PCA, the top three (independent) axes together explained 74.9% of variation (Table 2). The first axis, explaining 33.2%, could be distinguished as a fire sustainability axis. Flame and smoulder duration had the heaviest loadings together with leaf dry mass and leaf nutrient concentrations (N and P). The second axis explained 22.5% of the variation and could be characterized as the decomposition
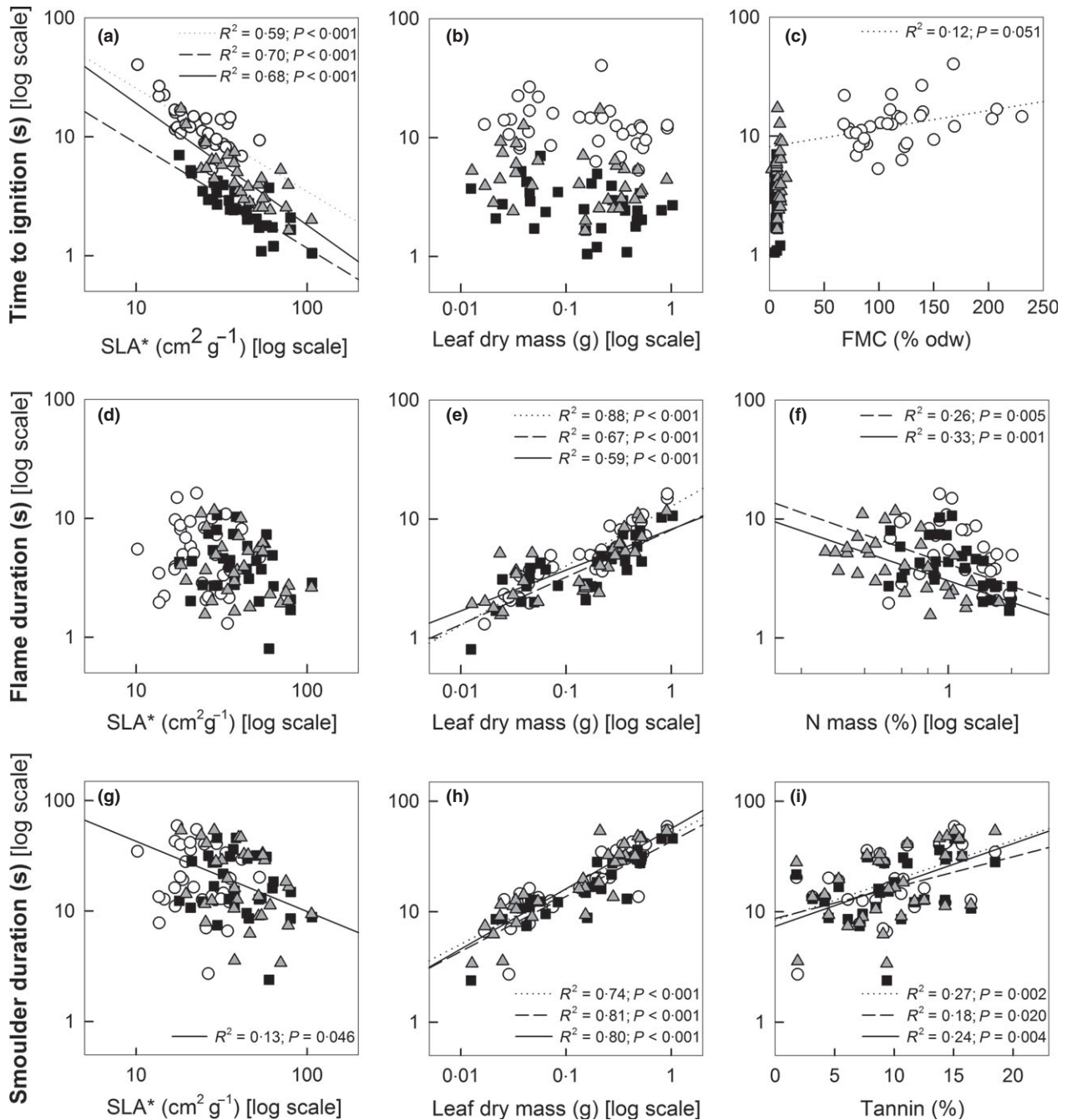
Fig. 3. Interspecific variation in TTI, FD and SD predicted by specific leaf area (SLA*) (a), (d), (g) and leaf dry mass (b), (e), (h); fuel moisture content (c), nitrogen concentration (f) and tannin concentration (i). All three material types are included, symbols as for Fig. 2. Significant relationships are represented with lines and their corresponding R^2- and P-values. Dotted lines represent fresh leaves, dashed lines represent dried leaves, and solid lines represent senesced leaves.

axis: lower values of lignin together with higher values for P led to higher decomposition rates. The third axis was almost as important as the second axis, explaining 19·2%. This was the ignitibility axis, with SLA* as the main driver. The key finding here is that ignitibility, sustainability (FD and SD combined) and decomposability each correlated most strongly with different axes and therefore could be said to be largely unrelated, or decoupled, from each other.

Discussion

FLAMMABILITY DECOUPLED FROM DECOMPOSABILITY

This study provides novel information about the decoupling of two litter fates as determined by species traits. To our knowledge, comparisons of the decomposition rates and flammability of the same range of species have not been made before. We found that ignitibility, fire sustain-
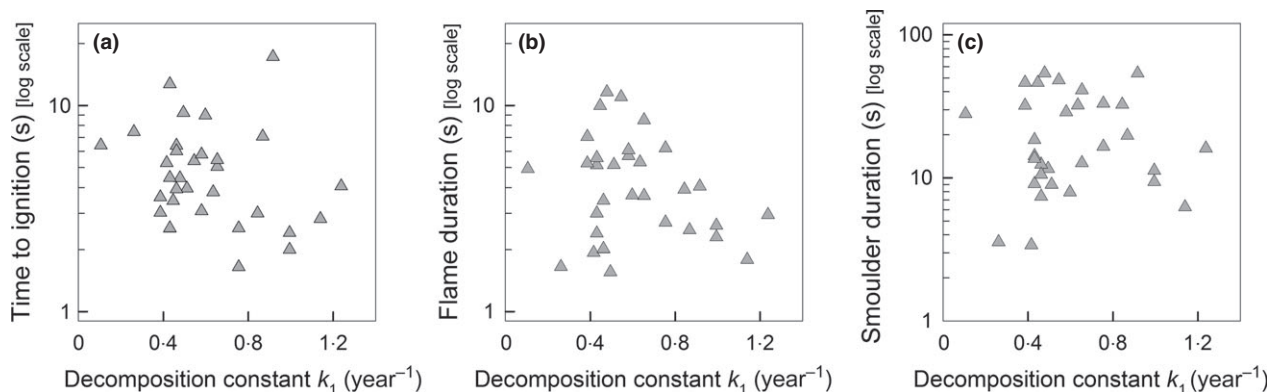
Fig. 4. Decomposition constant k_1 vs. the three flammability parameters (a) time to ignition ($R^2 = 0.06$, $P = 0.194$); (b) flame duration ($R^2 = 0.05$, $P = 0.242$); and (c) smoulder duration ($R^2 < 0.01$, $P = 0.943$).

Table 2. Component matrix of the first three axes, based on a principal component analysis (PCA) for senesced leaves. The input variables are decomposition constant k_1, time to ignition (TTI), flame duration (FD), smoulder duration (SD), dry mass, specific leaf area (SLA*), N, P, lignin and tannin concentrations. The three axes together explain 74·9% of the variation

	1st axis: 33·2%	2nd axis: 22·5%	3rd axis: 19·2%
Decomposition constant k_1 (year^{-1})	−0·371	0·728	0·067
Log TTI (s)	0·098	−0·188	−0·942
Log FD (s)	0·913	0·098	0·173
Log SD (s)	0·813	0·496	0·055
Log dry mass (g)	0·760	0·424	0·310
Log SLA* (cm^2 g^{-1})	−0·365	−0·134	0·865
Log N (%)	−0·696	0·415	0·009
Log P (%)	−0·516	0·670	0·014
Lignin (%)	0·224	−0·615	0·352
Tannin (%)	0·413	0·476	−0·172

ability and decomposability were largely unrelated, with different combinations of traits driving their variation.

This decoupling could represent the different mechanisms involved. Namely, decomposition is an ongoing process with a steady and slow release of carbon, while fires lead to infrequent carbon release bursts. And, whereas combustion (fire) is a physicochemical reaction, decomposition is mainly a microbial process. The speed of combustion will peak under hot and dry conditions (Scott *et al.* 2014), while decomposition by soil fauna is favoured under warm and moist conditions (Swift, Heal & Anderson 1979; Gholz *et al.* 2000; Makkonen *et al.* 2013). For fresh leaves, herbivory is another release mechanism for the fixed carbon in plants. Although herbivory can be quite high in some ecosystems (Cebrian 1999), this was not part of this study.

Fast- and slow-decomposing species varied 11-fold in k_1. This variation has potentially strong effects on the build-up of the litter layer and therefore on the availability of surface fuels for fire. Because decomposability and flammability are decoupled, we might consider three contrasting scenarios for litter fates and nutrient release rates: (i) species with fast-decomposing leaves will never build up a deep litter layer and, therefore, their flammability is not relevant because there will not be enough litter (fuel) to carry potential surface fires. (ii) Slow-decomposing species that are (highly) flammable can build up litter layers of significant depth. These species have the highest likelihood of developing intense and frequent fires because of their flammable characteristics. (iii) Slow-decomposing species with a low flammability form a smaller risk of uncontrollable fires because their leaves are less flammable.

TRAIT RELATIONSHIPS UNRAVELLED

Chemical leaf traits

We found that chemical leaf traits had strong effects on decomposability and on the sustainability of fire, but in different ways. Specifically, we found that decomposition was driven mostly by lignin and P, consistent with previous reports that litter with lower lignin/nutrient ratios is more decomposable (Coûteaux, Bottner & Berg 1995; Berg *et al.* 1996; Cornwell *et al.* 2008). In general, variation in decomposability seems to be related to a global spectrum of leaf carbon and nutrient economics (Cornwell *et al.* 2008); that is, decomposition rates are high for thin leaves with high nutrient concentrations, high photosynthetic rates and low reinforcement of cell walls (e.g. with lignin). Species with these leaf traits can potentially achieve quick returns on their carbon and nutrient investments in leaves, compared to thick, tough and recalcitrant leaves with low photosynthetic rates (Santiago 2007). In contrast, variation in flammability parameters does not show consistent relationships with that in leaf carbon and nutrient economics.

Lignin, tannins and ammonium phosphates (which contain N and P) are known to reduce combustibility by promoting char formation during the depolymerization phase (pyrolysis) of a fire (Green 1992; Celzard *et al.* 2011; Drysdale 2011; Scarff, Gray & Westoby 2012). In a competing pathway with char, fewer flammable tars (combustible volatiles) are formed which, by reacting with oxygen,

could be consumed in flames (DeBano, Neary & Ffolliott 1998). Indeed, we found that the FD was shorter at higher concentrations of N and P, which agrees with the findings of King & Vines (1969); Mak (1982) and Scarff & Westoby (2008). Higher tannin concentrations were correlated with prolonged SDs, which is the characteristic phase of char formation. Thus, although the recalcitrant compounds of lignin and tannins decrease both the decomposition and combustion rates, N and P have opposite effects for decomposition (positive) and fire (negative). This makes it difficult to infer carbon and nutrient release from species' variation in leaf traits.

Moisture content

Moisture content is generally accepted to be a strong determinant of fuel ignitibility (Byram 1959; Plucinski & Anderson 2008; Ganteaume *et al.* 2009; Sullivan *et al.* 2012). Indeed, here we showed that the higher moisture content of fresh material resulted in notably longer times to ignition than in dried or senesced material of the same species (see boxplots in Fig. 1). However, within any given material type, FMC was not a strong predictor of TTI, except in combination with other traits (Table S6). The FMC values that we measured in the fresh leaves (after transporting them to the laboratory in zip-locked bags), varying from 67·9 to 230·7%, covered the range of live FMCs that were found in the field by Caccamo *et al.* (2012; 80·6–142·5%) and mentioned by Bond & van Wilgen (1996; 50–250%). Furthermore, in real bush fires, fuels are a mix of live and dead material, and dead FMCs below 15% are not unusual (Bond & van Wilgen 1996; Matthews 2014). If we combined the FMC of all three material types in one analysis, thereby accounting for a very wide range of FMC, the moisture effect was much stronger ($R^2 = 0.55$, $P < 0.001$).

Specific leaf area

In fire literature, it is often stated that surface area-to-volume ratio (SA : V) is the most important factor for ignitibility, next to FMC (Bond & van Wilgen 1996; Gill & Moore 1996). However, specific leaf area (SLA; ratio of leaf area to leaf mass) has received far less attention regarding its relationship with flammability. One exception is recent work by Murray, Hardstaff & Phillips (2013), who found that higher SLA leaves had shorter TTI (as also found here). We found that SLA* showed a much stronger correlation with TTI than did SA : V. SLA does not only account for the dimensional aspects, but includes the density of the material as well ($1/SLA = 1/density \times 1/thickness$). Perhaps by including leaf density, we better account for the actual accessibility (porosity) for heat and oxygen (required for combustion) and the rate of moisture loss.

We were surprised that ignitibility (TTI) and decomposability (k_1) were not related via SLA*. Thinner, less dense leaves (higher SLA) are generally found to decompose fast

(Cornelissen 1996; Vaieretti *et al.* 2005; Santiago 2007; Cornwell *et al.* 2008). In our data set, however, SLA* and decomposition were unrelated. We do not rule out that a positive relationship between TTI and decomposition (via SLA) might exist in larger data sets. The overall pattern emerging from our study is that different combinations of traits drove the variation in decomposability, ignitibility and sustainability; these different relationships resulted in the observed decoupling of decomposability and flammability.

IMPLICATIONS

Carbon and nutrient fluxes

Decomposition and fire are two main fates for the carbon and nutrients fixed in plants, herbivory being a third. Changes in climate and vegetative composition can affect both ecosystem-level decomposition rate (Coûteaux, Bottner & Berg 1995; Gholz *et al.* 2000) and fire likelihood (IPCC 2012; Hughes & Steffen 2013). If decomposition rates decrease, for example due to a drought period, fewer nutrients are released and the litter will accumulate, which leads to an increased bush fire risk (Raison, Woods & Khanna 1986; Mousseau *et al.* 2014). On the other hand, the plant production could be slowed down during a drought, so less potential fuel will accumulate (Pausas & Bradstock 2007). By increasing fire occurrence, more carbon and nutrients will be lost to the atmosphere (Bowman *et al.* 2009). The complexity of the direct and indirect feedbacks makes it hard to predict what will happen to carbon and nutrient stocks. Based on the predictions of the Intergovernmental Panel on Climate Change, the increase in extreme droughts and heat will increase the risks of wildfires (IPCC 2012). Knowing which plant species and leaf traits make the vegetation more flammable, directly or indirectly through litter accumulation, is therefore invaluable information for the reliable modelling of nutrient and carbon fluxes. The study presented here contributes quantitative data to help us understand the complex processes and interactions of fire and decomposition.

Fire behaviour

Across 32 species from four vegetation types (dominated by sclerophyllous evergreen species), we demonstrated that species differ both in the decomposability of leaf litter and in the intrinsic flammability of their leaves and litter. This can have impacts at a landscape level. When it is known which species dominate in specific areas, an estimation of the corresponding fuel build-up and flammability can be made. For example, after the catastrophic 2009 Black Saturday fires in Victoria (southern Australia), an attempt has been made to make a guide of less flammable native species, which could be promoted around properties to reduce the fire intensity from garden plants (CFA 'landscaping for bushfire' 2011). We aspire to have the information on

decomposition rates and flammability used in fire behaviour models. By including the leaf traits in fire behaviour models, more accurate predictions can be made on where a fire is likely to start and, once a fire has started, some estimates can be made on the likely fire intensity and spread [e.g. PHOENIX RapidFire (Tolhurst, Shields & Chong 2008); Forest Flammability Model (Zylstra 2011)]. This will contribute to better prognoses for potential fire danger and behaviour. This could help forest managers, fire fighters and residents to make better informed decisions and to improve our predictive power of fire regimes in more natural areas under global changes.

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Data accessibility

Data for this manuscript are accessible at the Dryad Digital Repository http://dx.doi.org/ 10·5061/dryad.m41f1 (Grootemaat *et al.* 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Explanation of abbreviations.
Table S2. Species list.
Table S3. Trait – decomposition results.
Table S4. Variance in leaf traits and flammability.
Table S5. Trait – flammability results.
Table S6. Multiple regressions.