

Plant traits and their effect on fire and decomposition

Saskia Grootemaat

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Department of Biological Sciences
Macquarie University
North Ryde, Sydney, NSW 2109 Australia

Principal supervisor: Dr. Ian J. Wright

Associate supervisors: Prof. Peter M. van Bodegom and Prof. Johannes H.C. Cornelissen

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Summary

Wildfires are a major disturbance worldwide with large effects on ecosystem functioning, species composition and nutrient cycling. A fundamental factor in wildfires is the fuel, namely, live and dead plant material. Plant species differ in their flammability, but the role of plant traits in this remains largely unknown. The decomposition rates of different plant materials (and species) can strongly affect the availability of fuel for potential wildfires. While the influence of leaf traits on litter decomposability is reasonably well studied, it has never been compared to the drivers of litter flammability. In this thesis I focused on these two important turnover processes of plant material, i.e., fire and decomposition. By comparing a wide range of species from south-eastern Australia, I investigated the existence of general relationships between plant traits, flammability and litter decomposability.

In experiments on individual leaves (*Chapter 2*) I found that morphological leaf traits (such as specific leaf area or dry mass) were most strongly correlated with interspecific variation in flammability, while decomposability was mainly driven by chemical traits. Similar results were found for bark, another important litter component of the Australian forests (*Chapter 4*). Bark ignitibility of smooth bark species was driven by bark mass per area, while decomposition was strongly associated with initial lignin concentration. Consequently, fire and decomposition, as two alternative fates for leaves or bark, were unrelated.

Next, I demonstrated that leaf traits which affect the flammability of individual leaves (e.g. specific leaf area) continue to affect flammability when scaling up to fuel beds (*Chapter 3*). Can we use these findings on interspecific variation in leaf trait – flammability relationships to improve predictions of fire behaviour? In *Chapter 5* I showed that the inclusion of leaf traits (especially leaf thickness) improved the prediction of individual leaf ignitibility.

Altogether, this suite of studies increased our understanding of trait-effects on leaf and bark flammability and decomposability. Including plant traits in future analyses could improve the estimation of fuel loads and the prediction of wildfires.

Statement

I, Saskia Grootemaat, declare that this thesis titled “*Plant traits and their effects on fire and decomposition*” is my own work and has not been submitted in any form for another degree at any other university or institution. I also certify that this thesis is an original piece of research and has been written by me. Any help or assistance that I have received has been appropriately acknowledged, and the contribution of co-authors has been indicated in the contribution section. All sources of information and literature used are cited in the thesis.

Saskia Grootemaat

November 2015

Contribution

Chapter 1. General introduction

I, Saskia Grootemaat (SG), performed the literature review and writing of this chapter. Constructive feedback was given by my supervisors, Ian J. Wright, Peter M. van Bodegom and Johannes H.C. Cornelissen.

Chapter 2. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species

Ian J. Wright, Peter M. van Bodegom, Johannes H.C. Cornelissen and William K. Cornwell were involved in concept development and gave constructive feedback on draft versions of the manuscript. Decomposition data were kindly provided by William K. Cornwell.

Concept: SG 70%

Data collection: SG 80%

Data analysis: SG 100%

Writing: SG 100% (with feedback from co-authors)

Chapter 3. Towards a better understanding of fuel bed flammability; scaling up from individual leaves

Johannes H.C. Cornelissen was involved in concept development. Peter M. van Bodegom helped with some statistical analysis. Ian J. Wright, Peter M. van Bodegom and Johannes H.C. Cornelissen all provided constructive feedback on draft versions of the manuscript.

Concept: SG 80%

Data collection: SG 100%

Data analysis: SG 90%

Writing: SG 90% (with feedback from co-authors)

Chapter 4. Bark fates explored: decomposition and flammability of 10 woody species from the Sydney region (eastern Australia)

Original concept by SG. Ian J. Wright, Peter M. van Bodegom and Johannes H.C. Cornelissen provided suggestions for experimental set-up and gave constructive feedback on draft versions of the manuscript Veronica Shaw contributed enormously by helping me with the extensive field and lab -work.

Concept: SG 100%

Data collection: SG 80%

Data analysis: SG 100%

Writing: SG 100%

Chapter 5. Models for leaf ignitibility based on leaf traits

The concept was developed as a collaboration between SG and Philip Zylstra. Half of the data came from experimental burns by SG. Additional data was provided by Philip Zylstra. Peter M. van Bodegom contributed with useful statistical advice.

Concept: SG 60%

Data collection: SG 50%

Data analysis: SG 70%

Writing: SG 90%

Chapter 6. General discussion

I, (SG), performed the literature review and writing of this chapter. Constructive feedback was given by my supervisors, Ian J. Wright, Peter M. van Bodegom and Johannes H.C. Cornelissen.

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So here it is, my PhD thesis. I am happy but also sad that it has come to an end. It has been such an adventurous journey! Moving to the other side of the world, starting my own project, fieldwork in unknown areas, and writing papers like “real scientists” do... I will be frankly honest, I could not have done it without the people around me.

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1. General introduction

Different plant species possess different characteristics which may confer selective advantages and disadvantages in certain habitats and situations. For example, species can differ in leaf size and shape, in their canopy branching pattern, in the chemical composition of tissues, and so forth. These characteristics, hereafter called “traits”, reflect the ecological and evolutionary history of the species and largely control processes like resource acquisition, growth and survival (Grime 1977; Reich *et al.* 2003; Westoby & Wright 2006). In this thesis I explore the role of plant traits in two important processes involved in the turnover of biomass, namely, fire and decomposition. By doing this I aim for a stronger fundamental understanding of the difference in and relationship between flammability and decomposability of different (but co-occurring) plant species based on their traits. Below I will describe the motivation for studying wildfires, followed by sections on fuel availability, litter dynamics (including decomposition), fuel flammability and flammability traits. I conclude this general introduction by providing an outline of this thesis including a short description of the different chapters and their key results.

The importance of studying wildfires

Wildfires are a common disturbance for ecosystems around the world (Krawchuk *et al.* 2009). Some plant species possess traits that make them more fire resistant, while other plant species are fire sensitive (Keeley *et al.* 2011; Scott *et al.* 2014). Thus, fire is a strong selective force which, over millions of years, has helped shape the distribution of global biomes through its effects on species composition and vegetation structure (Bond & Keeley 2005; Pausas & Keeley 2009).

Depending on their size, frequency and intensity wildfires can have diverse impacts on our environment. For example, regular fires keep grassland areas open and thereby help conserve a high diversity of plant and animal species (Bond & Parr 2010). By contrast, wildfires in tropical evergreen forests typically lead to species loss and drastic deterioration of forest structure (Cochrane 2003; Barlow & Peres 2008). Animal populations are affected

by wildfire too, both directly (i.e. mortality) and indirectly due to changes in the post-fire environment (e.g. altered habitats and food supply) (Smith 2000; Gill 2012). In addition, smoke from wildfires can lead to human health problems, air pollution and disruption of air transport (Cochrane 2003). Especially when people live within the wildland urban interface, wildfires have the potential to destroy lives and material goods (Gill, Stephens & Cary 2013).

Under current and predicted global climate change more extreme weather events are likely (Hasson *et al.* 2009; IPCC 2013). This will strongly affect *fire regimes* (fire frequency, intensity and season of occurrence; *sensu* Gill 1975). More specifically, some regions of the world will experience a higher frequency and intensity of wildfires, sometimes associated with extreme fire behaviour or fire storms. Other regions might experience less frequent wildfires, e.g. due to higher rainfall or lack of fuel connectivity (Krawchuk *et al.* 2009; Cary *et al.* 2012). With changing climate and fire regimes, many ecological associations will be affected. For example, the structure and composition of vegetation types will change, as well as rates and the extent of biomass (fuel) accumulation (Cary *et al.* 2012). Therefore, it is of particular importance to understand these ecological processes, so we can predict and be prepared for future changes.

Wildfires themselves are a substantial source of greenhouse gases (e.g. CO₂, CH₄, N₂O), CO, NO_x and smoke particles, and these gases and particles have impacts on global warming, biogeochemical cycles and air quality (Page *et al.* 2002; Scott *et al.* 2014). The combustion of vegetation contributes ~ 2.0 – 2.5 Pg C to the atmosphere each year (van der Werf *et al.* 2010; Randerson *et al.* 2012), compared to ~ 8.6 – 10 Pg C per year from the combustion of fossil fuels (Le Quéré *et al.* 2014; van der Werf *pers. comm.*). These emissions from wildfires are often said to be balanced out due to post-fire regrowth (van der Werf *et al.* 2010; Le Quéré *et al.* 2014), but whether this carbon uptake is indeed in balance with the carbon emissions depends on the rate of vegetation recovery and the fire regime (Williams *et al.* 2012). For example, recent modelling work by Kelley & Harrison (2014) showed that although wildfire occurrence is likely to increase in Australia over the next century, a ~10% increase in carbon storage can be expected due to resprouting of fire-adapted trees and forest encroachment in semi-arid areas.

Wildfires do not only affect nutrient fluxes to the atmosphere but also influence nutrient cycling of the affected ecosystems. Within soils, fires affect both nutrient inputs (e.g. by

means of mineral ash) and nutrient losses (e.g. due to volatilization, leaching and erosion), and this has various consequences for plant productivity, diversity and microbial activity (Raison 1980; Christensen 1987; Neary *et al.* 1999). In Australia, the post-fire increase in plant growth on previously infertile soils is often explained by the so-called “ash-bed effect” (Humphreys & Craig 1981; Warcup 1981). The ash contains nutrients that were previously locked up in plant material. This together with a very common increase in soil pH leads to increased availability of soil nutrients for plant growth. Growing conditions for plants can be further improved through changes in the microbial composition and associated mineralisation processes (Christensen 1987).

The effects of wildfires on aboveground species composition and ecosystem functioning are very diverse. At a landscape scale species richness may remain the same, may temporarily increase due to short-lived pioneer species, or may decline due to increased mortality (Gill 1999). The effects of wildfire differ between ecosystems and are highly dependent on the fire regime. At the individual plant level, wildfires can destroy aboveground biomass such as leaves, stems or entire plants. Many perennial plants can recover from this damage by resprouting from epicormic buds, roots or lignotubers (Trabaud 1987) while others may regenerate from seeds that were stored in the seedbank or that were released from the canopy during the fire (e.g. from serotinous fruits as seen in many *Banksia* species). The plants that survive the wildfire or invade the burnt area can profit from the altered post-fire conditions such as lack of competition and enhanced resource availability (Bond & van Wilgen 1996).

Apart from the effects of fire on plants, plants themselves have an influence on fire behaviour. Unlike other ecosystem disturbances like storms, floods or landslides, fires are dependent on organic matter as fuel for their propagation and hence depend on plant availability and connectivity (Bond & Keeley 2005; Murphy, Williamson & Bowman 2011; O’Donnell *et al.* 2011). Plant effects can be direct, e.g. by available biomass (productivity) or by having a lower or higher intrinsic flammability, but can also be indirect, e.g. by providing shade or wind shelter to the understorey, which therefore retains more moisture and is less likely to burn (Cochrane 2003).

For these many reasons, wildfires are a fascinating study object. A better understanding of fire, as an integral part of ecosystem functioning, is desirable, especially in the context of our changing climate. A better understanding has potential to improve nutrient flux models

and enhance our predictions for ecosystem modelling (e.g., estimating species composition, vegetation structure and ecosystem functioning). Also, by gaining more insight into the role of plants in fire behaviour, we can be better prepared for wildfires and adjust ecosystem management and firefighting practises accordingly. This will promote not only human safety but can also help us in preserving biodiversity. In the next sections I will further define the scope and focus of this thesis.

Fuel availability

Weather conditions (e.g. temperature, wind, rainfall) and topography (e.g. slope, aspect) are very important for the development and behaviour of wildfires (Barrows 1951). However, it is the *fuel* that burns, and without available flammable fuel there cannot be a fire. The more material there is to burn, the higher the potential fire intensity (Byram 1959). Higher fuel loads can lead to more intense fires with larger flame heights, can promote the spread of flames into the elevated fuel and canopy layers, and can lead to greater difficulties for fire suppression overall (Hines *et al.* 2010).

Fuel can be roughly distinguished into two types: that from living plants and that from dead plant material (i.e. standing dead material and material in the litter layer). In both cases the fuel availability depends mostly on biomass accumulation as determined by plant growth (productivity) and biomass losses, e.g. by herbivory and decomposition (Cebrian 1999). Plant growth is driven by climate and weather, season, atmospheric CO₂ concentration and soil conditions. In general, vegetative productivity is highest under moist and warm conditions and lowest under dry or cold conditions (Whittaker 1975). A drought, for example, can strongly affect fuel availability and connectivity by preventing herbs and grasses from growing (Murphy, Williamson & Bowman 2011). Weather and seasonal patterns also have an influence on the rate of senescence. For example, senescence of broadleaved species is triggered by dry or cold conditions, to prevent damage from moisture stress (Gan & Amasino 1997). Independent of whether the biomass is still attached to living plants or has become part of the litter layer, in both cases it can act as potential fuel for a wildfire.

Similarly to plant growth, biomass loss by means of litter decomposition is driven by climate, but depends also on litter traits (e.g. morphological and chemical characteristics),

and the composition and abundance of soil-organisms (Berg & McClaugherty 2003). This will be further discussed in the next section.

As outlined above, there are multiple processes to be taken into account when estimating fuel availability. When land managers are concerned about the fuel load and the corresponding risks for wildfires, or want to optimise biodiversity, they can remove live and dead vegetation by means of mechanical removal or prescribed burning. A good understanding of fuel load dynamics is therefore desirable.

Litter dynamics

Besides living plants, dead plant material (i.e. both standing dead material and material in the litter layer) plays a major role in wildfires. It supplies fires with fine surface fuel and it can act as ladder fuels, which can lead to crown fires by supporting the burning of elevated fuels (Gould, McCaw & Cheney 2011). The build-up of the litter layer is regulated by litter inputs and outputs. Litter *input* is determined by leaves, twigs, bark and fruits that fall from trees and shrubs, both after senescence and after being knocked off during a storm. This litter fall varies per season, is highly species-specific, but also varies from plant to plant depending on the plants' size and vigour (e.g. Pook, Gill & Moore 1997; Crockford & Richardson 1998). Litter *output* is determined by several processes, e.g. leaching of soluble nutrients, physical degradation by UV radiation, decomposition by (micro-) organisms, or combustion in a wildfire (Austin & Vivanco 2006; Cornwell *et al.* 2009, Kazakou *et al.* 2009). Quantitatively, decomposition and fire are the two dominant processes causing litter output. All else being equal, when the degradation/decomposition rate of litter is high, less dead plant material (i.e. potential fuel) will accumulate.

In most Australian forests the accumulated litter reaches an equilibrium or “steady-state fuel load” after a fire-free period (Raison, Woods & Khanna 1986; Gould, McCaw & Cheney 2011). The accumulation of litter (input) is then in balance with the decomposition (output). The time needed to reach this equilibrium varies widely with forest type and environmental conditions. For example, in sub-alpine eucalypt forests of south-east Australia, equilibrium was reached after ~10 years without major disturbances (Raison, Woods & Khanna 1986). By comparison, in dry eucalypt forest of south-west Australia (dominated by *Eucalyptus marginata*) equilibrium was reached after ~15 years (Gould, McCaw & Cheney 2011). Although in equilibrium, these steady-state fuel loads can lead

to serious wildfire risks. While fuel amounts of 10 – 12 t.ha⁻¹ can already create control problems for fire fighters under extreme weather conditions, the equilibrium of sub-alpine eucalypt forests easily reached fuel loads between 13 and 23 t.ha⁻¹ (Raison, Woods & Khanna 1986) and ~12.5 t/ha for *E. marginata* forest (Gould, McCaw & Cheney 2011).

Here I propose that fire and decomposition can be seen as two alternative fates for litter in fire-prone ecosystems. While fire is a rapid chemical reaction leading to a pulse-wise carbon release, decomposition is mostly a slow microbial process leading to a steady carbon release. Nevertheless, these two turnover processes have several things in common; they are both key drivers of fuel accumulation, they are both highly dependent on weather conditions, and variation in morphological and chemical properties of the fuel/litter (i.e. traits) affects both the combustion properties and decomposition rate. Another direct link between the two processes is that the flammability of litter is strongly influenced by its decomposition stage (Zhao *et al.* 2014); namely, at a given moisture content, further decomposed twigs ignited easier and burned faster.

The influence of morphological and chemical characteristics (traits) on leaf decomposability is reasonably well understood. For example, under standardised conditions, leaves with higher lignin concentrations, lower specific leaf area (SLA; ratio of leaf area to dry mass) and lower nutrient concentrations show lower decomposition rates (Cornelissen 1996; Pérez-Harguindeguy *et al.* 2000; Cornwell *et al.* 2008; Fortunel *et al.* 2009). By contrast, the decomposability of other plant material, especially bark, has received little attention to this point. Therefore, and because bark litter is an important fuel for wildfires in Australia, part of this thesis (*Chapter 4*) is dedicated to identify which morphological and chemical traits define bark decomposability.

The driving forces behind interspecific variation in leaf *flammability*, however, have not been investigated as completely as have the drivers of leaf decomposition. Consequently, this formed a major goal of this thesis. Next, the two litter fates, fire and decomposition, have not been compared explicitly in the context of trait variation until now. Can we expect that litter which decomposes easily, also burns easily? For instance, thin leaves with a higher surface area-to-volume ratio will decompose faster (Swift, Heal & Anderson 1979) and ignite more quickly (Gill & Moore 1996) due to a relative large contact area for decomposition or pyrolysis to take place. At the same time another trait, like leaf litter moisture content, can have opposite effects. Higher litter moisture contents will speed up

the decomposition process, but will delay the potential ignition. So, how does the combined effect of several traits affect litter decomposability versus flammability when compared across multiple species? And, based on these trait-fate relationships, to what extent are the two fates related to each other and to what extent are they decoupled?

Fuel flammability¹ and plant traits

In addition to fuel *availability*, fuel *flammability* is very important for estimating potential wildfire occurrence and behaviour. Firstly, the conditions of the available fuel are influenced by weather conditions such as relative humidity, air temperature, solar radiation and wind speed. For instance, hot, dry or windy weather will dry out the fuel which makes it more susceptible to fire. Secondly, fuel intrinsic traits can affect the flammability: under equal conditions some fuels are more flammable than others, and this statement holds when comparing the flammability of different plant species (e.g. Gill & Moore 1996; Murray, Hardstaff & Phillips 2013; Grootemaat *et al.* 2015).

The most widely recognised fuel trait influencing fuel flammability is moisture content (e.g. Plucinski & Anderson 2008; Ganteaume *et al.* 2009). Fuels with higher moisture levels take more time to ignite because they require more energy for water evaporation and preheating of the fuel (Byram 1959; Possell & Bell 2013). An important consideration here is the origin of the fuel. While the moisture content of living tissues is largely regulated by the plants' physiology, the characteristics of dead fuel in the litter layer are largely dependent on the weather conditions (Matthews 2006; Matthews, Gould & McCaw 2010). However, the moisture dynamics in both cases are strongly affected by morphological traits of the fuel particles. For example, thin leaves with high surface area-to-volume ratios (SA:V) tend to lose moisture more easily due to a relative larger area for heating and drying to take place (Brown 1970). For most leaves SA:V is determined by leaf thickness (Roderick *et al.* 1999). Thinner leaves (leaves with higher values for SA:V) have been shown to have shorter ignition times (Montgomery & Cheo 1971; Gill & Moore 1996). Recent findings by Murray *et al.* (2013) and Grootemaat *et al.* (2015) suggest that specific leaf area (SLA; ratio of leaf area to dry mass; $\text{cm}^2 \cdot \text{g}^{-1}$) might be a better predictor for leaf

¹ I acknowledge that “flammability” is an ambiguous term, and that it would be better to use more precise terminology like “ignitibility” or “flame duration”. However, for the sake of simplicity of this introduction, I will mainly use the term “flammability” here. A detailed explanation of the different flammability parameters and better use of the terminology can be found in Chapters 2-5.

ignitibility than surface area-to-volume ratio or thickness alone. SLA does not only account for the dimensional aspects of the leaf (like thickness or SA:V), but includes tissue density as well ($SLA = 1/\text{thickness} * 1/\text{density}$; Witkowski & Lamont 1991; Wilson, Thompson & Hodgson 1999). A higher tissue density leads to a lower ignitibility, presumably through the higher quantity or compactness of cell wall material (Roderick *et al.* 1999) which accordingly needs more time for volatilisation during the thermal degradation process (Sullivan & Ball 2012).

The shape and arrangement of plant parts are also important for fuel flammability and potential fire behaviour. For example, in litter beds with a higher packing ratio due to smaller or less curly fuel particles, oxygen supply may be limited as a result of the limited physical space for air (Scarff & Westoby 2006; Schwilk & Caprio 2011). This leads to a less favourable fuel-to-air ratio (*Chapter 3*). In living plants the architecture of branches and leaves will determine the fuel connectivity and this affects the ability of flame-spread from one leaf (or branch) to another (*Chapter 5, Fig. 1*).

Plant chemistry can affect flammability too. Higher values of nutrient concentrations in leaves have been shown to reduce flammability (King & Vines 1969; Mak 1982; *Chapter 2 and 4*), whereas higher terpene concentrations in leaf litter tend to increase flammability (Ormeño *et al.* 2009).

How this interspecific variance in flammability can affect wildfire occurrence and behaviour at a landscape scale depends on the species composition and abundance, and on the litter accumulative characteristics of the species. When certain plants dominate the vegetation type, their intrinsic flammability will likely control the wildfire behaviour because of their larger fuel input (litter quantity). However, non-additive effects have been found in leaf litter of a temperate forest and tundra (van Altena *et al.* 2012; de Magalhães & Schwilk 2012) due to a “dominance effect” of species with a higher flammability (litter quality).

In spite of the importance and complexity of fuel flammability, the combined effect of multiple fuel traits is still largely unclear. While research on plant functional traits has bloomed in the last two decades (e.g. Westoby & Wright 2006), which has led to a better understanding of ecological processes and land-ecosystem properties in general, the important (combinations of) traits underpinning flammability have not been studied comprehensively as such. There is increasing evidence that variation in plant traits affects

wildfire behaviour (as discussed above and in Schwilk 2015). However, some authors argue that laboratory based fuel flammability experiments are not suitable for upscaling to real-world wildfire behaviour because the plant parts have been taken out of their natural fuel context (Fernandes & Cruz 2012). To deal with this controversy, parts of this thesis are especially designed to test the usefulness of single leaf measurements for the flammability of fuel beds (*Chapter 3*) and wildfire behaviour modelling (*Chapter 5*). I believe that a better understanding of the flammability of individual leaves can improve our understanding of fire behaviour in fuel beds and in entire ecosystems. Therefore, this work, which is focused on small scale flammability traits (i.e. individual leaves, bark samples and fuel beds), can be seen as a stepping stone for larger scale fire science.

Research objectives and thesis outline

In this thesis I aim for a better understanding of species-specific trait effects on litter decomposability and flammability. I will investigate the possible existence of general trends in biomass turnover processes for a wide range of species. Such trends would have potential to improve predictions of litter accumulation and wildfire behaviour in Australian ecosystems, as well as for other fire-prone ecosystems worldwide.

This thesis consists of a general introduction, four data chapters, and a general discussion. The data chapters are presented as stand-alone manuscripts for publication in international journals; their contents are summarised below. Because of this format, there is some duplication between the different data chapters, the general introduction and the discussion chapter. However, each of these chapters has a very distinct aim and study approach.

Chapter 2 - Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species²

By means of experimental burns on individual leaves of 32 perennial species from New South Wales, I investigated which morphological and chemical leaf traits are responsible for interspecific variation in leaf flammability. I compared these results with previously

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Chapter 1

established relationships between leaf traits and decomposability on the same species, to explore if these two litter fates (fire and decomposition) are coupled based on underlying trait-driven mechanisms. I found that interspecific variation in time-to-ignition was mainly explained by SLA and moisture content. Flame and smouldering duration were largely explained by leaf dry mass, and to a lesser degree by leaf N, P and tannin concentrations. The variation in the decomposition constant k across species was unrelated to the flammability parameters. Moreover, decomposability was driven by other combinations of leaf traits, namely lignin and P concentrations. With different combinations of traits driving their variation, leaf ignitibility, fire sustainability and decomposability were largely unrelated.

Chapter 3 - Towards a better understanding of fuel bed flammability: scaling up from individual leaves

Building up from individual leaf flammability to fire behaviour in fuel beds, I designed a conceptual framework to investigate how leaf traits can affect the flammability of fuel beds through their intrinsic flammability and their indirect effects by means of fuel bed packing. To test this conceptual framework, I burned monospecific fuel beds of 25 species (out of the 32 species from *Chapter 2*) and combined the results from the two studies (i.e. incorporating results from *Chapter 2* into *Chapter 3*). I demonstrate that leaf traits continue to affect flammability when scaling up from individual leaves to fuel beds.

Chapter 4 - Bark fates explored: decomposition and flammability of 10 woody species from the Sydney region (eastern Australia)

While most previous work on decomposition and functional traits has focused on leaves, another important component of the litter layer in Australia is bark. Eucalypt trees and other species of the Myrtaceae family tend to shed their bark, some of them on an annual basis. This leads to spectacular accumulations of bark on the forest floor and bark-ribbons hanging down from the branches and trunks. In this chapter I studied the bark decomposability and flammability of 10 common tree species from the Sydney region. By doing this, and comparing it to the relative decomposability and flammability of leaves from the same species, I aimed for a better understanding of aboveground litter

accumulation. Overall, bark decomposed slower and was less flammable than leaves. As I found for leaves, decomposability and flammability of bark were largely unrelated because they are underpinned by different combinations of morphological and chemical traits.

Chapter 5 - Models for leaf ignitibility based on leaf traits

Accurately predicting leaf ignitibility is important for estimating flame length and rate of spread in biophysical mechanistic models for wildfire behaviour. In this chapter I combined and compared the impact of the most obvious predictors for leaf ignitibility, namely, temperature, moisture content, leaf thickness and tissue density (and to a lesser extent leaf [N] and [P]). Based on a dataset of 32 Australian species, ranging in their moisture content and burned at different temperatures, 11 *a priori* models for leaf ignitibility were presented and evaluated by model selection analysis. For validation, the models were compared with observed values for leaf ignitibility as found by two other studies. The models including leaf thickness, tissue density or SLA performed best for our own dataset. This was sustained in the model validation (according to the Mean Squared Error), where particularly the model that included leaf thickness was better than the other models. Hence, I conclude that it is important to include leaf traits, and leaf thickness in particular, to parameterise leaf ignitibility in fire prediction models.

Chapter 6 – General discussion

In the final chapter of my thesis, I summarise the main findings of my research and I briefly touch on the potential implications of this work for ecosystem managers and modellers working on carbon fluxes and wildfire behaviour. Lastly, I discuss directions for future research.

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2. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species³

Saskia Grootemaat^{a*}, Ian J. Wright^a, Peter M. van Bodegom^{bc}, Johannes H. C. Cornelissen^b and William K. Cornwell^d

^a Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

^b System Ecology, Faculty of Earth and Life Sciences, VU University, 1081 HV Amsterdam, The Netherlands

^c Institute of Environmental Sciences, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands

^d Biological, Earth and Environmental Science, University of New South Wales, Sydney, NSW 2052, Australia

* Corresponding author: saskia.grootemaat@mq.edu.au

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Summary

1. In fire-prone 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 twofold: (i) to determine which morphological and chemical leaf traits drive flammability; and (ii) to determine if 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 standardised 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. Among 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, i.e. 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' effects 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 bushfire, or by micro-organisms as part of the decomposition 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 leaf economic spectrum (Wright *et al.* 2004; Santiago 2007; Freschet, Aerts & Cornelissen 2012), which describes differences among species in several inter-correlated 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 ratio (Scarff & Westoby 2006; Engber & Varner 2012; de Magalhães & Schwilk 2012; van Altena *et al.* 2012), while individual leaf traits like thickness, moisture content, phosphorus concentration 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 hypothesise 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 with 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 (TTI⁴; a proxy for ignitibility), flame duration (FD⁴) and smoulder duration (SD⁴; 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 nutrient fluxes and could potentially improve the modelling of ecosystem processes.

⁴ An overview of the abbreviations used in this paper can be found in Table 2.1.

Table 2.1 Explanation of abbreviations

Abbreviation	Description	Unit
TTI	Time-to-ignition; time from insertion into the furnace to the first visible flame	seconds
FD	Flame duration; time from the first visible flame until no more flames could be seen	seconds
SD	Smoulder duration; time from the end of the last visible flame until the glowing phase died out	seconds
SA	One sided leaf surface area	cm ²
SLA*	Ratio of leaf area to leaf mass, measured on the actual state of the leaf material as it was: fresh area/fresh weight, dried area/dried weight, senesced area/senesced weight	cm ² .g ⁻¹
SA:V	Two sided leaf surface area-to-volume ratio	cm ⁻¹
FMC	Fuel moisture content, defined as a percentage of leaf oven dry weight	% odw
N	Nitrogen concentration	% mass
P	Phosphorus concentration	% mass
k_1	Decomposition constant after one year; a higher k -value corresponds to faster decomposition rates ($M_t = M_0 e^{-kt}$)	year ⁻¹

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; Wright & Westoby 2003) and a detailed description of the sites can be found in Wright *et al.* (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 Ku-ring-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 cm², which is about the minimum size to obtain meaningful flammability data when leaves are burned individually (see below). These 32 species (Table 2.2) 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 to 45 cm²) 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; de Magalhães & Schwilk 2012; van Altena *et al.* 2012). We expect that traits other than leaf size play a role when oxygen is not limiting.

Table 2.2 Species list

Genus	Species	Family	Rainfall ^a	Soil P ^b
<i>Acacia</i>	<i>doratoxylon</i>	Fabaceae	low	high
<i>Acacia</i>	<i>havilandiorum</i>	Fabaceae	low	low
<i>Allocasuarina</i>	sp.	Casuarinaceae	high	high
<i>Astrotricha</i>	<i>floccosa</i>	Araliaceae	high	high
<i>Banksia</i>	<i>marginata</i>	Proteaceae	high	low
<i>Brachychiton</i>	<i>populneus</i>	Malvaceae	low	low
<i>Corymbia</i>	<i>gummifera</i>	Myrtaceae	high	low
<i>Dodonaea</i>	<i>viscosa</i> subsp. <i>spatulata</i>	Sapindaceae	low	high
<i>Eremophila</i>	<i>glabra</i>	Myoporaceae	low	high
<i>Eremophila</i>	<i>longifolia</i>	Myoporaceae	low	high
<i>Eriostemon</i>	<i>australasius</i>	Rutaceae	high	low
<i>Eucalyptus</i>	<i>dumosa</i>	Myrtaceae	low	low
<i>Eucalyptus</i>	<i>haemastoma</i>	Myrtaceae	high	low
<i>Eucalyptus</i>	<i>intertexta</i>	Myrtaceae	low	high
<i>Eucalyptus</i>	<i>socialis</i>	Myrtaceae	low	low
<i>Eucalyptus</i>	<i>umbra</i>	Myrtaceae	high	high
<i>Geijera</i>	<i>parviflora</i>	Rutaceae	low	high
<i>Grevillea</i>	<i>speciosa</i>	Proteaceae	high	low
<i>Hakea</i>	<i>dactyloides</i>	Proteaceae	high	low
<i>Hakea</i>	<i>tephrosperma</i>	Proteaceae	low	high
<i>Hakea</i>	<i>teretifolia</i>	Proteaceae	high	low
<i>Lambertia</i>	<i>formosa</i>	Proteaceae	high	low
<i>Lasiopetalum</i>	<i>ferrugineum</i>	Malvaceae	high	high
<i>Lomatia</i>	<i>silaiifolia</i>	Proteaceae	high	high
<i>Macrozamia</i>	<i>communis</i>	Zamiaceae	high	high
<i>Persoonia</i>	<i>levis</i>	Proteaceae	high	low
<i>Pultenaea</i>	<i>daphnoides</i>	Fabaceae	high	high
<i>Santalum</i>	<i>acuminatum</i>	Santalaceae	low	low
<i>Syncarpia</i>	<i>glomulifera</i>	Myrtaceae	high	high
<i>Synoum</i>	<i>glandulosum</i>	Meliaceae	high	high
<i>Triodia</i>	<i>scariosa</i>	Poaceae	low	low
<i>Xylomelum</i>	<i>pyriforme</i>	Proteaceae	high	high

^a Low rainfall sites receive approximately 387 mm.year⁻¹, high rainfall sites 1220 mm.year⁻¹.

^b Low soil phosphorus levels are below 132 µg.g⁻¹; high soil phosphorus levels are above 250 µg.g⁻¹ (Wright et al. 2001)

Material types

During a bushfire 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 (> 12h) until the time of the burning experiments. These experiments were run within 72 hours after picking. By using the zip-locked bags we aimed to minimise 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 72h 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 hours 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 cm²) was estimated with a LI-3100C area meter (LI-COR, Nebraska, USA). For terete leaves (e.g. *Allocasuarina* spp., *Hakea teretifolia* and *Acacia havilandiorum*), one-sided leaf area was calculated as projected area * $\pi/2$. The volume of the terete leaves was calculated as $\pi(\text{diameter}/2)^2 * \text{length}$. For broadleaved species leaf volume (cm³) was calculated as one-sided leaf area multiplied by leaf thickness. Specific leaf area (SLA) 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 hours 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:

$$FMC = \frac{(actual\ weight - dry\ weight)}{dry\ weight} * 100\%$$

Eqn. 2.1

Data on chemical leaf traits were taken from Cornwell’s decomposition experiment (2006). In short, 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 (6 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 x 10 x 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 approximately 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 time-to-ignition (TTI) as a proxy for ignitibility; while sustainability was represented both by flame duration (FD) and smoulder duration (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 (1) the temperature in the furnace was set (so flame temperature or heat release could not be measured) and (2) 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):

$$M_t = M_0 e^{-kt}$$

Eqn. 2.2

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 one 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 (*Macrozamia 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 2.3). Leaves with higher nutrient concentration and lower lignin concentration showed faster decomposition rates. SLA* was unrelated to litter decomposition rate in this dataset ($P = 0.495$).

Table 2.3 Trait - decomposition results. Bivariate regressions between traits of senesced leaves and the decomposition constant (k_1). R^2 and P -values are given (significant relationships in bold). The direction of the relation is expressed by (+) for positive relationships and (-) for negative relationships.

Traits	R^2	P
Log width	0.01	0.520
Log thickness	0.11	0.060 (-)
Log surface area	<0.01	0.973
Log volume	<0.01	0.911
Log dry mass	<0.01	0.839
Log SLA*	0.02	0.495
Log SA:V	0.02	0.474
Log N	0.15	0.036 (+)
Log P	0.22	0.008 (+)
Lignin	0.35	<0.001 (-)
Tannin	0.02	0.430

Differences in flammability among species

All three parameters of leaf flammability (time-to-ignition, flame duration and smoulder duration) differed significantly among the 32 species ($P < 0.001$, Table 2.4). 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 S2.1 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 seconds (*Brachychiton populneus*) to 17.2 seconds (*Santalum acuminatum*) (Fig. 2.1 a; Table S2.1). Flame duration varied 7.5-13.3 fold among species (depending on the material), whereas smoulder duration varied 15.9-21.8 fold (Fig. 2.1 b, c; Table S2.1). 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. 2.1 a). The differences in flame and smoulder durations between the three material types were far less obvious (Fig. 2.1 b, c), although statistically significant (Table 2.4, $P < 0.001$). Compared to the variation in FD and SD explained by material types, the species-effect was much stronger (effect size species $>$ material, Table 2.4).

Table 2.4 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	Df	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

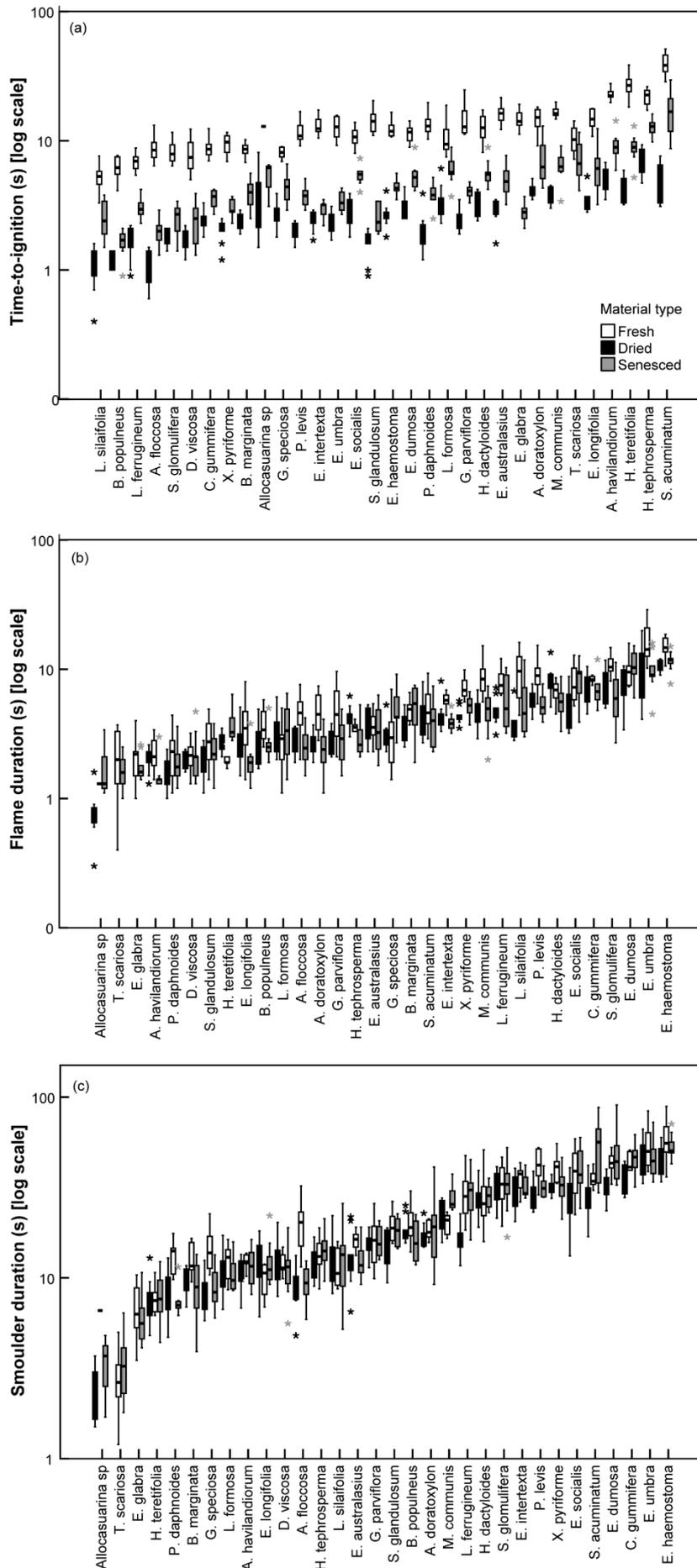


Fig. 2.1 Variance in flammability response across the species; (a) time to ignition, (b) flame duration, (c) smoulder duration (all in seconds, log-scale). Species are ordered from lowest to highest values; N = 10 per box (with some exceptions).

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. 2.2a, 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. 2.2c, $R^2 = 0.59-0.75$, 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. 2.3e, h). We checked this by dividing each of FD and SD by dry leaf mass (Fig. 2.2d). A similar relationship was found: mass-normalised FD and SD were tightly correlated, and positively so.

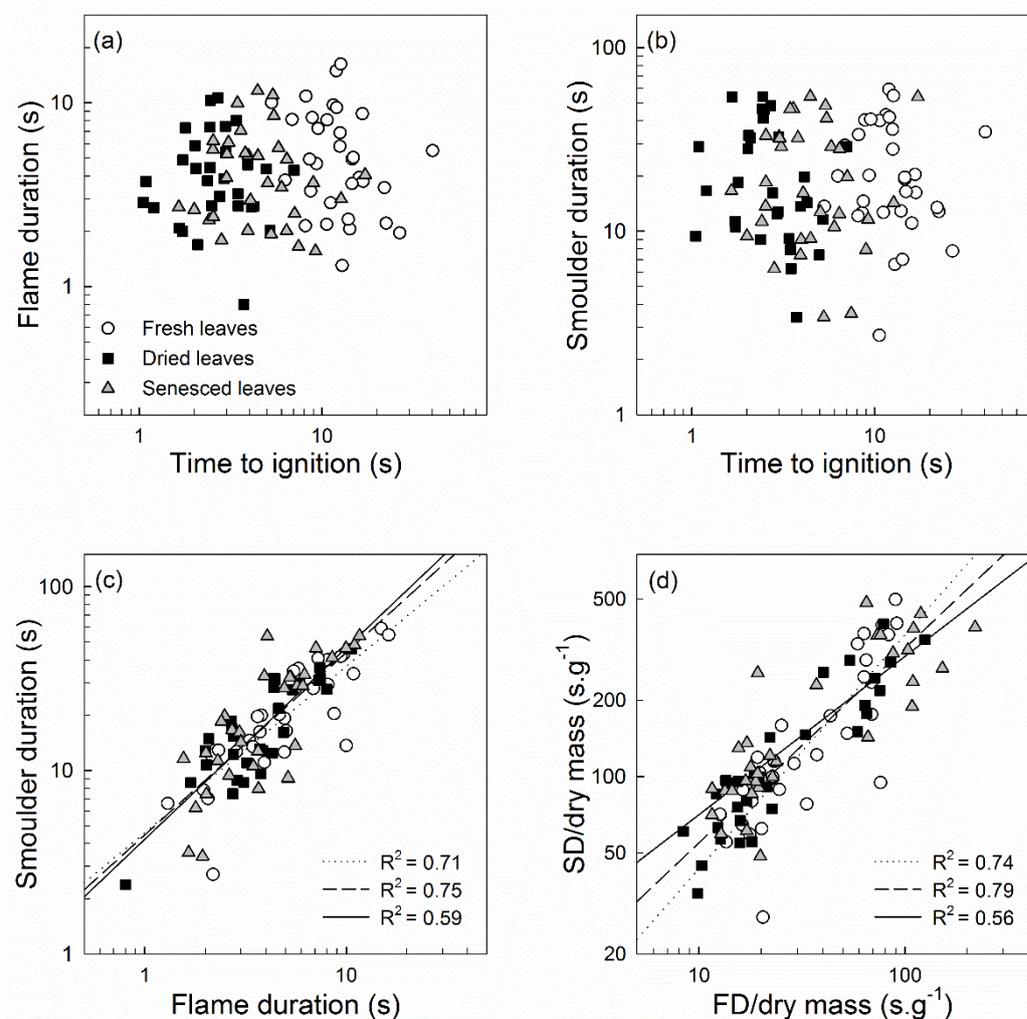


Fig. 2.2 Pairwise relationships of the three flammability parameters (a) TTI-FD, (b) TTI-SD, (c) FD-SD, and (d) FD/dry mass-SD/dry mass. Significant relationships are represented with lines and their corresponding R^2 -values (all $P < 0.001$). Dotted lines represent fresh leaves, dashed lines represent dried leaves and solid lines represent senesced leaves. All axes are log-scaled.

Leaf traits as drivers of flammability*Time-to-ignition*

Variation among species in time-to-ignition 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 S2.2). 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. 2.3a). Species with a higher SLA* ignited more quickly than species with lower SLA*. As expected, fuel moisture content (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. 2.3c). SA:V was negatively correlated with TTI ($R^2 = 0.13, P = 0.044$ for fresh material; Table S2.2), 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 S2.3). 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 ignitability for dried leaves, providing an additional 3% explanatory power. The total explained variation in time-to-ignition was 79, 89 and 83% for the fresh, dried and senesced material types, respectively.

Flame duration

As expected, larger (and heavier) leaves had longer flame durations than smaller leaves. Leaf dry mass was the most important driver of FD, explaining 59-88% of variation among species (Fig. 2.3e) ($R^2 = 0.88, 0.67$ and 0.59 for fresh, dried and senesced leaves respectively, all $p < 0.001$). Interestingly, SLA* hardly showed any relation with flame duration (all $P > 0.084; R^2 \leq 0.10$) (Fig. 2.3d, Table S2.2). Secondly, leaf chemistry turned out to have an influence on flame duration. Leaves with higher nitrogen concentrations flamed for a shorter period of time (Fig. 2.3f) ($R^2 = 0.26, P = 0.005$ for dried material; $R^2 = 0.33, P = 0.001$ for senesced material). Also, phosphorus concentration was related to a decrease in flame duration ($R^2 = 0.15, P = 0.041$ for dried material; $R^2 = 0.15; P = 0.037$ for senesced material; Table S2.2).

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 S2.3). 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 S2.3).

Smoulder duration

Similar to flame duration, heavier leaves smouldered for a longer period of time than smaller leaves (R^2 ranging from 0.74-0.81; Fig. 2.3h). A significant positive effect of tannins was also noted (Fig. 2.3i) ($R^2 = 0.27, 0.18$ 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 smoulder duration.

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 material types, adding 5-9% to the explained variation (Table S2.3). For dried and senesced leaves, SLA* and lignin were selected by the model, adding small but significant amounts to the additional explained variation ($\leq 8\%$; Table S2.3). Altogether, 84, 92 and 93% of the total variation in smoulder duration was explained by the leaf traits for the three material types (Table S2.3).

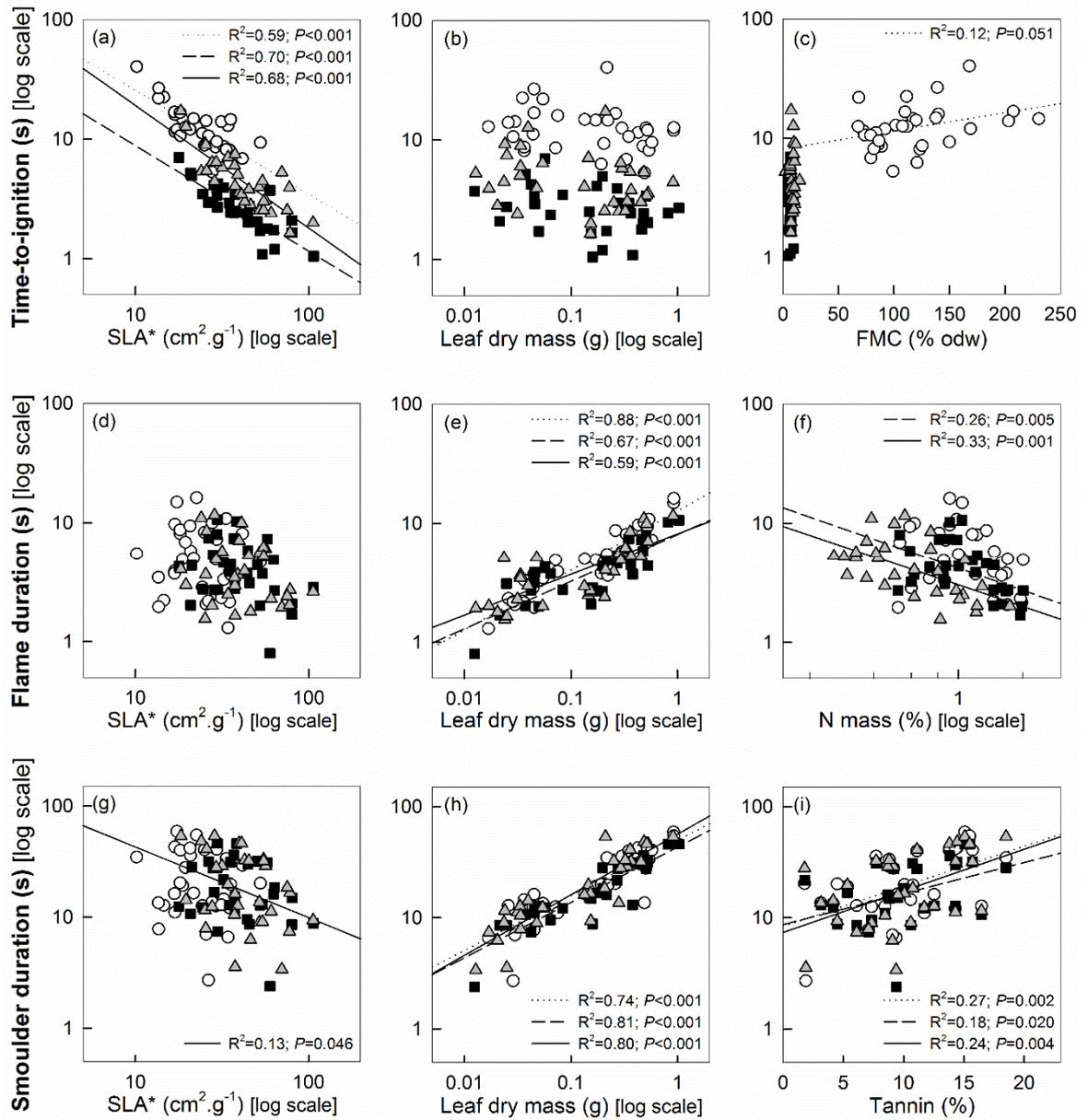


Fig. 2.3 Interspecific variation in TTI, FD and SD predicted by Specific Leaf Area (SLA*) (a), (d), (g) and leaf dry mass (b), (e), (h); fuel moisture content (c), nitrogen concentration (f) and tannin concentration (i). All three material types are included, symbols as for Fig. 2.2. Significant relationships 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.

Decomposition and flammability

All three flammability parameters showed a clear lack of relationship with the litter decomposition constant k_1 . TTI was unrelated to k_1 across all species (Fig. 2.4a; $R^2 = 0.06$, $P = 0.194$); 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. 2.4b), meaning that there were no rapidly decomposing species with long flame durations. Smoulder duration did not show any relationship with the decomposition constant k_1 (Fig. 2.4c).

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 2.5). 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 characterised as the decomposition 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.

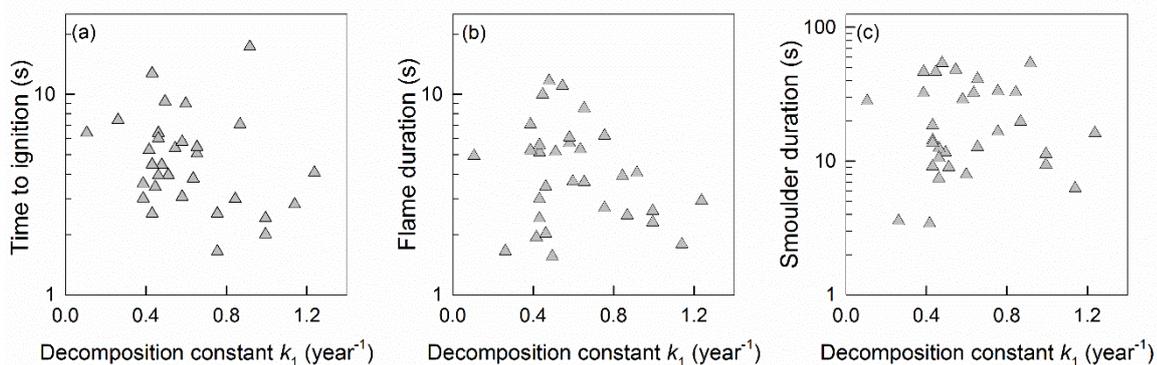


Fig. 2.4 Decomposition constant k_1 versus the three flammability parameters (a) time to ignition ($R^2 = 0.06$, $P = 0.194$); (b) flame duration ($R^2 = 0.05$, $P = 0.242$); and (c) smoulder duration ($R^2 < 0.01$, $P = 0.943$).

Table 2.5 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

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-sustainability 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 *et al.* 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), i.e. 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 depolymerisation phase (pyrolysis) of a fire (Green 1992; Celzard *et al.* 2011; Drysdale 2011; Scarff *et al.* 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 *et al.* 1998). Indeed, we found that the flame duration 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 smoulder durations, 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.1.1). However, *within* any given material type FMC was not a strong predictor of TTI,

except in combination with other traits (Table S2.3). The FMC values that we measured in the fresh leaves (after transporting them to the lab in zip-locked bags), varying from 67.9-230.7%, covered the range of live fuel moisture contents 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 bushfires, fuels are a mix of live and dead material, and dead fuel moisture contents 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 fuel moisture content (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 & Philips (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 ($1/\text{SLA} = \text{leaf thickness} * \text{tissue density}$; Witkowski & Lamont 1991; Wilson *et al.* 1999). 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 dataset, 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 datasets. 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 of 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 *et al.* 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 bushfire 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 of 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 *et al.* 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 paper 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

Table S2.1 Variance in leaf traits and flammability. For each material type mean minimum and maximum values are given for the selected flammability parameter or leaf trait (with the corresponding variance in brackets); the last column shows the variation within and among species. [continued on next page]

	Material type	Min, max (x-fold variance)	Variation within – among species (%)
Time-to-ignition (s)	Fresh	5.3, 40.4 (7.6)	18.3 – 81.7
	Dried	1.1, 7.0 (6.7)	27.9 – 72.1
	Senesced	1.6, 17.2 (10.5)	22.4 – 77.6
Flame duration (s)	Fresh	1.3, 16.2 (12.5)	25.7 – 74.3
	Dried	0.8, 10.6 (13.3)	28.9 – 71.1
	Senesced	1.6, 11.6 (7.5)	29.5 – 70.5
Smoulder duration (s)	Fresh	2.7, 59.2 (21.8)	19.1 – 80.9
	Dried	2.4, 46.0 (19.3)	16.7 – 83.3
	Senesced	3.4, 54.0 (15.9)	19.6 – 80.4
Leaf length (mm)	Fresh	29.0, 129.3 (4.5)	14.4 – 85.6
	Dried	24.8, 127.9 (5.2)	12.0 – 88.0
	Senesced	24.8, 128.9 (5.2)	18.2 – 81.8
Effective leaf width (mm)	Fresh	3.9, 50.2 (12.9)	7.4 – 92.6
	Dried	3.1, 42.8 (13.8)	7.9 – 92.1
	Senesced	3.0, 36.2 (12.1)	11.9 – 88.1
Leaf thickness (mm)	Fresh	0.28, 1.25 (4.5)	7.8 – 92.2
	Dried	0.30, 1.01 (3.4)	15.6 – 84.4
	Senesced	0.30, 0.99 (3.3)	21.9 – 78.1
Surface Area (cm²)	Fresh	1.1, 42.7 (40.0)	6.7 – 93.3
	Dried	0.8, 32.6 (43.3)	10.2 – 89.8
	Senesced	0.7, 27.8 (41.9)	10.4 – 89.6
Dry mass (g)	Fresh	0.02, 0.92 (55.0)	12.5 – 87.5
	Dried	0.01, 1.03 (82.6)	11.8 – 88.2
	Senesced	0.01, 0.91 (71.4)	18.9 – 81.1
Specific Leaf Area (cm² g⁻¹)	Fresh	10.2, 52.7 (5.2)	8.1 – 91.9
	Dried	17.9, 106.9 (6.0)	14.9 – 85.1
	Senesced	18.3, 106.3 (5.8)	12.2 – 87.8
Surface Area : Volume (cm⁻¹)	Fresh	18.8, 122.2 (6.5)	8.7 – 91.3
	Dried	22.8, 136.3 (6.0)	13.9 – 86.1
	Senesced	24.8, 127.5 (5.1)	12.2 – 87.8

	Material type	Min, max (x-fold variance)	Variation within – among species (%)
Fuel Moisture Content (% odw)	Fresh	67.9, 230.7 (3.4)	N/A
	Dried	4.5, 9.7 (2.2)	N/A
	Senesced	2.1, 15.0 (7.1)	N/A
N (% mass)	Fresh	0.52, 2.01 (3.9)	N/A
	Dried	0.52, 2.01 (3.9)	N/A
	Senesced	0.26, 1.74 (6.7)	N/A
P (% mass)	Fresh	0.018, 0.135 (7.5)	N/A
	Dried	0.018, 0.115 (6.4)	N/A
	Senesced	0.002, 0.051 (25.5)	N/A
Lignin (% mass)	Fresh	8.0, 37.5 (4.7)	N/A
	Dried	8.7, 37.5 (4.3)	N/A
	Senesced	8.0, 37.5 (4.7)	N/A
Tannin (% mass)	Fresh	1.8, 18.5 (10.3)	N/A
	Dried	1.8, 18.5 (10.3)	N/A
	Senesced	1.8, 18.5 (10.3)	N/A

Table S2.2 Trait-flammability results. Bivariate regressions between leaf traits and flammability parameters. R^2 - and P -values are given for the different material types (significant relationships in bold, $P < 0.05$). The direction of the relation is expressed by (+) for positive relationships and (-) for negative relationships.

Traits	Log TTI			Log FD			Log SD		
	Fresh	Dried	Senesced	Fresh	Dried	Senesced	Fresh	Dried	Senesced
Length	$R^2 = 0.02$ $P = 0.426$	0.01 0.647	0.01 0.550	0.33 (+) 0.001	0.12 (+) 0.056	0.11 (+) 0.067	0.16 (+) 0.022	0.20 (+) 0.013	0.16 (+) 0.023
Log width	$R^2 = 0.15 (-)$ $P = 0.055$	0.29 (-) 0.005	0.21 (-) 0.018	0.37 (+) 0.001	0.32 (+) 0.003	0.33 (+) 0.002	0.56 (+) < 0.001	0.42 (+) < 0.001	0.40 (+) 0.001
Log thickness	$R^2 = \mathbf{0.47 (+)}$ $P < \mathbf{0.001}$	0.10 (+) 0.082	0.20 (+) 0.011	0.00 0.962	0.06 0.186	0.12 (+) 0.049	0.00 0.839	0.00 0.884	0.05 0.240
Log surface area	$R^2 = \mathbf{0.20 (-)}$ $P = \mathbf{0.011}$	0.34 (-) 0.001	0.28 (-) 0.002	0.73 (+) < 0.001	0.46 (+) < 0.001	0.46 (+) < 0.001	0.64 (+) < 0.001	0.59 (+) < 0.001	0.58 (+) < 0.001
Log volume	$R^2 = 0.09 (-)$ $P = 0.096$	0.32 (-) 0.001	0.22 (-) 0.006	0.80 (+) < 0.001	0.53 (+) < 0.001	0.53 (+) < 0.001	0.70 (+) < 0.001	0.61 (+) < 0.001	0.63 (+) < 0.001
Log dry mass	$R^2 = 0.07$ $P = 0.137$	0.09 0.106	0.06 0.167	0.88 (+) < 0.001	0.67 (+) < 0.001	0.59 (+) < 0.001	0.74 (+) < 0.001	0.81 (+) < 0.001	0.80 (+) < 0.001
Log SLA*	$R^2 = \mathbf{0.59 (-)}$ $P < \mathbf{0.001}$	0.70 (-) < 0.001	0.68 (-) < 0.001	0.01 0.589	0.10 (-) 0.084	0.06 0.188	0.02 0.491	0.08 0.139	0.13 (-) 0.046
Log SA:V	$R^2 = \mathbf{0.13 (-)}$ $P = \mathbf{0.044}$	0.07 0.169	0.01 0.554	0.31 (-) 0.001	0.40 (-) < 0.001	0.45 (-) < 0.001	0.29 (-) 0.001	0.25 (-) 0.004	0.38 (-) < 0.001
FMC	$R^2 = 0.12 (+)$ $P = 0.051$	0.08 0.133	0.00 0.943	0.08 0.124	0.01 0.654	0.00 0.786	0.01 0.605	0.03 0.334	0.01 0.677
Log N	$R^2 = 0.00$ $P = 0.956$	0.04 0.310	0.01 0.643	0.09 0.106	0.26 (-) 0.005	0.33 (-) 0.001	0.03 0.369	0.02 0.458	0.06 0.193
Log P	$R^2 = 0.01$ $P = 0.686$	0.03 0.360	0.02 0.475	0.05 0.244	0.15 (-) 0.041	0.15 (-) 0.037	0.02 0.491	0.00 0.788	0.00 0.999
Lignin	$R^2 = 0.04$ $P = 0.259$	0.00 0.905	0.01 0.621	0.03 0.335	0.01 0.719	0.04 0.272	0.02 0.504	0.02 0.458	0.00 0.794
Tannin	$R^2 = 0.04$ $P = 0.283$	0.01 0.565	0.00 0.806	0.05 0.245	0.08 0.140	0.09 0.105	0.27 (+) 0.002	0.18 (+) 0.020	0.24 (+) 0.004

Table S2.3 Multiple regressions (P -values, R^2 and additional explained variation) of the three fire parameters: (1) time-to-ignition, (2) flame duration and (3) smoulder duration, for each material type, with the following traits selected: Specific Leaf Area (SLA*), leaf dry mass, fuel moisture content (FMC), nitrogen (N), phosphorus (P), lignin, and tannin -concentrations.

(1) Log time-to-ignition					
Material type	Trait	Sig (P)	Model R^2	Additional explained variation	AIC
Fresh	Log SLA*	<0.001	0.61	61%	-125
	FMC	<0.001	0.77	16%	-139
Dried	Log SLA*	<0.001	0.79	79%	-136
	Log dry mass	0.001	0.86	7%	-145
	Lignin	0.018	0.89	3%	-150
Senesced	Log SLA*	<0.001	0.76	76%	-127
	Log dry mass	0.002	0.83	7%	-135

(2) Log flame duration					
Material type	Trait	Sig (P)	Model R^2	Additional explained variation	AIC
Fresh	Log dry mass	<0.001	0.86	86%	-137
Dried	Log dry mass	<0.001	0.61	61%	-113
	Log P	<0.001	0.78	17%	-128
	Log SLA*	0.007	0.84	6%	-134
Senesced	Log dry mass	<0.001	0.54	54%	-107
	Log N	0.001	0.69	15%	-117

(3) Log smoulder duration					
Material type	Trait	Sig (P)	Model R^2	Additional explained variation	AIC
Fresh	Log dry mass	<0.001	0.76	76%	-122
	Tannin	0.001	0.84	8%	-133
Dried	Log dry mass	<0.001	0.79	79%	-126
	Tannin	<0.001	0.88	9%	-140
	Log SLA*	0.014	0.90	2%	-143
	Lignin	0.018	0.92	2%	-148
Senesced	Log dry mass	<0.001	0.79	79%	-118
	Log SLA*	<0.001	0.87	8%	-132
	Tannin	<0.001	0.92	5%	-143
	Lignin	0.046	0.93	1%	-146

3. Towards a better understanding of fuel bed flammability; scaling up from individual leaves

Saskia Grootemaat^a; Ian J. Wright^a; Peter M. van Bodegom^b; Johannes H.C. Cornelissen^c

^a Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

^b Institute of Environmental Sciences, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands

^c System Ecology, Faculty of Earth and Life Sciences, VU University, 1081 HV Amsterdam, The Netherlands

Summary

1. Predicting vegetation feedback to wildfire behaviour is a high research priority. For upscaling from leaf traits to wildfire behaviour we need to know if the same leaf traits are important for the flammability of (i) individual leaves, and (ii) multiple leaves packed in fuel beds. Based on a conceptual framework, we hypothesised that fuel packing properties, through oxygen limitation, would overrule the effects of individual leaf morphology and chemistry.
2. To test this hypothesis we compared the results of two experiments, respectively addressing individual leaf flammability and monospecific fuel bed flammability of 25 perennial species from eastern Australia.
3. Across species, fuel bed packing ratio and bulk density scaled negatively with fire spread and positively with maximum temperature and burning time. Species with ‘curlier’ leaves, higher specific leaf area, lower tannin concentrations and lower tissue density promoted faster fire spread through fuel beds.
4. We found that species with shorter individual leaf ignition times showed faster fire spread, shorter burning times and lower temperatures in fuel beds. Leaf traits that affect the flammability of individual leaves (e.g. specific leaf area), continue to do so even when packed in fuel beds.
5. While previous studies have focused on either flammability of individual plant particles or fire behaviour in fuel beds, this is the first time that an overarching combination of the two approaches was made for a wide range of species. Our framework and findings provide a robust basis for the upscaling of wildfire behaviour based on interspecific variation in morphological and chemical leaf traits.

Keywords: bulk density, fuel beds, leaf traits, packing ratio, rate of spread, specific leaf area, surface fires, tissue density

Introduction

Wildfires are a common phenomenon around the world and form an integral part of the carbon cycle (Bowman *et al.* 2009) and ecosystem dynamics (Bonan 2008; Scott *et al.* 2014). Furthermore, they can form a threat to life and assets. How often, how intense and where wildfires are occurring, depends not only on climate and weather conditions, but also on the particular fuel properties, i.e., the vegetation characteristics (Schwilk 2015). In high intensity wildfires any plant matter will likely burn. However, under mild conditions or at the start of a fire, material properties of organic fuels, like moisture content or leaf dimensions, can strongly influence fire behaviour (Scarff & Westoby 2006; Plucinski & Anderson 2008). In a previous study we showed that morphological and chemical traits of different plant species had strong and differential effects on the ignitability and fire sustainability of individual leaves (Grootemaat *et al.* 2015; see also Murray, Hardstaff & Phillips 2013). For example, species with higher specific leaf area (SLA; leaf area per dry mass) showed shorter ignition times. Species with higher concentrations of leaf nitrogen (N), phosphorus (P) and tannins showed shorter flame durations and prolonged smouldering, presumably by directing the combustion process towards charring rather than tarring (Scarff, Gray & Westoby 2012; Sullivan & Ball 2012).

In (litter) fuel beds on the soil surface, however, bulk density (mass of fuel per fuel bed volume) and packing ratio (particle volume per fuel bed volume) are assumed to be stronger drivers of fire spread than leaf chemical traits (de Magalhães & Schwilk 2012; Van Alena *et al.* 2012; Cornwell *et al.* 2015). Based on principles of air-flow, more densely packed fuel beds are restricted in their oxygen supply and will therefore be hindered in their combustion (Byram 1959; Rothermel 1972; Santoni *et al.* 2014). In general, species with larger leaves are known to pack less densely and therefore can be regarded as “more flammable” since they burn with higher rates of spread and higher energy outputs (Scarff & Westoby 2006; Schwilk & Caprio 2011; de Magalhães & Schwilk 2012). But, a critical knowledge gap constraining our ability to upscale from individual leaf traits to surface fire behaviour, is the lack of understanding of the linkages, across species, between flammability properties of individual leaves and those of fuel beds composed of the same leaves (Varner *et al.* 2015). Indeed previous studies, including the above-mentioned ones, have addressed either one or the other (flammability of individual leaves *or* fuel beds) but never the combination of the two.

This new challenge to link flammability properties of individual leaves to those of leaf fuel beds formed the basis of our conceptual framework (Fig. 3.1). Here we considered and integrated the effects of individual leaf morphological traits (3rd level) as the drivers of packing ratio and bulk density (2nd level). These fuel bed properties (packing ratio and bulk density) were the expected proximate drivers of fuel bed flammability, as described here by maximum temperature, rate of spread, burning time and fuel consumption (1st level, Fig. 3.1).

In this study we quantified the relative importance of leaf morphological traits and packing on the sustainability (here indicated by burning time), combustibility (here: maximum temperature, heat released and rate of spread) and consumability (here: fuel consumption) of fire burning through fuel beds consisting of monospecific leaves (Table 3.1). It is important to distinguish these different components of flammability (which additionally may include ignitibility), because these components are not necessarily positively correlated and express different aspects of fire (Anderson 1970; White & Zipperer 2010). In addition, we also evaluated whether leaf chemical traits (leaf N, P, lignin and tannin concentrations) could explain fuel bed flammability. Our aim was hence to gain a better insight into the leaf trait effects on flammability when considering fuel beds. By working on actual leaves (as opposed to artificial materials like wood wool and sticks, which most models are based on; Rothermel 1972), we aimed for a comprehensive and field-relevant understanding of the complexity in flammability of different species.

We examined if the same drivers were important for the “flammability” of (i) individual leaves and (ii) fuel beds. Based on the literature (Scarff & Westoby 2006; Engber & Varner 2012; Cornwell *et al.* 2015) and our conceptual framework, we hypothesised for fuel beds with a fixed volume (1) that leaf size and “curliness” (Fig. 3.2) would be the main drivers of fuel bed packing and therefore bulk density, with larger and curlier leaves forming more aerated fuel beds (i.e. a lower packing ratio) thereby leading to a higher so-called “reaction velocity” (Rothermel 1972) which implies a higher combustibility (e.g. higher rate of spread) and larger fuel consumption (Fig. 3.1). SLA, the most important driver for ignitibility of individual leaves in our previous study (Grootemaat *et al.* 2015), is the inverse of the product of leaf thickness and tissue density (Witkowski & Lamont 1991; Wilson, Thompson & Hodgson 1999). We hypothesised (2) that SLA could play an integrative but minor role in the fuel bed properties through its association with (a) leaf thickness and curliness as determinants of packing ratio, and with (b) tissue density as a determinant of

bulk density (Fig. 3.1). Since we expected that the physical arrangement of the leaves (i.e. the packing ratio) and the resulting air-to-fuel ratio would dominate the flammability of fuel beds, we hypothesised (3) to find only very weak effects of leaf chemistry (N-, P-, lignin- or tannin concentrations), if any at all. Overall, when scaling up from individual leaves to fuel beds across multiple species we hypothesised (4) that the species' flammability status would not necessarily hold because different leaf traits are deemed to be important at different scales.

We tested these hypotheses on 25 perennial species from fire-prone ecosystems in Australia, by comparing the traits and flammability parameters of their individual leaves (Grootemaat *et al.* 2015) with the traits and flammability parameters of foliage fuel beds as measured in standardised experiments.

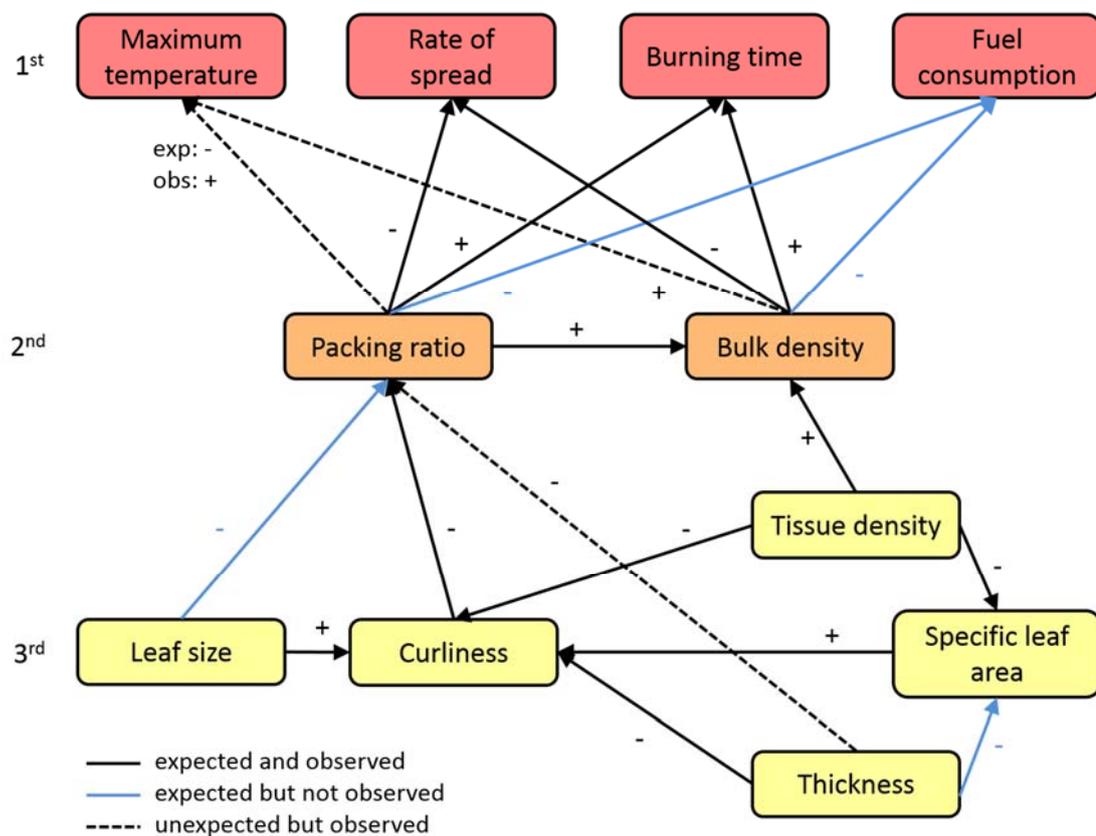


Fig. 3.1. Conceptual framework of how the flammability parameters in our study (1st level) can be driven by fuel bed properties (2nd level: packing ratio and bulk density) and how these are affected by individual leaf traits (3rd level: leaf size, curliness, leaf density and thickness -as part of specific leaf area). Positive relationships are represented with a plus (+), negative relationships with a minus (-).

Table 3.1 Overview of the flammability parameters measured during the experimental burns. The first six variables were measured in fuel beds; the last four variables came from our previous work on flammability of individual leaves in a muffle furnace at 400°C (Grootemaat *et al.* 2015). The numbers given are species-means.

Parameter	Description	Flammability component	Unit	Range (x-fold variation)
-Ignition frequency	Percentage of replicates that truly ignited (with flames rather than smouldering)	Ignitibility	%	33.3 - 100 (3.0)
-Maximum temperature	Mean maximum temperature for 5 sensors	Combustibility	°C	480 - 753 (1.6)
-Total heat released	Energy output; area under the temperature-time curve	Combustibility	°C * min	200 - 2620 (13.1)
-Rate of spread	Distance from the ignition point to the edge of the ring, divided by time to edge	Combustibility	cm.s ⁻¹	0.05 - 0.64 (12.8)
-Burning time	Fire duration; time from ignition at a sensor until the fire dies out at that sensor (mean of 5 sensors, threshold used is 50°C)	Sustainability	s	61 - 1407 (23.0)
-Fuel consumption	Percentage weight lost	Consumability	%	67 - 98 (1.5)
-Time to ignition	Time from the insertion of a leaf into a muffle furnace (400°C) until the first visible flame	Ignitibility	s	1.1 - 7.0 (6.7)
-Flame duration	Time from the first visible flame until no more flames could be seen	Sustainability	s	0.8 - 10.6 (13.3)
-Smoulder duration	Time from the end of the last visible flame until the glowing phase died out	Sustainability	s	2.4 - 46.0 (19.3)
-Total burning time	Sum of flame- and smoulder duration for individual leaves in the muffle furnace	Sustainability	s	3.2 - 56.7 (17.8)

Material and methods

Species selection and leaf collection

To compare the flammability of individual leaves with the flammability in fuel beds, the same evergreen perennials were used as in Grootemaat *et al.* (2015). However, for some species it was unrealistic to collect enough material and therefore we ended up using a subset of 25 species (out of 32; see Table S3.1 for the species list). The leaves were collected from four different sites in New South Wales, eastern Australia (previously used and described by Wright, Reich & Westoby 2001). Two sites were located in Ku-ring-gai Chase National Park, Sydney (average annual rainfall 1233 mm; Australian Bureau of Meteorology); two other sites were located in the drier Round Hill Nature Reserve (570 km inland from Sydney), with an average annual rainfall of 383 mm. Within each rainfall zone there was a site with nutrient-rich soil (phosphorus levels $> 250 \mu\text{g.g}^{-1}$) and nutrient-poor soil (phosphorus levels $< 132 \mu\text{g.g}^{-1}$). By dispersing sampling across these four different sites and vegetation types (closed forest; open forest; eucalypt-cypress pine woodland; mallee woodland) we ended up with a species set covering 13 families, with a variety of growth forms (trees, shrubs, a cycad and a hummock grass) and a wide interspecific range of leaf traits (Table S3.2).

As our model-material, green air-dried leaves were used because it was relatively easy to collect adequate amounts of material for most of the species and because it suited the purpose of this study, namely comparing the flammability of individual leaves with the flammability of fuel beds. The green leaves were picked fresh from the branches and were, after transport to the laboratory in paper bags, air-dried on benches until they reached equilibrium weight.

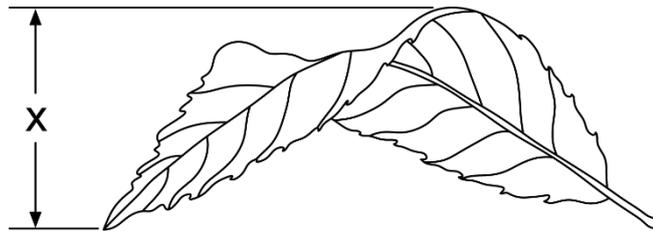


Fig. 3.2 Leaf curliness (x) in mm was measured as the maximum perpendicular height of the leaf when positioned on a flat surface.

Trait and fuel bed measurements

Leaf traits were measured on 10 individual leaves per species. For this purpose, representative fully expanded outer-canopy leaves were used. Leaf length (mm), width (mm), thickness (mm) and mass (g) were measured following standard protocols (Pérez-Harguindeguy *et al.* 2013). Leaf size (cm²), measured as one-sided leaf area, was estimated by using a LI-3100C area meter (LI-COR, Lincoln, NE, USA). For terete leaves (e.g. *Allocasuarina sp.*, *Hakea tephrosperma* and *Acacia havilandiorum*), one-sided leaf area was calculated as scanned area * $\pi/2$. The volume of the terete leaves was calculated as $\pi(\text{thickness}/2)^2 * \text{length}$. For broad-leaved species leaf volume (cm³) was calculated as one-sided leaf area multiplied by leaf thickness. Specific leaf area (SLA) was calculated as the one-sided area of a fresh green leaf divided by its oven-dried mass (Pérez-Harguindeguy *et al.* 2013). Leaf “curliness” (mm) was measured as the maximum absolute height when positioned on a flat surface (Fig. 3.2, after Engber & Varner 2012). This measurement of leaf curliness has its limitations (e.g. needles tend to fall flat), but it gives us some indication of the 3D-shape of the leaves, beyond leaf length, width, thickness and area.

Subsamples were held apart (n = 3 per species) for determination of fuel moisture content (FMC) and leaf chemistry (carbon, nitrogen and phosphorus concentration in mass %). After oven drying (>72h at 60°C) FMC was calculated as the percentage of moisture based on the oven dry weight. The subsamples for C and N were dried, ground and analysed with an elemental analyser (FlashEA 1112, Thermo Fisher Scientific, Rodano, Italy). Phosphorus concentration was measured colorimetrically, after digestion in a 1:4 mixture of 37% HCl and 65% HNO₃ (by volume) (Murphy & Riley 1962). Tannin and lignin concentrations for these species came from a previous study by Cornwell (2006). 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 Follin-Denis method (Allen *et al.* 1974).

Fuel bed bulk density (g.cm⁻³) was calculated as the mass of the sample divided by fuel bed volume. Packing ratio (cm³.cm⁻³, i.e. dimensionless) was expressed as particle (leaf) volume per fuel bed volume. Figure 3.3 gives a schematic impression of the difference between packing ratio and bulk density based on a fuel bed with a fixed volume. An extended overview of all the measured traits and fuel bed measurements can be found in Table S3.2.

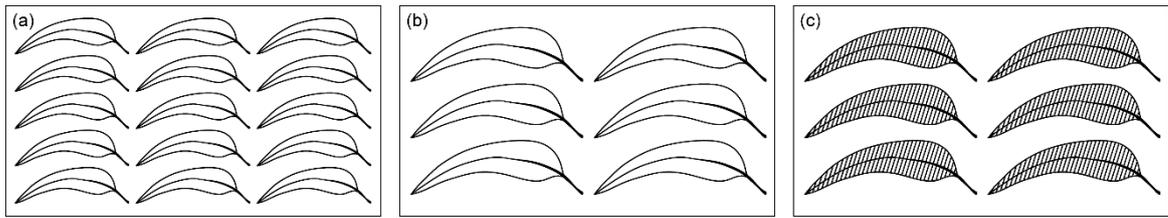


Fig. 3.3 Schematic representation of the difference between packing ratio and bulk density in fuel beds with a fixed volume. The left frame (a) has a higher packing ratio than the middle frame (b) and therefore also a higher bulk density. The right and middle frame have the same packing ratio, but the right frame (c) has a higher bulk density due to higher tissue density, as represented by dark lines.

Experimental fuel bed burns

Experimental burns were performed on monospecific fuel beds consisting of green air-dried leaves. The experiments were run in the Fire Laboratory of Amsterdam for Research in Ecology (FLARE), at VU University in Amsterdam, The Netherlands. The fuel beds were burned following the procedure as described by Van Altena *et al.* (2012). In short, on the days before the experimental burns, the samples, which were all at equilibrium moisture content under ambient lab-conditions, were weighed and sealed in plastic bags to keep the moisture content constant until the time of burning. Each bag was opened shortly before the burn and the air-dried leaves were placed loosely in a steel mesh ring (25 cm in diameter, 3 cm high). The leaves were equally distributed over the ring until the ring was full, resulting in an equal fuel bed volume for all replicates (1473 cm³). The number of replicates for each species depended on the availability of material (Table S3.1). For some species we only had enough material for one replicate, but, since the replicates *within* species are pseudo-replicates and the replicates *between* species are true replicates, this was not a problem for our experimental design. The burns were blocked in time, so that one sample of each species was burned in random order on a particular day. This would prevent any systematic effects of changes in air humidity and temperature in FLARE during the experiment (van Altena *et al.* 2012).

The filled ring was placed on a fire-resistant plate beneath a fume hood with a constant moderate draft. Samples were ignited by lighting a cotton disk (folded twice), injected with 1 ml of ethanol (96%), which was placed in the middle of the ring. Six thermocouples (1 mm type K) were positioned approximately 1 cm above the leaves. One of these

thermocouples was located above the centre of the ring, while the tips of the other five thermocouples were equally distributed around the ring with a distance of 6.25 cm from the ring's centre. Temperature was logged every second. The flammability parameters that were measured during each burn included ignition frequency (%), maximum temperature (°C), an approximation to total heat released (°C * min), rate of spread (cm.s⁻¹), burning time (s) and fuel consumption (% mass loss) (Table 3.1).

Data analysis

First we evaluated whether room temperature, air-humidity, and fuel moisture differences affected the results. The variation in room temperature (17.0-25.1°C), air-humidity (55.6-85.4%) and fuel moisture content (4.6-8.4% oven dry weight) was evenly distributed across the replicates and no relationships were found with the selected fire parameters. Altogether, the burns had an ignition frequency of 97%. Two replicates of *Eucalyptus intertexta* and one replicate of *A. havilandiorum* did not ignite properly and were therefore omitted from further analysis. Maximum temperature, total heat released and burning time were calculated from time-temperature curves which were saved by a data logger. Since air-temperatures $\geq 50^\circ\text{C}$ would normally not occur in the lab under ambient conditions, we took this as a safe threshold value; at temperatures above 50°C we considered there to be a fire.

Before statistical analysis, individual measurements of the replicates were averaged for each species, and trait- and flammability parameters were log-transformed to satisfy the assumptions of normality and homogeneity of variance. In some cases we had to exclude *Triodia scariosa* (a C4 hummock grass) from the analysis because we lacked the individual leaf flammability parameters and some trait measurements. In those cases we ran the analyses with 24 species instead of 25. Fuel consumption showed a clearly non-normal distribution and therefore non-parametric Spearman's rho correlations were used for analyses related to fuel consumption. For the other flammability parameters, Pearson correlations and linear regressions were used to test for relationships between leaf traits, fuel bed properties and flammability. To evaluate the relationships between fuel bed properties and flammability parameters as constrained by the combined influences of various leaf traits, a multivariate redundancy analysis (RDA) was run in the “vegan” package in R, scaled to deal with the different units of expression.

For comparison of the flammability of individual leaves with the flammability in fuel beds, four flammability parameters from a previous study were used, namely: time-to-ignition, flame duration, smoulder duration and total burning time, of individual leaves burned in a muffle furnace at 400°C (Table 3.1). Details of these measurements can be found in Grootemaat *et al.* (2015). Bivariate regressions were used to test for relationships between the flammability of individual leaves and the flammability of fuel beds across the 25 species.

All statistical analyses were carried out with SPSS Statistics V21.0 (IBM, USA) or with R (version 3.0.0; R Development Core Team 2013).

Results

Flammability of the fuel beds

There was considerable variation among the 25 species in their flammability parameters (Fig. 3.4; Table 3.1). Species-mean maximum temperature varied between 480 and 753°C. Total heat released varied 13-fold, between 200 and 2620°C * min and this was mainly due to burning time ($r = 0.99$, $P < 0.001$) and less to maximum temperature ($r = 0.69$, $P < 0.001$; Table S3.3). Rate of spread showed *c.* 13-fold variation, ranging from 0.05 cm.s⁻¹ (*Santalum acuminatum*) to 0.64 cm.s⁻¹ (*Lomatia silaifolia*). Total burning time varied 23-fold, from 61 (*L. silaifolia*) to 1407 seconds (*H. tephrosperma*). Rate of spread and burning time were strongly correlated in our dataset ($r = 0.93$, $P < 0.001$; Table S3.3). Interestingly, fuel consumption varied relatively little across the species: for 23 of 25 species, between 82 (*S. acuminatum*) and 98% (*Macrozamia communis*) of the material was consumed (Fig. 3.4g and h). Two species had clearly lower fuel consumption: *Eucalyptus dumosa* and *Eucalyptus socialis*, with a mean fuel consumption of 67 and 68%, respectively. The fire spread slowly through these fuel beds, with small flames compared to the other species. Consequently, a thick layer of black-charred and partly unburnt leaves remained after the experimental burns.

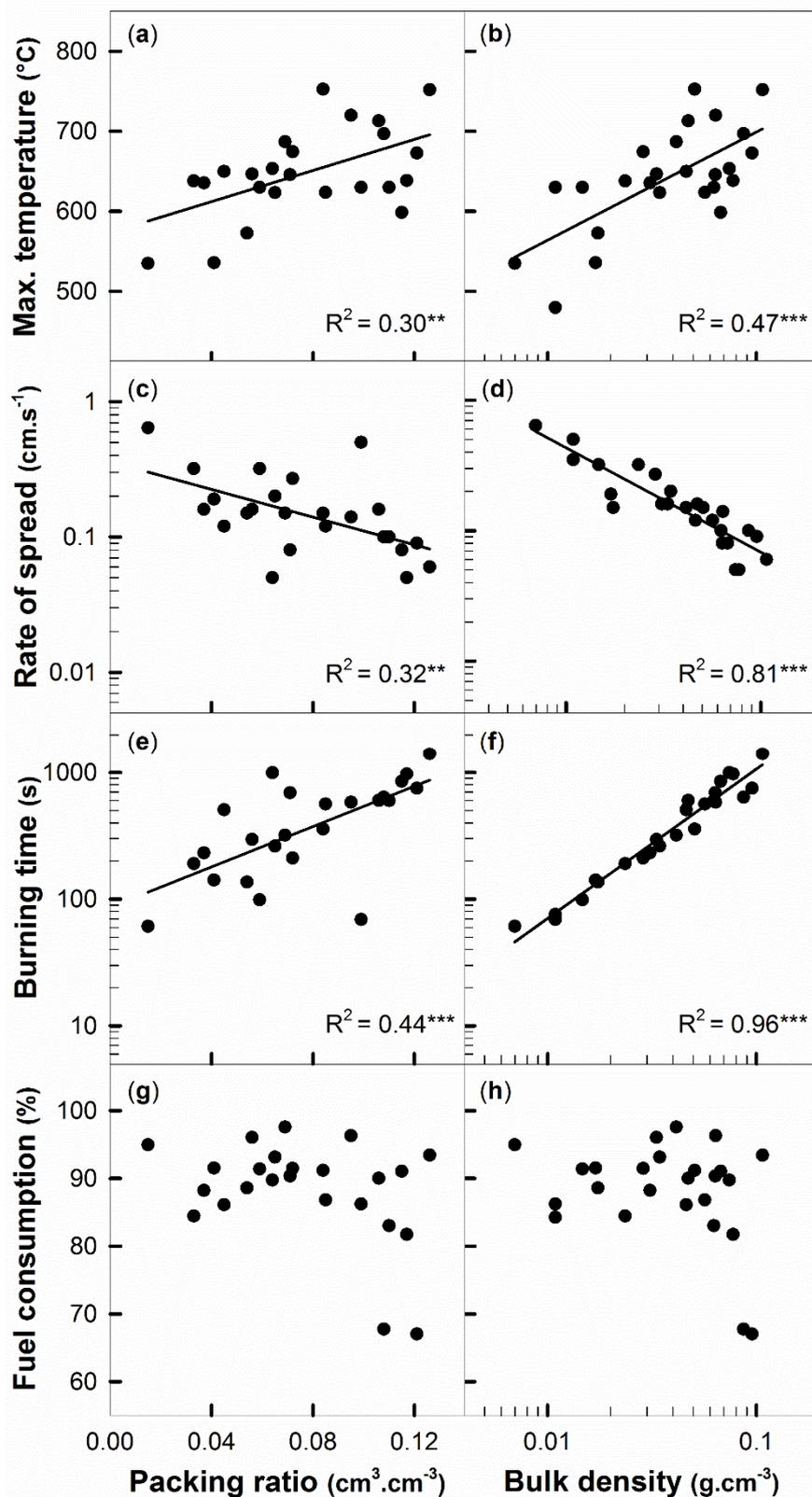


Fig. 3.4. Bivariate relationships between the four flammability parameters and packing ratio or bulk density. Each dot represents a species-mean. Significant relationships are represented with solid lines and corresponding R^2 -values. **, $P < 0.01$; ***, $P < 0.001$.

Which fuel properties drive variation in fuel bed flammability?*Packing ratio and bulk density*

Several leaf- and fuel bed traits were correlated with the combustibility and fire sustainability of the fuel beds (Table S3.3). The more available fuel, the higher the maximum temperatures (Fig. 3.4a and b). Higher rates of spread, shorter burning times and a lower heat release for species with lower packing ratios (more aerated fuel beds) were found (Fig. 3.4c and e; Table S3.3). However, bulk density turned out to be a better predictor of our flammability parameters than packing ratio. Bulk density was by far the most important driver for rate of spread (negatively; $R^2 = 0.81$, $P < 0.001$; Fig. 3.4d) and burning time (positively; $R^2 = 0.96$, $P < 0.001$; Fig. 3.4f). Fuel beds with a higher bulk density (more mass per fuel bed-volume) showed a slower spread of the fire, a longer burning time and consequently a higher heat release. Although packing ratio was positively related to bulk density ($r = 0.70$, $P < 0.001$; Table S3.3; Fig. S3.1), the results here suggest that a factor related to the residual variance between these fuel bed properties contributes to the additional predictive power of bulk density. As discussed in the following paragraphs, interspecific variation in packing ratio and in bulk density are indeed driven by different leaf traits (Fig. S3.2).

Individual leaf traits

In addition to the effects of packing ratio and bulk density on the flammability parameters, we found effects of individual leaf traits on the combustibility and sustainability of fire in the fuel beds. Species with larger leaves had a tendency to burn with lower maximum temperatures ($R^2 = 0.14$, $P = 0.071$; Fig. 3.5a). Curlier leaves and leaves with higher SLA showed lower maximum temperatures when burned in the fuel beds ($R^2 = 0.54$, $P < 0.001$ for curliness; $R^2 = 0.19$, $P = 0.028$ for SLA; Fig. 3.5b and c). Species with thicker leaves burned with higher maximum temperatures ($R^2 = 0.21$, $P = 0.026$; Fig. 3.5d). Tissue density, the other component of SLA, showed no effect on maximum temperature (Fig. 3.5e).

Fuel beds made up of larger leaves showed higher rates of spread ($R^2 = 0.17$, $P = 0.046$; Fig. 3.5f) and shorter burning times ($R^2 = 0.25$, $P = 0.013$; Fig. 3.5k). Curliness and SLA however, were stronger drivers than leaf size for rate of spread (Fig. 3.5g and h) and burning time (Fig. 3.5l and m) (all $P < 0.001$). These effects of SLA on rate of spread and burning time can be mostly ascribed to tissue density (Fig. 3.5j and o) and not to leaf thickness (Fig.

3.5i and n). No relationships were found between morphological leaf traits and fuel consumption (Fig. 3.5p-t).

Unexpectedly, interspecific variation in leaf chemistry also had an effect on the flammability in fuel beds. Species with higher tannin concentrations showed a lower rate of spread ($R^2 = 0.16$, $P = 0.05$; Fig. 3.6a) and a lower fuel consumption ($\rho = 0.44$, $P = 0.030$; Fig. 3.6b). Even when the mostly smouldering species *E. dumosa* and *E. socialis* (see above) were removed from the analysis regarding fuel consumption, the data still showed a negative trend ($R^2 = 0.16$, $P = 0.064$).

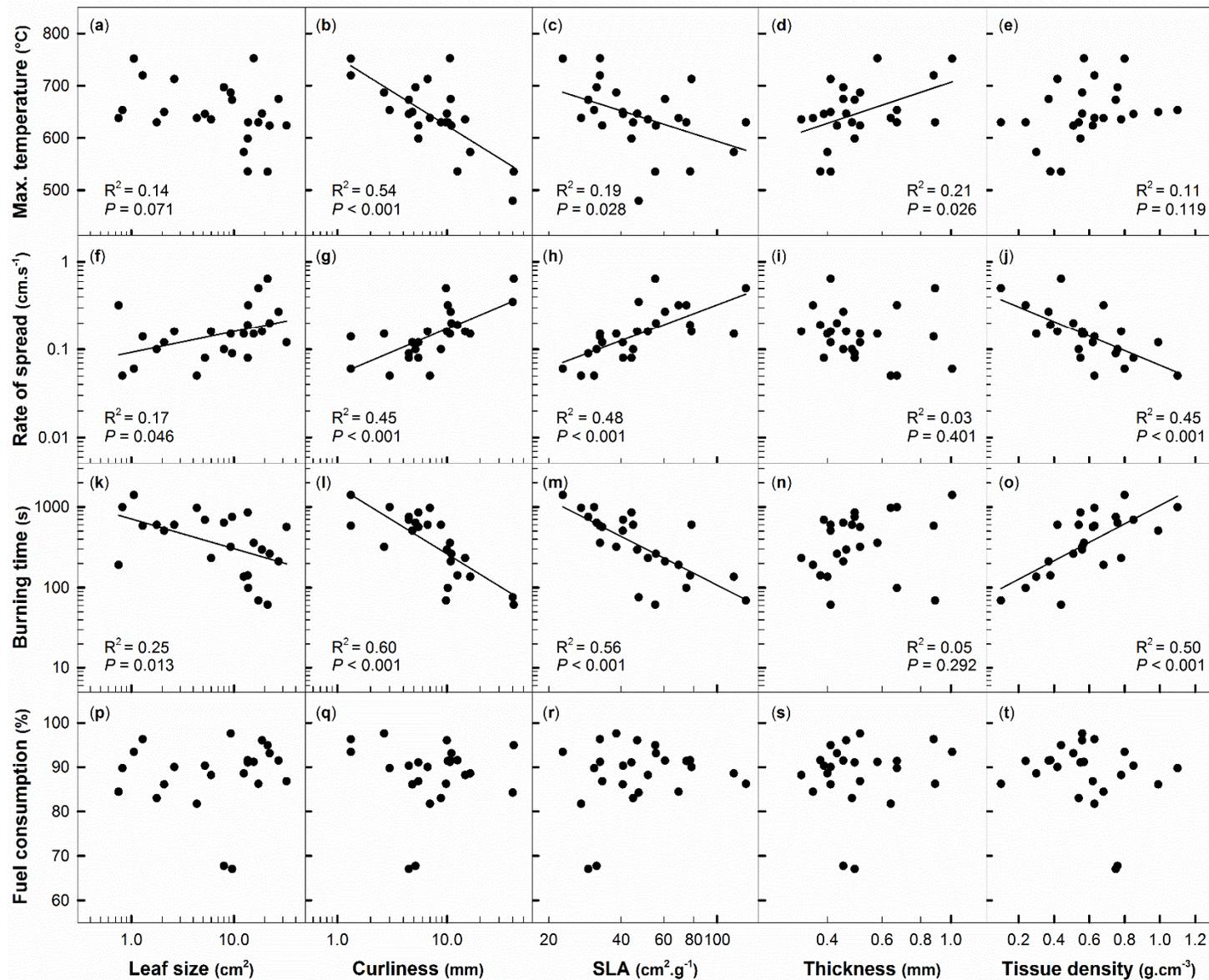


Fig. 3.5 Bivariate relationships of four flammability parameters and five leaf traits. Each dot represents a species-mean. Significant relationships ($P < 0.05$) are represented with a solid line.

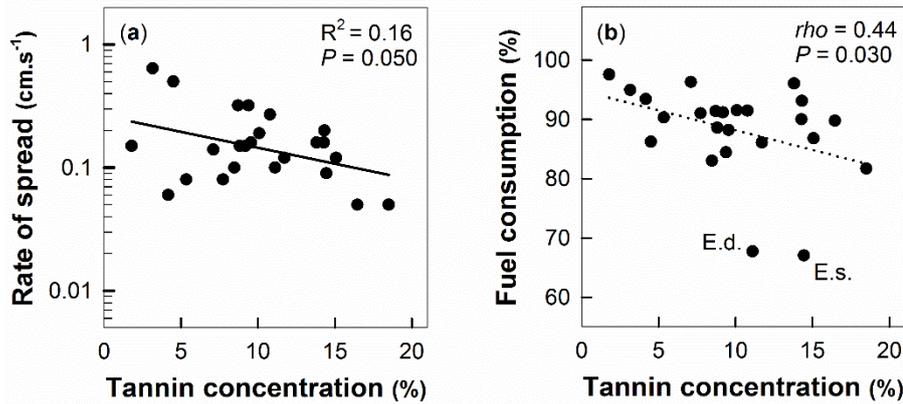


Fig. 3.6 Effects of tannin concentration on (a) rate of spread, and (b) fuel consumption. When *Eucalyptus dumosa* (E.d.) and *Eucalyptus socialis* (E.s.) were excluded from the analysis (panel b), the data still showed a negative trend ($R^2 = 0.16$, $P = 0.064$).

Combined leaf trait effects

The interrelatedness among the morphological leaf traits complicate identifying the contribution of individual leaf traits on fuel bed properties and flammability. Therefore, we ran a redundancy analysis, quantifying what proportion of variance in fuel bed properties and flammability could be explained by all leaf traits combined. The two first RDA axes together explained 56% of the total variance (Fig. 3.7). Bulk density, strongly related to the first axis, was in line with burning time and rate of spread (as seen before in Fig. 3.4), and was mostly driven by SLA (as mainly associated to variation in tissue density), curliness and leaf size (Fig. 3.7). Packing ratio (in line with maximum temperature) was more closely related to the second RDA axis, where leaf thickness and/or surface area per volume were the strongest drivers. In Figure S3.2 an overview can be found of how the morphological leaf traits are related to packing ratio and bulk density in a multivariate space in the absence of flammability parameters.

Does the status in species' flammability hold for individual leaves versus fuel beds?

Interspecific variation in time-to-ignition for individual leaves showed strong correlations with four out of five flammability parameters as measured in fuel beds (Table 3.2). Species with leaves that required more time for ignition burned with higher maximum temperatures when burned in a fuel bed ($R^2 = 0.37$, $P = 0.002$), meaning that it took more energy to ignite them, but once they were burning they produced more heat (e.g. thick, tough leaves).

Similarly, species with longer time-to-ignition released more energy when burned in a fuel bed ($R^2 = 0.67$, $P < 0.001$), showed a lower rate of spread ($R^2 = 0.59$, $P < 0.001$) and had prolonged burning times ($R^2 = 0.66$, $P < 0.001$). Time-to-ignition and fuel consumption were unrelated. The other individual leaf flammability parameters (flame duration, smoulder duration and total burning time) were all unrelated to the fuel bed parameters (all $P > 0.167$, Table 3.2).

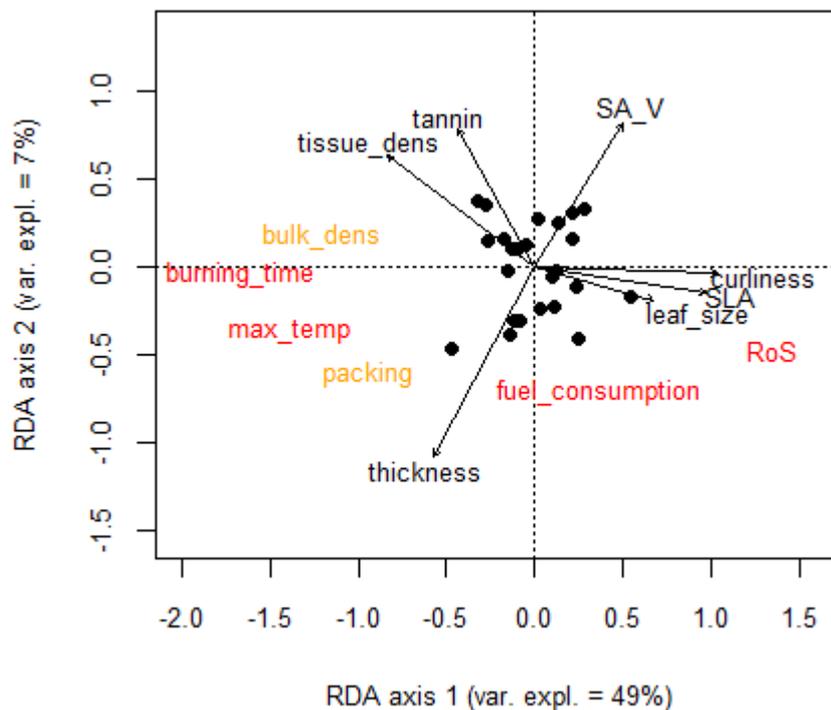


Fig. 3.7 Redundancy analysis of the flammability of 24 Australian species. Each dot represents a species-mean. Flammability results are described by maximum temperature (max_temp), rate of spread (RoS), burning time and fuel consumption (in red). Fuel bed properties (in orange) are packing ratio (packing) and bulk density (bulk_dens). Leaf traits (in black) are tissue density (tissue_dens), tannin concentration, surface area per volume ratio (SA_V), curliness, specific leaf area (SLA), leaf size and thickness. In combination, the first two axes explained 56% of the total variance.

Table 3.2 Individual leaf flammability versus flammability in fuel beds. All correlations are based on linear regressions except the last column (fuel consumption) where non-parametric Spearman's rho was used. Individual leaf time-to-ignition showed significant relationships with four out of five fuel bed flammability parameters (in bold).

Individual leaves	Fuel beds				
	Maximum temp. (°C)	(log) Total heat released (°C*min)	(log) Rate of spread (cm.s ⁻¹)	(log) Burning time (s)	Fuel consumption (%)
(log) Time-to-ignition (s)	R² = 0.37(+) P = 0.002	R² = 0.67(+) P < 0.001	R² = 0.59(-) P < 0.001	R² = 0.66(+) P < 0.001	rho = 0.11 P = 0.607
(log) Flame duration (s)	R ² = 0.04 P = 0.364	R ² = 0.05 P = 0.279	R ² = 0.02 P = 0.573	R ² = 0.02 P = 0.515	rho = 0.09 P = 0.680
(log) Smoulder duration (s)	R ² = 0.00 P = 0.999	R ² = 0.08 P = 0.187	R ² = 0.09 P = 0.167	R ² = 0.04 P = 0.326	rho = 0.07 P = 0.762
(log) Total burning time (s)	R ² = 0.00 P = 0.883	R ² = 0.08 P = 0.192	R ² = 0.07 P = 0.204	R ² = 0.04 P = 0.344	rho = 0.09 P = 0.686

Discussion

Vegetation characteristics can have large effects on wildfire behaviour (Schwilk 2015) and a crucial step in predicting surface fire behaviour is the upscaling from individual fuel particles (e.g. leaves) to fuel beds (Varner *et al.* 2015). However, previous studies have focused on either a) the flammability of individual plant particles or b) fire behaviour in fuel beds. To our knowledge, this is the first time that data on individual leaf flammability was coupled with data of fire behaviour in fuel beds.

Previous fire modelling work has been based on artificial materials (e.g. wood wool and sticks, Rothermel 1972) or has focussed on vegetation types as a whole (e.g. grasslands, shrublands, dry or wet eucalypt forests, pine plantations; Cruz *et al.* 2015). Although these latter models are “fuel type specific”, by lumping the species characteristics together they fail to acknowledge species-specific differences in flammability. It is true that in real-world scenarios fuel beds will be comprised of mixed litter from multiple species. Indeed, we strongly encourage flammability studies on fuel bed mixtures as in van Altena *et al.* (2012) and de Magalhães & Schwilk (2012). The study presented here, however, was particularly focused on the upscaling from individual leaf properties to fuel bed flammability. Therefore we chose to limit ourselves to monospecific fuel beds only. We investigated the flammability of a wide range of species, and placed our work within an over-arching conceptual framework that helps integrating the results.

Putting the conceptual framework to the test (Figure 3.1)

Expected and observed

Variation in leaf packing ratio and bulk density of fuel beds from 25 mostly woody, evergreen Australian species were strongly related to variation in their flammability; this agrees with the findings of many previous studies (e.g., Rothermel 1972; Plucinski & Anderson 2008; de Magalhães & Schwilk 2012). When there was more fuel to be consumed per sample volume (i.e. higher bulk density), this led to higher maximum temperatures, slower rates of spread, longer burning times, and higher heat release.

Higher packing ratios were related to higher bulk densities (in fuel beds with a fixed volume), but this was not a one-to-one relationship. Moreover, bulk density showed much stronger relationships with the flammability parameters than did packing ratio, which

indicates a strong role for intrinsic leaf properties and afterlife effects of dead plant material (Schwilk 2015).

We consider the values for bulk density in our study (0.007 - 0.107 g.cm⁻³) a fair representation of the real world. Undisturbed litter in south eastern France had a mean bulk density of 0.043 g.cm⁻³ (Ganteaume *et al.* 2011) and values ranging from 0.010 to 0.152 g.cm⁻³ have been reported elsewhere (Plucinski & Anderson 2008; Ganteaume *et al.* 2009; de Magalhães & Schwilk 2012). Bulk density was strongly negatively related to leaf curliness and SLA. This agrees with findings in previous studies where relationships were found between specific leaf area and maximum fire temperature of subarctic plant materials (Van Altena *et al.* 2012), and rate of spread, time-to-ignition, sustainability and flame height in a temperate mixed conifer forest (Supporting information from de Magalhães & Schwilk 2012). The effects of SLA on bulk density were mainly related to tissue density and this had impacts on the fuel bed flammability. For dried leaves, tissue density is related to the number of plant cells and cell wall thickness. When there is more cell wall material per leaf volume, this leads to higher tissue densities (Roderick *et al.* 1999). This again leads to higher energy contents (more available fuel) and therefore higher temperatures, longer burning times and slower rates of spread under controlled conditions.

Several authors (Rothermel 1972; Papió & Trabaud 1990; Gill & Moore 1996) indicated that the ratio of surface area per volume (SA:V) is of major significance for particle flammability. Indeed we found SA:V to be the most important driver of packing ratio, but, as discussed before, interspecific variation in bulk density had much stronger effects on the fuel bed flammability than the variation in packing ratio alone and this is principally driven by variation in tissue density. Since tissue density is a component of SLA (Wilson, Thompson & Hodgson 1999), we consider SLA as a better alternative for SA:V when estimating leaf flammability.

Expected but not observed

Based on the reasoning that fuel beds with higher packing ratios have less physical space for airflow and oxygen supply (Scarff & Westoby 2006; Santoni *et al.* 2014), we expected that packing ratio would control the reaction velocity and therewith also the consumability (completeness of fuel consumption) (Rothermel 1972). However, except for two *Eucalyptus* species (*E. dumosa* and *E. socialis*) there was no clear indication of severe oxygen limitation on the measured flammability parameters. No relationships were found

between the morphological leaf traits or fuel bed properties with fuel consumption. In general most of the fuel was consumed eventually and only a small percentage of *unburnt* material was left behind (max. 12% of initial weight, *E. socialis*, data not shown). This suggests that the fires were generally fairly complete in their combustion and not seriously limited by oxygen supply. Instead, the fuel load per volume, as described by bulk density, seemed to be the driving force of differences in flammability across our samples (Whelan 1995; NSW Rural Fire Service 2012).

In contrast with the literature (Scarff & Westoby 2006; Cornwell *et al.* 2015) leaf size (as one sided surface area) was not related to packing ratio in our dataset. We noticed that large flat leaves (like those from *Eucalyptus haemastoma*) were densely packed despite their leaf length or leaf size. Instead, leaf curliness and thickness were clearly more important for the packing ratio of our species than leaf size *per se* (as in Engber & Varner 2012). Small but curly leaves can still have more aerated fuel beds than large flat leaves and therefore we suggest that both leaf size and curliness should be considered when making estimations for packing ratios and bulk density.

Unexpected but observed

We hypothesised that fuel beds with a lower packing ratio (and therefore a lower bulk density) would burn at higher temperatures because they would not be limited in their oxygen supply. However, we found the opposite trend: at higher packing ratios and bulk densities, higher maximum temperatures were reached. This suggests again (a) that there was no severe oxygen limitation in our fuel beds, and (b) the more fuel there was (mass per fuel bed volume), the more organic material there was for heat to be released.

We were surprised that the fire-retardant properties of tannins, as found in previous research (Celzard *et al.* 2011; Grootemaat *et al.* 2015), showed up in our results. Apparently the flammability of leaves in a fuel bed is not just about packing and bulk density; our results indicate that the chemistry of leaves can still have effects on the flammability when scaling up from individual leaves to fuel beds. Therefore, in combination with the impacts of morphological traits, this shows that it is important to examine the vegetative composition, in terms of the functional leaf traits of its species, when dealing with wildfires (Schwilk 2015).

Individual leaf flammability versus flammability in fuel beds

Although one might expect that the total burning time of individual leaves would relate positively to the burning time in fuel beds, we did not find that in our results. This confirms our expectation that the physical arrangement of leaves within the fuel bed largely overruled the effects of intrinsic leaf chemistry and morphology on the flammability in fuel beds (Scarff & Westoby 2006; but see Ormeño *et al.* 2009 for terpene effects in litter beds). However, individual leaf time-to-ignition was correlated with several parameters of flammability in fuel beds, including rate of fire spread. The latter can be seen as a chain of ignition-steps; the easier individual leaves ignite, the quicker the fire will spread from one leaf to another. This is most likely a consequence of the thickness and density of the leaves (both components of SLA). In our previous study, interspecific variation in SLA was found to be the main driver of time-to-ignition ($R^2 = 0.70$, $P < 0.001$; Grootemaat *et al.* 2015). These effects of SLA continue to affect flammability when scaling up from individual leaves to fuel beds, both directly via tissue density, and indirectly via leaf curliness and packing ratio (Fig. 3.1, Fig. 3.7). This is further evidence that tissue-level variations among species can have important implications at larger scales. Our finding that the species' flammability ranking held roughly when scaling up from ignitibility of individual leaves to flammability of fuel beds provides important information for the estimation of ignition likelihood and rate of spread in wildfires.

Conclusions

The spatial arrangement of fuel and fuel specific particle properties both have strong influences on the spread and severity of a fire, especially under mild weather conditions (Byram 1959; Turner & Romme 1994). Here we have demonstrated that a better understanding of fire dynamics at a fine spatial scale (e.g. individual leaf ignitibility) provides useful information for fire behaviour modellers working at coarser spatial scales, by means of upscaling. Leaf traits that affect the flammability of individual leaves, continue to do so even when packed in fuel beds. Tissue density has received little attention in models so far (Rothermel 1972; Scott & Burgan 2005), but based on our results, we suggest that dry leaf curliness and tissue density (by itself or as part of SLA) could improve the predictions of surface fire behaviour.

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Supporting information

Table S3.1 Species list

Genus	Species ^a	Family	Rainfall ^b	Soil P ^c	No. of replicates
<i>Acacia</i>	<i>doratoxylon</i>	Fabaceae	low	high	5
<i>Acacia</i>	<i>haviandiorum</i>	Fabaceae	low	low	2
<i>Allocasuarina</i>	sp.	Casuarinaceae	high	high	5
<i>Astrotricha</i>	<i>floccosa</i>	Araliaceae	high	high	5
<i>Brachychiton</i>	<i>populneus</i>	Malvaceae	low	low	6
<i>Corymbia</i>	<i>gummifera</i>	Myrtaceae	high	low	6
<i>Dodonaea</i>	<i>viscosa spatulata</i>	Sapindaceae	low	high	1
<i>Eremophila</i>	<i>longifolia</i>	Myoporaceae	low	high	5
<i>Eucalyptus</i>	<i>dumosa</i>	Myrtaceae	low	low	3
<i>Eucalyptus</i>	<i>haemastoma</i>	Myrtaceae	high	low	6
<i>Eucalyptus</i>	<i>intertexta</i>	Myrtaceae	low	high	6
<i>Eucalyptus</i>	<i>socialis</i>	Myrtaceae	low	low	4
<i>Geijera</i>	<i>parviflora</i>	Rutaceae	low	high	6
<i>Hakea</i>	<i>dactyloides</i>	Proteaceae	high	low	4
<i>Hakea</i>	<i>tephrosperma</i>	Proteaceae	low	high	2
<i>Hakea</i>	<i>teretifolia</i>	Proteaceae	high	low	1
<i>Lambertia</i>	<i>formosa</i>	Proteaceae	high	low	1
<i>Lasiopetalum</i>	<i>ferrugineum</i>	Malvaceae	high	high	6
<i>Lomatia</i>	<i>silaiifolia</i>	Proteaceae	high	high	6
<i>Macrozamia</i>	<i>communis</i>	Zamiaceae	high	high	5
<i>Persoonia</i>	<i>levis</i>	Proteaceae	high	low	3
<i>Santalum</i>	<i>acuminatum</i>	Santalaceae	low	low	3
<i>Syncarpia</i>	<i>glomulifera</i>	Myrtaceae	high	high	4
<i>Synoum</i>	<i>glandulosum</i>	Meliaceae	high	high	6
<i>Triodia</i>	<i>scariosa</i>	Poaceae	low	low	5

^a Species names following PlantNET (online reference from the National Herbarium of New South Wales)

^b Low rainfall sites receive approximately 383 mm rainfall per year, high rainfall sites 1233 mm (Australian Bureau of Meteorology)

^c Low soil phosphorus levels are below 132 $\mu\text{g}\cdot\text{g}^{-1}$; high soil phosphorus levels are above 250 $\mu\text{g}\cdot\text{g}^{-1}$ (Wright et al. 2001)

Table S3.2 Overview of the trait and fuelbed measurements.

Traits	Description	Units	Range (mean)
Packing ratio	Particle volume per fuel bed volume	(cm ³ cm ⁻³)	0.02 - 0.13 (0.08)
Bulk density	Mass of sample per fuel bed volume	g.cm ⁻³	0.007 - 0.107 (0.05)
Fuel moisture content	Based on oven dry weight	% odw	5.0 - 7.8 (6.2)
Leaf curliness	Maximum perpendicular height from the leaf surface, when positioned on a flat surface	mm	1.3 - 40.7 (10.3)
Leaf thickness	Thickness between border and midrib	mm	0.33 - 1.01 (0.53)
Leaf length	Length between the base and the tip	mm	43 - 128 (91)
Leaf width	Measured as the maximum diameter of an imaginary circle within the leaf	mm	3 - 43 (18)
Leaf size	One sided surface area	cm ²	0.8 - 32.6 (10.9)
Leaf dry mass	Oven dry weight	g	0.01 - 1.03 (0.26)
Leaf SA:V	Two sided leaf surface area per leaf volume	cm ⁻¹	22.8 - 84.1 (44.8)
Specific leaf area	One sided leaf area per dry mass	cm ² .g ⁻¹	22.9 - 131.9 (52.6)
Tissue density	Leaf mass per volume	g.cm ⁻³	0.10 - 1.10 (0.59)
Leaf N	Nitrogen concentration	% mass	0.60 - 2.19 (1.27)
Leaf P	Phosphorus concentration	% mass	0.016 - 0.110 (0.056)
Leaf lignin	Lignin concentration	% mass	8.7 - 37.5 (20.9)
Leaf tannin	Soluble polyphenols	% mass	1.8 - 18.5 (9.9)

Table S3.3 Correlation matrix of the bivariate relationships between the flammability parameters and fuel bed properties. The relationships of fuel consumption are presented in italic because here the non-parametric Spearman's rho was used, rather than a Pearson correlation. Positive relationships are represented with a plus (+), negative relationships with a minus (-).

	(log) Heat released (°C*min)	(log) Rate of spread (cm.s⁻¹)	(log) Burning time (s)	Fuel consumption (%) (Spearman)	Packing ratio (cm³.cm⁻³)	(log) Bulk density (g.cm⁻³)
Maximum temperature (°C)	r = 0.691 (+) <i>P</i> < 0.001	r = 0.431 (-) <i>P</i> = 0.031	r = 0.622 (+) <i>P</i> = 0.001	<i>rho</i> = 0.135 <i>P</i> = 0.521	r = 0.546 (+) <i>P</i> = 0.006	r = 0.685 (+) <i>P</i> < 0.001
(log) Heat released (°C*min)		r = 0.917 (-) <i>P</i> < 0.001	r = 0.989 (+) <i>P</i> < 0.001	<i>rho</i> = 0.142 <i>P</i> = 0.497	r = 0.680 (+) <i>P</i> < 0.001	r = 0.985 (+) <i>P</i> < 0.001
(log) Rate of spread (cm.s⁻¹)			r = 0.926 (-) <i>P</i> < 0.001	<i>rho</i> = 0.218 <i>P</i> = 0.296	r = 0.563 (-) <i>P</i> = 0.004	r = 0.902 (-) <i>P</i> < 0.001
(log) Burning time (s)				<i>rho</i> = 0.175 <i>P</i> = 0.402	r = 0.660 (+) <i>P</i> < 0.001	r = 0.978 (+) <i>P</i> < 0.001
Fuel consumption (%)					<i>rho</i> = 0.264 <i>P</i> = 0.212	<i>rho</i> = 0.208 <i>P</i> = 0.317
Packing ratio (cm³.cm⁻³)						r = 0.695 (+) <i>P</i> < 0.001

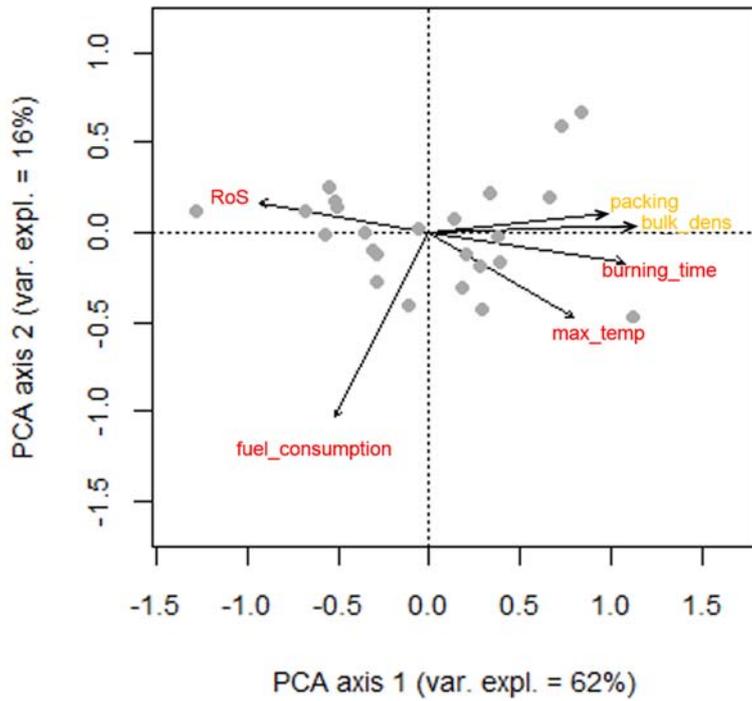


Fig. S3.1 Principle component analysis of the four flammability parameters (in red) and the two fuel bed properties (in orange) together. The two axes together explain 78% of the total variance. The grey dots represent species-mean scores.

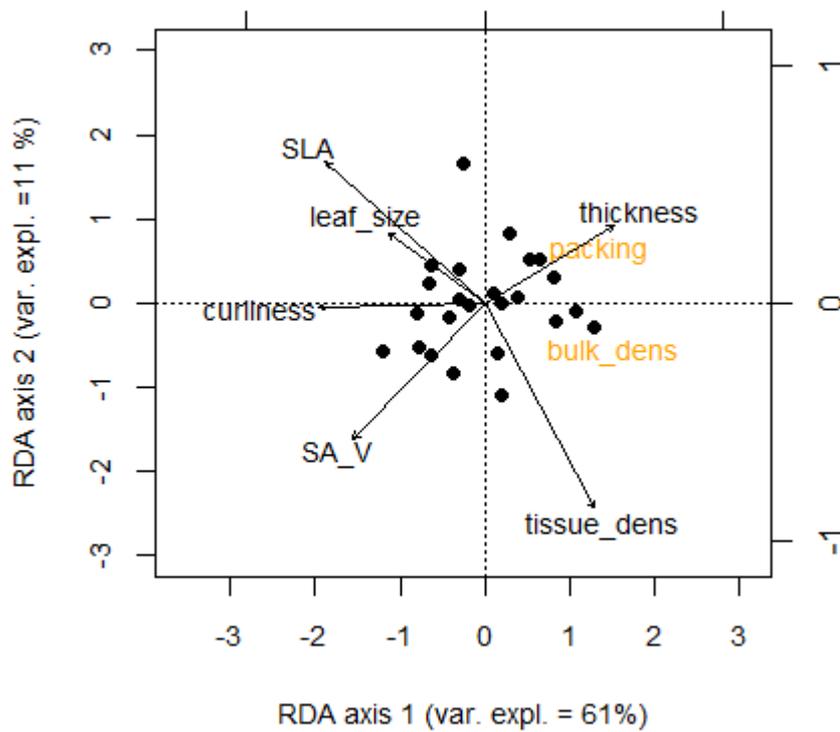


Fig. S3.2 RDA plot of the two fuel bed properties (packing ratio and bulk density, in orange) as constrained by the morphological leaf traits. The two axes together explain 72% of the total variance. The black dots represent species-mean scores.

4. Bark fates explored: decomposition and flammability of 10 woody species from the Sydney region (south-eastern Australia)

Saskia Grootemaat^a; Ian J. Wright^a; Peter M. Van Bodegom^b; Johannes H. C. Cornelissen^c; Veronica Shaw^a

^a Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

^b Institute of Environmental Sciences, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands

^c System Ecology, Faculty of Earth and Life Sciences, VU University, 1081 HV Amsterdam, The Netherlands

Summary

1. Bark shedding is a remarkable feature of the Australian forests. In spite of the enormous quantitative contribution of bark to the aboveground litter, little is still known about the fates of dead bark. In this study, we investigated the relative decomposability and flammability of bark from 10 woody species of the Sydney region. Also, we determined whether (combinations of) morphological and chemical traits could explain the interspecific variation in bark decomposability and flammability to the same extents as it does for leaves.
2. To explore the decomposability of bark, a common garden decomposition experiment was run for two years. In parallel, duplicates of the samples were burned in a muffle furnace to test for ignitability (time-to-ignition), fire sustainability (flame and smoulder duration) and combustibility (total mass burnt per combustion duration).
3. Considerable variation in bark decomposability and flammability was found, both within and across species. Overall, bark decomposed more slowly than leaves, especially in the first year. Bark took longer to ignite than leaves, and burned more slowly.
4. The variation in bark (and leaf) decomposition was mainly driven by lignin concentration. Each flammability parameter was driven by different traits; e.g. bark time-to-ignition was negatively correlated with nitrogen concentration, while flame and smoulder duration were highly defined by sample mass. Interspecific variation in mass-standardised flame duration, however, correlated positively with copper and negatively with phosphorus concentrations. Consequently, bark decomposability and flammability parameters showed no correlation across the 10 species as they are underpinned by different traits.
5. Despite its contribution to surface litter and complementary to all the work that has been done on leaves, this is the first time that decomposability and flammability of bark were quantified and compared across multiple species. By taking species-specific bark traits into consideration better estimations of fuel loads, fire risks and carbon loss dynamics can be made.

Keywords: decay, litter components, surface fire, traits, woody debris

Introduction

Bark is unequivocally a special feature in the Australian forests. With a great variety of types (e.g. smooth bark, stringy-bark, ironbark; Fig. 4.1) it is often used in floras as the first key for tree identification of the *Eucalyptus* genus (Millett 1969; Brooker & Kleinig 1990; Robinson 2003). Many species of *Eucalyptus* and other genera in the Myrtaceae family shed their bark annually, which leads to spectacular accumulations of bark on the forest floor and ribbons hanging down from the trunk and branches. This gives the forests of south-eastern Australia, which are mostly dominated by *Eucalyptus*, their unique appearance.

This bark shedding, especially of the “smooth bark species”, happens mainly in the Australian summer, often around December (Lamb 1985; Crockford & 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 & Richardson 1998). Potential adaptive value of the bark shedding is thought to include promoting photosynthesis by the living tissues of the trunk (Aschan & Pfanz 2003; Cernusak & Hutley 2011), and eliminating pathogens and sap-feeding herbivores (Paine *et al.* 2010). It has also been proposed to be a simple physical consequence of lateral stem increment, especially of thick-walled smooth bark (Jacobs 1955). Some authors speculate that the loose hanging bark could promote the fire spread from the surface layer up to the canopy by acting as “ladder fuels” (Gould, McCaw & Cheney 2011), thereby potentially benefitting pyrophytic tree species to promote their own competitive position (Bond & Midgley 1995).

While we know relatively little about the *causes* of bark-shedding, we know even less about the ecological *effects*. The cast 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* forest (McColl 1966; Woods & Raison 1983; Lamb 1985), the other chief components being leaves, twigs and fruits. This 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 & 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 been dropped on the forest floor several processes can

potentially affect the bark-litter, namely: (a) leaching of water-soluble nutrients, (b) breakdown of the woody material by UV light or fragmentation, (c) decomposition by (micro-) organisms, or (d) combustion in a wildland fire (Cornwell *et al.* 2009). In this study we mainly focused on the latter two processes.

For *leaves*, another important component of the litter layer, decomposition and flammability are reasonably well understood. Apart from environmental conditions (air temperature, litter moisture content, UV radiation), leaf decomposition is strongly driven by the 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 & Raison 1983; Berg & McClaugherty 2003), while recalcitrant structural compounds (like lignin) slow the decomposition process down, especially in the later stages (Melillo, Aber & Muratore 1982; Berg & McClaugherty 2003). Under controlled conditions, leaf ignitibility (a measurement for the ease of ignition) is strongly driven by specific leaf area (Murray *et al.* 2013; Grootemaat *et al.* 2015), while mass-standardised flame and smoulder durations are mainly determined by leaf chemistry (Grootemaat *et al.* 2015).

This growing understanding of leaf decomposition and flammability, and the underlying role of traits therein, contrasts with the lack of understanding of the drivers (traits) for bark decomposition and flammability. Comparative studies on (dead) bark fates and rates from multiple species are rare. The only study that we are aware of which explicitly included bark decomposition (Johnson *et al.* 2014) suggested 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 & Ashton 1968; Frejaville, Curt & Carcaillet 2013). However, these studies only looked at a limited set of species and bark-traits.

The aim of this study was to lay a foundation for predicting surface litter (fuel) accumulation in Australian forests dominated by species of the Myrtaceae family. We therefore investigated the relative decomposability and flammability of a range of tree species, while paying special attention to bark - because bark is such an important and understudied component of the litter layer in these forests. We endeavoured to unravel 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, while we expected substantial interspecific variation in bark decomposability based on their great visual differences in morphology, we also expected that bark would generally decompose more slowly than leaves, because it contains more structural compounds like 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) we expected to find a difference in bark flammability between “stringy-barks” and “smooth barks”; namely, stringy-barks would ignite more easily and tend to smoulder for longer when compared to smooth barks. When comparing mass-standardised combustion of bark and leaves, we expected 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 hypothesised that decomposability and flammability would not be 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).

In order to address these questions and expectations, we quantified the decomposability of bark chunks (~13 cm²) and leaf material for 10 woody species of the Sydney region, Australia, in a 2-year common garden decomposition experiment. In parallel we quantified the flammability of duplicate samples burned in a muffle furnace.

Material and methods

Site description and species selection

Ten tree species with characteristic bark features were selected in Ku-ring-gai Chase National Park (two study sites: “West Head” and “Bobbin Head”) and the Blackwall Mountain Reserve (one study site), all located north of Sydney (New South Wales,

Australia). The soils in Ku-ring-gai Chase National Park are predominantly sandy (derived from Hawkesbury Sandstone) and very low in nutrients, particularly phosphorus, with values ranging between 30 and 80 mg.kg⁻¹ P (Leishman & Thomson 2005). Blackwall Mountain Reserve is located on the northern site of Broken Bay (33°30'26"S, 151°20'0"E). The reserve is located on the interface between Hawkesbury and Narrabeen Sandstones (i.e. infertile sandy soil; Gosford City Council, 1996). Because of the proximity of the three sites, the climate is very similar. Long-term climate data (last ≥ 50 years) indicate a mean annual temperature of 17°C and a mean annual rainfall of 1332 mm (Australian Bureau of Meteorology⁵).

Tree species were selected based on their bark characteristics (Table 4.1), abundance and their contribution of bark to the litter layer. All species were part of the Myrtaceae family, and we deliberately chose species with visually different bark types, including “smooth barks” and “stringy-barks” (Fig. 4.1). Although the stringy-bark species (*Eucalyptus eugenioides* and *Syncarpia glomulifera*) do not shed their bark as vigorously as the other species, they were included for comparison and because of their importance in fire spread (further discussed below).

Material collection and trait measurements

Bark

The bark of nine individual trees per species was collected in December 2012 and stored in paper bags under ambient conditions. 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 size: after air-drying the bark was split into pieces with a one sided surface area of approximately 13 cm². We decided to use this size because it 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).

⁵ Average climate data based on all available data from the following weather stations: Narara Research station, Duffys Forest and the Riverview Observatory.

Table 4.1 Species list and additional bark information for the 10 species used in this study.

Species	Location	Bark type ^c	Field observations
<i>Angophora costata</i>	West Head ^{ab}	Smooth bark	Bark comes off in large patches, leaving the entire tree (trunk + branches) orange/salmon coloured.
<i>Angophora hispida</i>	West Head ^a	Full bark	Shrub-tree up to 4m high. Bark is curly, more fibrous than smooth bark. Comes off from the younger branches.
<i>Corymbia gummifera</i>	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.
<i>Corymbia maculata</i>	Blackwall Mountain	Smooth bark	Bark comes off in patches similar to <i>Angophora costata</i> . The old bark is grey/purple, while the new bark (underneath the old layer) is green.
<i>Eucalyptus eugenioides</i>	Bobbin Head	Stringy bark	Typical stringy-bark with long fibers. Bark comes occasionally off in strips but we had to pull it off.
<i>Eucalyptus haemastoma</i>	West Head ^a	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.
<i>Eucalyptus pilularis</i>	Blackwall Mountain	Part bark	Bark comes off in long strips. The bark is a considerable component of the litter layer. Trunk is white once the bark is shed except from the trunk-base which remains grey and fibrous.
<i>Eucalyptus piperita</i>	Bobbin Head	Part bark	Grey fibrous trunk, upper limbs are white/yellow. Bark comes off from the upper limbs in long ribbons, partly curled.
<i>Eucalyptus punctata</i>	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.
<i>Syncarpia glomulifera</i>	West Head ^a	Stringy bark	Typical stringy-bark with long fibers. Bark comes occasionally off in strips but we had to pull it off.

^a Also abundant at Bobbin Head

^b Also abundant at Blackwall Mountain

^c Bark types following Robinson 2003; the “full bark” and “part bark” division says something about the distribution of the bark on the trunk, not about the material properties as such.

Leaves

To investigate if the decomposability and flammability of bark are related to the decomposability and flammability of leaves, we ran our experiments in parallel with leaves of the same 10 tree species. Freshly senesced leaves 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 replicates of bark, which were true replicates of nine individual trees, the replicates for leaves came out of a bulk-sample from ~10-40 individual trees per species. The samples were stored in paper bags under ambient conditions until the time of the experiments.

Trait measurements

Subsamples of bark and leaves were kept separate for trait measurements (Table S4.1). Length and width were measured with a ruler. Thickness (mean of 3 measurements for bark) was measured with a thickness gauge and dry mass was determined by weighing the samples 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, Nebraska, USA). The volume of the bark samples was estimated by using the gravimetric (water replacement) method. The volume of the leaves, however, was calculated as leaf area multiplied by average leaf thickness. Tissue density was calculated as mass divided by volume. Tensile strength for the bark samples was measured by means of a 3 mm punch-test, using an Instron machine, model 5542 (Instron, Norwood, Massachusetts, USA). Fuel moisture contents were measured on subsamples just before the experimental burns were carried out. These samples were measured at their air-dry (equilibrium) weight and remeasured after 24h of oven drying at 105°C. The fuel moisture content was then expressed as a percentage of the oven dried weight:

$$FMC = \frac{(\text{actual weight} - \text{dry weight})}{\text{dry weight}} * 100\%$$

Eqn. 4.1

Energy content (MJ.kg⁻¹) of ground bark and leaf material was measured with a Parr 6400 calorimeter (Parr Instrument Company, Moline, Illinois, USA). Detailed extraction methods for analysing bark and leaf chemistry can be found in the supporting information (Text S4.1). In short, carbon and nitrogen were measured with a CHN combustion analyser (Rayment & Lyons 2011). Calcium, copper, potassium, magnesium and phosphorus concentrations were quantified by acid digestion (Martinie & Schilt 1976). Tannins were quantified following Dalzell & Kerven (1998), and lignin, cellulose and ash concentrations were measured with an ADF extraction method (Rowland & Roberts 1994).



Fig. 4.1 Examples of the variability of bark morphology among different tree species. (a) *Eucalyptus punctata*, note the vast accumulation of bark-slabs near the trunk; (b) shedding of the bark from a young *Angophora costata* stem; (c) *Syncarpia glomulifera*, a typical stringy-bark.

Decomposition experiment

Litterbags (20 x 15 cm) made of fiberglass fly screen mesh (1.5-2 mm) were filled with approximately 3 pieces of bark of $\sim 13 \text{ cm}^2$ each, or 1.0 gram of intact senesced leaves. These litterbags were placed in a common litter bed at Macquarie University Fauna Park, North Ryde (33°46'9"S, 151°6'46"E) in January 2013. This woodland consists mainly of Turpentine (*Syncarpia glomulifera*) forest, one of the characteristic vegetation types 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), which is very similar to the climate of the collection sites. During the two years of our experiment the weather conditions at our experimental site were slightly warmer (18.4°C in 2013; 18.5°C in 2014) compared to the long-term average for this region (17.3°C). The year 2013 was slightly wetter (1425 mm) while 2014 was somewhat drier (1180 mm). An overview of the seasonal pattern of rainfall and temperature during our study period can be found in Fig. 4.2. Since the experiment was carried out in a common garden experiment, we consider the weather conditions to be the same for all our samples.

Three batches of samples (A, B, C) with corresponding retrieval dates (Table S4.2) were distributed at random on the cleared forest floor and staked down with 10 cm long nails. Large trees surrounded our plots and therefore the samples were shaded/semi-shaded for

most of the time. Also, we deliberately left the samples uncovered, so natural processes like revegetation and litter fall could continue as per normal. We started the decomposition experiment with 270 bark litter bags (10 species x 9 replicates x 3 retrieval times) and 180 leaf litter bags (10 species x 6 replicates x 3 retrieval times). After 3 months one replicate of each species (both for bark and leaf samples) was harvested to get an early impression of the decomposition rate. We decided to harvest the first batch of leaves (A) after 3.5 months. Since the decomposition of bark was significantly slower, we left the bark (batch A) for a later harvest (Table S4.2). The two other harvest moments were after 12 and 24 months (bark and leaves). After harvesting the bags, samples were dried at 60°C for ≥ 10 days until equilibrium mass was achieved. The remaining mass was weighed after any dirt had been brushed from the samples.

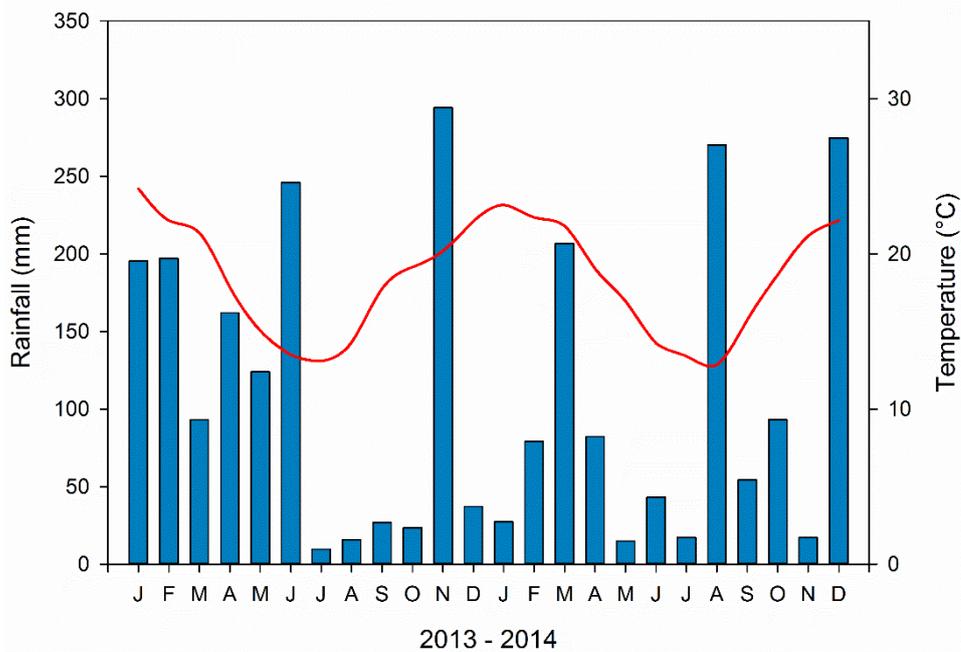


Fig. 4.2 Rainfall and temperature for the years 2013 and 2014. Rainfall from Turrumurra weather station, 3.8 km from Macquarie University campus; temperature from Riverview Observatory, 7.0 km from Macquarie University campus (www.bom.gov.au).

Experimental burns

Leaves were burned as described by Grootemaat *et al.* 2015. In short: Samples were horizontally inserted into a muffle furnace (Charles Moloney, Sydney) with a set internal temperature of 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 approximately 8 mm above the centre of each sample to provide a source of ignition (Gill & Moore 1996). This spark gun was inserted simultaneously with the leaf and removed as soon as the leaf ignited. During the entire burning process the furnace door was kept open to provide abundant oxygen and to permit the filming of the processes within the furnace. The furnace was used in a well-ventilated room without strong drafts. Three thermocouples (type K, chromel-alumel) were adjusted to a steel cradle perpendicular to the opening of the furnace. The thermocouples were connected to a computer via a CR10WP-data logger (Campbell Scientific, Logan, Utah, USA). When the average temperature value of the 3 thermocouples was c. 400°C (+/- 10°C) leaf samples were inserted.

A similar set-up was used for the experimental burns on bark, with a few adjustments: the bark samples were not held by tongs for the entire duration of the combustion, but inserted by tongs and left on a stainless steel grill (2.4 mm thick, spaced 1 cm apart). The remaining ash was collected in a stainless steel dish (99 x 99 x 18 mm) which was custom made to fit underneath the grill. However, the mass of the remaining ash was undetectable on a scale with 3 digits and therefore we consider the burns as complete combustions.

The combustion process was filmed and subsequently analysed by using the digital video editor “VideoPad” (NCH Software, Canberra, Australia). This set-up 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

The decomposition constant k is often used to describe the rate of decomposition (Olson 1963). In this study, however, we chose to report the percentage mass lost rather than a k -value, because (a) there was no exponential trend in our data, which forms the basis of these

decomposition models; and (b) the decomposition constant k averages the decomposition rate over the different stages (months) and is very dependent on variations in temperature and moisture content (Woods & Raison 1983). Several other decomposition models have been proposed for leaves and coarse woody debris (Harmon *et al.* 2004; Adair *et al.* 2008; Cornwell & Weedon 2014) but they cannot always account for the complexity of the litter, nor for the complex heterotrophic interactions (Facelli & Pickett 1991). Therefore we considered it more insightful to simply report the percentage mass lost at a given (standard) point in time.

Variance component analyses were run to differentiate the total variance in decomposability and flammability into within-species and among-species components. Since the variation in bark FD and SD were 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. This gives us insight into tissue-level properties, namely, flame and smoulder duration per gram material.

Subsequently, measurements were averaged per species and the flammability parameters and trait measurements were log transformed to satisfy the assumptions of normality and homogeneity of variance. Linear regressions were used to compare (a) decomposability (as % mass lost) of leaves and bark, (b) flammability (as ignitibility, sustainability and combustibility) of leaves and bark, and (c) decomposability and flammability for a given material. Because bark SD/mass was not normally distributed, the non-parametric Spearman’s ρ was used to test for correlations with bark SD/mass. One-way ANOVAs were used to compare the ignitibility and sustainability of stringy-barks with the other (smooth-like) bark types.

Bivariate regressions were used to quantify which traits affected the decomposition and flammability of bark and leaves, and this analysis was followed by stepwise multiple linear regressions to quantify how the measured traits together could explain the variation in bark and leaf decomposability and flammability. ANCOVAs were used to test if the slopes from the bivariate regressions differed for the two material types.

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 to 22-60% for the leaves (Fig. 4.3). In the second year the rate of bark decomposition nearly approached that of leaves, which (depending on species) led to 27-72% mass loss for bark and 56-92% mass loss for leaves after the full 24 months (Fig. 4.3). 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 chapter. Considered after 12 months, there was a marginally significant tendency for leaf decomposition to be correlated with bark decomposition ($R^2 = 0.34$, $P = 0.075$; Fig. 4.4). However, after 24 months there was no relationship ($P = 0.411$).

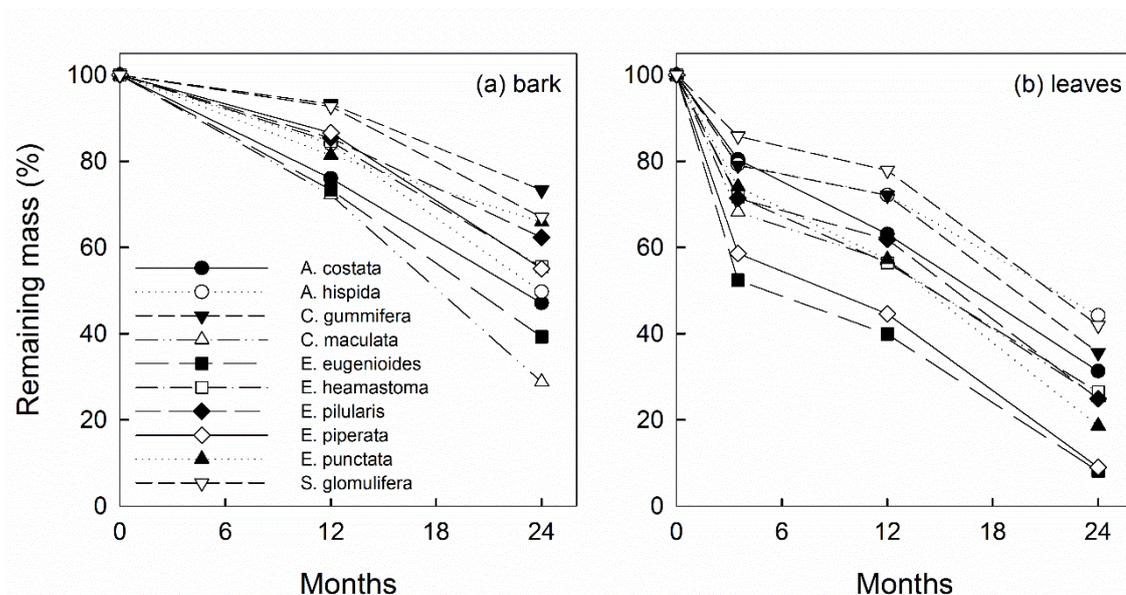


Fig. 4.3 Decomposition of (a) bark and (b) leaves over a period of 24 months, starting in January 2013 (summer in the southern hemisphere). Decomposition is presented as the percentage remaining mass of the initial litter samples (species-means).

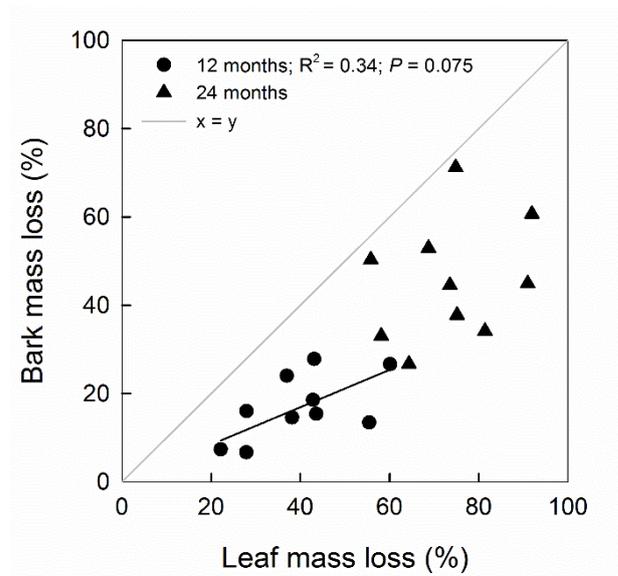


Fig. 4.4 Decomposability of leaves (% mass loss) versus decomposability of bark (% mass loss) from 10 woody species from the Sydney region. Each dot represents a species-mean.

Bark versus leaf flammability⁶

There was considerable variation in bark and leaf flammability, both within and among species (Fig. 4.5). Overall, bark material needed more time for ignition than did leaves (species means: 2.6-14.0 s versus 1.9-4.2 s, respectively; Fig. 4.5a). Bark flamed and also smouldered for longer than leaves, even after standardisation by mass (Fig. 4.5b, c). In line with this, bark was less combustible (4.9-7.5 mg.s⁻¹) than leaves (9.8-18.3 mg.s⁻¹) (Fig. 4.5d). Bark from the stringy-bark species (*E. eugenioides* and *S. glomulifera*) showed 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 $P \geq 0.392$). *Eucalyptus punctata*, which is characterised by very thick smooth bark, had the longest time-to-ignition and highest SD/mass. Bark and leaf flammability were unrelated, considering all four parameters of flammability (all $P \geq 0.322$). For example, species with fast ignitable leaves did not necessarily have fast ignitable bark.

⁶ The most widely recognised trait influencing fuel flammability is moisture content. Because all leaf and bark samples were air-dried (under ambient conditions) before the experimental burns, they varied little in moisture content (species-means ranging from 11.8-14.4% for bark, and 7.3-10.0% for leaves). Apart from a significant correlation with bark TTI ($R^2 = 0.40$, Table S4.3), interspecific variation in fuel moisture content had no strong effects on the measured flammability parameters (all $P \geq 0.05$; Table S4.3; results for leaves not shown). Because all samples were stored under similar conditions, we consider it fair to make the comparison between bark and leaf flammability.

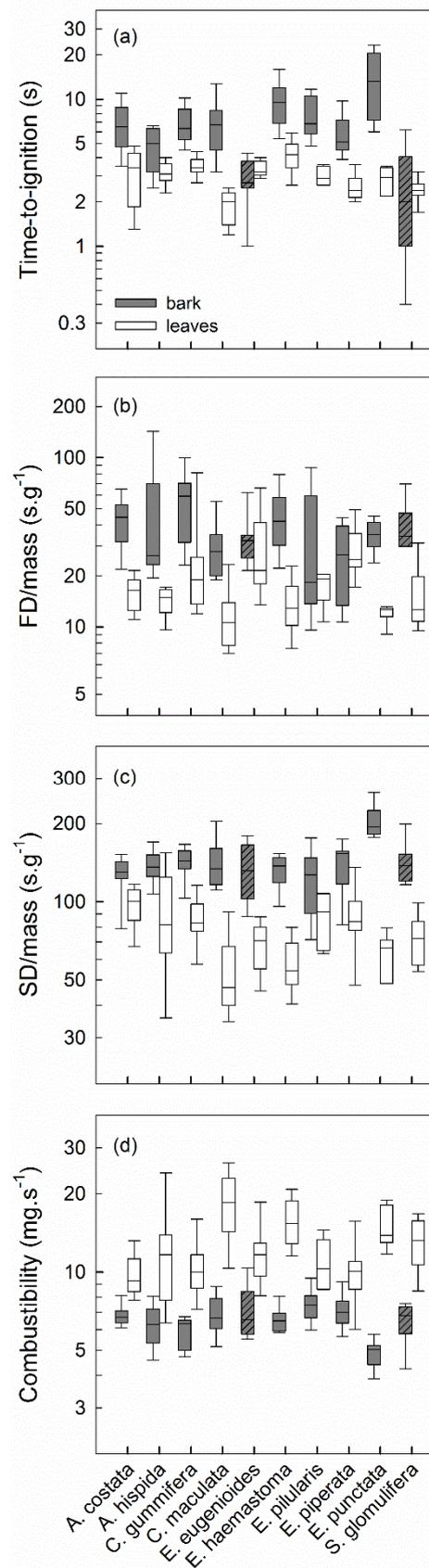


Fig. 4.5 Flammability of bark (dark-grey) and leaves (white) as described by (a) time-to-ignition, (b) mass-standardised flame duration, i.e. FD/mass, (c) mass-standardised smoulder duration, i.e. SD/mass, and (d) combustibility. The hatched boxes characterise the stringy-barks.

Decoupling of decomposition and flammability as 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 4.2). The relevant traits for the two turnover processes will be discussed below.

Table 4.2 Decomposition after 12 and 24 months (percentage mass loss of initial samples) versus the different flammability parameters, i.e., time-to-ignition (TTI), mass-standardised flame duration (FD/mass), mass-standardised smoulder duration (SD/mass), and combustibility. Results (R^2 or ρ and P -values) are presented for bark and leaves. No significant relationships were found (all $P \geq 0.180$).

Material	Mass loss after x months	Flammability parameter	R^2 (or ρ)	P
Bark	12	TTI	0.005	0.854
		Log FD/mass	0.002	0.894
		SD/mass	$\rho: -0.091$	0.803
		Combustibility	0.054	0.517
	24	TTI	0.066	0.475
		Log FD/mass	0.188	0.211
		SD/mass	$\rho: -0.321$	0.365
		Combustibility	0.213	0.180
Leaves	12	TTI	0.001	0.947
		Log FD/mass	0.168	0.239
		SD/mass	0.092	0.395
		Combustibility	0.005	0.845
	24	TTI	0.004	0.869
		Log FD/mass	0.204	0.190
		SD/mass	0.088	0.404
		Combustibility	0.000	0.953

Decomposition

Both after 12 and 24 months, initial lignin concentration was the strongest predictor of bark decomposition ($R^2 = 0.66$ and 0.63 respectively; Table S4.3, Fig. 4.6a), followed by cellulose concentration ($R^2 = 0.57$ and 0.43 ; Table S4.3). Considered after 12 months, energy content and tissue C concentration also explained a substantial portion of variation in bark decomposition (R^2 0.55-0.56; both negatively); however, after 24 months these trends were no longer significant. Other traits suspected to have an influence on decomposability, e.g. tissue density or tensile strength (based on studies on leaves, Kazakou *et al.* 2009), had no effect on bark decomposability. Using stepwise multiple regressions⁷ to quantify how the measured traits together could explain the variation in bark

⁷ Traits in consideration for the stepwise multiple regressions are presented in Table S4.4

decomposability, tannin concentration added another 21% (12 months) and 18% (24 months) to the explained variation, on top of the 66 and 63% already explained by lignin (Table 4.3). That is, these two traits together explained 81-87% of variation in bark decomposition.

As for bark, initial lignin concentration was also the most important driver for leaf decomposition ($R^2 = 0.64$ and 0.55 ; Table 4.3, Fig. 4.6a) with an additional 27% explained by leaf thickness after 24 months (i.e., total $R^2 = 0.82$; Table 4.3). 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. 4.6a). Therefore, we could not conclude that there was a common decomposability-lignin function *across* tissue types.

Flammability – bark

Several traits were important for the ignitibility, sustainability and combustibility of bark. Bark area per mass (BAM; $\text{cm}^2 \cdot \text{g}^{-1}$), analogous to specific leaf area (SLA; $\text{cm}^2 \cdot \text{g}^{-1}$), did not affect ignitibility when all species were included (Fig. 4.6b, $R^2 = 0.10$, $P = 0.385$). However, as noted before, the two stringy-bark species (*E. eugenoides* and *S. glomulifera*) were quite different from the other species in their morphology and ignitibility. Once these were excluded, BAM showed a strong negative relationship with time-to-ignition of the smooth bark species ($R^2 = 0.89$, $P < 0.001$). Considering all species, nitrogen concentration turned out to be the most important driver of bark ignitibility (Fig. 4.6c, $R^2 = 0.69$, $P = 0.003$): at higher N-concentrations, bark samples took less time to ignite. Calcium concentration added another 27% to the explained variance of bark ignitibility when we looked at the combined effect of traits in a multiple regression (Table 4.3). Fuel moisture content delayed the bark ignition ($R^2 = 0.40$, Table S4.3), but this moisture effect was not strong enough, or sufficiently independent from the [N] and [Ca] effects, to show up in the multiple regression results.

As mentioned above, 88% and 97% of variation in flame and smoulder durations, respectively, was explained by sample mass. When we standardised FD and SD by dry mass a far larger proportion of variance was accounted for by the within-species (error) term, than by the among-species term (88 and 71% within species, 12 and 29% among species; Table S4.5). Also, bark combustibility showed more variation within than among species (73% versus 27%; Table S4.5). 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 little among species (at least, compared to variation within any given species). Consequently, interspecific correlations between these traits and other measured properties should be treated with some degree of caution.

Variation among species in bark FD/mass was most strongly associated with copper concentration ($R^2 = 0.54$) or by lignin concentration ($R^2 = 0.49$; Table S4.3, Fig. 4.6d), both relationships being positive in sign. Phosphorus concentration added another 26% to the explained variance by [Cu] in the multiple regression model (Table 4.3); at a given [Cu], bark samples with higher [P] had shorter flame durations per gram material. [Ca] and [Mg] together explained 80% of the variation in combustibility among species (Table 4.3). Higher concentrations of Ca and Mg lowered the combustibility.

Flammability – leaves

As found in our previous study (Grootemaat *et al.* 2015), specific leaf area (SLA) was the most important driver for leaf TTI. Species with higher SLA ignited more quickly ($R^2 = 0.79$, $P = 0.001$; Table 4.3, Fig. 4.6b). Similarly but less markedly than was the case for bark, more variation in leaf FD/mass, SD/mass and combustibility was found at the within-species level than at the among-species level (36, 33 and 35%; Table S4.5). Nonetheless, leaf FD/mass was negatively correlated with potassium concentration ($R^2 = 0.44$; Table 4.3). None of the measured leaf traits were correlated with SD/mass or with combustibility. Consequently, no traits were selected for a model based on stepwise multiple regressions.

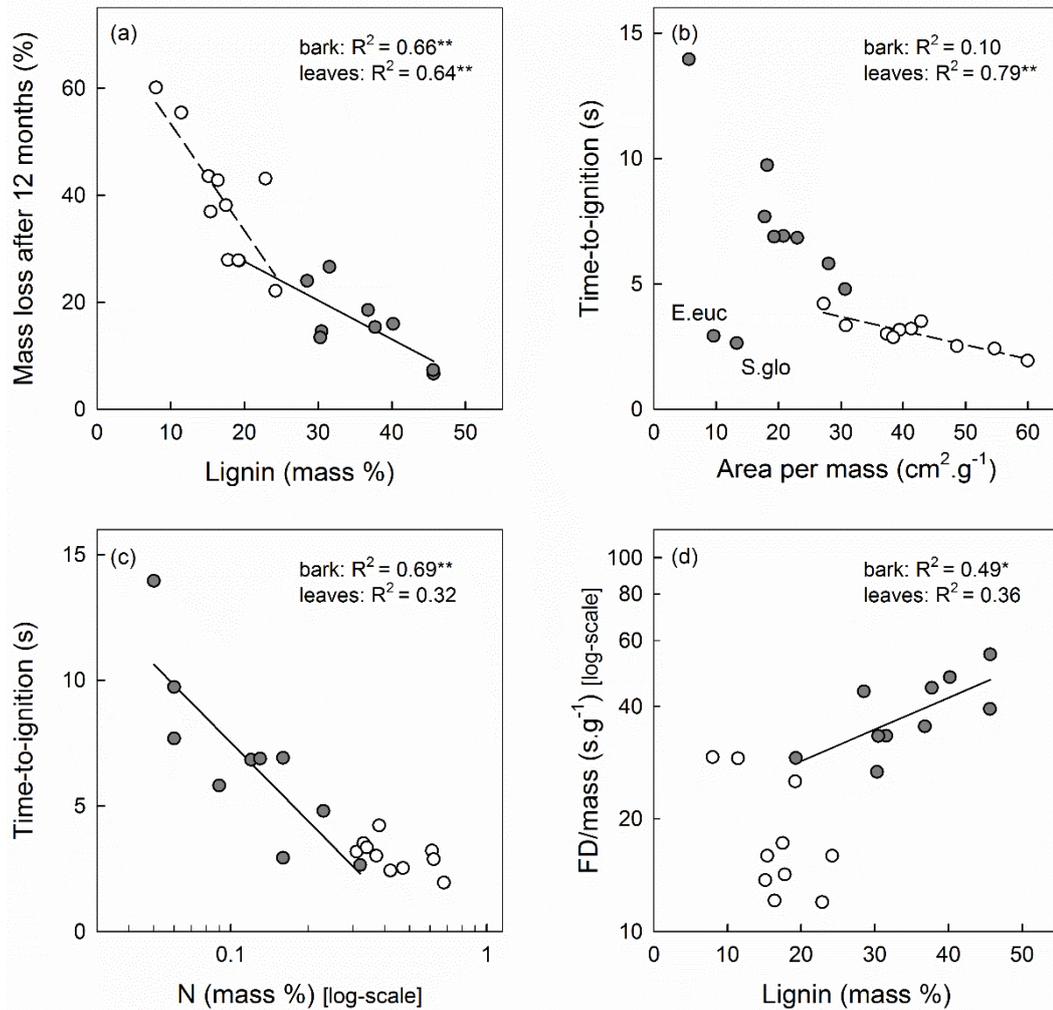


Fig. 4.6. Relationships for interspecific variation in (a) decomposability, (b + c) ignitibility, (d) mass-standardised flame duration, and a selection of traits (initial lignin concentration, area per mass, initial nitrogen- and lignin concentration, respectively) for bark (dark-grey) and leaves (white). Significant ($P \leq 0.05$) relationships are represented with a regression line. In (b) E.euc = *Eucalyptus eugenioides*, S.glo = *Syncarpia glomulifera* (both stringy-barks); when the stringy-barks were excluded from the analysis, bark time-to-ignition was strongly driven by bark area per mass (BAM; $R^2 = 0.89^{***}$). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 4.3 Traits with significant importance for decomposition after 12 months, decomposition after 24 months, time-to-ignition, flame duration (per gram material), smoulder duration (per gram material) and combustibility after stepwise multiple regressions; both for bark and leaves. Relationships are based on species-means.

Material	Mass loss 12 months (%)	Mass loss 24 months (%)	TTI (s)	Log FD/mass (s.g⁻¹)	SD/mass (s.g⁻¹)	Combustibility (mg.s⁻¹)
Bark	Lignin (-) <i>P</i> = 0.004 <i>R</i> ² = 0.66	Lignin (-) <i>P</i> = 0.006 <i>R</i> ² = 0.63	Log [N] (-) <i>P</i> = 0.003 <i>R</i> ² = 0.69	Log [Cu] (+) <i>P</i> = 0.016 <i>R</i> ² = 0.54	N/A	Log [Ca] (-) <i>P</i> = 0.029 <i>R</i> ² = 0.47
	Tannins (-) <i>P</i> = 0.013 Tot <i>R</i> ² = 0.87	Tannins (-) <i>P</i> = 0.037 Tot <i>R</i> ² = 0.81	Log [Ca] (+) <i>P</i> < 0.001 Tot <i>R</i> ² = 0.96	[P] (-) <i>P</i> = 0.019 Tot <i>R</i> ² = 0.80		Log [Mg] (-) <i>P</i> = 0.012 Tot <i>R</i> ² = 0.80
Leaves	Lignin (-) <i>P</i> = 0.005 <i>R</i> ² = 0.64	Lignin (-) <i>P</i> = 0.015 <i>R</i> ² = 0.55	SLA (-) <i>P</i> = 0.001 <i>R</i> ² = 0.79	Log [K] (-) <i>P</i> = 0.037 <i>R</i> ² = 0.44	N/A	N/A
		Thickness (-) <i>P</i> = 0.015 Tot <i>R</i> ² = 0.82				

Discussion

Bark has several functions when it is still attached to the trunk. Next to the transport of photosynthates by the phloem, bark is important for structural support, protection against pests and fire, water storage and/or carbon acquisition by photosynthesis. Accordingly, large variations in morphological and chemical bark traits have been described (Paine *et al.* 2010; Poorter *et al.* 2014; Rosell *et al.* 2014). In spite of the substantial contribution of bark to the litter layer in Australian forests, comparative studies of (dead) bark fates and associated mass loss rates have rarely been undertaken. In this study we focused on the decomposability and flammability of bark from 10 woody species and compared the results with the decomposability and flammability of leaves, since leaves and bark are the two major components of litter in dry sclerophyll forests (Lamb 1985; Crockford & Richardson 1998). By doing so, we aimed for a better understanding of the processes causing litter (fuel) accumulation on the forest floor, and hence a better prediction of the potential fire risk.

Slow decomposition of bark

The 10 woody species from the Sydney region differed in their bark and leaf decomposition rates. Higher interspecific lignin concentrations slowed the decomposability of leaf material, as has been found before (Melillo, Aber & Muratore 1982; Adair *et al.* 2008; Freschet *et al.* 2012), and a similar pattern (but with a different slope) was found for bark. Bark had higher initial lignin concentrations than leaves and this could be an explanatory factor for the slower decomposition rates of bark when compared to leaves, especially in the first year. Other reasons for the slow start (lag-phase) of bark decomposition could be local nutrient limitation since bark had lower [N] than leaves (Table S4.1), priority effects among decomposers (i.e. the decomposers prefer leaves over bark) and/or allelopathy between decomposers (Cornwell & Weedon 2014).

The lower decomposability of bark presumably provides a long-term slow release of nutrients to the forest soil (Lamb 1985; O'Connell 1997; Johnson *et al.* 2014), and also leads to accumulation of fuel for a potential fire (Hines *et al.* 2010). In contrast, the rapid initial decomposition in leaves, likely associated with leaching of water-soluble compounds (Woods & Raison 1983; Berg & McClaugherty 2003) and higher initial concentrations of N and P (Cornwell *et al.* 2008), releases nutrients relatively quickly.

After one year, a positive association (very weak at best) was found between the decomposability of leaves and bark, but this disappeared after 24 months. That is, we found no clear evidence that species with more decomposable leaves also have more decomposable bark. This raises the question of the extent to which decomposition rates of different material types (and underlying chemistry too) should be expected to be coordinated as part of a species' ecological strategy (*sensu* Freschet *et al.* 2010a). This will be further discussed below.

Flammability of bark is lower than that of leaves

While previous studies of bark flammability have typically focused on bark that is still attached to the tree, e.g. quantifying the ability of bark to protect the valuable vascular cambium (Uhl & Kauffman 1990; Pinard & Huffman 1997; Lawes *et al.* 2011), our study compared the flammability of bark chunks as components of the litter layer. The 10 species used in this study differed in their bark flammability, the various indices of flammability varying 1.5- to 5.4-fold among species. In general, bark took longer to ignite than leaves, and burned more slowly. The slower combustion of bark leads to longer fire residence times, and this is likely to lead to higher soil temperatures and plant mortality (Neary *et al.* 1999; Gagnon *et al.* 2010).

The fire sustainability of bark (and leaves) was strongly mass driven; the more mass available, the longer the flame and smoulder duration, and therefore the lower the combustibility. Although this may seem an obvious result, it means that the species-specific contribution of bark to the litter layer can be very important for the duration of a surface fire. We acknowledge also that the size and shape of bark particles can be important through their effect on the packing of litter (fuel) beds and the resulting airflow and oxygen supply (as found in fuel beds made up of leaves, Scarff & Westoby 2006; *Chapter 3*).

Once we standardised by area and sample mass, the variation in FD and SD was mostly accounted for by within species variation. This led to two observations: (a) even though the bark samples showed a huge variety in bark morphology and chemistry, once ignited, the flame and smoulder durations among species hardly varied; and (b) even after standardising by mass, the bark samples still showed longer flame and smoulder durations than the leaf samples. The latter could be explained by bark being richer in structural compounds (e.g. lignin; Fig. 5d), which have a higher thermal stability and therefore take more time, or

higher temperatures, for combustion (Philpot 1970; Di Blasi 2008). In addition, the greater particle thickness (Table S4.1) may also have contributed to low bark flammability by constraining heat supply to the inner parts of bark chunks.

Ignitibility is of special importance for wildfires, since highly ignitable material is likely to start a wildfire more easily. Also, fire spread can be seen as an accumulation of ignition steps (Rothermel 1972; *Chapter 5*). The stringy-barks (*E. eugenoides* and *S. glomulifera*) showed shorter ignition times than did the smooth bark species. This is not only relevant for understanding fire spread but also especially relevant for firefighting, since stringy-barks form firebrands (large embers) which can travel for miles and start a new fire in unburnt forest (so-called “spotting”) (Hines *et al.* 2010; Ellis 2011). The strongest driver of interspecific bark ignitibility in our dataset was nitrogen concentration; bark samples higher in [N] ignited more quickly. This contradicts our understanding that N, at least in ammonium phosphates, has fire retardant properties (Duquesne *et al.* 2003), but we do not know the relation between [N] and ignitibility when it is part of other chemical compounds. However, we think that the “fibrosity” of the bark may play an important role too. The small loose fibres of stringy-barks may catch alight more easily than smooth bark surfaces (Jacobs 1955). Even though we took great care in measuring several morphological traits, an index of bark “fibrosity” was not included.

Leaf ignitibility was strongly driven by SLA (leaf area per mass), as found previously (Murray, Hardstaff & Phillips 2013; Grootemaat *et al.* 2015). Similarly, when the stringy-barks were excluded from the analysis, a strong relationship was found between the SLA-analogue BAM (bark area per mass) and ignitibility. This is important information for our understanding of ignitibility and this could improve fire prediction models.

The remaining interspecific variation in bark FD/mass was mostly driven by copper concentration and secondly by [P]. While P has known flame retardant properties (Green 1992; Scarff, Gray & Westoby 2012), we do not have an explanation for the apparent flame-prolonging effects of [Cu]. The lower combustibility of bark at higher concentrations of Ca and Mg agrees with the common perception that the presence of cations, or higher nutrient concentrations in general, promotes the formation of chars during the depolymerisation phase of a fire (pyrolysis), at the expense of volatile tar formation. This makes the fuel less flammable (King & Vines 1969; Mak 1982). Similarly, this is how we can explain the

additional impact of [Ca] on bark TTI (i.e., at higher Ca concentrations the samples take longer to ignite).

Decoupling of decomposition and flammability

For a given material (i.e. bark or leaves), decomposability and flammability were unrelated when compared across the 10 species. This is a confirmation of our previous findings on leaves (Grootemaat *et al.* 2015), and the results here suggest a similar “decoupling” for bark. At a given decomposition rate, a full range of bark ignitibility, fire sustainability and combustibility are possible. However, the *stage* of decomposition will also affect the flammability, as was shown for twigs in recent work by Zhao *et al.* (2014). This decoupling of the two turnover processes is likely a consequence of the different drivers for decomposition and flammability. Indeed, bark decomposition was largely driven by lignin concentrations, while bark ignitibility was mainly driven by its nutrient concentrations (i.e. [N] and [Ca]), or BAM when considering the smooth barks only.

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 a mix of carbon turnover rates and litter accumulation. The bark contribution of some species to the litter layer in dry sclerophyllous forests can be very substantial (up to ~45%; McColl 1966; Lamb 1985). Combined with differences in decomposability and flammability, this makes it important to consider the species composition for estimating nutrient fluxes and assessing fuel loads and their flammability. In view of the 10 species used here, special attention could be given, for example, to *Eucalyptus pilularis*, because its bark can dominate the litter layer locally (due to a very high bark-production, not quantified in this study) and its relatively low decomposability (38% lost after 24 months). Also, its ribbons tend to hang down from the main branches and trunk, thereby serving as ladder fuels. This is important information for estimating fire behaviour, and adjusting forest management and firefighting techniques accordingly.

Plant organ coordination and ecological strategies

We found that the turnover rates of leaf and bark (by means of decomposition and combustion) were largely unrelated. Should this come as a surprise or can we explain it by

the lack of functional coordination between these two plant materials? In previous studies it has been shown that species with leaf traits promoting fast growth also have stem and root traits promoting fast growth (Freschet *et al.* 2010b; Reich 2014). Next, species with leaf traits promoting fast growth showed higher decomposition rates (and therewith presumably nutrient fluxes), based on their so-called trait “afterlife” effects (Cornelissen 2001; Santiago 2007; Cornwell *et al.* 2008). Freschet *et al.* (2012; 2013) found that the decomposability of leaves, stems and roots were positively coordinated, both in a subarctic flora and in ecosystems worldwide. This can be ascribed to the underlying structure and chemistry of the plant materials; plants with a “slow” strategy generally invest more in structural compounds (e.g. lignin) than “fast” plants do, and this makes them more resistant to decomposition. Should we therefore expect that species with leaf traits that promote fast growth and which results in highly-decomposable litter, also produce rapidly decomposing bark? We consider a strong coordination between leaves and bark unlikely, because of the very different functions they fulfil. While the main function of leaves is carbon acquisition by means of photosynthesis (and thereby promoting plant growth), bark transports photosynthates, gives structural support, protects the tree from pests and fire and helps with water storage (Niklas 1999; Rosell *et al.* 2014) - but in some cases can also contribute to the carbon acquisition by photosynthetic bark (Aschan & Pfanz 2003; Cernusak & Hutley 2011). Because of these fundamental different functions we think that bark production and decomposability is unrelated to the “fast-slow” plant economics spectrum *sensu* Reich (2014).

Next to decomposition, combustion is another fate of plant litter. One could assume that (leaf) litter of species with a “slow” strategy is more recalcitrant and therefore more difficult to ignite, or slower in its combustion. Indeed we found that species with low SLA (as often found in “slow” species; Reich 2014) were less ignitable. However, no relationship was found between SLA and mass loss by decomposition. So far, no evidence has been found for the theory that flammability is related to the “fast-slow” plant economics spectrum or to decomposability. Moreover, decomposition and combustion of bark and leaves are driven by different traits and are therefore unrelated.

Concluding remarks

For the first time, bark decomposability and flammability were quantified for a set of species. Bark decomposability varied across species and this could be ascribed to differences in initial lignin concentration. Bark decomposition was slower than leaf decomposition, which could lead to a relative domination of bark in the litter layer. However, this would also depend on the relative rates of litter fall and composition (input of leaf and bark litter respectively). This species-specific litter input is also important for estimating fire risks, since fuel availability (mass) is a major driver of fire duration. Even though the bark ignitibility of the different species varied, once the bark was alight there were no large interspecific differences in combustibility or in flame or smoulder -durations.

A litter bed is mostly a mixture of leaves and bark (and twigs), and the rate of fire spread through this litter bed is largely dependent on the ignitibility of the *leaves* (since they are the first plant parts to ignite due to their high surface area-to-volume ratio; Gill & Moore 1996; *Chapter 3*). *Bark* needs more time for ignition, but when it does ignite it will lead to longer flame and smouldering durations of the litter bed. This can lead to more extensive thermal damage to the local soil flora and fauna (Neary *et al.* 1999; Gagnon *et al.* 2010).

Different (combinations of) traits were associated with bark *decomposability* and *flammability parameters*, respectively. Consistent with the pattern for leaves, found here and previously by us (Grootemaat *et al.* 2015), bark decomposability and flammability were therefore unrelated i.e. “decoupled”. Altogether, we believe that the estimation of fuel loads and consequently of fire risks can be improved by taking species-specific traits of both leaves and bark into consideration.

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Supporting information

Table S4.1 Trait measurements, decomposability measurements and flammability measurements based on species' means, n = 9. Measurements marked with an asterisk (*) are not independent since we standardised by bark-size at the beginning of the experiment.

Trait	Bark (range; x-fold variation)	Leaves (range, x-fold variation)
One sided surface area (cm ²)	10.9-16.5; 1.5*	13.0-38.1; 2.9
Thickness (mm)	0.99-7.11; 7.2	0.33-0.81; 2.5
Dry mass (g)	0.40-2.20; 5.6*	0.27-1.02; 3.8
Density (g/cm ³)	0.22-1.13; 5.1	0.33-0.74; 2.2
Area per mass (cm ² /g)	5.63-30.67; 5.4 (BAM)	27.23-59.97; 2.2 (SLA)
Tensile strength (Newton/mm)	3.75-53.75; 14.3	N/A
Moisture content - before burning (% odw)	11.8-14.4; 1.2	7.3-10.0; 1.4
Energy content (MJ/kg)	18.7-20.2; 1.1	20.8-22.8; 1.1
C (%)	44.5-48.9; 1.1	48.2-51.9; 1.1
Ca (%)	0.02-0.96; 48.0	0.36-1.01; 2.9
Cu (mg/kg)	1.15-8.37; 7.3	2.97-22.03; 7.4
K (%)	0.01-0.15; 15.0	0.05-0.35; 6.5
Mg (%)	0.01-0.16; 16.0	0.14-0.28; 1.9
N (%)	0.05-0.32; 6.4	0.31-0.68; 2.2
P (mg/kg)	22.1-63.4; 2.9	66.6-367.7; 5.5
Lignin (%)	19.3-45.7; 2.4	8.0-24.2; 3.0
Cellulose (%)	36.1-53.8; 1.5	19.0-44.1; 2.3
Ash (%)	0.05-1.05; 21.0	0.06-1.16; 18.2
Tannins (%)	0.08-33.64; 420.5	0.96-31.95; 33.3
Decomposition after 12 months (% mass loss)	6.7-27.8; 4.2	22.1-60.1; 2.7
Decomposition after 24 months (% mass loss)	26.7-71.2; 2.7	55.8-91.9; 1.6
Time-to-ignition (s)	2.6-14.0; 5.4	1.9-4.2; 2.2
Flame Duration (s)	11.2-94.2; 8.4	6.0-16.4; 2.7
FD/mass (g/s)	26.8-47.9; 1.8	12.0-29.3; 2.4
Smoulder Duration (s)	55.0-566.6; 10.3	22.0-79.0; 3.6
SD/mass (g/s)	122.5-205.4; 1.7	53.1-97.3; 1.8
Combustibility (mg/s)	4.9-7.5; 1.5	9.8-18.3; 1.9

Table S4.2 Retrieval dates of the samples in our decomposition experiment. “N” is the number of replicates per species.

	Bark	Leaves	Months since start date
Start date	9 January 2013	19 January 2013	N/A
1 st trial (1 replicate from batch A)	10/04/2013 (n=1)	19/04/2013 (n=1)	3 months
1 st retrieval (leaves only, batch A)	N/A	02/05/2013 (n=5)	3.5 months
2 nd trial (1 replicate from batch B)	02/09/2013 (n=1)	N/A	8 months
2 nd retrieval (batch B)	09/01/2014 (n=8)	17/01/2014 (n=6)	12 months
3 rd retrieval (batch C)	08/01/2015 (n=9)	08/01/2015 (n=6)	24 months
4 th retrieval (bark only, batch A)	09/07/2015 (n=8)	N/A	30 months

Table S4.3 Bivariate regressions between bark traits and several parameters of decomposability and flammability. Significant relationships ($P < 0.05$) are presented in bold, followed by the sign of these relationships in parentheses; (+) for positive, (-) for negative relationships.

Bark traits	Mass loss 12 months (%)	Mass loss 24 months (%)	TTI (s)	Log FD/mass (s/g)	SD/mass (s/g)	Combustibility (mg/s)
Surface area	$R^2 = 0.03$ $P = 0.655$	$R^2 = 0.01$ $P = 0.852$	$R^2 = 0.17$ $P = 0.232$	$R^2 = 0.04$ $P = 0.597$	$\rho = 0.20$ $P = 0.590$	$R^2 = 0.02$ $P = 0.711$
Log Thickness	$R^2 = 0.06$ $P = 0.483$	$R^2 < 0.01$ $P = 0.860$	$R^2 < 0.01$ $P = 0.932$	$R^2 < 0.01$ $P = 0.947$	$\rho = 0.26$ $P = 0.467$	$R^2 = 0.12$ $P = 0.326$
Log Dry mass	$R^2 = 0.04$ $P = 0.587$	$R^2 = 0.02$ $P = 0.673$	$R^2 = 0.19$ $P = 0.209$	$R^2 = 0.01$ $P = 0.741$	$\rho = 0.10$ $P = 0.777$	$R^2 = 0.29$ $P = 0.107$
Log Density	$R^2 = 0.03$ $P = 0.652$	$R^2 = 0.02$ $P = 0.730$	$R^2 = 0.13$ $P = 0.313$	$R^2 = 0.02$ $P = 0.728$	$\rho = 0.16$ $P = 0.663$	$R^2 = 0.04$ $P = 0.596$
Area per mass	$R^2 = 0.06$ $P = 0.509$	$R^2 = 0.01$ $P = 0.798$	$R^2 = 0.10$ $P = 0.384$	$R^2 = 0.04$ $P = 0.580$	$\rho = 0.07$ $P = 0.855$	$R^2 = 0.10$ $P = 0.378$
Log Tensile strength	$R^2 = 0.05$ $P = 0.519$	$R^2 = 0.11$ $P = 0.359$	$R^2 = 0.28$ $P = 0.113$	$R^2 = 0.03$ $P = 0.609$	$\rho = 0.12$ $P = 0.751$	$R^2 = 0.01$ $P = 0.800$
Moisture content	$R^2 = 0.05$ $P = 0.522$	$R^2 < 0.01$ $P = 0.919$	$R^2 = 0.40$ (+) $P = 0.049$	$R^2 = 0.01$ $P = 0.852$	$\rho = 0.22$ $P = 0.533$	$R^2 = 0.01$ $P = 0.742$
Energy content	$R^2 = 0.55$ (-) $P = 0.014$	$R^2 = 0.19$ $P = 0.212$	$R^2 = 0.28$ $P = 0.116$	$R^2 = 0.26$ $P = 0.129$	$\rho = 0.14$ $P = 0.701$	$R^2 < 0.01$ $P = 0.939$
Log C	$R^2 = 0.56$ (-) $P = 0.012$	$R^2 = 0.29$ $P = 0.108$	$R^2 = 0.13$ $P = 0.304$	$R^2 = 0.31$ $P = 0.093$	$\rho = 0.01$ $P = 0.987$	$R^2 < 0.01$ $P = 0.910$
Log Ca	$R^2 = 0.06$ $P = 0.483$	$R^2 < 0.01$ $P = 0.943$	$R^2 = 0.61$ (+) $P = 0.008$	$R^2 = 0.04$ $P = 0.607$	$\rho = 0.23$ $P = 0.532$	$R^2 = 0.47$ (-) $P = 0.029$
Log Cu	$R^2 = 0.09$ $P = 0.400$	$R^2 = 0.07$ $P = 0.465$	$R^2 = 0.04$ $P = 0.568$	$R^2 = 0.54$ (+) $P = 0.016$	$\rho = 0.41$ $P = 0.244$	$R^2 = 0.29$ $P = 0.107$
Log K	$R^2 = 0.32$ $P = 0.090$	$R^2 = 0.30$ $P = 0.104$	$R^2 = 0.20$ $P = 0.201$	$R^2 = 0.03$ $P = 0.640$	$\rho = 0.03$ $P = 0.945$	$R^2 < 0.01$ $P = 0.879$
Log Mg	$R^2 = 0.12$ $P = 0.330$	$R^2 = 0.03$ $P = 0.615$	$R^2 = 0.62$ (+) $P = 0.007$	$R^2 < 0.01$ $P = 0.924$	$\rho = 0.05$ $P = 0.894$	$R^2 = 0.12$ $P = 0.318$
Log N	$R^2 < 0.01$ $P = 0.893$	$R^2 = 0.04$ $P = 0.562$	$R^2 = 0.69$ (-) $P = 0.003$	$R^2 = 0.06$ $P = 0.498$	$\rho = 0.01$ $P = 0.987$	$R^2 = 0.03$ $P = 0.638$
P	$R^2 = 0.22$ $P = 0.173$	$R^2 = 0.22$ $P = 0.168$	$R^2 = 0.03$ $P = 0.613$	$R^2 = 0.03$ $P = 0.628$	$\rho = 0.44$ $P = 0.200$	$R^2 = 0.03$ $P = 0.613$
Lignin	$R^2 = 0.66$ (-) $P = 0.004$	$R^2 = 0.63$ (-) $P = 0.006$	$R^2 = 0.01$ $P = 0.811$	$R^2 = 0.49$ (+) $P = 0.025$	$\rho = 0.37$ $P = 0.293$	$R^2 = 0.25$ $P = 0.144$
Cellulose	$R^2 = 0.57$ (+) $P = 0.011$	$R^2 = 0.43$ (+) $P = 0.038$	$R^2 = 0.10$ $P = 0.375$	$R^2 = 0.38$ $P = 0.056$	$\rho = 0.49$ $P = 0.150$	$R^2 = 0.18$ $P = 0.227$
Log Ash	$R^2 < 0.01$ $P = 0.932$	$R^2 = 0.01$ $P = 0.854$	$R^2 = 0.29$ $P = 0.106$	$R^2 = 0.40$ $P = 0.052$	$\rho = 0.13$ $P = 0.725$	$R^2 = 0.01$ $P = 0.840$
Tannins	$R^2 = 0.06$ $P = 0.503$	$R^2 = 0.05$ $P = 0.547$	$R^2 = 0.03$ $P = 0.626$	$R^2 = 0.14$ $P = 0.296$	$\rho = 0.30$ $P = 0.405$	$R^2 = 0.10$ $P = 0.364$

Table S4.4 Traits selected as input for multiple stepwise regressions for bark and leaves. Bark area and bark dry mass are not species specific traits, but were manipulated when we standardised by bark-size; therefore we measured the area and dry mass explicitly for the bark samples that were used in the experimental burns (marked with an asterisk, *). When we ran the analysis for mass standardised flammability parameters (i.e. FD/mass, SD/mass and combustibility) dry mass was excluded as input from the multiple regressions (α).

Bark	Leaves
Surface area	Surface area
Surface area_flammability*	
Log Thickness	Thickness
Log Dry mass α	Dry mass α
Log Dry mass_flammability* α	
Log Density	Density
Area per mass (BAM)	Area per mass (SLA)
Log Tensile strength	N/A
Moisture content	Moisture content
Energy content	Energy content
Log C	Log C
Log Ca	Log Ca
Log Cu	Log Cu
Log K	Log K
Log Mg	Log Mg
Log N	Log N
P	Log P
Lignin	Lignin
Cellulose	Cellulose
Log Ash	Log Ash
Tannins	Log Tannins

Table S4.5 Variance component analysis for two decomposition and six flammability parameters (based on MINQUE – Minimum Norm Quadratic Unbiased Estimation).

Material	Parameter	Variation within species (%)	Variation among species (%)
Bark	Decomposition 12 months	39.8	60.2
	Decomposition 24 months	43.2	56.8
	Log TTI	42.9	57.1
	Log FD	45.9	54.1
	Log FD/mass	88.0	12.0
	Log SD	20.4	79.6
	Log SD/mass	71.4	28.6
	Log combustibility	72.7	27.3
Leaves	Decomposition 12 months	42.8	57.2
	Decomposition 24 months	44.1	55.9
	Log TTI	57.9	42.1
	Log FD	48.6	51.4
	Log FD/mass	64.3	35.7
	Log SD	34.4	65.6
	Log SD/mass	66.7	33.3
	Log combustibility	65.0	35.0

Text S4.1 Extraction methods for leaf and bark chemistryCarbon and nitrogen

0.25 g of sample was weighed out into a tin foil capsule which was placed into the induction furnace of a LECO Truspec CHN combustion analyser set at 1100°C and calibrated on EDTA. The carbon present was combusted to CO₂ which was determined with an infrared detection cell. The nitrogen present was combusted to N₂, NO₂ and NO. The oxides were reduced to N₂ which was determined quantitatively using a thermal conductivity cell.

(Rayment, G.E. & Lyons, D.J. (2011) *Soil Chemical Methods: Australasia*. CSIRO Publishing. Handbook section 6B2, p75.)

Other elements (acid digestions)

0.25 g of sample was weighed out and digested with 15 ml of 5:1 nitric-perchloric acid. The digested sample was made up to a volume of 25 ml and the elemental concentrations were then determined by ICPAES.

(Martinie, G.D. & Schilt, A.A. (1976) *Wet oxidation efficiencies of perchloric acid mixtures for various organic substances and the identities of residual matter*. *Analytical Chemistry*, 48, 70-74.)

Tannin analysis

0.2 g of sample was weighed out and extracted 3 times with 8 ml of 70% acetone for 45 minutes with the extracts made up to 25 mL volume. 1 ml of extract was heated with 5 ml of 19:1 butanol-HCl at 95°C for 45 minutes in a water bath. The extracts were analysed at a wavelength specific to the tannin in question. Bound tannin is measured by adding 5 ml of Butanol HCl to the extraction residue and heating as above. Please note that these samples have been quantified using a condensed tannin stock prepared from *Acacia aneura* (mulga) which was the best fit we could find for the range of samples in question. As a consequence these values should be reported as relative numbers rather than absolutes.

(Dalzell, S.A. & Kerven, G.L. (1998) *A rapid method for the measurement of Leucaena spp proanthocyanidins by the proanthocyanidin (butanol/HCl) assay*. *Journal of the Science of Food and Agriculture*, 78, 405-416.)

Lignin and Cellulose analysis (ADF extraction)

ADF analysis measures cellulose + lignin + ash content. ADF reagent was prepared from CTAB (cetyltrimethylammonium bromide) and H₂SO₄. 1.0 g of sample was extracted with 45 ml of ADF reagent at 100°C for 70 minutes. The samples were then filtered, rinsed and dried at 60°C for 12 hrs. The dried samples were then reacted with 25 mL of cold 72% H₂SO₄ for 3 hours; then filtered and rinsed again prior to ashing at 500°C for three hours.

(Rowland, A.P. & Roberts, J.D. (1994) *Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods*. *Communications in Soil Science and Plant Analysis*, 25, 269-277.)

5. Models for leaf ignitibility based on leaf traits

Saskia Grootemaat^a, Phil Zylstra^b, Peter van Bodegom^c

^a Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

^b School of Biological Sciences, University of Wollongong, Wollongong, NSW 2522, Australia

^c Institute of Environmental Sciences, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands

Summary

1. For almost 100 years fire scientists have tried to predict fire behaviour. Because of the complexity of wildfires, which includes impacts of weather, fuel conditions and topography, predicting fire behaviour is a real challenge. Leaf traits have received relatively little attention as predictive factors so far. We hypothesised that leaf traits like leaf thickness, tissue density or specific leaf area would improve the estimation of leaf ignitability (expressed as time-to-ignition, TTI) compared to basic ignition models that only include temperature and fuel moisture content.
2. By means of experimental burns on individual leaves from 32 Australian plants species at a gradient of temperatures and with a range of fuel moisture contents, we compared 11 *a priori* models to define which combination of parameters would best describe leaf TTI. Next, we validated our models by comparing the values for TTI as predicted by our models with observed values from two other datasets.
3. The results from the model selection analysis showed that including leaf thickness, density or SLA improved the estimation of leaf TTI by 10-18% compared to the model based on temperature and fuel moisture contents only. Foliar nitrogen or phosphorus concentration did not significantly improve the predictions.
4. Our models performed well in the validation tests. In 8 out of 9 cases the models which included leaf traits had lower Mean Squared Errors compared to the basic model. The model that included leaf thickness (next to temperature and moisture content) performed best, with a reduced Mean Squared Error from 0.091 to 0.061 (all leaves) and from 0.167 to 0.028 (fresh leaves only).
5. This study provides the first cross-species, cross-temperature model of TTI, which is a critical component in biophysical mechanistic modelling of wildfire behaviour. It quantifies the importance of morphological and (to a lesser extent) chemical traits to leaf ignitability; thereby allowing future work to examine how changes to climate or management may affect landscape flammability. This will help us predicting shifts in ecosystem functioning, biodiversity, terrestrial carbon balances and risks to human life.

Keywords: fire behaviour modelling, flammability, leaf thickness, model selection analysis, moisture content, Specific Leaf Area, wildland fires

Introduction

Large areas of the Earth's surface are prone to wildfires (Krawchuk *et al.* 2009). These fires play an important role in controlling ecosystem distribution and vegetation composition worldwide (Bond & Keeley 2005; Bond & Parr 2010; Pausas & Keeley 2009). Depending on the size, frequency and intensity of the fires they can have enormous impacts on our environment. For example, large uncontrolled fires can cause erosion and ecosystem degradation (Doerr, Shakesby & MacDonald 2009; Neary *et al.* 1999; Pausas *et al.* 2008), change the diversity of plants (Bond & Parr 2010), change the habitat conditions for animals (Smith 2000), increase the emission of CO₂ and smoke particles (Page *et al.* 2002; Bowman *et al.* 2009; van der Werf *et al.* 2010), and are sometimes associated with loss of lives and material goods (Gill, Stephens & Cary 2013). For all these reasons it is of outmost importance to predict wildfire behaviour as accurately as possible.

For almost 100 years scientists have tried to come up with predictive models or guidelines for wildfire behaviour (Sullivan 2009a, b, c; Cruz *et al.* 2015; Scott *et al.* 2014). By means of field studies and laboratory based experiments our understanding of fire behaviour has certainly increased. Yet, there is still much to learn, and one of the main challenges remains connecting lab-based results with real-life situations in the field (Varner *et al.* 2015). One way to bridge this gap is by developing models which build up from the flammability of the smallest particles involved in fire, e.g. leaves, and then adding complexity step by step (Zylstra *in prep.*).

To date, fire researchers recognise that wildfire behaviour and potential fire spread are basically dependent on three factors, namely, weather conditions (e.g. temperature, wind, rainfall), topography (e.g. slope) and fuel characteristics (e.g. moisture content) (Barrows 1951). In this study we focused on the fuel characteristics, since fuel -type, -size and -arrangement can have large effects on the ignitibility, spread and intensity of fires (e.g. Brown & Davis 1973; Bond & van Wilgen 1996).

Different plant species have been shown to differ in their flammability, both in experiments on individual leaves (Gill & Moore 1996; Murray, Hardstaff & Phillips 2013; Grootemaat *et al.* 2015), and in experiments on fuel beds (Kane, Varner & Hiers 2008; de Magalhães & Schwilk 2012; *Chapter 3*). Both morphological and chemical leaf traits have been identified as drivers of interspecific variation in fuel flammability (Grootemaat *et al.* 2015; Varner *et al.* 2015). For example, long and curly leaves decrease fuel bed density, thereby

increasing oxygen flow throughout the fuel bed (Scarff & Westoby 2006; Schwilk & Caprio 2011); this can lead to fires with a higher intensity, shorter duration, or higher fuel consumption (Engber & Varner 2012; *Chapter 3*). Higher values of nutrient concentrations have been shown to reduce flammability (Mak 1982; *Chapters 2 and 4*); while higher leaf litter terpene concentrations tend to increase flammability (Ormeño *et al.* 2009).

We acknowledge that “flammability” can be a confusing term, and it is often divided into ignitibility, sustainability and combustibility (Anderson 1970). In this study we focused on the *ignitibility* of leaves because (a) without ignition there is no fire, and (b) fire spread can be seen as a chain of ignition steps (Fig. 5.1; *Chapter 3*). Investigating the thresholds at which flames from one leaf can ignite another leaf is critical to predicting flame heights and fire spread, and this is also useful information for predicting if a surface fire will develop into a crown fire or not (Fig. 5.1b). Many fire behaviour models do not consider leaf ignitibility explicitly, although it is an essential component in biophysical mechanistic models such as that of Zylstra (2011, 2014a; Fig. 5.2). We used leaves as our fuel of interest because they are usually the first plant parts to ignite in a wildfire due to their high surface area to volume ratio (Gill and Moore 1996). And, next to twigs and bark, leaves form the major fuel component in surface fires.

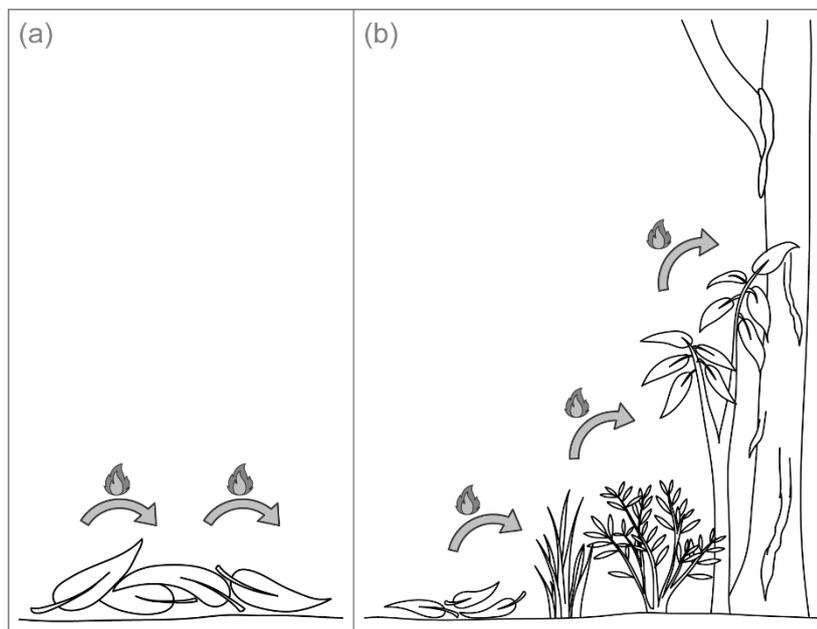


Fig. 5.1 A schematic overview of stepwise ignitions. Flames from one leaf can ignite another leaf when leaves are (a) part of the litter layer, or (b) still attached to the plant. By means of this chain of ignition steps the fire can spread through different layers of the vegetation.

Drivers of leaf ignitibility

Ignitibility itself has two components, namely the minimum temperature for piloted ignition (“endotherm” *sensu* Philpot 1970) and the ignition delay time (hereafter referred to as time-to-ignition; TTI). Throughout this paper we focus on TTI. As suspected drivers of individual leaf time-to-ignition, we highlight the following traits:

Fuel Moisture Content (FMC)

The principal trait affecting leaf ignitibility is fuel moisture content (FMC) (Plucinski & Anderson 2008; Ganteaume *et al.* 2009). Leaves with higher moisture levels take longer to ignite as they require more energy for water evaporation and preheating of the fuel (Byram 1959; Possell & Bell 2013). The moisture content of *living plants* (especially perennials) is largely regulated by species’ physiology and the time of year. However, extreme weather conditions like droughts can lead to plant moisture stress (McDowell *et al.* 2008). Live fuel moisture content can be measured by remote sensing and this is very useful information for the estimation of leaf ignitibility (Chuvieco *et al.* 2002; Caccamo *et al.* 2012; Yebra *et al.* 2013). The moisture content of *litter* (dead plant material) is strongly dependent on weather conditions. Driven by fluctuating levels of relative humidity, rainfall, air temperature, solar radiation and wind speed, litter moisture content is defined by a continuous interplay of absorbing water and drying out (Matthews 2006; Matthews, Gould & McCaw 2010). These moisture dynamics of litter beds are strongly affected by leaf morphological traits like size, surface area-to-volume and curliness. In general, thin leaves with high surface area-to-volume ratios absorb and lose moisture more easily, while curly leaves promote drying in fuel beds through lower bulk densities and therefore increased airflow (Kreye *et al.* 2013).

Surface area-to-volume ratio (SA:V) or leaf thickness

In general, leaves with higher surface to volume ratios (SA:V) ignite more quickly due to a relative larger area for heating and drying to take place (Brown 1970). For most leaves SA:V is determined by leaf thickness (Roderick *et al.* 1999). Consequently, both thickness and SA:V have been used to describe ignitibility. Thinner leaves (leaves with higher values for SA:V) have been shown to have shorter ignition times (Montgomery & Cheo 1971; Gill & Moore 1996).

Specific leaf area (SLA)

Next to the evident effects of moisture content and SA:V on leaf ignitibility as described above, recent findings (Murray, Hardstaff & Phillips 2013; Grootemaat *et al.* 2015) suggest that specific leaf area (SLA; ratio of leaf area to dry mass; $\text{cm}^2 \cdot \text{g}^{-1}$) is a better predictor of TTI than surface area-to-volume ratio or thickness alone. SLA does not only account for the dimensional aspects of the leaf (like thickness or SA:V), but includes tissue density as well ($1/\text{SLA} = \text{leaf thickness} * \text{tissue density}$) (Witkowski & Lamont 1991; Wilson, Thompson & Hodgson 1999). A higher tissue density leads to a lower ignitibility, presumably through the higher quantity or compactness of cell wall material (Roderick *et al.* 1999) which accordingly needs more time for volatilisation during the thermal degradation process (Sullivan & Ball 2012). Despite the potential importance for ignitibility, tissue density has received little attention in fire behaviour models so far (Rothermel 1972; Scott & Burgan 2005). This could potentially change in the near future since worldwide databases with information on leaf traits are increasingly becoming available. Because of the importance of SLA and nutrient concentrations as explanatory traits in carbon gain strategies (e.g. Wright *et al.* 2004) and carbon release (e.g. decomposability; Brovkin *et al.* 2012; Freschet, Aerts & Cornelissen 2012), these traits are now widely measured and documented by plant ecologists (e.g. TRY, Kattge *et al.* 2011). We suggest that this information could be of use for leaf ignitibility models.

Chemistry

As commonly accepted, high concentrations of essential oils in plants (e.g. *Eucalyptus* sp.) make the leaves more flammable. However, the measurement of these oils, mostly consisting of terpenes, is quite elaborate and goes beyond the routine measurements of most plant- or fire ecologists (Boland *et al.* 1991). As a result there is only very limited scientific evidence for effects of terpenes on ignitibility (Ormeño *et al.* 2009). By contrast, given the importance of nitrogen and phosphorus in biogeochemical cycles, foliar [N] and [P] are available for a large number of species. Some studies indicate that nutrient concentrations may affect the ignitibility of leaves. Philpot (1970) found that phosphorus delayed the thermal decomposition of cellulose (pyrolysis), and it has been suggested that phosphorus could work as fire retardant by favouring the production of char over flammable tars (Scarff & Westoby 2008; Scarff, Gray & Westoby 2012). Although these effects of leaf nutrient

composition might be small compared to other leaf traits like thickness or moisture content, they still merit investigation as potential contributors to the prediction of leaf ignitibility.

Towards a better prediction of leaf ignitibility

Leaf ignitibility is a broadly measured aspect of flammability (Pérez-Harguindeguy *et al.* 2013). However, It has not been explicitly considered in fire behaviour models (Sullivan 2009a, b, c) until the recent biophysical, mechanistic approach of Zylstra (2011) in the Forest Flammability Model (FFM, Fig. 5.2). While some studies have quantified TTI at a range of temperatures for particular species (e.g. Xanthopoulos & Wakimoto 1993) or for a large set of species at one convective heating temperature (e.g. Gill & Moore 1996), the combination of a range of species *and* a range of temperatures has not been made before. The exception to this is the TTI equation of Zylstra (2011) which achieves high predictive accuracy for six species across eight temperatures using FMC, leaf thickness and the number of sides of the leaf as a component of SA:V. This model, however, was built on data from six sclerophyllous species only, and was restricted in the number of leaf traits included.

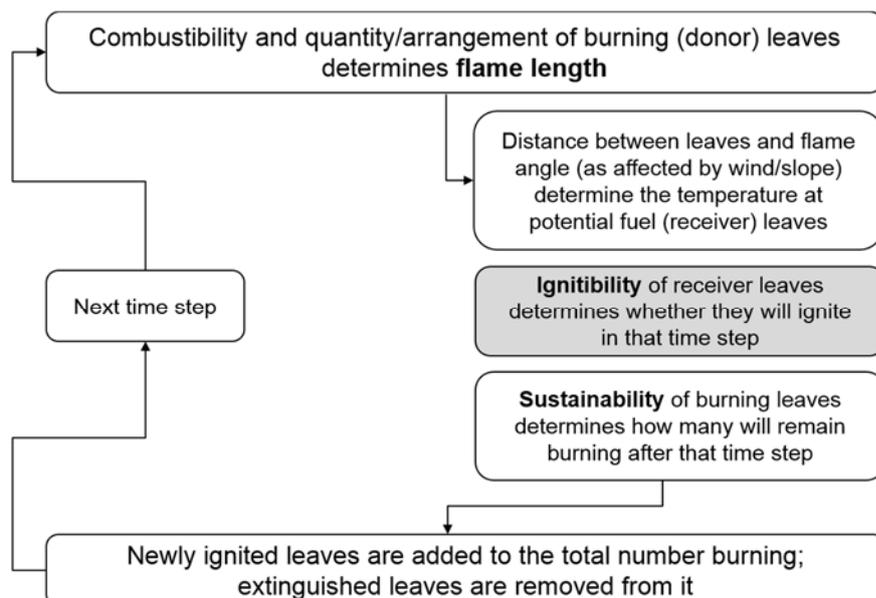


Fig. 5.2 A simplified description of estimating flame length as part of fire behaviour modelling after Zylstra's Forest Flammability Model (Zylstra 2011; Zylstra *in prep.*). Flame length per time step is determined by the numbers of leaves burning, their arrangement and their flammability. Leaf ignitibility (in grey) forms an essential building block of this estimation.

Based on results from our previous studies (Grootemaat *et al.* 2015; this thesis), leaf traits like SLA or tissue density form strong candidates to improve leaf ignitibility equations relative to Zylstra (2011), and also leaf nutrient concentration may be worth some extra investigation (Philpot 1970; Mak 1982; Scarff & Westoby 2008). The aim of our study, therefore, was to replicate the methodology of Zylstra (2011) for a wider domain and number of traits, investigating the influence of possible drivers such as tissue density, SLA, nitrogen and phosphorus -concentration. We aimed to build a robust model of TTI that can be applied across species and for a full range of convective temperatures, as required for the mechanistic modelling approach. We specifically focused on the following questions: (i) Which combinations of leaf traits provide the best model to describe leaf TTI? And (ii) Do our leaf-ignition models perform well for leaves from a wide range of species and ecosystems?

To answer these questions we used a dataset with 150 entries from leaf ignition times for 32 perennial species from fire prone areas in eastern Australia. Leaves of these species were burned at a gradient of temperatures and with a range of fuel moisture contents. With different leaf traits as predictors (i.e., moisture content, leaf thickness, tissue density and leaf chemistry), we built 11 different *a priori* ignition models based on our understanding of the physical processes involved. We compared and ranked these models by using model selection analysis (Burnham & Anderson 2002; Symonds & Moussalli 2011). The best models were evaluated by comparing predicted ignition times with observed values for 56 species (172 entries) from two other datasets (i.e., Gill & Moore 1996 and Zylstra 2011).

Materials and methods

Dataset specifications

The dataset that was used to build our leaf ignitibility models was based on experimental burns of individual leaves from 32 perennial species from eastern Australia. The leaves were collected at four study sites which differed in climate (especially rainfall) and soil nutrient status (Table 5.1), and consequently consisted of different vegetation types. The two wetter sites were located in Ku-ring-gai Chase National Park, north of Sydney, with an average annual rainfall of 1333 mm. The drier sites, with an average annual rainfall of 421 mm, were located in Round Hill Nature Reserve, 580 km inland (west) from Sydney. The use of these four distinct vegetation types expanded our range of growth forms and plant

traits without actually focussing on the patterns due to rainfall or soil nutrient status. The 32 species were all evergreen perennials, representing 14 different families of distant lineages (Table 2.2, page 40). The set consisted of species with a variety of growth forms (i.e., trees, shrubs, one cycad and one grass), average leaf sizes (1-45 cm²) and morphologies (e.g. both broad- and needle-leaved species). Leaf traits for these species are well documented (Wright, Reich & Westoby 2001; Wright & Westoby 2002, 2003) and the dataset contains measurements for leaf thickness (mm), tissue density (g.cm⁻³), specific leaf area (cm².g⁻¹), and foliar nitrogen and phosphorus concentration.

For the practicality of this study, and because of the nature of the validation datasets, we focused on green leaves freshly picked from plants in the field and dried to a range of moisture contents. Over 15 individual plants per species were used for the collection of our samples. Some of the leaves were stored in zip-locked bags to minimize moisture loss (*sensu* Pérez-Harguindeguy *et al.* 2013), others were stored in paper bags and air-dried under ambient conditions until they were used in the experimental burns. By doing so we ended up with a wide gradient of fuel moisture contents (FMC; Eqn. 5.1), which was defined as a percentage of oven dry weight:

$$FMC = \frac{(actual\ weight - dry\ weight)}{dry\ weight} * 100\%$$

Eqn. 5.1

Subsamples were measured at their actual weight just before the experimental burns, and remeasured after 24h of drying at 105°C (*sensu* Matthews 2010). FMCs ranged from 4.3 to 230.7%.

Leaf samples of the 32 species were burned individually in a muffle furnace at set temperatures varying between 295 and 612°C (9 temperature classes, Table S5.1). A more detailed description of the experimental burns can be found in Grootemaat *et al.* 2015, although it is import to notice that those experiments were all performed at 400°C whereas this study deals with a temperature range. In short, leaves (n = 6-10 per species, per temperature class, per moisture level) were horizontally placed in the middle of the furnace, *c.* 3.5 cm above a cradle with three thermocouples (type K, chromel-alumel). A high frequency electrical spark gun was held *c.* 8 mm above each specimen to provide a source of ignition (*sensu* Gill & Moore 1996). This spark gun was removed once the leaves had

ignited. The entire combustion process in the furnace was filmed and later on analysed by using the digital video editor “VideoPad” (NCH Software, Canberra, ACT, Australia). This experimental set-up allowed us to measure TTI as the difference in time between the insertion of the leaf and the first visible flame. Since ignitibility is commonly seen as a result of temperature and moisture content, the gradient of temperatures at which the leaves were burnt and the variation in moisture content as described before gave us a large spectrum to work with, i.e. for building and testing leaf ignitibility models.

Table 5.1 Description of the datasets and study sites characteristics. Long term mean annual rainfall and temperature (based on all available years) from the Australian Bureau of Meteorology (www.bom.gov.au).

Dataset	Study sites <i>Vegetation type</i> <i>Location</i>	Climate <i>Annual rainfall</i> <i>Mean annual temperature (min, max)</i>	Soil type <i>- nutrient status</i>	No. species	No. of data entries <i>(species-means)</i>	Dominant species
This study	Open woodland Kuring-Gai NP 33°41'38"(S) 151°08'35"(E)	1333 mm ⁽¹⁾ 12.3, 22.2 °C ⁽²⁾	Yellow-gray sand (Hawkesbury sandstone) - Low nutrient	9	94 - fresh and air-dried samples tested at 9 temperatures	<i>Eucalyptus haemastoma</i> , <i>Corymbia gummifera</i> , <i>Hakea dactyloides</i> , <i>Lambertia formosa</i>
	Closed forest Kuring-Gai NP 33°34'44"(S) 151°17'32"(E)	1333 mm ⁽¹⁾ 12.3, 22.2 °C ⁽²⁾	Red-brown clay (weathered volcanic dyke) - High nutrient	10	20 - fresh and air-dried samples tested at 408°C	<i>Syncarpia glomulifera</i> , <i>Eucalyptus umbra</i> , <i>Synoum glandulosum</i>
	Open shrub mallee Round Hill 32°58'35"(S) 146°08'45"(E)	421 mm ⁽³⁾ 10.9, 25.1 °C ⁽³⁾	Loamy red sand (Quaternary dune system) - Low nutrient	5	14 - fresh and air-dried samples tested at 309°C and 408°C	<i>Eucalyptus dumosa</i> , <i>Eucalyptus socialis</i>
	Dry open woodland Round Hill 32°58'00"(S) 146°09'17"(E)	421 mm ⁽³⁾ 10.9, 25.1 °C ⁽³⁾	Light red clay (residual deposits Mt Hope volcanics) - High nutrient	8	22 - fresh and air-dried samples tested at 309°C and 408°C	<i>Eucalyptus intertexta</i> , <i>Geijera parviflora</i> , <i>Brachychiton populneus</i>
Gill & Moore 1996	Horticulturally grown Australian plants Australian National Botanical Gardens (and surroundings)	N/A (likely watered) 6.4, 20.7 °C ⁽⁴⁾	N/A (likely fertilised)	50	80 - fresh and oven-dried samples tested at 254°C	N/A
Zylstra 2011	Montane to sub-alpine open forest Kosciusko NP 36°20'51"(S) 148°31'30"(E)	1752 mm ⁽⁵⁾ 2.0, 13.6 °C ⁽⁵⁾	Granitic silty clay to loam, (Kosciuszko batholith)	6	92 - fresh and oven-dried samples tested at 8 temperatures	<i>Eucalyptus pauciflora</i> , <i>Eucalyptus stellulata</i> , <i>Daviesia mimosoides</i> , <i>Bossiaea foliosa</i>

Weather stations used: (1) Riverview Observatory; (2) Duffys Forest; (3) Lake Cargelligo airport; (4) Queanbeyan Bowling Club; (5) Thredbo Village.

Trait selection for models

We started with a very basic model for leaf ignitibility, including furnace air temperature and leaf moisture content only (model 1, Table 5.2). Based on our understanding of the processes related to leaf ignitibility we then included leaf thickness as a predictor (model 2). As an alternative to this model, we also built a model that was based on temperature, moisture content and tissue density (model 3). As a step up from these models we combined leaf thickness and tissue density in model 4. Since leaf thickness and tissue density are by definition (i.e. mathematically) combined in SLA, we also built a model based on temperature, moisture content and SLA (model 5) for comparison with model 4. In theory, model 4 and model 5 should give us the same outcomes. In model 6 and 7, foliar nitrogen and phosphorus concentrations were added. Finally, for fresh leaves only, model 8-11 included just temperature, temperature and thickness, temperature and tissue density or temperature and SLA, respectively. These models could serve as alternative formulations for estimating ignition delay times when leaves are still attached to the plants and no information of the moisture content is available.

Table 5.2 Regression models examining the effects of leaf traits on leaf ignition delay time (logTTI), ranked from best to poorest performing model based on their AIC_c-values. *k* is the number of parameters included in the model (plus one for the intercept). Temp = furnace temperature (°C), FMC = fuel moisture content (% oven dry weight), Thickn = leaf thickness (mm), dens = tissue density (g.mm⁻³), SLA = specific leaf area (cm.g⁻¹), [N] = nitrogen concentration (%), [P] = phosphorus concentration (%). The prefix “log” refers to the base 10 logarithm.

Ranking	Candidate models	R ²	<i>k</i>	AIC _c	Akaike weight (<i>w</i>)
1	(5) Temp, logFMC, logSLA	0.887	4	-624.5	0.68
2	(4) Temp, logFMC, logThickn, dens	0.887	5	-623.0	0.32
3	(6) Temp, logFMC, logSLA, log[N]	0.890	5	-603.9	0.00
4	(7) Temp, logFMC, logSLA, log[P]	0.890	5	-603.1	0.00
5	(2) Temp, logFMC, logThickn	0.818	4	-553.1	0.00
6	(3) Temp, logFMC, dens	0.810	4	-546.5	0.00
7	(1) Temp, logFMC	0.712	3	-486.5	0.00
8	(9) Temp, logThickn (fresh leaves only)	0.789	3	-247.4	0.58
9	(11) Temp, logSLA (fresh leaves only)	0.787	3	-246.8	0.42
10	(10) Temp, dens (fresh leaves only)	0.687	3	-224.1	0.00
11	(8) Temp (fresh leaves only)	0.526	2	-202.1	0.00

Calculations and model selection analysis

Species-mean data for TTI and most leaf traits (all except tissue density) were log-transformed to satisfy the assumptions of normality and homogeneity of variance. Bivariate linear regressions were run to quantify the predictive power of the leaf traits separately, and to confirm the direction of these associations. Next we built the 11 previously described models by means of multiple linear regressions. To compare these models, and calculate the relative importance of the individual predictors (traits), we used model selection analysis as described by Burnham & Anderson (2002) and Symonds & Moussalli (2011).

We used Akaike's Information Criterion (AIC; Eqn. 5.2) modified for small sample sizes (AIC_c; Eqn. 5.3) to rank our set of *a priori* models. The model with the lowest AIC_c value represents the best approximating model for the dataset under consideration. The AIC_c takes into account how well the model fits the data, but models with fewer parameters (*k*) will be favoured to avoid the problem of overfitting. We calculated the Akaike weight (*w_i*; Eqn. 5.4) which represented the probability that model “*i*” was the best approximating model for a given dataset.

$$AIC = n \left[\ln \left(\frac{RSS}{n} \right) \right] + 2k$$

Eqn. 5.2

$$AIC_c = \frac{AIC + 2k(k + 1)}{(n - k - 1)}$$

Eqn. 5.3

$$w_i = \frac{\exp \left(-\frac{1}{2} \Delta_i \right)}{\sum_{r=1}^R \exp \left(-\frac{1}{2} \Delta_r \right)}$$

Eqn. 5.4

Where *RSS* is the residual sum of squares of the model; *n* is the sample size; *k* is the number of parameters included in the model plus one for the intercept; Δ_i is the difference in AIC_c between the best model and each of the other models.

Model validation

To evaluate our models, we compared leaf ignition times based on our models (TTI_{exp}) with observed ignition times (TTI_{obs}) of 56 species from two other studies, i.e., Gill & Moore 1996 and Zylstra 2011. These two studies were executed with a similar experimental set-up but included species from different vegetation types and the leaves were burned at different temperatures (Table S5.1).

The Gill & Moore dataset included 50 Australian species, horticulturally grown in Canberra. Leaves were collected from plants growing in the Australian National Botanical Gardens (44 species), on CSIRO Black Mountain campus (five species), and on the campus of the Australian National University (one species). The 50 species represented 19 distinct families and covered a wide range of leaf traits like leaf thickness and leaf chemistry. Samples of these species were burned at 254°C (corrected temperature, see Table S5.1) for both fresh and oven-dried leaves. The oven-dried leaves were dried at 95°C for at least 22 hours. Moisture contents for the fresh leaves were given, but the values for the oven-dried leaves were not reported. Compared to the oven-dried leaves of the Zylstra dataset (1.4%; dried at 105°C for 24h) we estimated the moisture content for the Gill & Moore leaves to be around 2%. We removed 12 data entries with tissue densities reported to be $> 1.0 \text{ g.cm}^{-3}$ since we considered these to be unrealistic (i.e., they would sink in water) and therefore due to errors in either measurement or reporting.

The Zylstra dataset included six montane and subalpine species from Kosciusko National Park (Table 5.1). Leaves were burned at eight temperature classes, ranging from 175 to 588°C (Table S5.1). Trait data for these species was available for moisture content and thickness. Tissue density was measured from representative samples for each species and values for nitrogen and phosphorus concentration were found in the literature for three of the six species (Bahamonde 2012; Fox & Morrow 1992; Woods & Raison 1983).

For the comparison of the three datasets, we firstly checked and standardised the furnace air temperatures. Our dataset was developed with the same apparatus (muffle furnace and spark gun) and largely followed the methodology of the Gill & Moore and Zylstra studies. However, the placement of thermocouples was slightly modified. Gill and Moore were not specific in regards to their placement of a thermocouple, so this could not be repeated. Zylstra was specific, but in recognition of the significant temperature gradient in the furnace, we decided to place three thermocouples (instead of one) perpendicular to the open

furnace door to provide a more accurate indication of the temperature within the furnace. Consequently, the temperature measurements of these three studies varied slightly. Since for all three datasets 70 mm Whatman filter paper had been used as a control, the temperature inside the furnace could be recalculated (“Standardising test temperatures”, Supplementary Information). Next, by means of regression analysis, the expected TTI values based on our models of interest (TTI_{exp}) were compared with the observed TTI values from the two combined validation datasets (TTI_{obs}). Mean squared errors (MSE), as an unbiased estimate of error variance, was calculated by dividing the residual sum of squares by the number of degrees of freedom.

Results

What are the best predictive drivers for leaf TTI?

As expected, higher furnace temperatures shortened the time-to-ignition, while higher fuel moisture contents led to longer TTIs ($R^2 = 0.19$ and 0.28 , respectively; Table 5.3). Thicker leaves took more time to ignite ($R^2 = 0.22$), but leaf density was unrelated to TTI. Leaves with higher SLA had shorter ignition times ($R^2 = 0.15$). Nitrogen and phosphorus concentration had no significant effect on TTI (Table 5.3).

Table 5.3 Relationships between the parameters and Log TTI, based on bivariate linear regressions for our complete dataset (150 data entries). R^2 and P -values are given. Positive correlations are marked with a plus (+), negative correlations with a minus (-).

Parameters	R^2	P
Temperature (-)	0.19	< 0.001
Log Moisture content (+)	0.28	< 0.001
Log Thickness (+)	0.22	< 0.001
Tissue density	0.02	0.061
Log SLA (-)	0.15	< 0.001
Log N	< 0.01	0.787
Log P	< 0.01	0.652

When we compared the seven models that we built based on our full dataset to explain the variance in TTI, model 1 (including temperature and moisture content only) showed the poorest performance ($R^2 = 0.712$, $AIC_c = -486.5$; Table 5.2). Including thickness or tissue density (model 2 or 3) did increase the explained variation in TTI by approximately 10% ($R^2 = 0.818$ and 0.810 , respectively). Adding extra parameters when comparing model fits is penalised in model selection analysis to avoid problems of overfitting (Cornwell & Weedon 2014), but even though model 2 and 3 had an extra parameter compared to model 1, their AIC_c values were lower (-553.1 and -546.5 ; Table 5.2).

When leaf thickness and tissue density were both included (model 4) this led to a second best prediction of TTI ($R^2 = 0.887$, $AIC_c = -623.0$, Table 5.2). Since SLA comprises both leaf thickness and tissue density, we expected the same result for model 4 and 5. Indeed, the R^2 of both models was exactly the same ($R^2 = 0.887$), while the model based on SLA had a lower AIC_c value due to the lower number of parameters ($k = 4$ instead of 5, Table 5.2). Adding [N] or [P] as explanatory traits improved the model based on SLA (or thickness and density) with 0.3% ($R^2 = 0.890$), but the AIC_c values were higher (-603.9 and -603.1). Altogether, the Akaike weight gave us a 68% probability that model 5 (temperature, moisture content, SLA) is the best approximating model for estimating TTI, followed by a 32% probability for model 4 (temperature, moisture content, leaf thickness and tissue density).

TTI models without known moisture contents for fresh leaves

When we compared the four models for fresh leaves only (i.e. model 8-11), the basic model based on temperature only (model 8) performed worst ($R^2 = 0.526$). Adding tissue density (model 10) increased the explained variation with 16% ($R^2 = 0.687$). However, the models including temperature and either leaf thickness (model 9) or SLA (model 11) performed best ($R^2 = 0.789$ and 0.787); these two models had both a reasonable probability of being the best predictor for TTI (Akaike weights of 0.58 and 0.42, respectively; Table 5.2).

Evaluation of the leaf ignitibility model*All leaves (model 1-7)*

By including leaf traits, five out of six models performed better than the basic model (model 1, $MSE = 0.091$, Fig. 5.3a) when we compared TTI_{exp} with TTI_{obs} . The model that included leaf thickness performed best, with a MSE of 0.061 (Fig. 5.3b), but also model 4 and 5 were an improvement compared to model 1 ($MSE = 0.074$ and 0.79 , respectively; Fig. 5.3c, Table 5.4). The additional inclusion of nitrogen or phosphorus concentration on top of SLA did not lower the MSE further, but still, model 6 and 7 had a lower MSE than model 1 (i.e., 0.080 and 0.086). Only model 3, which adds merely tissue density on top of temperature and fuel moisture content, performed worse compared to the basic model ($MSE = 0.104$, Table 5.4).

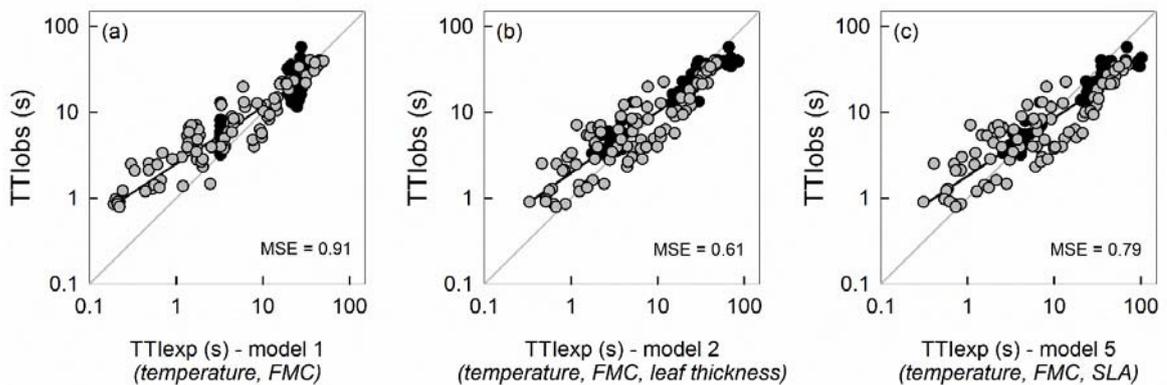


Fig. 5.3 Relationships between expected TTI (TTI_{exp}) and observed TTI (TTI_{obs}) after comparison with the validation datasets. The black bullets represent the Gill & Moore data, the grey bullets represent the Zylstra data. The grey line is a 1:1 reference line ($x = y$). (a) TTI_{exp} as a function of temperature and fuel moisture content (model 1); (b) TTI_{exp} as function of temperature, fuel moisture content and leaf thickness (model 2); (c) TTI_{exp} as a function of temperature, fuel moisture content and specific leaf area (model 5). MSE is given for each association between TTI_{exp} and TTI_{obs} .

Fresh leaves only (model 8-11)

When comparing TTI_{exp} and TTI_{obs} for fresh leaves, the basic model which included temperature only (model 8) showed the worst performance ($MSE = 0.167$, Fig. 5.4a). In all cases including leaf traits improved the accuracy of the predictions. Again, the model that included leaf thickness performed best, with a MSE of 0.028 (Fig. 5.4b). Including density led to a MSE of 0.073 (Table 5.4), and including SLA led to a MSE of 0.049 (Fig. 5.4c).

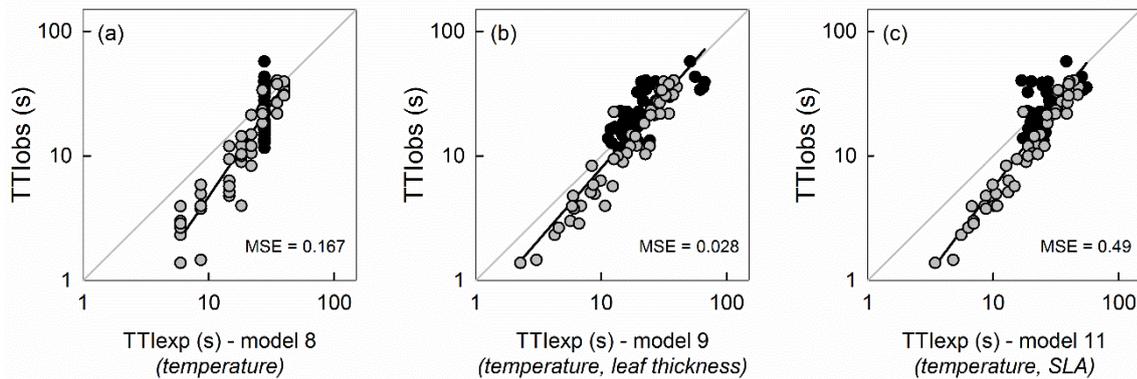


Fig. 5.4 Relationship between TTI_{exp} and TTI_{obs} for fresh leaves only. Black bullets represent the Gill & Moore data, grey bullets represent the Zylstra data. The grey line is a 1:1 reference line ($x = y$). (a) TTI_{exp} is a function of temperature (model 8); (b) TTI_{exp} is a function of temperature and leaf thickness (model 9); (c) TTI_{exp} is a function of temperature and specific leaf area (model 11). MSE is given for each association between TTI_{exp} and TTI_{obs} .

Table 5.4 Equations for Log TTI with the parameter estimates included based on the Grootemaat dataset. Mean squared errors (MSE) are given for the relationships between Log TTI_{exp} and Log TTI_{obs} after comparison with the validation datasets (Gill & Moore 1996, Zylstra 2011). Temp = furnace temperature (°C), FMC = fuel moisture content (% oven dry weight), Thickn = leaf thickness (mm), dens = tissue density (g.mm⁻³), SLA = specific leaf area (cm.g⁻¹), [N] = nitrogen concentration (%), [P] = phosphorus concentration (%). The prefix “log” refers to the base 10 logarithm.

Model	Equation	Validation MSE
(1)	= -0.003*Temp + 0.494*logFMC + 1.123	0.091
(2)	= -0.002*Temp + 0.463*logFMC + 0.821*logThickn + 1.320	0.061
(3)	= -0.003*Temp + 0.548*logFMC + 0.738*dens + 0.666	0.104
(4)	= -0.002*Temp + 0.513*logFMC + 0.712*logThickn + 0.631*dens + 0.903	0.074
(5)	= -0.002*Temp + 0.517*logFMC - 0.693*logSLA + 2.163	0.079
(6)	= -0.002*Temp + 0.525*logFMC - 0.719*logSLA + 0.089*log[N] + 2.177	0.080
(7)	= -0.002*Temp + 0.525*logFMC - 0.705*logSLA + 0.050*log[P] + 2.227	0.086
(8)	= -0.002*Temp + 1.951 (<i>fresh leaves only</i>)	0.167
(9)	= -0.002*Temp + 0.895*logThickn + 2.222 (<i>fresh leaves only</i>)	0.028
(10)	= -0.002*Temp + 0.591*dens + 1.1653 (<i>fresh leaves only</i>)	0.073
(11)	= -0.002*Temp - 0.475*logSLA + 2.739 (<i>fresh leaves only</i>)	0.049

Discussion

Our results demonstrate that leaf TTI could be predicted with a satisfying precision across temperatures and a wide domain of species, leaf traits and moisture conditions. By analysing such a diverse range of species, our models do not only provide fairly robust predictions for other species and ecosystems, but we have been able to empirically test the influence of potential drivers (leaf traits) on leaf TTI and provided indications of the strength of their influences.

The best predictors for leaf ignition delay time

Our results showed that the inclusion of leaf traits, especially leaf thickness, improved the prediction of leaf TTI. This is not completely new, as leaf thickness has been mentioned before as an important factor for leaf ignitibility (e.g. Brown 1970; Montgomery & Cheo 1971; Gill & Moore 1996). However, also the inclusion of tissue density (separately, or combined with leaf thickness in SLA) improved the estimation of TTI in our own dataset. Contrary to expectations from previous studies (Philpot 1970; Mak 1982; Scarff & Westoby 2008), neither leaf [N] or [P] showed a significant effect.

When we compared the expected values of TTI (TTI_{exp}) based on our models, with the observed values of TTI (TTI_{obs}) from the Gill & Moore and Zylstra datasets, the models that included leaf thickness (i.e. model 2 and model 9) performed best. Also the models that included SLA performed better than the model which was merely based on temperature and fuel moisture content. Thus, we conclude that it is indeed important to include leaf traits as parameters for leaf ignitibility. And, by doing this, the estimation of flame length and rate of fire spread in biophysical mechanistic fire behaviour models will be improved.

The inclusion of leaf traits in fire behaviour models also depends on the availability of information for the species in question. Thanks to datasets such as TRY (Kattge *et al.* 2011) our TTI model may be applied in many cases, because leaf thickness and SLA, two widely measured traits, are actually the best predictors of leaf TTI next to temperature and moisture content. Also, measurements of plant traits by means of remote sensing (e.g. Ustin & Gamon 2010; Houborg, Fisher & Skidmore 2015) are very promising in this respect. Knowing what species or functional plant types are growing where, combined with the information on the species specific traits and the live fuel moisture contents (Chuvieco *et*

al. 2002; Caccamo *et al.* 2012; Yerba *et al.* 2013) will lead to better estimations of fuel flammability and the prediction of fire risks. It would be especially valuable to quantify how well leaf thickness and SLA help predict TTI in fire-prone ecosystems outside of Australia, for example in Canadian pine forests, Mediterranean shrublands or African savannas. As long as similar experimental set-ups are used, comparisons of datasets can be made; and the ignitability equation, including the effects of leaf traits, can be further fine-tuned.

Significance of this work for fire behaviour modelling

Accurately predicting leaf ignition delay time is important for estimating flame length and rate of spread in biophysical mechanistic models such as (Zylstra 2011; 2014a, b). In combination with weather, topography and other fuel descriptors, leaf ignitability is critical to the question: “At temperature x , and considering plant species with leaf traits y , will the leaves at location z ignite within a given time?” This information will be of use for ecosystem management practices and firefighting operations. For example, the FFM has already been used to identify positive fire-flammability feedbacks that traditional models had failed to detect (Zylstra 2013), but by incorporating the ignitability equations presented here, we can extend the use of the FFM to more diverse ecosystems with leaf traits outside of the domain of the original Zylstra (2011) TTI equation.

Some authors argue that small scale laboratory flammability experiments are not suitable for upscaling to real-world, full-scale wildfire behaviour because (i) by performing flammability experiments on discrete fuel elements (e.g. leaves or twigs) the fuel elements are taken out of their overall fuel context; and (ii) the laboratory studies are executed at lower temperatures or energy levels and do not replicate the same heat transfer mechanisms and combustion processes as in wildfires (Fernandes & Cruz 2012). We sympathise with the first argument and we would like to emphasise that our work presented here is only a first step, namely to better predict individual leaf ignitability. In addition to this, information is needed about the architecture of the plants and the ecosystem composition to bridge the gap between laboratory results and wildfire behaviour in the field. Our equations should therefore not be considered as solutions in isolation, but can be used to inform our understanding of flammability and fire only if they are integrated into a model that properly considers the surrounding context. However, we disagree with the second argument. We

believe that laboratory studies are of use for wildfire behaviour modelling because the same physical and chemical processes are at play. Even though maximum temperatures and energy fluxes may be higher at a wildfire, leaves do not just ignite at these extreme conditions but will ignite whenever the conditions are right. These ignition thresholds are well-presented by laboratory flammability experiments and provide valuable information for further upscaling. Therefore, careful interpretation of trait-based effects on flammability are useful and, together with an integration of flammability research and databases on plant traits, this may lead to interesting predictions (Varner *et al.* 2015)

Changing climate, for example, is promoting species change in the Amazonian Chiquitano forests of Brazil (Devisscher *et al.* 2016), the tropical montane cloud forests near the Andean tree line (Oliveras *et al.* 2014) and other areas of the Amazon (Olivares *et al.* 2015). How might the changing traits (related to the species change) affect the nature and strength of flammability-feedbacks? Burns *et al.* (2015) found that *E. regnans* forests in south-eastern Australia have a $\geq 92\%$ chance of ecosystem collapse by 2067, with a significant part of the impact being due to fire. The flammability of these forests is related to crown death, which in turn depends on time since fire and associated species composition changes and growth (Lindenmayer *et al.* 2011, Taylor *et al.* 2014). Could a better understanding of these fire-traits-flammability feedbacks inform targeted intervention strategies?

In addition to ecological conservation implications, fire behaviour models are also used to inform decision making in wildfire suppression (firefighting) scenarios. Typical questions asked by fire fighters and Incident Control Teams are: “Is it safe to send fire fighters to that particular area? Do we need to evacuate? How much time do we have?” If leaf traits affect the likelihood for fire to ignite new plant strata and thereby increasing the fire intensity (e.g. larger flame heights, higher rates of spread), then we argue that quantifying that likelihood will facilitate better, more informed decision-making.

Concluding remarks

Our study has highlighted the importance of certain morphological leaf traits (i.e., leaf thickness, density and SLA) on leaf TTI and found little support for the expected influence of others (i.e. leaf [N] and [P]). Including leaf traits in the ignitability equation can improve the prediction of flame heights and rate of spread, and, together with information on species composition, this can expand our knowledge of landscape flammability. If the assembly of

leaf traits will change in an area, e.g. due to species succession, management influences or climate change, this will affect the flammability of the ecosystem.

Leaf flammability, however, is not only underpinned by ignitibility, but burning duration (sustainability) and combustibility are important aspects too. Future work on leaf flammability should therefore focus on the ways that leaf traits affect combustibility and sustainability of burning leaves. Next, the physical arrangement (or architecture) of living plants needs more investigation. How far are the leaves from each other? And how does this effects the threshold level for at which flames from one leaf can ignite other leaves?

We expect that this work, in combination with ongoing work on plant-trait modelling and remote sensing will improve our understanding and predictive power of fire behaviour. Hopefully this will contribute to the conservation of biodiversity and ecosystem functioning of fire-prone vegetation types while ensuring human safety at the same time.

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Supporting information

Standardising test temperatures

As several datasets were used, the temperatures for each were standardised using the measured TTI values for filter paper controls. The first Grootemaat ranged temperature dataset (G1) was used as the standard because more thermocouples (i.e. three) were utilised in the muffle furnace compared to the Zylstra 2011 or Gill & Moore 1996 setup (one thermocouple). The standardising process was to fit a function to the Grootemaat filter paper controls to find an expected TTI per temperature (Fig. S1, Eq. S1), rearrange this equation to find an expected temperature per TTI (Eq. S2), and then correct the values of all test temperatures using this function (Table S1).

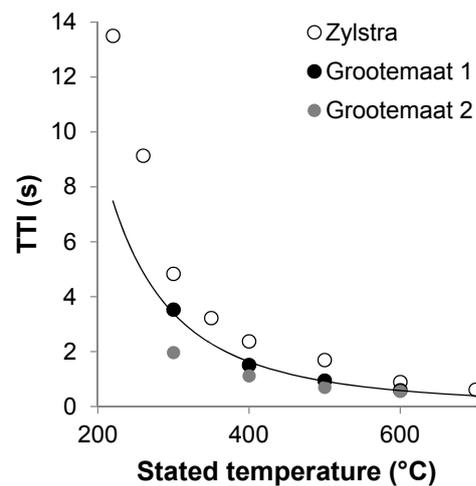


Figure S5.1 Curve for estimating furnace temperatures based on the ignition times of filter paper. Dataset G1 (Grootemaat 1, 300-400-500-600°C) was used as the standard (fitted trend line).

$$TTI = 7010282T^{-2.549}$$

Eqn. S5.1

$$T = \frac{TTI^{\frac{1}{-2.549}}}{7010282}$$

Eqn. S5.2

Table S5.1 Corrections of furnace temperatures based on the ignition times of filter paper (controls). Codes for the different datasets are as follows: G1 = Grootemaat 1, ranged dataset (fresh leaves), G2 = Grootemaat 2, ranged dataset (intermediate moisture contents), G300 = Grootemaat 300°C (air-dried leaves), G400 = Grootemaat 400°C (fresh and air-dried leaves), GM = Gill & Moore 1996, Z = Zylstra 2011.

Dataset	Original temperature (°C)	Standardised temperature (°C)
G1	300	295
G300	300	309
G2	300	372
G1/G400	400	408
G2	400	464
G1	500	496
G2	500	557
G1	600	596
G2	600	612
GM	400	254
Z	220	175
Z	260	203
Z	300	261
Z	350	306
Z	400	345
Z	500	394
Z	600	507
Z	700	588

6. General discussion

What have we learned?

An overarching goal of this thesis was to determine which plant traits are responsible for the interspecific variation in plant flammability and decomposability. More specifically, I quantified the effects of variation in morphological and chemical traits among species from south-east Australia on the flammability of individual leaves, fuel beds and bark chunks, and on bark decomposability. I compared the underlying drivers of species' flammability and decomposability with each other in order to gain a better understanding of the relationship between these two major litter fates, i.e., being consumed during a wildfire or being decomposed by micro-organisms. The key results are summarised below, and implications and future research directions are briefly discussed next.

The role of traits for interspecific variation in flammability of individual leaves

To investigate the effects of leaf traits on individual leaf flammability, I burned leaves from 32 perennial species under controlled conditions in a muffle furnace set at 400°C (*Chapter 2*). Variation among species in leaf time-to-ignition (a proxy of *ignitibility*) was largely driven by morphological traits like SLA, leaf surface area or leaf thickness, and not by chemical traits like N, P, lignin or tannin concentrations. The strongest predictor of leaf time-to-ignition in this particular dataset was SLA. Species with higher SLA ignited more quickly than species with lower SLA. Interestingly, SLA was also a strong driver of *fuel bed* flammability (as further discussed below; *Chapter 3*). Fuel moisture content was important for the ignition time of fresh leaves, but not for air-dried (green) or air-dried senesced leaves.

Can the inclusion of leaf traits in ignitibility equations improve the prediction of fire behaviour? I tested different combinations of leaf traits as predictors for leaf ignitibility (*Chapter 5*). In addition to air temperature and fuel moisture content (which are both known to be important parameters in fire behaviour models; Xanthopoulos & Wakimoto 1993;

Sullivan 2009 a, b; Cruz *et al.* 2015), I evaluated the effects of including leaf thickness, tissue density, SLA, and nitrogen and phosphorus concentration to estimate leaf time-to-ignition. For my dataset, the inclusion of leaf thickness and density (separately, combined or expressed as SLA) led to better predictions of measured leaf time-to-ignition than a model which was based on temperature and moisture content only. This effect was sustained during model validation (considering two independently collected datasets), showing that particularly leaf thickness lowered the Mean Squared Error. Thus, it is indeed important to include leaf traits as parameters for leaf ignitability. By doing this, the estimation of flame length and rate of fire spread in biophysical mechanistic fire behaviour models can potentially be improved. Also, by taking leaf traits into account, future studies can examine how changes to climate or management (and therefore changes in species and trait composition) may affect landscape flammability.

Interspecific variation in leaf flame and smouldering duration (both proxies of fire *sustainability*) were mostly driven by leaf dry mass; when there was more leaf material to be burned (i.e. higher leaf mass) the leaves flamed and smouldered for longer. Higher concentrations of leaf N and P shortened the flame duration, possibly by promoting the formation of a heat insulating char layer during pyrolysis (Scarff & Westoby 2008; Scarff, Gray & Westoby 2012). Leaves with higher tannin concentrations showed prolonged smouldering. What are the implications of this interspecific variation in flame and smouldering duration of leaves for wildfires on a landscape scale? Unexpectedly, I did not find any relationships between flame and smoulder duration of individual leaves and flammability parameters in *fuel beds* (Chapter 3). However, it could be worth investigating (e.g. by modelling) if the fire sustainability of individual leaves *in situ* on living plants will affect fire behaviour.

The role of leaf traits for the flammability of fuel beds

Based on information from the literature (e.g., Scarff & Westoby 2006; Engber & Varner 2012) and my findings in Chapter 2, I designed a conceptual framework that builds up from individual leaf traits, via fuel bed packing, to fire behaviour in fuel beds. I put this framework to the test by burning monospecific fuel beds of 25 species (out of the 32 species from Chapter 2) and I combined the results of the experiments on individual leaves and fuel beds.

Across species, the spatial arrangement of fuel (described by packing ratio) and the intrinsic leaf traits showed strong correlations with maximum temperature during fire, fire spread and burning time. Bulk density of the fuel beds turned out to be a better predictor for the flammability parameters than packing ratio itself. This suggests that a factor related to the residual variance between packing ratio and bulk density contributed to the additional explanatory power of bulk density. Indeed, different leaf traits underpinned the interspecific variation in packing ratio and bulk density. Packing ratio was largely driven by leaf thickness or surface area-per-volume, while bulk density was more closely associated with SLA, leaf curliness and leaf size.

When comparing the results of individual leaf flammability with the flammability of fuel beds, species with shorter individual leaf ignition times (*Chapter 2*) were also shown to be more flammable in fuel beds (e.g. by faster rates of fire spread, *Chapter 3*). The important finding here is that leaf traits which affect individual leaf flammability (like SLA) continue to affect flammability when scaling up from individual leaves to fuel beds. Again, these results suggested that the inclusion of leaf traits could improve fire behaviour models. It gave me extra motivation to test this, and a first step was made in *Chapter 5* where I showed that the inclusion of leaf traits improved the prediction of *individual* leaf ignitibility (as summarised above). The confirmation that species with highly ignitable individual leaves indeed have a higher rate of fire spread through *fuel beds* (by means of a chain of ignition steps; *Chapter 3*) agrees with the underlying theory of biophysical mechanistic models such as assumed in the Forest Flammability Model (Zylstra 2011). Namely, the model makes explicit use of the thresholds at which flames from one leaf can ignite another leaf. This is critical information to predict flame heights and fire spread in fuel beds, the understorey, or in a forest as a whole.

Flammability of bark chunks

Compared to leaf flammability, far less is known about the drivers of interspecific variation in bark flammability. Bark chunks of 10 local woody species varied considerably in their ignitibility measured under standardised conditions in a muffle furnace. Ranging from 2.6 to 14.0 seconds, some species took more time to ignite than others. Although all samples were air-dried, some interspecific variance in moisture content was found and species with higher moisture contents at air-dry equilibrium took longer to ignite. When considering

smooth-bark species only (8 of the 10 species), bark area per mass ($\text{cm}^2\cdot\text{g}^{-1}$) was the strongest predictor of time-to-ignition. Chunks with higher bark area per mass ignited more quickly. This is analogous to our findings on leaf flammability, where interspecific variation in area per mass (SLA) was the strongest predictor of time-to-ignition. When all bark species were included, initial nitrogen concentration showed a negative relationship with bark ignitibility, but more research is needed to fully understand this relationship.

Flame and smouldering durations of the bark samples were largely driven by sample mass of the bark chunks, and therefore there was a considerable variation in flame and smouldering duration both within and among the 10 species. To put it simply, the more material there is to be consumed (burned), the longer the flame and smoulder duration (residence time). Although this may seem an obvious result, it quantifies how the species-specific contribution of bark to the litter layer can be very important for the duration of a surface fire.

In general bark was less “flammable” than leaves. Bark took more time to ignite and, when standardised by sample mass, bark burned for longer (i.e. higher flame and smoulder durations per unit sample mass) compared to leaves. Thus, leaves burn more fiercely, but bark burns for longer. In a surface fire, the prolonged smouldering of bark may have extended consequences for the local soil flora and fauna, by means of thermal damage (Neary *et al.* 1999; Gagnon *et al.* 2010). Also, the prolonged burning of bark is of particular importance when considering firebrands, which can start new fires when spread by wind (i.e. “spotting”; Hines *et al.* 2010; Ellis 2011).

Decomposability of bark chunks

Relatively little is known about bark decomposability. Here, considerable variation in bark decomposition was found among bark material from 10 woody species from the Sydney area. After two years, species-mean bark mass loss varied from 27% to 72%. Variation in bark mass loss was mostly correlated with initial lignin concentration, and secondly with cellulose concentration. Species with higher initial concentrations of these structural compounds decomposed slower, as has been found for leaf litter in numerous studies (e.g. Berg & McClaugherty 2003; Cornwell *et al.* 2008; Fortunel *et al.* 2009).

Bark decomposed more slowly than leaves, especially in the first year of the experiment. After 12 months 7-28% of the initial bark samples was lost, compared to 22-60% of leaves (of the same species). This is important information for estimating litter accumulation (and consequently fuel loads) in fire-prone ecosystems. It can also help us to estimate carbon fluxes, as further discussed below.

Decoupling of flammability and decomposability

Flammability and decomposability of plant material were unrelated when we compared them in bivariate regressions. In *Chapter 2*, focusing on leaf material, the decomposition constant k_1 did not show any association with time-to-ignition, flame duration or smoulder duration (all $P \geq 0.19$). A similar result was found for bark chunks when we compared percentage mass lost (after 12 and 24 months) with time-to-ignition, mass standardised flame and smoulder duration, or combustibility (all $P \geq 0.18$).

How to explain this decoupling? Flammability and decomposability of plant material were underpinned by different combinations of traits. While flammability of leaves (*Chapters 2, 3 and 4*) and bark (*Chapter 4*) was mostly correlated with *morphological* traits like SLA or bark area per mass, decomposability was chiefly driven by *chemical* traits, especially initial lignin concentration. Given this we now have a solid, mechanistic understanding for why fire and decomposition, as two alternative fates for biomass, are unrelated or “decoupled”.

The leaf economic spectrum (Wright *et al.* 2004) and the “fast-slow” plant economics spectrum (Reich 2014) describe correlated sets of traits important for carbon gain, water use and nutrient acquisition strategies, and thus for plant growth. In previous studies it has been shown that leaf economic traits which promote fast growth (e.g. high SLA or high nitrogen concentration) also promote rapid leaf litter decomposition (Cornelissen *et al.* 2001; Santiago 2007; Cornwell *et al.* 2008). However, apart from the relationship between SLA and ignitibility, no strong evidence has been found that flammability is linked to the “fast-slow” economic spectrum. In this thesis I showed that flammability and decomposability of plant material are driven by different traits and that the two fates did not show any form of relationship.

This decoupling of the two fates means that plant material which is slow to decompose (e.g. due to high lignin concentrations) does not necessarily ignite more easily or more slowly.

At a given decomposition rate, a full range of ignitibility, fire sustainability and combustibility are possible. However, the *stage* of decomposition will also affect the flammability of plant material, as was shown by recent work of Zhao *et al.* (2014). Namely, at a given moisture content, further decomposed twigs of a given species had a lower tissue density and therefore ignited easier and burned faster. They were also more flammable because low tissue density led to faster rates of water loss under dry conditions.

The decoupling of flammability and decomposability potentially leads to three different types of scenarios in a forest: (1) Fast decomposing species, for which the flammability of the material might be of little relevance for estimating fire risk because there is a quick breakdown of the biomass and therefore only ever a low fuel load. However, this is strongly dependent on the patterns of litter fall and the resulting litter quantity (fuel load). In case there is a continual layer of senesced leaves, and if these leaves are highly flammable, they will play a role in estimating fire risk. (2) Slow decomposing species with low flammability, for which the slow decomposition can lead to high fuel loads. However, this does not directly translate to high fire risks in case the litter has a relatively low flammability (e.g. species from a temperate rainforest were found to have significantly lower rates of fire spread than species from an adjacent *Eucalyptus* forest (Peacock & Iaconis 2015), although no such differences in flammability were found by Clarke *et al.* (2014). And (3) Slow decomposing species with high flammability. This third scenario is potentially the most important for forest managers: because of the slow decomposition, the litter can accumulate to extremely high fuel loads. And, if a fire starts, there is enough flammable fuel to support a fire of high intensity, with large flame heights and high rates of fire spread. In most forests, however, there will be a mix of relatively fast and slow decomposing species, and species with high and low flammability characteristics. Estimating the actual fire risk is therefore not an easy task. At the end of this general discussion I will describe some suggestions to improve future predictions on fuel flammability and fire risks (see *New research directions*).

Implications

Fuel management planning

In fire-prone ecosystems close to urban areas, land managers generally aim for limiting the risks of wildfires while also maintaining a wide variety of forest functions (e.g. biodiversity conservation, facilitating tourism, timber and paper production, carbon storage, providing water catchments, and so forth; Palo, Uusivuori & Mery 2001). The management of these natural areas is not an easy task given that there are so many demands and different processes at play. When it comes to fuel management it is useful to know what the fuel inputs and outputs are. Litter accumulation and understorey growth can be considered as fuel inputs, while decomposition, mechanical removal and prescribed burning are key fuel outputs. A good understanding of the processes within the ecosystem, together with the management goals, financial and social support, will determine if fuel management activities will take place and be successful.

In *Chapter 4* I showed that bark decomposed slower than leaves and had a lower flammability. Therefore bark can dominate the litter layer and this is indeed easily apparent in many Australian forests. However, litter fall varies with temperature, rainfall, season and species (Crockford & Richardson 1998; Gan & Amasino 1997), and also within species depending on the size and vigour of the plants (e.g. Pook, Gill & Moore 1997). Only a few studies have thus far focused on bark accumulation (e.g. Woods & Raison 1983; Lamb 1985; Pook, Gill & Moore 1997) and very few have explicitly addressed bark decomposition, with the exception of recent work on three species in a northern hardwood forest of the United States (Johnson *et al.* 2014). I am not aware of any bark decomposability studies for Australian forests, which is surprising given the enormous contribution of bark to the litter layer (especially by *Eucalyptus* species) and the substantial variation in relevant bark traits, such as thickness (Rosell *et al.* 2014). The lack of information on bark decomposition rates formed the motivation to devote one chapter of this thesis to bark decomposability (*Chapter 4*). I found a considerable variation in bark decomposition across species and this will determine, together with the interspecific variation in bark-shedding, how much bark will accumulate on the forest floor.

As more specific information on litter/fuel dynamics will become available, better management decisions can be made. For example, given that mass-standardised bark material decomposes slower and burns for longer compared to leaves (*Chapter 4*), and

given that prolonged durations of temperatures above 60°C can lead to thermal damage and mortality of soil flora and fauna (Neary *et al.* 1999; Gagnon *et al.* 2010), land managers can opt for local mechanical removal of bark to promote the conservation of certain target species. However, a good understanding of ecosystem dynamics is needed since (bark) litter can also be beneficial by regulating temperature and moisture retention of the upper soil (Facelli & Pickett 1991).

Another example of fuel management planning is the protection of water catchments. To prevent the negative effects of surface run off and erosion due to uncontrolled wildfires, and the resulting reduction in water quality, the area around dams undergoes frequent low-intensity prescribed burning. The (fine) fuel load around the dams is therefore reduced, and the occurrence of severe uncontrolled fires is minimised. An example of these practices can be found at Mangrove Creek Dam which is the primary reservoir for water supply to residents of the Central Coast, Australia (Gosford Bush Fire Management Committee 2011; Gosford City Council 2012).

Estimation of carbon and nutrient fluxes

I proposed that fire and decomposition can be seen as two major alternative fates for organically-bound carbon in fire-prone ecosystems (*Chapter 1*) - while also acknowledging that herbivory (Cebrian 1999) and degradation by UV radiation (Austin & Vivanco 2006) can be very important in particular situations (but probably less so for bark than for leaf material). Even though the underlying mechanisms of fire and decomposition are essentially different, the rate of combustion and decomposition are both associated with variation in morphological and chemical traits of the fuel/litter (Cornwell *et al.* 2008; Grootemaat *et al.* 2015). In this thesis I showed that flammability and decomposability are driven by different combinations of traits, providing new, quantitative explanations for how and why they are uncorrelated or “decoupled” (see *Decoupling of flammability and decomposability*). When determining these two fates for carbon flux modelling, precision can be added by including trait-based effects as found in this thesis. For example, species with high SLA leaves will ignite easier than species with low SLA leaves. And, in agreement with the literature, I found that species with lower lignin concentrations are more decomposable (both for leaves *and* bark).

When it comes to the estimation of nutrient fluxes (e.g. nitrogen and phosphorus) as influenced by fire and decomposition the story becomes quite complex. Decomposition of organic matter makes nutrients available for uptake by plants. Changes in environmental conditions, such as shifts in temperature or rainfall, will affect the decomposition. In general, decomposition peaks under warm and moist conditions, but when it becomes too warm or too moist the activity of decomposer organisms may decline (Swift, Heal & Anderson 1979). Decomposition processes can be disturbed by the occurrence of a wildfire; the volatilisation of organic matter and increased mortality of decomposers will both have negative effects on decomposition (Neary *et al.* 1999). Fires may also affect the nutrient stoichiometry, which is very important for plant performance and biogeochemical cycling (Elser *et al.* 2010). Different chemical elements have different temperatures at which they are volatilised. For instance, nitrogen and sulphur volatilise roughly at temperatures > 300°C, phosphorus and potassium at > 750°C and calcium and magnesium at > 1500°C (Scott *et al.* 2014). So, fire intensity will affect the local chemical composition of the soil.

When studying the effects of fires on nutrient availability, depending on the research focus the outcomes may seem to be contradictory. Christensen (1987) wrote about this:

“The literature on fire is a bit like the Holy Scripture; by careful selection of results, one can ‘prove’ for example that fire increases, decreases or has no effect on nutrient availability, or that fires result in considerable or negligible loss of nutrient capital from ecosystems.”

This range of possible outcomes of fire effects on nutrient fluxes is determined by the different mechanisms and timeframes studied. Short-term (direct) and long-term (indirect) effects need to be considered, as well as the different nutrient pools. Wildfires may lead (for example but not exclusively) to:

- Soil/litter nutrient loss, due to volatilization (direct);
- Soil nutrient loss due to leaching (mostly direct);
- An increased availability of nutrients to plants by the deposition of ash and heating of the soil (direct);
- An increased availability of nutrients to plants by increased mineralisation rates of soil organic matter (indirect);
- Altered nutrient stoichiometry (mostly direct).

(Raison 1980; Christensen 1987). These nutrient fluxes are very important for plant growth, and studies linking fire, soil fertility and plant function (e.g. Giovannini, Lucchesi & Giachetti 1990) are very important but also rather rare. In this study I looked at the effects of nutrient concentration on plant flammability, but not at the effects of fire on nutrient availability for plants. New research that would focus on fire-nutrient-plant feedbacks, by comparing interspecific variation in plant flammability parameters, pre- and post-fire nutrient pools and post-fire plant traits, for different ecosystems and soil types, could give us more insight into these complex ecological processes.

New research directions

In this thesis I studied the effects of leaf traits on *individual leaf flammability*. In combination with the already existing literature on individual leaf flammability (e.g. Mak 1982; Gill & Moore 1996; Murray, Hardstaff & Phillips 2013) I believe we now have a general understanding of the combined effects of morphological leaf traits and nutrient concentration on leaf ignitibility and fire sustainability for a wide range of species. However, in this thesis I focused on plant species from south-east Australia only. Although I worked with species that covered a wide range of leaf traits (e.g., one-sided leaf area varying from 1 to 43 cm², leaf thickness varying from 0.3 to 1.3 mm), it would be very interesting to see how the leaf traits and flammability patterns hold when examining other fire-prone ecosystems (e.g. Mediterranean shrublands, northern hemisphere pine forests or African grasslands). Another factor that has not been explicitly quantified for a wide range of species is the impact of terpenes on leaf flammability (except for 6 species from southern France and Spain; Ormeño *et al.* 2009); this could be a challenge for future research.

Fuel bed experiments have been performed all over the world, for a wide range of vegetation types. These experiments include experiments on litter from oak and mixed conifer forests in California (Engber & Varner 2012; de Magalhães & Schwilk 2012), litter layers from representative forests and shrublands in southern France (Ganteaume *et al.* 2011), Australian litter (e.g., Scarff & Westoby 2006; *Chapter 3*) and litter from a wide range of gymnosperms (Cornwell *et al.* 2015). As long as similar set-ups are used, the results of these studies could be combined in a meta-analysis to investigate if there are universal trends in fuel bed flammability worldwide. Such meta-analysis has not yet been done. Next, fuel bed flammability studies on species mixtures and non-additive effects of dominant species deserve more attention (van Altena *et al.* 2012; de Magalhães & Schwilk 2012), and experiments on controlled mixtures of plant parts (e.g., leaves & twigs or leaves & bark) could lead to new insights (e.g. van Altena *et al.* 2012).

When it comes to the characteristics and fates of *bark* many questions still remain: Why is there not such an apparent bark shedding in other ecosystems around the world? Why do some Australian tree species shed their bark so extensively, while other species in the same genus do not shed their bark at all? And, depending on the vegetation type, how much bark is shed on a yearly base, and how does this relate to the amount of litter from other organs (i.e., leaves, twigs and fruits)? In this thesis I quantified the decomposability and

flammability of bark chunks from 10 species from the Sydney region (south-east Australia). It would be fascinating to examine how these results relate to future results from other bark shedding species such as *Eucalyptus globulus*, which is native to southern Victoria and Tasmania but has been cultivated worldwide, mainly for paper pulp production (Turnbull 1999).

Another challenge that remains is the use of trait-based data to make predictions for ecosystem functioning and management practices on a landscape scale. How can we bridge the gap between small-scale trait measurements and large scale ecosystem dynamics? The use of models that allow for the inclusion of plant traits will likely improve the precision of predictions for carbon and nutrient fluxes.

A first attempt was made to improve the leaf ignitability equation in a biophysical mechanistic fire behaviour model (i.e., FFM, Zylstra 2011) by evaluating the impact of including leaf traits on the estimation of leaf ignition delay time (*Chapter 5*). A next step would be to do something similar for flame durations (fire sustainability) of individual leaves for a wide range of species. Using this information in combination with the physical arrangement of leaves in the litter layer, or the architecture of living plants would be another challenge. Data from extensive plant trait databases like TRY (Kattge *et al.* 2011) together with estimates of plant traits from remote sensing (Ustin & Gamon 2010; Houborg, Fisher & Skidmore 2015) will give us a good indication of the characteristics of certain vegetation types, and future measurements on twig, branch and bark traits could further improve this. Knowing what species or functional plant types are growing where, combined with the information on the species specific traits and the live fuel moisture contents (Chuvieco *et al.* 2002; Caccamo *et al.* 2012; Yebra *et al.* 2013) will lead to better estimations of fuel flammability and the prediction of fire risks in the future. This information may be of use for ecosystem management practices and firefighting operations. Hopefully this will contribute to the conservation of biodiversity and ecosystem functioning of fire-prone vegetation types while ensuring human safety at the same time.

While challenges remain, the research as presented in this thesis has given us new insights into the flammability of individual leaves, fuel beds and bark chunks. Also, for the first time, bark decomposition for a set of Australian species has been quantified. Leaf and bark traits as the drivers of decomposition and flammability have been identified, and it was shown that interspecific variation in decomposability and flammability, as two alternative fates, are mostly unrelated.

“I will be a hummingbird; I will do the best I can”

Wangari Maathai

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