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Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits

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Abstract

1. Flammability is an important plant trait, relevant to plant function, wildfire behaviour and plant evolution. However, systematic comparison of plant flammability across ecosystems has proved difficult because of varying methodologies and assessment of different fuels comprising different plant parts. We compared the flammability of plant species at the leaf-level (most commonly used in flammability studies) and shoot-level (which retains aspects of plant architecture). Furthermore, we examined relationships between leaf functional traits and flammability to identify key leaf traits determining shoot-level flammability.
2. We collated and analysed existing leaf- and shoot-level flammability data from 43 common indigenous perennial New Zealand plant species, along with existing data on leaf morphological and chemical traits.
3. Shoot-level flammability was decoupled from leaf-level flammability. Moreover, leaf-level rankings of flammability were not correlated with rankings of flammability of plants derived from expert opinion based on field observations, while shoot-level rankings had a significant positive relationship. Shoot-level flammability was positively correlated with leaf dry matter content (LDMC), phenolics and lignin, and negatively correlated with leaf thickness.
4. *Synthesis*. Our study suggests that shoot-level measurements of flammability are a useful and easily replicable way of characterizing the flammability of plants, particularly canopy flammability. With many parts of the world becoming more fire-prone, due to anthropogenic activities, such as land-use change and global warming, this finding will help forest and fire managers to make informed decisions about fuel management, and improve modelling of fire-vegetation-climate feedbacks under global climate change. Additionally, we identified some key, widely measured leaf traits, such as leaf dry matter content (LDMC), that may be useful surrogates for plant flammability in global dynamic vegetation models.

KEYWORDS
fire ecology, functional traits, leaf chemistry, leaf flammability, plant architecture, shoot flammability

1 | INTRODUCTION

Plant flammability describes the ability of plant biomass to ignite and sustain a flame when exposed to fire (Gill & Zylstra, 2005; Pausas, Keeley, & Schwilk, 2017). Plants fuel most of the wildfires on earth and plant flammability plays a central role in determining the intensity and severity of wildfires (Beckage, Platt, & Gross, 2009; Pausas et al., 2017; Simpson et al., 2016). In recent years, wildfire activity has increased in terms of area burned and the frequency of high severity fires, and many parts of the Earth that are not normally fire-prone have experienced devastating wildfires (Anonymous, 2017; Doerr & Santín, 2016; Flannigan et al., 2013; Miller, Safford, Crimmins, & Thode, 2009; Westerling, 2016). This trend is mainly due to anthropogenic activities (such as land-use change and extensive fire prevention activities), and human-induced climate change, which contributes to higher temperatures, increased drought frequency and intensity, altered forest composition and productivity, increased vegetation dryness and longer fire seasons (Abatzoglou & Williams, 2016; Flannigan, Stocks, Turetsky, & Wotton, 2009; Jolly et al., 2015; Le Page et al., 2017). Management of wildfires requires accurate characterization of plant flammability (Chuvieco, González, Verdú, Aguado, & Yebra, 2009; Dimitrakopoulos, 2001; White & Zipperer, 2010). An understanding of plant flammability can also inform fundamental research. For instance, flammability is recognized as a core plant functional trait (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013) and is a key factor in understanding the evolution of land plants (Pausas & Moreira, 2012; Schwilk & Ackerly, 2001), particularly given the 420 million-year shared history of plants and fire (Glasspool, Edwards, & Axe, 2004; He, Belcher, Lamont, & Lim, 2016; Scott, 2018). Flammability can influence the fitness, survival, reproduction and distribution of plants, as seen by the evolution of flammability strategies in fire-prone environments (Bond & Midgley, 1995; Mutch, 1970; Pausas et al., 2017). Recently, there have been renewed efforts in plant flammability research to tackle fundamental topics such as the evolution of plant flammability (Archibald et al., 2018; Battersby, Wilmshurst, Curran, McGlone, & Perry, 2017; Pausas et al., 2017), and in an applied context to provide information useful for fire management (Krix & Murray, 2018; Wyse et al., 2016; Zylstra, 2018), building on past work in such areas (Bond & Midgley, 1995; Gill, 1981; Kerr, Schwilk, Bergman, & Feldman, 1999; Mutch, 1970). However, there is still considerable debate on how best to measure plant flammability and therefore, how to appropriately quantify this important plant trait (Schwilk, 2015; Varner, Kane, Kreye, & Engber, 2015).

Quantification of flammability is not straightforward. Plant flammability can be separated into four different components: (a) ignitibility (ignition delay time or temperature required to ignite any fuel); (b) combustibility (how much temperature the fuel emits or heat release rate); (c) sustainability (how long the fuel continues to burn); and (d) consumability (how much of the fuel is consumed during a fire) (Anderson, 1970; Martin et al., 1994; White & Zipperer, 2010). Moreover, plant flammability has been measured using a variety of methods (White & Zipperer, 2010), at multiple levels (leaf, shoot, whole plant) and for different fuel types (canopy and litter) (Jaureguiberry, Bertone, & Diaz, 2011; Murray, Hardstaff, & Phillips, 2013; Pausas, Alessio, Moreira, & Segarra-Moragues, 2016; Pausas & Moreira, 2012; Schwilk & Caprio, 2011). Most flammability experiments have been conducted in the laboratory on small plant components (i.e. leaves, leaf litter, small twigs or needles, bark, woody debris) due to ease of sample collection and manipulation during burning (Ganteaume, Jappiot, Lampin, Guijarro, & Hernando, 2013; Grootemaat, Wright, Bodegom, Cornelissen, & Shaw, 2017; Kauf, Fangmeier, Rosavec, & Španjol, 2015; Mason, Frazao, Buxton, & Richardson, 2016; Zhao, Logtestijn, Werf, Hal, & Cornelissen, 2018). It has been argued that these fine-level laboratory tests do not scale up to predict canopy flammability or crown fire in the field, at least in part because they do not adequately account for plant architecture (Fernandes & Cruz, 2012).

High-intensity crown fires are mostly initiated from surface fuels that, with the necessary environmental conditions, climb into the canopy using understorey shrubs and low-lying branches as ladder fuels (Blauw, Logtestijn, Broekman, Aerts, & Cornelissen, 2017; Wang, Wonkka, Grant, & Rogers, 2016). Some ecosystems (e.g. grasslands, shrublands, and North American boreal forest) are more prone to crown fires due to their vegetation structure, where canopies extend to the ground and act as ladder fuels (Bradstock & Gill, 1993; Kafka, Gauthier, & Bergeron, 2001). With the increasing occurrence of crown fires worldwide, there is an urgent need to better characterize canopy fuel characteristics (Cruz, Alexander, & Wakimoto, 2003; Mitsopoulos & Dimitrakopoulos, 2007). While burning entire plants is more appropriate for understanding crown fire behaviour (Etlinger & Beall, 2005; Stephens, Gordon, & Martin, 1993; White, DeMars, & Bishop, 1997), this approach is logistically challenging and expensive (Jaureguiberry et al., 2011; Pausas & Moreira, 2012). In response to this challenge, a low-cost device for measuring shoot-flammability was developed by Jaureguiberry et al. (2011) and has been promoted because it facilitates rapid measurement of the relative flammability of many species (Perez-Harguindeguy et al., 2013; Schwilk, 2015). Additionally, the plant flammability rankings derived from these shoot-level measurements are highly correlated with independent rankings determined by expert opinion based on observation of plant flammability in the field (Wyse et al., 2016), suggesting that the shoot-level measurements might scale up to canopy flammability. Despite these advances, the outcomes from different methodologies and levels of flammability measurements are often incomparable, providing conflicting information when attempts are made to upscale to whole plant flammability or fire behaviour in the field (White & Zipperer, 2010). Thus, to better characterize plant flammability and to improve predictions of flammability across different fuel levels, it is essential to compare the flammability of different fuel types quantified using different methodologies.

The flammability of plants is likely to be related to their functional traits. Some traits, such as the retention of dead plant matter, presence of volatile chemicals, and high leaf dry matter content (LDMC), can enhance flammability, whereas other traits, such as high moisture content, thick leaves, and high fuel density, decrease flammability (Anderson, 1970; Cornelissen et al., 2003; Murray et al., 2013; Pausas et al., 2016; Simpson et al., 2016). Among these traits, leaf physical and chemical traits affect ignitibility, combustibility and sustainability of single leaves (Alessio et al., 2008; Grootemaat, Wright, Bodegom, Cornelissen, & Cornwell, 2015; Murray et al., 2013), whereas fuel loading, branching pattern and other architectural traits are important determinants of whole-plant flammability (Fernandes & Cruz, 2012; Schwilk, 2003; Zylstra et al., 2016). Several studies have sought to predict flammability and fire behaviour from functional traits at leaf, litter, whole plant, and ecosystem levels (Grootemaat, 2015; Schwilk & Caprio, 2011; Simpson et al., 2016; Zylstra et al., 2016). It is expected that shoot-level measurements provide an appropriate quantification of canopy flammability (Schwilk, 2015) as the shoots preserve the architecture of the plant (Jaureguiberry et al., 2011; Wyse et al., 2016). Because of this, understanding the relationships between traits and shoot flammability should enhance our knowledge of how certain species may influence crown fires. While several studies have estimated plant and community flammability at individual-, ecosystem-, or biome-level by measuring shoot-level flammability (e.g. Burger & Bond, 2015; Calitz, Potts, & Cowling, 2015; Jaureguiberry et al., 2011; Padullés Cubino, Buckley, Day, Pieper, & Curran, 2018; Wyse et al., 2016), few have quantitatively assessed trait-flammability relationships. Calitz et al. (2015) compared ordinal trait values, including leaf size, leaf texture, leaf density and twigginess (number of twigs per unit volume), to shoot flammability, and found that plants with small leaves and high twigginess had relatively high flammability. However, Calitz et al. (2015) identified few robust trait-flammability relationships and concluded that other, unmeasured traits better predicted flammability, or that the measured traits interacted to influence flammability. Leaves are usually the first parts of a plant to be ignited and mostly burn along with terminal branches during fires (Belcher, 2016; Midgley, Kruger, & Skelton, 2011; Murray et al., 2013), and so leaf traits are expected to influence plant flammability. In addition, leaves are a fuel component that is strongly linked to fire behaviour, and leaf traits are increasingly used to understand the pattern of fire behaviour in the field (Schwilk & Caprio, 2011; Zylstra et al., 2016). Leaf traits can also reflect the architecture of a shoot as a narrow, frequently branched shoot often has many small leaves, whereas thick shoots typically support fewer, bigger leaves (Corner, 1949; Westoby & Wright, 2003). Moreover, the chemistry of a plant shoot can be reflected by leaf traits, for example, broad leaves contain more water and needle leaves often contain more volatile components (Materić et al., 2015; Rowe & Scotter, 1973). Given these links with fire behaviour, shoot architecture and shoot chemistry, leaf traits are expected to influence the burning characteristics of a shoot, and an improved understanding of these relationships would help to upscale from leaf-level functional traits to fire behaviour in different biomes (Archibald et al., 2018; Schwilk, 2015). Finally, for many species, leaf traits are comparatively easy to measure and there are extensive data held in large global databases (e.g. TRY; Kattge et al., 2011). Therefore, if we can identify quantitative relationships between shoot flammability and leaf morphological and chemical traits, these extensive global trait databases can be unlocked to predict shoot flammability across many species.

We used measurements of leaf functional traits, and leaf- and shoot-level flammability taken across 43 common indigenous perennial New Zealand plant species to (a) explore how flammability differs between leaf- and shoot-level measurements for the same species; (b) compare the leaf-level (Mason et al., 2016) and shoot-level (Wyse et al., 2016) flammability rankings with the flammability of the same species in field conditions as determined by expert opinion (Fogarty, 2001); and (c) explore which suites of leaf traits, if any, are correlated with shoot flammability. While a recent study by Ganteaume (2018) compared leaf and litter bed level flammability, to our knowledge, ours is the first study to compare the most commonly used plant flammability measurement (i.e. leaf-level flammability) to an approach (shoot-level flammability) that retains aspects of plant architecture, and which then assesses each approach against independently determined rankings derived from expert opinion of field-based fire behaviour.

2 | MATERIALS AND METHODS

2.1 | Species used in this study

To assess plant flammability and its relationships with leaf functional traits, we compiled existing flammability and functional trait data for 43 common indigenous New Zealand plant species across 35 families. Species were chosen based on the availability of both the functional trait and flammability data on the same species. These species comprised twenty-two angiosperm trees, five coniferous trees, five ferns (including three tree ferns), one long-lived forb, one grass, six shrubs, and three lianas. The species were collected from a broad range of habitats on the North, South and Stewart Islands of New Zealand. Data were obtained using leaves from 10–40 individuals per species for the leaf-level data, and single 70 cm-long shoots from 6 to 21 individual plants per species for the shoot-level data. For details describing the species and their sampling see Table S1, Mason et al. (2016), Wyse et al. (2016) and Padullés Cubino et al. (2018).

2.2 | Functional trait measurements

We obtained leaf morphological and chemical trait data from Mason et al. (2016), or the Manaaki Whenua-Landcare Research Traits

Database (https://ecotraits.landcareresearch.co.nz/). In those studies, at least ten fully expanded leaves from each species were used to measure the functional traits (Figure S1, Table S3). The leaf area, perimeter, length and width were measured from digital images (Epson Expression 10000XL scanner) and WinFOLIA Pro V. 2012 software (Regent Instruments Inc.). Leaf thickness was measured with callipers, and fresh mass was recorded for all leaves. Leaf volume was calculated by multiplying the leaf area by the thickness and used to calculate leaf surface area to volume ratio (SA:V). The leaves were then oven-dried at 60°C for 48 hr to obtain the leaf dry mass (LDM), which was used to calculate specific leaf area (SLA) and LDMC. Among the chemical traits, percent nitrogen (N) and phosphorus (P) were calculated using the acid digest and colorimetric methods of Blakemore et al. (1987). The percent acid detergent cellulose and percent acid detergent lignin were determined using the acid detergent method described by Rowland and Roberts (1994). The percent condensed tannins was calculated using the vanillin method of Broadhurst and Jones (1978) and total phenols were quantified using the method of Price and Butler (1977).

2.3 | Flammability trait measurements

We collated shoot-level flammability data of 43 plant species from Wyse et al. (2016), Padullés Cubino et al. (2018) and D. Donkers, M. A. Alam, J. Bréda, S. Blackwood, D. O'Connell, and T. J. Curran (unpublished data), while the leaf-level flammability data for the same species were obtained from Mason et al. (2016). To measure shoot-level flammability, 70 cm-long terminal shoots of woody plants or ferns, and the lower 70 cm parts of herbs or grasses were burnt in the apparatus described by Jaureguiberry et al. (2011) as modified by Wyse et al. (2016). First, the samples were laid horizontally on the grill on the top of the apparatus, taking care to preserve their natural arrangement. The burners and a blowtorch were positioned below the grill. The burners maintained the grill temperature at *c*.150°C throughout the burning period, while the blowtorch provided an ignition source for the samples. After preheating the samples on the grill for two minutes, the blowtorch was turned on for 10 s to provide the ignition. Measurements started immediately after the blowtorch was turned off. Four flammability traits (Table 1) were assessed to characterize flammability of plants at the shoot-level. At least eight individual shoot samples were used in burning for each species with the exception of *Polystichum vestitum* (*n* = 6) and *Agathis australis* (*n* = 7) (Table S1) (for details see Wyse et al., 2016).

To measure leaf-level flammability, single leaves of each plant species were burnt in a muffle furnace (chamber size 380 × 180 × 128 mm) at an oven temperature of 400–430°C, and attached to two thermocouples: one on the hot plate and one at the centre of the oven. At least five individual leaves were burnt from each species, and the entire leaf area was combusted in each burning trial. Leaf temperature was calculated using the thermocouple attached to the centre of the leaf (Mason et al., 2016). A data logger (Campbell 21X) was used to record temperature readings from each of the thermocouples at intervals of 0.5 s. Three flammability traits—leaf temperature at smoke production (smoke temperature), leaf temperature at ignition (ignition temperature) and rate of temperature increase from the time of smoke production to maximum recorded leaf temperature (rate of heat release)—were calculated (for details see Mason et al., 2016).

2.4 | Field-level plant flammability ranking by expert opinion

Flammability rankings based on expert opinion were taken from Fogarty (2001) for a subset of the species. These rankings were derived from a quantitative analysis of ordinal classifications of plant flammability (High, Moderate/High, Moderate, Low/Moderate, Low) based on field observations by 59 fire managers of species' burning characteristics during wildfires or prescribed burns across New Zealand. Forty-two indigenous New Zealand species (mostly trees and shrubs) were ranked using the average flammability score derived from observations by fire managers. Of the 42 species assessed

TABLE 1 The variables used in this study to assess flammability at both the shoot and leaf levels

Level	Parameter	Measurement method
Shoot	Ignition percentage (%) as ignitibility	Percentage of sample that ignited during the burning of the sample
	Maximum temperature (°C) as combustibility	Highest temperature measured during burning of the sample
	Burn time (s) as Sustainability	The duration of flaming combustion
	Burnt biomass (%) as Consumability	Percentage of fuel consumed by fire during burning
Leaf	Ignition temperature (°C) as ignitibility	Temperature required to ignite the leaf
	Smoke temperature (°C) as ignitibility	Temperature required to produce smoke from the leaf
	Heat release rate (°C) as combustibility	Rate of temperature increase from the time of smoke production to maximum temperature

by Fogarty (2001), we retained only those species that were common with our leaf- (n = 28) and shoot-level (n = 31) data.

2.5 | Data analysis

A principal component analysis (PCA) was conducted, including four shoot-level flammability traits and three leaf-level flammability traits (Table 1). This PCA allowed us to examine the relationships between these different flammability traits. A shoot-only PCA and a leaf-only PCA were used to rank species by both shoot and leaf-level flammability based on the first component PCA score at each level (following Wyse et al., 2016). This component explained the majority of the variation in the data in each level (shoot-level: 83% (Figure S2a) and leaf-level: 77% [Figure S2b]). We used Spearman's rank correlation to compare the flammability ranking based on leaf (28 species) and shoot (31 species) data with the rankings as determined by expert opinion (Fogarty, 2001), to understand how the flammability of plants at the leaf and shoot levels correlated with the flammability of plants in the field.

In addition, separate PCAs were conducted using leaf morphological and chemical traits to visualize their covariation across species (Figure S3). All PCAs were performed using the *princomp* function from *stats* package in R version 3.4.1 (R Core Team 2017) using the correlation matrices of the data as the variables were measured using different units.

Also, the sum of squares data from an analysis of variance (ANOVA) was used to partition variance in each flammability trait into among-species and within-species components.

To explore how the leaf traits were related to the components of shoot flammability, generalized linear models (GLM) were used to establish the strength and direction of leaf traits contributing to each measured flammability trait. GLMs used a Gamma error distribution with a log link function determined by the distribution of the response variables in quantile-quantile plots. Multicollinearity between the functional traits was assessed using Pearson's correlation coefficient (Figure S1) and variance inflation factors (VIF). VIF was calculated using the function *vif* in the R package *car* (v 3.0-0) (John & Sanford, 2011). Due to strong correlations between some traits, we restricted our analyses to nine, uncorrelated traits that maximized the trait variation analysed ($-0.6 < r < .6$; VIF < 3) (Dormann et al., 2013; Zuur, Ieno, & Elphick, 2010). Leaf dimensions were highly correlated, so only leaf length was included in the analysis and leaf width and perimeter were removed. LDM and SLA were included instead of leaf area and SA:V, while leaf phosphorus and phenolics were included, and nitrogen and tannins removed. To allow better comparisons with existing studies, when faced with a choice between two highly correlated traits, we retained the one that had been more widely used in other studies as a predictor of flammability. All predictor variables were standardized using the *scale* function in R prior to analysis so that parameter estimates were on a comparable scale. For each GLM, we calculated the variance function based R-squared values (R^2) (Zhang, 2017) using the R package *rsq* (v 1.1) (Zhang, 2018) to assess model fit. Due to missing values for some traits, 39 species were included in the GLM analysis. Also, we calculated the Pearson Correlation Coefficients between the leaf traits and shoot flammability traits (Table S6). All analyses were performed using functions and routines implemented in the R software package version 3.4.1 (R Core Team, 2017).

3 | RESULTS

3.1 | Flammability differences between leaf and shoot level

Principal component analysis of the plant flammability data showed that leaf-level flammability traits were orthogonal to shoot-level flammability traits (Figure 1). The first two components of the PCA represented most of the variation (81%) in the data. The first PCA axis explained 49.6% of the variation and was mainly associated with the four shoot flammability traits, whereas the second axis explained 31.6% of the variation and was mainly associated with leaf flammability traits. All shoot-level flammability traits were negatively loaded on PCA axis 1 (ignition percentage: −0.458; maximum temperature: −0.498; burn time: −0.460 and burnt biomass: −0.481), while two of the leaf-level flammability traits had positive (ignition temperature: 0.547 and smoke temperature: 0.592) and the third had negative (rate of heat release: −0.518) loadings on the second axis. At the shoot-level, species with a low PCA score for all four traits on both axes were more flammable, whereas species with a high PCA score for ignition temperature and heat release

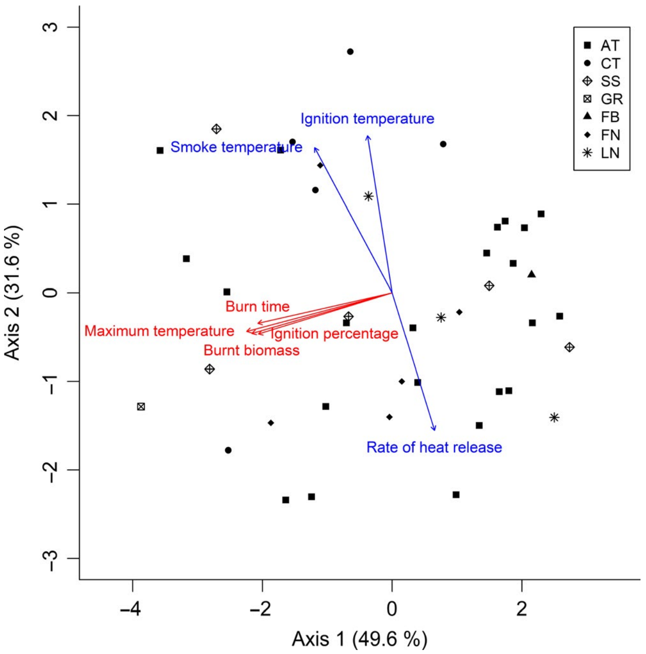

FIGURE 1 Principal component analysis (PCA) of the four shoot-level flammability traits (red vectors: ignition percentage, maximum temperature, burn time and burnt biomass) and three leaf-level flammability traits (blue vectors: ignition temperature, smoke temperature and rate of heat release). Each point is a species mean score. AT, Angiosperm tree; CT, Conifer tree; FB, Forb; FN, Fern; GR, Grass, LN, Liane; SS, Shrub [Colour figure can be viewed at wileyonlinelibrary.com]

rate on the first axis and a low PCA score for all three traits on the second axis were more flammable at the leaf-level.

3.2 | Comparing plant flammability at the leaf and shoot level to expert opinion at the field level

The species leaf-level flammability ranking was not correlated with the flammability ranking of plants based on expert opinion derived from field observation (Spearman's $\rho = -0.279$, $p = .17$; Figure 2a). However, the flammability ranking at the shoot-level was positively correlated with the flammability ranking of plants based on expert opinion (Spearman's $\rho = 0.70$, $p < .0001$; Figure 2b).

3.3 | Relationships between leaf functional traits and shoot flammability

The proportion of variance in all the shoot flammability traits was found to be higher between (58% and 68%) than within species (32% and 42%) (Table S5). All four shoot flammability traits were related to leaf functional traits, with a suite of leaf morphological and chemical traits being most associated with shoot-level flammability. The amount of variation explained by leaf traits varied from the highest for combustibility ($R^2 = 0.63$) to the lowest for consumability ($R^2 = 0.41$). The leaf traits that significantly contributed to explaining each of the flammability traits were LDMC, leaf thickness, phenolics and lignin (Table 2). Overall, among all leaf traits, LDMC was most strongly associated with flammability and showed a positive relationship with all flammability traits (Table 2, Figure 3). Plants with high LDMC ignited faster, burnt at a higher temperature, burnt longer, and had greater biomass consumption. Leaf thickness was another morphological trait negatively related to ignitibility ($p < .05$) with thick-leaved plants taking longer to ignite (Table 2, Figure 3), although the significant relationship did not hold when the thick-leaved plant (*Phormium tenax*) was excluded from the analysis. In contrast, leaf length, LDM, and SLA made minor contributions to explaining the shoot flammability traits (Table 2; Table S6).

Lignin was the most important leaf chemical trait and was significantly positively associated with all shoot flammability traits except ignitibility (Table 2, Figure 3). Phenolic content was another important chemical trait and had a significant, positive association with combustibility ($p < .01$). In contrast, both phosphorus and cellulose were not significantly associated with shoot flammability (Table 2).

4 | DISCUSSION

4.1 | Plant flammability differs at the leaf and shoot levels

Our study demonstrates that measurements of shoot-level flammability are decoupled from leaf-level flammability, which suggests that

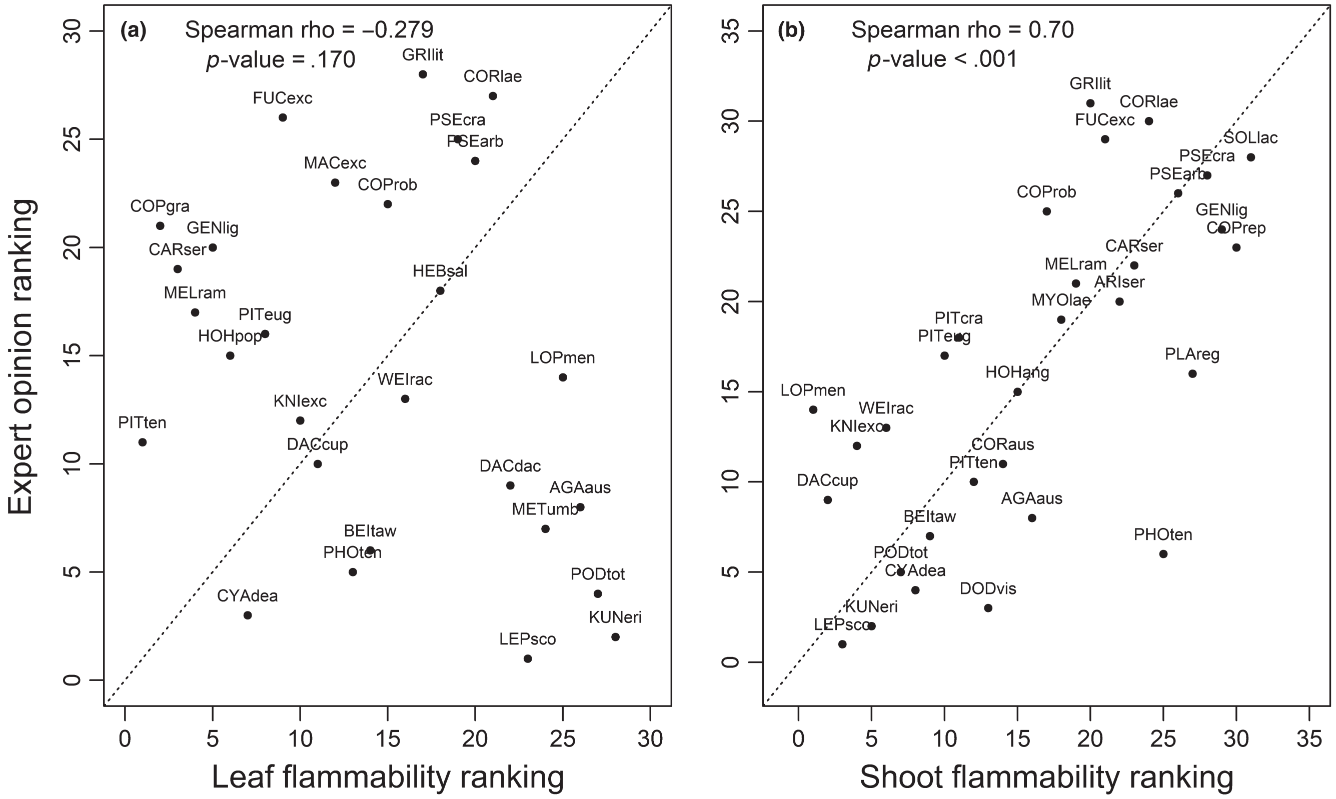

FIGURE 2 Comparison of species flammability rankings derived from both leaf-level (a) and shoot-level (b) data with those determined by Fogarty (2001) using expert opinion. The dashed line indicates where points would lie in a perfect correlation between both ranking systems. Lower numbers indicate higher flammability. See Table S1 for species codes

TABLE 2 Contribution of leaf functional traits to shoot flammability as determined by generalized linear models

Traits	Ignition percentage (%)	Maximum temperature (°C)	Burn time (s)	Burnt biomass (%)
Leaf length	0.031 ± 0.07	0.072 ± 0.05	−0.032 ± 0.17	0.019 ± 0.14
Leaf dry mass	0.026 ± 0.10	0.041 ± 0.08	0.020 ± 0.28	−0.045 ± 0.22
Leaf dry matter content	0.177 ± 0.09*	0.158 ± 0.07*	0.567 ± 0.24*	0.617 ± 0.18**
Leaf thickness	−0.180 ± 0.08*	−0.043 ± 0.06	−0.107 ± 0.21	−0.293 ± 0.17
Specific leaf area	−0.071 ± 0.09	−0.15 ± 0.07	0.108 ± 0.24	0.269 ± 0.19
Phosphorus	−0.015 ± 0.06	−0.043 ± 0.04	−0.138 ± 0.17	−0.009 ± 0.13
Phenolics	0.102 ± 0.06	0.123 ± 0.04*	0.068 ± 0.16	0.197 ± 0.13
Lignin	0.114 ± 0.08	0.209 ± 0.06**	0.502 ± 0.21*	0.432 ± 0.17*
Cellulose	0.017 ± 0.08	−0.016 ± 0.06	−0.045 ± 0.21	−0.104 ± 0.16
R^2	0.48	0.63	0.56	0.41

Note: Values represent coefficient estimates ± SE of the slopes, and p values.
*p < .05.
**p < .01.

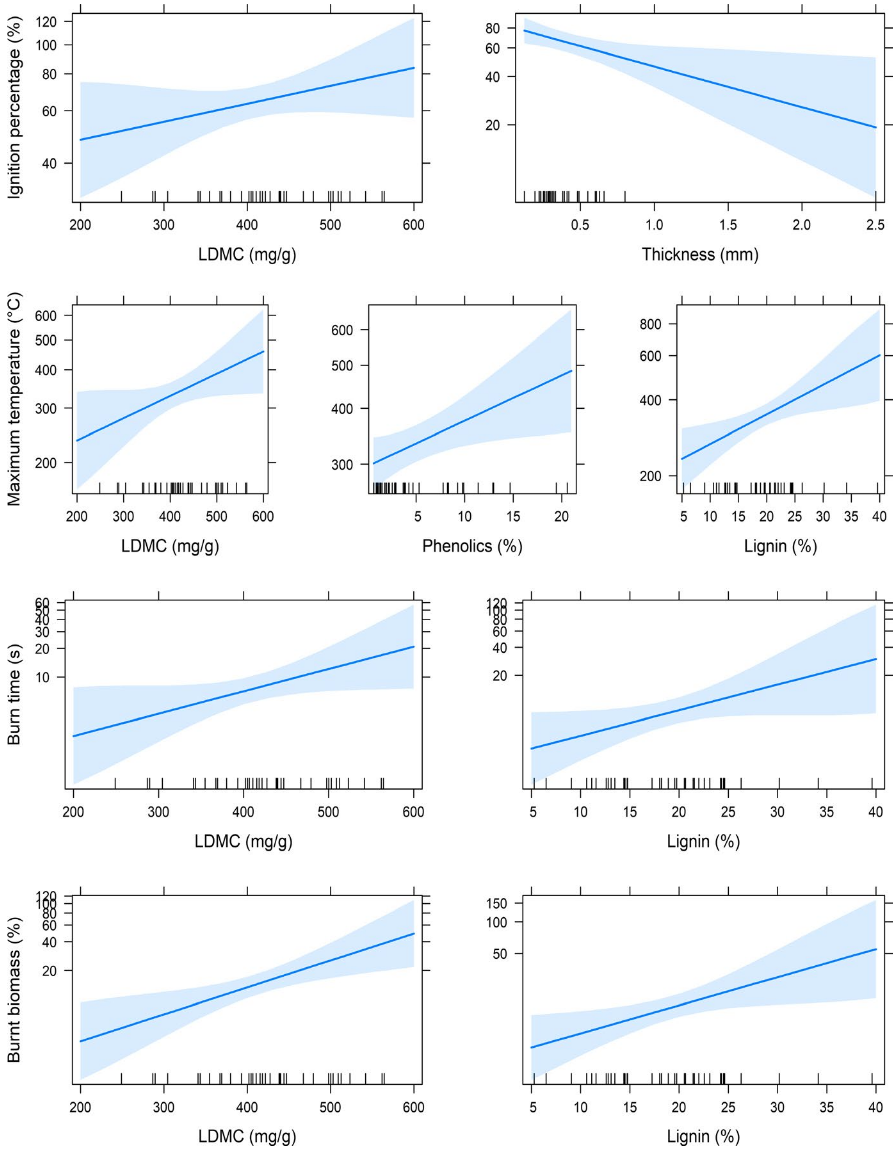

FIGURE 3 Effect plots showing the predicted (blue line) relationship of the shoot flammability traits as a function of the significant leaf functional traits from the generalized linear models. The blue envelope represents the 95% confidence interval. Observed trait data are represented by the small black lines on the *x*-axes. The plots show the relationship between the flammability traits and each of the functional traits in the model where other variables were held constant [Colour figure can be viewed at wileyonlinelibrary.com]

care must be taken when comparing plant flammability assessments conducted using different fuel levels. Leaf-level studies are common in fire ecology and fire evolution studies because they are easier to conduct, and leaves are usually the plant component that ignites first and is assumed to drive flammability (Etlinger & Beall, 2005; Gill & Zylstra, 2005; Pickett et al., 2009; Zylstra et al., 2016). However, with the increasing importance of obtaining accurate estimates of plant flammability for land management, it is important to understand how leaf-level tests correlate with flammability measurements conducted at larger levels. To our knowledge, this is the first study to quantitatively compare proxies for canopy flammability at two levels across a wide range of species.

The lack of correlation between leaf- and shoot-level flammability is likely to be explained by differences in the amount and arrangement of the fuel being burned. While in leaf-level studies a single leaf is burnt, the shoot-level study uses a 70 cm-long shoot as fuel, which contains multiple leaves, twigs and small branches. The flammability of vegetation is influenced by fuel arrangement, continuity, and quantity (Martin et al., 1994), and our results suggest that these principles apply at the shoot level. The arrangement of leaves and twigs at the shoot level likely reflects the way that fire burns through a plant canopy, with the propagation of fire from twig to twig on a shoot similar to propagation from branch to branch in a canopy. The burning of single leaves may be more relevant to litter fires (Ganteaume, 2018; Grootemaat, Wright, Bodegom, & Cornelissen, 2017; Varner et al., 2015), albeit without the more realistic representation of fuel bulk density that comes with burning leaf litter mixes.

Another possible explanation for the decoupling of the leaf- and shoot-level flammability relates to the measurement methods. Leaf flammability was calculated by burning a single leaf in a muffle furnace at an oven temperature of 400–430°C, without applying any ignition source (Mason et al., 2016), as has been done in several other studies (Krix & Murray, 2018; Krix, Phillips, & Murray, 2019; Montgomery & Cheo, 1971; Murray et al., 2013). Exposing the leaf to such high temperatures in the absence of a flame is likely to remove any volatile oils present in the leaf before they ignite, and thus overestimate the ignition time of a leaf. Leaf volatile organic compounds (VOCs; e.g. tannins, terpenes, isoprenoids and phenolics) increase plant flammability (Alessio et al., 2008; Chetehouna et al., 2009; Owens, Lin, Taylor, & Whisenant, 1998; Pausas et al., 2016), and phenolic concentrations were positively correlated with shoot-flammability in our study. Species with high VOCs are likely to be slow to ignite unless a flame is used (Martin et al., 1994), suggesting that methods that use an ignition source are better suited to measuring the ignitibility of these species.

These potential differences in measurement methods could be resolved by direct comparisons of leaf-level tests in a muffle furnace with and without an ignition source, but we could find no such studies (see Data S1, Table S4). However, we can indirectly compare results with and without an ignition source by assessing whether different methods produced similar relationships between leaf traits and flammability. In doing so, we found similar trait–flammability relationships between the methods (Table S4). This provides support for the contention that the leaf flammability measured in a muffle furnace is similar whether or not an ignition source is used. Thus, we conclude that the lack of correlation between shoot and leaf flammability in our study was unlikely to be due to methodological differences (absence of an ignition source), but recommend direct tests of this for confirmation.

Given that the level of the fuel material influences measurements of flammability, which level best represents whole-plant and potentially ecosystem flammability? Ultimately, addressing this question requires burning whole plants in the laboratory and plant communities in the field and comparing the results to predictions of fire behaviour based on tests on plant parts. However, our finding that shoot-level, but not leaf-level flammability, rankings were correlated with rankings by experts suggests that shoot-level tests will upscale better than leaf-level tests to whole plant or ecosystem flammability. In his instructions to respondents of his expert survey, Fogarty (2001) asked fire managers to isolate the flammability of the species they were assessing from that of the vegetation that was burning and to pay particular attention to how well species burnt in a head fire or during high-intensity burn-offs. This focussed questioning of a substantial pool of experts (*n* = 59) lends credence to the findings of that study. However, as Fogarty (2001) acknowledged, further empirical testing in the laboratory and the field is needed to confirm his findings.

4.2 | Shoot flammability is related to leaf functional traits, including LDMC, leaf thickness, and lignin and phenolic concentrations

Leaf traits explained a substantial proportion of variation in shoot flammability components (48%, 63%, 56%, and 41% for ignitibility, combustibility, sustainability and consumability, respectively), with the four most important traits (individually and in combination) being LDMC, leaf thickness, lignin content, and phenolic content. LDMC was the leaf trait most strongly correlated with shoot flammability and was positively related to all four traits of shoot flammability, suggesting that higher dry matter content resulted in higher flammability. This result confirms the suggestion in the standardized trait measurement handbooks that LDMC is an important trait positively related to flammability (Cornelissen et al., 2003; Perez-Harguindeguy et al., 2013). LDMC is closely related to the water content and tissue density of the leaves. High dry matter content indicates low water content and high dry mass per volume of the tissue (Garnier & Laurent, 1994; Perez-Harguindeguy et al., 2013; Shipley & Vu, 2002; Wilson, Thompson, & Hodgson, 1999). Hence, the higher shoot flammability of the species with high LDMC content in this study was likely due to the low water content of the leaves, which therefore require less energy to combust (Chuvieco et al., 2009; Pompe & Vines, 1966). Additionally, the higher available dry tissue mass per volume allows the fuels to ignite more rapidly, burn with higher intensity for longer, and causes higher biomass consumption (Chuvieco, Aguado, & Dimitrakopoulos, 2004; Cowan

& Ackerly, 2010; Dimitrakopoulos & Papaioannou, 2001; De Lillis, Bianco, & Loreto, 2009; Perez-Harguindeguy et al., 2013). LDMC is a trait that is relatively easy to measure and is widely available in global trait databases (e.g. Kattge et al., 2011; Kleyer et al., 2008; Tavşanoğlu & Pausas, 2018), potentially making it a useful predictor of plant flammability.

Leaf thickness was another morphological trait related to shoot-level flammability, with thick-leaved plants igniting more slowly. Leaf-level experiments have demonstrated that thicker leaves take longer to ignite and release less heat during burning, contributing to the fire retardance of plants (Grootemaat et al., 2015; Mason et al., 2016; Montgomery & Cheo, 1971). However, such findings are not universal; Murray et al. (2013) found no relation between leaf thickness and leaf flammability. Interestingly, leaf thickness was the only trait that reduced ignitibility at both the shoot- and leaf-level in our study, although these two levels of flammability were orthogonal. This may be because leaves are the first component to ignite during fire irrespective of the fuel levels and suggests that ignitibility is influenced by leaf thickness at any fuel level. While this finding matches that of most other studies, we recommend that it be treated cautiously, as the significant negative relationship between ignitability and leaf thickness in our study is mostly driven by the thick-leaved perennial herb *Phormium tenax*.

Lignin content of leaves was the chemical trait most strongly correlated with shoot flammability, with flammability increasing with leaf lignin content. Tissues with high lignin content have low water storage capacity (Berry & Roderick, 2005) and high energy content (Demirbas, 2002; Hough, 1969; McKendry, 2002) and burn hotter and longer after ignition (Fernandes, 2013). Although lignin reduces tissue combustibility at the pyrolysis stage (Grootemaat et al., 2015; Xu & Ferdosian, 2017), once lignin-rich tissues ignite, it intensifies the fire, producing high temperatures due to its high energy content. Phenols were also correlated with shoot flammability: plant species with high phenolic compound concentrations had higher combustibility at the shoot level. Phenolic compounds (flavonoids, phenolic acids, tannins, terpenes) are often produced in plants during stress (Fernandes, 2013; Ormeno, Fernandez, & Mévy, 2007). Phenols are strongly positively related to plant flammability in several other studies (Keith, 2012; Ormeno et al., 2009; Owens et al., 1998; White, 1994) because fuels high in phenolic compounds have high calorific values (Núñez-Regueira, Proupın-Castineiras, & Rodrıguez-Anón, 2002; Núñez-Regueira, Rodriguez-Anon, Proupin, Mourino, & Artiaga-Diaz, 2005), which makes them burn more intensely. Collectively, these trait correlations demonstrate how different leaf morphological and chemical traits influence shoot flammability and highlight the significance of considering leaf functional traits to explain shoot flammability. Although several of the leaf traits we evaluated contribute to shoot flammability, LDMC is clearly the most important. While leaf-level traits were related to shoot flammability, architectural traits (e.g. spatial arrangement of leaves and twigs, branch ramification, and retention of dead material) are also likely to influence shoot-level flammability (Perez-Harguindeguy et al., 2013; Schwilk, 2003). However, none of these measurements currently exist for our study species. Future studies should examine whether architectural traits are more important drivers of shoot flammability than leaf traits.

Our study demonstrates the importance of fuel level when measuring plant flammability and shows for the first time that leaf- and shoot-level flammability is decoupled. This decoupling suggests that caution is needed when leaf-level measurements are scaled up to predict the flammability of larger plant parts or fire behaviour. For the species that we considered, shoot-level flammability was highly correlated with plant-level flammability, as determined by expert opinion based on field observations, and hence is likely a useful way to characterize plant flammability. However, shoot flammability research is in its infancy, with only several hundred species (ca 300) tested so far globally (Burger & Bond, 2015; Calitz et al., 2015; Jaureguiberry et al., 2011; Padullés Cubino et al., 2018; Wyse et al., 2016). Thus, there is a need to identify widely measured traits that could be used as a surrogate for shoot-level flammability. To this end, our study has identified several key leaf traits (LDMC, thickness, phenolics, and lignin) that are strongly correlated with shoot flammability. Some of these traits (e.g. LDMC with 4,941 species entries in the TRY trait database (Kattge et al., 2011) and 1735 species in the LEDA trait database (Kleyer et al., 2008)) have been widely measured globally. Assuming the relationships described here hold when more coniferous trees and deciduous trees are assessed, LDMC could act as a surrogate for the shoot- and perhaps plant-level flammability in global dynamic vegetation models, facilitating improved modelling of fire-climate-vegetation feedbacks associated with global change.

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AUTHORS' CONTRIBUTIONS

This study was conceived by T.J.C., M.A.A., G.L.W.P. and S.V.W. and designed by M.A.A., T.J.C., G.L.W.P., S.V.W. and H.L.B. Analyses were conducted by M.A.A., H.L.B., S.V.W., J.J.S. and G.L.W.P. M.A.A. wrote the first draft, which was then revised and approved by all co-authors.

DATA AVAILABILITY STATEMENT

Data associated with this manuscript are archived and made publicly available on Figshare: https://doi.org/10.6084/m9.figshare.9738917.v1 (Alam et al. 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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